MASARYK
UNIVERSITY
Faculty of Science

Tree-soil interactions in natural temperate forests in space and time

Ph.D. Dissertation

Pavel Daněk

Supervisor
Ing. Pavel Šamonil, Ph.D.

Department of Botany and Zoology
Brno 2021

Bibliografický záznam

Autor	Mgr. et Mgr. Pavel Daněk Přírodovědecká fakulta, Masarykova univerzita Ústav botaniky a zoologie
Název práce	Interakce mezi stromy a půdou v přirozených temperátních lesích v prostoru a čase
Studijní program	Ekologická a evoluční biologie
Specializace	Botanika
Vedoucí práce	Ing. Pavel Šamonil, Ph.D.
Akademický rok	2020/2021
Počet stran	238
Klíčová slova	interakce stromů a půdy; temperátní les; vývrat; ekosystémový inženýr; dynamika lesa; *Fagus sylvatica*; *Picea abies*; listový opad; mrtvé dřevo; pedogeneze; půdní chemie; biomechanické a biochemické vlivy stromů; zmlazení stromů

Bibliographic entry

Author	Mgr. et Mgr. Pavel Daněk Faculty of Science, Masaryk University Department of Botany and Zoology
Title of Thesis	Tree-soil interactions in natural temperate forests in space and time
Degree programme	Ecological and Evolutionary Biology
Field of Study	Botany
Supervisor	Ing. Pavel Šamonil, Ph.D.
Academic year	2020/2021
Number of Pages	238
Keywords	tree-soil interactions; temperate forest; uprooting; ecosystem engineer; forest dynamics; *Fagus sylvatica*; *Picea abies*; leaf litter; deadwood; pedogenesis; soil chemistry; biomechanical and biochemical effects of trees; tree regeneration

Abstrakt

Stromy a půda se vzájemně ovlivňují mnoha způsoby a jejich interakce mohou v některých případech vést ke vzniku zpětných vazeb, které určují vývoj lesních společenstev. Půda je pro stromy významná tím, že jim poskytuje fyzickou oporu a látky nezbytné k růstu, zejména vodu a živiny. Zároveň i stromy různými způsoby ovlivňují půdu a v této práci jsou uvažovány dva hlavní typy takových vlivů: biochemické a biomechanické. Mezi ty první se řadí například vliv stromů na chemismus půdy působením rozkládajícího se listového opadu nebo mrtvého dřeva. Druhý typ zahrnuje různé účinky stromů, které mohou vést jak k mobilizaci půdy, tak k její stabilizaci. Nejvýraznějším z těchto účinků je vyvracení stromů, během něhož obvykle vznikají dvě specifická mikrostanoviště (jáma a kupa) které mohou hrát významnou roli ve vývoji půd i lesních společenstev. Cílem této práce je prozkoumat různé aspekty interakce stromů a půd jak z hlediska toho, jakými způsoby stromy ovlivňují půdu, tak toho, jaký má půda význam pro stromy. Zároveň se budu soustředit i na identifikaci možných zpětných vazeb vyplývajících z těchto dvou směrů působení.

Práce se zabývá třemi užšími tématy: vlivem stromů na fyzikální a chemické vlastnosti půdy prostřednictvím vývratů a rozkládajících se kmenů, biogeomorfologickými aspekty biomechanického působení stromů a rolí půdy v dynamice populací buku (*Fagus sylvatica*) a smrku (*Picea abies*) v Boubínském pralese.

Pedogeneze ve vývratech probíhala rychleji v jamách než na kupách a byla pomalejší v hlubších půdních horizontech než ve svrchních. Doba potřebná k tomu, aby půdní horizonty znova dosáhly tloušťku, kterou měly před narušením, se pohybovala od 5 do > 16 000 let. Fyzikální a chemické vlastnosti půdy byly nejvíce závislé na hloubce v půdním profilu, dále mikrostanovišti (jáma nebo kupa) a potom na době od narušení. Důležitou roli hrála textura půdy, ovšem na rozdíl od výsledků týkajících se půdní morfologie se chemické rozdíly mezi mikrostanovišti s rostoucí intenzitou zvětrávání a vyluhování snižovaly. Rozkládající se kmeny nejvíce ovlivňovaly svrchních 20 cm půdy a zpočátku způsobily zvýšení obsahu živin, pH a kationtové výměnné kapacity. Z modelů vývoje pro jednotlivé chemické vlastnosti vyplynulo, že by vliv kmenů na půdu kulminoval během 12–60 let a přestal být patrný po 39–229 letech.

Biomechanické vlivy stromů (BVS) byly v Boubínském pralese pozorovány u více než poloviny živých i ležících mrtvých stromů. Nejčastějším vlivem byla stabilizace půdy, ale z hlediska celkové plochy a objemu ovlivňěné půdy dominovaly vývraty. Další studie ukázala intenzifikaci BVS podél gradientu nadmořské výšky od nížin do hor. Tato intenzifikace byla způsobena především vyšší četností vývratů související s vyšším výskytem větrných bouří.

Abychom mohli posoudit roli půd v lesní dynamice Boubínského pralesa, analyzovali jsme nejprve komplexitu jejich prostorové struktury. Ze tří hlavních zjištěných gradientů půdních vlastností byla za většinu pozorované prostorové komplexity půd zodpovědná hydromorfologie (ovlivnění vodou). Ta byla také hlavním faktorem určujícím rozložení populací buku a smrku, s tím že buk převažoval na sušších stanovištích a smrk na vlhčích. Během zdokumentovaných 38 let vývoje lesa buk expandoval na všech hlavních půdách, což bylo způsobeno především jeho vyšším dorůstáním a nižší mortalitou. Na terestrických půdách se rozdíl v mortalitě mezi dřevinami projevoval především v postupném odumíráním jednotlivých stromů, zatímco na hydromorfních půdách byl spojen především s důsledky silné větrné bouře. I přes podobné celkové zastoupení obou druhů v zápoji byl buk mnohem hojnější ve zmlazení. Frekvence semenáčků obou druhů se zvyšovala s rostoucím zastoupením vlastního druhu v zápoji, ale pro starší zmlazení nabývalo na významu ovlivnění půdy vodou. Zatímco zmlazení buku vykazovalo pozitivní vazbu na místa s bukovým listovým opadem a bylo hojné na nedisturbované půdě, kde bylo opadu hodně, smrk zmlazoval především na mikrostanovištích, kde byla akumulace bukového opadu nižší, tedy především na mrtvém dřevě a na vývratových kupách. Toto naznačuje existenci pozitivní zpětné vazby mezi bukem a půdou, jejímž prostřednictvím může buk bránit zmlazování smrku, aniž by přitom limitoval vlastní obnovu.

Abstract

Trees and soils interact in many ways, and these interactions may in some cases lead to the emergence of feedbacks with consequences for forest dynamics. Soils are essential for trees as they provide them with physical support and different substances necessary for tree growth, such as water and nutrients. On the other hand, trees also affect the soil in various ways and the two main types of tree influence considered in this thesis are biochemical and biomechanical. The former include, e.g., the effects of trees on soil chemistry through the decomposition of litter and deadwood. The latter comprise various effects of trees that can lead to both soil displacement and stabilization. The most prominent such effect is tree uprooting, a process that typically leads to the formation of two distinct microsites, a pit and a mound, which can be important for their role in soil formation and forest dynamics. The aim of this thesis is to explore different aspects of tree-soil interactions, focusing both on how trees affect soil and what is the importance of soil for trees, and also to try to find evidence of possible feedbacks resulting from these two ways of action.

Three specific topics are addressed in the thesis: effects of trees on soil physical and chemical properties through uprooting and decaying logs, biogeomorphological aspects of biomechanical effects of trees and the dynamics of beech (*Fagus sylvatica*) and spruce (*Picea abies*) in and old-growth forest with respect to soils.

Post-uprooting pedogenesis proceeded faster in uprooting pits than on mounds and was slower in deeper soil horizons than in the upper ones. The modelled time required for horizons to reach their pre-disturbance thickness ranged from 5 to > 16,000 years. Soil physical and chemical properties were best explained by depth within the soil profile, followed by microsite (pit or mound) and time since disturbance. Soil texture played an important role and, in contrast to the results from soil morphology, chemical differences between the microsites decreased with increasing intensity of weathering and leaching. Decaying logs had the strongest effects on the top 20 cm of soil and initially caused an increase in nutrients, pH and cation exchange capacity. Their influence on the soil peaked in 12–60 years and was modelled to disappear after 39–229 years.

Biomechanical effects of trees (BETs) in an old-growth forest (Boubín) were observed for more than half of both living and dead lying trees. Soil stabilization was the most frequent function but in terms of the total soil area and volume affected, uprootings predominated. In another study, we observed an intensification of BETs along an elevation gradient from lowlands to mountains, which was mostly caused by an increase in the frequency of uprooting associated with higher windstorm activity.

To assess the role of soils in forest dynamics in Boubín, we first analyzed the complexity of their spatial pattern. Of the three major soil property gradients identified, hydromormorphology (soil wetness) was the one responsible for most of the observed soil spatial complexity. It was also the main factor determining the spatial distribution of beech and spruce populations, with beech predominating on drier sites and spruce on the wetter ones. Over the documented 38 years of forest development, beech expanded on all major soils, which was mostly caused by its higher recruitment and lower mortality rates. On terrestrial soils, the difference in mortality between species was manifested gradually through the death of individual trees, whereas on hydromorphic soils it was mainly related to a single strong windstorm. Despite the similar overall representation of the two species in the canopy, beech was much more abundant in regeneration. Seedling occurrence of both species increased with the species' proportion in the canopy, but for older regeneration soil wetness became more important. While beech regeneration showed a positive association with its own litter and was common on the litter-rich undisturbed soil, spruce occurred mostly on microsites with lower beech litter accumulation, such as deadwood and uprooting mounds. This indicates a positive tree-soil feedback in beech through which it can suppress its competitor, while not harming its own regeneration.

Poděkování / Acknowledgements

Pavlovi za uvedení do tajů lesa, půdy a bourbonu.

Členům pralesního týmu  [Modrá kočka] za všechny milé chvíle strávené v pralesích, na Lidické i jinde.

Lidem na ÚBZ za přátelské a inspirativní prostředí.

I thank Jonathan and Łukasz for their cooperation, inspiration and pleasant company on our Czech roadtrips.

Všem blízkým lidem, zejména Barboře, Martinovi, Radce, Stance, Tomášovi a Zuzaně.

Rodičům za všechno možné i nemožné.

A v neposlední řadě všem českým i světovým (pra)lesům, v čele s Boubínem.

Author contributions to the papers in the thesis

Paper 1 Šamonil P., **Daněk P.**, Schaetzl R.J., Vašíčková I., Valtera M. 2015. Soil mixing and genesis as affected by tree uprooting in three temperate forests. *European Journal of Soil Science* 66: 589–603.

PŠ, PD and RJS conceived the ideas; RJS helped select research sites in Michigan contributed significantly to methodology; PŠ, PD, IV and MV collected data; PD analysed the data; PŠ led the manuscript writing; all authors discussed the final version of the manuscript.

Paper 2 Šamonil P., **Daněk P.**, Schaetzl R.J., Tejnecký V., Drábek O. 2018. Converse pathways of soil evolution caused by tree uprooting: A synthesis from three regions with varying soil formation processes. *Catena* 161: 122–136.

PŠ, PD and RJS conceived the ideas; RJS helped select research sites in Michigan contributed significantly to methodology; PŠ and PD collected data; VT and OD carried out laboratory soil analyses; PD analysed the data; PŠ led the manuscript writing; all authors discussed the final version of the manuscript.

Paper 3 Šamonil P., **Daněk P.**, Baldrian P., Tláskal V., Tejnecký V., Drábek O. 2020. Convergence, divergence or chaos? Consequences of tree trunk decay for pedogenesis and the soil microbiome in a temperate natural forest. *Geoderma* 376: 1–16.

PŠ, PD, PB and VTl conceived the ideas; PŠ collected data; VTe and OD carried out laboratory soil analyses; VTl carried out microbial analyses; PD led the pedological data analysis; PB led the microbial data analysis; PŠ and PB led the manuscript writing; all authors discussed the final version of the manuscript.

Only the part concerning pedogenesis is considered for the purposes of this thesis.

Paper 4 Šamonil P., **Daněk P.**, Senecká A., Adam D., Phillips J.D. 2018. Biomechanical effects of trees in an old-growth temperate forest. *Earth Surface Processes and Landforms* 43: 1063–1072.

PŠ, PD and JDP conceived the ideas; PŠ and AS collected data; DA processed tree census data; PD led the data analysis; PŠ led the manuscript writing; all authors discussed the final version of the manuscript.

Paper 5 Šamonil P., **Daněk P.**, Adam D., Phillips J.D. 2017. Breakage or uprooting: How tree death type affects hillslope processes in old-growth temperate forests. *Geomorphology* 299: 76–84.

PŠ, PD and JDP conceived the ideas; PŠ collected data; DA processed tree census data; PD led the data analysis; PŠ led the manuscript writing; all authors discussed the final version of the manuscript.

Paper 6 **Daněk P.**, Šamonil P., Phillips J.D. 2016. Geomorphic controls of soil spatial complexity in a primeval mountain forest in the Czech Republic. *Geomorphology* 273: 280–291.

PD, PŠ and JDP conceived the ideas; PŠ collected data; PD analysed the data; PD and PŠ led the manuscript writing; all authors discussed the final version of the manuscript.

Paper 7 **Daněk P.**, Šamonil P., Vrška T. 2019. Four decades of the coexistence of beech and spruce in a Central European old-growth forest. Which succeeds on what soils and why? *Plant and Soil* 437: 257–272.

PD and PŠ conceived the ideas; PD collected and analysed the data; PD led the manuscript writing; all authors discussed the final version of the manuscript.

Paper 8 **Daněk P.**, Šamonil P., Hort L. Canopy trees drive regeneration of a spruce-beech forest through forest floor alteration. Submitted to *Forest Ecology and Management.*

PD and PŠ conceived the ideas; PD collected and analysed the data; PD led the manuscript writing; all authors discussed the final version of the manuscript.

Preface

When looking at a tree growing out of the soil, what goes through a scientist's mind and the questions they ask can be greatly influenced by their scientific specialization and the associated way of perceiving nature. A person trained in botany might wonder whether the soil's nutrient status, moisture or reaction are suitable for this particular tree species. Or vice versa, they may be able to read the soil conditions based on the tree's species identity. A Norway spruce, for instance, has quite different requirements than a pubescent oak. A pedologist or geomorphologist, on the other hand, would likely think about different aspects. How is the soil chemistry affected by tree litter decomposition? Is the tree base bent, possibly indicating downslope soil movement, or is the tree large enough so that it can stabilize the soil? The tree may even be long gone, but certain signs of its former presence, such as uprooting mounds, can remain visible to the observant eye for thousands of years. I started out as a botanist, but while working on this thesis I learned to also appreciate the other facets of the sophisticated tree-soil relationship. Perhaps this thesis can help broaden someone else's perspective too, whatever their background.

Contents

Introduction

Trees and soil are two key components of forest ecosystems that exhibit various mutual interactions, but have long been studied within different scientific fields. As living organisms, trees have primarily been an object of interest for biological sciences, especially botany and ecology. Soils, while also containing a non-negligible biological component, have traditionally been studied within Earth sciences, mainly pedology and geomorphology. The interactions within plant-soil systems were recognized already in the agriculture of early civilizations (the Mayans, the Chinese and the Romans), but their wider scientific appreciation has come only in the last several decades (Ehrenfeld et al. 2005).

1.1 Effects of trees on soil

Trees affect soil throughout their lives, at the moment of their death, and even afterwards. They can do so through virtually every body part, however the most intense contact usually occurs in the root zone. Traditionally, organisms (including trees) are considered one of the five main soil-forming factors, along with parent material, climate, topography and time (Jenny 1941). For the purposes of this thesis, I will consider two main groups of trees' effects on soil: *biochemical* and *biomechanical* (Pawlik 2013; Pawlik et al. 2016). Besides these, trees can also exert impact on soil physical properties (temperature, water content) or biological components (Ehrenfeld et al. 2005).

By modifying the environment in ways that modulate the availability of resources to other species trees act as *ecosystem engineers* (Jones et al. 1994) and cases where there are stronger evolutionary consequences can be referred to as *niche construction* (Odling-Smee et al. 2003; Corenblit et al. 2011; Pawlik et al. 2016). Based on the concept of extended phenotype (Dawkins 1982), which also considers the effects a gene has on its environment, not just within the body of an organism, Phillips (2009) views soils as *extended composite phenotypes* of various biota, including trees.

1.1.1 Biochemical effects

Trees have a high ability to filter gases and particles from the atmosphere (Binkley 1996). The resulting throughfall deposition is dependent on pollutant concentrations and tree canopy characteristics which can differ between species. *Fagus sylvatica* stands with a leaf area index of 6 and a 6-month leaf retention period showed about half the throughfall deposition of nitrogen and sulphur compounds compared to the evergreen *Picea abies* stands with a leaf area index of 10 (Rothe et al. 2002).

Some tree species have developed symbiotic relationships with nitrogen-fixing microorganisms and can substantially increase nitrogen input to the soil (Binkley 1996; Santi et al. 2013; Baldrian 2017). *Robinia pseudoacacia* invasion in a pine–oak forest was observed to significantly increase nitrogen concentrations in the A horizon (1.3–3.2 times) as well as net N-mineralization (5–13 times) and nitrification (25–120) rates (Rice et al. 2004).

An important effect on soil chemistry is through tree litter (Sayer 2006). Litter quality varies significantly between species and the differences are also reflected in the soil. Finzi et al. (1998a) reported large differences in C and N content in forest floor under six tree species in a northern hardwood forest in Connecticut. The C and N pools were smallest beneath *Acer saccharum* and highest beneath *Tsuga canadensis,* while the opposite was true for soil pH (Finzi et al. 1998b). A similar pattern was found for European tree species where the forest floor C and N contents increased in the order *Fraxinus excelsior* = *Tilia cordata* = *Acer pseudoplatanus* < *Quercus robur* = *Fagus sylvatica* << *Picea abies* (Vesterdal et al. 2008). The reverse order applies for topsoil pH under these species (Augusto et al. 2002). Besides leaf litter, trees affect soil also with root litter and root exudates (Spielvogel et al. 2014).

Trees also affect soil through decaying deadwood. Deadwood decomposition can have similar effects as the decomposition of tree litter and was shown to increase concentrations of C, N, P and Ca in soils under logs of different species, especially in acidic and nutrient-poor soils (Minnich et al. 2021). However, it is not clear how deep these effects reach and how long they last (Spears et al. 2003).

1.1.2 Biomechanical effects

While biochemical effects of trees always work gradually and need some time to manifest themselves, biomechanical ones can act abruptly when coupled with processes that are instantaneous. This is best exemplified by tree uprooting, but can also be associated with other dynamic events, such as the fall of part of the trunk or a large branch.

Trees can both cause soil displacement and act against it. The latter involves situations where living or dead trees slow or stop the downslope movement of soil by physically obstructing particle transport (Pawlik 2013). This stabilizing effect is also called bioprotection (Naylor 2005) and depending on their root system strength and structure, trees can protect slopes from different kinds of mass wasting processes, e.g., landslides (Rickli & Graf 2009; Stokes et al. 2009). If the logs from dead trees lie parallel to slope contours, they may exert damming effect and act as sedimentation traps (LaMarche 1968).

Trees can displace soil actively through root and stem axial and radial growth. As roots grow, they exert radial pressure of up to 0.9 MPa (Bennie 1991), which may be enough to intensify the weathering of softer rocks (Jackson & Sheldon 1949). Root and stem growth contributes to a downslope flux of soil (Gabet et al. 2003) and its other manifestations include root mounds and baumsteins. Root mound is a small microtopographical elevation around the base of a trunk (Hoffman & Anderson 2014) and baumsteins are rock fragments displaced by tree growth (Phillips & Marion 2006).

When a tree dies (and does not uproot), its root system starts to decay and the processes of soil displacement described above reverse. Channels after decomposing roots are gradually infilled by the surrounding soil (Gabet et al. 2003) and stump rotting can lead to the formation of a surface depression (stump hole) that is infilled with material from its immediate vicinity, including litter or previously displaced baumsteins (Phillips & Marion 2006).

Last but not least, trees are able to mediate (or transfer) energy to the soil. A classic example is tree uprooting (described in detail below), a process during which the energy of wind or another external agent (or just the tree's own gravitational potential energy) is mediated through the body of the tree to the roots and soil. Even if the wind force is not strong enough to cause uprooting, it can still act on the soil by agitating the tree, leading to root movement (Schaetzl et al. 1989). A concentrated flow of water associated with standing or lying trees may cause local erosion on their downslope side and was described as stemwash and trunkwash, respectively (Phillips et al. 2017).

Tree uprooting

Tree uprooting (or treethrow) is the fall of a tree trunk during which the root plate is torn out of the soil, and can have various causes, e.g., wind, overloading of the crown by ice or snow, weakening of the tree roots by rot or the fall of another tree (Schaetzl et al. 1989; Šamonil et al. 2010). It is the most noticeable way trees modify their environment and the resulting microtopographical features may reach impressive dimensions. Root plate areas can reach up to 40 m^2 (Šamonil et al. 2014) and their volumes can be as high as 60 m^3 (Phillips et al. 2017). Uprooting is typically associated with the formation of two distinctive microtopographical features – a depression (or pit) in the place where the tree with its root system was originally located, and a mound where the uprooted material accumulates. These features, together referred to as a pit-mound, are gradually flattened by erosion, but may remain visible for more than 6000 years (Šamonil et al. 2013). The time it takes, on average, for the whole surface of a given area to be uprooted is called rotation period (Šamonil et al. 2010). Depending on uprooting intensity and pit-mound dimensions this period can be of varying length. The shortest rotation period of 300–500 years was estimated in a *Quercus rubra–Fagus grandifolia* forest in Pennsylvania (Denny & Goodlett 1956), but most studies report higher values, e.g., 1250 years from a *Fagus sylvatica–Abies alba* stand in the Czech Republic (Šamonil et al. 2009) or 4120 years in *Picea abies*-dominated forests in the Polish Tatra Mountains (Strzyżowski et al. 2018). These are, however, only hypothetical average values and in reality some places will be disturbed less and some more frequently (Norton 1989). On landscape scale, uprooting can transport significant amounts of soil. In a *Fagus sylvatica*-dominated old-growth forest, the average volume of soil related to tree uprooting was 3.5 m^3 ha^{-1} $year^{-1}$(Šamonil et al. 2020).

Although the initial disturbance by uprooting is mechanical, it also has a substantial impact on the course of soil formation, leading to changes in both the physical and chemical soil properties. Tree uprooting initially locally resets pedogenesis by mixing the soil (Schaetzl et al. 1990), and soils in areas with frequent windthrow may thus be younger and with less developed horizonation than soils in places where such disturbance is less common (Kramer et al. 2004). At the same time, however, the rates of pedogenesis in the uprooting pits and mounds can differ both from those in the undisturbed soil and, even more so, from each other. Soils in pits are typically more developed than those on mounds (although rarely it can be the other way around, see Šamonil et al. 2010), which is manifested through higher horizon thicknesses, lower soil reaction and cation exchange capacity (CEC) or lower concentrations of basic cations (Veneman et al. 1984; Schaetzl et al. 1990; Kramer et al. 2004; Šamonil et al. 2010). This is caused by several factors, including more water percolating through the pit, higher humus content, more intense leaching, and non-freezing temperatures there due to higher snow accumulation in the winter (Dwyer & Merriam 1981; Veneman et al. 1984; Schaetzl et al. 1990; Šamonil et al. 2010). As opposed to pits, mounds tend to be drier, warmer during the growing season (but potentially colder during winter as they have less snow cover) and accumulate less litter (Dwyer & Merriam 1981; Beatty 1984; Schaetzl et al. 1990; Peterson & Campbell 1993; Simon et al. 2011).

Windstorms, a major cause for uprooting, represent the most common forest disturbance in Europe (Schelhaas et al. 2003). However, susceptibility to wind damage varies among tree species and so does their tendency for uprooting. One of the most susceptible European trees is *Picea abies* (Jactel et al. 2017), particularly when growing on waterlogged soils (Dobbertin 2002).

1.1.3 Implications for soil spatial pattern

The effects of trees leading to the intensification of certain pedogenetic processes can ultimately result in such large changes in the soil that it actually changes its taxonomic classification. An important process in this respect is podzolization which is known to be intensified by certain types of vegetation, e.g., conifers (Lundström et al. 2000). About 80 years of *Picea abies* monoculture were enough to cause significant increase in weathering processes and removal of elements in soils previously occupied by *Fagus sylvatica* (Sohet et al. 1988). These effects are typically highly localized below the canopies of individual trees, as observed, for instance, in the case of strong local podzolization around *Tsuga heterophylla* and *Pseudotsuga menziesii* trees in British Colombia (Crampton 1982). This can lead to increases in local soil diversity and spatial complexity (Phillips 2013) and the emergence of mid-scale spatial patterns in the range of meters (Bruckner et al. 1999; Valtera et al. 2013; Gruba et al. 2020).

1.2 Importance of soils for trees

For trees, as for other plants, soil is an essential substrate that provides their bodies physical support and supplies them with what they cannot obtain from the air, mainly water and nutrients.

The support provided to trees depends on soil type and is species-specific. Data from tree-pulling experiments showed that, e.g., *Abies grandis* had a significantly better anchorage than *Picea sitchensis* and that the anchorage of the latter was strongest on peat and poorest on gleyed mineral soils (Nicoll et al. 2006). Lower susceptibility to wind damage on peatlands than on mineral soils was also found for *Picea abies* and *Pinus sylvestris* (Suvanto et al. 2016).

Soil texture and water content determine soil water availability for trees, which is generally highest in silty soils and lowest in sandy soils but can also be increased by organic matter content (Leuschner & Ellenberg 2017). Low water availability can completely prevent tree occurrence and episodic drought-related water shortages lead to decline in tree growth (Bréda et al. 2006). However, drought resistance of different tree species varies, as is the case for example with *Picea abies* and *Fagus sylvatica*. Although *P. abies* grew faster than *F. sylvatica* in favorable conditions, its diameter increments decreased significantly under extreme drought, while no difference was found for the broadleaf (Rötzer et al. 2017). Excess water availability can be as damaging to trees as much as water shortage due to oxygen deprivation in roots or impaired nutrient uptake (Schmull & Thomas 2000; Kreuzwieser & Gessler 2010). Such conditions may appear as a result of waterlogging, to which species are differently adapted. For instance, *Quercus robur* is able to generate roots even below the water table and thus tolerate water-saturated soils better than *Fagus sylvatica* (Dreyer 1994; Schmull & Thomas 2000). If a species is not adapted to tolerate excess water in the soil, it can avoid it by developing a shallow root system, as is often the case with *P. abies* (Leuschner & Ellenberg 2017).

1.3 Tree-soil feedbacks

The two-way nature of the effects within the tree–soil system may lead to a number of possible feedbacks. Binkley & Giardina (1998) give three hypotheses why tree species affect soil differently, based on the tightness of the relationship between the tree's actions and their effect on its fitness. The tight-weave hypothesis applies in situations when the effects of a tree on soil result from direct selection to improve a tree's fitness, thus creating a positive feedback. If the effects do not directly influence a tree's fitness but are rather a side effect of another process that does, this is called a loose-weave connection. Such effects may not necessarily be beneficial to the tree, but they should not be more negative than the positive effects of the primary trait. Finally, a frayed pattern is when the effects are byproducts of ecological interactions not in direct relation to the tree's fitness.

Ehrenfeld et al. (2005) distinguish also other characteristics of tree–soil feedbacks, including specificity (whether the feedback is specific, e.g., to one individual, species, functional group or trees in general), whether they are qualitative/quantitative, scale (spatial and temporal), sign (positive/negative) and complexity (a simple two-component loop, or a more complicated system of multiple components and their interaction).

I will further discuss several examples of feedbacks that can have an impact on forest dynamics and are reasonably well detectable, i.e., in terms of the above-mentioned criteria, they could be described as tight-weave or species-specific, operating on a relatively small spatial scale (meters) but a wider temporal scale (years to hundreds of years), both positive and negative and not overly complex.

A positive tree-soil feedback was described from a mosaic of *Tsuga canadensis* and *Acer saccharum* forests, where regeneration of *Tsuga* in *Acer* dominated stands was impaired by the effects of *Acer* litter in the forest floor, while the regeneration of *Acer* in *Tsuga* stands appeared limited by low nitrogen supply in *Tsuga* soils (Frelich et al. 1993; Binkley & Giardina 1998). The negative effect of tree litter on the establishment of certain tree species is a common phenomenon (Sayer 2006). The low nutrient reserves in the seeds of small-seeded (and often pioneer or shade-intolerant) species only can support limited radicle and hypocotyl growth of seedlings, so a thick litter layer can represent an impermeable barrier for these species. Besides *Tsuga,* this also applies to other conifers, e.g., different spruce species (Simard et al. 1998; Asplund et al. 2018; Han et al. 2018). Larger-seeded conifers (e.g., firs), however, do not show such limitation, or at least not so strong (Knapp & Smith 1982; Simard et al. 1998). Similar to Frelich et al. (1993), also other authors reported lower suitability of broadleaved litter for conifer seedlings (Simard et al. 1998; Asplund et al. 2018), supporting the existence of an important tree-soil feedback.

Another feedback between trees and soils can arise through uprooting. The pit and mound microtopographies created by uprooting act as unique microhabitats in the forest and depending on local environmental conditions and the requirements of a particular tree species, both pits and mounds can be either more or less suitable for the species' regeneration, compared to the undisturbed forest floor. The only universal phenomenon is the exposure of bare soil on young pits and mounds, which can make them a suitable microsite for the regeneration of early-successional and light-seeded species (Peterson et al. 1990; Kern et al. 2019). Pits become an unsuitable microsite for two main reasons, litter accumulation and excess wetness. The negative effects of litter on regeneration of some species were discussed above and have also been observed in connection with broadleaved litter accumulation in pits (Beatty & Sholes 1988; Simon et al. 2011). Waterlogging in pits may be a problem for seedlings in areas with a generally high water table (Hörnberg et al. 1997), but its effects vary depending on the species of both the seedling and the uprooted tree. *Picea* and *Betula* regeneration was more successful in shallower, drier, pits (created by uprooted *Picea* trees with shallower root system compared to other tree species), while *Alnus* seedlings did not show such preference (Vodde et al. 2010; Vodde et al. 2015). Under certain conditions, however, the increased moisture availability in pits can be beneficial to plants as was the case after a catastrophic windthrow in Pennsylvania, where soil dryness and high surface temperature on mounds made them a less suitable microsite (Peterson & Pickett 1990). More often, however, mounds appear to be a better microsite for tree growth (Lyford & MacLean 1966; Šebková et al. 2012; Šamonil et al. 2016; Kern et al. 2019).

Aims of the thesis and research questions

Within the broad topic of tree-soil interactions, this study targets three areas using the results of eight papers. Papers 1–3 explore the effects of trees on pedogenesis (physical and chemical soil properties) through uprooting and decaying logs. Although these processes have been studied previously, little is known especially about their temporal progressions, which we studied using chronosequences from pit-mound microtopographies and soil below decaying *Fagus sylvatica* logs. Papers 4–5 focus on the biogeomorphological aspects of biomechanical effects of trees on soil, specifically on assessing the frequency and importance of all distinguishable effects of trees in an old-growth forest and comparing the importance of tree death-related effects across different types of forests, neither of which has been done before. Finally, in papers 6–8 we studied the dynamics of *F. sylvatica* and *Picea abies* in an old-growth forest with respect to soils. The first step was to identify the main patterns of soil spatial complexity and its sources (Paper 6). Then we explored the relationship of the two tree species to soils and its dynamics over four decades. The last paper deals with the regeneration of *F. sylvatica* and *P. abies* and its relation to soils and tree-created microsites. Specific research questions follow.

Impacts of trees on pedogenesis (physical and chemical soil properties)

- What is the progress of post-uprooting pedogenesis in different soils and how does it differ between treethrow pits and mounds? How long does it take for a soil horizon to regain its pre-disturbance thickness? What are the patterns of post-uprooting development of soil physical and chemical properties? (Papers 1, 2)
- To what depth do decaying tree trunks affect soil properties? What changes do they cause and how long do these effects last? (Paper 3)

Biomechanical effects of trees on soil

- How frequent are different biomechanical effects of trees in a temperate old-growth forest? How important are they in terms of areas and volumes associated with them? (Paper 4)
- What is the structure of long-term biomechanical effects of trees related to two types of tree mortality – breakage and uprooting? How does it change along an elevational gradient represented by four Central European forests? (Paper 5)

The dynamics of *Fagus sylvatica* and *Picea abies* in an old-growth forest with respect to soils

- What are the main patterns and sources of soil spatial complexity in Boubín old-growth forest? (Paper 6)
- How does the distribution of *F. sylvatica* and *P. abies* in Boubín reflect soil spatial pattern? How did tree populations of *F. sylvatica* and *P. abies* in Boubín change between 1972 and 2010 with respect to soils and what were the responsible drivers? (Paper 7)
  What are the main drivers of *F. sylvatica* and *P. abies* regeneration occurrence in Boubín? How important is the role of canopy trees and their ability to modify their environment? (Paper 8)

Material and methods

This is only a brief overview of the study sites, data collected and statistical approaches. Detailed information can be found in the individual papers.

Study sites

The papers included in this thesis use data collected in five Czech and one US (Michigan) locations. These sites span an altitudinal range from 152 to 1109 m a.s.l., lie on different types of bedrock with various soils, and have different climatic conditions with mean annual temperatures between 5.1 and 9.9 °C, and mean annual precipitation between 545 and 1121 mm (Table 1). In the Czech Republic, vegetation ranges from an alluvial forest in the lowest site, through *Fagus sylvatica*-dominated stands to a *Picea abies*-dominated forest in the highest altitude. Northern hardwood forests predominate in Michigan. All Czech sites are old-growth forests under strict nature protection. Two of these sites, Žofín and Boubín virgin forests, have never been cut and have been protected since 1838 and 1858, respectively (Šebková et al. 2011; Janík et al. 2016), making them among the oldest forest reserves in Europe (Welzholz & Johann 2007). In addition, all Czech sites have a long tradition of forest research in the form of repeated tree censuses. During these, position, diameter, species and several other characteristics of all living and dead trees with DBH > 10 cm are recorded. The first censuses were carried out in the 1970s (Průša 1985) and have been repeated several times since then.

Data sets

Soil development after tree uprooting (Papers 1, 2) was studied in 46 pit-mound pairs from three regions with soils of different degree of weathering and leaching, represented by the Razula (Haplic Cambisols), Žofín (Entic Podzols) and Upper Peninsula (Albic Podzols) sites.

Table 1 Study sites.

Site	Country	Altitude (m)	MAT (°C)	MAP (mm)	Geology	Soils	Main tree species
Ranšpurk	CZ	152–155	9.9	545	sandy and loamy sediments	Gleysols, Fluvisols	*Fraxinus angustifolia, Acer campestre, Carpinus betulus, Quercus robur*
Upper Peninsula	US	215–270	5.1	800	outwash	Podzols	*Acer saccharum, A. rubrum, Q. rubra, Pinus strobus, Tsuga canadensis*
Razula	CZ	660–810	6.5	1121	mudstone, siltstone	Cambisols	*Fagus sylvatica, Abies alba*
Žákova hora	CZ	727–806	6.1	781	migmatite, gneiss, amphibolite	Cambisols, Podzols, Stagnosols	*F. sylvatica, Picea abies, Acer pseudoplatanus*
Žofín	CZ	736–829	6.2	866	granite	Cambisols, Podzols, Gleysols, Histosols	*F. sylvatica, P. abies*
Boubín	CZ	926–1109	4.9	1067	gneiss	Podzols, Cambisols, Gleysols, Stagnosols, Leptosols, Histosols	*P. abies, F. sylvatica*

The age of pit-mound microtopographies was assessed using several dating techniques. Tree-census data were used to determine the age of the youngest (< 37 years) uprooting events, ^{210}Pb dating (including ^{137}Cs and ^{226}Ra) to date treethrow events younger than ca. 200 years, dendrochronological dating for features less than ca. 400 years old, and radiocarbon dating for the oldest microtopographies (Šamonil et al. 2013). The oldest pit-mounds at each study site were 220, 1688 and 6089 years old, respectively. Soil profiles were described and sampled in 1.5 m deep trenches excavated along the pit-mound pairs and in control profiles nearby. Soil samples were analyzed for 38 physical and chemical properties.

For Paper 3, organic material and mineral soil horizons were sampled from and under 24 decaying *Fagus sylvatica* logs and at adjacent control sites in Žofín. Soil samples were taken from the upper mineral A horizon and at depths of 5 and 10 cm below the A horizon base and analyzed for a wide range of chemical properties. Ages of the decaying logs were assessed dendrochronologically and ranged from 8 to 52 years.

Biomechanical effects of trees (BETs; Paper 4) were evaluated in Boubín on a set of 3956 standing or lying trees. We considered 10 BETs: tree uprooting, root mounding, bioprotection, trunk baumsteins (rock fragments displaced by trunk growth), root baumsteins, stump hole infilling, trunk and root systems displacements, depressions formed after trunk fall, stemwash, and trunkwash.

To quantify the long-term biomechanical effects of tree uprooting/breakage (Paper 5) we combined data from repeated tree censuses with site- or species-specific models for soil area and volume affected by dying trees, based on tree DBH. We worked with data from four sites (Ranšpurk, Žákova hora, Žofín and Boubín) where life histories of 55,492 trees were available in total. Areas and volumes affected by uprooting were modelled based on 1035 measured treethrow pit-mound pairs. Tree diameters at base were measured for 3649 trees and the volume of tree root system was derived from species-specific allometric equations for belowground biomass.

Soil survey in Boubín (Papers 6–8) was carried out on a regular square grid with a lateral spacing of ca. 22 m. At each of the grid points diagnostic horizons and other features of 1 m deep soil profiles were used to determine the soil taxonomical unit (STU) according to the WRB system.

The development and current state of *Fagus sylvatica* and *Picea abies* populations in Boubín (Papers 7, 8) was assessed from repeated tree censuses carried out in 1972, 1996 and 2010.

For Papers 7 and 8 we also collected data on tree regeneration in Boubín. First, we censused all tree regeneration with DBH between 1 and 10 cm in 116 circular plots of 10 m radius. Next, in a subset of 46 of these plots, we placed rectangular single-microsite (intact soil, treethrow pits and mounds, stumps or deadwood) plots on which we censused all regeneration with DBH < 10 cm. For seedlings (height < 15 cm), we also recorded in which seedbed (beech litter, mosses or bare substrate) they grew.

Statistical analyses

We used various modeling techniques ranging from simple linear regression (OLS, ordinary least squares) through GLM (generalized linear models) to GLMM (generalized linear mixed models). Bootstrapping (Efron 1979) was used for nonparametric testing and computation of confidence intervals. For soil complexity analysis we applied and extended existing methods based on graph theory (Phillips et al. 2015). Vast majority of analyses were performed in R (R Core Team 2020).

Main results

Impacts of trees on pedogenesis through uprooting (Papers 1, 2)

Post-uprooting pedogenesis was always more rapid in pits than on mounds and was slower for deeper lying horizons (E and B) than for the upper ones (O and A). The time required for a soil horizon to reach the same thickness as was observed at undisturbed sites ranged from 5 (O horizon in pits on Haplic Cambisols) to > 16,000 years (E horizon on mounds on Albic Podzols; Fig. 1).

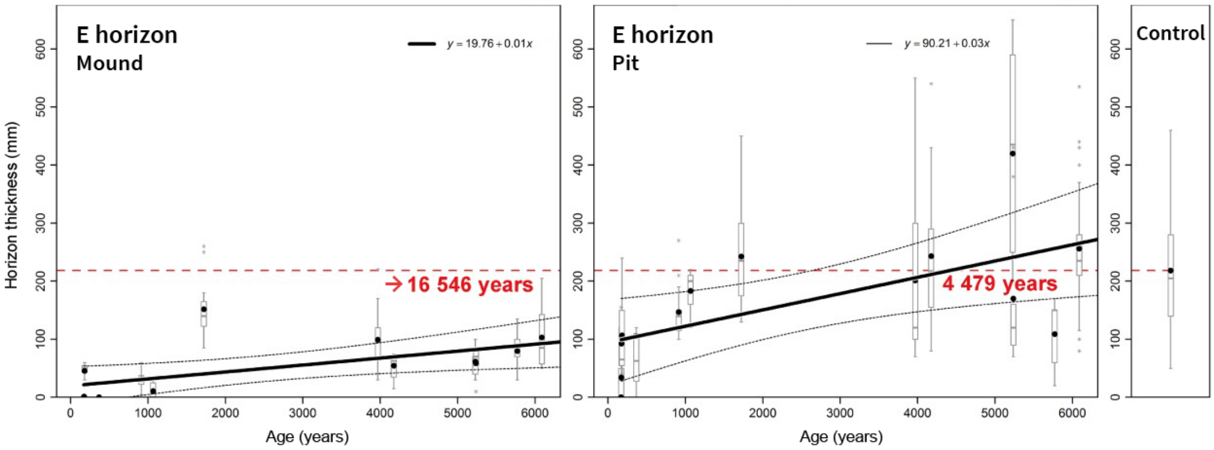


Fig. 1 E horizon thickness development as a function of time on Albic Podzols in Upper Peninsula, Michigan. Even on the oldest (> 6000 years) uprooting mounds, the E horizons did not reach the average thickness found on undisturbed soil (control). In the pits, however, it took an average of about 4500 years (Paper 1).

Concerning soil physical and chemical properties, depth along the soil profile was the most important explanatory variable in all three regions, followed by microsite (pit or mound) and then age (time since disturbance). On fine-textured soils with less intensive pedogenesis (Haplic Cambisols), tree uprooting increased the local variability of pedogenic processes by changing melanization and hydromorphic processes and by mineral alteration. Conversely, on the coarse-textured Albic Podzols, the post-uprooting pedogenesis was much less diversified between the microsites, despite rapid podzolization in pits and slower podzolization on mounds. This suggests that in more highly developed soils, responses to disturbance may be more limited than in less-developed soils, leading to weaker polygenetic effects of uprooting (Fig. 2).

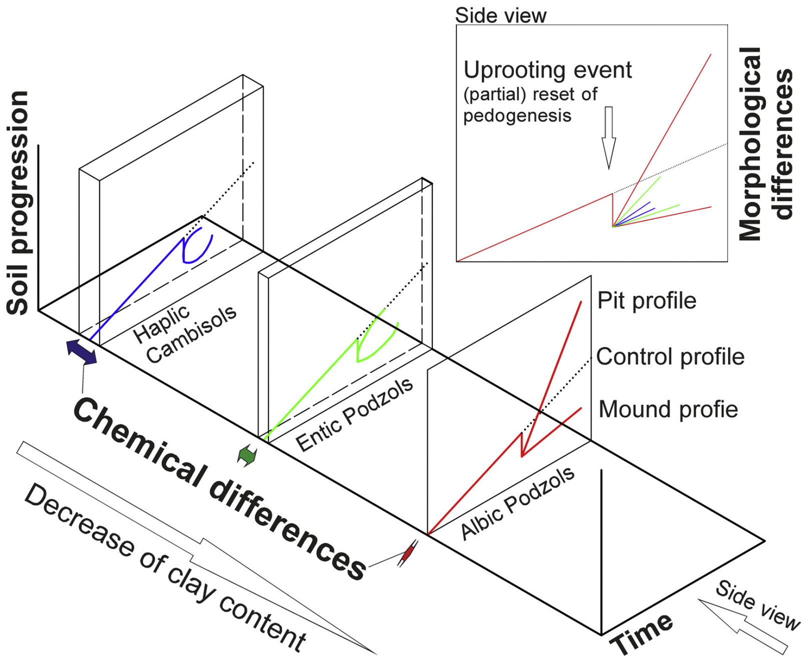


Fig. 2 Conceptual model of post-disturbance soil formation in three soil regions, on Haplic Cambisols, Entic Podzols, and Albic Podzols. Although morphological data indicate a non-linear pedogenesis, chemical data suggest a convergent mode of soil formation, more so the higher the coarse fraction content of the soil (Paper 2).

Effects of decaying tree logs on pedogenesis (Paper 3)

During the first stages of log decay, the underlying soil responded with a substantial increase in nutrients, pH and CEC. The effect of log decay was strongest within the uppermost 20 cm of soil, but for some soil properties the models predicted it to reach down to 60 cm. The maximum divergence from control sites was reached 12–60 years following trunk fall, after which most soil properties slowly converged back to their initial level (Fig. 3). The modelled convergence times ranged between 39 and 229 years with a median of 53 years.

Biomechanical effects of trees (Papers 4, 5)

Biomechanical effects of trees (BETs) were observed in 59% of standing and 51% of lying dead trees and approximately one tenth of trees showed both bioprotective and bioerosive effects. Significant differences were observed between tree species (e.g., less treethrows

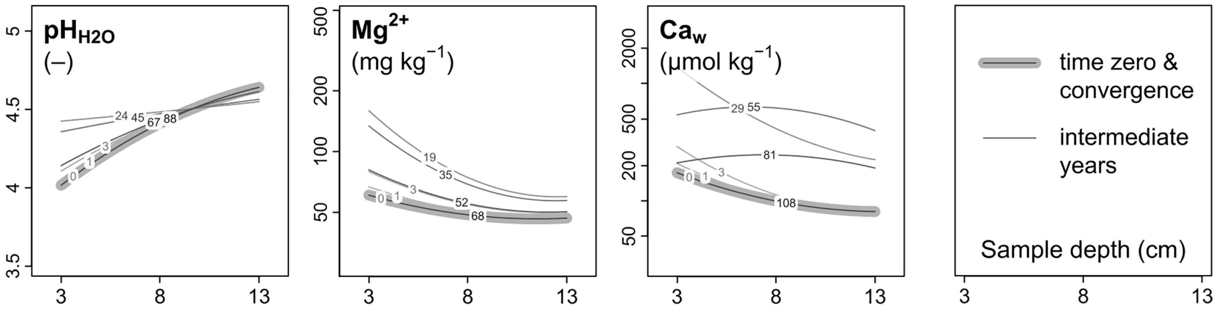


Fig. 3 Development of pH and contents of two base cations in soil under decaying *Fagus sylvatica* logs modelled as a function of soil depth and time. The models assume convergence, i.e. that as the log decays, the values begin to change but eventually they return back to the state at time zero (thick line). The time course of this process is shown by thin lines marked by the decay times (in years), which they correspond to (Paper 3).

in *Abies alba* than in *Picea abies* and *Fagus sylvatica*) as well as between size categories. A bioprotective function was the most frequently observed phenomenon, but treethrows dominated when affected soil areas and volumes were considered. The total soil area affected by the BETs was 342 m^2 ha^{-1} and the associated soil volume was 322 m^3 ha^{-1} (Fig. 4).

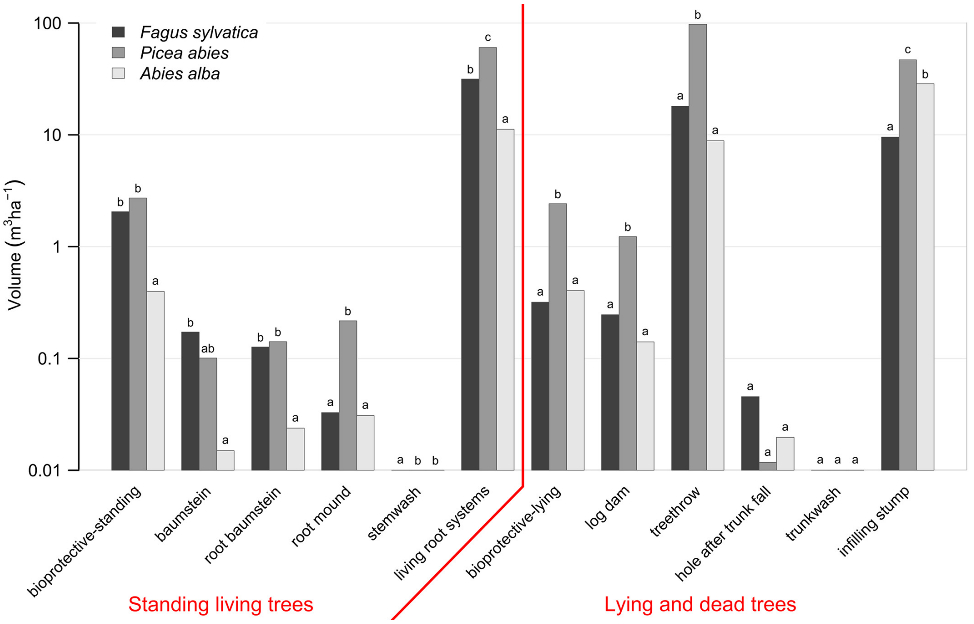


Fig. 4 Volume of soil and regolith associated with different types of biomechanical effects of trees in Boubín, according to the three main tree species (Paper 4).

BETs intensified with increasing elevation and this pattern was mostly related to the effects of dying trees, especially those that uprooted. In the lowlands, an average of 2.7 m^3 ha^{-1} year^{-1} was associated with all BETs, while in the highest mountain site it averaged 7.8 m^3 ha^{-1} year^{-1}. Effects of dying trees and particularly treethrows represented about 70% of all BETs at both mountain sites, while it was 58% at the highland site and only 32% at the lowland site. This shows a more important role of BETs in hillslope processes in the mountains, partly due to a higher frequency of windstorms there (Table 2).

Table 2 Average characteristics of forest dynamics between the 1970s and 2000s at the study sites. Largest differences between sites are in uprooting-related values (Paper 5).

		Lowlands	Highlands	Mountains	
Property	Unit	Ranšpurk	Žákova Hora	Žofín	Boubín
Frequency					
Survivors	ind. ha^{-1} period^{-1}	130.4^{a}	178.9^{c}	128.1^{a}	172.9^{b}
Recruits	ind. ha^{-1} year^{-1}	4.4^{d}	3.2^{c}	2.7^{b}	1.0^{a}
Standing dead trees	ind. ha^{-1}	5.3^{a}	6.5^{a}	9.3^{b}	17.1^{c}
Broken trees	ind. ha^{-1} year^{-1}	1.6^{a}	1.5^{a}	1.9^{b}	1.9^{b}
Uprooted trees	ind. ha^{-1} year^{-1}	0.7^{b}	0.6^{a}	1.6^{c}	1.9^{d}
Area					
Surviving basal area	m^{2} ha^{-1} period^{-1}	43.9^{c}	38.9^{b}	44.8^{c}	37.1^{a}
Increment of basal area	m^{2} ha^{-1} year^{-1}	1.3^{a}	1.7^{c}	1.3^{a}	1.4^{b}
Basal area of standing dead trees	m^{2} ha^{-1}	2.3^{a}	1.6^{a}	3.7^{b}	5.0^{c}
Basal area of broken trees	m^{2} ha^{-1} year^{-1}	0.7^{ab}	0.7^{b}	1.1^{c}	0.6^{a}
Area of treethrow pit-mounds	m^{2} ha^{-1} year^{-1}	1.5^{a}	2.7^{b}	9.6^{c}	10.3^{d}
Volume					
Surviving root systems volume	m^{3} ha^{-1} period^{-1}	53.0^{d}	29.2^{a}	41.2^{b}	46.2^{c}
Increment of root systems	m^{3} ha^{-1} year^{-1}	1.5^{a}	1.5^{a}	1.6^{b}	2.3^{c}
Root systems of standing dead trees	m^{3} ha^{-1}	3.9^{b}	1.6^{a}	4.6^{b}	8.5^{c}
Root systems of broken trees	m^{3} ha^{-1} year^{-1}	0.9^{b}	0.7^{a}	1.4^{c}	1.0^{b}
Volume of treethrow root plates	m^{3} ha^{-1} year^{-1}	0.2^{a}	0.6^{b}	4.2^{c}	4.3^{c}

ind. = individuals

Soil spatial complexity in Boubín (Paper 6)

Within six reference soil groups (Leptosols, Cambisols, Podzols, Stagnosols, Gleysols and Histosols) and 37 second-level soil units we identified three main gradients: (i) degree of weathering and leaching processes, (ii) hydromorphology (water influence), and (iii) proportion of rock fragments. The factor responsible for most of the observed soil spatial complexity ($\lambda_1 = 14.7$) was hydromorphology ($\lambda_1 = 8$). Both degree of weathering and hydromorphology exhibited significant sequentiality, which indicates that the spatial pattern of soils respected these two gradients. A partial spatial coherence of these two gradients also suggests synergistic influences of topography, climate, (hydro)geology and biomechanical and biochemical effects of trees. On the other hand, the spatial pattern of the proportion of rock fragments appeared random in all respects, indicating primary control of local geology and Quaternary biogeomorphological processes (Fig. 5).

Fagus sylvatica and *Picea abies* vs. soils in Boubín (Papers 7, 8)

The spatial distribution of populations of *F. sylvatica* (beech) and *P. abies* (spruce) primarily reflected a gradient of soil hydromorphism, with beech dominating drier soils and spruce dominating wetter soils (Fig. 6). Over the 38 years, beech expanded on all major soils (Fig. 7), yet the most important drivers differed. The only driver acting in favor of spruce on certain terrestrial soils was its faster radial growth. However, the effect was

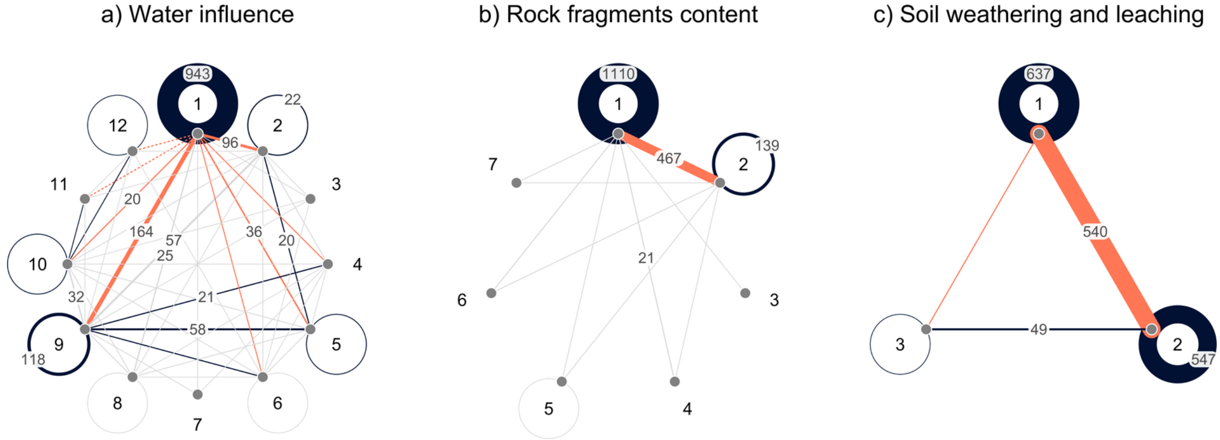


Fig. 5 Soil spatial complexity in Boubín as manifested within the three main gradients of soil properties. Spatial complexity decreased from a) to c). E.g., in a), the numbered points (1–12) represent the levels of the gradient of water influence from the least to the most hydromorphic soils. Spatial adjacency (neighborhood) frequency within the sampling 22-m square grid is denoted by straight lines (between levels) and circles (self-adjacency within one level). Line thickness corresponds to the observed frequency and line color denotes its (non)randomness: random (gray), more frequent than random (dark) and less frequent (orange; Paper 6).

weaker than the effect of drivers that prioritized beech, mainly tree mortality. Fine-scale mortality (deaths of individual trees) was more significant on terrestrial soils, while the effect of coarse-scale mortality (deaths from a single severe windstorm event) increased towards hydromorphic soils. Beech was also more successful in recruitment than spruce. Certain soils (Histosols and Albic Podzols) diverged from the general trends because of their different disturbance regimes and specific tree-soil interactions.

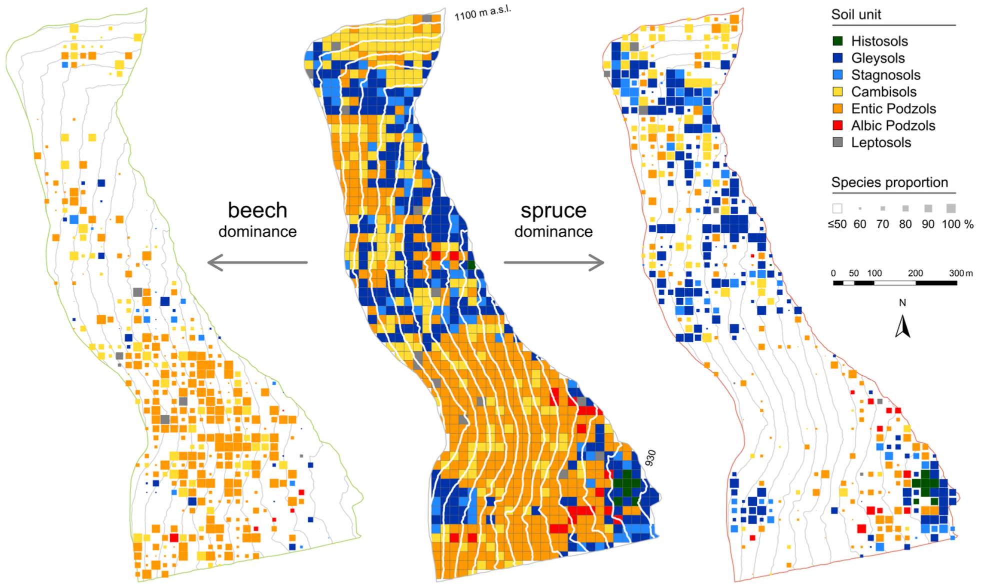


Fig. 6 Dominance of beech on terrestrial soils (left) and spruce on hydromorphic soils (right) in Boubín (Paper 7).

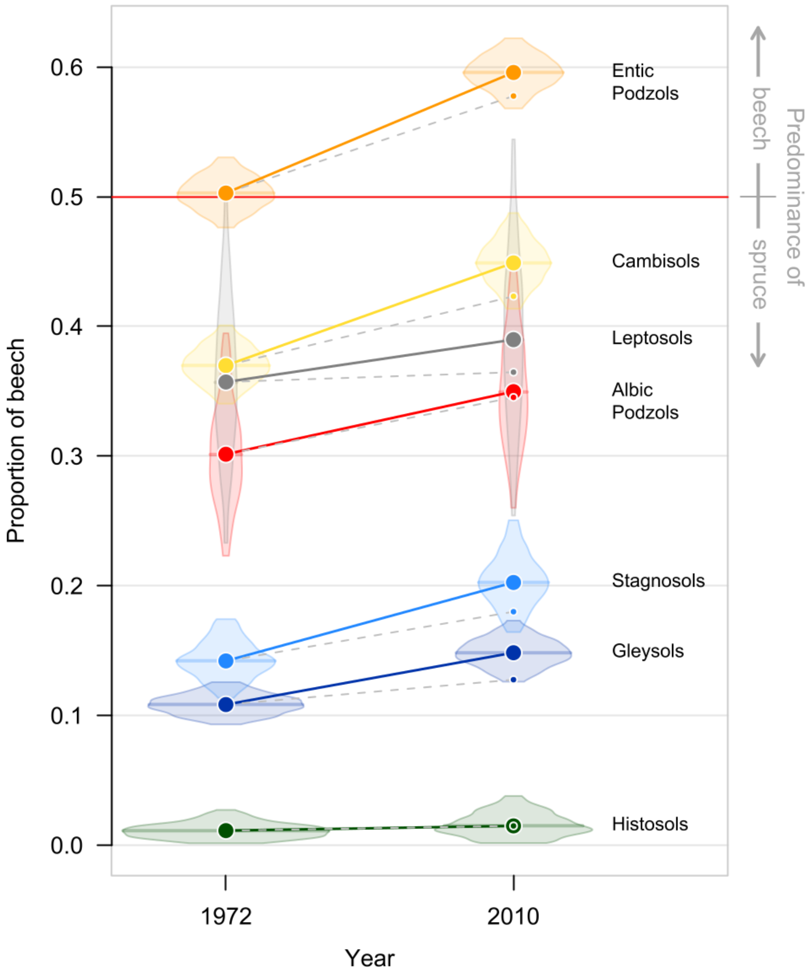


Fig. 7 The proportion of beech increased on most soils over the four decades and the increase was higher on terrestrial soils. Mean proportions by soils are plotted with their bootstrap distributions truncated at the inner 95%. Dashed lines show the theoretical development without the occurrence of the Emma windstorm (Paper 7).

Although beech was overall slightly less abundant in the canopy than spruce, it strongly outnumbered spruce in regeneration. Beech showed an affinity for beech litter-rich microsites and terrestrial soils, while spruce was more common on deadwood and moister soils and its response to the seedbed was microsite-specific. The regeneration of both species was positively related to the proportion of their own species in the canopy, but much more so in seedlings than in older regeneration cohorts, where soil wetness was more important (Fig. 8). Both species exhibited an ability to modify their environment in favor of their own regeneration. Beech mainly by producing deep litter in which establishment is difficult for smaller-seeded species, and spruce by creating alternative microsites (deadwood, treethrow mounds) where its regeneration is more likely to get established.

The results of both studies suggest that beech has been steadily expanding in Boubín over the last forty years and, given its high dominance in regeneration, this trend is likely to continue unless interrupted by severe disturbance providing more suitable microsites and available light for spruce regeneration.

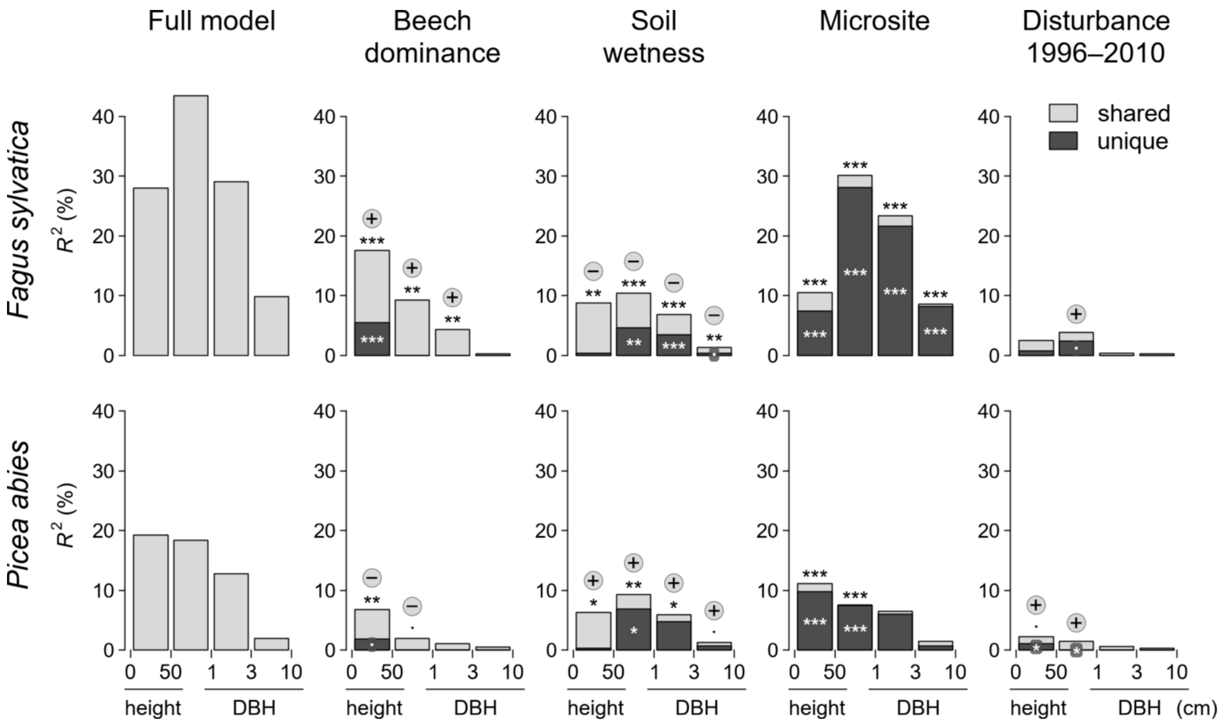


Fig. 8 The importance of the studied factors for different cohorts of beech and spruce regeneration, based on their explained variance (R^2). Canopy composition (beech dominance) was more important for seedlings than for older regeneration, while soil wetness and microsite retained their influence even for saplings and small trees. The first bar chart in a row shows the total variance explained by all variables, and the contributions of individual variables follow. Dark and light parts of bars mark the unique variance explained by each variable, and the explained variance it shares with other variable(s), respectively. Stars inside the dark areas denote the statistical significance of the unique effects of variables, while stars above bars mark the significance of total effects of variables (., $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). For significant continuous variables, the sign of their effect (+/−) is displayed above bars (Paper 8).

Conclusion

There are many different ways in which trees and soils may interact, and at least some of them were explored in this thesis. Trees were shown to affect soils on various spatial and temporal scales, ranging from highly localized processes such as stemwash whose influence is more or less limited to a part of a tree's lifespan, to uprootings through which a single tree can disturb tens of square meters of soil and the resulting microtopographies may persist for thousands of years. Soils, on the other hand, were responsible for the main spatial distribution pattern of beech (*Fagus sylvatica*) and spruce (*Picea abies*) trees in Boubín old-growth forest. Finally, since certain effects of trees, such as uprooting or litter and deadwood production, also influenced the chances of trees to regenerate, positive feedbacks between trees and soils emerged.

References

Asplund J., Hustoft E., Nybakken L., Ohlson M., Lie M.H. 2018. Litter impair spruce seedling emergence in beech forests: a litter manipulation experiment. *Scandinavian Journal of Forest Research* 33: 332–337.

Augusto L., Ranger J., Binkley D., Rothe A. 2002. Impact of several common tree species of European temperate forests on soil fertility. *Annals of Forest Science* 59: 233–253.

Baldrian P. 2017. Forest microbiome: Diversity, complexity and dynamics. *FEMS Microbiology Reviews* 41: 109–130.

Beatty S.W. 1984. Influence of Microtopography and Canopy Species on Spatial Patterns of Forest Understory Plants. *Ecology* 65: 1406–1419.

Beatty S.W., Sholes O.D. V. 1988. Leaf litter effect on plant species composition of deciduous forest treefall pits. *Canadian Journal of Forest Research* 18: 553–559.

Bennie A.T. 1991. Growth and mechanical impedance. In Waisel Y., Eshel A., Kafkafi U. (eds.), Plant roots: The hidden half, pp. 393–414. Marcel Dekker, Inc., New York.

Binkley D. 1996. The influence of tree species on forest soils: Processes and patterns. In Mead D.J., Cornforth I.S. (eds.), Proceedings of the Trees and Soils Workshop, pp. 1–33. Agronomy Society of New Zealand, Canterbury.

Binkley D., Giardina C. 1998. Why do tree species affect soils? The Warp and Woof of tree–soil interactions. *Biogeochemistry* 42: 89–106.

Bréda N., Huc R., Granier A., Dreyer E. 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science* 63: 625–644.

Bruckner A., Kandeler E., Kampichler C. 1999. Plot-scale spatial patterns of soil water content, pH, substrate-induced respiration and N mineralization in a temperate coniferous forest. *Geoderma* 93: 207–223.

Corenblit D., Baas A.C.W., Bornette G., Darrozes J., Delmotte S., Francis R.A., Gurnell A.M., Julien F., Naiman R.J., Steiger J. 2011. Feedbacks between geomorphology and biota controlling Earth surface processes and landforms: A review of foundation concepts and current understandings. *Earth-Science Reviews* 106: 307–331.

Crampton C.B. 1982. Podzolization of soils under individual tree canopies in Southwestern British Columbia, Canada. *Geoderma* 28: 57–61.

Dawkins R. 1982. The Extended Phenotype. The Gene as the Unit of Selection. Oxford University Press.

Denny C.S., Goodlett J.C. 1956. Microrelief resulting from fallen trees. In Denny C.S. (ed.), Surficial geology and geomorphology of Potter Country Pennsylvania, pp. 59–66. Washington.

Dobbertin M. 2002. Influence of stand structure and site factors on wind damage comparing the storms Vivian and Lothar. *Forest Snow and Landscape Research* 77: 187–205.

Dreyer E. 1994. Compared sensitivity of seedlings from 3 woody species (*Quercus robur* L, *Quercus rubra* L and *Fagus silvatica* L) to water-logging and associated root hypoxia: effects on water relations and photosynthesis. *Annales des Sciences Forestières* 51: 417–428.

Dwyer L.M., Merriam G. 1981. Influence of Topographic Heterogeneity on Deciduous Litter Decomposition. *Oikos* 37: 228.

Efron B. 1979. Bootstrap Methods: Another Look at the Jackknife. *The Annals of Statistics* 7: 1–26.

Ehrenfeld J.G., Ravit B., Elgersma K. 2005. Feedback in the plant-soil system. *Annual Review of Environment and Resources* 30: 75–115.

Finzi A.C., Van Breemen N., Canham C.D. 1998a. Canopy tree–soil interactions within temperate forests: Species effects on soil carbon and nitrogen. *Ecological Applications* 8: 440–446.

Finzi A.C., Canham C.D., Van Breemen N. 1998b. Canopy tree–soil interactions within temperate forests: Species effects on pH and cations. *Ecological Applications* 8: 447–454.

Frelich L.E., Calcote R.R., Davis M.B., Pastor J. 1993. Patch formation and maintenance in an old-growth hemlock-hardwood forest. *Ecology* 74: 513–527.

Gabet E.J., Reichman O.J., Seabloom E.W. 2003. The effects of bioturbation on soil processes and sediment transport. *Annual Review of Earth and Planetary Sciences* 31: 249–273.

Gruba P., Mulder J., Pacanowski P. 2020. Combined effects of soil disturbances and tree positions on spatial variability of soil pH_{CaCl2} under oak and pine stands. *Geoderma* 376: 114537.

Han A.R., Kim H.J., Jung J. Bin, Park P.S. 2018. Seed germination and initial seedling survival of the subalpine tree species, *Picea jezoensis*, on different forest floor substrates under elevated temperature. *Forest Ecology and Management* 429: 579–588.

Hoffman B.S.S., Anderson R.S. 2014. Tree root mounds and their role in transporting soil on forested landscapes. *Earth Surface Processes and Landforms* 39: 711–722.

Hörnberg G., Ohlson M., Zackrisson O. 1997. Influence of bryophytes and microrelief conditions on *Picea abies* seed regeneration patterns in boreal old-growth swamp forests. *Canadian Journal of Forest Research* 27: 1015–1023.

Jackson G., Sheldon J. 1949. The Vegetation of Magnesian Limestone Cliffs at Markland Grips Near Sheffield. *The Journal of Ecology* 37: 38.

Jactel H., Bauhus J., Boberg J., Bonal D., Castagneyrol B., Gardiner B., Gonzalez-Olabarria J.R., Koricheva J., Meurisse N., Brockerhoff E.G. 2017. Tree Diversity Drives Forest Stand Resistance to Natural Disturbances. *Current Forestry Reports* 3: 223–243.

Janík D., Král K., Adam D., Hort L., Samonil P., Unar P., Vrska T., McMahon S. 2016. Tree spatial patterns of *Fagus sylvatica* expansion over 37 years. *Forest Ecology and Management* 375: 134–145.

Jenny H. 1941. Factors of soil formation. A system of quantitative pedology. McGraw-Hill, New York.

Jones C.G., Lawton J.H., Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* 69: 373.

Kern C.C., Schwarzmann J., Kabrick J., Gerndt K., Boyden S., Stanovick J.S. 2019. Mounds facilitate regeneration of light-seeded and browse-sensitive tree species after moderate-severity wind disturbance. *Forest Ecology and Management* 437: 139–147.

Knapp A.K., Smith W.K. 1982. Factors influencing understory seedling establishment of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in southeast Wyoming. *Canadian Journal of Botany* 60: 2753–2761.

Kramer M.G., Sollins P., Sletten R.S. 2004. Soil carbon dynamics across a windthrow disturbance sequence in southeast Alaska. *Ecology* 85: 2230–2244.

Kreuzwieser J., Gessler A. 2010. Global climate change and tree nutrition: Influence of water availability. *Tree Physiology* 30: 1221–1234.

LaMarche V.C. 1968. Rates of Slope Degradation as Determined from Botanical Evidence White Mountains California. *Geological Survey Professional Paper* 352: 341–377.

Leuschner C., Ellenberg H. 2017. Ecology of Central European Forests. Vegetation Ecology of Central Europe, Volume I. Springer International Publishing, Switzerland.

Lundström U.S., van Breemen N., Bain D. 2000. The podzolization process. A review. *Geoderma* 94: 91–107.

Lyford W.H., MacLean D.W. 1966. Mound and Pit Microrelief in Relation to Soil Disturbance and Tree Distribution in New Brunswick, Canada. Harvard Forest Paper No. 15: 1–20.

Minnich C., Peršoh D., Poll C., Borken W. 2021. Changes in Chemical and Microbial Soil Parameters Following 8 Years of Deadwood Decay: An Experiment with Logs of 13 Tree Species in 30 Forests. *Ecosystems* 24: 955–967.

Naylor L.A. 2005. The contributions of biogeomorphology to the emerging field of geobiology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 219: 35–51.

Nicoll B.C., Gardiner B.A., Rayner B., Peace A.J. 2006. Anchorage of coniferous trees in relation to species, soil type, and rooting depth. *Canadian Journal of Forest Research* 36: 1871–1883.

Norton D.A. 1989. Tree windthrow and forest soil turnover. *Canadian Journal of Forest Research* 19: 386–389.

Odling-Smee J., Laland K.N., Feldman M.W. 2003. Niche construction. The neglected process in evolution. Princeton University Press.

Pawlik Ł. 2013. The role of trees in the geomorphic system of forested hillslopes – A review. *Earth-Science Reviews* 126: 250–265.

Pawlik Ł., Phillips J.D., Šamonil P. 2016. Roots, rock, and regolith: Biomechanical and biochemical weathering by trees and its impact on hillslopes—A critical literature review. *Earth-Science Reviews* 159: 142–159.

Peterson C.J., Campbell J.E. 1993. Microsite Differences and Temporal Change in Plant Communities of Treefall Pits and Mounds in an Old-Growth Forest. *Bulletin of the Torrey Botanical Club* 120: 451–460.

Peterson C.J., Carson W.P., Mccarthy B.C., Pickett S.T.A. 1990. Microsite variation and soil dynamics within newly created treefall pits and mounds. *Oikos* 58: 39–46.

Peterson C.J., Pickett S.T.A. 1990. Microsite and Elevational Influences on Early Forest Regeneration after Catastrophic Windthrow. *Journal of Vegetation Science* 1: 657–662.

Phillips J.D. 2009. Soils as extended composite phenotypes. *Geoderma* 149: 143–151.

Phillips J.D. 2013. Sources of spatial complexity in two coastal plain soil landscapes. *Catena* 111: 98–103.

Phillips J.D., Marion D.A. 2006. Biomechanical effects of trees on soil and regolith: Beyond treethrow. *Annals of the Association of American Geographers* 96: 233–247.

Phillips J.D., Šamonil P., Pawlik Ł., Trochta J., Daněk P. 2017. Domination of hillslope denudation by tree uprooting in an old-growth forest. *Geomorphology* 276: 27–36.

Phillips J.D., Schwanghart W., Heckmann T. 2015. Graph theory in the geosciences. *Earth-Science Reviews* 143: 147–160.

Průša E. 1985. Die Böhmischen Und Mährischen Urwälder – Ihre Struktur Und Ökologie. Academia, Praha.

R Core Team. 2020. R: A language and environment for statistical computing.

Rice S.K., Westerman B., Federici R. 2004. Impacts of the exotic, nitrogen-fixing black locust (*Robinia pseudoacacia*) on nitrogen-cycling in a pine-oak ecosystem. *Plant Ecology* 174: 97–107.

Rickli C., Graf F. 2009. Effects of forests on shallow landslides – Case studies in Switzerland. *Forest Snow and Landscape Research* 82: 33–44.

Rothe A., Huber C., Kreutzer K., Weis W. 2002. Deposition and soil leaching in stands of Norway spruce and European Beech: Results from the Hoglwald research in comparison with other European case studies. *Plant and Soil* 240: 33–45.

Rötzer T., Biber P., Moser A., Schäfer C., Pretzsch H. 2017. Stem and root diameter growth of European beech and Norway spruce under extreme drought. *Forest Ecology and Management* 406: 184–195.

Šamonil P., Antolík L., Svoboda M., Adam D. 2009. Dynamics of windthrow events in a natural fir-beech forest in the Carpathian mountains. *Forest Ecology and Management* 257: 1148–1156.

Šamonil P., Egli M., Steinert T., Norton K., Abiven S., Daněk P., Hort L., Brandová D., Christl M., Tikhomirov D. 2020. Soil denudation rates in an old-growth mountain temperate forest driven by tree uprooting dynamics, Central Europe. *Land Degradation, Development* 31: 222–239.

Šamonil P., Král K., Hort L. 2010. The role of tree uprooting in soil formation: A critical literature review. *Geoderma* 157: 65–79.

Šamonil P., Schaetzl R.J., Valtera M., Goliáš V., Baldrian P., Vašíčková I., Adam D., Janík D., Hort L. 2013. Crossdating of disturbances by tree uprooting: Can treethrow microtopography persist for 6000 years? *Forest Ecology and Management* 307: 123–135.

Šamonil P., Valtera M., Schaetzl R.J., Adam D., Vašíčková I., Daněk P., Janík D., Tejnecký V. 2016. Impacts of old, comparatively stable, treethrow microtopography on soils and forest dynamics in the northern hardwoods of Michigan, USA. *Catena* 140: 55–65.

Šamonil P., Vašíčková I., Daněk P., Janík D., Adam D. 2014. Disturbances can control fine-scale pedodiversity in old-growth forests: is the soil evolution theory disturbed as well? *Biogeosciences* 11: 5889–5905.

Santi C., Bogusz D., Franche C. 2013. Biological nitrogen fixation in non-legume plants. *Annals of Botany* 111: 743–767.

Sayer E.J. 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological Reviews of the Cambridge Philosophical Society* 81: 1–31.

Schaetzl R.J., Burns S.F., Small T.W., Johnson D.L. 1990. Tree uprooting: Review of types and patterns of soil disturbance. *Physical Geography* 11: 277–291.

Schaetzl R.J., Johnson D.L., Burns S.F., Small T.W. 1989. Tree uprooting: review of terminology, process, and environmental implications. *Canadian Journal of Forest Research* 19: 1–11.

Schelhaas M.-J., Nabuurs G.-J., Schuck A. 2003. Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology* 9: 1620–1633.

Schmull M., Thomas F.M. 2000. Morphological and physiological reactions of young deciduous trees (*Quercus robur* L., *Q. petraea* [Matt.] Liebl., *Fagus sylvatica* L.) to waterlogging. *Plant and Soil* 225: 227–242.

Šebková B., Šamonil P., Janík D., Adam D., Král K., Vrška T., Hort L., Unar P. 2011. Spatial and volume patterns of an unmanaged submontane mixed forest in Central Europe: 160 years of spontaneous dynamics. *Forest Ecology and Management* 262: 873–885.

Šebková B., Šamonil P., Valtera M., Adam D., Janík D. 2012. Interaction between tree species populations and windthrow dynamics in natural beech-dominated forest, Czech Republic. *Forest Ecology and Management* 280: 9–19.

Simard M.-J., Bergeron Y., Sirois L. 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. *Journal of Vegetation Science* 9: 575–582.

Simon A., Gratzer G., Sieghardt M. 2011. The influence of windthrow microsites on tree regeneration and establishment in an old growth mountain forest. *Forest Ecology and Management* 262: 1289–1297.

Sohet K., Herbauts J., Gruber W. 1988. Changes caused by Norway spruce in an ochreous brown earth, assessed by the isoquartz method. *Journal of Soil Science* 39: 549–561.

Spears J.D.H., Holub S.M., Harmon M.E., Lajtha K. 2003. The influence of decomposing logs on soil biology and nutrient cycling in an old-growth mixed coniferous forest in Oregon, U.S.A. *Canadian Journal of Forest Research* 33: 2193–2201.

Spielvogel S., Prietzel J., Leide J., Riedel M., Zemke J., Kögel-Knabner I. 2014. Distribution of cutin and suberin biomarkers under forest trees with different root systems. *Plant and Soil* 381: 95–110.

Stokes A., Atger C., Bengough A.G., Fourcaud T., Sidle R.C. 2009. Desirable plant root traits for protecting natural and engineered slopes against landslides. *Plant and Soil* 324: 1–30.

Strzyżowski D., Fidelus-Orzechowska J., Żelazny M. 2018. Sediment transport by uprooting in the forested part of the Tatra Mountains, southern Poland. *Catena* 160: 329–338.

Suvanto S., Henttonen H.M., Nöjd P., Mäkinen H. 2016. Forest Ecology and Management Forest susceptibility to storm damage is affected by similar factors regardless of storm type : Comparison of thunder storms and autumn extra-tropical cyclones in Finland. *Forest Ecology and Management* 381: 17–28.

Valtera M., Šamonil P., Boublík K. 2013. Soil variability in naturally disturbed Norway spruce forests in the Carpathians: Bridging spatial scales. *Forest Ecology and Management* 310: 134–146.

Veneman P.L.M., Jacke P. V., Bodine S.M. 1984. Soil formation as affected by pit and mound microrelief in Massachusetts, USA. *Geoderma* 33: 89–99.

Vesterdal L., Schmidt I.K., Callesen I., Nilsson L.O., Gundersen P. 2008. Carbon and nitrogen in forest floor and mineral soil under six common European tree species. *Forest Ecology and Management* 255: 35–48.

Vodde F., Jõgiste K., Engelhart J., Frelich L.E., Moser W.K., Sims A., Metslaid M. 2015. Impact of wind-induced microsites and disturbance severity on tree regeneration patterns: Results from the first post-storm decade. *Forest Ecology and Management* 348: 174–185.

Vodde F., Jõgiste K., Gruson L., Ilisson T., Köster K., Stanturf J.A. 2010. Regeneration in windthrow areas in hemiboreal forests: The influence of microsite on the height growths of different tree species. *Journal of Forest Research* 15: 55–64.

Welzholz J., Johann E. 2007. History of protected forest areas in Europe. In Frank G., Parviainen J., Vandekerkhove, K. Latham J., Schuck A., Little D. (eds.), COST Action E27 Protected Forest Areas in Europe – Analysis and Harmonisation (PROFOR): Results, Conclusions and Recommendations, pp. 17–40. Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW), Vienna.

Paper 1

Soil mixing and genesis as affected by tree uprooting in three temperate forests

Pavel Šamonil
Pavel Daněk
Randall J. Schaetzl
Ivana Vašíčková
Martin Valtera

European Journal of Soil Science 66 (2015), 589–603

Abstract

The purpose of this study was to identify general patterns of pedoturbation by tree uprooting in three different, forested landscapes and to quantify post-disturbance pedogenesis. Specifically, our study illustrates how the effects of ‘tree-throw’ on soils gradually become diminished over time by post-uprooting pedogenesis. We studied soil development within 46 pit-mounds in two regions of the Czech Republic, one on Haplic Cambisols and one on Entic Podzols. A third study site was in Michigan, USA, on Albic Podzols. Uprooting events were dated by using tree censuses, dendrochronology and radiometry. These dates provided information on several chronosequences of pedogenesis in the post-uprooting pits and mounds, dating back to 1816 AD (dendrochronological dating, Haplic Cambisols), 322 AD (median of calibration age, ^{14}C age = 1720 ± 35 BP, Entic Podzols) and 4077 BC (^{14}C age = 5260 ± 30 BP, Albic Podzols). Post-uprooting pedogenesis was most rapid in pits and slowest on mounds. Linear chronofunction models were the most applicable for pedogenesis, regardless of whether the soils were in pit or mound microsites. These models allowed us to estimate the time required for horizons in such disturbed sites to obtain the equivalent thicknesses of those in undisturbed sites. These ranged from 5 (O horizon in pits on the Haplic Cambisols) to > 16 000 years (E horizon on mounds on the Albic Podzols). On the Albic Podzols, development of eluvial and spodic horizon thicknesses suggested that pathways involving divergent pedogenesis may occur at these small and localized spatial scales.

P. Šamonil[a], *P. Daněk*[a,b], *R.J. Schaetzl*[c], *I. Vašíčková*[a,d], *M. Valtera*[a]

[a] Department of Forest Ecology, The Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Brno, Czech Republic [b] Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic [c] Department of Geography, Michigan State University, East Lansing, Michigan, USA [d] Department of Forest Botany, Dendrology and Geobiocoenology, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic

1 Introduction

Tree uprooting is important in the evolution of some forest soils. In temperate, beech-dominated European forests, approximately one-third of all trees die as a result of uprooting, implying that, theoretically within 500–3000 years, every location in these forests is likely to be disturbed (Šamonil et al. 2010a, 2013). As a large tree topples, it tears up a lens of soil and leaves an irregularly shaped pit. The soil in the lens slowly detaches from the roots and subsides into an irregular mound, some of which falls and washes back into the pit (Fig. 1). Tree uprooting ('tree-throw') interrupts the generally slow but progressive evolution of soils that involves mineral weathering, decomposition of organic matter, vertical segregation of their products into distinct horizons, and the resultant formation of organized soil profiles. Tree-throw disrupts this progression and is a regressive process (Johnson & Watson-Stegner 1987). Tree uprooting mainly affects soil horizonation, as it mixes materials that were originally systematically stratified. The post-fall re-establishment of horizonation processes and profile differentiation is affected by the microtopography that results from uprooting. The pits receive additional in-washed litter and minerals, and are the loci for additional percolating water, which usually facilitates horizon development and translocation. In contrast, mound soils are subject to reduced leaching, increased desiccation and runoff, and possibly accelerated erosion.

With few exceptions (Vassenev & Targulian 1995), previous studies have focused on only a few pit-mound pairs at a single location. Our data come from multiple disturbance sites in three temperate forests in the Czech Republic and Michigan, USA. Our data also benefit from recent advances in tree-throw dating techniques (Šamonil et al. 2013). Our Michigan site includes the oldest reported uprooting features in the world, some more than 6000 years old, and our data for the Czech Republic include pit-mound pairs that are 1700 years or older (Šamonil et al. 2010a, 2013).

Fig. 1 Tree-throw pit-mound created during the storm in Zofin on 18 January 2007.

Our goal was to determine the patterns of mixing by tree uprooting, and the subsequent re-establishment of soil horizons and profiles, and to develop chronofunctions for these processes and to quantify rates of post-disturbance pedogenesis.

2 Materials and methods

2.1 Study sites

The study sites are at Zofin and Razula in the Czech Republic (CR), and at three locations in the eastern part of the Upper Peninsula of Michigan, USA (Fig. 2 and Table 1). They are all at latitudes 45–50°N and span a gradient of soil leaching and weathering, with highly leached, weathered and acidic Albic Podzols on sandy glacial outwash in Michigan, intermediate Entic Podzols on granite at Zofin, and Haplic Cambisols (soil classification according to Michéli et al. 2007) on flysch at Razula. We avoided very shallow and extremely stony soils at Zofin and Razula (Hyperskeletic and Epileptic Cambisols and Podzols, and Leptosols). Soil textures become sandier from the Haplic Cambisols (Razula), through the Entic Podzols (Zofin) to the Albic Podzols (Michigan). This gradient was associated with increasing longevity of pit-mound micro-topographies (Šamonil et al. 2009, 2013).

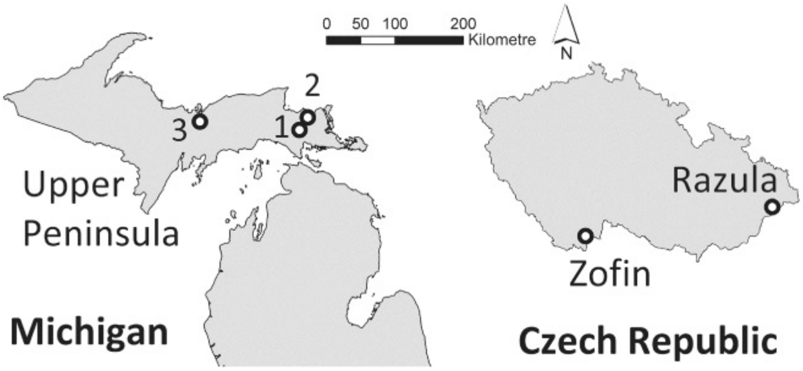


Fig. 2 Location of the Razula and Zofin study areas in the Czech Republic and the research sites in Michigan, USA. For latitude and longitude see Table 1.

Tree uprooting is the most important disturbance factor in these forest ecosystems, although there are others, such as rare fires in Michigan and infrequent mammalian burrowing at all sites. The Michigan sites were located within managed forests that were last cut at least 40 years ago. The old-growth forest at Zofin has been under protection since 1838, and historical documents suggest it has never been cut. The old-growth forest at Razula has been under protection since 1933, and was affected by infrequent selective cutting and grazing before then (Table 1).

2.2 Dating

We selected tree-throw pit-mounds for potential dating by using stratified random techniques at both the Razula (in total 1562 pit-mounds studied in detail, Šamonil et al. 2009) and Zofin sites (1733 pit-mounds, Šamonil et al. 2014). In Michigan, tree-throw features were selected more subjectively (70 pit-mounds studied in detail, Šamonil et al. 2013). Dating techniques were adapted to expected different longevities of pit-mounds in individual localities (Šamonil et al. 2013). Dendrochronological dating was used at all sites, radiometric dating was not applied in Razula and tree census was not used in Michigan.

Table 1 Overview of the physical and ecological conditions associated with each of the three study sites

Feature/locality	Razula	Zofin	Upper Peninsula
Parent material	Flysch	Granite	Outwash
Soil taxonomy	Haplic Cambisols	Entic Podzols	Albic Podzols
Location/latitude, longitude	49.36°N, 18.38°E	48.67°N, 14.70°E	46.32°N, 85.06°W; 46.44°N, 84.82°W; 46.37°N, 86.70°W
Average soil reaction (pH_{H_2O}) in B horizon/dimensionless ± SD / n	5.1 ± 0.4 / 23	4.5 ± 0.2 / 14	5.1 ± 0.2 / 17
Cation exchange capacity in B horizon/mmol+/kg ± SD / n	130.77 ± 38.31 / 23	65.6 ± 17.9 / 14	40.9 ± 11.8 / 17
Soil texture fraction < 0.01 mm in B horizon/% ± SD / n	34.20 ± 11.6 / 23	2.5 ± 1.7 / 14	0.2 ± 0.8 / 17
Soil texture fraction < 0.002 mm in B horizon/% ± SD / n	12.7 ± 5.9 / 23	0.25 ± 0.59 / 14	0.1 ± 0.4 / 17
Forest type	Fir-beech forest	(Spruce)-fir-beech forest	Hardwoods
Main tree species	*Fagus sylvatica, Abies alba*	*Fagus sylvatica, Picea abies, Abies alba*	*Acer saccharum, A. pensylvanicum, A. rubrum, Quercus rubra, Tsuga canadensis, Pinus* spp.
Range of altitudinal gradient / m a.s.l.	600–812	730–837	215–270
Mean annual precipitation / mm	1057	900	800
Average seasonal maximum of snow cover depth / cm	75–100	75–100	circa 100
Mean average temperature / °C	5.0–6.0	4.3	5.1
Maximal observed pit-mound longevity / year	220	1688	6089

Tree-census data were used to establish the ages of the youngest (< 37 years) uprooting events in Zofin and Razula. This method involves repeated measurements (during the 1970s, 1990s and 2000s) of the dimensions of all trees with the diameter at breast height ≥ 10 cm within the reserves. We used ^{210}Pb (lead) dating (and also including ^{137}Cs (caesium) and ^{226}Ra (radium)) of soil material deposited within the tree-throw pits to date disturbance events younger than about 200 years. Dendrochronological dating was applied only to live trees, yielding a useful age range of about 400 years. Radiocarbon (^{14}C) dating was used for features older than 100 years. The age of the tree-throw events in Michigan was taken as the radiocarbon dates of buried wood or the pre-fall buried A horizons in the mound profiles (profile B in Fig. 3 in Schaetzl 1986; Šamonil et al. 2013). The various dating methods have different ranges of validity. Where these ranges overlapped, we cross-validated estimates of tree-throw ages (Šamonil et al. 2013). In total, we successfully dated 37 pit-mounds in Razula, 178 pit-mounds in Zofin and 14 pit-mounds in Michigan (Šamonil et al. 2009, 2013).

The dates that we report reflect various ages, relative to the disturbance events. Minimum ages of the events are reported by dendrochronological data for trees that had rooted on a dated pit-mound, or had recently grown in gaps formed during uprooting events, and some data from tree-censuses, as well as ^{210}Pb- and ^{14}C-dates from the sedimentation funnel within the tree-throw pit. Real (best actual) age estimates of disturbance events were obtained by complete tree-census data and by coring trees that grew in the vicinity of pit-mounds but had germinated before the disturbance event. Release in radial growth of these trees was used to establish the date of the uprooting event. Finally, radiocarbon dates of remnants of uprooted trunks in mounds provided maximum ages (see details in Šamonil et al. 2009, 2013).

2.3 Soil selection and characterization

We selected only the most precisely dated pit-mounds for this study (14 pit-mounds in both Razula and Michigan; 18 pit-mounds in Zofin). The 46 sites were described and sampled in 1.5-m deep and 0.6-m wide trenches along the axes of the pit-mound pairs (profile A in Fig. 3). The soil horizonation across the face of the trenches was carefully sketched (Table 2). We sampled by horizons in the trench and at fixed depths in the pit and mound, and also in an adjacent undisturbed reference pedon at depths of 5, 15, 30, 50 and 100 cm. About 700 samples (Fig. 4-6) were analysed for the main processes in soils: transformation and translocation of organic compounds (such as humification); weathering and leaching processes (mineral formation and alteration, clay illuviation); and oxidation-reduction processes (Šamonil et al. 2010b), and complemented and verified the morphological survey. Within this study we refer to some characteristics of the sorption complex, including exchangeable Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}, exchangeable acidity (Al+H) and effective cation exchange capacity (CEC). These were all analysed according to Gillman & Sumpter (1986; $BaCl_2$-compulsive exchange procedure, native pH).

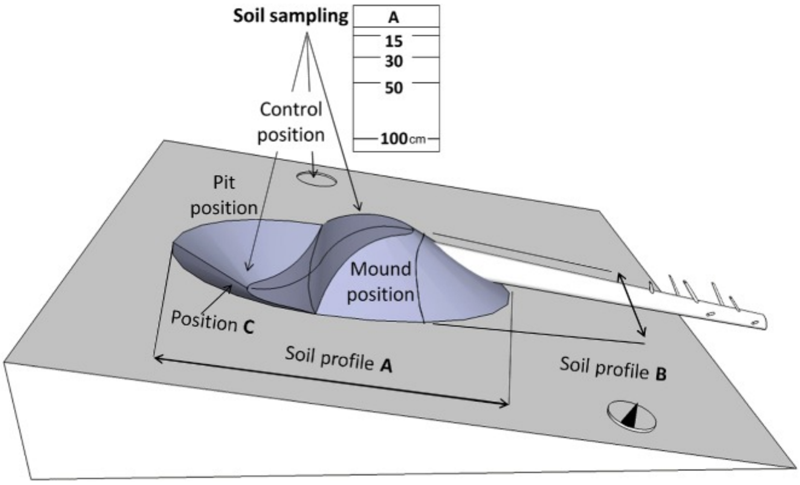


Fig. 3 A schematic pit-mound pair and uprooted tree trunk, with positions of sampled profiles on pit, mound and undisturbed control sites.

2.4 Development of soil chronofunctions

We quantified pedogenesis in the pits and mounds in terms of the thicknesses of newly-formed horizons as compared with the equivalent horizons in the reference pedons. Intensity of horizon development in terms of colour and chemical evolution were noted but not quantified in this study. We modelled the relationships between horizon thickness and the age of the disturbance event, which was taken as the new time$_{zero}$ for soil formation. We applied generalized

Table 2 Soil horizons used.

Group of horizons		Description of individual horizons
Terrestrial upper **organic horizons**	O	**L** = litter organic horizon
		F = fermented organic horizon
		H = humification organic horizon
Uppermost **mineral soil horizons** enriched with organic matter	A	A**m** = mollic horizon
		A**u** = umbric horizon
Eluvial horizons	E	**Ep** = eluvial (= Albic) podzolic horizon
Metamorphic and illuvial horizons	B	B**v** = cambic horizon
		B**vs**, B**s** = spodic horizon without illuviation process; Bs = lower spodic horizon in Albic Podzols; Bvs = sole spodic horizon in Entic Podzols
		B**h** = spodic horizon of organic substances illuviation
		B**hs** = spodic horizon of illuviation of complexes of sesquioxides and organic substances
		Bs**m**, Bhs**m** = ortstein horizon
		B**t** = argic horizon
		B**x** = fragipan (like) horizon
		B**w** = weakly developed B horizon in terms of soil colour or soil structure
Substratum horizons	C	**C** = substratum (unconsolidated) horizon, without features of pedogenesis, physically weathered bedrock is accepted
	R	**R** = bedrock, unweathered rock

Additional symbols	Description	Example
()	Weakly obvious horizon or properties	(E), B(h)s, (Bv)C, A(Ep)
AE, AB, BC	Transitional horizon	BvsC, ABv1, ABvs, BC
1, 2, 3...	Order of separated zones of one horizon	C1, C2, C3, 1BC, 2BC, 3BC
f	Burried (= fossil) undisturbed horizon	fA
g	Hydromorphic properties	BvgC

Organic horizons based on Klinka et al. (1997) and mineral horizons on World Reference Base and Czech taxonomies (Michéli et al., 2007; Němeček et al., 2011).

linear models (GLMs) and linear models with generalized least squares (GLS), using R software (http://www.R-project.org/). Horizon thicknesses were represented by mean values across individual pit-mound transects. Characterizing horizon thickness as medians, $Q_{0.8}$ values and linear mixed-effects models (computed on original data with individual mounds as a random effect) all gave similar responses.

Chronosequence data were fitted to linear, quadratic and hyperbolic statistical models and evaluated for goodness of fit. Linear and quadratic models have been widely applied (Schaetzl et al. 1994), but there have been limited applications of the hyperbolic model, $y = x/(b + ax)$. When both a and b are positive the function increases for positive values of x (age), with an initial slope of $1/b$ and a horizontal asymptote of $1/a$. The development of several soil properties appears to be hyperbolic (Schaetzl & Anderson 2005). Because non-positive values of response are not allowed in this parametrization, hyperbolic models could only be used with chronosequences where zero means do not occur. The homoscedasticity of residuals from linear models was tested with the Breusch-Pagan test (Breusch & Pagan 1979), and if significant ($\alpha = 0.05$) the model was

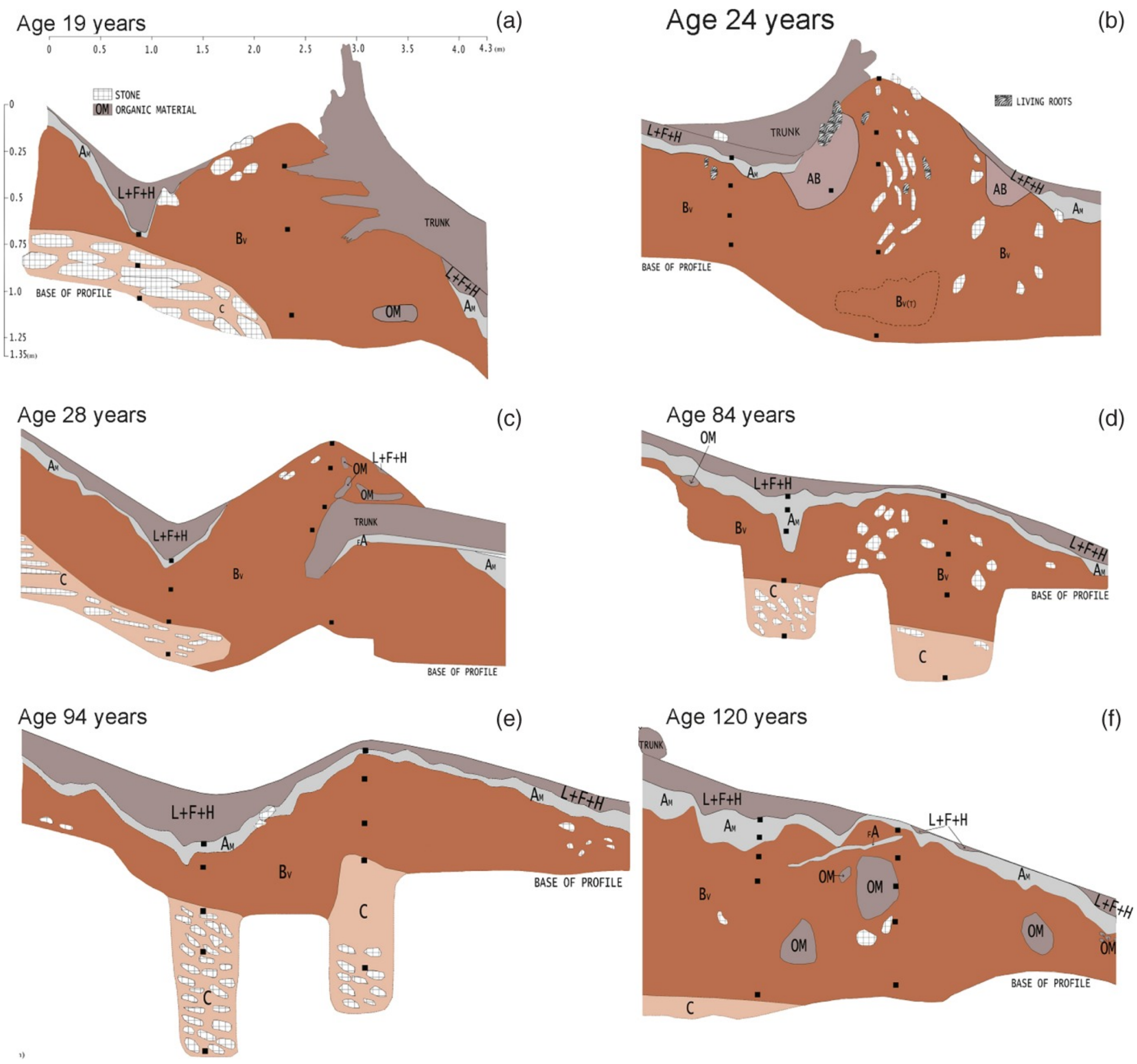


Fig. 4 Soil horizonation in selected pit-mound pairs (a–f) in Haplic Cambisols at Razula. Black squares are sampled locations. For horizon codes, see Table 2. Ages are derived from tree census and dendrochronology.

re-fitted using generalized least squares (GLS). Because the complexity of soil development gave greater variance in horizon thicknesses at older sites, two models with variances taken as fixed and power functions of age were compared with Akaike's information criterion (AIC) adjusted for small sample size (AICc):

$$\mathrm{AICc} = \mathrm{AIC} + 2k(k+1)/(n-k-1)$$

where k is the number of model parameters and n is the sample size (Akaike 1974). Only models significant at $\alpha = 0.05$ were accepted. Quadratic models had to be significantly better than the corresponding linear model to be accepted. As another measure of goodness of fit, a generalization of the coefficient of determination R^2 (Nagelkerke 1991) was computed.

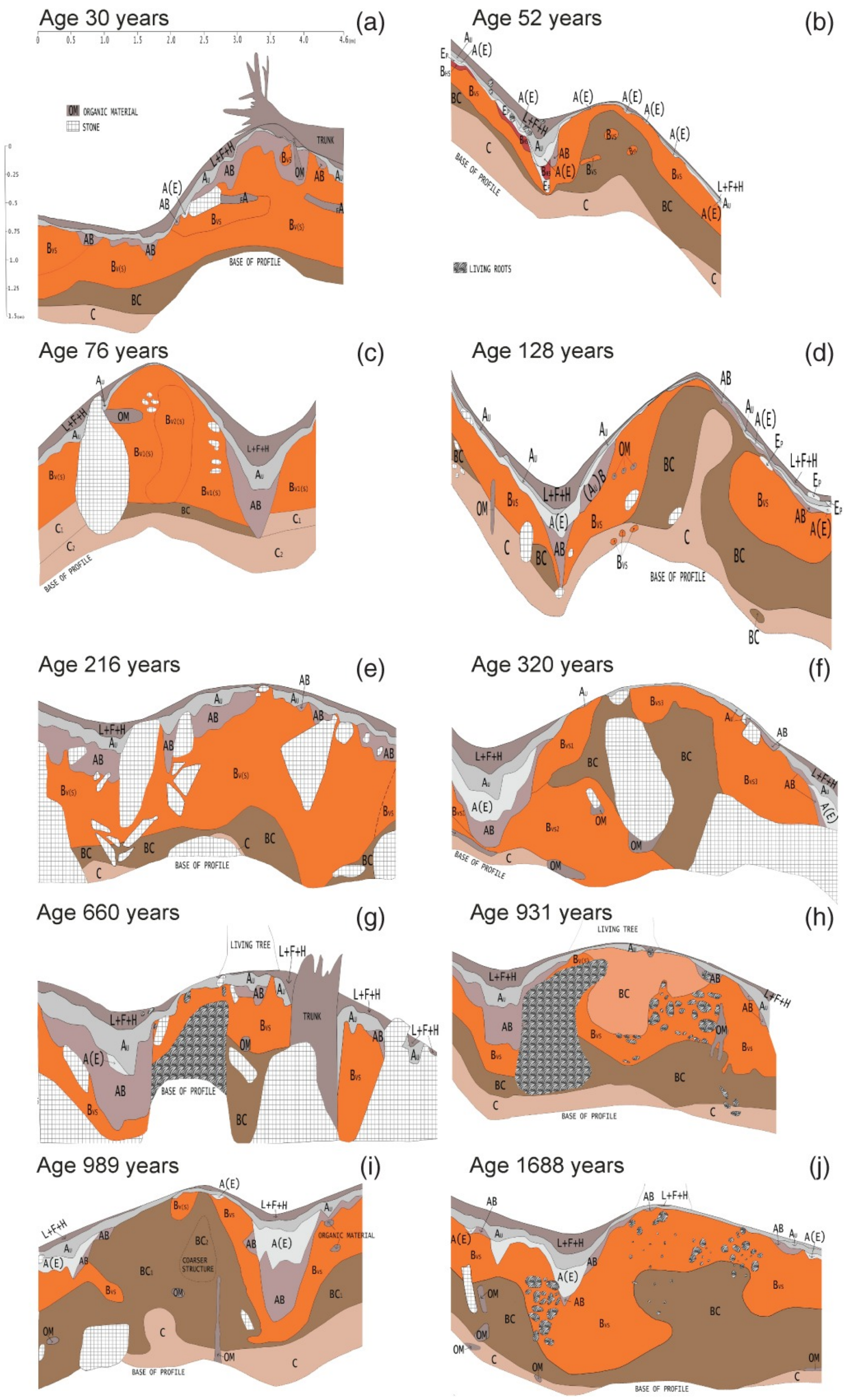


Fig. 5 Soil horizonation in selected pit-mounds (a–j) in Entic Podzols at Zofin. For details, see Fig. 4 and Table 2. Ages are derived from tree census, dendrochronology and radiometry data.

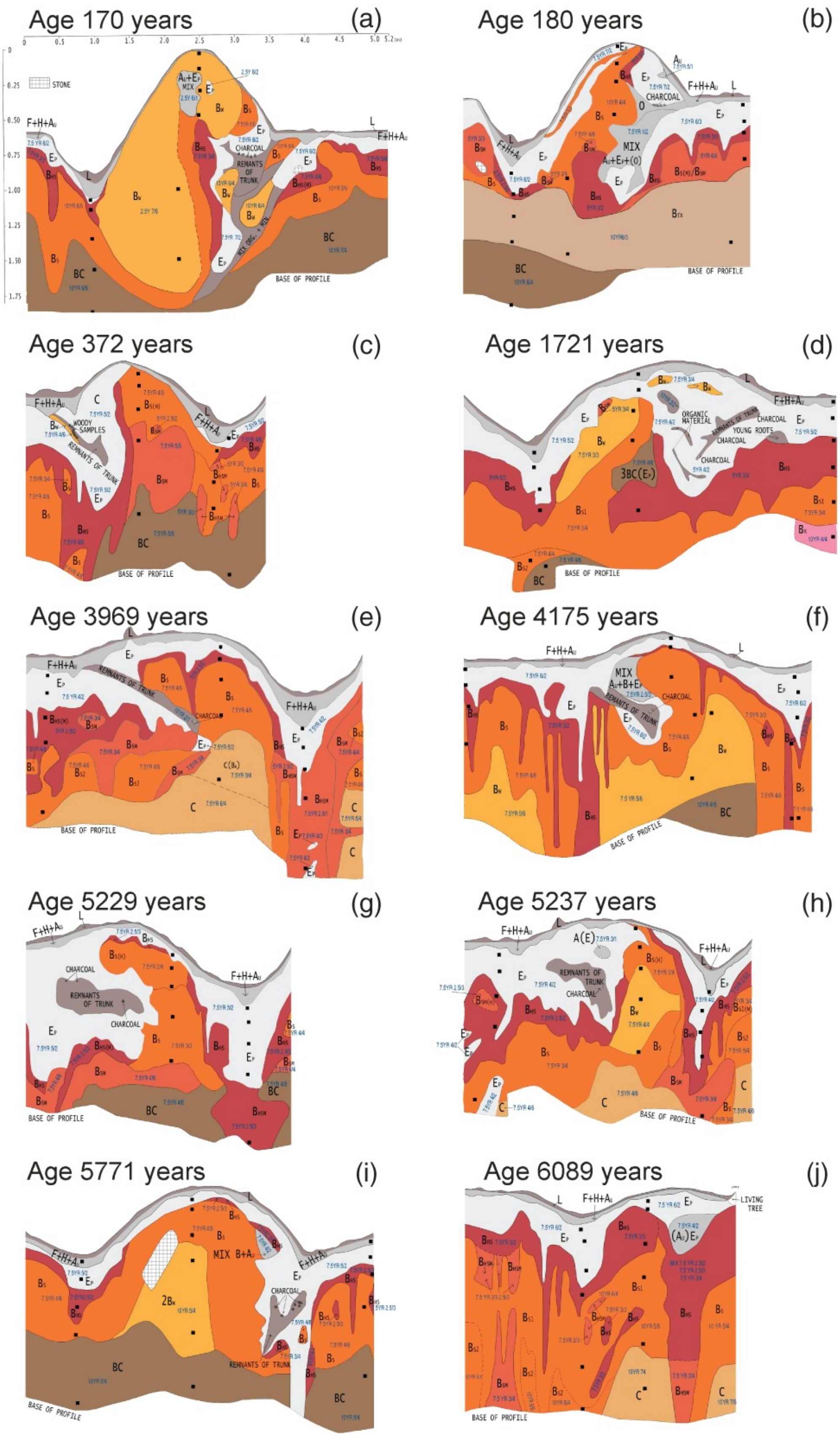


Fig. 6 Soil horizonation in pit-mounds (a–j) in Albic Podzols in Michigan site. For details, see Fig. 4 and Table 2. Ages are derived from dendrochronology and radiometry data.

3 Results

3.1 Soil morphology

Soil morphology and laboratory analyses confirmed that weathering and leaching processes were tracing podzolization at Zofin and Michigan and brunification at Razula. However, evidence of clay translocation, melanizing complexation or hydromorphic processes were also observed in disturbed and control undisturbed microsites, particularly at Razula.

Because they lack E horizons and have little B horizon variability, soil morphologies in pit-mounds on Haplic Cambisols (Fig. 4) were simpler and less informative than those in the Entic Podzols (Fig. 5). This was especially so for the complex and clearly defined horizonation of the Albic Podzols (Fig. 6) (see also Fig. S1). The more diffuse boundaries in the Haplic Cambisols also made precise distinctions and depth measurements more difficult. At our sites, profile morphologies (horizon sequences, thicknesses and transitions) within pits and mounds always differed from those at control sites.

Elongate solitary rocks in the disturbed soils often come to rest vertically (Fig. 4b,f, 5c,e–g), with many slumping back to the horizontal only after the pit becomes in-filled. In the more lithic soils at Zofin and Razula, we often observed signs of bedrock excavation by uprooting where the bottoms of the tree-throw pits reach the R horizon (Fig. 4a,c,e, 5e–g). In mounds, E, B and C horizon remnants were also often vertical, particularly in sites on gentle slopes (Fig. 6a–c). In mounds on steeper slopes, horizon fragments were tilted, vertical or over-turned (see Fig. 5a,b). Where horizons were over-turned intact (Schaetzl 1986), they indicate rotation of the lens about a hinge close (usually < 2 m) to the uprooted tree. The horizons usually retained their original sequence, but were upturned or inverted. Various soil properties such as orientation of cutans and size of soil aggregate structure, helped to identify upturned horizons, particularly in Haplic Cambisols.

The deposition of uprooted material increases the solum thickness on mounds because it overlies the original soil. Such soil deepening was clearest in Haplic Cambisols, where mixed upturned cambic horizons were barely distinguishable from the undisturbed B and BC horizons beneath (Fig. 4a–c). Below some mounds we observed buried soil horizons that appear to date from earlier disturbances (Fig. 6a,j).

The O and A horizons were thicker in the pits and thinner on mounds in all three regions (Fig. 4-6), especially in the Haplic Cambisols (Fig. 4a–f, 'funnel-like' forms). Increasing thicknesses of A horizons were also observed at the mound edges, and attributed to erosion and sedimentation during mound deterioration.

New O and A horizons in pits were clearly distinguishable at all sites, even the youngest, indicating the rapidity of pedogenesis there. The effects of runoff water flowing into pits and associated erosion/sedimentation on pedogenesis differed between sites. In the Albic Podzols, the organic matter that accumulated in the pit O horizons led to the rapid acidification and eluviation of the upper part of the mineral soil below, forming exceptionally thick E horizon tongues below the pit centre (Fig. 6a–j). Consequently, CEC, exchangeable cation contents (particularly Ca, Mg and K) and base saturation were small in the upper mineral horizons of pit soils. These processes have had a rapid impact on the soils in the pits, especially in Michigan, largely because of the small surface area and rapid permeability of the sandy Michigan soils.

Litter also accumulated in the pits on the finer-textured Haplic Cambisols (Fig. 4a–f) but the larger clay content and base status of the flysch parent material inhibited leaching and facilitated the melanizing complexing of humus on clay minerals, thus forming thick A, but no E, horizons. The finer textures and better base status also promoted more active assemblages of soil fauna, and consequent mixing of litter into the mineral soil. This also contributes to the formation of A horizons, with larger CEC values and nutrient contents in the Haplic Cambisols than in the thick O horizons of the Podzols.

Pit soils in the Entic Podzols were morphologically intermediate between Albic Podzols and Haplic Cambisols and had thick A horizons but also thin E horizons (Fig. 5b,f,g,i,j). Thus all of the pits were sites of organic matter accumulation, but the impacts were mainly governed by texture and base status. Inflow of water into the pits, coupled with poor permeabilities in the fine-textured Haplic Cambisols, often led to the formation of hydromorphic properties in BvgC horizons (Table 2), but this was not observed in the sandier soils.

Material from pre-disturbance lower subsoils (BC and C horizons) was commonly excavated and incorporated into the mounds. In older mounds this material had developed into Bs or Bw horizons (Fig. 4d, 5b–d,f,h,j, 6a,c–i, 7b). Although Bhs horizons usually had Munsell colours of 5YR–7.5YR 3/3 and darker (Schaetzl & Anderson 2005), Bs horizons were lighter and yellower (7.5YR 4/6, 10YR 4/6, 4/4 and 5/6), and substratum horizons were even lighter. This process was morphologically less obvious in flysch parent materials, on soils with deep B horizons and where trees had shallow root systems and uprooting pits. Post-disturbance pedogenic horizonation was readily observed within this originally subsoil material because of the absence of noticeable pre-disturbance horizons.

Some morphologic features and pedogenic processes were specifically associated with particular localities. In Michigan, soil below uprooted trunk fragments was frequently more eluviated than adjacent undisturbed soil. Some decayed trunks left hemi-cylindrical traces of E and Bhs horizons in the underlying soil (Fig. 6g,h). Buried A and E horizon materials under mounds without the trunk present left more planar traces. Hemi-cylindrical traces were distinguished by digging transects orthogonal to the direction of tree fall (Fig. 2, profile B). The presence and shape of E and Bhs horizons indicate relatively rapid post-disturbance pedogenesis in the soils beneath the uprooted tree. Fallen trunks, which were sometimes charred, gradually decomposed and became a source of organic acids, which may assist in the podzolization process. We refer to the E and Bhs horizons buried beneath the mound as ‘covert Podzols’ (Fig. 6c–i, 7a,c).

The non-charred remains of trunks were not observed in mounds older than about 375 years. The older ^{14}C dates reported here and in Šamonil et al. (2013) were based on charcoal found at the contact with the buried soil, below the mound, sensu Schaetzl (1986). In the oldest mounds, the little charcoal that remained was fragile. However, the thickness of the underground zone of the E horizon in these older mounds was substantial (Fig. 6g, 7a). In the finer-textured soils of the Czech Republic, woody materials remained for only a few decades after the uprooting event (Fig. 4c). According to Šamonil et al. (2009) the oldest existing uprooted trunks in the Czech beech-dominated old-growth forests were 50–60 years old (calculated in Razula).

3.2 Chronofunctions of soil development

Of the many chronofunction models tested for the development of soil horizon thickness, the linear model was most often the best fit (at $\alpha = 0.05$, Table 3). Although the quadratic model was often

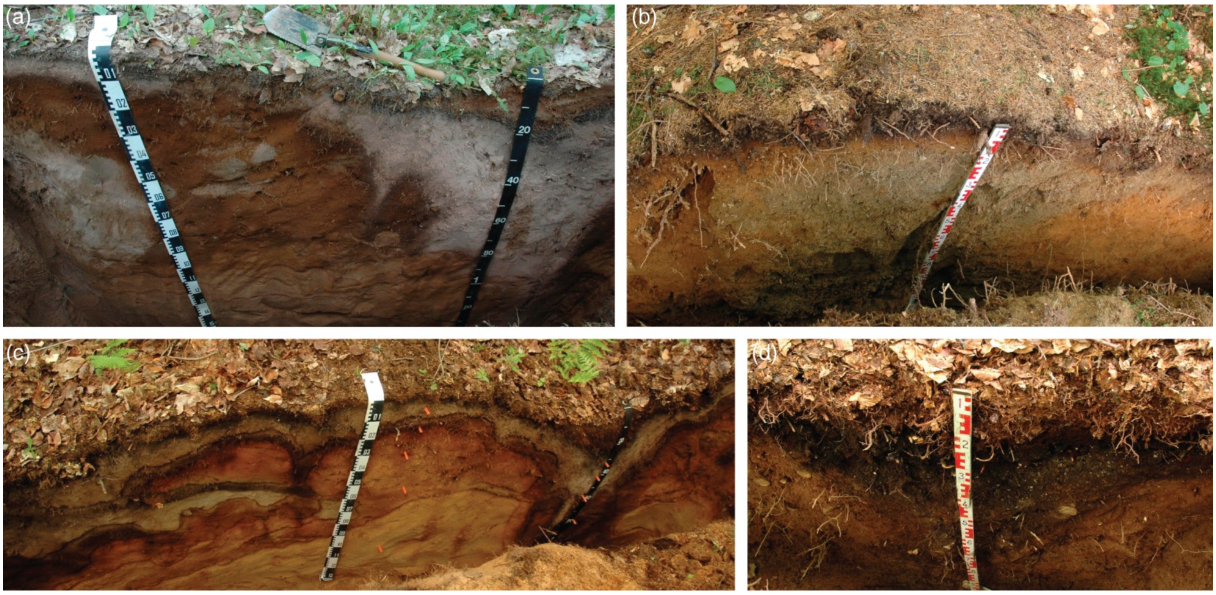


Fig. 7 Pit-mound profiles. (a) Albic Podzol pit-mound profile dated 3217 BC (median of calibration age, ^{14}C age = 4480 ± 35 BP. Note the strongly developed covert E horizon in the buried soil beneath the mound and the strong new E and Bhs horizons in the pit, and the thin, new E and Bhs horizons in the mound. (b) Incipient spodic horizonation in a mound dated 1882 AD on an Entic Podzol at Zofin uplifted substratum material (dendrochronological dating). (c) Complete profile of a pit-mound pair on Albic Podzols in Michigan dated to 1957 BC (median of calibration age, ^{14}C age = 3600 ± 30 BP). Note the thick E and B horizons in the pit, and thinner horizons in the mound. This site also shows a good example of a buried soil beneath the mound. (d) Organo-mineral sedimentation funnel in a pit in an Entic Podzol in Zofin dated to 1844 AD (dendrochronological).

equally statistically significant, the addition of the quadratic component often did not contribute any additional significance.

In a number of cases, the chronofunction model for horizon thicknesses in pit soils did not intersect at the origin, but was markedly positive at time$_{\text{zero}}$ (Fig. 8d, 9d, 9f). This finding suggests that the initial development of the given horizon was non-linear; horizons began to form quickly after the disturbance event and the rate of development slowed with time. Alternatively, some soil characteristics associated with the pit soils, as in the B horizon, were not completely re-set by the disturbance event.

In contrast, the extrapolated chronofunction model for several mounds showed negative intercepts at time$_{\text{zero}}$ (Fig. 8c, 9e). This suggests that the onset of pedogenic horizonation was delayed, with for instance some acidification required before chelation, or the formation of a loose Bs horizon before the development of a Bhs. (Franzmeier & Whiteside 1963). No one chronofunction model worked best for both pit and mound soils at any site, with various models best for similar horizons in different microsites, and others for different horizons at one type of microsite.

Mathematical models were not statistically significant at $\alpha = 0.05$ for some O and A horizons in both pits and mounds (Table 3), mostly in Entic Podzols, as these have O and A horizons of variable thicknesses, even in the reference profiles (Šamonil et al. 2011). Local variability of O and A horizons within pits and mounds was common and did not increase with time. Instead, increased variation with time was observed in the successfully-modelled E and Bhs horizons on Albic Podzols (Fig. 9), the chronofunctions of which required widening confidence intervals with time.

Table 3 Soil chronofunctions tested with Akaike information criterion (AICc), coefficient of determination (R^2) and P-values.

			Linear model			Quadratic model			Hyperbolic model		
Locality, soils	Horizon	Microsite	AIC	R^2	P	AIC	R^2	P	AIC	R^2	P
Razula, Haplic Cambisols	O	Pit	172	0.20	0.074	175	0.20	0.211	**164**	**0.46**	**0.034**
	O	Mound	**138**	**0.71**	**< 0.001**	145	0.60	0.002	–	–	–
	Am	Pit	**167**	**0.53**	**< 0.001**	170	0.53	0.005	**168**	**0.55**	**0.016**
	Am	Mound	**128**	**0.90**	**< 0.001**	129	0.91	< 0.001	–	–	–
Zofin, Entic Podzols	O	Pit	178	0.09	0.215	177	0.26	0.101	–	–	–
	O	Mound	**156**	**0.31**	**0.016**	159	0.32	0.052	–	–	–
	Au	Pit	213	0.13	0.142	**204**	**0.54**	**0.003**	**200**	**0.41**	**0.004**
	Au	Mound	202	0.06	0.332	205	0.06	0.635	–	–	–
	Bvs	Mound	**133**	**0.81**	**< 0.001**	**129**	**0.91**	**< 0.001**	–	–	–
Michigan, Albic Podzols	O	Pit	134	0.22	0.089	137	0.26	0.188	–	–	–
	O	Mound	116	0.21	0.103	**115**	**0.44**	**0.043**	**111**	**0.40**	**0.024**
	Au	Pit	98	0.04	0.513	99	0.19	0.322	97	0.14	0.119
	Au	Mound	92	0.20	0.103	93	0.30	0.138	**80**	**0.43**	**0.031**
	Ep	Pit	**170**	**0.42**	**0.013**	169	0.54	0.014	–	–	–
	Ep	Mound	**145**	**0.42**	**0.013**	146	0.51	0.02	–	–	–
	Bhs	Pit	**179**	**0.35**	**0.013**	181	0.40	0.061	171	0.34	0.056
	Bhs	Mound	**132**	**0.51**	**0.002**	134	0.57	0.004	–	–	–

Statistically significant models ($\alpha = 0.05$) are in bold; bold for quadratic models only where the quadratic component added additional significance; dash – hyperbolic model could not be fitted because of zero values in the response variable; for horizon codes see Table 2.

All of the best-fit chronofunctions exhibited positive slopes, indicative of progressive increasing soil horizon and profile thicknesses after uprooting for soils in both pits and mounds, which suggests that pedogenic processes are not easily reversible. This trend was especially apparent in the Albic Podzols (Fig. 9a–f). Mineral horizon thinning occurred in Entic Podzols, but only rarely, and not at all in Haplic Cambisols and Albic Podzols (Fig. 8, 10, 9).

Chronofunctions indicated that Michigan Albic Podzol E and Bhs horizons thickened faster in pits than on mounds (Fig. 9c–f). Differences in E horizon development between mounds and pits, as indicated by thickness, was only just significant ($P = 0.08$). Increasing pedogenic differences between soil development in pits and in mounds over time show that uprooting and the subsequent micro-topography affected the rates of pedogenesis at a pedon-to-pedon scale. We did not observe similar trends at the Czech sites, the chronofunctions of which suggested ambiguous or convergent trajectories of pedogenic development in pits and mounds (Fig. 8, 10).

3.3 Rates of pedogenesis

We used the chronofunctions to estimate how long it would take for horizon thicknesses in pit and mound microsites to match those in the adjacent reference pedons (Fig. 8, 10, 9). Pedogenic development in pits was considerably faster than on mounds. The O horizons in pits on Haplic Cambisols reached the average reference pedon thickness after only 5 years, whereas on mounds an equivalent thickness was achieved after about 150 years (Fig. 8a,b). The more rapid thickening in pits is because in these micro-topographic low areas litter can accumulate as it washes or is

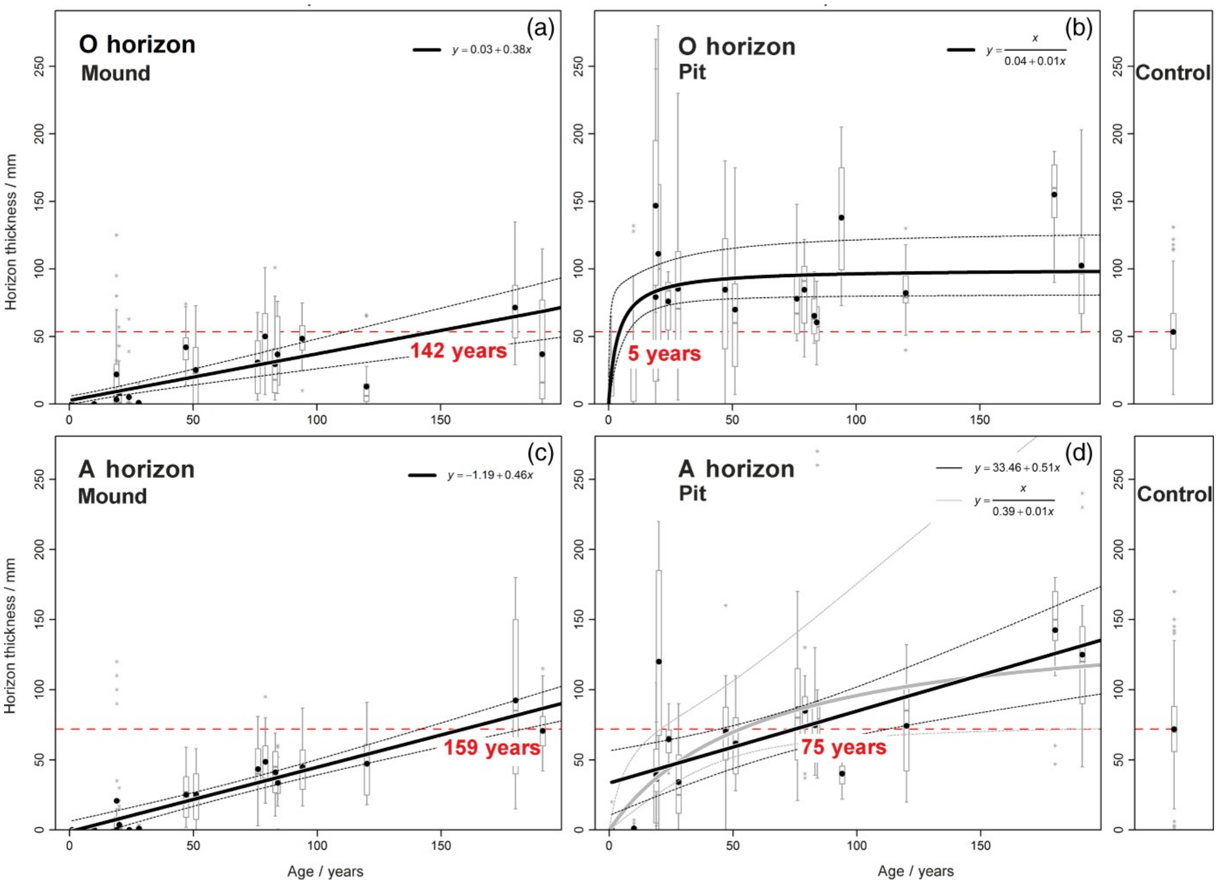


Fig. 8 Boxplots of O (a,b) and A (c,d) horizon thickness chronofunctions on Haplic Cambisols at Razula, with the middle 50% in box, whiskers extending over the remainder of the data range and outliers as stars. Means are represented by circles; medians by thick lines. Each boxplot represents one pit or mound; the means for the aggregated reference pedons are red dashed lines. Where the chronofunction is statistically significant, the best model is a solid black line with the 95% confidence intervals as dashed lines; the second best is solid grey. The best model equation uses AICc for evaluation. The red dashed line is the corresponding mean thickness in undisturbed reference profiles, with the time required for the best model to match them shown in red.

blown in. Litter in pits also decays more slowly because of cooler and moister conditions and thicker snow cover.

Similarly, A horizons in Haplic Cambisol pits were as thick as in undisturbed reference pedons after only 75 years (Fig. 8d). On mounds the equivalent development period was about 160 years (Fig. 8c). The A horizon thickness was connected most closely with age ($R^2 = 0.9$) on Haplic Cambisol mounds. The A horizon development on Albic Podzols was the slowest and on mounds it reached the same thickness as on undisturbed positions after about 240 years (Fig. 9b). On Entic Podzols, modelling of A horizon thickness was successful only for the pit soils, where it reached the value of the control pedons after about 45 years (Fig. 10a).

The chronofunctions for both pit and mound sites confirmed that development of E and B horizons was slower than for O or A horizons. On Entic Podzols, the B horizons in mounds had reached the average thickness of the undisturbed pedons after about 590 years (Fig. 10b). The Bhs horizons in mounds (as well as the O and E horizons) in the Albic Podzols (Michigan site) never reached the thicknesses observed in the reference pedons throughout the entire >6000-

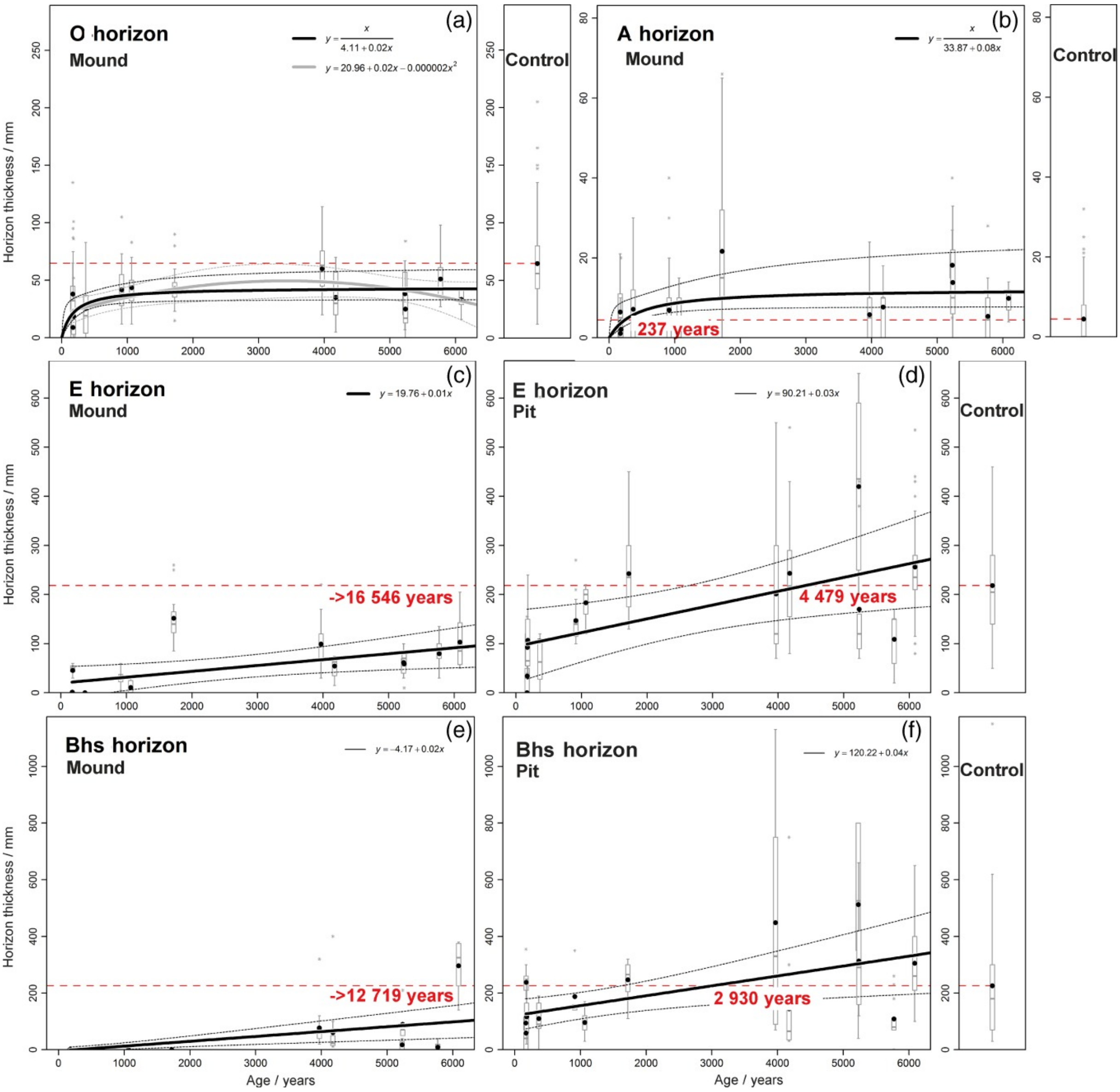


Fig. 9 Boxplots of O (a), A (b), E (c,d) and Bhs (e,f) horizon thickness chronofunctions in Albic Podzols on the Michigan sites. For details see Fig. 8 and Table 2.

year chronosequence. In these soils the chronofunction model for E and Bhs horizons on mounds extrapolated to reference pedon thicknesses after more than 16 500 and more than 12 700 years, respectively (Fig. 9c,e). These data reflect not only the slower development of mound soils in general, but also the fact that Bhs horizons take thousands of years to form, even in undisturbed soils. In contrast, the corresponding E and Bhs horizons in the pits were extrapolated to the reference soil thicknesses after only about 4500 and 3000 years, respectively (Fig. 9d,f). Although the chronofunctions indicated an initial lag in Bhs development, it was then faster than for the E horizons in both pits and mounds.

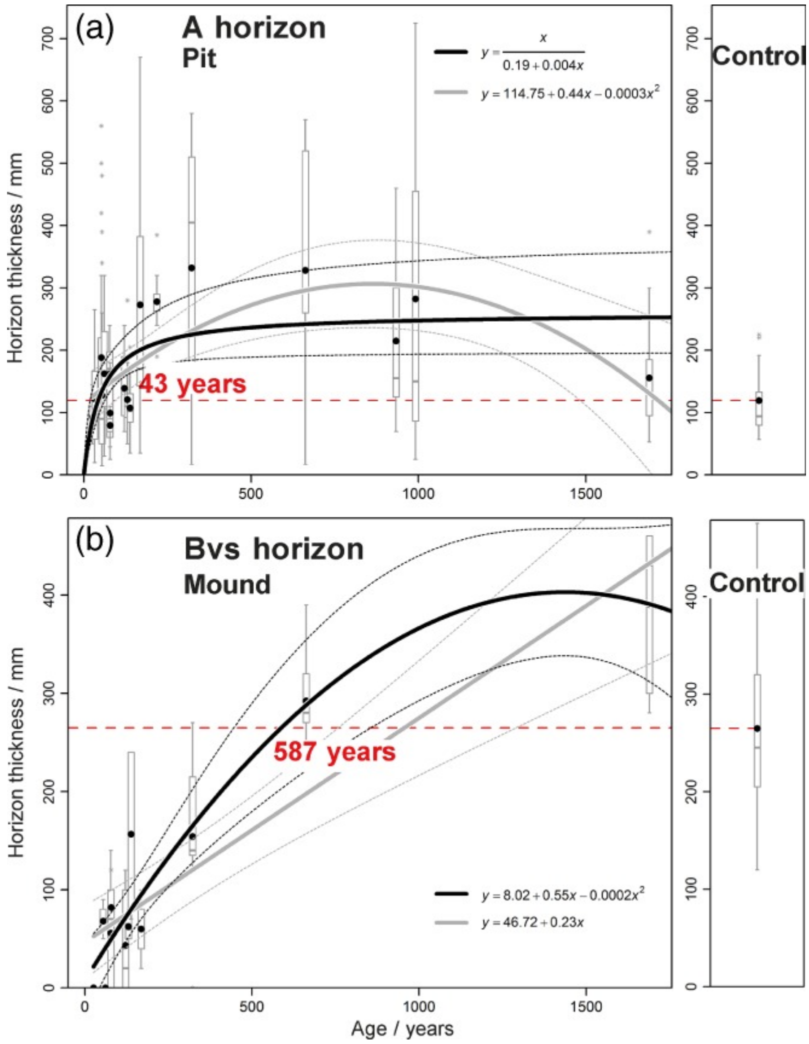


Fig. 10 Boxplots of A (a) and Bvs (b) horizon thickness chronofunctions for pits and mounds on Entic Podzols at the Zofin site. For details see Fig. 8 and Table 2.

4 Discussion

4.1 Pedogenesis on tree-throw pit-mounds

Morphological features of soils have long been a valuable source of information about the effects of uprooting on pedogenesis (Schaetzl 1986, 1990; Bormann et al. 1995). With only a few exceptions (Vassenev & Targulian 1995), the earlier studies focused on single sites, and few compared the effects of uprooting on and pedogenesis between different regions. These limited data suggest that it is difficult to generalize about the effects of pedoturbation on pedogenesis. Our own earlier studies suggest that conclusions based on Albic Podzols are not readily transferable to regions with different pedogenic regimes (Šamonil et al. 2010a,2010b).

Most of the earlier studies lack precise dates for the uprooting events (Veneman et al. 1984; Bormann et al. 1995). Many also assume linear rates of post-uprooting pedogenesis. Although often satisfactory, the automatic assumption of linearity for soil development can be misleading (Schaetzl et al. 1994). Linear models may underestimate regressive elements in pedogenesis (Johnson et al. 1990) and fail to account for the general complexity of pedogenesis.

However, earlier studies within the Albic Podzol region of Michigan have shown that rapid soil development occurs in pits, but that pedogenesis is slower on mounds (Schaetzl 1990; Šamonil et al. 2010a). Four thousand to 10 000 years are required for the development of a spodic (roughly comparable to a Bhs) horizon on level ground in the USA and Canada (see Franzmeier & Whiteside 1963; Barrett & Schaetzl 1992). Our results show how variable estimates of these rates become when micro-topographic effects are factored in. Uprooting microsites within a given landscape not only have widely varying rates of pedogenesis, but also different time$_{zero}$. Pit-mound pairs can occur within a metre or two of each other, cumulatively leading to much small-scale spatial variability. Uprooting micro-topography both resets the pedogenic clock and mediates rates of post-disturbance pedogenesis (Phillips 2013).

Albic Podzols in pits show rapid development, probably driven by large infiltration rates, resulting from deep snow, and because of the increased amounts of organic acids, because of the deeper thicker litter. Corresponding mound soils develop more slowly, again affected by the micro-topographic shape and form that sheds both water and litter, and because the micro-topographic upper components freeze in winter, leading to runoff in spring, and they therefore lose some water and litter (Schaetzl 1990).

At most of our sites in Michigan and Zofin, unlike those studied by Veneman et al. (1984), pit-mound features >500 years old do not have soil profile stratigraphy (horizon thicknesses and proportions) corresponding to those in undisturbed reference pedons. Our data from Michigan agree more with Bormann et al. (1995), who observed slow development of E horizons on tree-throw mounds in Alaska. They observed 1.1-cm thick E horizons after 150 years and 2.1-cm thick E horizons after 350 years. According to Bormann et al. (1995), the Bhs horizon was thicker (2.1 cm at 150 years and 3.8 cm at 350 years). The slower initial development of the mound Bhs horizon than of the E horizon in our results may be related to the deposition of loose pre-disturbance Bs, Bw, BC or C horizon materials, which only later qualify as Bhs.

We usually observed increasing soil horizon thicknesses with time at all sites, pointing to progressive soil development (Johnson et al. 1990). Examples of thinning of soil horizons over time in our results were rare. Some authors (see Vassenev & Targulian 1995; Šamonil et al. 2010a,b) have speculated from limited soil data about the possibilities of regressive development and suggest that pit O and A horizons may eventually become thinner as the uprooting micro-topography gradually becomes levelled, thus eliminating the special pedogenic conditions in the pits. This idea was not generally supported by our chronofunctions.

We also note that if the lower boundary of the E (or any) horizon in a formerly disturbed or undisturbed microsite extends below the depth of rooting the probability of rejuvenation of these horizons through new uprooting is very small. Vassenev & Targulian (1995) concluded that soil horizon thicknesses will never approximate those of undisturbed control sites in large pit-mounds.

'Tonguing' of E and B horizons is a common morphologic feature below tree-throw pits (Fig. 6, 7). Schaetzl (1990) described deep E and B horizon tongues in a tree-throw pit dated by ^{14}C to be 2010 ± 70 BP. Similar tongues had developed in tree-throw pits that were only 1000 years old. At our sites, we observed that tonguing markedly increases with time, leading to an increase in the variability of horizon thicknesses and boundary irregularities between microsites and with time. Increased horizon thickness variability with time was also described by Barrett & Schaetzl (1993) on undisturbed Albic Podzol sites, all at least 4000 years old.

Divergence increased between pits and mounds in the rates and degree of podzolization, as shown by the modelled horizon thickness chronofunctions. This mediation of soil evolution by micro-topography (Phillips 2001) should be confirmed by soil chemical characteristics (Myster &

Malahy 2008). This divergent development only operates at the spatial scale of tree-throw microtopography (Lepš & Rejmánek 1991).

Vassenev & Targulian (1995) observed rapid disintegration of the remains of the pre-uprooting illuvial (B) horizon in mounds. The rapid increase in the thickness of the new spodic horizon in mounds on our Entic Podzols, may relate to the disintegration of pre-uprooting soil structures. However, this contradicts Schaetzl's (1990) finding of slower weathering and formation of spodic horizons on Albic Podzol mounds. As noted earlier, our results may be obscured by difficulties in the differentiation of newly formed from pre-disturbance B horizons in mounds.

Our 'covert podzols' merit further attention, perhaps in relation to 'basket' or 'egg cup' podzols (Bloomfield 1953; Schaetzl 1990). The gradual decomposition of uprooted, and sometimes burnt, trunks, which are a source of organic acids for podzolization, may explain the larger proportion of C in illuvial horizons developed after disturbances in mountain podzolic soils in Alaska (Kramer et al. 2004). It may also be connected to the surprisingly large concentrations of C in mineral soils on tree-throw mounds (Liechty et al. 1997). Even charcoal is not entirely stable in soils; estimates place mean residence times at 3000–12 000 years (Preston & Schmidt 2006). Different forms of pyrogenic carbon originating during the fire event can also be the source of organic acids in the podzolization process (Haumaier & Zech 1995; Preston & Schmidt 2006) and thus it can facilitate the development of the buried soil. In addition to large localized variation in chelating capacity, podzolization processes can be locally intensified with extra percolation water. The sandy soil textures and deep snow cover at the Michigan site facilitate deep percolation and accelerate pedogenesis (Schaetzl & Isard 1996). It appears that this effect can also penetrate into and through even a thick tree-throw mound (Fig. 6).

The lack of significance of the regression models for five of the chronofunctions does not necessarily imply that these profiles have developed chaotically. Post-disturbance pedogenic development may be too complex for the models (Walker et al. 2010). The lack of significance for the Zofin model may be related to the exceptionally large local pedodiversity and soil variability (Šamonil et al. 2011, 2014). Pedodiversity and the formation of non-linear networks can limit the applicability of chronofunctions (Walker et al. 2010; Phillips 2015).

Extrapolations from findings on the impact of tree-throw on soils from the pit-mound scale to stands and landscapes are difficult and may conclude that the overall effect of uprooting is to rejuvenate soils of the whole landscape, although in a piecemeal fashion, and thus inhibit soil formation from achieving some sort of terminal stage (Bormann et al. 1995). This interpretation is complicated by the non-random occurrences of new disturbances, which are least probable in pits (Šebková et al. 2012). Soils in pits may develop to such a point, and so rapidly, that future disturbances cannot obliterate them, because the bottoms of the horizons extend below the depth of rooting. Thus, post-disturbance lower subsoil development in pits may be irreversible.

As well as effects on horizon development, uprooting also affects soil thickness by the lateral transfer of soil and regolith material from pit to mound, obscuring the link between soil depth and topography (Gabet & Mudd 2010). In lithic soils, weathering and pedogenesis can be locally stimulated and mineral nutrients replenished by the excavation and subsequent weathering of fresh bedrock (Phillips et al. 2005).

4.2 Methodological issues

Several studies have documented the thick accumulation of organic matter in tree-throw pits and the rapid pedogenesis that it facilitates (Schaetzl 1990; Šamonil et al. 2010a). However, few have paid equal attention to the newly formed soils in mounds. By studying the generally slower and divergent soil development in mounds, a more complete picture emerges of the pedogenic effects of uprooting and the consequent pit-mound topography.

However, the assessment of soil development in mounds is difficult because mound soil materials have a history of previous pedogenesis. Therefore, sampling mound tops must take into account the pedoturbation process and origin of soil material. Our recommendation is to study soil morphology within entire mounds and to sample where post-disturbance pedogenesis is most visible (uplifted substratum material), even if this is not the mound summit.

We dated material from sediments in the narrow funnels in the pits of very old tree-throws on Entic Podzols. The intersection of the funnel with the organically poor BC and C horizons in some profiles made the application of ^{210}Pb and ^{14}C dating easier, especially on the pit face opposite the mound (position C in Fig. 3). However, there is still a possibility of contamination by extraneous material. In sandy sediments, the measuring of magnetic susceptibility may facilitate the location of a transition zone between disturbed soils and underlying soil material not affected by tree-throw.

Supporting Information The following supporting information is available in the online version of this article: Fig. S1. Albic Podzol pit-mound profile older than 5200 years. Note the thick E and B horizons in the pit, the thin, new E and Bhs horizons in the mound, and the covert E horizon in the buried soil beneath the mound.
https://doi.org/10.1111/ejss.12245

Acknowledgements The authors thank their colleagues from the 'Blue Cat research team' for field data measurement, Péter Szabó from the Institute of Botany ASCR for English proofreading and Ian Baillie for English proofreading and general manuscript improvement, and Jay Strahan from Michigan State University for assistance in the field. The research was supported by the Czech Science Foundation (project No. P504/11/2135) and Czech Ministry of Education and Sports and AMVIS (project No. LH12039).

References

Akaike H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19: 716–723.

Barrett L.R., Schaetzl R.J. 1992. An examination of podzolization near Lake Michigan using chronofunctions. *Canadian Journal of Soil Science* 72: 527–541.

Barrett L.R., Schaetzl R.J. 1993. Soil development and spatial variability on geomorphic surfaces of different age. *Physical Geography* 14: 39–55.

Bloomfield C. 1953. A study of podzolization. Part II. The mobilization of iron and aluminum by the leaves and bark of Agathis australis (Kauri). *Journal of Soil Science* 4: 17–23.

Bormann B.T., Spaltenstein H., McClellan M.H., Ugolini F.C., Cromack K. Jr., Nay S.M. 1995. Rapid soil development after windthrow disturbance in pristine forests. *Journal of Ecology* 83: 747–

757.

Breusch T.S., Pagan A.R. 1979. A simple test for heteroscedasticity and random coefficient variation. *Econometrica* 47: 1287–1294.

Franzmeier D.P., Whiteside E.P. 1963. A chronosequence of Podzols in northern Michigan. II. Physical and chemical properties. Michigan State University. *Agricultural Experiment Station: Quarterly Bulletin* 46: 21–36.

Gabet J.E., Mudd S.M. 2010. Bedrock erosion by root fracture and tree throw: a coupled biogeomorphic model to explore the humped soil production function and the persistence of hillslope soils. *Journal of Geophysical Research* 115: 1–14.

Gillman G.P., Sumpter M.E. 1986. Modification of the compulsive exchange method for measuring exchange characteristics of soils. *Australian Journal of Soil Research* 17: 61–66.

Haumaier L., Zech W. 1995. Black carbon – possible source of highly aromatic components of soil humic acids. *Organic Geochemistry* 23: 191–196.

Johnson D.L., Watson-Stegner D. 1987. Evolution model of pedogenesis. *Soil Science* 143: 349–366.

Johnson D.L., Keller E.A., Rockwell T.K. 1990. Dynamic pedogenesis: new views on some key soil concepts, and a model for interpreting quaternary soils. *Quaternary Research* 33: 306–319.

Klinka K., Fans J., Krestov P. 1997. Towards a Taxonomic Classification of Humus Forms; Third Approximation. Scientia Silvica, Extension Series No. 9. Forestry Sciences Department, The University of British Columbia, Vancouver.

Kramer M.G., Sollins P., Sletten R.S. 2004. Soil carbon dynamics across a windthrow disturbance sequence in southeast Alaska. *Ecology* 85: 2230–2244.

Lepš J., Rejmánek M. 1991. Convergence or divergence: what should we expect from vegetation succession? *Oikos* 62: 261–264.

Liechty H.O., Jurgensen M.F., Mroz G.D., Gale M.R. 1997. Pit and mound topography and its influence on storage of carbon, nitrogen, and organic matter within an oldgrowth forest. *Canadian Journal of Forest Research* 27: 1992–1997.

Michéli E., Schad P., Spaargaren O. (eds) 2007. World Reference Base for Soil Resources 2006, First Update 2007. World Soil Resources Reports No 103, FAO, Rome.

Myster R.W., Malahy M.P. 2008. Is there a middle way between permanent plots and chronosequences? *Canadian Journal of Forest Research* 38: 3133–3138.

Nagelkerke N.J.D. 1991. A note on the general definition of the coefficient of determination. *Biometrika* 78: 691–692.

Němeček K., Muhlhanselová M., Macků J., Vokoun J., Vavříček D., Novák P. 2011. Taxonomický klasifikační systém půd České republiky. Česká Zemědělská Univerzita v Praze, Praha.

Phillips J.D. 2001. Divergent evolution and the spatial structure of soil landscape variability. *Catena* 43: 101–113.

Phillips J.D. 2013. Evaluating taxonomic adjacency as a source of soil map uncertainty. *European Journal of Soil Science* 64: 391–400.

Phillips J.D. 2015. The robustness of chronosequences. *Ecological Modelling* 298: 16–23.

Phillips J.D., Marion D.A., Luckow K., Adams K.R. 2005. Nonequilibrium regolith thickness in the Ouachita Mountains. *The Journal of Geology* 113: 325–340.

Preston C.M., Schmidt M.W.I. 2006. Black (pyrogenic) carbon: a synthesis of current knowledge and uncertainties with special consideration of boreal regions. *Biogeosciences* 3: 397–420.

Šamonil P., Antolík L., Svoboda M., Adam D. 2009. Dynamics of windthrow events in a natural fir-beech forest in the Carpathian Mountains. *Forest Ecology and Management* 257: 1148–1156.

Šamonil P., Král K., Hort L. 2010a. The role of tree uprooting in soil formation: a critical literature review. *Geoderma* 157: 65–79.

Šamonil P., Tejnecký V., Borůvka L., Šebková B., Janík D., Šebek O. 2010b. The role of tree uprooting in Cambisol development. *Geoderma* 159: 83–98.

Šamonil P., Valtera M., Bek S., Šebková B., Vrška T., Houška J. 2011. Soil variability through spatial scales in a permanently disturbed natural spruce-fir-beech forest. *European Journal of Forest Research* 130: 1075–1091.

Šamonil P., Schaetzl R.J., Valtera M., Goliáš V., Baldrian P., Vašíčková I. et al. 2013. Crossdating of disturbances by tree uprooting: can treethrow microtopography persist for 6,000 years? *Forest Ecology, Management* 307: 123–135.

Šamonil P., Vašíčková I., Daněk P., Janík D., Adam D. 2014. Disturbances can control fine-scale pedodiversity in old-growth forest: is the soil evolution theory disturbed as well? *Biogeosciences* 11: 5889–5905.

Schaetzl R.J. 1986. Complete soil profile inversion by tree uprooting. *Physical Geography* 7: 181–189.

Schaetzl R.J. 1990. Effects of treethrow microtopography on the characteristics and genesis of Spodosols, Michigan, USA. *Catena* 17: 111–126.

Schaetzl R.J., Anderson S. 2005. Soils. Genesis and Geomorphology. Cambridge University Press, New York.

Schaetzl R.J., Isard S.A. 1996. Regional-scale relationships between climate and strength of podzolization in the Great Lakes region, North America. *Catena* 28: 47–69.

Schaetzl R.J., Barrett L.R., Winkler J.A. 1994. Choosing models for chronofunctions and fitting them to data. *European Journal of Soil Science* 45: 219–232.

Šebková B., Šamonil P., Valtera M., Adam D., Janík D. 2012. Interaction between tree species populations and windthrow dynamics in natural beech-dominated forest, Czech Republic. *Forest Ecology and Management* 280: 9–19.

Vassenev I.I., Targulian V.O. 1995. Windthrow and Taiga Pedogenesis (Regimes, Processes, Morphogenesis of Soil Successions). Nauka, Moscow (in Russian with English summary).

Veneman P.L.M., Jacke P.V., Bodine S.M. 1984. Soil formation as affected by pit and mound microrelief in Massachusetts, USA. *Geoderma* 33: 89–99.

Walker L.R., Wardle D.A., Bargett R.D., Clarkson B.D. 2010. The use of chronosequences in studies of ecological succession and soil development. *Journal of Ecology* 98: 725–736.

Paper 2

Converse pathways of soil evolution caused by tree uprooting: A synthesis from three regions with varying soil formation processes

Pavel Šamonil
Pavel Daněk
Randall J. Schaetzl
Václav Tejnecký
Ondřej Drábek

Catena 161 (2018), 122–136

Abstract

Post-disturbance pedogenetic pathways were characterized in three landscapes representing different degrees of weathering and leaching. Tree uprooting has been the main form of disturbance in all three landscapes. We hypothesized that the pedogenetic effect of trees due to uprooting is mainly governed by the regional degree of pedogenesis, which in turn affects soil and landscape evolution.

The three regions were characterized by a chronosequence of treethrow pit-mound pairs, from fresh to almost leveled forms. Two sequences originated from the Czech Republic, one on Haplic Cambisols and one on Entic Podzols. The third and the oldest chronosequence, in Michigan, USA, was on Albic Podzols (dating back to 4080 BCE). We analyzed 38 chemical and physical soil properties for 700 samples from 42 pit-mound pairs in these regions. Ordination and regression techniques allowed us to evaluate the effect of sample depth, microsite (pit, mound, and undisturbed control position), and age of the soils formed after uprooting.

Depth was the most significant variable in all regions ($p < 0.001$), followed by microsite location, and then age (time since disturbance). The significance of these variables decreased with increasing weathering and leaching intensity. The results suggest that intense pedogenesis, as at the Michigan site, decreases the polygenetic impacts of uprooting on soil development pathways. On Haplic Cambisols, disturbances increased the local variability of pedogenic processes by changing melanization and hydromorphic processes, as well as by mineral alteration. Conversely, on Albic Podzols, we found comparative chemical uniformity in post-uprooting pedogenesis between microsites, despite rapid podzolization in pits and slower podzolization on mounds. The general chemical convergence of pedogenesis in these landscapes towards vertically-dominated podzolization may limit divergence of pedogenic pathways after a disturbance. The formation and translocation of labile organic matter-sesquioxide complexes in the uppermost podzolic horizons in Entic Podzols was a key threshold, in that it changed the pedochemical, ecological and biogeomorphic role of the treethrow features in the soil and landscape evolution. Although treethrow pits were accumulation sites for soil elements in Haplic Cambisols and Entic Podzols, they were microsites of intense leaching and elemental loss in Albic Podzols.

P. Šamonil[a], *P. Daněk*[a,b], *R.J. Schaetzl*[c], *V. Tejnecký*[d], *O. Drábek*[d]

[a] Department of Forest Ecology, The Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Brno, Czech Republic [b] Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic [c] Department of Geography, Environment, and Spatial Sciences, Michigan State University, East Lansing, Michigan, USA [d] Department of Soil Science and Soil Protection, Faculty of Agrobiology, Food and Natural Resources, Czech University of Life Sciences Prague, Prague, Czech Republic

1 Introduction

Tree uprooting is the most evident and significant biogeomorphic disturbance agent in many forest soils (Fig. 1, Schaetzl et al. 1989, Phillips & Marion 2006, Pawlik et al. 2016a). For example, in temperate, central European, primeval forests approximately 30% of all trees die as a result of uprooting, and theoretically, within 500–3000 years every site in such forests is likely to be disturbed by uprooting (e.g., Skvorcova et al. 1983). So-called rotation periods, showing how often an area equivalent to an entire area is disturbed (Pickett & White 1985), are comparable or even shorter in other temperate or boreal forests (review by Šamonil et al. 2010a).

Fig. 1 An extremely large, complex root plate formed by uprooting on Entic Podzols during the Kyrill storm in Zofin, Czech Republic, in 2007. Tape represents 1 m. Photo by Pavel Šamonil.

From a general theoretical perspective, biomechanical soil disturbances are an important source of the kind of local, transient changes that are usually associated with deterministic chaos. A self-organizing, chaotic, and unpredictable mode of soil behavior may be a substantial component of the usually-assumed non-chaotic mode (Walker et al. 2010, Phillips 2013c). Both chaotic and non-chaotic modes contribute soil evolution on all scales, but their individual effects are little known. Focusing on non-chaotic soil behavior in experiments, mathematical models and interpretations can result in simplifications or even false results in soil and biogeomorphic studies (see Peckham 2009). The predominance of a self-organizing component in the evolution of a soil landscape leading to divergent evolution is the most evident such example (Phillips 1993), which represents a converse direction and an important alternative to the traditionally-assumed convergent evolution (see Phillips 2001). Although differences in initial conditions and local perturbations are gradually smoothed in convergent evolution, leading to decreased soil spatial variability, differences nonetheless persist and can even increase, producing a more variable soil cover; this is one example of divergent soil evolution. In any case, when pedogenesis is dynamically unstable and chaotic, the effects of small disturbances such as those associated with pedologic influences of individual trees become exaggerated over time (Phillips 2000, Phillips 2013a, Phillips 2013b, Toomanian et al. 2006, Milan et al. 2009, Borujeni et al. 2010, Phillips & Van Dyke 2016). Using pedomorphology data, Šamonil et al. (2015) found possible divergent soil evolution after tree uprooting in Albic Podzols, wheres other soil units expressed different post-disturbance evolutionary pathways. These findings suggest a regionally-specific role of tree uprooting in pedogenesis, although the direction of post-uprooting erosion-sedimentation processes and the specifics of microclimate within treethrow pits and mounds seem to be universal (the mound is generally drier, has a higher radiation balance and a wider amplitude of temperature with comparison to the pit, see Beatty & Stone 1986). However, such pedomorphic results only minimally inform us about complex soil formation processes, and need to be validated by pedochemical analyses. Datasets from different soil regions can fundamentally help improve still-unsupported theoretical derivations regarding the switching of soil behavior modes on pedon scales, the role of deterministic chaos, and the directions of post-disturbance evolutionary trajectories in soils.

Most of the case studies on uprooting so far have focused on Spodosols, and most of the research has been on single sites in the US, Canada and Russia (Skvorcova & Ulanova 1977, Schaetzl 1990, Small et al. 1990, Bormann et al. 1995, Kramer et al. 2004). Only few such studies are truly comparative, using pedochemical data from different soil regions (Skvorcova et al. 1983, Vassenev & Targulian 1995). Nonetheless, these studies suffer from a relatively low amount of data and inaccurate (or lack of) dating of uprooting events. These geographical and methodological limitations fundamentally reduce our ability to study post-disturbance pedogenetical pathways and do little to help derive conceptual generalities regarding the effect of uprooting disturbances on pedogenesis and eco-evolution dynamics (Corenblit et al. 2011, Pawlik et al. 2016b). Here, we focus on this still unsolved issue and compare the pedogenetic impacts of uprooting on dated chronosequences from multiple landscapes.

Our primary hypothesis is that trees do not affect pedogenesis through uprooting in a universal way, but rather various or even opposing post-disturbance evolutionary trajectories can arise, depending on the intensity of regional soil evolution processes. This hypothetically causes regionally-specific feedbacks in the tree-soil coevolution system (see Šamonil et al. 2014). The specific purposes of this study are to evaluate the effects of sample depth, microsite (pit, mound, and undisturbed control position), and age of soils since tree uprooting in three different soil regions. Using these data, we aim to build a general conceptual model of post-uprooting pedogenetical pathways. This model is made possible by existing tree uprooting research performed in three soil regions, where since 2006 (regions of Haplic Cambisols, Entic Podzols and Albic Podzols) we precisely dated a number of uprooting events (Šamonil et al. 2009, Šamonil et al. 2013), studied the formation of the forest floor on treethrow microsites (Šamonil et al. 2008a, Šamonil et al. 2008b), and assessed pedomorphic (Šamonil et al. 2015), biogemorphic (Šamonil et al. 2016, Phillips et al. 2017), and limited pedochemical processes (standard laboratory extract methods used solely on Haplic Cambisols by Šamonil et al. 2010b in studies of post-uprooting pedogenesiswere deepen using voltammetry of microparticles and diffuse reflectance spectroscopy by Tejnecký et al. (2015). These modern methods allowed us to develop a much deeper understanding of composition of mixed chemical extracts of Al, Fe, Si, and Mn).

2 Materials and methods

2.1 Study sites

Our three soil regions are in the Czech Republic (CR)–the Razula and Zofin forest reserves–and the Upper Peninsula of Michigan, USA (Fig. 2 and Table 1). The regions all have humid climates, and together they roughly span a gradient of texture and intensity of pedogenesis (see von Zezscheitz et al. 1973), with (1) strongly weathered, leached and acidic Albic Podzols on pure sandy outwash in Michigan (2) intermediate severity of podzolization, including clay destruction, on acidic Entic Podzols on loamy sand granite residuum at Zofin, and (3) clay formation without its destruction on Haplic Cambisols (Michéli et al. 2007) on loam or clay-loam flysch residuum at Razula (Fig. 3; Table 1) Precipitation decreases along this gradient. Mean slope inclination ranges from 8° (Zofin) to 19° (Razula). All forests are dominated by broadleaf species, specifically by *Fagus sylvatica* in both Czech sites and *Acer* spp. in Michigan (Table 1, Šamonil et al. 2011, Šamonil et al. 2016).

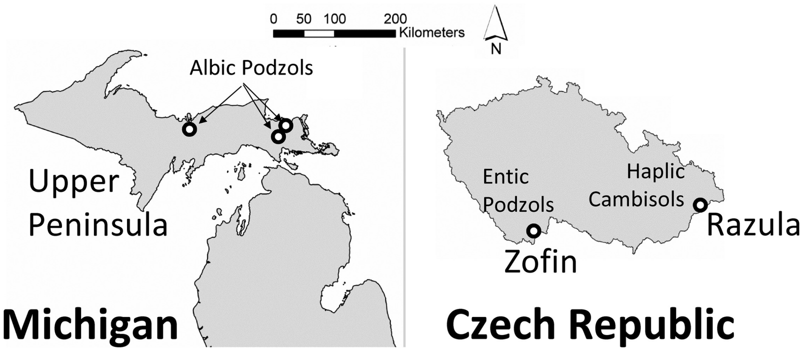


Fig. 2 Locations of the three study sites. For details see Table 1.

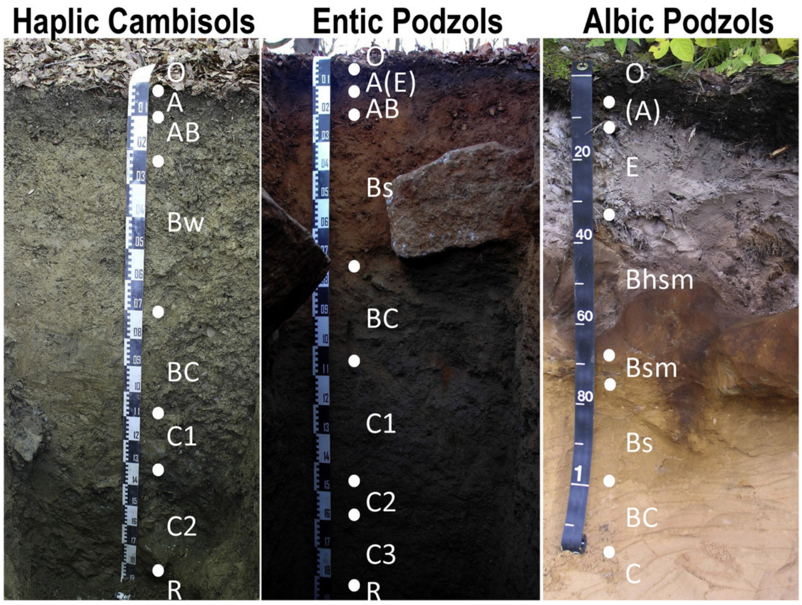


Fig. 3 Typical (control) soil profiles at each of the three study sites. Descriptions of upper organic horizons were made according to Klinka et al. (1997). Mineral horizons were described according to Němeček et al. (2011) and Michéli et al. (2007).

We examined soils within treethrow pits and on mounds at sites that represented the most typical soils of the region, avoiding wet (soil having hydromorphic properties or even stagnic, gleyic or histic horizons) and stony sites (classified according to Michéli et al. 2007 as Leptosols or Hyperskeletic, Leptic and Lithic Lower Soil Units of the other soils units). The gradient in clay content was associated with increasing activity of erosion and slope processes, and therefore with decreasing longevity of treethrow pit-mound pairs (Šamonil et al. 2015; Table 1).

Tree uprooting has been common in the recent past at all three study sites (Šamonil et al. 2011, Šamonil et al. 2016, Phillips et al. 2017). Other disturbance agents, such as fire in Michigan and mammalian burrowing (wild boar or woodchuck) are uncommon but worthy of mention here. Data were collected in Michigan in managed forests that were last selectively cut at least 40

Table 1 Overview of the physical and ecological conditions associated with each of the three study sites

Feature/locality	Razula	Zofin	Upper Peninsula
Soil taxonomy (WRB 2007)	Haplic Cambisols	Entic Podzols	Albic Podzols
Parent material	Flysch	Granite	Outwash
Location (Lat., Long.)(°)	49.36 N, 18.38 E	48.67 N, 14.70 E	46.32 N, 85.06 W; 46.44 N, 84.82 W; 46.37 N, 86.70 W
Average soil reaction (pH-H_2O) in B horizon ± SD (n)	5.1 ± 0.4 (23)	4.5 ± 0.2 (14)	5.1 ± 0.2 (17)
Cation exchange capacity in B horizon ($mmol^+$/kg) ± SD (n)	130.7 ± 38.31 (23)	65.6 ± 17.9 (14)	40.9 ± 11.8 (17)
Soil texture fraction < 0.01 mm in B horizon (%) ± SD (n)	34.2 ± 11.6 (23)	2.5 ± 1.7 (14)	0.2 ± 0.8 (17)
Soil texture fraction < 0.002 mm in B horizon (%) ± SD (n)	12.7 ± 5.9 (23)	0.25 ± 0.59 (14)	0.1 ± 0.4 (17)
Forest type	fir-beech forest	(spruce)-fir-beech forest	hardwoods
Main tree species	*Fagus sylvatica, Abies alba*	*Fagus sylvatica, Picea abies, Abies alba*	*Acer saccharum, A. pensylvanicum, A. rubrum, Quercus rubra, Tsuga canadensis, Pinus* spp.
Range of altitudinal gradient (m a.s.l.)	600–812	730–837	215–270
Mean annual precipitation (mm)	1057	900	800
Average seasonal maximum of snow cover depth (cm)	75–100	75–100	Circa 100
Mean average temperature (°C)	5.0–6.0	4.3	5.1
Maximal observed pit-mound longevity (year) (Šamonil et al. 2013)	220	1690	6183

years ago. The core zone of Zofin reserve has never been cut and has been under protection since 1838. The old-growth forest at Razula has been under protection since 1933, but was affected by infrequent selective cutting and grazing prior to that time (Table 1). We selected these sites as representative of the natural picture of local post-disturbance pedogenesis.

2.2 Dating of uprooting events

In total, 1562 (Razula) and 1733 (Zofin) pit-mound pairs were studied in terms of their dimensions, morphology, degree of trunk decay (where applicable), and organic horizon characteristics (Šamonil et al. 2009, Šamonil et al. 2014). Subsets of these were selected for dating using stratified random techniques. In Michigan, we used a more subjective technique for selection of 70 pit-mound sites to study and date. We applied our self-named “cross dating” procedure to establish the ages of the uprooting events. This method integrates dendrochronological, tree census and radiometric (isotopes ^{137}Cs, ^{210}Pb, ^{226}Ra, ^{14}C) techniques to establish the ages of pit-mound pairs, and hence, the age of the treethrow event. In all, we dated 178 treethrow pit-mound pairs in Zofin, 37 in Razula, and 14 in Michigan. Dating techniques as well as the results are described in detail by Šamonil et al. 2009, 2013.

2.3 Soil selection and characterization

Soil data were collected for 14 of the most precisely dated pit-mound pairs of different age in each region (42 total). These sites represent three rough chronosequences, one on Haplic Cambisols (from 1988 to 1816 CE), one on Entic Podzols (from 1979 to circa 320 CE), and one on Albic Podzols (from 1842 CE to circa 4080 BCE). The morphology of the soils in all of the 42 uprooting features were described from ca 1.5 m deep and 0.6 m wide trenches along the axis of the pit-mound pair (profile A in Fig. 4; Šamonil et al. 2015). Although treethrow pit–mounds were oriented in a multitude of directions, relative to slope inclination, downslope orientation predominated. The control profiles occurred on the same landscape position as did the relevant disturbed profiles. The selected control areas did not express footprints of former disturbance (although we assumed that the control profiles could have been disturbed in deep past). We sampled all soil horizons at depths of 5, 15, 30, 50, and 100 cm directly in excavated trenches, in addition to other horizons occurring between these depths in their specific position in the trench, across the three microsites (pit, mound, undisturbed reference pedon). In total, 700 soil samples were sampled and analyzed for standard chemical and physical characteristics. We chose these analyses to characterize the dominant pedogenic processes in these soils: transformation and translocation of organic compounds (humification, melanization etc.); weathering and leaching processes (formation and alteration of minerals, clay illuviation, podzolization, etc.); and oxidation-reduction processes.

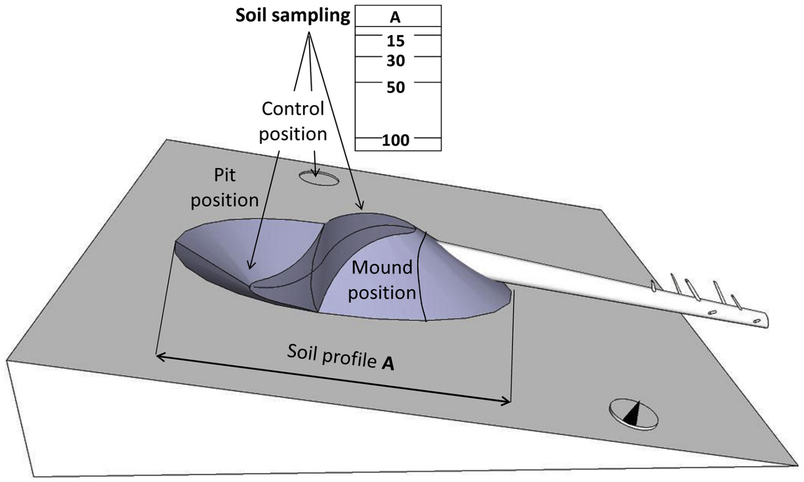


Fig. 4 A schematic treethrow pit-mound pair still with uprooted trunk, with locations of sampled profiles on microsites – pit, mound, and undisturbed control.

All soil samples were analyzed according to the procedures outlined in Zbíral 2002, 2003 and Zbíral et al. (2004): exchange soil reaction (pH-KCl) – 0.2 M KCl; active soil reaction (pH-H_2O); color quotient (Q4/6) – calculated using the equation Q4/6 = E465/E665, where E465 and E665 are the extinctions (0.05 M $Na_4P_2O_7$ extract) at wavelengths 465 and 665 nm (Chen et al. 1977); total organic C (Cox) – spectrophotometric approach after oxidation by H_2SO_4 + $K_2Cr_2O_7$ according to ISO (1995); C content in total humic substances (C–THS), and separately in humic acids (C–HA) and in fulvic acids (C–FA) – all in $Na_4P_2O_7$; total N content according to Kjeldahl (Bremner 1996); exchangeable Ca^{2+}, Mg^{2+}, K^+, Na^+, exchangeable acidity (Al+H) and effective cation exchange capacity (CEC) – all according to Gillman (Gillman & Sumpter 1986; $BaCl_2$-compulsive exchange procedure, native pH); and particle-size distribution according to Casagrande (Bernhardt 1994). Concentrations of elements in the various liquid extracts were measured using an atomic absorption spectrophotometer (GBC 932 AB Plus) and with a Specol 221 UV/VIS spectrophotometer.

The contents of crystalline, amorphous and labile Fe, Al, Mn and Si forms were determined for all samples by simple extraction methods. Although the extracted forms of Fe and Al can be classified into these three forms (Courchesne & Turmel 2008), for Mn and Si, this division is less clear (Guest et al. 2002).

1. The contents of reactive-exchangeable and weakly organics bond forms (Fe_k, Al_k, Mn_k, Si_k) were determined by using 0.5 M KCl (37.27 $g\,l^{-1}$) (1:10, *v*/*w*), according to Drábek et al. 2003, Drábek et al. 2005.
2. The contents of sum of exchangeable, organic and particularly amorphous forms and organic complexes (Fe_{ox}, Al_{ox}, Mn_{ox}, Si_{ox}) were determined with acid ammonium oxalate, according to Courchesne & Turmel (2008), with 0.2 M of ammonium oxalate at pH 3 (at a ratio of 0.25:10, *w*/*v*).
3. The contents of sum of exchangeable, organic, amorphous and mainly crystalline forms (Fe_d, Al_d, Mn_d, Si_d) were determined by extraction with a dithionite–citrate solution (DC) (McKeague et al. 1971) at a ratio of 0.5:25 (*w*/*v*), according to Courchesne & Turmel (2008).

Tejnecký et al. (2015) examined in detail the mineralogy of these extracts using voltammetry of microparticles and diffuse reflectance spectroscopy and Šamonil et al. (2010b) published local pedochemical data regarding uprooted Cambisols. The data from Zofin and Michigan, as well as summary syntheses and the conceptual model, have not been published previously.

2.4 Data analysis

Using soil data from the 42 treethrow sites we assessed the importance of three characteristics on soil development: (i) depth, (ii) age (after disturbance by tree uprooting), and (iii) microsite location (pit, mound, undisturbed, i.e. control position), using a set of redundancy analyses (RDA), separately for each region. Because the age of the soils sampled at the currently undisturbed (control) microsites is unknown, and soils here are always older than those on the pit-mound pair itself, only the data from pits and mounds were used when examining the effects of age. This approach resulted in two kinds of analyses (with and without data from controls).

In each RDA, one of these three characteristics was used as explanatory variable; the remaining two (or one) were included as covariates. In addition, the effect of age, together with its interactions with both sampling depth and microsite, were analyzed with the net effect of these two variables partialled out. We did not include control profiles in these calculations, as explained above. Response (dependent) variables in all RDAs were the 32 measured physical and chemical soil properties. The explained variation was computed using permutationally adjusted R^2 (Peres-Neto et al. 2006) based on 10,000 permutations. To avoid possible problems with autocorrelation of data from the same microsite and within a pit–mound pair, we used a three-level hierarchical block randomization scheme, respecting the autocorrelation resulting from sampling design (Manly 2006). Microsite blocks containing data from individual pits or mounds (or controls) were nested in pit–mound blocks and randomizations were only allowed to occur within each level of hierarchy. This permutation scheme ensured that potential autocorrelation affected also null distributions of test statistics derived from the randomized data which prevented the occurrence of falsely significant results (particularly in age-related analyses).

We also studied the relationship between individual soil properties and the three variables used in the RDA (depth, age and microsite). Using generalized linear models (GLM) with gaussian and gamma distributions, we started with a full model including all three explanatory variables and all their interactions. Two variants were fitted, with sampling depth added as either a linear or quadratic term. The model was then reduced by backwards selection, dropping non-significant terms ($\alpha = 0.05$) with the highest p values one at a time, until only significant terms remained. The structure of the residuals from this analysis was then inspected, and from the models that were satisfactory in this respect, the final one was chosen using AIC. As in the case of RDA, the autocorrelation within microsites on individual pit–mound pairs had to be taken into account, and the significance of individual terms was tested using the same randomization scheme as described above. All analyses were performed in R (R Core Team 2015).

3 Results and discussion

3.1 Soil forming processes and differences between soil regions

Data from chemical and physical laboratory analyses confirmed that weathering and leaching processes are following traditional podzolization pathways at the Zofin and Michigan sites (Table 2, Fig. 3, Fig. 5). According to the fulvate-complex theory of podzolization (McKeague et al. 1978, Buurman 1984, Lundström et al. 2000, Buurman & Jongmans 2005) unsaturated organo-metallic complexes are formed in litter on the forest floor (O and A horizons) and subsequently mobilized and precipitated in the B (spodic) horizon upon saturation of organic molecules through metal complexation (see forms of Fe, Al and C in Fig. 5). In such soils, high acidities often lead to clay destruction as well (Schaetzl & Thompson 2015). Alternatively, in the finer-textured soils at the Razula site, secondary (clay) mineral formation pathways are also operating (Table 2, Tejnecký et al. 2015). As expected, terrain pedomorphology (see Šamonil et al. 2015) as well as soil analyses showed evidence of clay translocation at the Razula, as argillans on peds and as clay-enriched B horizons. Melanization and hydromorphic (redox) processes were also observed in disturbed and control undisturbed microsites as well, particularly in Razula. These processes were supported by occurrence of cambic Bwg horizon with stagnic properties in some pits (e.g. Table 2), unimodal development of total organic carbon within the pit (Fig. 5), direction of C and Mn forms to the pit (Fig. 7) as well as by former findings of Šamonil et al. (Šamonil et al. 2010b, Šamonil et al. 2015) and Tejnecký et al. (2015).

Contrary to our expectations, active as well as exchangeable soil reactions were both higher in the Albic Podzols (range of pH-H_2O = 4.1–6.3) than the Entic Podzols (range of pH-H_2O = 3.6–5.0, see also Table 1). This difference can be partly elucidated by significantly higher cation exchange capacities (up to 250 mmol$^+$/kg) and organic matter contents in the Entic Podzols. The higher CEC in Entic Podzols was naturally accompanied by increased exchangeable acidities, as well as H^+concentrations. Higher amounts of organic matter frequently support soil acidification and some of this effect can be also due to the different vegetation covers of the three forest ecosystems.

Although CEC and pH were mutually positively correlated in the Cambisols at Razula, similar correlations were negative for Podzols. The negative correlations may have been caused by the formation of organo-mineral complexes between soil organic matter and short-range order Al

Table 2 Examples of soil chemical and physical properties for disturbed and adjacent undisturbed soil profiles in the three soil regions.

Soil unit / Locality	Microsite and age (years)	Soil horizon	Sample depth (cm)	pH-KCl	Nt (%)	Cox (%)	C-HA/FA	Q4/6	CEC (mmol+/kg)	Al+H (mmol+/kg)	Ca^{2+} ($mmol^{+}/kg$)	Mg^{2+} ($mmol^{+}/kg$)	K^{+} ($mmol^{+}/kg$)	Al_k (mg/kg)
Haplic Cambisols (Razula)	Control	A	5	3.85	0.49	4.73	0.91	6.22	180.0	36.0	148.0	20.8	5.0	107.6
		AB	15	3.53	0.30	2.75	0.79	8.10	168.0	80.0	77.6	13.5	1.8	554.1
		Bw	30	3.67	0.22	2.13	1.25	7.59	165.0	40.0	126.0	19.0	2.7	441.9
		Bw	50	3.68	0.12	1.85	1.07	7.37	174.0	72.0	89.2	16.2	2.5	558.5
		(B)C	100	3.85	0.11	1.10	1.00	5.16	178.0	20.0	168.0	14.5	3.0	136.9
	Pit (192)	A	5	3.92	0.43	5.00	1.32	6.59	191.0	42.0	163.0	16.7	4.7	79.7
		AB	15	3.96	0.38	4.25	1.10	7.37	187.0	34.0	169.0	14.8	2.8	51.7
		Bw	30	4.10	0.34	3.83	1.00	6.01	178.0	22.0	175.0	15.1	2.7	32.2
		Bw(g)	50	4.69	0.21	3.23	1.07	6.49	183.0	24.0	167.0	18.7	3.6	97.3
		C	80	3.89	0.11	0.98	1.83	5.19	201.0	0.0	261.0	19.3	5.0	0.0
	Mound (192)	A	5	3.63	0.26	3.23	2.05	6.82	179.0	68.0	88.8	20.6	8.4	468.8
		AB	15	3.59	0.20	2.10	4.20	5.97	220.0	72.0	163.0	23.1	6.2	541.1
		Bw	30	3.67	0.13	1.60	4.78	5.72	245.0	36.0	259.0	27.6	5.6	222.1
		Bw	50	3.76	0.12	1.48	4.00	5.57	221.0	28.0	246.0	27.6	4.4	150.9
		C	100	3.56	0.12	1.43	1.22	5.82	193.0	60.0	135.0	29.8	4.1	471.6
Entic Podzols (Zofin)	Control	A	3	3.04	1.00	14.38	1.89	8.21	177.0	26.5	72.0	7.9	4.1	242.4
		A(E)	9	3.04	0.44	7.50	1.22	7.04	94.1	26.5	21.4	5.6	0.9	495.0
		(A)B	15	3.49	0.30	5.72	0.50	10.29	75.2	25.5	10.9	3.8	0.3	775.1
		Bs	30	3.96	0.14	3.32	0.35	9.94	43.6	13.8	9.8	4.5	0.9	500.1
		BC	50	4.22	0.10	1.08	0.38	9.38	41.6	4.6	6.0	2.7	0.3	198.3
		C	100	4.10	0.06	0.65	0.56	9.74	20.0	2.0	6.7	3.0	0.6	174.8
	Pit (991)	A	5	3.09	0.94	10.77	1.07	8.28	103.0	33.7	16.6	7.0	3.0	609.4
		A	15	3.40	0.74	10.29	0.95	8.30	107.0	33.7	15.0	5.4	1.9	751.0
		A(E)	30	3.42	0.64	8.95	0.81	7.49	84.5	30.6	9.8	4.3	0.9	741.7
		AB	50	3.78	0.22	4.38	0.60	8.15	62.9	20.9	7.7	3.7	1.0	684.1
		C	100	4.19	0.10	0.99	0.50	7.69	29.4	5.1	7.5	3.4	1.1	224.4
	Mound (991)	A	3	3.50	0.60	8.75	1.05	8.75	96.4	25.0	16.2	5.4	3.2	544.3
		Bs	15	4.05	0.18	1.83	0.44	8.44	32.2	10.7	5.8	3.0	1.0	384.8
		BC	30	4.28	0.11	1.59	0.33	9.24	34.5	6.6	7.8	3.1	0.8	215.5
		BC	50	4.31	0.07	0.55	0.43	6.57	23.1	4.6	6.6	3.2	1.0	174.1
		(B)C	100	4.35	0.05	0.55	0.39	7.56	17.7	4.6	5.5	3.1	1.0	146.3
		C	120	4.30	0.08	0.70	0.89	7.11	9.1	2.6	5.1	3.1	1.1	149.8
Albic Pozdols (Michigan)	Control	E	5	3.43	0.04	0.63	1.20	4.53	29.0	10.0	8.8	3.6	0.5	18.1
		E	15	3.74	0.02	0.43	0.04	4.09	23.2	6.8	5.8	2.4	0.1	17.8
		Bhs	30	3.95	0.12	1.73	0.32	8.18	53.7	39.4	9.8	3.4	1.8	241.4
		Bhs	50	4.03	0.10	1.59	0.35	7.50	44.0	33.9	9.4	3.3	0.8	193.1
		Bs	100	4.74	0.04	0.24	0.10	6.50	29.9	6.8	6.4	2.6	0.7	16.2
	Pit (3969)	AE	5	3.71	0.04	1.15	1.38	4.01	23.4	6.6	7.2	3.2	0.9	11.5
		E	15	3.67	0.03	0.41	0.50	4.03	17.4	6.6	1.6	1.6	1.0	16.3
		E	30	3.63	0.03	0.34	0.57	4.14	44.5	7.6	2.4	1.8	0.9	31.1
		Bhs(m)	50	4.11	0.07	1.14	0.31	7.69	44.9	31.0	6.0	2.5	1.0	135.1
		Bhs(m)	100	4.30	0.05	0.88	0.37	8.11	41.7	28.6	3.0	1.8	0.9	108.5
	Mound (3969)	A(E)	5	3.50	0.05	0.70	1.03	4.80	29.4	15.2	2.6	1.2	0.8	34.5
		Bhs	15	3.99	0.07	1.25	0.46	8.34	55.8	37.2	10.2	3.0	0.8	165.6
		Bs	30	4.54	0.04	0.52	0.50	7.44	29.5	13.8	8.2	2.9	0.5	50.3
		Bs	50	4.60	0.03	0.71	0.40	6.39	27.4	11.6	8.2	3.1	0.6	39.1
		B(C)	100	4.81	0.02	0.19	0.78	7.11	16.1	4.6	6.0	3.0	0.6	12.4

Table 2 (continued)

Soil unit / Locality	Fe_k (mg/kg)	Mn_k (mg/kg)	Al_{ox} (mg/kg)	Fe_{ox} (mg/kg)	Mn_{ox} (mg/kg)	Si_{ox} (mg/kg)	Al_d (mg/kg)	Fe_d (mg/kg)	Mn_d (mg/kg)	Si_d (mg/kg)	Fraction 2–0.1 mm (%)	Fraction 0.1–0.05 mm (%)	Fraction 0.05–0.01 mm (%)	Fraction < 0.01 mm (%)
Haplic Cambisols (Razula)	1.8	537.0	2553	4364	1801	172	3083	20,377	1830	820	45	15	24	16
	1.7	346.7	2829	4668	1529	163	3156	20,702	1564	765	42	15	24	19
	0.5	184.0	2556	4260	1556	196	3017	22,177	1581	934	23	11	22	35
	0.3	121.0	2552	4000	1391	191	3016	22,017	1398	947	22	10	22	46
	0.0	116.9	1881	4212	1366	217	2618	21,082	1429	878	18	8	24	51
	19.9	699.8	1956	4292	1456	148	2374	17,967	1516	841	64	12	17	7
	2.0	471.4	1986	3482	1433	162	2488	17,172	1545	825	45	16	25	14
	4.9	470.5	1951	3678	1426	134	2550	17,537	1556	745	47	14	23	17
	0.5	242.7	1745	3024	1194	149	2315	18,582	1230	843	37	15	25	24
	0.3	85.4	918	1958	2627	249	990	10,012	2704	616	47	13	21	20
	3.0	248.8	2169	3146	863	159	2563	18,762	897	854	46	10	18	26
	0.2	101.1	2106	3589	634	178	2541	23,292	652	1132	34	9	18	36
	0.3	93.4	1628	3194	640	209	2096	22,637	656	1208	34	11	17	38
	0.0	128.6	1452	2916	724	185	1950	20,617	771	1056	40	11	16	33
	0.7	131.8	2030	3024	1897	187	2457	22,182	1867	1152	48	8	13	31
Entic Podzols (Zofin)	152.8	6.4	2400	5045	12	32	2565	8967	0	850	93	4	4	0
	139.8	1.6	3117	8331	10	152	2395	16,278	8	1400	78	14	6	2
	102.6	2.1	12,256	28,135	43	700	10,430	39,346	63	1500	72	17	10	2
	15.6	0.5	19,140	16,785	43	2072	14,460	24,937	46	2000	85	8	6	1
	2.1	0.3	14,004	2791	29	3500	7810	9739	28	2450	90	5	5	0
	0.3	0.8	6478	1332	99	1568	3905	12,001	105	1550	93	4	4	0
	322.9	6.8	3908	9928	20	128	2860	14,587	25	950	78	15	7	0
	186.2	19.6	6147	12,741	48	252	5090	20,959	66	1650	78	14	8	0
	118.8	8.1	6354	12,980	34	192	5295	23,536	69	1650	72	17	12	0
	49.2	2.9	9694	16,324	43	524	8100	26,448	78	1400	78	7	13	3
	2.2	1.3	6216	2668	102	916	4480	8533	89	950	83	14	4	0
	107.4	42.0	6416	7871	86	352	5420	16,246	118	1050	74	17	10	0
	10.1	4.1	13,214	14,462	85	1392	9720	23,096	101	2200	74	6	8	3
	2.0	1.0	16,983	5526	66	3496	10,195	13,230	75	2200	85	6	9	3
	0.7	0.5	10,769	3233	67	2524	5720	10,540	73	1900	85	8	8	0
	0.4	0.8	6424	1747	67	1428	3230	8207	76	1900	91	5	4	0
	0.3	0.8	4074	1199	105	860	2375	8722	120	1700	81	10	9	0
Albic Pozdols (Michigan)	2.5	0.1	108	90	2	0	65	1647	13	50	78	14	6	3
	2.0	0.0	85	123	1	0	115	1681	14	0	90	5	5	0
	36.1	0.6	5077	6075	8	544	3930	8024	19	500	84	12	4	0
	21.8	0.6	3426	3824	9	160	2945	5646	23	200	83	14	4	0
	3.0	0.1	2104	832	10	596	1865	1444	21	250	93	5	3	0
	1.9	0.4	51	71	3	60	75	1254	19	0	84	13	4	0
	2.0	0.0	62	69	2	76	280	1429	16	0	84	14	3	0
	4.7	0.1	93	146	3	44	205	1649	12	0	84	13	4	0
	20.8	1.6	3518	3915	22	428	2835	5046	30	0	83	15	3	0
	9.2	0.5	2822	1640	7	184	2025	2063	12	0	79	18	3	0
	5.0	0.1	149	111	2	32	175	1471	17	0	73	19	7	1
	25.9	0.7	3012	2918	8	264	2620	4359	20	50	80	16	5	0
	3.5	0.6	3566	1178	15	856	2335	2100	25	300	80	17	4	0
	1.7	0.3	3690	1641	11	976	2290	2813	24	50	78	17	4	1
	1.2	0.5	1579	459	16	556	540	1159	25	0	80	18	3	0

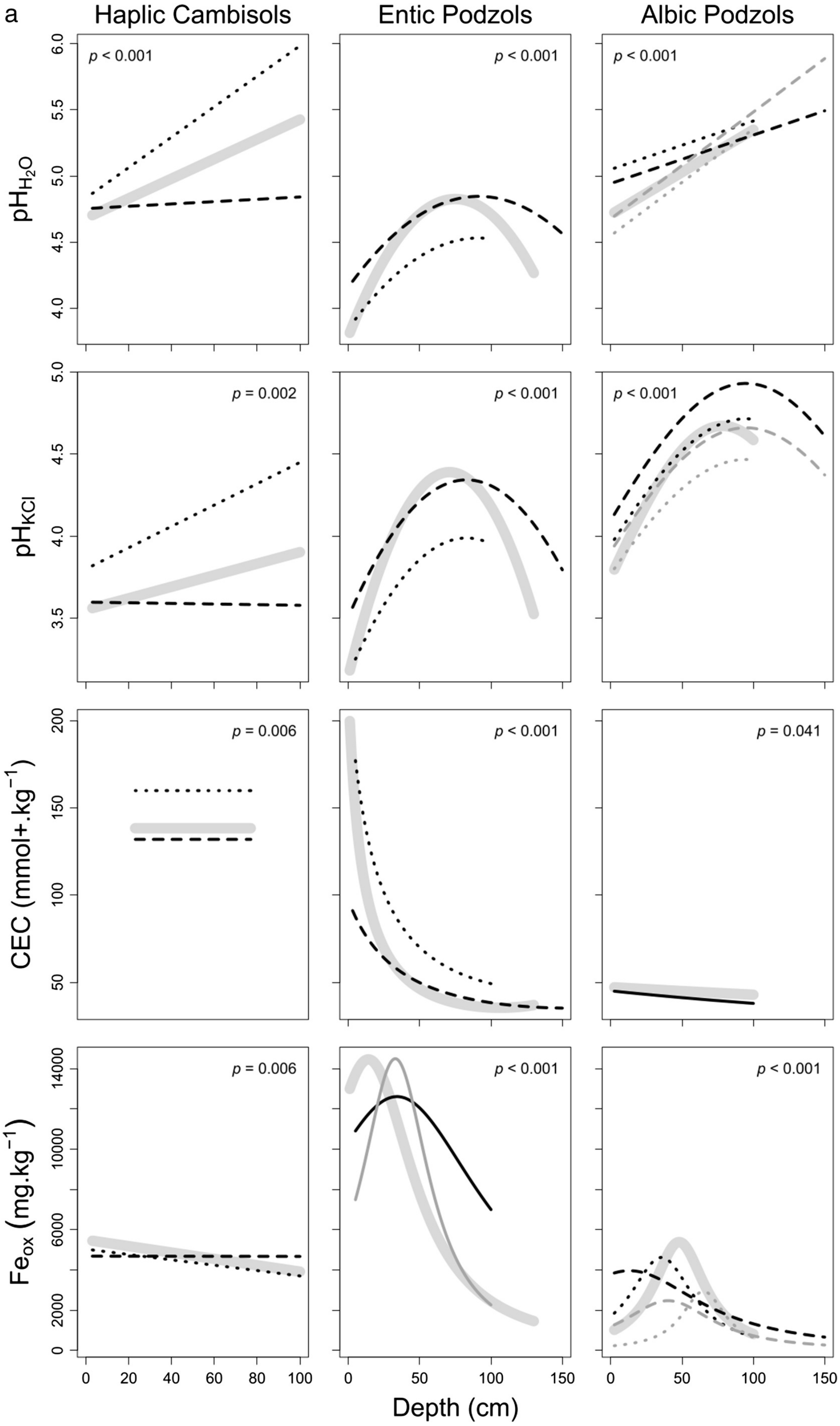


Fig. 5 Significant models of the selected soil properties, in relation to the sample depth, microsite and age. Ages of young and old pits or mounds correspond to the youngest and oldest dated uprooting events within each soil unit (19 and 250 years on Haplic Cambisols, 32 and 1690 on Entic Podzols and 168 and 6089 years on Albic Podzols, respectively).

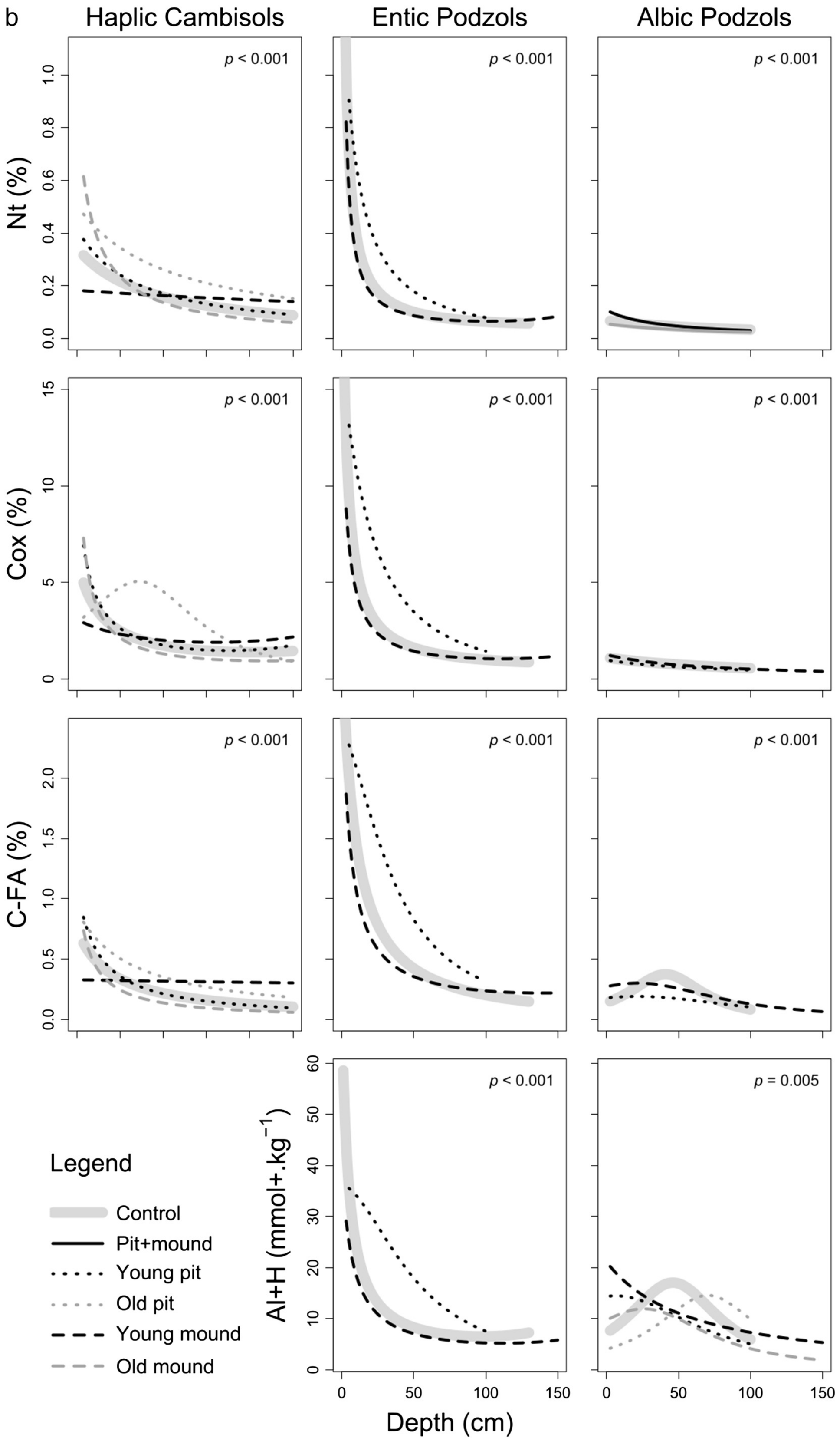


Fig. 5 *(continued)*

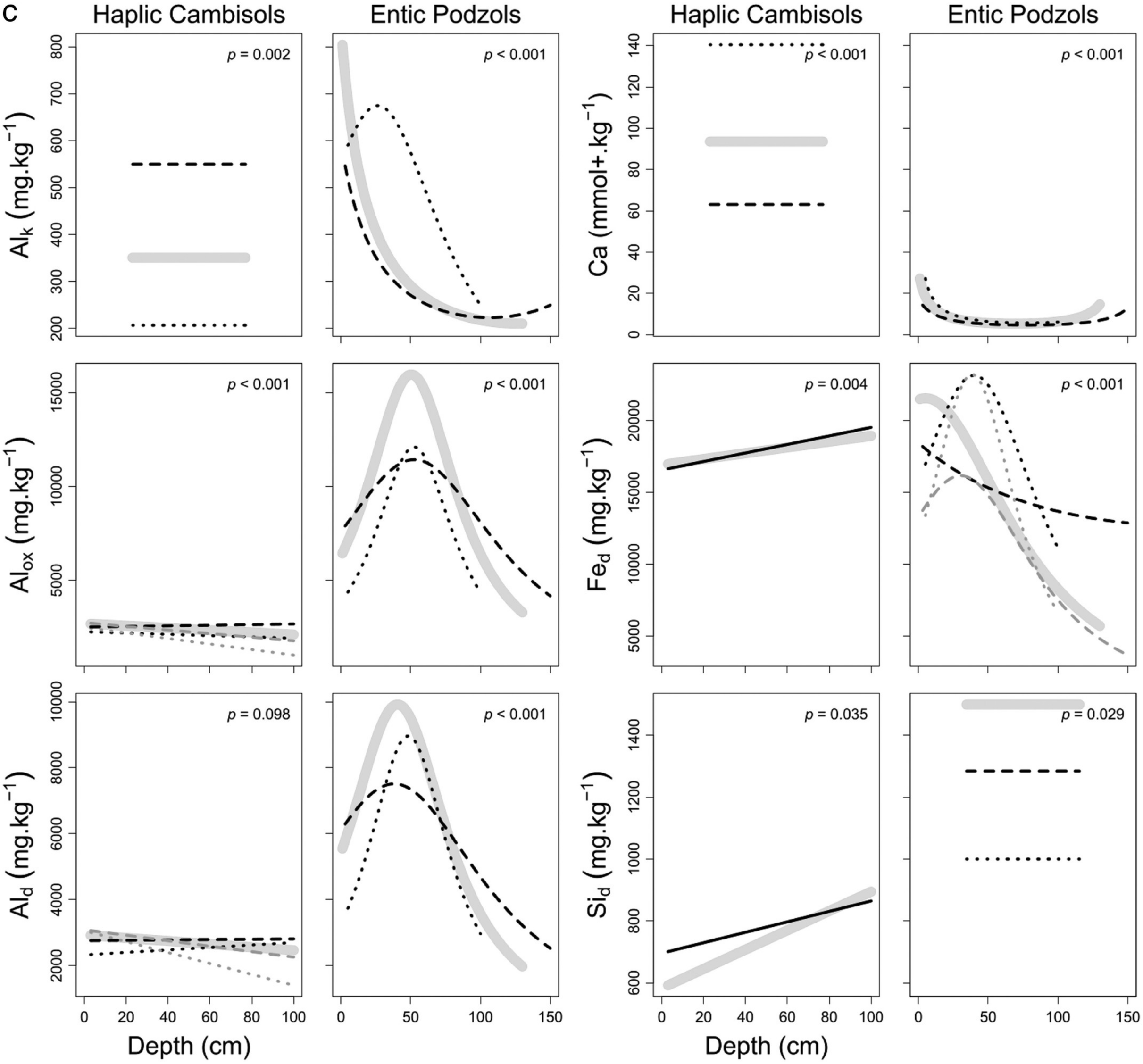


Fig. 5 *(continued)*

and Fe phases (Fe_{ox}, Al_{ox}, see Grand & Lavkulich 2013). Organo-mineral complexes, together with organic compounds, represented the main components of cation exchange capacity on Entic and Albic Podzols. Therefore amount of carbon, and its forms and complexes were strongly correlated with CEC (Fig. 6, Fig. 7, Table 2, see Grand & Lavkulich 2013). Although complexation of organic matter with metallic compounds can also have significant podzolization potential in Cambisols (Titeux et al. 2002), it was only minimally present in our profiles, through the translocation of organic carbon (Cox), and specially fulvic acids (C-FA), in older treethrow pits. Cation exchange capacities were probably preferentially driven by clay contents (Table 1, Šamonil et al. 2010b), although the role of organic matter cannot be considered negligible (e.g. Gruba & Mulder 2015) in the Haplic Cambisols (Fig. 5, Fig. 6, Fig. 7).

Contents of amorphous and crystalline forms of Fe and Al and their organic complexes were significantly lower in B horizons of Albic Podzols than in Haplic Cambisols, and particularly in

Entic Podzols – despite the intense podzolization at the Michigan site (Table 2, Fig. 3, Šamonil et al. 2015, Schaetzl et al. 2015, Schaetzl & Rothstein 2016). This relationship can be attributed to significantly lower concentrations of Al and Fe in the quartz-rich outwash parent materials in Michigan. Contents of **organic C** and its specific forms (C-HA, C-FA) were the highest on Entic Podzols (Table 2, Fig. 5). The results of laboratory analyses show that Albic Podzols on outwash had significantly lower buffer potential and relatively low amounts of fulvic acids, but, obviously, in sufficient amounts to initiate illuviation of labile organic matter-sesquioxide complexes. A similar observation was made by Stützer (1999) in shallow podzolic soils in mountain areas. Relatively low buffering capacity of soil on outwash is reflected in relatively rapid post-disturbance pedogenesis, as observed by Schaetzl (1986) and Šamonil et al. (2015) (see review by Lundström et al. 2000).

3.2 Role of sample depth in soil data

Sample depth was the most important variable with respect to post-disturbance soil development ($p < 0.001$, Table 3); it was more significant than either age or microsite. Sample depth explained nearly 13% of the variability on Haplic Cambisols, and 14.9% on Entic Podzols. In the most podzolized region, on Albic Podzols, depth explained only 6.0% of the data variability. This lower proportion reflected the age-dependent deepening of unimodal (or bimodal) concentrations of the fractions of C, Al, Fe and Si from eluviation and illiviation of labile organo-mineral complexes (Fig. 5). These components reached their maximal concentrations in the mid-B horizon (Bhs, Bhsm, Fig. 5). Higher concentrations of amorphous and crystalline Fe in the uppermost horizons (Fe_{ox}, Fe_d in Fig. 5) within disturbed microsites on Albic Podzols showed repeated mobilization of these complexes after their former immobilization in pre-disturbance spodic horizons. Tanskanen & Ilvesniemi (2004) observed such re-precipitation of metallic complexes in soils disturbed by plowing. Tree uprooting has obviously had similar effects in these forested landscapes.

The **unimodal shapes of concentrations** of many soil properties in profiles resulted in their orthogonal relationship to sample depth and hence, the lack of linear statistical fit (Fig. 6). On the other hand, for the Haplic Cambisols the extensive sorption of C on particles of the clay-rich soil matrix led to a sharp decrease of C with depth, as well as connected N concentrations, usually along **exponential decay trajectories**. Increases with depth also occurred for crystalline Fe (Fed) in the Haplic Cambisols, which was unlike soils in both regions of Podzols. The highest concentrations of Fed in medial soil horizons of Podzols illustrated the pedogenic origin of this fraction, rather than geogenic. This predominance was even more visible in Al forms (Fig. 5, Fig. 6, Fig. 7).

Clay contents, soil reaction (pH-H_2O, pH-KCl), and Si_{ox} concentrations belonged in the category of soil properties that had similar relationships with sample depth in all three studied regions. All of these properties increased with depth. Although all these properties are affected by pedogenesis, their increasing values with depth indicates (especially in case of Si_{ox}) the significant role of bedrock in their constitution (e.g. appearance of weathered claystones on flysch at Razula reserve and weathered granite at Zofin).

Table 3 Results of ordination analyses. Statistically significant results are in bold and marked with asterisks (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). For details about settings of analyses, see Section 2.4.

Site	Variable	Explained data variability (%)	*P* value	
Haplic Cambisols (Razula)	**depth**	**12.7**	**< 0.001**	***
	microsite	**7.3**	**< 0.001**	***
	age	2.7	0.397	
	age × microsite	**2.3**	**0.045**	*
	age × depth	**1.1**	**0.004**	**
	depth × microsite	**4.0**	**< 0.001**	***
Entic Podzols (Zofin)	**depth**	**14.9**	**< 0.001**	***
	microsite	**4.8**	**0.001**	***
	age	0.9	0.912	
	age × microsite	0.5	0.793	
	age × depth	0.3	0.405	
	depth × microsite	**3.0**	**< 0.001**	***
Albic Podzols (Michigan)	**depth**	**6.0**	**< 0.001**	***
	microsite	2.1	0.076	
	age	3.7	0.117	
	age × microsite	0.6	0.873	
	age × depth	**1.1**	**0.020**	*
	depth × microsite	0.8	0.058	

3.3 Evolutionary trajectories, and the general role of microsite and age in pedogenesis

We can assume that the microsite and its interaction with time since the disturbance event can be viewed as one possible alternative within the soil development pathway system, i.e. it may be a factor of soil non-linearity or polygenesis (Johnson & Watson-Stegner 1987). Each microsite potentially presents a specific developmental trajectory in soils below, because the site changes the local microclimate (Beatty & Stone 1986), flora (von Oheimb et al. 2007) and hydrology (Schaetzl 1990), as well as characteristics of the forest floor.

Statistically, the significance of microsite decreased with increasing degree of podzolization (Table 3). The largest proportion of data variation by microsite was explained on Haplic Cambisols (7.3%, $p < 0.001$), less so on Entic Podzols (4.8%, $p < 0.001$), and least on Albic Podzols (2.1%, $p = 0.076$). Moreover, in soil regions without strong illuviation of organic matter-sesquioxide complexes (Haplic Cambisols and Entic Podzols), an additional 3–4% of the data variability was explained by interactions of microsite with depth, or even with age (Haplic Cambisols, 2.3%, $p = 0.045$).

The age of treethrow features was particularly important as an explanatory variable on Haplic Cambisols, where it obtained statistical significance in interactions with the depth and microsite (Table 3). In the Albic Podzol region, age was significant only in its interaction with depth. Age exceeded the level of statistical significance in all calculations on Entic Podzols as well (Table 3). The low significance of the age variable on Entic Podzols could be connected with the high local soil variability (Šamonil et al. 2011) and diversity (Šamonil et al. 2014), i.e., there exists a relatively high importance of the local soil environment.

Evaluation of post-disturbance pedogenet pathways requires simultaneous considering of the effect of microsite, time and depth. Our data (Table 3, Fig. 5a,b, 7) generally clearly show that soils in post-disturbance microsites are pedochemically closer to undisturbed (control) soils at the Michigan site, where soil weathering and leaching were the most intense. In other words, although neoformation of podzolic E and Bhs horizons here is extremely rapid in pits and much slower on mounds (e.g. Al+H in Fig. 5, Table 2, Šamonil et al. 2015), its pedochemical properties are nearly the same in all microsites. We speculate that the pedogenic impact of pit and mound microtopography is reduced by predominance of vertical podzolization and by the limitation of lateral processes in the extremely poor, acidic and permeable parent materials of Michigan. In the sandy parent materials at the Michigan site, there is no evidence of lateral podzolization (Sommer et al. 2001; see also Schaetzl et al. 2015).

Alternatively, soils in the Cambisol region (Razula) were the most variable after disturbance, with respect to soil chemistry and physics data (Table 3, Fig. 5, Fig. 7). The secondary (clay) mineral formation (Table 1, Table 2, Tejnecký et al. 2015), which are key pedogenetical process in Cambisols (e.g. Schaetzl & Thompson 2015), was here supplemented by strong melanization connected with bioturbation by soil fauna (Šamonil et al. 2008a, Šamonil et al. 2008b), clay illuviation, clay mineral alteration (Tejnecký et al. 2015) and hydromorphic processes (Schaetzl 1990). This finding can be associated with the decreasing number of statistically significant models of individual soil properties with increasing severity of podzolization in regions (Fig. 5). Although we report on 27 valid statistical models for Haplic Cambisols, we found only 23 such models on Entic Podzols using the same technique, and only 15 models on Albic Podzols.

3.4 Equivocal pedogenetical role of disturbed microsites

Although microclimatic differences across microsites seem to be universal, i.e., mounds are often drier and warmer than pit microsites in the same landscape (Beatty & Stone 1986, Schaetzl 1990), our data suggest that – the role of treethrow microsites as a factor of the soil polygenesis, was more equivocal. Of the 38 evaluated soil properties, only amorphous and crystalline forms of manganese and aluminum (Mn_{ox}, Mn_d, Al_{ox}, Al_d) always had maximal concentrations in treethrow pits, probably due to redoximorphic processes for manganese and accumulation of organic matter and associated organically-bound Al and poorly crystalline aluminosilicates (Fiedler & Kalbitz 2003). In Albic Podzols, the formation of thick E horizons, indicative of extreme podzolization, acidification, and nutrient loss (the lowest amounts of Ca^{2+}, Mg^{2+}, and K^+, and high exchangeable acidities) were most commonly observed in pits. This finding agrees with those of others, who described this process in detail (Bormann et al. 1995, Cremeans & Kalisz 1988, Schaetzl 1990, Schaetzl & Follmer 1990, Kabrick et al. 1997). Alternatively, accumulation of nutrients, as well as higher CEC and pH values, occurred within pit soils on Haplic Cambisols and Entic Podzols. This key difference in the pedogenetic role of treethrow mounds and pits is likely due to the high buffer capacities of the clay minerals in Haplic Cambisols (see also Šamonil et al. 2010b) and the lowered importance of translocation of organic matter-sesquioxide complexes in Entic Podzols. In this region, we sometimes found weak E horizons in some very old treethrow pits (Šamonil et al. 2015) but generally these soils still did not exhibit pedomorphic formation of eluvial E and illuvial Bhs horiozons. Our results suggest that the start of eluviation of labile organic matter-sesquioxide complexes from the upper mineral horizons is a key threshold point in the development of soils in pits, representing a transition in post-uprooting microsites from accumulation to leaching. Prior to this point, pedogenetic development on treethrow sites is similar to that on Cambisols, even in soils with spodic properties. In a humid climate such as in our study, this point can be reached on poor rock in less time. On bedrock with the higher buffering power, it probably takes longer.

3.5 Evolution of undisturbed soils

Soils on microtopographically flat (control) sites were generally intermediate in character between pit and mound sites. However, such soils are also considerably older, and hence often have higher amounts of clay, crystalline and amorphous forms of Al, Si and partially also Fe and Mn. Such forms of metals may require hundreds or thousands of years to develop (e.g. Arduino et al. 1984, Pai et al. 2004). Hence, they are correlated with control positions because of the greater age of these soils. Unfortunately, the longevity of undisturbed formation of control profiles is not exactly known and can be only estimated. If we assume that many sites have rotation periods of 900–1400 years (Šamonil et al. 2009, Šamonil et al. 2013), then each site within the studied forest landscapes has theoretically been disturbed circa 8 times during the Holocene. Nevertheless, the duration of the rotation period does not exclude possibility of, locally much longer time periods between disturbances (cf. Šamonil et al. 2013). Instead, the rotation period provides only information about mean disturbance dynamics. Some sites will be frequently disturbed but others will remain undisturbed for thousands of years. Evaluation of age and denudation rates in undisturbed profiles is challenge for future research.

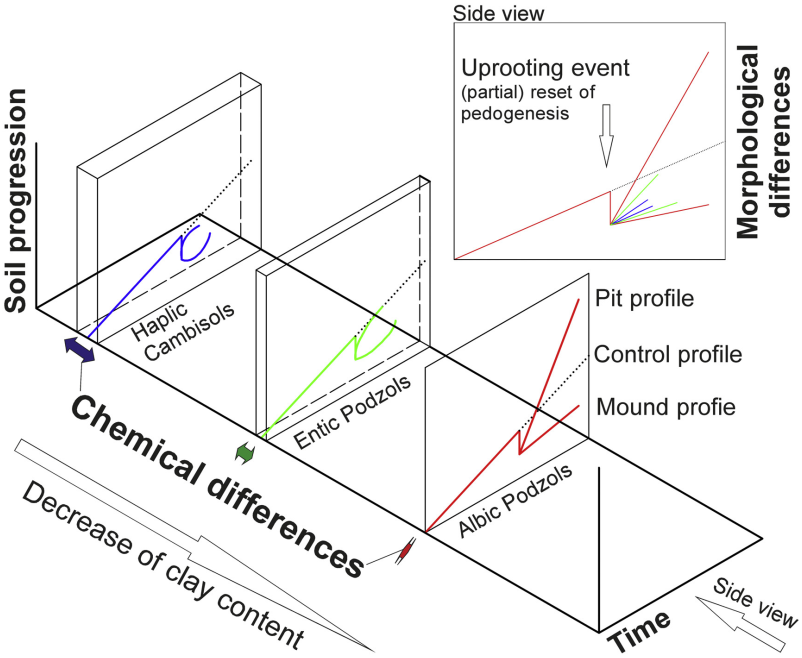
3.6 Pedomorphology versus pedochemistry

Šamonil et al. (2015) observed increasing differences in E horizon thicknesses over time between pit and mound sites. They hypothesized that this finding was due to divergent pedomorphic soil evolution, initiated by uprooting. Our current results are not in contradiction with these former findings. Instead, our current data on soil chemistry provide a more complete picture of soil formation and suggest that, in terms of soil chemistry, similar soil formation processes operate across all the microsites (Fig. 8).

3.7 Effect of long-term development of soil landscape

Long-term changes in soils could also influence current post-disturbance pedogenetical pathways. Some soil and landscape studies in northern Michigan revealed postglacial non-linear soil formation, at least in parts of the landscape (see Johnson et al. 1990). In the Albic Podzol region, clay-enriched lower horizons with argillic properties were repeatedly noted in soils that have spodic horizons in the upper profile (Šamonil et al. 2015). This horizon sequence generally is taken to imply that podzolization is preceded by clay illuviation (see bisequal soils in Schaetzl 1996, Bockheim 2003, Schaetzl & Thompson 2015). Based on our results from these three regions with soils of varying textures, we can generally derive expected changes in post-uprooting pedogenesis due to movement in regional soil evolution. The long-term sequencing of lessivage on region scale followed by podzolization will lead to qualitative flattening and homogenization of post-disturbance soil evolutionary trajectories at local scales. In other words, the assumed convergence of soil chemistry on a landscape scale towards vertically-dominated podzolization locally causes convergence of post-disturbance pedogenetical pathways.

Fig. 8 Conceptual model of post-disturbance soil formation (red, green, and blue lines, respectively) in the three soil regions, on Haplic Cambisols, Entic Podzols, and Albic Podzols. Although morphological data point to non-linear pedogenesis, chemical differences suggest post-disturbance, polygenetic soil formation.



3.8 Feedbacks from soil disturbance to forest development

Changes in soil development, as impacted by tree uprooting, have strong effects on forest regeneration. The affinity of woody species to mound microsites has long been known (see Nakashizuka 1989, Palmer et al. 2000, von Oheimb et al. 2007, Simon et al. 2011, Šebková et al. 2012, Šamonil et al. 2016). This affinity is presumably due to the usually unfavorable microclimate of pit sites. The wetter and colder character of pit is likely an advantage for organisms only in dry and arid regions. Pits are also sites of higher seed predation by small mammals (e.g. Simon et al. 2011), and juvenile plants by fungal pathogens (e.g. Šamonil et al. 2008b). Most importantly, organic matter accumulation within pits can be thick, which inhibits the successful germination of seedlings (Beatty & Stone 1986, Šamonil et al. 2008a, Šamonil et al. 2008b). This divergence can be even more significant after leaching and acidification of pit soils becomes enhanced in the post-disturbance years. The decreasing probability of successful establishment of plants within pits can, in turn, alter the spatial pattern of trees within the forested landscape (Szwagrzyk & Czerwczak 1993, Janík et al. 2016) and hence, the spatial distribution of additional uprooting disturbances (Šamonil et al. 2014).

Our results also suggest that the self-reinforcing pedologic influences of trees (SRPIT) model (Phillips & Marion 2004, Phillips 2008) needs refinement. The SRPIT model treats all former tree sites as a single microsite, without distinguishing between pits and mounds, or stump decay sites. Our results suggest that pedogenetic feedbacks cause rejuvenation on mounds, but progressive leaching in pits.

4 Conclusions

Post-uprooting pedogenetical pathways were compared between treethrow pits, mounds and undisturbed control profiles in three regions with different soil textures and intensities of weathering and leaching. Sample depth was the most significant variable in all three regions ($p < 0.001$) followed by microsite, and finally age since disturbance. Increasing contents of coarse fractions in soils and increasing intensity of podzolization caused chemical homogenization of post-uprooting pedogenetical pathways between the microsites. Results suggest that, in more highly developed soils, responses to disturbance may be more limited than in less-developed soils, which may decrease the polygenetic effects of uprooting. Convergent or divergent development can differ according to what soil property one is concerned with, or even broad classes of properties (e.g., soil morphology vs. soil chemistry).

The start of eluviation of labile organic matter-sesquioxide complexes from the upper mineral horizons is a key threshold in the pedogenesis in pits, representing a transition in post-uprooting microsites from accumulation to leaching. An occurrence of such threshold point can cause a type of mode switching of soil behavior. For centuries, disturbance can result in divergence; eventually, however, a threshold is approached, and a convergent mode is encountered across the landscape.

Acknowledgements The authors thank their colleagues Barbora Šebková, Martin Valtera, Petra Doleželová and Ivana Vašíčková from the 'Blue Cat research team', and our colleagues from Michigan State University, Jay Strahan and Caitlin Clark, for assistance in the field. We especially thank Jonathan D. Phillips from 'Blue Cat research team' and University of Kentucky for great suggestions relevant to non-linear dynamics of the Earth systems. Research was supported by the Czech Science Foundation (project No. 16-15319S) and by the Czech University of Life Sciences Prague (internal student project No. CIGA 20162016).

References

Arduino E., Barberis E., Carraro F., Forno M.G. 1984. Estimating relative ages from iron-oxide/total-iron ratios of soils in the Western Po Valley, Italy. *Geoderma* 33: 39–52.

Beatty S.W., Stone E.L. 1986. The variety of soil microsites created by tree falls. *Canadian Journal of Forest Research* 16: 539–548.

Bernhardt C. 1994. Particle size Analysis – Classification and Sedimentation Methods. Springer, London.

Bockheim J.G. 2003. Genesis of bisequal soils on acidic drift in the Upper Great Lakes region, USA. *Soil Science Society of America Journal* 67: 612–619.

Bormann B.T., Spaltenstein H., McClellan M.H., Ugolini F.C., Cromack Jr. K., Nay S.M. 1995. Rapid soil development after windthrow disturbance in pristine forests. *Journal of Ecology* 83: 747–757.

Borujeni I.E., Mohammadi J., Salehi M.H., Toomanian N., Poch R.M. 2010. Assessing geopedological soil mapping approach by statistical and geostatistical methods: a case study in the Borujen region, central Iran. *Catena* 82: 1–14.

Bremner J.M. 1996. Nitrogen-total. In: Sparks (Ed.), Methods of soil analysis. Part 3. Chemical methods. Number 5 in Soil Science Society of America Book Series. Soil Science Society of America, Inc. and American Society of Agronomy, Madison, Wisconsin, pp. 1085–1121.

Buurman P. (Ed.) 1984. Podzols. Van Nostrand Reinhold Soil Science Series. New York, USA.

Buurman P., Jongmans A.G. 2005. Podzolization and soil organic matter dynamics. *Geoderma* 125: 71–83.

Chen Y., Senesi N., Schnitzer M. 1977. Information provided on humic substances by E4/E6 ratios.

Soil Science Society of America Journal 41: 352–358.

Corenblit D., Baas A.C.W., Bornette G., Darrozes J., Delmotte S., Francis R.A., Gurnell A.M., Julien F., Naiman R.J., Steiger J. 2011. Feedbacks between geomorphology and biota controlling earth surface processes and landforms: a review of foundation concepts and current understandings. *Earth-Science Reviews* 106: 307–331.

Courchesne F., Turmel M.C. 2008. Extractable Al, Fe, Mn and Si. In: Carter M.R., Gregorich E.G. (Eds.), Soil Sampling and Methods of Analysis, 2nd ed. Canadian Society of Soil Science, CRC Press, pp. 307–315.

Cremeans D.W., Kalisz P.J. 1988. Distribution and characteristics of windthrow microtopography on the Cumberland Plateau of Kentucky. *Soil Science Society of America Journal* 52: 816–821.

Drábek O., Borůvka L., Mládková L., Kočárek M. 2003. Possible method of aluminium speciation in forest soils. *Journal of Inorganic Biochemistry* 97: 8–15.

Drábek O., Mládková L., Borůvka L., Száková J., Nikodem A., Němeček K. 2005. Comparison of water-soluble and exchangeable forms of Al in acid forest soils. *Journal of Inorganic Biochemistry* 99: 1788–1795.

Fiedler S., Kalbitz K. 2003. Concentrations and properties of dissolved organic matter in forest soils as affected by the redox regime. *Soil Science* 168: 793–801.

Gillman G.P., Sumpter M.E. 1986. Modification of the compulsive exchange method for measuring exchange characteristics of soils. *Australian Journal of Soil Research* 17: 61–66.

Grand S., Lavkulich M. 2013. Potential influence of poorly crystalline minerals on soil chemistry in Podzols of southwestern Canada. Eur. J. *Soil Science* 64: 651–660.

Gruba P., Mulder J. 2015. Tree species affect cation exchange capacity (CEC) and cation binding properties of organic matter in acid forest soils. *Science of the Total Environment* 511: 655–662.

Guest C.A., Schulze D.G., Thompson I.A., Huber D.M. 2002. Correlating manganese X-ray absorption near-edge structure spectra with extractable soil manganese. *Soil Science Society of America Journal* 66: 1172–1181.

ISO 1995. ISOIDIS 14235. Soil quality. In: Determination of Organic Carbon in Soil by Sulfochromic Oxidation. International Organization for Standardization, Berlin, Vienna and Zurich.

Janík D., Král K., Adam D., Hort L., Šamonil P., Unar P., Vrška T. 2016. Tree spatial patterns of *Fagus sylvatica* expansion over 37 years. *Forest Ecology and Management* 375: 134–145.

Johnson D.L., Watson-Stegner D. 1987. Evolution model of pedogenesis. *Soil Science* 143: 349–366.

Johnson D.L., Keller E.A., Rockwell T.K. 1990. Dynamic pedogenesis: new views on some key soil concepts, and a model for interpreting quaternary soils. *Quaternary Research* 33: 306–319.

Kabrick J.M., Clayton M.K., McBratney A.B., McSweeney K. 1997. Cradle-knoll patterns and characteristics on drumlins in northeastern Wisconsin. *Soil Science Society of America Journal* 61: 595–603.

Klinka K., Fans J., Krestov P. 1997. Towards a Taxonomic Classification of Humus Forms; Third Approximation. Scientia Silvica, Extension Series No. 9. Forestry Sciences Department, The University of British Columbia, Vancouver.

Kramer M.C., Sollins P., Sletten R.S. 2004. Soil carbon dynamics across a windthrow disturbance sequence in southeast Alaska. *Ecology* 85: 2230–2244.

Lundström U.S., van Breemen N., Bain D. 2000. The podzolization process. A review. *Geoderma* 94: 91–107.

Manly B.F.J. 2006. Randomization, Bootstrap and Monte Carlo Methods in Biology. CRC Press.

McKeague J.A., Brydon J.E., Miles N.M. 1971. Differentiation of forms of extractable ion and aluminum in soils. *Soil Science Society of America Proceedings* 35: 33–38.

McKeague J.A., Ross G.J., Gamble D.S. 1978. Properties, criteria of classification and concept of genesis of podzolic soils in Canada (55-60 pp). In: Mahaney W.C. (Ed.), Quaternary soils. Third York Quaternary Symposium, Toronto 1976, Geo Abstracts Ltd., Norwich, England.

Michéli E., Schad P., Spaargaren O. 2007. World Reference Base for Soil Resources 2006, First Update 2007. World Soil Resources Reports No 103. FAO, Rome.

Milan H., Garcia-Formaris I., Gonzalez-Posada M. 2009. Nonlinear spatial series analysis from unidirectional transects of soil physical properties. *Catena* 77: 56–64.

Nakashizuka T. 1989. Role of uprooting in composition and dynamics of an oldgrowth forest in Japan. *Ecology* 70: 1273–1278.

Němeček K., Mühlhanselová M., Macků J., Vokoun J., Vavříček D., Novák P. 2011. Taxonomický klasifikační systém půd České republiky. Česká zemědělská univerzita, Praha.

von Oheimb G., Friedel A., Bertsch A., Härdtle W. 2007. The effects of windthrow on plant species richness in a Central European beech forest. *Plant Ecology* 191: 47–65.

Pai C.W., Wang M.K., Zhuang S.Y., King H.B. 2004. Free and non-crystalline fe-oxides to total iron concentration ratios correlated with 14C ages of three forest soils in central Taiwan. *Soil Science* 169: 582–589.

Palmer M.W., McAlister S.D., Arévalo J.R., DeCoster J.K. 2000. Change on the understory during 14 years following catastrophic windthrow in two Minnesota forests. *Journal of Vegetation Science* 11: 841–854.

Pawlik, Ł., Migoń P., Szymanovski M. 2016a. Local- and regional-scale biomorphodynamics due to tree uprooting in semi-natural and managed montane forests of the Sudetes Mountains, Central Europe. *Earth Surface Processes and Landforms* 41: 1250–1265.

Pawlik, Ł., Phillips J.D., Šamonil P. 2016b. Roots, rock, and regolith: biomechanical and biochemical weathering by trees and its impact on hillslopes – a critical literature review. *Earth-Science Reviews* 159: 142–159.

Peckham S.D. 2009. Geomorphometry and spatial hydrologic modeling. *Developments in Soil Science* 33: 579–602.

Peres-Neto P.R., Legendre P., Dray S., Borcard D. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87: 2614–2625.

Phillips J.D. 1993. Chaotic evolution of some coastal plain soils. *Physical Geography* 14: 566–580.

Phillips J.D. 2000. Signatures of divergence and self-organization in soils and weathering profiles. *Journal of Geology* 108: 91–102.

Phillips J.D. 2001. Divergent evolution and the spatial structure of soil landscape variability. *Catena* 43: 101–113.

Phillips J.D. 2008. Soil system modelling and generation of field hypotheses. *Geoderma* 145: 419–425.

Phillips J.D. 2013a. Nonlinear dynamics, divergent evolution, and pedodiversity. In: Ibanez J.J., Bockheim J. (Eds.), Pedodiversity. CRC Press, Boca Raton, FL, pp. 59–82.

Phillips J.D. 2013b. Sources of spatial complexity in two coastal plain soil landscapes. *Catena* 111: 98–103.

Phillips J.D. 2013c. Networks of historical contingency in Earth surface systems. *Journal of Geology* 121: 1–16.

Phillips J.D., Marion D.A. 2004. Pedological memory in forest soil development. *Forest Ecology and Management* 188: 363–380.

Phillips J.D., Marion D.A. 2006. Biomechanical effects of trees on soil and regolith: beyond treethrow. *Annals of the American Association of Geographers* 96: 233–247.

Phillips J.D., Van Dyke C. 2016. Principles of geomorphic disturbance and recovery in response to storms. *Earth Surface Processes and Landforms* 41: 971–979.

Phillips J.D., Šamonil P., Pawlik L., Trochta J., Daněk P. 2017. Domination of hillslope denudation by tree uprooting in an old-growth forest. *Geomorphology* 276: 27–36.

Pickett S.T.A., White P.S. (Eds.) 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, San Diego.

R Core Team 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Austria, Vienna URL. http://www.R-project.org/

Šamonil P., Král K., Douda J., Šebková B. 2008a. Variability in forest floor at different spatial scales in a natural forest in the Carpathians: effect of windthrows and mesorelief. *Canadian Journal of Forest Research* 38: 2596–2606.

Šamonil P., Šebková B., Douda J., Vrška T. 2008b. Role of position within the windthrow in forest floor chemistry in the flysch zone of the Carpathians. *Canadian Journal of Forest Research* 38: 1646–1660.

Šamonil P., Antolík L., Svoboda M., Adam D. 2009. Dynamics of windthrow events in a natural fir-beech forest in the Carpathian mountains. *Forest Ecology and Management* 257: 1148–1156.

Šamonil P., Král K., Hort L. 2010a. The role of tree uprooting in soil formation: a critical literature review. *Geoderma* 157: 65–79.

Šamonil P., Tejnecký V., Borůvka L., Šebková B., Janík D., Šebek O. 2010b. The role of tree uprooting in Cambisol development. *Geoderma* 159: 83–98.

Šamonil P., Valtera M., Bek S., Šebková B., Vrška T., Houška J. 2011. Soil variability through spatial scales in a permanently disturbed natural spruce-fir-beech forest. *European Journal of Forest Research* 130: 1075–1091.

Šamonil P., Schaetzl R.J., Valtera M., Goliáš V., Baldrian P., Vašíčková I. 2013. Crossdating of disturbances by tree uprooting: can treethrow microtopography persist for 6,000 years? *Forest Ecology and Management* 307: 123–135.

Šamonil P., Vašíčková I., Daněk P., Janík D., Adam D. 2014. Disturbances can control fine-scale pedodiversity in old-growth forest: is the soil evolution theory disturbed as well? *Biogeosciences* 11: 5889–5905.

Šamonil P., Daněk P., Schaetzl R.J., Vašíčková I., Valtera M. 2015. Soil mixing and evolution as affected by tree uprooting in three temperate forests. *European Journal of Soil Science* 66: 589–603.

Šamonil P., Valtera M., Schaetzl R.J., Adam D., Vašíčková I., Daněk P., Janík D., Tejnecký V. 2016. Impacts of old, comparatively stable, treethrow microtopography on soils and forest dynamics in the northern hardwoods of Michigan, USA. *Catena* 140: 55–65.

Schaetzl R.J. 1996. Spodosol-Alfisol intergrades: bisequal soils in NE Michigan, USA. *Geoderma* 74: 23–47.

Schaetzl R.J. 1986. Complete soil profile inversion by tree uprooting. *Physical Geography* 7: 181–189.

Schaetzl R.J. 1990. Effects of treethrow microtopography on the characteristics and genesis of Spodosols, Michigan, USA. *Catena* 17: 111–126.

Schaetzl R.J., Follmer L.R. 1990. Longevity of treethrow microtopography: implications for mass wasting. *Geomorphology* 3: 113–123.

Schaetzl R.J., Rothstein D. 2016. Temporal variation in the strength of podzolization as indicated by lysimeter data. *Geoderma* 282: 26–36.

Schaetzl R.J., Thompson M.L. 2015. Soil Genesis and Geomorphology, 2nd ed. Cambridge Univ., Press, Cambridge, USA (778 pp).

Schaetzl R.I., Burns S.F., Johnson D.L., Small T.W. 1989. Tree uprooting: review of impacts on forest ecology. *Vegetatio* 79: 165–176.

Schaetzl R.J., Luehmann M.D., Rothstein D. 2015. Pulses of podzolization: the importance of spring snowmelt, summer storms, and fall rains on spodosol development. *Soil Science Society of America Journal* 79: 117–131.

Šebková B., Šamonil P., Valtera M., Adam D., Janík D. 2012. Interaction between tree species populations and windthrow dynamics in natural beech-dominated forest, Czech Republic. *Forest Ecology and Management* 280: 9–19.

Simon A., Gratzer G., Sieghardt M. 2011. The influence of windthrow microsites on tree regeneration and establishment in an old growth mountain forest. *Forest Ecology and Management* 262: 1289–1297.

Skvorcova E.B., Ulanova N.G. 1977. Certain aspects of the influence of blowdowns on a forest biogeocenoses. *Moscow University Soil Science Bulletin* 32 (1–5): 77–78.

Skvorcova E.B., Ulanova N.G., Basevic V.F. 1983. Ekologiceskaja rol vetrovalov. Lesnaja Promyslennost. Moskva, Russia.

Small T.W., Schaetzl R.J., Brixie J.M. 1990. Redistribution and mixing of soil gravels by tree uprooting. *Professional Geographer* 42: 445–457.

Sommer M., Halm D., Geisinger C. 2001. Lateral podzolization in a sandstone catchment. *Geoderma* 103: 231–247.

Stützer A. 1999. Podzolisation as a soil forming process in the alpine belt of Rondane, Norway. *Geoderma* 91: 237–248.

Szwagrzyk J., Czerwczak M. 1993. Spatial patterns of trees in natural forests of East-Central Europe. *Journal of Vegetation Science* 4: 469–476.

Tanskanen N., Ilvesniemi H. 2004. The amount of secondary Al in two ploughed podzolic forest soils. *Geoderma* 119: 249–260.

Tejnecký V., Šamonil P., Matys Grygar T., Vašát R., Ash C., Drahota P., Šebek O., Němeček K., Drábek O. 2015. Transformation of iron forms during soil formation after tree uprooting in a natural beech-dominated forest. *Catena* 132: 12–20.

Titeux H., Brahy V., Bruno D. 2002. Metal complexing properties of forest floor leachates might promote incipient podsolization in a Cambisol under deciduous forest. *Geoderma* 107: 93–107.

Toomanian N., Jalalian A., Khamedi H., Eghbal M.K., Papritz A. 2006. Pedodiversity and pedogenesis in Zayandeh-rud valley, central Iran. *Geomorphology* 81: 376–393.

Vassenev I.I., Targulian V.O. 1995. Windthrow and Taiga Pedogenesis (regimes, processes, morphogenesis of soil successions). Nauka, Moscow. Russia.

Walker L.R., Wardle D.A., Bargett R.D., Clarkson B.D. 2010. The use of chronosequences in studies of ecological succession and soil development. *Journal of Ecology* 98, 725–736.

Zbíral J. 2002. Analýza půd I. Ústřední kontrolní a zkušební ústav zemědělský, Brno. Czech Republic.

Zbíral J. 2003. Analýza půd II. Ústřední kontrolní a zkušební ústav zemědělský, Brno, Czech Republic.

Zbíral J., Honsa I., Malý S., Čižmár D. 2004. Analýza půd III. Ústřední kontrolní a zkušební ústav zemědělský, Brno. Czech Republic.

von Zezscheitz E., Schwertmann U., Ulrich B. 1973. Die podsolierungsstadien von braunerden aus schieferschutt. *Zeitschrift für Pflanzenernährung und Bodenkunde* 136: 40–52.

Paper 3

Convergence, divergence or chaos? Consequences of tree trunk decay for pedogenesis and the soil microbiome in a temperate natural forest

Pavel Šamonil
Pavel Daněk
Petr Baldrian
Vojtěch Tláskal
Václav Tejnecký
Ondřej Drábek

Geoderma 376 (2020), 114499

Abstract

The biochemical effects of trees may significantly influence local pedogenesis as well as pedocomplexity, biodiversity and forest dynamics on both stand and landscape scales. One such effect is the decay of tree trunks, which is driven by organisms, and especially by the microbiome. Decomposition modifies soil formation, which due to the existence of many feedbacks affects the composition of the decomposer community. We aimed to uncover general trends in the evolution of Entic Podzols as well as individual trajectories of soil properties below decaying beech trunks in an old-growth mountain forest. In particular, we used mathematical models to distinguish soil convergence, divergence and chaotic behaviour to enhance a general theory of pedogenesis. We further aimed to calculate the depth and time of convergence if this scenario is prevailing in the study plot. Pedogenetic pathways were assessed regarding the changing composition of fungal and bacterial communities in soils to obtain a complex picture of the decaying trunk-soil microbiome system.

We sampled the decaying wood layer under 24 lying beech trunks and corresponding organic horizons on adjacent control microsites occupied by decaying beech leaves. At the same time we sampled underlying mineral soil horizons at both microsites (wood vs. leaves), all on Entic Podzols and granite (in total 192 soil samples). Individual trunk fall events were dated using precise dendrochronology, with the resulting chronosequence covering trunks lying for 8–52 years. We analysed decomposition processes (with a wide spectra of organic acids and ions analysed), soil chemistry (28 additional soil properties assessed), and the microbiome composition in both decaying organic matter and soils (relative abundances of the 200 most common bacterial and fungal OTUs analysed).

During the first stage of trunk decay, underlying Entic Podzols responded with a significant increase of nutrients, pH, and CEC, and the maximal divergence compared to control sites was reached between 12 and 60 years after the trunk fall. Subsequently, a majority of soil properties slowly converged over a few decades to match the soil properties of control sites. The modelled convergence point occurred at ages between 39 (SO_4^{2-}) and 229 (Al_w) years, with a median convergence time of 53 years. The majority of soil properties converged within 20 cm below the trunk, but mathematical models predicted footprints of some soil properties down to depths of ca 60 cm. In addition, 11 soil properties did not converge at any depth, and for some properties the models even diverged. Differences in bacterial and fungal communities between below-trunk and control positions were relatively minor. Pedochemical drivers of fungal and bacterial communities (nutrients content, N_{tot}, C_{ox}, Al, Fe, Mn forms) changed significantly in the mineral soil below trunks, and the microbiome partly reflected these depth-related changes. However, we propose that there is a threshold between organic and mineral soil horizons limiting the impacts of trunk decay and pedogenesis in changes to the microbiome.

P. Šamonil[a,b], *P. Daněk*[a,c], *P. Baldrian*[d], *V. Tláskal*[d], *V. Tejnecký*[e], *O. Drábek*[e]

[a] Department of Forest Ecology, The Silva Tarouca Research Institute, Brno, CZ [b] Department of Forest Botany, Dendrology and Geobiocoenology, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, CZ [c] Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, CZ [d] Laboratory of Environmental Microbiology, Institute of Microbiology of the Czech Academy of Sciences, Prague, CZ [e] Department of Soil Science and Soil Protection, Faculty of Agrobiology, Food and Natural Resources, Czech University of Life Sciences Prague, Prague, CZ

1 Introduction

Individual trees may locally accelerate, slow or redirect pedogenetic pathways. Trees affect soils via biomechanical processes such as root mounding (Hoffman & Anderson 2013), and biochemically through metabolism and body parts decay (Binkley & Giardina 1998). These are strong point impacts, but they can also be expressed at stand and landscape scales. Recent studies have suggested that tree influences may contribute to the exceptional but still weakly explained spatial pedocomplexity of some mountain forests (including the Žofinský Prales Reserve in the Czech Republic, where this study took place – Šamonil et al. 2014). The discovery of the significant effects of individual trees on soil evolution in landscapes has led to modifications of the evolutionary theory of pedogenesis (e.g. Phillips 2001, Phillips 2009, Roering et al. 2010, Šamonil et al. 2014). Pedocomplexity is closely interconnected with disturbance regimes, land use, and biodiversity (Nachtergale et al. 2002, Daněk et al. 2016), issues extending beyond life sciences to the whole of human society.

The decomposition of lying trunks is one of the characteristic biochemical influences of trees in soils in old-growth forests, where they may potentially be a source of local non-linearity in soil evolution and spatial pedocomplexity. For example, lying trunks cover approximately 4% of the area in Central European old-growth forests (e.g. Průša 1985). Due to ongoing tree mortality and gradual lying trunk decomposition, the underlying soils are constantly changing. However, the information remains in the soil memory, potentially for long time periods. Soil properties do not necessary homogenize in time and space. Examples of divergent or chaotic soil evolution have already been recognized (Phillips 2001, Šamonil et al. 2015, see below). Moreover, soils locally affected by trees influence the new generation of trees (Simon et al. 2011). The complex system of decaying wood – i.e. the community of decomposers and soils, with many hidden feedbacks – has still not been sufficiently described and requires further attention.

Current publications generally agree on the significant impact of decomposing trunks on soils, but they differ in their evaluations of the outcome of these processes. While for example Kayahara et al. (1998) and Dhiedt et al. (2019) described the positive effects of decomposing trunks on nutrient contents and increases in soil CEC, Spears & Lajtha (2004) found the opposite. Hence, additional studies are needed to obtain a more general picture of the process in various ecosystems. Pedogenetic studies have generally ignored the potentially important role of soil organisms such as fungi and bacteria in pedogenesis under lying tree trunks. We aimed to expand on the traditional pedogenetic approach by studying changes of the microbial community during beech trunk decay (see Mäkipää et al. 2017, Peršoh & Borken 2017) and a detailed analysis of the products of trunk decay affecting pedogenesis.

Both divergent soil development and deterministic chaos in soils (Phillips 2001) are significant alternatives to the traditionally accentuated soil convergence. Divergence or chaotic behaviour can be very local processes that take place on a fine spatial scale due to the influence of an individual tree, against the background of a general soil convergence in the landscape. But many other scenarios are possible. Potentially, only some soil properties may diverge while others converge. Such non-linear pedogenesis and the coexistence of different directions in evolutionary soil trajectories have not yet been given much scientific attention, although they may have a significant impact on the spatial complexity of soils and the dynamics of the whole forest landscape.

In our study we focused on the influence of decaying *Fagus sylvatica* L. trunks in a region of enormous soil complexity, where Entic Podzols represent the main soil unit. The aims of the study were (i) to determine individual evolutionary trajectories of soil properties and the general trends in soils under decomposing *Fagus sylvatica* trunks, (ii) to find evidence pointing to the convergence, divergence, or chaos in soils influenced by a trunk, and (iii) to calculate the depth and time of convergence if this process is predominant. Furthermore, we asked (iv) what is the composition of the soil microbiome along the gradient of trunk decay. The results should deepen our understanding of soil complexity sources in old-growth forests and, subsequently, a better understanding of the impacts of human forest management in mountain forest ecosystems when all trunks are removed.

2 Terminology

Within this study we refer to "convergent soil development" as the process where differences in studied soil properties decrease along a gradient of soil depth or along a gradient of time. We used a standard chronosequence approach, i.e. space-for-time substitution, to study the effect of age (e.g. Bockheim 1980). "Divergent development" is the opposite process where differences in soil quality increase along depth or time gradients (see Phillips 2001). Chaotic development represents a specific scenario of significantly increasing variance of a studied soil property without significant changes in its mean value (Phillips et al. 1996, Phillips 2006).

3 Material and methods

3.1 Study area

The research was carried out in the Žofínský Prales Reserve in the Novohradské Mts. (hereinafter Zofin). The reserve is located along an altitudinal gradient ranging between 735 and 830 m a.s.l. Mild NW slopes predominate. The bedrock is nearly homogeneous and consists of porphyritic and biotite granite (CGS 2019). Soils are characteristically podzolized, acidic, and sandy (Šamonil et al. 2011). Annual average temperature in Zofin is about 4.3 °C and annual average rainfall is about 704 mm (CHMU 2019). Plant communities can be most often classified into the association *Galio odorati-Fagetum*. Long-term forest dynamics are driven by fine scale disturbances with infrequent occurrences of severe winds or biotic disturbances (Šamonil et al. 2013a). *Fagus sylvatica* dominates in Zofin (62% of the volume of living trees), followed by *Picea abies* (34%). *Abies alba* and sporadic broadleaves (e.g. *Acer pseudoplatanus*, *Ulmus glabra*) represent 3% and 1% of the living tree volume, respectively.

3.2 Data collection – trunk selection

We sampled organic and mineral soil horizons on positions of decaying beech trunks and adjacent control positions (we call these positions "microsites"). To select appropriate beech trunks we used two extensive datasets:

- In total 3020 dendrochronological cores had been taken by a regular randomized approach through the whole reserve between 2008 and 2012 for the purpose of studying disturbance history (see details in Šamonil et al. 2013a). Here we focused on precise dendrochronological dating of lying beeches according to methodology by Šamonil et al. (2013b).

- A detailed soil map, with soils classified in 5 replications on each of 353 square plots of area 1958 m^2 (see details in Šamonil et al. 2011). Based on a total of 1765 shallow profiles and penetrations by a soil borer, we assessed the occurrence of soil units. For the purposes of this paper, we selected areas with predominantly Entic Podzols and disregarded areas occupied by other soils (Haplic Cambisols, Dystric Cambisols, Albic Podzols, Glesols, Stagnosols, Histosols, Fluvisols, Leptosols, IUSS Working Group WRB 2014)

These two data sources were interconnected by choosing a set of ca 50 beech trunks at different degrees of decomposition on the Entic Podzols, surrounded by cored trees. We dendrochronologically dated the death of each trunk with an accuracy of 1–5 years. Then, for soil and microbiology data, we chose 24 trunks with the highest degree of certainty in dating accuracy, evenly covering a gradient of ages from 8 to 52 years. The time since the tree death roughly corresponded with a stage of trunk decomposition. Trunks lying for 8 years were still compact and solid (i.e. hard at a 3-level classification by Průša 1985). while all trunks lying for more than 33 years occurred in final degree of decomposition (decayed according to Průša 1985). Trunks lying between 8 and 33 years appeared characteristically intermediately decomposed (partly rotten). Selected trunks were randomly distributed within the ForestGEO plot of area 25 ha, and the distance between two adjacent trunks usually exceeded 40 m.

3.3 Data collection – Soil sampling

At distances ¼ and ¾ along their length, soil samples were taken under each of 24 lying trunks in autumn 2015. In shallow excavated profiles, all soil horizons present were described in terms of soil morphology (Schoeneberger et al. 1998) and soils were classified according to the IUSS Working Group WRB (2014). Samples were taken from just under the decomposing trunks, the upper mineral A horizon, and at depths of 5 and 10 cm below the A horizon base. We call these deepest samples as Bs-upper and Bs-lower. Corresponding samples from the 2 sampling points below each trunk were merged. As a result, under each of the 24 trunks chosen for soil and microbiology analyses, 4 mixed samples were taken along the gradient of soil depth (including one sample from organic horizon, i.e. decaying trunk). The boundaries between organic and mineral horizons as well as the lower boundary of upper mineral A horizon were deliberately taken into account, and these horizons were not mixed with others to best determine the potential course of podzolization, which is initiated just below the A horizon. The thickness of the A horizon was most often 5 cm of sampling depth, so modifications of sampling depth were minor. Samples associated with trunk microsite are denoted by the symbol W – wood.

Control profiles were excavated 2 m away from the soil profiles under trunks, i.e. two control points close to each trunk. The sampling strategy and subsequent mixture of correspond samples were the same as with trunk microsites, except that the organic horizons did not represent decomposed wood, but decomposing leaves, with litter, fermented, and humification horizons (see Klinka et al. 1997, Jabiol 2013). Control samples are denoted by the symbol L – litter. A similar sampling scheme was used by Stutz et al. (2017). All samples were frozen immediately after sampling, and altogether 192 samples were taken for laboratory analysis. Bulk densities below the trunk were similar to those in control positions.

3.4 Laboratory analyses

3.4.1 Soil chemistry

The samples were dried at laboratory temperature and sieved through 2 mm sieves (except for analysis of low molecular mass organic acids, see below). Organic horizons were ground to this fraction. We focused on a wide spectrum of chemical soil characteristics: (i) First we were interested in characteristics associated with humification and the transformation of organic matter in soils. (ii) Second, we were interested in soil qualities expressing the degree of weathering and leaching processes, especially podzolization. (iii) Third, we determined soil properties suggesting the nutrition requirements of the organisms present.

Dry and homogenized samples were analysed according to the following procedures by Zbíral 2002, Zbíral 2003, Zbíral et al. 2004: active (pH_{H_2O}) and exchange (pH_{KCl}) soil reaction – 0.2 M KCl;; total organic C (Cox) – using a spectrophotometric approach after oxidation by H_2SO_4 + $K_2Cr_2O_7$; total N content according to Kjeldahl (Bremner 1996); exchangeable base cations Ca^{2+}, Mg^{2+}, K^+, Na^+, effective cation exchange capacity (CEC), base saturation (BS), and exchangeable acidity (Al+H) – all according to Gillman & Sumpter (1986; $BaCl_2$-compulsive exchange procedure, native pH). Concentrations of elements in the various liquid extracts were subsequently measured using a Specol 221 UV/VIS spectrophotometer and an atomic absorption spectrophotometer (GBC 932 AB Plus).

All mineral samples were analysed in terms of the contents of amorphous, labile and organically bound Fe, Al, Mn and Si forms by extraction methods. Whereas extracted Fe and Al can be classified into these three forms relatively reliably (Courchesne & Turmel 2008), for Si and Mn this division is less clear (Guest et al. 2002). Tejnecký et al. (2015) analysed the mineralogy of such extracts in detail using diffuse reflectance spectroscopy and voltammetry of microparticles. We used the approach of Drábek et al. 2003, Drábek et al. 2005 to determine contents of reactive-exchangeable and weakly organics bond forms. The labile forms were extracted in 0.5 M KCl (37.27 $g\,l^{-1}$) (1:10, v/w), and are indicated by the subscript "k" (Fe_k, Al_k, Mn_k, Si_k). 0.2 M acid ammonium oxalate (according to Courchesne & Turmel 2008 at a ratio of 0.25:10, w/v, pH 3) was used to detect the contents of the sum of exchangeable, organic and particularly amorphous forms. The amorphous forms are indicated by the subscript "ox" (Fe_{ox}, Al_{ox}, Mn_{ox}, Si_{ox}). Primarily organically bound forms were determined using extraction by $Na_4P_2O_7$ at pH 10 (Schnitzer et al. 1958); these are indicated by the subscript "p" (Fe_p, Al_p, Si_p, Mn_p).

Low molecular mass organic acids (LMMOA) in soils were analysed in samples that were thawed at laboratory temperature (25 °C) before water extraction for LMMOA analysis. Unfrozen samples represented a "fresh" state of actual soil moisture. These were subjected to a deionised water (conductivity $< 0.055\ \mu S\,cm^{-1}$, Crystal Adrona and simultaneously $< 2\ ng\,l^{-1}$ TOC) extraction (ratio soil/water 1:10 w/v, 1 h extraction on a reciprocal shaker at a stable laboratory temperature 20 °C). The suspension was then centrifuged at 4000 rpm for 10 min, then extracts were filtered through a 0.45 µm nylon membrane filter (Cronus Membrane Filter Nylon, GB). In aqueous extracts, the following chemical parameters were analysed: contents of LMMOA, inorganic anions by means of ion chromatography (IC; see details below), and contents of selected elements (Al_w, Ca_w, Fe_w, K_w, Mn_w, Mg_w) using an inductively-coupled plasma-optical emission spectrometer (ICP-OES; iCAP 7000, Thermo Scientific, USA). All results were recalculated using soil moisture to soil dry mass ($\mu mol\,kg^{-1}$ and $\mu eq\,kg^{-1}$).

Major LMMOA (lactate, acetate, formate, malate, oxalate and citrate) and inorganic (NO^{3-}, PO_4^{3-} and SO_4^{2-}) anions were determined by means of ion-exchange chromatography with suppressed conductivity using an ICS 1600 ion chromatograph (Dionex, USA) equipped with an IonPac AS11-HC (Dionex, USA) guard and analytical columns. The eluent composition was 1–35.2 mM KOH with a linear gradient 1–65 min (0.55 mM KOH min^{-1}); flow rate was set to 1 ml min^{-1}. Detailed descriptions of IC analyses were described in Hubova et al. (2018).

To suppress eluent conductivity, an ASRS 300 – 4 mm suppressor (Dionex, USA), and Carbonate Removal Device 200 (Dionex, USA) were used. Chromatograms were processed and evaluated using the software Chromeleon 6.80 (Dionex, USA). Standards were prepared from 1 g l^{-1} anion concentrates (Analytika, CZ and Inorganic Ventures, USA) and deionised water (conductivity < 0.055 µS cm^{-1}; Crystal Adrona, Latvia) in the range of 0.1–40 mg l^{-1}. Limits of detection were calculated from the 3:1 signal-to-noise ratio (Shabir 2003), and for determined organic acids the limits of detection were: 0.25 µmol l^{-1} for lactate, 0.46 µmol l^{-1} for acetate, 0.53 µmol l^{-1} for propionate, 0.27 µmol l^{-1} for formate, 0.55 µmol l^{-1} for butyrate, 0.28 µmol l^{-1} for malate, 0.23 µmol l^{-1} for tartrate, 0.43 µmol l^{-1} for maleate, 0.24 µmol l^{-1} for oxalate and 0.34 µmol l^{-1} for citrate.

3.4.2 DNA extraction and amplification

Organic and mineral samples were homogenized, weighed, freeze-dried and weighed again before DNA extraction. Total DNA was extracted in triplicates from 300 mg of sample material using a modified SK method (Sagova-Mareckova et al. 2008) and cleaned with a GeneClean Turbo Kit (MP Biomedicals, USA). Extracted and pooled DNA was then used as a template for the amplification of the hypervariable region V4 of the 16S rRNA gene using the barcoded primers 515F and 806R (Caporaso et al. 2012). Amplification of the fungal ITS2 region was performed using barcoded gITS7 and ITS4 (Ihrmark et al. 2012). PCR amplification of fungal and bacterial DNA was performed as described previously (Žifčáková et al. 2016). Amplicons were purified, pooled and sequenced on the Illumina MiSeq to obtain pair-end sequences of 2 × 250 bp.

Bacterial and fungal rRNA gene copies were quantified by qPCR using the 1108f and 1132r primers for bacteria (Wilmotte et al. 1993, Amann et al. 1995) and FR1 and FF390 primers for fungi (Prévost-Bouré et al. 2011). The fungal:bacterial rRNA gene ratio (F:B) was calculated by dividing rRNA gene copy numbers. To compare soils with deadwood communities we utilized sequence data of deadwood fungi and bacteria from the same trunks that were sampled and analysed as published previously (Baldrian et al. 2016, Tláskal et al. 2017), using the same laboratory procedures except for the use of the NucleoSpin Soil Kit (Macherey-Nagel, Germany) for duplicated DNA extraction from 200 mg of wood sample material.

3.5 Data processing

3.5.1 Pedogenetic pathway

To investigate the general effects of microsite (under wood versus the litter control) and sample depth in the whole data set, we used multidirectional direct linear redundancy analysis (RDA) in Canoco for Windows 4.5 software (Ter Braak and Šmilauer 2002). The lower amount of analysed soil properties in the uppermost organic horizons led to the fact that RDA analyses were calculated separately for organic and mineral soil. Significance of factors was tested separately for sample depth and microsite using a Monte Carlo test with 4999 permutations and variance partitioning approach. Data were standardized according to the "species" data (Ter Braak & Šmilauer

2002). Because we expected the importance of the decayed trunk to decrease in soils of increasing depth, we tested the microsite effects at individual sample depths.

One weakness of multidimensional analysis is the low plasticity of the models used, which was limiting mainly in uncovering the shapes of pedogenetic pathways. Therefore, we used linear mixed-effects models (LMM) to investigate detailed pathways in relation to the effect of the lying trunk, the effect of sampling depth, and the time the trunk had been decaying (time) on measured soil properties. When necessary, the dependent variable was log-transformed, and microsite nested within the site (i.e. site/microsite in LMM notation) was used as a random effect.

We first fitted a set of models without accounting for the effect of time. These included all 7 possible models with some or all of depth (taken as either a linear or a quadratic term), microsite and their interaction as explanatory variables. Furthermore, we considered a convergent model in which the value of a soil property differed between the two microsites at shallow depths, but with this difference decreasing with increasing soil depth there was no difference. We call this point where the difference disappears the convergence depth, and since it is not a linear model parameter it could not be estimated while fitting the LMM. Instead, we found the optimum value for this parameter within the interval 3–100 cm by minimizing the Akaike information criterion (AIC) of the model.

For models with the time variable included we considered two scenarios, convergence and a general trend. The convergent model assumed that there was no difference between the microsites at time zero (the moment of trunk fall) and any impact of the lying dead wood disappeared after a certain time (convergence time). We defined two convergent models, which differed in the development of the difference between the microsites between time zero and the convergence time. The development was either unimodal (modelled by a quadratic curve) or more complicated (a cubic curve). Similar to convergence depth, convergence time was determined as that for which the model reached the lowest AIC (with the interval 5–1000 years). The model for the general trend included a quadratic term of depth, a quadratic term of time and their interaction as explanatory variables. For convergence models the time variable for control microsites was set to the value of the convergence time (i.e. the optimum value in case of the final model or the one currently tested during optimization) while for general trend model it was set to zero (see Appendix A for the derivation of convergence models).

Performance of the models was measured by their AIC, which was increased by 2 for convergence models as a penalization for estimation of the convergence parameter. We first identified the best model among those that did not include time. Generally, we chose the one with the lowest AIC, but prioritized the convergence model if it was not significantly worse than the best model (i.e. its AIC was not more than 4 units higher than that of the best model; Burnham & Anderson 2004). In other words, we selected the convergence model unless there was substantial evidence against it. The reason for this is because of the assumption that the influence of the decaying log is indeed likely depth-limited, and thus this model is likely more pedologically relevant. A time-specific model was considered only if it performed substantially better than the best depth-only model.

Confidence intervals (CI) for the convergence parameters (depth and time) were computed from 100 bootstrap resamples. For individual resampling units we took the complete data from each microsite pair (24 units in total). We report only those convergence parameters (and their confidence intervals) for which the optimization converged (a minimum AIC was found for some value within the target interval) and the optimum value was inside the confidence interval. These

CIs can be interpreted independently from the overall comparison of model performance based on AIC. Particularly in the case of time-specific models, it may happen that although the time-convergence model did not perform significantly better than the depth-only models, the CI for its time-convergence parameter could have been narrow. This means that although there was not a universal pattern in the development of the soil after the decaying log started to influence it (the time variable itself was not significant), the period after which the soil returns to its initial condition could still be estimated. The narrower the CI, the more useful this estimate is.

We considered chaotic behaviour to be the situation when the development of a property could take any direction. This results in no universal temporal trend in the development of the differences between the below-trunk sample and the control but rather a clear increase in variance of these differences with time. We searched for evidence of this behaviour separately in each of the three depths (3, 8 and 13 cm) for each studied soil property using generalized least squares (GLS) models. For each case we fitted four GLS models with the observed difference between the below-trunk and control values as the dependent variable: 1) a null (intercept-only) model, 2) a linear-trend model with trunk age as an explanatory variable, 3) a null model with variance modelled as a power function of trunk age, and 4) a linear-trend model with age both as an explanatory variable and a covariate for modelling variance (the same as in model 3). Among these four models, chaotic behaviour corresponds to model 3, and we considered it plausible if this model performed significantly better than models 1 and 2, was not significantly outperformed by model 4, and the estimated power exponent for variance was positive. Again, a model was considered significantly better performing if its AIC was at least 4 units lower than that of a competing model. For LMM and GLS fitting we used the *nlme* package (Pinheiro et al. 2019) in R (R Core Team 2019).

3.5.2 Bioinformatic workflow and statistical analyses

The sequencing data were processed using SEED v 2.1.05 (Větrovský et al. 2018). Briefly, pair-end reads were merged using fastq-join (Aronesty 2013). Sequences with ambiguous bases were omitted, as were sequences with a mean quality score below 30. Chimeric sequences were detected using UCHIME implementation in USEARCH 8.1.1861 (Edgar 2010) and deleted, and sequences shorter than 200 bp were also removed. Filtered sequences were clustered using the UPARSE algorithm implemented in USEARCH 8.1.1861 (Edgar 2013) at a 97% similarity level. OTU construction was done together with previously published (Baldrian et al. 2016; Tláskal et al. 2017) sequences obtained from wood samples of proximal trunks to enable comparisons between mineral soil and wood inhabiting taxa. The most abundant sequences were taken as representative for each OTU. To assign taxonomy, the closest hits at a genus or species level were identified using BLASTn 2.5.0 against the Ribosomal Database Project (Cole et al. 2014) and GenBank databases. Sequences identified either as no hits or as nonbacterial/nonfungal were discarded. To assign putative ecological functions to fungal OTUs, fungal genera of the best hit were classified into ecophysiological categories (e.g., white-rot, brown-rot, saprotroph, yeast, ectomycorrhiza) based on the published literature. The definition of categories was the same as in (Tedersoo et al. 2014). Fungal OTUs not assigned to a genus with known ecophysiology and those assigned to genera with unclear ecophysiology remained unassigned. Sequence data have been deposited into the NCBI database under the accession number PRJNA558885.

Multivariate analysis of microbial abundance data with environmental variables was performed using *vegan* package 2.5–5 (Oksanen et al. 2019) in R 3.6.0 (R Core Team 2019). The function *adonis* was used to test for significant differences in community composition among compartments (WO – deadwood, LO – litter, WA – upper mineral A soil horizon below deadwood, LA – upper mineral A soil below the litter, WBs-upper – mineral soil 5 cm below A horizon in the deadwood microsite, LBs-upper – mineral soil 5 cm below the A horizon in litter microsite) based on the Hellinger distance of the datasets containing relative abundances of the 200 most abundant bacterial and fungal OTUs. Permutation in *adonis* was constrained to individual sites using the *strata* option to filter out possible spatial effects. Two-dimensional non-metric multidimensional scaling (NMDS) ordination analysis on Hellinger distances was performed in R with the package vegan and the function *metaMDS*. Environmental variables were fitted using the function *envfit* to the ordination diagram as vectors with 999 permutations. Square rooted values of variables with non-normal distribution were used for fitting. Only significant variables with high R^2 values were displayed in resulting plots. Differences at $p < 0.05$ were regarded as statistically significant. Microbial abundance (qPCR) was tested by a pairwise comparison of deadwood and litter at the corresponding site using a pairwise Wilcoxon test.

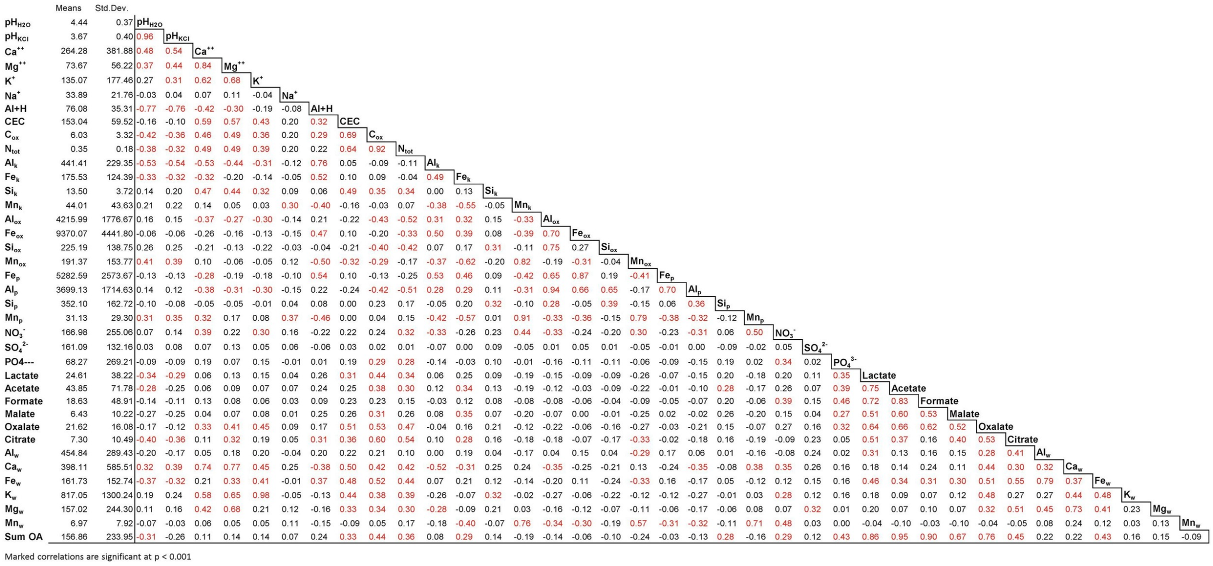
4 Results

4.1 Relationship between soil properties

Mean values and standard deviations of 38 soil properties show a general picture of acidic podzolized soils with a predominance of amorphous and organically bound fractions of Al and particularly Fe (Fig. 1). Cation exchange capacity was highly variable, generally weak, and dependent on the amount of organic matter in soils. The amount of organic C was relatively high. The concentrations of nutrients were changeable and generally low, with Ca the most common. Many soil properties were naturally correlated with each other (Fig. 1). The highest correlation (r = 0.98) was found between concentrations of K in the water extract, which imitates the soil solution and easily available forms, and available K^+ based on Gillman's approach. There was a correlation (r = 0.96) between active and exchangeable soil reaction values, but their large differences reflected a highly acidic soil environment. Many relations were statistically significant at $\alpha = 0.001$ (Fig. 1), and models of property behaviour in soil were also sometimes very similar (see below). As mentioned above, concentrations of base cations in the water extract (Ca_w, Mg_w, K_w) developed similarly as the concentrations of cations in standardized and the more powerful Gillman's extract. Concentrations of active, organically bound and amorphous forms of metals and metaloids gradually increased with increasing powerful extraction, and their models resembled each other (maximal correlation coefficients between these forms of elements were 0.28–0.94). This suggests that there was a similar proportion of forms in many samples. As expected there was a high correlation between C_{ox} and N_{tot} (r = 0.92) and between characteristics of the sorption complex.

4.2 Trunk decay

The multidirectional redundancy analysis revealed a significantly different chemical composition in decomposed trunks versus leaf material in the control profile (Table 1, Fig. 2). Trunks had a higher proportion of organic carbon but a lower proportion of total nitrogen; differences in the nitrogen anion NO^{3-} were minor. We also found higher values of active and exchange soil reaction and simultaneously lower concentrations of water-extracted Al and Fe (Al_w, Fe_w) in woody material compared to leaves. Concentrations of organic acids were slightly higher in wood as well,



	Means	Std.Dev.	pH$_{H2O}$	pH$_{KCl}$	Ca^{++}	Mg^{++}	K^{+}	Na^{+}	Al+H	CEC	C$_{ox}$	N$_{tot}$	Al$_{k}$	Fe$_{k}$	Si$_{k}$	Mn$_{k}$	Al$_{ox}$	Fe$_{ox}$	Si$_{ox}$	Mn$_{ox}$	Fe$_{p}$	Al$_{p}$	Si$_{p}$	Mn$_{p}$	NO$_3^-$	SO$_4^{2-}$	PO$_4^{3-}$	Lactate	Acetate	Formate	Malate	Oxalate	Citrate	Al$_{w}$	Ca$_{w}$	Fe$_{w}$	K$_{w}$	Mg$_{w}$	Mn$_{w}$
pH$_{H2O}$	4.44	0.37																																					
pH$_{KCl}$	3.67	0.40	0.96																																				
Ca^{++}	264.28	381.88	0.48	0.54																																			
Mg^{++}	73.67	56.22	0.37	0.44	0.84																																		
K^{+}	135.07	177.46	0.27	0.31	0.62	0.68																																	
Na^{+}	33.89	21.76	-0.03	0.04	0.07	0.11	-0.04																																
Al+H	76.08	35.31	-0.77	-0.76	-0.42	-0.30	-0.19	-0.08																															
CEC	153.04	59.52	-0.16	-0.10	0.59	0.57	0.43	0.20	0.32																														
C$_{ox}$	6.03	3.32	-0.42	-0.36	0.46	0.49	0.36	0.20	0.29	0.69																													
N$_{tot}$	0.35	0.18	-0.38	-0.32	0.49	0.49	0.39	0.20	0.22	0.64	0.92																												
Al$_{k}$	441.41	229.35	-0.53	-0.54	-0.53	-0.44	-0.31	-0.12	0.76	0.05	-0.09	-0.11																											
Fe$_{k}$	175.53	124.39	-0.33	-0.32	-0.32	-0.20	-0.14	-0.05	0.52	0.10	0.09	-0.04	0.49																										
Si$_{k}$	13.50	3.72	0.14	0.20	0.47	0.44	0.32	0.09	0.06	0.49	0.35	0.34	0.00	0.13																									
Mn$_{k}$	44.01	43.63	0.21	0.22	0.14	0.05	0.03	0.30	-0.40	-0.16	-0.03	0.07	-0.38	-0.55	-0.05																								
Al$_{ox}$	4215.99	1776.67	0.16	0.15	-0.37	-0.27	-0.30	-0.14	0.21	-0.22	-0.43	-0.52	0.31	0.32	0.15	-0.33																							
Fe$_{ox}$	9370.07	4441.80	-0.06	-0.06	-0.26	-0.16	-0.13	-0.15	0.47	0.10	-0.20	-0.33	0.50	0.39	0.08	-0.39	0.70																						
Si$_{ox}$	225.19	138.75	0.26	0.25	-0.21	-0.13	-0.22	-0.03	-0.04	-0.21	-0.40	-0.42	0.07	0.17	0.31	-0.11	0.75	0.27																					
Mn$_{ox}$	191.37	153.77	0.41	0.39	0.10	-0.06	-0.05	0.12	-0.50	-0.32	-0.29	-0.17	-0.37	-0.62	-0.20	0.82	-0.19	-0.31	-0.04																				
Fe$_{p}$	5282.59	2573.67	-0.13	-0.13	-0.28	-0.19	-0.18	-0.10	0.54	0.10	-0.13	-0.25	0.53	0.46	0.09	-0.42	0.65	0.87	0.19	-0.41																			
Al$_{p}$	3699.13	1714.63	0.14	0.12	-0.38	-0.31	-0.30	-0.15	0.22	-0.24	-0.42	-0.51	0.28	0.29	0.11	-0.31	0.94	0.66	0.65	-0.17	0.70																		
Si$_{p}$	352.10	162.72	-0.10	-0.08	-0.05	-0.05	-0.01	0.04	0.08	0.00	0.23	0.17	-0.05	0.20	0.32	-0.10	0.28	-0.05	0.39	-0.15	0.06	0.36																	
Mn$_{p}$	31.13	29.30	0.31	0.35	0.32	0.17	0.08	0.37	-0.46	0.00	0.04	0.15	-0.42	-0.57	0.01	0.91	-0.33	-0.36	-0.15	0.79	-0.38	-0.32	-0.12																
NO$_3^-$	166.98	255.06	0.07	0.14	0.39	0.22	0.30	0.16	-0.22	0.22	0.24	0.32	-0.33	-0.26	0.23	0.44	-0.33	-0.24	-0.20	0.30	-0.23	-0.31	0.06	0.50															
SO$_4^{2-}$	161.09	132.16	0.03	0.08	0.07	0.13	0.05	0.06	-0.06	0.03	0.02	0.01	-0.07	0.00	0.09	-0.05	0.01	0.05	0.01	-0.05	-0.01	0.00	-0.09	-0.02	0.05														
PO4---	68.27	269.21	-0.09	-0.09	0.19	0.07	0.15	-0.01	0.01	0.19	0.29	0.28	-0.14	-0.03	0.10	-0.01	-0.16	-0.11	-0.11	-0.06	-0.09	-0.15	0.19	0.02	0.34	0.02													
Lactate	24.61	38.22	-0.34	-0.29	0.06	0.13	0.15	0.04	0.26	0.31	0.44	0.34	0.06	0.25	0.09	-0.19	-0.15	-0.09	-0.09	-0.26	-0.07	-0.15	0.20	-0.18	0.20	0.11	0.35												
Acetate	43.85	71.78	-0.28	-0.25	0.06	0.09	0.07	0.07	0.24	0.25	0.38	0.30	0.12	0.34	0.13	-0.19	-0.12	-0.03	-0.09	-0.22	-0.01	-0.10	0.28	-0.17	0.26	0.07	0.39	0.75											
Formate	18.63	48.91	-0.14	-0.11	0.13	0.08	0.06	0.03	0.09	0.23	0.23	0.15	-0.03	0.12	0.08	-0.08	-0.08	-0.06	-0.04	-0.09	-0.05	-0.07	0.20	-0.06	0.39	0.15	0.46	0.72	0.83										
Malate	6.43	10.22	-0.27	-0.25	0.04	0.07	0.08	0.01	0.25	0.26	0.31	0.26	0.08	0.35	0.07	-0.20	-0.07	0.00	-0.01	-0.25	0.02	-0.02	0.26	-0.20	0.15	0.04	0.27	0.51	0.60	0.53									
Oxalate	21.62	16.08	-0.17	-0.12	0.33	0.41	0.45	0.09	0.17	0.51	0.53	0.47	-0.04	0.16	0.21	-0.12	-0.22	-0.06	-0.16	-0.27	-0.03	-0.21	0.15	-0.07	0.27	0.16	0.32	0.64	0.66	0.62	0.52								
Citrate	7.30	10.49	-0.40	-0.36	0.11	0.32	0.19	0.05	0.31	0.36	0.60	0.54	0.10	0.28	0.16	-0.18	-0.18	-0.07	-0.17	-0.33	-0.02	-0.18	0.16	-0.19	-0.09	0.23	0.05	0.51	0.37	0.16	0.40	0.53							
Al$_{w}$	454.84	289.43	-0.20	-0.17	0.05	0.18	0.20	-0.04	0.20	0.22	0.21	0.10	0.00	0.19	0.04	-0.17	0.04	0.15	0.04	-0.29	0.17	0.06	0.01	-0.16	-0.08	0.24	0.02	0.31	0.13	0.16	0.15	0.28	0.41						
Ca$_{w}$	398.11	585.51	0.32	0.39	0.74	0.77	0.45	0.25	-0.38	0.50	0.42	0.42	-0.52	-0.31	0.25	0.24	-0.35	-0.25	-0.21	0.13	-0.24	-0.35	-0.08	0.38	0.35	0.26	0.16	0.18	0.14	0.24	0.11	0.44	0.30	0.32					
Fe$_{w}$	161.73	152.74	-0.37	-0.32	0.21	0.33	0.41	-0.01	0.37	0.48	0.52	0.44	0.07	0.21	0.12	-0.14	-0.20	0.11	-0.24	-0.33	0.16	-0.17	0.05	-0.12	0.12	0.15	0.16	0.46	0.34	0.31	0.30	0.51	0.55	0.79	0.37				
K$_{w}$	817.05	1300.24	0.19	0.24	0.58	0.65	0.98	-0.05	-0.13	0.44	0.38	0.39	-0.26	-0.07	0.32	-0.02	-0.27	-0.06	-0.22	-0.12	-0.12	-0.27	-0.01	0.03	0.28	0.12	0.16	0.18	0.09	0.07	0.12	0.48	0.27	0.27	0.44	0.48			
Mg$_{w}$	157.02	244.30	0.11	0.16	0.42	0.68	0.21	0.12	-0.16	0.33	0.34	0.30	-0.28	-0.09	0.21	0.03	-0.16	-0.12	-0.07	-0.11	-0.06	-0.17	-0.06	0.08	0.07	0.32	0.01	0.20	0.07	0.10	0.07	0.32	0.51	0.45	0.73	0.41	0.23		
Mn$_{w}$	6.97	7.92	-0.07	-0.03	0.06	0.05	0.05	0.11	-0.15	-0.09	0.05	0.17	-0.18	-0.40	-0.07	0.76	-0.34	-0.30	-0.19	0.57	-0.31	-0.32	-0.11	0.71	0.48	0.03	0.00	-0.04	-0.10	-0.03	-0.10	-0.04	-0.05	0.08	0.24	0.12	0.03	0.13	
Sum OA	156.86	233.95	-0.31	-0.26	0.11	0.14	0.14	0.07	0.24	0.33	0.44	0.36	0.08	0.29	0.14	-0.19	-0.14	-0.06	-0.10	-0.24	-0.03	-0.13	0.28	-0.16	0.29	0.12	0.43	0.86	0.95	0.90	0.67	0.76	0.45	0.22	0.22	0.43	0.16	0.15	-0.09

Marked correlations are significant at $p < 0.001$

Fig. 1 Mean values, standard deviations and correlation coefficients in a correlation matrix of soil properties. The full data set was included; relationships of samples to microsite or horizon were not take into account in calculations. Marked correlations (red) are statistically significant at α = 0.001. For the coding of soil properties see Section 3.4.

while the concentration of PO_4^{3-} was slightly higher in leaf material. The mean time of convergence of the decaying trunk to the characteristics of the control profile was 40–50 years (Fig. 3c, see below).

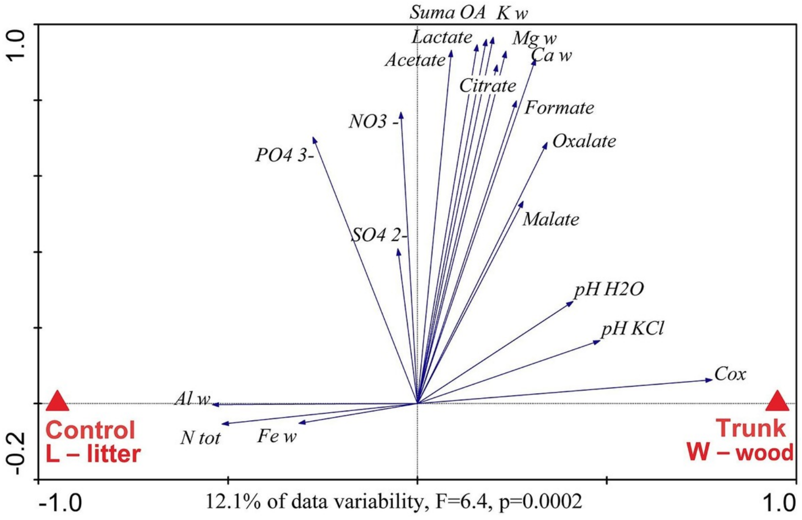


Fig. 2 The results of redundancy analysis focused on differences in the chemistry of decomposed *Fagus sylvatica* trunks and leafs in control profiles. Adjustment of analysis is visible in Table 1, coding of properties in Section 3.4.

4.3 General effects of microsite and sample depth in the mineral soil

The redundancy analysis (RDA) showed a significant role of microsite (wood versus litter) and sample depth in the mineral soil (Table 1, Fig. 4). The effect of microsite was significant in all horizons and depths, and slightly decreased along the gradient of sample depth. These results should be considered to be averages about the whole data set, and cannot be used to evaluate the

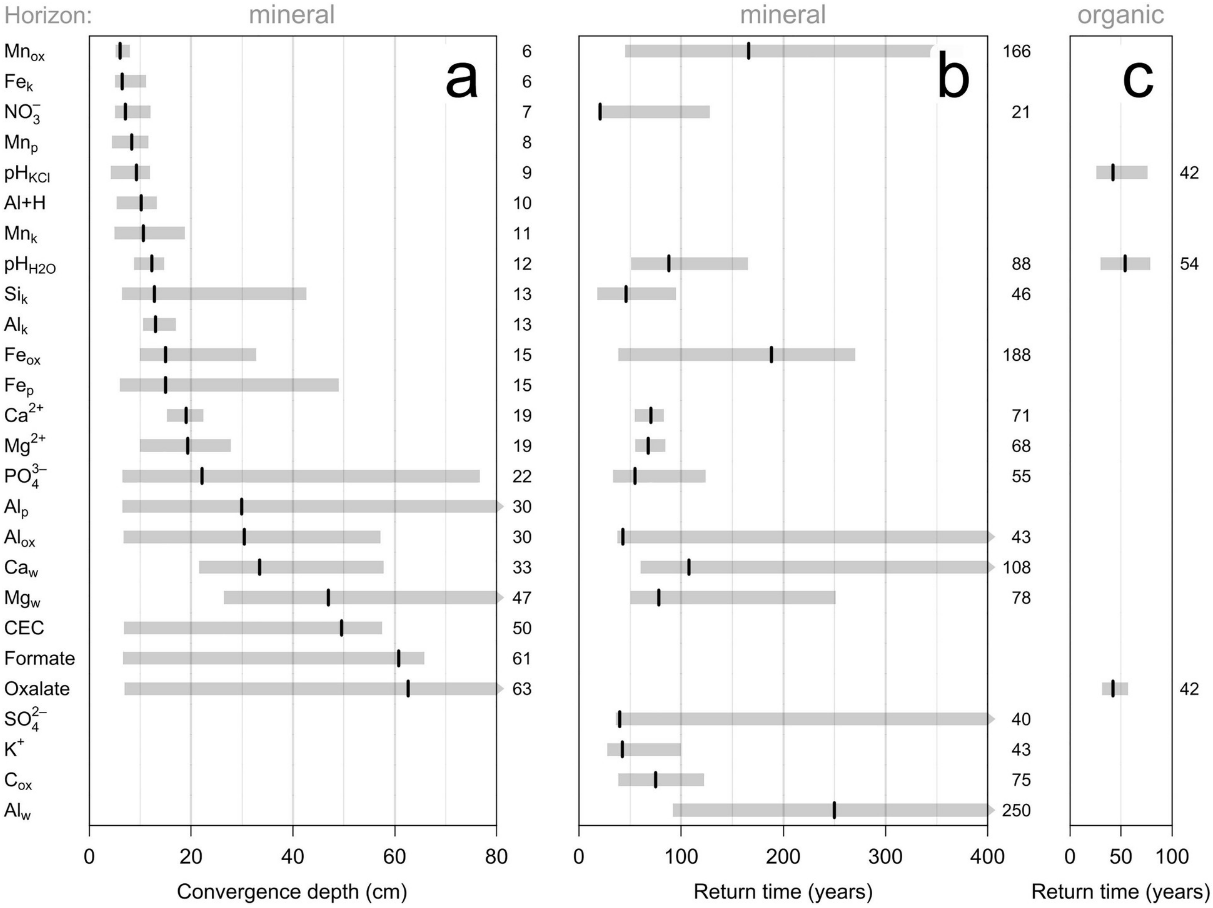


Fig. 3 Estimates of a) convergence depths (depth at which the difference in a measured soil characteristic between the soil under decaying trunks and control sites disappears) and return times (times after which values of a measured characteristic affected by decaying trunks return to the initial values) for b) mineral soil horizons and c) organic horizons. Vertical black bars show estimated mean values (displayed also numerically to the right of the plots) and horizontal grey bars give 95% confidence intervals.

detailed shape and range of individual soil properties. For that purpose, we calculated individual models (see below).

In general, individual characteristics developed predictably along the depth gradient (Fig. 4), following the transitions between organic, upper mineral A, and deeper spodic horizons. Soil characteristics of biogenic origin (C_{ox}, N_{tot}, organic acids etc.) decreased with sample depth. On the other hand, characteristics of rather geogenous origin (e.g. amorphous forms of Si, Al, Fe) increased with increasing sample depth. Increased values of active and exchangeable pH with sample depth was clearly related to a greater the decrease of exchangeable acidity, which was higher than the decrease in the concentration of basic cations bound to the low soil clay content, especially in organic matter. The cation exchange capacity decreased with the depth as well, which is in line with the decreasing concentrations of C_{ox}.

The mineral soil below the trunk generally had higher amounts of nutrients than control, especially very active forms found in the water extract (Fig. 4). The higher exchangeable acidity and higher concentration of Al in the KCl extract are naturally related. Soils affected by trunk decay also generally showed higher active and exchange soil reaction, cation exchange capacity, and concentrations of some organic acids (lactate, oxalate etc.).

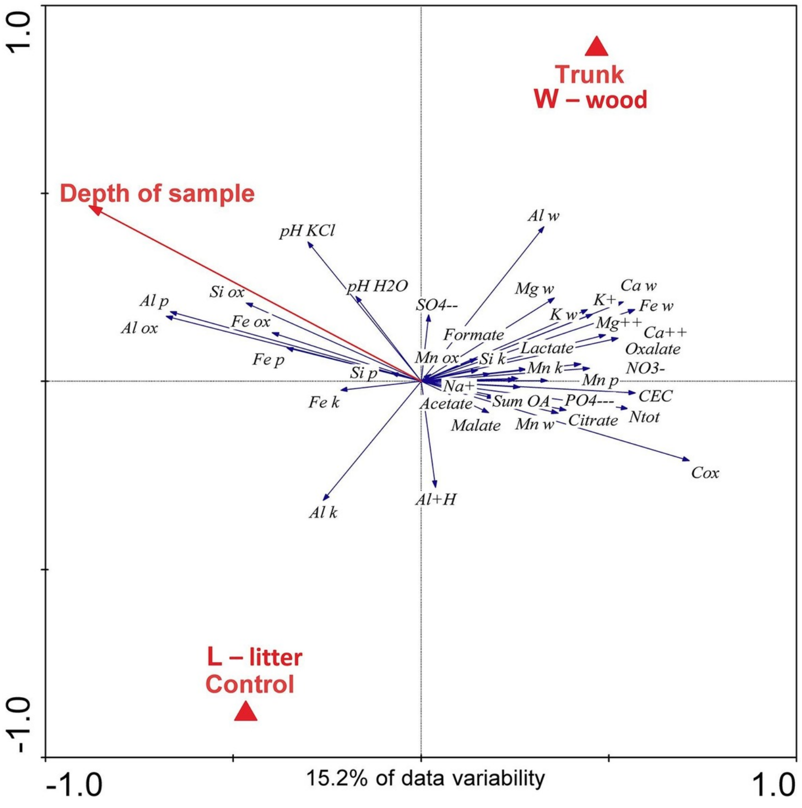


Fig. 4 The result of redundancy analysis focused on differences is mineral soils below decomposing trunks (W – wood) and control profiles (below leaf litter – L), and on the effect of sample depth in soil chemistry. Adjustment of analysis is visible in Table 1, coding of properties in Section 3.4.

4.4 Detailed pedogenetic pathways in the mineral soil

All 38 soil properties separately showed a significant relationship to the soil sample depth. The relation to microsite could be classified into 6 groups (Fig. 5). Only 5 soil properties showed no difference between the profile under the trunk and the control profile (group A in Fig. 5). These were amorphous and organically bound forms of Si, Na content and some organic acids. Some of these properties were found in very low concentrations across the entire dataset (Na, acetate, malate), and therefore it is not surprising that their models were insignificant. Concentrations of Si forms were not limiting, but more reflect geogenic factors and not the presence of lying trunks.

A total of 22 soil characteristics (58%) converged below the trunk at different depths towards the control values (groups B, C, D, F in Fig. 5). The model depths of convergence, along with the widths of the confidence intervals, are shown in Fig. 3a. For 7 chemical soil properties, values below the trunk were significantly higher than in the control and converged at a very low depth of about 10 cm (group B). These included the most active form of Si (Si_k), all evaluated forms of Mn, both types of soil reaction and NO^{3-}. Below, at depths between 19 and 65 cm, 8 characteristics converged (group C). Most of these were basic anions or cations of nutrients, effective CEC, and oxalate concentrations. A total of 7 soil characteristics were higher in the control profile than under the trunk. Five of them converged just below the trunk (group D), and included organically bound and amorphous forms of Fe, active Al, as well as exchangeable acidity. With the exception of the active Fe_k, which already converged in the A horizon, the other characteristics converged within a maximum of 13 cm depth. Organically bound and amorphous forms of Al were significantly lower under the trunk than in the control profile, and converged only at considerable depth (group F).

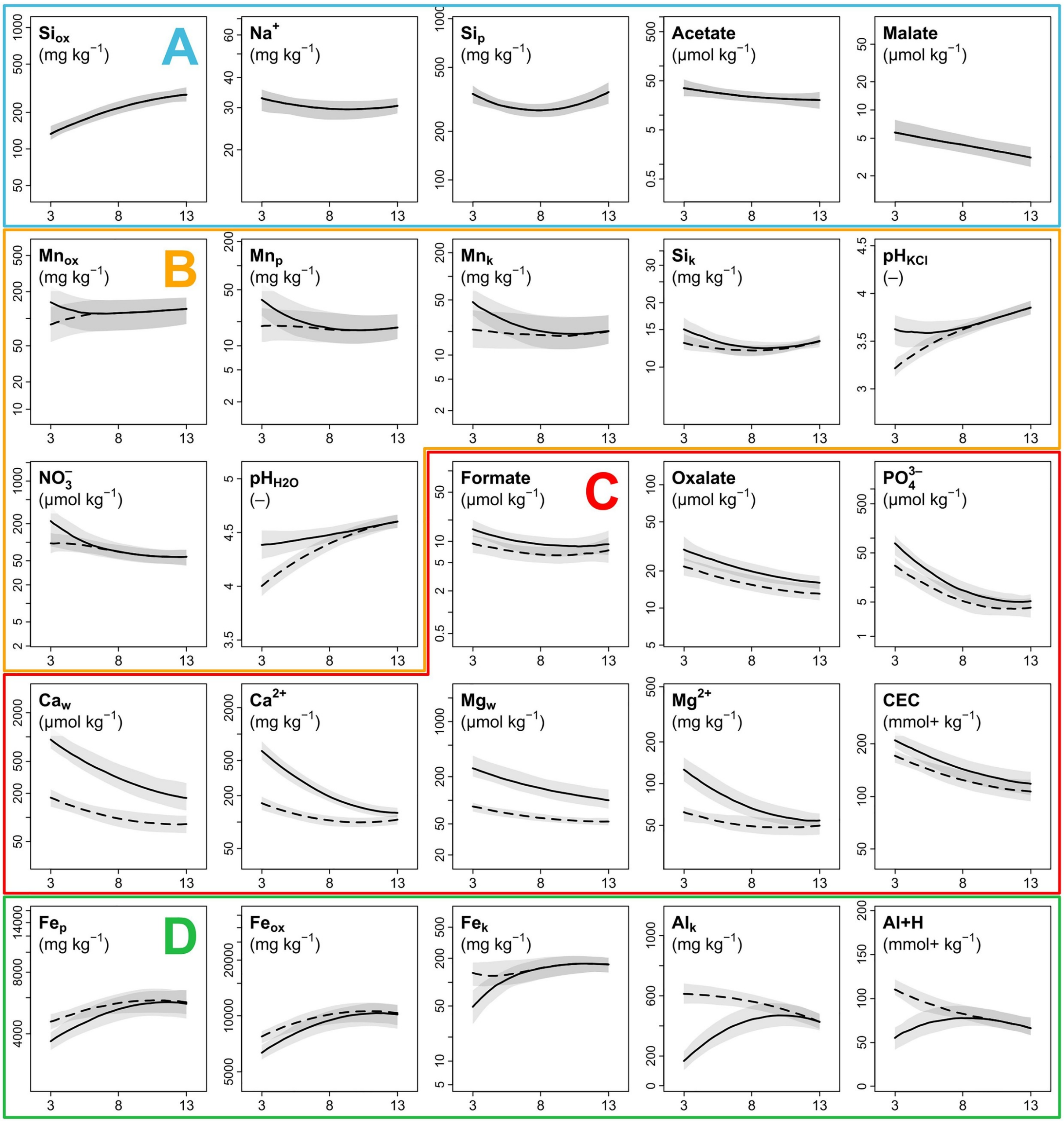


Fig. 5 Modelled values of soil characteristics with respect to soil depth. Lines of two types are shown if there were significantly different values under decaying trunks (solid line) and in control sites (dashed line). Grey areas surrounding the lines represent 95% confidence intervals.

Altogether, 11 soil properties did not converge at any depth, or the models even diverged. All of them were positively influenced by the presence of the trunk (group E in Fig. 5). These comprised organic C and N contents in soil, some organic acids as well as very mobile concentrations of nutrients (K) and metals (Fe$_W$, Al$_W$, Mn$_W$).

For 11 chemical soil properties, the age of the decomposing trunk was statistically significant, and it was possible to model the pedogenetic soil pathways in detail along the age and depth gradients (Fig. 6). With the exception of amorphous Al, all properties were very dynamic (contents of nutrient cations and anions, extracts with weakly aggressive agents – H_2O, KCl). Most of these characteristics belonged to groups B, C and E in Fig. 5, i.e. convergence models predom-

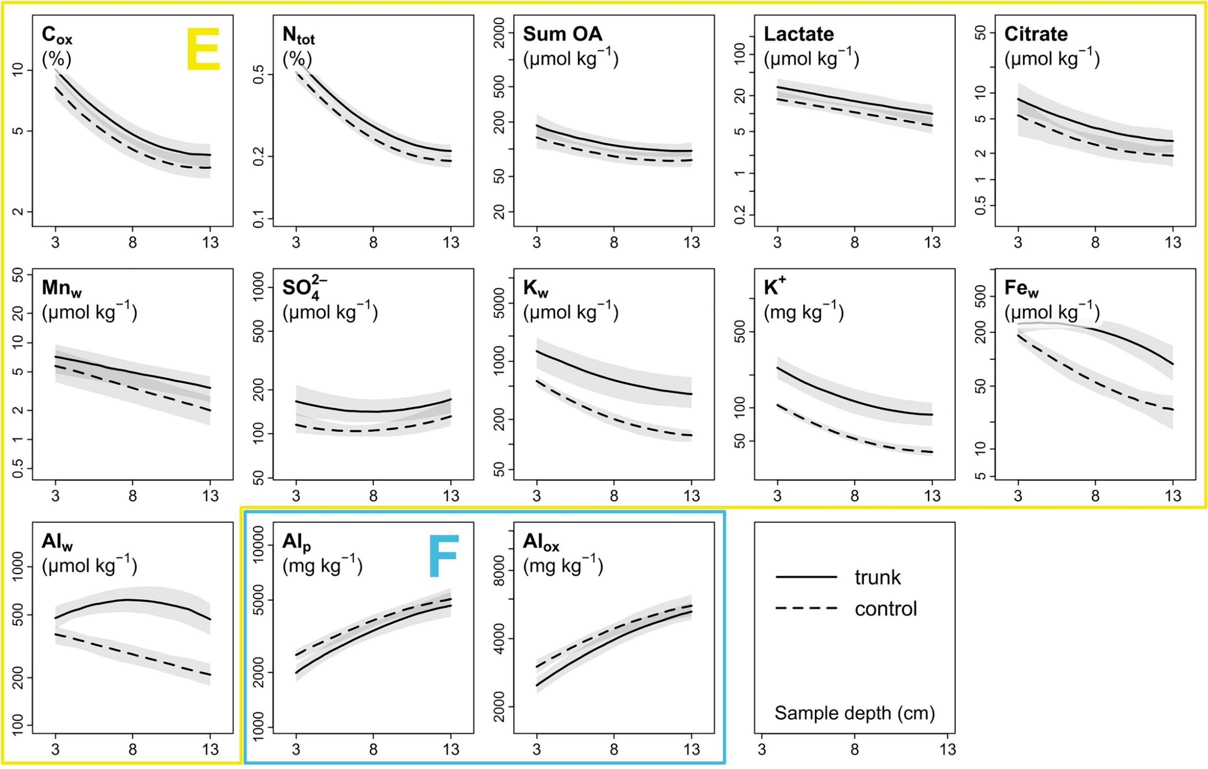


Fig. 5 *(continued)*

inated. With the decomposition of the trunk, these models showed a gradual deviation in the developmental trajectory from the control profile to stage of maximal divergence, and then usually convergence back to control values. The maximal divergence ranged between 12 and 60 years, averaging 25 years after the tree fall. The modelled convergence point back to the control values occurred at ages between 39 (SO_4^{2-}) and 229 (Al_w) years (Fig. 3b). This long-term response of water-extracted Al is quite surprising, considering the known seasonal variability of these forms. The median convergence time for analysed soil properties was 53 years.

We found only very limited evidence for chaotic behaviour in soil development. Only three property-depth combinations exhibited signs of chaotic development (Appendix B), and given that 114 tests were performed in total, these may have been just due to random results within the 5% Type I error rate. Furthermore, in all these three instances a well-fitting model with depth or age was found. Therefore, chaotic soil development under a decaying tree trunk does not appear to be a likely scenario.

4.5 Effects of deadwood on the microbiome composition

To explore the effects of changes in soil chemistry induced by deadwood decomposition, microbial communities were compared in decaying deadwood versus in leaf litter (i.e. two corresponding organic horizons), and in mineral soils under decomposing trunks versus under leaf litter. The communities of both fungi and bacteria in decaying leaves and wood were significantly different ($p < 0.0001$), with the wood community expressing a much higher composition variability than that in leaf litter (Fig. 7). Members of the bacterial order *Rhizobiales* genera *Rhodoplanes* and *Bradyrhizobium* were enriched in leaf litter (Fig. 8). The genera *Nitrospirillum* and *Steroidobacter* were abundant in wood.

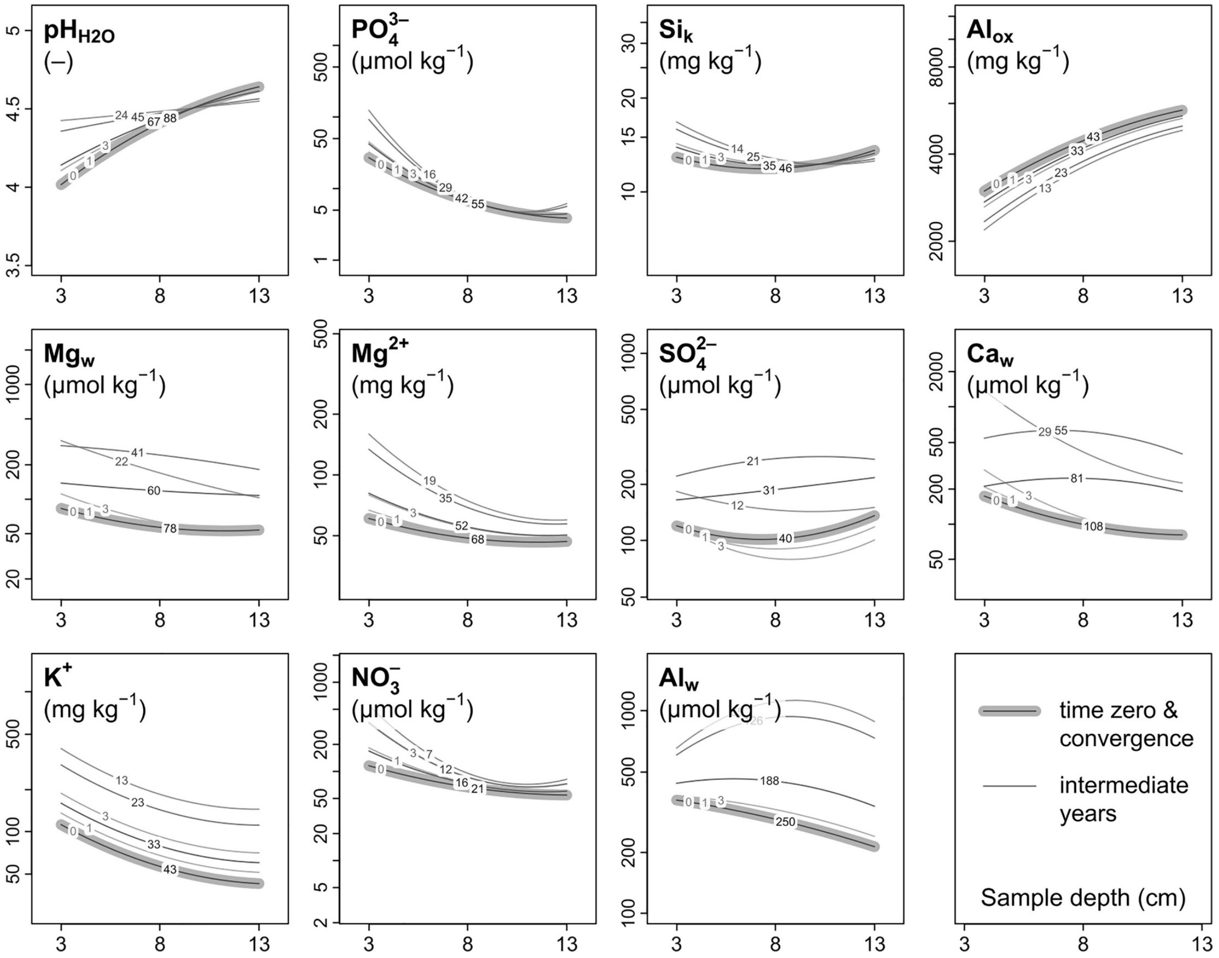


Fig. 6 Modelled values of soil characteristics with respect to soil depth and time of trunk decay. All models assume convergence, i.e. as the trunk decays the values start to change but eventually they return back to the state at time zero (thick line). The temporal progression of this process is depicted by thin lines marked with the time of decay (in years) to which they correspond.

Soil communities were dominated by Proteobacteria that represented around 50% of the whole community, followed by Actinobacteria, Firmicutes and Acidobacteria. The most abundant bacterial genera in soil were *Rhodoplanes* and *Halochromatium* (Fig. 8). Another genera enriched in soil in comparison with litter were *Beggiatoa* and *Thiogranum*. Importantly, bacterial communities were significantly different between soil horizons ($p = 0.001$, $R^2 = 0.131$), and this was consistent below both the trunk (W-wood) and the leaves (L, Fig. 9B). This horizon effect was stronger for bacteria than for fungi (see below). The effect of decomposing wood (sites under trunks versus under leaves) on bacterial community in mineral soils was significant as well ($p = 0.004$, $R^2 = 0.034$), and likely resulted from higher C and N availability under wood than under litter (Fig. 9B). However, the interaction of horizon and position effect was not significant. *Gammaproteobacteria* showed a preference for sites rich in Fe, while *Betaproteobacteria* occurred at higher pH at sites rich in Ca, Mg and Mn (Appendix C).

Fungal communities in decomposing wood and leaves were dominated by *Mycena, Megacollybia, Fomes, Hyphodontia, Ganoderma* and *Kretzschmaria*. Mineral soil horizons were rich in *Inocybe, Piloderma, Cenococcum* and *Amanita* (Fig. 8). In the soil below wood we did not find typical wood decomposers. Fungal communities in the A horizon and upper Bs horizon were significantly dif-

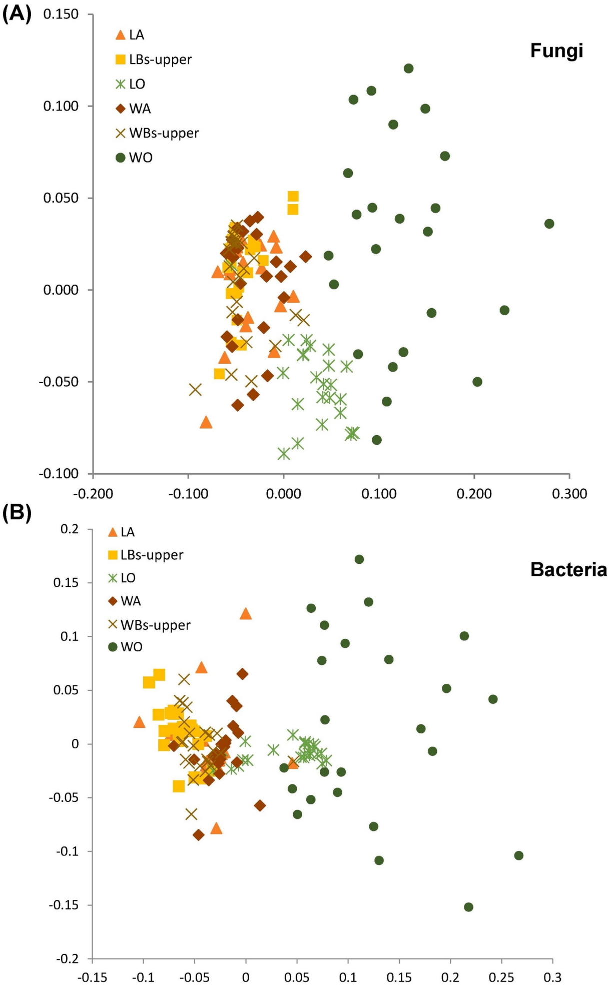


Fig. 7 Two-dimensional NMDS of fungal (A) and bacterial (B) communities in decomposing wood, litter and soil in Zofin. The dataset contained the top 200 OTUs of bacteria or fungi.

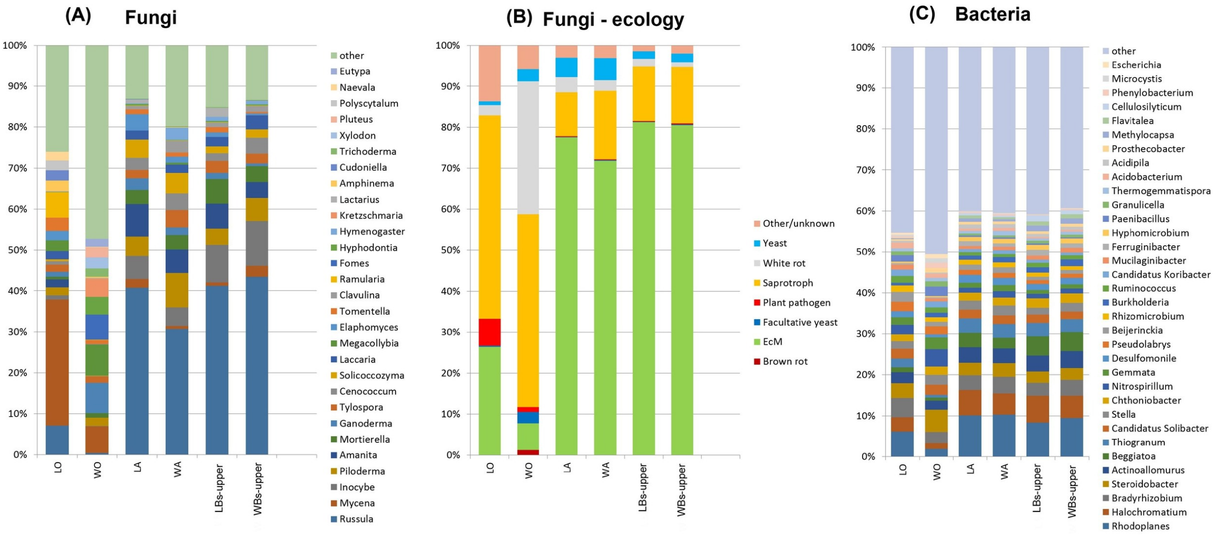


Fig. 8 Composition of fungal communities (A), fungal ecological groups (B) and bacterial communities (C) in decomposing wood, litter and soil in Zofin.

ferent (i.e. soil horizon effect, $p = 0.001$, $R^2 = 0.033$) as were those from the soil below the wood and below the litter (i.e. decomposing wood effect, $p = 0.001$, $R^2 = 0.022$, Fig. 9A) where difference in C and N availability was a strong driver of the microbial community. At the class level, fungal

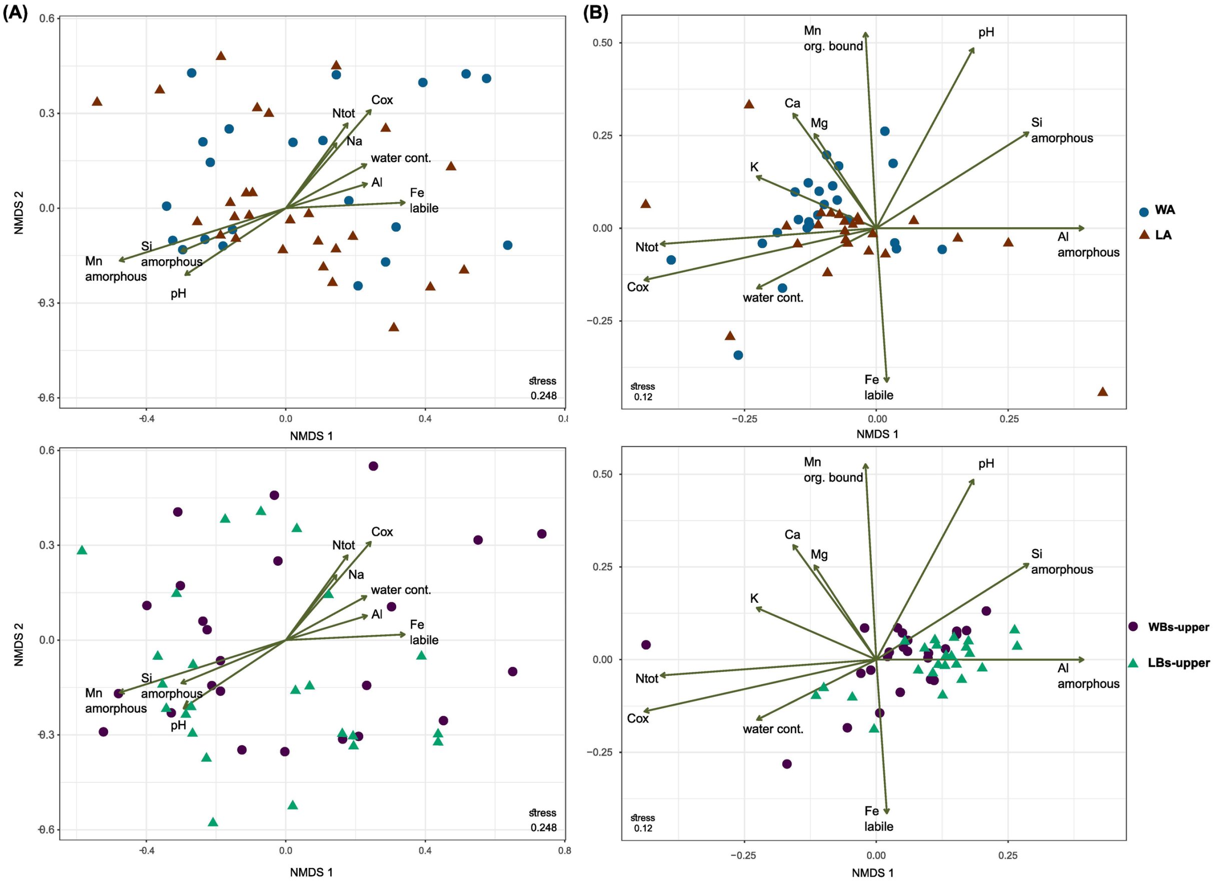


Fig. 9 Two-dimensional NMDS of microbial communities in soils of the A and Bs-upper horizons under litter and under wood in Zofin. The ordination of individual sites for fungi (A) and bacteria (B) are shown. The vectors show environmental variables with significant ordination to NMDS axes ($p <$ 0.05) and high R^2 values. Samples from both horizons are shown in separate panels for clarity.

taxa did not display a preference for sites with a higher content of some nutrient with the except of *Eurotimycetes* OTUs, which occurred preferentially at high pH sites rich in Si, Mn, C and N (Appendix C).

According to fitted nutrient concentrations onto the microbial multidimensional ordination, the composition of fungal communities was generally most influenced by the content of nutrients, C_{ox} and N_{tot}, but also by the concentrations of Mn, Al, Si, Fe and Na. Similarly, the composition of bacterial communities among individual microsites was driven by C_{ox}, N_{tot}, Mg^{2+}, Mn, K, Ca, Al, Fe, and Si (Fig. 9, Appendix D).

The content of fungal biomass was similar in wood and litter ($2.1 \times 10^8 \pm 0.3 \times 10^8$ of rDNA copies g^{-1} and $2.3 \times 10^8 \pm 0.8 \times 10^8$), and significantly higher than in soil where it ranged between $0.14 \times 10^8 \pm 0.02 \times 10^8$ and $0.26 \times 10^8 \pm 0.05 \times 10^8$); however, differences between A and Bs-upper horizons and between soils under litter and wood were not significant (Fig. 10). In bacteria, litter was most rich with $18.0 \times 10^8 \pm 1.8 \times 10^8$ of rDNA copies g^{-1}, while the fewest bacteria were found in deadwood ($2.7 \times 10^8 \pm 0.9 \times 10^8$). Soils harboured between $7.7 \times 10^8 \pm 0.5 \times 10^8$ and $9.9 \times 10^8 \pm 1.0 \times 10^8$ rDNA copies g^{-1}, and the differences between soils under litter and wood were not significant; the ratio of fungi and bacteria in soils was between 0.018 and 0.028 (Table 1).

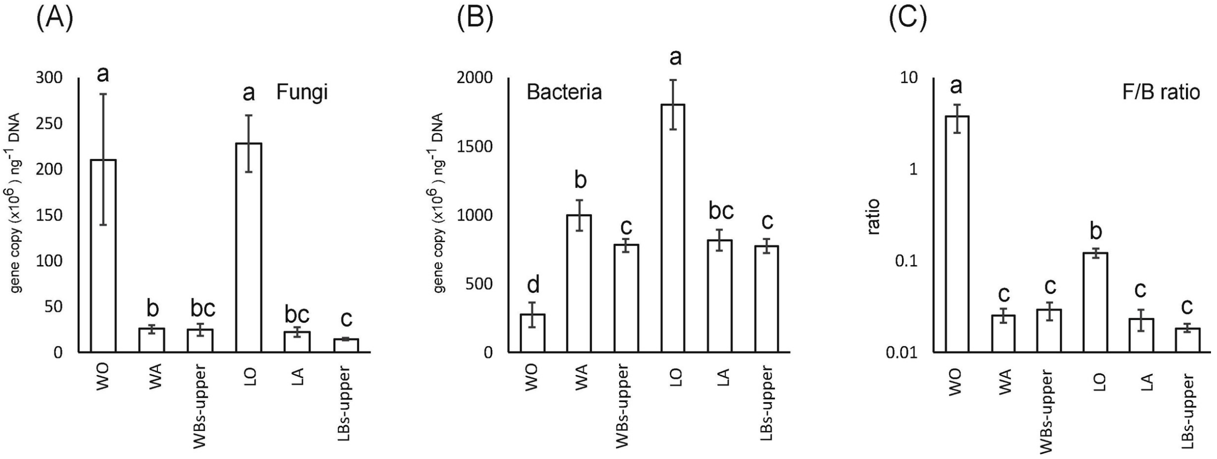


Fig. 10 Biomass content of A) fungi, B) bacteria and C) fungal/bacterial biomass ratio in decomposing wood, litter and soil in Zofin. The data show means and standard errors of counts (× 10^6) of A) 18S rRNA B) 16S rRNA gene copies in 1 ng of DNA.

Table 1 Adjustment of multidirectional redundancy analyses (RDA) and their results.

Environmental data	Covariable data	Soil layer	Average depth of sample (cm)	No. samples	No. soil properties	Explained variability (%)	p-value	F-value
Sample depth (cm)	Microsite	All mineral	3–13	144	38	13.1	< 0.001	21.3
Microsite	Sample depth	All mineral	3–13	144	38	6.2	< 0.001	9.6
Microsite		O horizont	0	48	20	12.1	< 0.001	6.4
Microsite		A harizont	3	48	38	15.4	< 0.001	8.0
Microsite		5 cm below A	8	48	38	8.5	< 0.001	4.3
Microsite		10 cm below A	13	48	38	6.7	0.004	3.3

5 Discussion

Along a gradient of weathering and leaching on acidic rocks in the temperate zone, Entic Podzols occupy a special position. From the point of view of pedogenesis, these are Podzols, soils with spodic horizons formed through the chemical destruction of clay particles and the gradual illuviation of organo-metallic complexes (Buurman & Jongmans 2005, Sauer 2007). However, from the perspective of the ecological role of soils in forest dynamics, these soils can be considered rather initial Cambisols than Podzols. In other words, the ecological role of soils in forest dynamics does not follow their genetic (and diagnostic) character in this case. Šamonil et al. 2015, Šamonil et al. 2018) found (during the research of biomechanical effects of trees due to tree uprooting) that Albic Podzols develop divergently after mechanical soil disturbances, but Haplic Cambisols develop convergently. From the viewpoint of typical genetic sequence of the soil evolution (with respect to more evolutionary trajectories, Huggett 1998), Entic Podzols appear roughly between Albic Podzols and Haplic Cambisols, and may express most the interesting responses to local mechanical or chemical disturbances. This was demonstrated by our current research here, where the majority of chemical soil properties expressed soil convergence but a significant proportion of properties developed in different or even opposite trajectories. Such a picture of opposing trajectories of soil properties was also described by Šamonil et al. 2015, Šamonil et al. 2018, who found podzolic horizon thicknesses exhibiting divergence in time, while chemical properties behaved convergently. These findings may supplement the traditional concept of soil evolution on the border between Cambisols and Podzols (see Schaetzl et al. 1994).

Using mathematical modelling we distinguished divergent, convergent and chaotic behaviors of individual soil properties. The majority converged by 25 cm below the decomposing trunk and during the first century after trunk fall. We expect that decreasing inputs of chemical compounds from gradually decomposing and shrinking beech trunk (potentially associated with changes in hydrological and microclimatological conditions, e.g. deadwood partly saturated by rainy water) and a still sufficient cation exchange capacity in Entic Podzols allowing the capture of the components drive pedogenetic convergence under deadwood. Unfortunately, as far as we know, comparable studies including detailed models with predictions of soil development do not exist. We can only generally support the results of Kayahara (1998), who found a positive effect of coniferous decaying trunks in the amount of nutrients in mineral soils (cf. Kayahara et al. 1996). A similar finding was observed by Dhiedt et al. (2019) below beech trunks on Umbrisols and Retisols in Belgium. In Cambisols in Germany, Stutz et al. (2017) found higher effective CEC, exchangeable Ca^{2+}, Mg^{2+}, and base saturation below beech trunks as well. The authors concluded that deadwood affects soil through the composition of added phenolic matter. We expect that beech deadwood produced more water extractable organic carbon (Stutz et al. 2019), and this DOC increased the mobility of Al and Fe. Also, higher contents of LMMOA under trunks consequently lead to lower contents of Al and Fe in soils (Hubová et al. 2018). These mentioned results are partly in contradiction with the conclusions of Spears & Lajtha (2004) concerning coniferous trunks on Andisols in Oregon, US. Similarly Goldin & Hutchinson (2013) described a rather acidifying effect of eucalyptus trunks on Regosols, Leptosols, Luvisols, and Solonetz in Australia. However, neither studied specific Entic Podzols below decaying *Fagus sylvatica* trunks. As suggested by Šamonil et al. (2018), it is likely that the resulting effect of a decomposing trunk is very dependent on the particular soil-forming process, notably the soil's ability to absorb the released nutrients and organic compounds. Entic Podzols in Zofin still retain this ability although continuing podzolization was evident. Entic Podzols are sensitive to biochemical tree influences, which may temporarily increase spatial soil complexity on local scales in forested landscapes.

The unimodal course of exchangeable acidity, Fe forms and active Al in the water extract, as well as the correlation between LMMOA and Fe forms (Fig. 1), may all indicate podzolization with an initiation of the illuviation of organo-metallic complexes under trunks. This process originates at the base of the A-horizon, in our case at an average depth of 8 cm. However, the evolution of the eluvial and illuvial horizons was not yet evident, because the dynamics of other soil properties did not follow this suggested trend. The soil was already podzolized but still had the ability to bind larger amounts of substances released during trunk decomposition. Nonetheless, the significant depths at which some characteristics converged to the control values (see below) as well as the non-convergent development of others (e.g. C_{ox}) strongly suggest that the ability of Entic Podzols to absorb released substances from trunks was relatively low. There was a clear movement of chemical compounds (e.g. LMMOA) produced by trunk decay to deeper soil horizons.

The biomass of both fungi and bacteria in soils was generally similar below the trunks and leaves, suggesting that leaching nutrients from decomposing wood does not support the growth of microorganisms to higher densities than in the surrounding soil. Despite the effects of decomposing trunks on soil properties, we found their effects on the microbial community composition to be minor. This is similar to that found in a comparison of fungi under litter and decomposing *Picea abies* trees in Finland, which were, however, distinctly different and showed soil colonization by wood-associated fungi (Mäkipää et al. 2017). While there were a few taxa with a preference for sites with higher concentrations of leached nutrients, most taxa did not show such preference. This is in contrast with the impact of living trees, which actively transfer exudates to underlying microbial communities and where fungi are determined by tree species and bacteria show a preference for particular rhizosphere habitats (Urbanová et al. 2015, Uroz et al. 2016). In our study, a higher abundance of fungi typically associated with decomposing wood was not observed in the soil under dead trees. In an experiment where the decomposing wood of multiple trees was incubated on top of *Picea abies* soil in the laboratory, both microbial biomass and community composition differed from controls and also among tree species (Peršoh & Borken 2017). The most pronounced differences in composition were among different habitats – wood, leaf litter and soil. Wood and litter, as a C rich and N limited substrate, hosted fungal saprotrophic degraders specialized for C uptake from recalcitrant polymers and bacteria known for N fixation or from associations with fungal hyphae (Uroz et al. 2012; Mäkipää et al. 2018). On the other hand, several bacterial taxa enriched in soil were chemolithotrophs and dominant fungi are known from ectomycorrhizal association with plant roots (Bahnmann et al. 2018, Lladó et al. 2018). In our study, soil fungi and bacteria within individual microsites were affected by soil chemistry that responded to trunk decomposition, with the most important being C_{ox}, N_{tot}, Mg^{2+}, Mn and Al. However, the wood-on-soil effects were weak, and for bacteria the wood influence was overridden by the influence of individual horizons. The minor response of the fungal community in this study is likely due to the high spatial variability of the community in decomposing wood, forest floor and upper mineral soil horizons, which is substantially higher than that of bacteria (Štursová et al. 2016, Baldrian et al. 2016; Tláskal et al. 2017).

6 Conclusion

The evolution of Entic Podzols below decaying *Fagus sylvatica* trunks was evaluated in an old-growth temperate mountain forest. Using extensive sampling and laboratory analyses, we obtained a detailed picture of the process of wood decay, pedogenetic pathways and the composition of fungal and bacterial communities in both organic matter and in underlying mineral soils. Soil convergence was the prevailing pedogenetic pathway, although some individual soil properties expressed chaotic or even divergent pointing.

Soils below the decaying trunk followed generally unimodal pedogenetical trajectory culminating about 25 years after trunk fall. After ca 53 years, soils typically converged to the characteristics of the control soil (i.e. below the leaves). The changes were marked especially in the uppermost soil horizons, but modelled wood decomposition footprints were found even at a depth of 60 cm for some soil properties. Changes in the composition of bacterial and fungal communities were greatly restricted to the litter layer and uppermost mineral horizon, despite the finding that many important chemical drivers differed significantly between the trunk and control sites, even in deeper soil horizons (CEC, Ca^{2+}, Mg^{2+}, Al_{ox}) or did not converge at all (C_{ox}, N_{tot}). There is likely an additional barrier preventing the deepening of the trunk effect in microbiome compositions in mineral soil. This is most likely associated with unmeasured physical properties of different environments and requires further attention.

Our results demonstrate the complexity of soil evolution, and highlight the necessity to study a wide spectrum of soil properties in detail. Using only a few properties, one might obtain a highly biased picture of pedogenesis. Biochemical effects of lying beech trunks certainly increase the spatial soil complexity but this effect is rather temporary. Human interventions preventing the presence of newly decaying logs, for example by trunk haulage, will thus most likely decrease the soil spatial complexity. The response of soil will be long-lasting and qualities may rejuvenate based on changed management practices.

Supplementary data Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2020.114499

Acknowledgements The authors would like to thank Ondřej Paták for help with data collection in Zofin. The project was supported by the Czech Science Foundation (project No. 19-09427S – attendance of Pavel Šamonil and Pavel Daněk in team; project No. 17-20110S – attendance of Petr Baldrian and Vojtěch Tláskal).

References

Amann R.I., Ludwig W., Schleifer K.H. 1995. Phylogenetic Identification and in-Situ Detection of Individual Microbial-Cells without Cultivation. *Microbiological Reviews* 59: 143–169.

Aronesty E. 2013. Comparison of Sequencing Utility Programs. *Open Bioinformatics Journal* 7: 1–8.

Bahnmann B., Mašínová T., Halvorsen R., Davey M.L., Sedlák P., Tomšovský M., Baldrian P. 2018. Effects of oak, beech and spruce on the distribution and community structure of fungi in litter and soils across a temperate forest. *Soil Biology and Biochemistry* 119: 162–173.

Baldrian P., Zrůstová P., Tláskal V., Davidová A., Merhautová V., Vrška T. 2016. Fungi associated with decomposing deadwood in a natural beech-dominated forest. *Fungal Ecology* 23: 109–122.

Binkley C., Giardina D. 1998. Why do tree species affect soils? The warp and woof of tree–soil interactions. *Biogeochemistry* 42: 89–106.

Bockheim J.G. 1980. Solution and use of chronofunctions in studying soil development. *Geoderma* 24: 71–85.

Bremner J.M. 1996. Nitrogen-total. In: Sparks, et al. (Eds.), Methods of Soil Analysis. Part 3. Chemical Methods. Number 5 in Soil Science Society of America Book Series. Soil Science Society of America, Inc. and American Society of Agronomy, Madison, Wisconsin, pp. 1085–1121.

Burnham K.P., Anderson D.R. 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. *Sociological Methods and Research* 33: 261–304.

Buurman P., Jongmans A.G. 2005. Podzolisation and soil organic matter dynamics. *Geoderma* 125: 71–83.

Caporaso J.G., Lauber C.L., Walters W.A., Berg-Lyons D., Huntley J., Fierer N., Owens S.M., Betley J., Fraser L., Bauer M., Gormley N., Gilbert J.A., Smith G., Knight R. 2012. Ultra-high-throughput microbial community analysis on the Illumina HiSeq and MiSeq platforms. *ISME Journal* 6: 1621–1624.

CGS, Geological map 1:50000, Czech Geological Survey, available at: www.geology.cz, last access: November 2019.

CHMU, average annual rainfall in period 1961–1990, Czech Hydrometeorological Institute, available at: www.chmu.cz, last access: November 2019.

Cole J.R., Wang Q., Fish J.A., Chai B.L., McGarrell D.M., Sun Y.N., Brown C.T., Porras-Alfaro A., Kuske C.R., Tiedje J.M. 2014. Ribosomal Database Project: data and tools for high throughput rRNA analysis. *Nucleic Acids Research* 42: D633–D642.

Courchesne F., Turmel M.C. 2008. Extractable Al, Fe, Mn and Si. In: Carter M.R., Gregorich E.G. (eds) Soil sampling and methods of analysis. 2nd ed. Canadian Society of Soil Science. CRC Press, Boca Raton, pp. 307–315.

Daněk P., Šamonil P., Phillips J.D. 2016. Geomorphic controls of soil spatial complexity in a primeval mountain forest in the Czech Republic. *Geomorphology* 273: 280–291.

Dhiedt E., De Keersmaeker L., Vandekerkhove K., Verheyen K. 2019. Effects of decomposing beech (*Fagus sylvatica*) logs on the chemistry of acidified sand and loam soils in two forest reserves in Flanders (northern Belgium). *Forest Ecology and Management* 445: 70–81.

Drábek O., Borůvka L., Mládková L., Kočárek M. 2003. Possible method of aluminium speciation in forest soils. *Journal of Inorganic Biochemistry* 97: 8–15.

Drábek O., Mládková L., Borůvka L., Száková J., Nikodem A., Němeček K. 2005. Comparison of water-soluble and exchangeable forms of Al in acid forest soils. *Journal of Inorganic Biochemistry* 99: 1788–1795.

Edgar R.C. 2010. Search and clustering orders of magnitude faster than BLAST. *Bioinformatics* 26: 2460–2461.

Edgar R.C. 2013. UPARSE: highly accurate OTU sequences from microbial amplicon reads. *Nature Methods* 10: 996–998.

Gillman G.P., Sumpter M.E. 1986. Modification of the compulsive exchange method for measuring exchange characteristics of soils. *Australian Journal of Soil Research* 17: 61–66.

Goldin S.R., Hutchinson M.F. 2013. Coarse woody debris modifies surface soils of degraded temperate eucalypt woodlands. *Plant Soil* 370: 461–469.

Guest C.A., Schulze D.G., Thompson I.A., Huber D.M. 2002. Correlating manganese Xray absorption near-edge structure spectra with extractable soil manganese. *Soil Science Society of America Journal* 66: 1172–1181.

Hoffman B.S.S., Anderson R.S. 2013. Tree root mounds and their role in transporting soil on forested landscapes. *Earth Surface Processes Landforms* 39: 711–722.

Hubova P., Tejnecky V., Ceskova M., Boruvka L., Nemecek K., Drabek O. 2018. Behaviour of aluminium in forest soils with different lithology and herb vegetation cover. *Journal of Inorganic Biochemistry* 181: 139–144.

Huggett R.J. 1998. Soil chronosequences, soil development, and soil evolution: a critical review. *Catena* 32: 155–172.

Ihrmark K., Bodeker I.T.M., Cruz-Martinez K., Friberg H., Kubartova A., Schenck J., Strid Y., Stenlid J., Brandstrom-Durling M., Clemmensen K.E., Lindahl B.D. 2012. New primers to amplify the fungal ITS2 region - evaluation by 454-sequencing of artificial and natural communities.

FEMS Microbiology Ecology 82: 666–677.

IUSS Working Group WRB 2014. World Reference Base for Soil Resources 2014. International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No. 106. FAO, Rome.

Jabiol B., et al. 2013. A proposal for including humus forms in the world reference base for soil resources (WRB-FAO). *Geoderma* 192: 286–294.

Kayahara G.J. 1998. Effect of Decaying Wood on the Weathering of Soils in Coastal British Columbia. Canada. *Northwest Science* 72: 74–76.

Kayahara G.J., Klinka K., Lavkulich L.M. 1996. Effects of decaying wood on eluviation, podzolization, acidification, and nutrition in soils with different moisture regimes. *Environmental Monitoring and Assessment* 39: 485–492.

Klinka K., Fons J., Krestov P. 1997. Towards a taxonomic classification of humus forms; third approximation. Scientia Silvica, Extension Series No. 9. Forestry Sciences Department, The University of British Columbia, Vancouver.

Lladó S., López-Mondéjar R., Baldrian P. 2018. Drivers of microbial community structure in forest soils. *Applied Microbiology and Biotechnology* 102: 4331–4338.

Mäkipää R., Leppänen S.M., Munoz S.S., Smolander A., Tiirola M., Tuomivirta T., Fritye H. 2018. Methanotrophs are core members of the diazotroph community in decaying Norway spruce logs. *Soil Biology and Biochemistry* 120: 230–232.

Mäkipää R., Rajala T., Schigel D., Rinne K.T., Pennanen T., Abrego N., Ovaskainen O. 2017. Interactions between soil- and dead wood-inhabiting fungal communities during the decay of Norway spruce logs. *ISME Journal* 11: 1964–1974.

Nachtergale L., Ghekiere K., De Schrijver A., Muys B., Luyssaert S., Lust N. 2002. Earthworm biomass and species diversity in windthrow sites of a temperate lowland forest. *Pedobiologia (Jena)* 46: 440–451.

Oksanen J., Blanchet F.G., Kindt R. et al. 2019. vegan: Community ecology package. R package version 2.5–5.

Peršoh D., Borken W. 2017. Impact of woody debris of different tree species on the microbial activity and community of an underlying organic horizon. *Soil Biology and Biochemistry* 115: 516–525.

Phillips J.D. 2001. Divergent evolution and the spatial structure of soil landscape variability. *Catena* 43: 101–113.

Phillips J.D. 2006. Deterministic chaos and historical geomorphology: A review and look forward. *Geomorphology* 76: 109–121.

Phillips J.D. 2009. Soils as extended composite phenotypes. *Geoderma* 149: 143–151.

Phillips J.D., Perry D., Carey K., Garbee A.R., Stein D., Morde M.B., Sheehy J. 1996. Deterministic uncertainty and complex pedogenesis in some Pleistocene dune soils. *Geoderma* 73: 147–164.

Pinheiro J., Bates D., DebRoy S., Sarkar D. 2019. R Core Team 2019. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-140.

Prévost-Bouré N.C., Christen R., Dequiedt S., Mougel C., Lelievre M., Jolivet C., Shahbazkia H.R., Guillou L., Arrouays D., Ranjard L. 2011. Validation and Application of a PCR Primer Set to Quantify Fungal Communities in the Soil Environment by Real-Time Quantitative PCR. *PLoS ONE* 6, e24166.

Průša E. 1985. Die böhmischen und mährischen Urwälder—ihre Struktur und Ökologie, Vegetace

ČSSR A15. Academia, Praha.

R Core Team 2019. A language and environment for statistical computing.

Roering J.J., Marshall J., Booth A.M., Mort M., Jin Q. 2010. Evidence for biotic controls on topography and soil production. Earth Planet. Sci. Lett. 298: 183–190. Sagova-Mareckova M., Cermak L., Novotna J., Plhackova K., Forstova J., Kopecky J. 2008. Innovative methods for soil DNA purification tested in soils with widely differing characteristics. *Applied and Environmental Microbiology* 74: 2902–2907.

Šamonil P., Daněk P., Schaetzl R.J., Vašíčková I., Valtera M. 2015. Soil mixing and genesis as affected by tree uprooting in three temperate forests. *European Journal of Soil Science* 66: 589–603.

Šamonil P., Doleželová P., Vašíčková I., Adam D., Valtera M., Král K., Janík D., Šebková B. 2013. Individual-based approach to the detection of disturbance history through spatial scales in a natural beech-dominated forest. *Journal of Vegetation Science* 24: 1167–1184.

Šamonil P., Valtera M., Bek S., Šebková B., Vrška T., Houška J. 2011. Soil variability through spatial scales in a permanently disturbed natural spruce-fir-beech forest. *European Journal Forest Research* 130: 1075–1091.

Šamonil P., Vašíčková I., Daněk P., Janík D., Adam D. 2014. Disturbances can control fine-scale pedodiversity in old-growth forest: Is the soil evolution theory disturbed as well? *Biogeosciences* 11: 5889–5905.

Šamonil P., Daněk P., Schaetzl R.J., Tejnecký V., Drábek O. 2018. Converse pathways of soil evolution caused by tree uprooting: A synthesis from three regions with varying soil formation processes. *Catena* 161: 122–136.

Šamonil P., Schaetzl R.J., Valtera M., Goliáš V., Baldrian P., Vašíčková I., Adam D., Janík D., Hort L. 2013. Crossdating of disturbances by tree uprooting: can treethrow microtopography persist for 6,000 years? *Forest Ecology and Management* 307: 123–135.

Sauer D., et al. 2007. Podzol: soil of the year 2007. A review on its genesis, occurrence, and functions. *Journal of Plant Nutrition and Soil Science* 170: 581–597.

Schaetzl R.J., Barrett L.R., Winkler J.A. 1994. Choosing models for chronofunctions and fitting them to data. *European Journal of Soil Science* 45: 219–232.

Schnitzer M., Wright J.R., Desjardins J.G. 1958. A comparison of the effectiveness of various extractans for organic matter from two horizons of a Podzol Profile. *Canadian Journal of Soil Science* 38: 49–53.

Schoeneberger P.J., Wysicki D.A., Benham E.C., Broderson W.D. 1998. Field Book for Describing and Sampling Soils. Natural Resources Conservation Service, USDA, National Soil Survey Center, Lincoln, NE.

Shabir G.A. 2003. Validation of high-performance liquid chromatography methods for pharmaceutical analysis: Understanding the differences and similarities between validation requirements of the US Food and Drug Administration, the US Pharmacopeia and the International Conference on Harmonization. *Journal of Chromatography* A, 987: 57–66.

Simon A., Gratzer G., Sieghardt M. 2011. The influence of windthrow microsites on tree regeneration and establishment in an old growth mountain forest. *Forest Ecology and Management* 262: 1289–1297.

Spears J.D.H., Lajtha K. 2004. The imprint of coarse woody debris on soil chemistry in the western Oregon cascades. *Biogeochemistry* 71: 163–175.

Štursová M., Bárta J., Šantručková H., Baldrian P. 2016. Small-scale spatial heterogeneity of ecosystem properties, microbial community composition and microbial activities in a temperate mountain forest soil. *FEMS Microbiology Ecology* 92: fiw185.

Stutz K.P., Dann D., Wambsganss J., Scherer-Lorenzen M., Lang F. 2017. Phenolic matter from deadwood can impact forest soil properties. *Geoderma* 288: 204–212.

Stutz K.P., Kaiser K., Wambsganss J., Santos F., Berhe A.A., Lang F. 2019. Lignin from white-rotted European beech deadwood and soil functions. *Biogeochemistry* 145: 81–105.

Tedersoo L., Bahram M., Polme S., Koljalg U., Yorou N.S., Wijesundera R., Ruiz L.V., Vasco-Palacis A.M., Thu P.Q., Suija A., Smith M.E., Sharp C., Saluveer E., Saitta A., Rosas M., Riit T., Ratkowsky D., Pritsch K., Poldmaa K., Piepenbring M., Phosri C., Peterson M., Parts K., Partel K., Otsing E., Nouhra E., Njouonkou A.L., Nilsson R.H., Morgado L.N., Mayor J., May T.W., Majuakim L., Lodge D.J., Lee S. S., Larsson K.H., Kohout P., Hosaka K., Hiiesalu I., Henkel T.W., Harend H., Guo L.D., Greslebin A., Grelet G., Geml J., Gates G., Dunstan W., Dunk C., Drenkhan R., Dearnaley J., De Kesel A., Dang T., Chen X., Buegger F., Brearley F.Q., Bonito G., Anslan S., Abell S., Abarenkov K. 2014. Global diversity and geography of soil fungi. *Science* 346: 1256688.

Tejnecký V., Šamonil P., Matys Grygar T., Vašát R., Ash C., Drahota P., Šebek O., Němeček K., Drábek O. 2015. Transformation of iron forms during soil formation after tree uprooting in a natural beech-dominated forest. *Catena* 132: 12–20.

Ter Braak C.J.F., Šmilauer P. 2002. CANOCO reference manual and CanoDraw for Windows User's guide: Software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca.

Tláskal V., Zrůstová P., Vrška T., Baldrian P. 2017. Bacteria associated with decomposing dead wood in a natural temperate forest. *FEMS Microbiology Ecology* 93, Fix157.

Urbanová M., Šnajdr J., Baldrian P. 2015. Composition of fungal and bacterial communities in forest litter and soil is largely determined by dominant trees. *Soil Biology and Biochemistry* 84: 53–64.

Uroz S., Oger P., Morin E. 2012. Distinct ectomycorrhizospheres share similar bacterial communities as revealed by pyrosequencing-based analysis of 16S rRNA genes. *Applied Environmental Microbiology* 78: 3020–3024.

Uroz S., Oger P., Tisserand E., et al. 2016. Specific impacts of beech and Norway spruce on the structure and diversity of the rhizosphere and soil microbial communities. *Scientific Reports* 6: 1–11.

Větrovský T., Baldrian P., Morais D. 2018. SEED 2: a user-friendly platform for amplicon high-throughput sequencing data analyses. *Bioinformatics* 34: 2292–2294.

Wilmotte A., Van der Auwera G., De Wachter R. 1993. Structure of the 16 S ribosomal RNA of the thermophilic cyanobacterium chlorogloeopsis HTF ('*Mastigocladus laminosus*') strain PCC-7518, and phylogenetic analysis. *FEBS Letters* 317: 96–100.

Zbíral J. 2002. Analýza půd I. Ústřední kontrolní a zkušební ústav zemědělský, Brno. Czech Republic.

Zbíral J. 2003. Analýza půd II. Ústřední kontrolní a zkušební ústav zemědělský, Brno. Czech Republic.

Zbíral J., Honsa I., Malý S., Čižmár D. 2004. Analýza půd III. Ústřední kontrolní a zkušební ústav zemědělský, Brno, Czech Republic.

Žifčáková L., Větrovský T., Howe A., Baldrian P. 2016. Microbial activity in forest soil reflects the changes in ecosystem properties between summer and winter. *Environmental Microbiology* 18: 288–301.

Paper 4

Biomechanical effects of trees in an old-growth temperate forest

Pavel Šamonil
Pavel Daněk
Anna Senecká
Dušan Adam
Jonathan D. Phillips

Earth Surface Processes and Landforms 43 (2018), 1063–1072

Abstract

The role of biomechanical effects of trees (BETs) in ecosystem and landscape dynamics is poorly understood. In this study, we aim to (i) describe a widely applicable methodology for quantifying the main BETs in soil, and (ii) analyze the actual frequencies, areas and soil volumes associated with these effects in a mountain temperate old-growth forest.

The research took place in the Boubínský Primeval Forest in the Czech Republic; this forest reserve, predominated by *Fagus sylvatica* L. and *Picea abies* (L.) Karst., is among the oldest protected areas in Europe. We evaluated the effects of 4000 standing and lying trees in an area of 10.2 ha from the viewpoint of the following features: tree uprooting, root mounding, bioprotection, trunk baumsteins (rock fragments displaced by trunk growth), root baumsteins, stump hole infilling, trunk and root systems displacements, depressions formed after trunk fall, stemwash, and trunkwash.

BETs were recorded in 59% of standing and 51% of lying dead trees (excluding the pervasive soil displacement by thickening trunks and roots and the infilling of decayed stumps). Approximately one tenth of the trees showed simultaneous bioprotective and bioerosion effects. Different tree species and size categories exhibited significantly different biomechanical effects.

A bioprotective function was the most frequent phenomenon observed, while treethrows prevailed from the viewpoint of areas and soil volumes affected. The total area influenced by the BETs was 342 m^2 ha^{-1}. An additional 774 m^2 ha^{-1} were occupied by older treethrow pit-mounds with already decayed uprooted trunks. The total volume of soil associated with the studied phenomena was 322 m^3 ha^{-1}, and apart from treethrows, volumes of the living and decaying root systems and bioprotective functions predominated. Other processes were not so frequent but still significant for biogeomorphology.

P. Šamonil[a], *P. Daněk*[a,b], *A. Senecká*[a,c], *D. Adam*[a], *J.D. Phillips*[a,d]

[a] Department of Forest Ecology, The Silva Tarouca Research Institute, Brno, Czech Republic [b] Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic [c] Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic [d] Earth Surface Systems Program, Department of Geography, University of Kentucky, Lexington, KY, USA

1 Introduction

The biomechanical effects of trees (BETs) are a potentially significant factor in biogeomorphology (e.g. Phillips et al. 2017) and pedocomplexity (e.g. Šamonil et al. 2014; Daněk et al. 2016). Nevertheless, apart from tree-uprooting dynamics, research on this issue has been only sporadic so far. Treethrow dynamics have been studied in greater detail, but most studies are from Albic Podzols regions in the United States, Canada and Russia, with other regions under-represented in treethrow research (see review by Šamonil et al. 2010).

Previous studies have demonstrated the significance of tree uprooting dynamics on biogeomorphology and pedology. Uprooted trees can move boulders heavier than 4 tons (Lutz 1960), their root-plates can reach areas of up to 40 m^2 (Šamonil et al. 2014) and volumes up to 60 m^3 (Phillips et al. 2017). Moreover, radiometric dating of treethrow features has revealed that typical post-disturbance pit-mound microtopography can persist for more than 6000 years (Šamonil et al. 2013b), and these forms can cover up to 90% of a forest area (Karpachevskiy et al. 1980). In some forested biomes, particularly in boreal forests, each position in a forest can be disturbed by uprooting an average of every 200 to 400 years (e.g. Bormann et al. 1995, assuming that tree establishment and uprooting is either spatially uniform or random – see review by Šamonil et al. 2010).

Other less visible BETs beyond uprootings have been studied sporadically, and moreover using various methods that limit comparisons. The studies that have been done have suggested that these processes can significantly affect hillslope processes. According to Bennie (1991), roots penetrating the soil and belowground rock can produce pressures of about 1.45 MPa, and significant combined biomechanical and biochemical influences can contribute to weathering processes and deepening of the soil and regolith (Shouse & Phillips 2016; Pawlik et al. 2016). However, soil close to the surface is lifted up by radial growth of roots and so-called root mounds are formed (Hoffman & Anderson 2013). Extruding radial soil is a component of biogenous creep, which in some ecosystems can be as important as abiotic creep (Caine 1986; Lehre 1987). Concentrated stemflow on standing or under lying tree trunks can cause the removal of forest floor or even mineral soil, processes that were termed by Phillips et al. (2017) as stemwash and trunkwash.

However, trees are not only a factor contributing to erosion and mass movement, but can also simultaneously operate against removal. The bodies of standing and lying trees block the transport of soil and regolith on slopes (Naylor 2005). The significance of the bioprotective function of trees has mainly been studied at a general level (e.g. correlation of erosion rates with forest cover), and it is widely accepted (see Pawlik et al. 2013). Because the age of trees in temperate old-growth forests can exceed 500 years (Šamonil et al. 2013a, unpublished) and decomposition of a lying trunk can take more than 100 years (e.g. Lombardi et al. 2008), localized sedimentation at tree sites is probably not negligible (Pawlik 2013; Pawlik et al. 2016).

Apart from the influence of treethrows in pedogenesis, the impact of the BETs in soils has only been evaluated on the landscape scale by rotation period calculations. In Arkansas, Phillips & Marion (2006) showed that an area equal to their entire study area was disturbed by soil displacement due to the radial growth of trunks every 6250 years on average. In contrast, the filling of decayed stump holes by soil required c. 43,500 years to disturb an equal area. As far as we know, other data on coarse spatial scales are lacking. Therefore, we have little knowledge on the structure of the BETs in forests and their role in hillslope dynamics. In this study we aim to (i) describe a detailed and universal methodology for studying the visible BETs, (ii) analyze the actual structure of the BETs in a temperate old-growth mountain forest, and (iii) discuss the implications of BETs for slope processes.

2 Material and Methods

2.1 Study site

Our research took place in the Boubínský Primeval Forest Reserve (hereinafter Boubin) in the Šumava Mountains in the Czech Republic (Fig. 1, Table 1). This forest reserve is the second oldest protected forest area in the Czech Republic and one of the oldest in Europe (Welzholz & Johann 2007). As far as we know the core zone of Boubin studied here has never been cut, and has been under strict protection since 1858. The old-growth forest occupies north-eastern slopes on crystalline rocks of the Bohemian Massif. The average slope is about 14.4°. The underlying bedrock is primarily schists, and biotite-rich gneisses. Geophysical data using ground penetration radar, seismic measurements and electrical resistivity tomography (not presented here) has uncovered solid unweathered compact rock 5–10 m below the current soil surface. Daněk et al. (2016) described exceptional local pedodiversity and pedocomplexity in Boubin consisting of 37 soil units (classified according to Michéli et al. 2007). Within the reserve we found a complex spatial pattern of soils driven particularly by topography (including microtopography formed by individual trees), hydrogeology and postglacial geomorphological processes (debris flow, rotational slumps, etc.). In Boubin, Podzols predominate on better-drained areas followed by Cambisols, while Gleysols predominate on spring and stream areas followed by Stagnosols and Histosols. Plant communities can be mostly classified into montane acidophilous or nutrient-rich *Fagus sylvatica* forests (phytosociological associations *Calamagrostio villosae–Fagetum sylvaticae*, *Mercuriali perennis–Fagetum sylvaticae*) and montane acidophilous *Picea abies* forests (associations *Calamagrostio villosae–Piceetum abietis*). Hydromorphic areas are dominated by wet *Picea abies* forests, usually with an abundance of mosses (*Soldanello montanae–Piceetum abietis*; see Chytrý 2013).

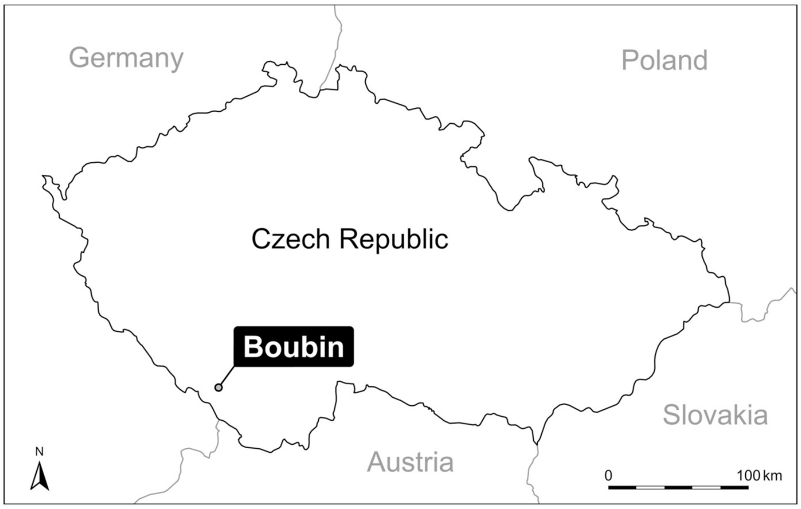


Fig. 1 Study area location map.

Table 1 Key characteristics of the studied sites relevant to environmental conditions, and history

Feature/locality	Boubínský Primeval Forest
Location (latitude, longitude)	48°58′43″ N, 13°48′43″ E
Parent material	gneiss, schists
Soil taxonomy, predominant soils (WRB 2007)	Podzols, Gleysols
Studied area (ha)	10.2
Range of altitudinal gradient (m a.s.l.)	925–1050
Mean annual precipitation (mm)	1067
Mean average temperature (°C)	4.9
Mean slope (deg)	14.4
Strictly protected since (year ad)	1858
Main tree species	*Fagus sylvatica*, *Picea abies*, (*Abies alba*)

2.2 Data collection and processing

Repeated tree censuses took place in 1972, 1996 and 2010 in the Boubin core zone with an area of 10.2 ha. During each census, the tree species, position, and health status (living, living broken tree, standing dead tree, tree stump, dead uprooted tree, etc.) of all living or dead tree individuals of diameter at breast height (DBH) ≥ 10 cm was recorded. Based on these measurements we created digital maps of trees showing the precise positions of trees in the forest (accuracy c. 0.5 m) along with detailed information about each tree (e.g. Šebková et al. 2011). This individual-based approach allowed us to study biogeomorphic features on the scale of the individual tree. In this 10.2 ha core area, there were 3956 standing trees or laying undecomposed tree trunks in 2016, and the following BETs were assessed (see Fig. 2, Supporting Information Fig. S1 (a)–(j)):

Treethrow (uprooting; sensu Šamonil et al. 2010) Root mound (sensu Hoffman & Anderson 2013) Bioprotective function of a standing tree (we focused on the deposition-promoting, transport-blocking effects; anchoring, erosion-prevention effect was not studied here, see Pawlik 2013) Bioprotective function of a lying tree, including a log dam (see Pawlik 2013) Trunk baumstein (sensu Phillips & Marion 2006) Root baumstein (a newly-established process that has never been studied before) Stump infilling (see Bolte et al. 2004 – using allometric equations, Phillips & Marion 2006 – using taproot depth, see d in Fig. S1(b)) Hole after trunk fall (a newly-established process that has never been studied before) Stemwash (sensu Phillips et al. 2017) Trunkwash (sensu Phillips et al. 2017) Trunk and root system displacement (sensu Bolte et al. 2004)

Other possible BETs were excluded from this study, due to the absence of easily-accessible footprints of such additional processes or their general absence in the locality. For example, root penetration to bedrock has been evaluated in Boubin using ground penetration radar, seismic and tomography measurements, and will be the subject of a future study expanding on our current results. We logically assumed that one tree can produce multiple biomechanical effects in soils. Individual processes were determined using the following key: Key to the BETs (the numbers listed at the end of each item indicate where to proceed).

1a A standing tree .... continue to point 2
1b A lying tree 10
2a A dead tree (roots decaying and being infilled by surrounding soil) .... *infilling stump*; 3

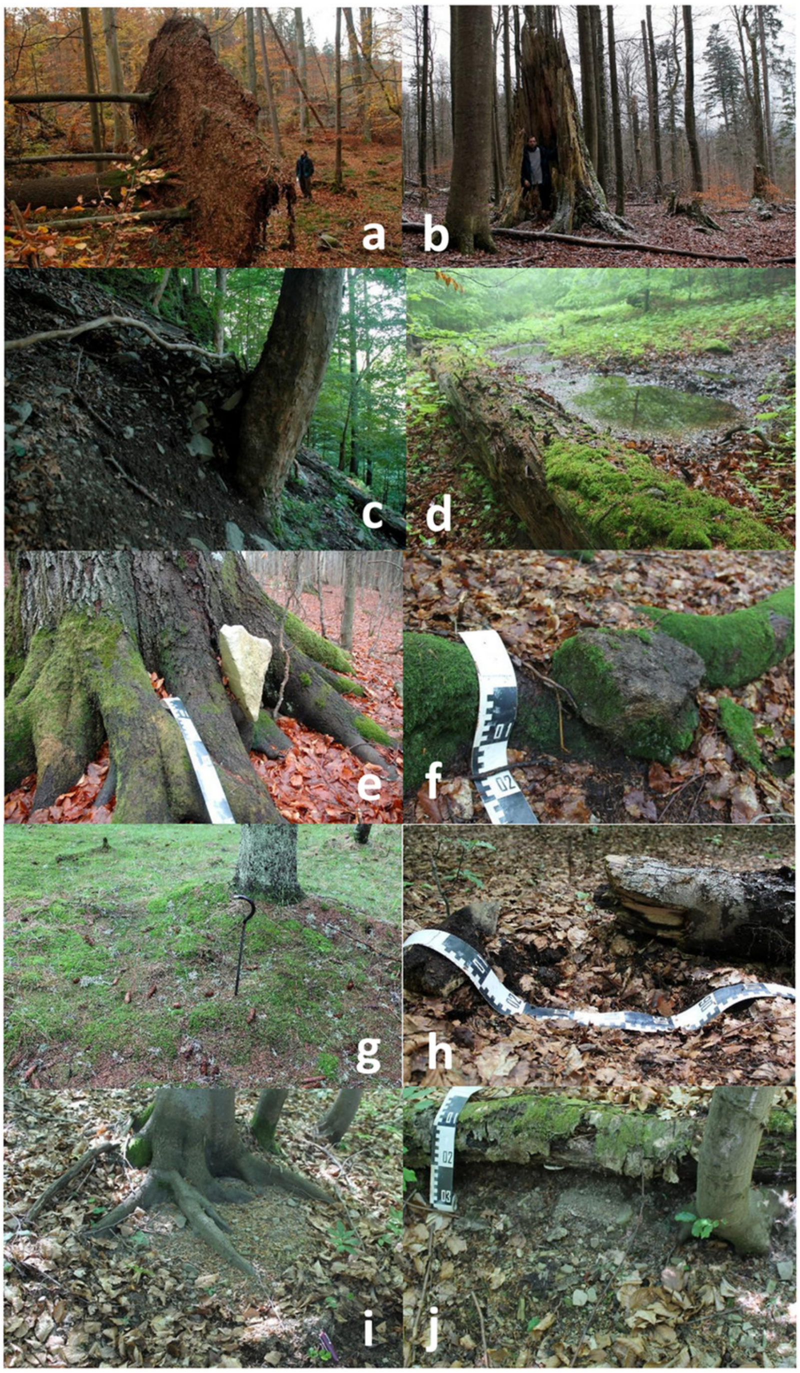


Fig. 2 Examples of evaluated processes: (a) treethrow, (b) stump infilling (inverse process to root system and trunk displacement, both processes root system and stem cylinder growth and decay were studied using general allometric equations), (c) the bioprotective function of a standing tree, (d) the bioprotective function of a lying tree including a log dam, (e) baumstein, (f) root baumstein, (g) root mound, (h) a hole after trunk fall, (i) stemwash, (j) trunkwash.

2b A living tree (soil is compressed and moved to all directions by radial growth of trees and roots) .... *trunk and root displacement*; 3

3 Organic material, mineral soil or (rarely) small rock fragments are removed from the vicinity of the trunk base. Material is characteristically accumulated in a small wall-like shape below the tree base. Bare mineral soil occurs between the accumulated material and trunk. (A result of material movement due to concentrated stemflow.) .... *stemwash*; 4

4 Organic material, mineral soil or rock fragments close to the tree trunk are about ≥ 0.1 m higher than in corresponding adjacent areas 5

5 Organic material, mineral soil or rock fragments are accumulated between the slope and trunk base or between the slope and partly exposed roots. Local terrain microtopography is

never convex close to the trunk base. If mineral material is deposited, it is typically mixed with organic material, without sharp transitions between soil horizons. (A result of material on a slope being prevented from moving.) .... *bioprotection*; 6

6 Organic material or mineral soil is at least about 0.1 m higher close to the tree trunk compared with corresponding adjacent areas. Organic material typically occurs on mineral soil without a mixture of soil horizons. (A result of material being uplifting due to trunk and root radial growth) .... *root mound*; 7

7 Rock fragments are present 8

8 Rock fragments are directly in contact with the tree trunk (including root haunches). Due to the radial growth of the trunk stones are moved predominantly horizontally, which is evidenced by an empty space forming on the trunk side of the stone. (If the tree trunk is in direct contact with the stone but there is no evidence of stone movement – e.g. the stone is too big, the stone does not experience radial pressure – then the case is not accepted to be a biomechanical process.) .... *baumstein*; 9

9 Rock fragments are not in direct contact with the trunk base but with the tree roots. Below the rock fragments there is a space resulting from the predominantly vertical movement of stones due to radial root growth .... *root baumstein*

10a Soil disturbance is visible close to the trunk or basal trunk part 11

10b No soil disturbance is visible close to the trunk or basal trunk part 12

11a Soil was disturbed by uprooted roots in the basal part of the trunk. Pit-mound microtopography is typically formed but mound or pit by themselves can be formed as well. (A result of tree uprooting and subsequent erosion–sedimentation processes.) .... *treethrow*; 12

11b In contact with a non-basal part of the tree trunk, pit-like microtopography is formed. (A result of tree breakage and soil displacement by the falling trunk.) .. *hole after trunk fall*; 12

12 Organic material, mineral soil or rock fragments are accumulated between the slope and the lying trunk or are even on lying trunk. The lying trunk usually crosses the fall line of the slope. In some cases, and particularly close to streams, material accumulated behind the trunk is water saturated, which is called a log dam .... *bioprotective function*; 13

13 Organic material, soil or (rarely) small rock fragments are missing below the lying trunk. The removed material is generally concentrated in a small wall-like form below. (A result of concentrated surface water flow and material movement.) .... *trunkwash*

We recorded the frequencies of individual processes as well as their horizontal areas and volumes of associated soil. Apart from detailed visual and tactual inspection, we used a thin soil corer, pedomorphological tests of soil properties (e.g. Schoeneberger et al. 1998; Schaetzl & Thompson 2015) and an ultrasonic meter. We accepted and measured only clearly visible effects of trees, and therefore we expect that at least the minimal extents of the biomechanical processes were evaluated. During areal and volumetric assessments, each form was approximated by basal geometric shapes (Fig. S1(a)–(j)).

While root baumsteins represent a spatially dispersive process without any characteristic pattern (rock fragments closer or farther from the trunk base are directly affected by roots), trunk baumsteins frequently produces typical 'stone ring' narrowly surrounding trunk base. We utilized this typical expression of the trunk baumstein during measurements because it is not so laboriousness as individual measurement of all affected rock fragments, which is necessary in root baumstein study. Uncertainties associated with calculation of areas and volumes of material associated with these processes seem to be similar because complex shapes of individual rock fragments have to be always approximated by simple geometric forms such as prism or cube in both cases. If 'stone ring' was only fragmental or too irregular, individual stones were measured and the trunk baustein was calculated identically to the root baumstein. The same is valid for fragmental expression of root mound.

Since calculating living trunk and root displacement and the inverse process of stump infilling using direct measurements was not possible in our locality, we used allometric equations according to Bolte et al. (2004). In our approach these processes are equal of the stem cylinder volume plus root volume. Estimates using DBH for *Fagus sylvatica* were also used for other broadleaf trees, while a model for *Picea abies* was also used for *Abies alba* Mill. The proportion of marginal tree species, other than *Picea abies* and *Fagus sylvatica*, within the studied area was 5.9%. Because radial growth of living roots and conversely decay of root systems and stump cylinders takes place in all living and dead trees without exception, respectively, we calculated these two processes for each living and analogous dead tree present. Because volumes of the root mounds represent visible subset of volumes of root systems, we did not insert this phenomenon to the summary of BETs per locality.

Compared to other phenomena, treethrows have enormous longevity, significantly exceeding the time period of trunk decomposition. In central European temperate forests, the longevity of treethrow pit mounds can reach 1700 years, and even 6000 years in other regions (Šamonil et al. 2013b). For this reason, we analyzed all visible treethrow pit-mounds within 118 random circular plots of 10 m radius (3.71 ha).

Relationships between DBH and areas or volumes affected by treethrows were modeled using linear, quadratic and cubic models. The best fitting model was then selected based on Akaike information criterion (AIC). Differences between effects of trees were tested using bootstrapping. For each combination of quantification (proportion, area or volume) and grouping (DBH class or species) the differences between all effects within groups (e.g. areas associated with *Fagus sylvatica*) and each effect between groups (e.g. areas associated with treethrow) were tested based on 1000 re-samplings. The probability that two compared quantities differ was calculated as $1 - q$, where q is the quantile overlap between the values obtained after re-sampling. Alpha level was set at 0.05 and possible problems resulting from multiple testing were addressed using a sequential Bonferroni-type procedure which controls the false discovery rate (Benjamini & Hochberg 1995). All analyses were performed in R (R Core Team 2016).

3 Results

3.1 Frequencies of biomechanical processes

In our approach, trunk and root system displacement and stump infilling were inherently linked to all 2600 living and all 1400 dead trees, respectively (see Fig. S1(a)–(j)). Beyond the universal and long-term soil displacement by thickening trunks and roots or the infilling of stem cylinders and root systems by surrounding soil, at least one other biomechanical phenomenon was observed in 58.7% of standing trees and 51.3% of lying dead trees. Standing trees are also more likely to show multiple effects. At least two biomechanical processes were recorded for 9.3% of standing and only 3.7% of lying tree individuals. The most common combination of multiple effects was the extrusion of rock fragments during radial growth and the bioprotective function of standing trunks. For lying trunks we observed most commonly the death of a tree by uprooting followed by the bioprotective function of the lying trunk. Approximately 10.5% of the lying trees expressing some BETs had simultaneously opposing phenomena, such as a blocking of slope processes as well as inducing their intensification.

Visible effects of bioprotection (that is, beyond the general increase in resistance associated with vegetation cover) was recorded for 40 to 50% of standing trees, depending on the tree species (Fig. 3), which suggests a considerable slope movement of soil and regolith. For lying trees this proportion decreased up to c. 20%. In 5% of cases the material accumulated behind fallen trunks was saturated by water and fluvial erosion was blocked (we call this phenomenon log dam).

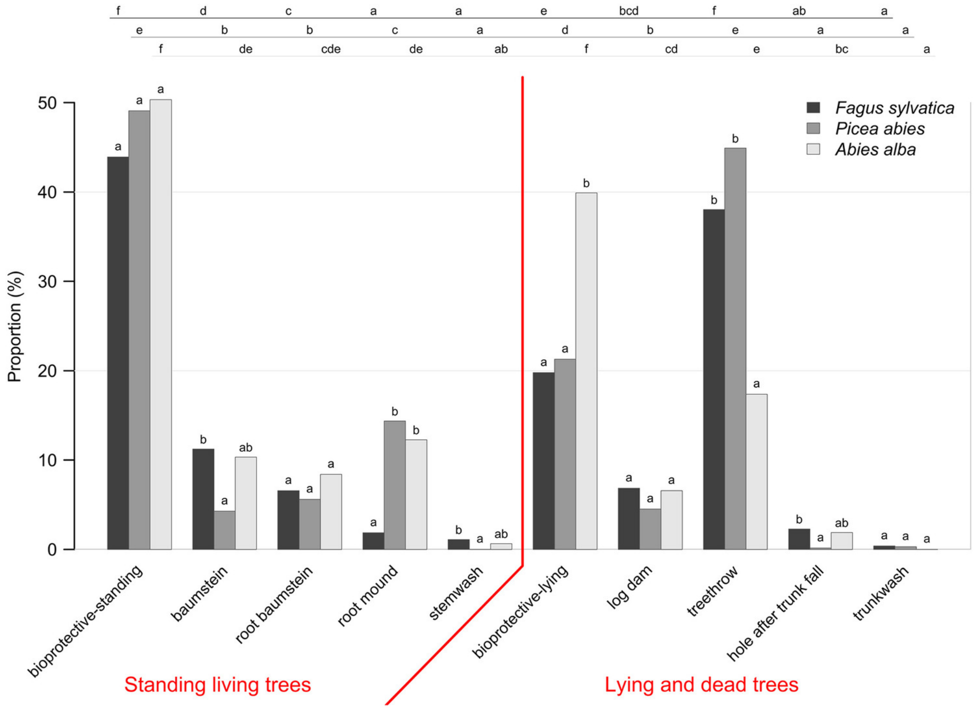


Fig. 3 Proportions of the recorded biomechanical effects of trees according to tree species. Small letters (a–f) indicate differences between proportions – if two bars share a common letter, there is not a significant difference between them and vice versa. The letters right above the bars show differences between species within a single effect while the letters in three rows in the top of the plot indicate differences between effects within each of the three species.

Treethrows are a significant phenomenon in this mountain temperate forest, as almost 40% of *Picea abies* individuals died due to uprooting. *Abies alba* and *Fagus sylvatica*, with generally deeper root architecture and less affinity for labile histic and gleyic soils, were uprooted in 13% and 32% of cases, respectively. Thus, treethrow dynamics were specific to the tree taxa.

Differences between species also emerged for other effects that were observed in less than 10% of tree individuals. While *Picea abies* expressed decreased frequency of root and trunk baumsteins compared to other tree species, *Fagus sylvatica* only rarely showed evidence of root mound. Stemwash, trunkwash and a hole after trunk fall were present only marginally, in 1% of cases.

The diameter of trees, and therefore their age, considerably influenced the observed occurrence of the phenomena studied (Fig. 4). With the exception of treethrows, the bioprotective function of trees was the most frequent phenomenon detected for larger-diameter trees. Bioprotection in the form of blocking downslope transport and promoting local deposition was recorded in standing trees with DBH ≥ 75 cm in nearly 58% of cases, compared to only 38% of cases for DBH ≤ 35 cm. The highest proportion of uprooted trees was found for intermediate-diameter trees with DBH between 35 and 75 cm.

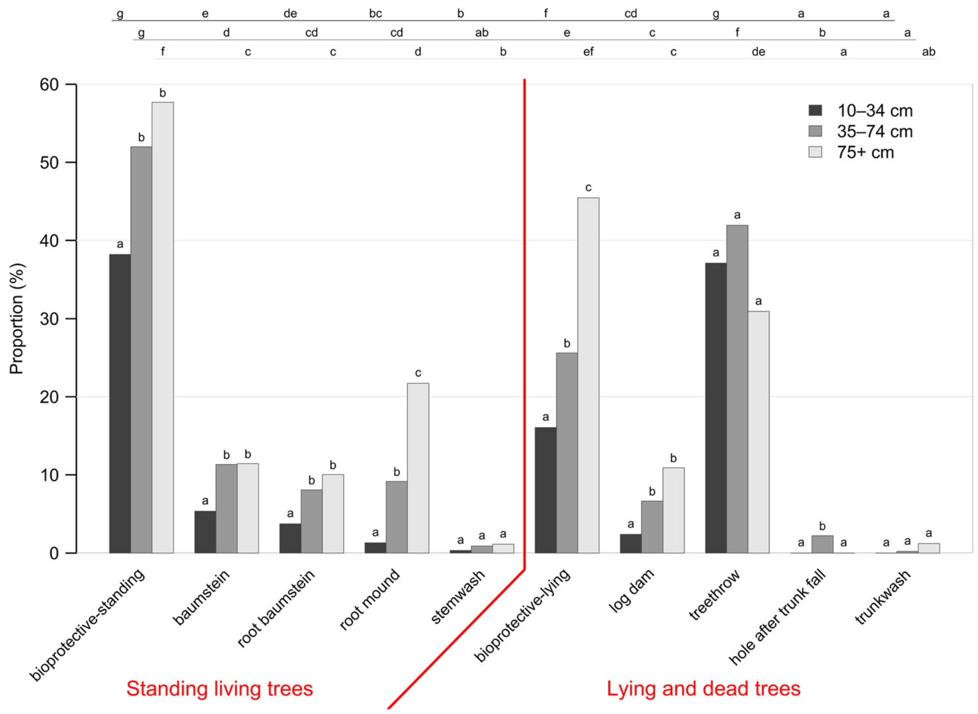


Fig. 4 Proportions of the recorded biomechanical effects of trees according to the diameter of trees at breast height. See Fig. 3 for details.

3.2 Areas of biomechanical effects

The total area of the studied biomechanical effects for the current generation of trees in Boubin was 342 $m^2\ ha^{-1}$. Recalculating the frequencies to the areas showed an increasing proportion of the biomechanical effects of dead and lying trees in the whole data set of BETs. In particular, areas of treethrows were exceptionally large (Fig. 5). Treethrows with the uprooted trunk still present covered 127 $m^2\ ha^{-1}$, and the area of all treethrow pit-mound features, including older microtopographical forms without uprooted trunks, reached 901 $m^2\ ha^{-1}$ (95% confidence interval = 783–1021 $m^2\ ha^{-1}$). The area of treethrows with an uprooted trunk still represented 37% of whole area of biomechanical effects, and even reached 43% for *Picea abies*, where pit-mounds were exceptionally large. The biomechanical effects connected with *Picea abies* were generally more important than expected, based on the proportion of tree species in the forest. While the proportion of *Picea abies* in Boubin was only 38%, the proportion of relevant biomechanical processes represented 59% of all effects.

From the viewpoint of area the second most important BETs was trunk displacement. Displacement of soil and rock fragments due to radial trunk growth occupied an area of 76 $m^2\ ha^{-1}$.

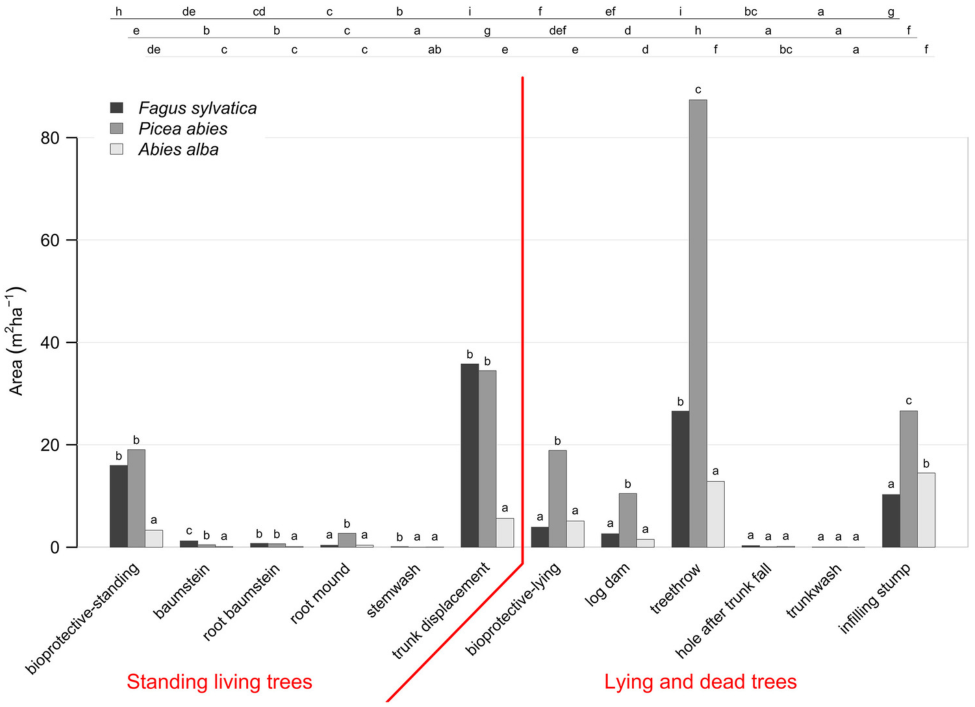


Fig. 5 Areas associated with the studied biomechanical effects of trees according to tree species. See Fig. 3 for details.

The opposite process, decay of dead stump cylinders and root systems known as stump infilling occupied an area of 51 m^2 ha^{-1}. Apart from *Picea abies* stumps, there were also thick stumps present from recently dying *Abies alba* (as a result of air pollution in the 1980s to the 1990s). The bioprotective functions of standing (38 m^2 ha^{-1}) and lying (28 m^2 ha^{-1}) trees were also not negligible, with log dams covering approximately half the area of lying trees. All other effects of trees covered ≤ 5 m^2 ha^{-1}.

Although the proportions of smaller- and intermediate-diameter trees on the site were almost equal in terms of area, the biomechanical effects of medium trees clearly predominated (Fig. 6). Interestingly, even though thick trees of DBH ≥ 75 cm represented only 14% of trees, they represented 34% of the area of biomechanical effects. These thick trees significantly contributed particularly to trunk displacement, baumstein, treethrow and stump infilling. The best fitting model between DBH and the most important process – treethrows – showed a linear relationship (AIC values for linear, quadratic and cubic model were 1741, 1836 and 1961, respectively) according to the equation $b = 0.15851 \times a$, where a is DBH (in centimeters) and b represents the area of treethrow pit-mounds (in m^2); relevant coefficient of determination $R^2 = 0.78$ (Fig. S2).

3.3 Volumes of biomechanical effects

A total of 322 m^3 ha^{-1} of soil and regolith was transported through studied biomechanical effects of the current generation of forest plus additional 57 m^3 ha^{-1} associated in former treethrow pit-mounds currently without uprooted trunk. A substantial proportion was represented by uprootings, which accounted for 39% of this volume (48% if all visible treethrow pit-mound forms are calculated), with an average volume of 2.8 m^3 $tree^{-1}$. The total volume of all treethrow forms, including microtopographical features already lacking the uprooted trunk, was 181 m^3 ha^{-1} (95%

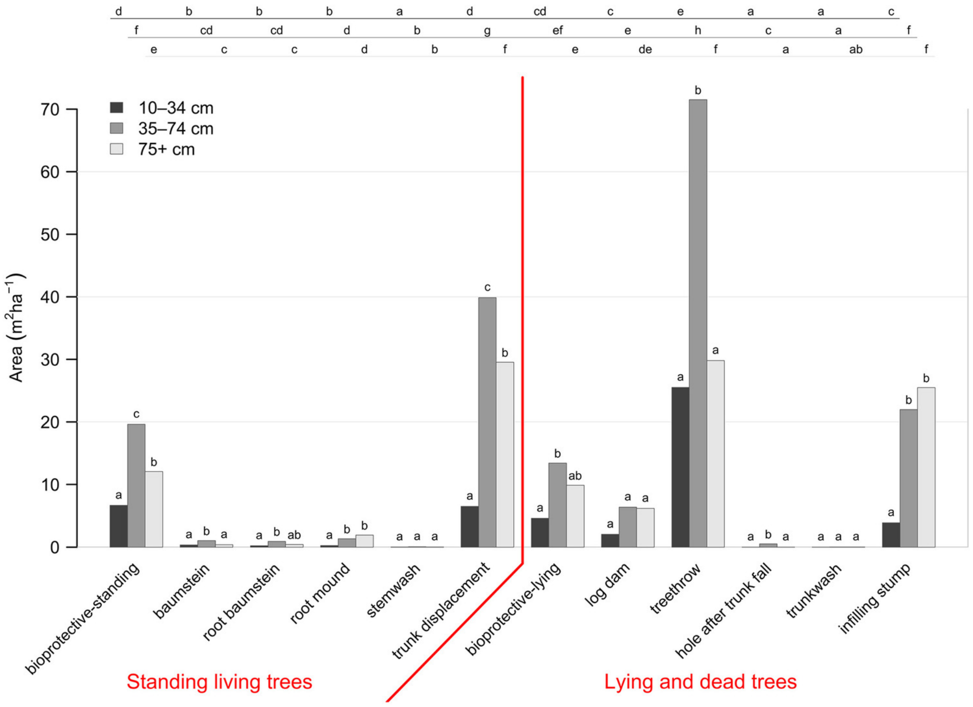


Fig. 6 Areas associated with the studied biomechanical effects of trees according to the diameter of trees at breast height. See Fig. 3 for details.

confidence interval = 152.7–214.5 m^3). In this study, *Picea abies* was most common among the more recent treethrows with a trunk still present (97 m^3 ha^{-1}). *Picea abies* was again the main tree species with which biomechanical phenomena were connected.

In terms of associated soil volume, the second most important effect of trees was the radial growth of roots and trunk displacement (103 m^3 ha^{-1}), followed by opposite process, i.e. infilling of decomposed stump cylinders and root systems, consisting of 85 m^3 ha^{-1} (Fig. 7). The bioprotective function of standing and lying trees represented 5 and 3 m^3 ha^{-1}, respectively. None of the additional effects, i.e. root mound, stemwash, trunkwash, a hole after trunk fall, and root baumstein, reached even 1 m^3 ha^{-1}.

Despite their lower proportion, from the viewpoint of associated soil volume, thick trees had the same significance as the predominant intermediate-diameter trees (Fig. 8). Whereas the studied biomechanical processes of thick trees with DBH ≥ 75 cm affected 152 m^3 ha^{-1}, intermediate-diameter trees with DBH from 35 to 75 cm affected 145 m^3 ha^{-1}. Even though trees of DBH < 35 cm represented 56% of tree individuals, they affected only 14% of the soil volume, notable through treethrows. This clearly suggests a non-linear relationship between tree dimensions and the volume of affected soil. The best fitting model between DBH and treethrows was a quadratic relationship (AIC values for linear, quadratic and cubic model were 1680, 1656 and 1699, respectively), according to the equation $b = 0.001209 \times a^2$, where a represents DBH (in centimeters) and b represents the volume of soil affected by uprooting (in m^3).

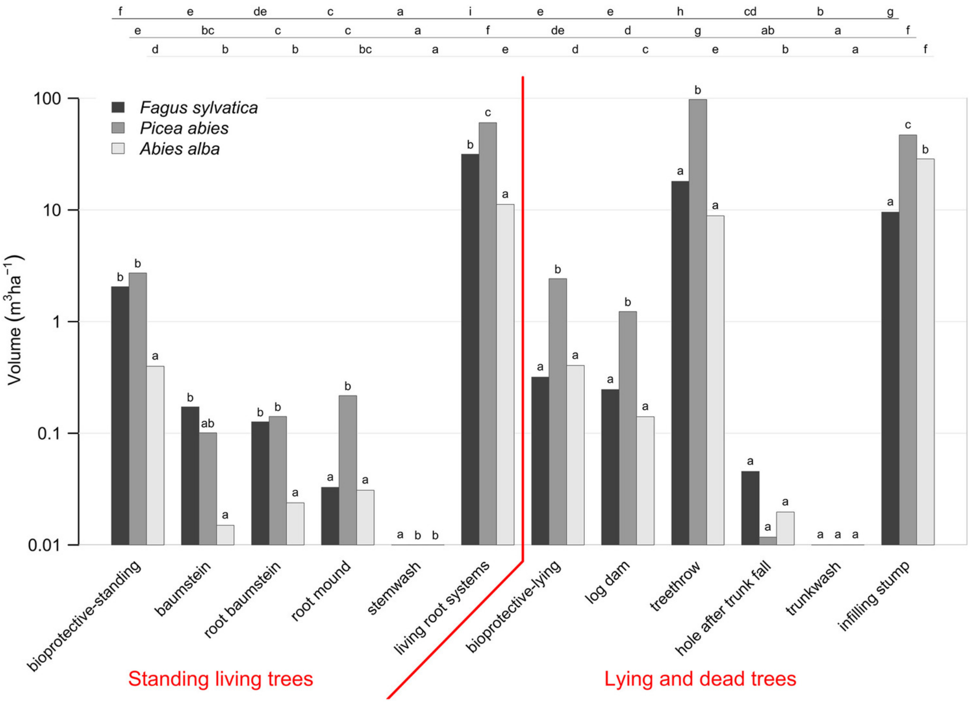


Fig. 7 Volumes of soil (organic and mineral horizons) and regolith associated with the studied biomechanical effects of trees according to tree species. See Fig. 3 for details.

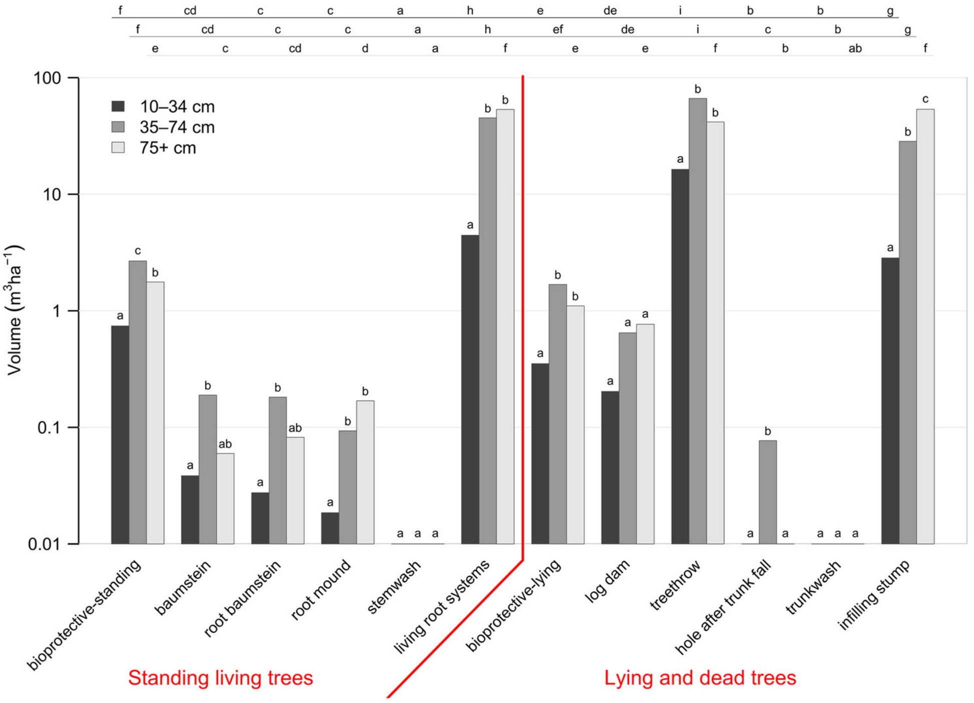


Fig. 8 Volumes of soil (organic and mineral horizons) and regolith associated with the studied biomechanical effects of trees according to the diameter of trees at breast height. See Fig. 3 for details.

4 Discussion

4.1 Magnitude and relative importance of BETs

The lower frequency of BETs in lying trunks compared to standing is most likely related to their shorter average lifespan. While the physical age of a tree in temperate mountain old-growth forests can exceed 400–500 years (e.g. Šamonil et al. 2013a), during which they actively (e.g. root mound) and passively (e.g. bioprotective function) participate in biogeomorphic processes, lying trunks decompose during no more than 100 years (e.g. Lombardi et al. 2008). Apart from shorter longevity the decreasing bioprotective function of the laying trees was also caused by their frequent orientation along the upslope–downslope axis. When the direction of the trunk is perpendicular to elevation contours, the bioprotective process proceeds only exceptionally, for example when the trunk is adjacent to a treethrow mound. *Abies alba* trunks persist even longer than other tree species, which probably amplify their increasing bioprotective function.

We also observed species specific effects in other studied phenomena. The earlier-mentioned affinity of *Picea abies* to soils with histic horizons without any rock fragments presumably decreased the frequency of trunk baumsteins and root baumsteins in this species. On the contrary, decreased evidence of root mound in *Fagus sylvatica* is obviously connected with its distinct root architecture with a higher proportion of deeper roots (e.g. Stokes et al. 2007).

The occurrence of root mounds significantly increased with increasing diameter of trees. However, even in the thickest trees its proportion reached only 21%. This suggest that the soil surrounding trunk bases was predominantly compacted during the radial growth of trees without its significant vertical displacement. Displacement was more visible in the largest trees where the biggest amount of material was transported by radial tree growth. Significantly increasing proportion of trunk and root baumsteins in thicker trees is probably associated with increasing probability of such trees to be in direct contact with rock fragments.

Stemwash and trunkwash were introduced by Phillips et al. (2017) in the Carpathians. Both phenomena were much more frequent on flysch in the Western Carpathians compared to on gneiss in the Šumava Mountains. Coarser fine earth (loamy coarse sand in Boubin versus clay in the Carpathians) and trunk bases covered by mosses probably decreased these processes in Boubin. Stemwash and trunkwash were both more frequently observed in *Fagus sylvatica*, which has smooth bark, but differences between tree species were not statistically significant.

An increasing proportion of the biomechanical effects of lying and dead trees after recalculating the frequencies of BETs to the areas and volumes of affected soil is in line with the results of Phillips & Marion (2006), who observed the same in hardwoods and coniferous forests in Arkansas, and Šamonil et al. (2013b) in central European mountain forests. These results probably follow from the widely observed non-linear relationship between individual tree dimensions and the volume of affected soil (see Roering et al. 2010; Sobhani et al. 2014). Total areas of treethrow pit-mound pairs in Boubin roughly corresponds with other central European studies, where pit-mounds usually covered between 4% and 30% of the area (see review by Šamonil et al. 2010).

Total volumes of soil associated with tree uprooting in Boubin generally agrees with results from several studies on other temperate forests on different bedrock. For example, Šamonil et al. (2016) found 214–225 $m^3 ha^{-1}$ of soil transported by uprootings on an outwash in Michigan, and Phillips et al. (2017) calculated 263 $m^3 ha^{-1}$ on flysch in the Czech Republic. Our results support the idea of a crucial role of treethrows in lateral biogeomorphological processes in some forest ecosystems (Gabet et al. 2003; Gallaway et al. 2009; Gabet & Mudd 2010; Phillips 2010). The average volume of single treethrow pit-mound pair reached 2.8 m^3 in Boubin, which is slightly above the average of previously published studies volumes of individual treethrow pit-mounds from 0.1 to 5.6 m^3 (see review by Pawlik 2013).

4.2 Geomorphic significance of BETs

Some BETs have been both widely recognized and extensively studied, such as effects of uprooting and of treethrow pit-mound topography (review by Šamonil et al. 2010), and the general bioprotective effects of forest cover (e.g. Stevens 1997). Others, e.g. mass displacement and stump cavity infilling, have been widely recognized (Phillips & Marion 2006), but there has been little research on the specific effects or efforts to quantify their impacts. Yet other BETs, such as trunk and stemwash, have received very little attention (Phillips et al. 2017) or, like holes created by trunkfall or root baumsteins, are assessed for the first time here. As far as we know, this is the first study to provide comparative, quantitative estimates of 11 different biomechanical effects or processes.

These results confirm the biogeomorphic importance of uprooting in temperate forests minimally influenced by harvesting and management. Especially in mountain forested landscapes, tree uprooting may represent a crucial biogemorphic agent of hillslope denudation (Phillips et al. 2017). Our results simultaneously confirm that while some processes (e.g. mass displacement by trunk and root growth) are ubiquitous and associated with all trees growing in soil or regolith, others are rarer and associated with only some individuals, such as stemwash and trunkwash. Spatial expression of the pattern of biogeomorphic processes will require future attention.

Results of this study also show a significant relationship between BETs and tree size and species. Because DBH is correlated with age (e.g. Šebková et al. 2012), and growth rates are typically non-linear, this suggests that BETs are likely to vary over the lifespan of an individual tree or a forest stand, and with changes in species composition. This further suggests the need for future magnitude–frequency type studies. For instance, what are the relative biogeomorphic impacts of *Picea abies* harvested and regrown every 80 years (a typical rotation age in the region), versus those that die and regenerate naturally every 100, 200, or 500 years?

The BETs documented in this study represent a non-trivial amount of geomorphic work. Though the effects are spatially concentrated, the 322 $m^3\,ha^{-1}$ represents a volume equivalent to a 32.2 mm thickness across the entire forest area. Even if these effects are only repeated every 200 to 500 years, this is equivalent to a rate of 0.161 to 0.064 $mm\,yr^{-1}$. In mass terms, with a typical bulk density of 1.1 $t\,m^{-3}$, 322 m^3 equates to 354 tonnes, or about 1.8 to 0.7 $t\,ha^{-1}\,yr^{-1}$ over 200 to 500 years. These rough estimates show that even under conservative guesses as to recurrence intervals, these BETs account for a significant amount of geomorphic work, in the same range as many measurements of fluvial denudation rates (e.g. Milliman & Syvitski 1992; Summerfield & Hulton 1994).

Also note that we concentrated on visible component of processes. Trees have important mechanical and biochemical effects deeper in the regolith, and where they contact bedrock, at the weathering front (Pawlik et al. 2016). Given this, and the conservative approach used to measure or estimate BETs in this study, their overall magnitude must be significantly greater than reported here.

This work also suggests that future work should specifically link BETs to forest management practices, rotation ages, and species compositions, as well as in different climate and topographic settings.

5 Conclusion

We analyzed in detail the visible biomechanical effects of 4000 trees in mountain old-growth forest soils in the Czech Republic. The bioprotective function was the most frequent phenomenon visible in some short-lived lying trunks, reflecting rapid hillslope processes in Boubin. The areas and volumes of the BETs were dominated by treethrow dynamics, followed by mass displacement due to radial growth of roots and trunk base and subsequently by stump infilling. These results demonstrate the ability of trees to significantly contribute to soil and landscape evolution. The total quantity of geomorphic work found here, even though incomplete and conservatively calculated, indicates magnitudes comparable to fluvial denudation rates.

Supporting information Fig. S1. A detailed approach for evaluating the measurement of biomechanical effects in the field and subsequent calculations of associated soil areas and volumes. (a) treethrow, (b) infilling stump, (c) bioprotective function of a standing tree, (d) bioprotective function of a lying tree including a log dam, (e) baumstein plus trunk displacement, (f) root baumstein, (g) root mound, (h) a hole after trunk fall, (i) stemwash, (j) trunkwash. Fig. S2. Relationship between diameter at breast height (DBH) of uprooted trees and area of the root plate (n = 446), grey band represents 95% confidence interval. Supporting information can be found at https://doi.org/10.1002/esp.4304

Acknowledgements The authors thank their colleagues from the 'Blue Cat research team' for field data measurement. This research was supported by Grantová Agentura České Republiky (the Czech Science Foundation), project No. 16-15319S, and partially by the Forests of the Czech Republic, state enterprise and the Šumava National Park, state contributory organization, contract No. 6/2016.

References

Benjamini Y., Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)* 57: 289–300.

Bennie A.T. 1991. Growth and mechanical impedance. In Plant Roots: The Hidden Half, Y Waisel, A Eshel, U Kafkafi (eds). Marcel Dekker: New York.

Bolte A., Rahmann T., Kuhr M., Pogoda P., Murach D., Gadow K. 2004. Relationships between tree dimension and coarse root biomass in mixed stands of European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* [L.] Karst.). *Plant and Soil* 264: 1–11.

Bormann B.T., Spaltenstein H., McClellan M.H., Ugolini F.C., Cromack K., Jr, Nay S.M. 1995. Rapid soil development after windthrow disturbance in pristine forests. *Journal of Ecology* 83: 747–757.

Caine T.N. 1986. Sediment movement and storage on alpine slopes in the Colorado Rocky Mountains. In Hillslope Processes, Abrahams A. (ed). Allen and Unwin: Boston, MA; pp. 115–137.

Chytrý M. (ed). 2013. Vegetace České republiky 4. Lesní a křovinná vegetace. Academia: Prague.

Daněk P., Šamonil P., Phillips J.D. 2016. Geomorphic controls of soil spatial complexity in a primeval mountain forest in the Czech Republic. *Geomorphology* 273: 280–291.

Gabet E.J., Reichman O.J., Seabloom E.W. 2003. The effect of bioturbation on soil processes and sediment transport. *Annual Review of Earth and Planetary Sciences* 31: 249–273.

Gabet J.E., Mudd S.M. 2010. Bedrock erosion by root fracture and treethrow: a coupled biogeomorphic model to explore the humped soil production function and the persistence of hillslope soils. *Journal of Geophysical Research* 115(F04005): 1–14.

Gallaway J.M., Martin Y.E., Johnson E.A. 2009. Sediment transport due to tree root throw: integrating tree population dynamics, wildfire and geomorphic response. *Earth Surface Processes and Landforms* 34: 1255–1269.

Hoffman B.S.S., Anderson R.S. 2013. Tree root mounds and their role in transporting soil on forested landscapes. *Earth Surface Processes and Landforms* 39: 711–722.

Karpachevskiy L.O., Cholopova L.B., Prosvirina A.P. 1980. O dinamike stroenija pocvennogo pokrova v lesnych biogeocenozach. *Pocvovedenie* 5: 40–49.

Lehre A.K. 1987. Rates of soil creep on colluvium-mantled hillslopes in north-central California. In Erosion and Sedimentation in the Pacific Rim, Beschta R., Blinn T., Grant C., Ice G., Swanson F. (eds). IAHS Press: Wallingford; pp. 91–100.

Lombardi F., Cherubini P., Lasserre B., Tognetti R., Marchetti M. 2008. Tree rings used to assess time since death of deadwood of different decay classes in beech and silver fir forests in the central Appenines (Molise, Italy). *Canadian Journal of Forest Research* 38: 821–833.

Lutz H.J. 1960. Movement of rocks by uprooting of forest trees. *American Journal of Science* 258: 752–756.

Michéli E., Schad P., Spaargaren O. (eds). 2007. World Reference Base for Soil Resources 2006, First Update 2007, World Soil Resources Reports No 103. FAO: Rome.

Milliman J.D., Syvitski J.P.M. 1992. Geomorphic/tectonic control of sediment discharge to the ocean: the importance of small mountainous rivers. *Journal of Geology* 100: 525–544.

Naylor L.A. 2005. The contributions of biogeomorphology to the emerging field of geobiology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 219: 35–51.

Pawlik Ł. 2013. The role of trees in the geomorphic system of forested hillslopes – A review. *Earth-Science Reviews* 126: 250–265.

Pawlik Ł., Migoń P., Owczarek P., Kacprzak A. 2013. Surface processes and interactions with forest vegetation on a steep mudstone slope, Stolowe Mountains, SW Poland. *Catena* 109: 203–216.

Pawlik Ł., Phillips J.D., Šamonil P. 2016. Roots, rock, and regolith: biomechanical and biochemical weathering by trees and its impact on hillslopes—A critical literature review. *Earth-Science Reviews* 159: 142–159.

Phillips J.D. 2010. The convenient fiction of steady-state soil thickness. *Geoderma* 156: 389–398.

Phillips J.D., Marion D.A. 2006. Biomechanical effects of trees on soil and regolith: beyond treethrow. *Annals of the Association of American Geographers* 96: 233–247.

Phillips J.D., Šamonil P., Pawlik L., Trochta J., Daněk P. 2017. Domination of hillslope denudation by tree uprooting in an old-growth forest. *Geomorphology* 276: 27–36.

R Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing: Vienna. https://www.r-project.org/

Roering J.J., Marshall J., Booth A.M., Mort M., Jin Q. 2010. Evidence for biotic controls on topography and soil production. *Earth and Planetary Science Letters* 298: 183–190.

Šamonil P., Doleželová P., Vašíčková I., Adam D., Valtera M., Král K., Janík D., Šebková B. 2013a. Individual-based approach to the detection of disturbance history through spatial scales in a natural beech-dominated forest. *Journal of Vegetation Science* 24: 1167–1184.

Šamonil P., Král K., Hort L. 2010. The role of tree uprooting in soil formation: a critical literature review. *Geoderma* 157: 65–79.

Šamonil P., Schaetzl R.J., Valtera M., Goliáš V., Baldrian P., Vašíčková I. 2013b. Crossdating of disturbances by tree uprooting: can treethrow microtopography persist for 6,000 years? *Forest Ecology and Management* 307: 123–135.

Šamonil P., Valtera M., Schaetzl R.J., Adam D., Vašíčková I., Daněk P., Janík D., Tejnecký V. 2016. Impacts of old, comparatively stable, treethrow microtopography on soils and forest dynamics in the northern hardwoods of Michigan, USA. *Catena* 140: 55–65.

Šamonil P., Vašíčková I., Daněk P., Janík D., Adam D. 2014. Disturbances can control fine-scale pedodiversity in old-growth forest: is the soil evolution theory disturbed as well? *Biogeosciences* 11: 5889–5905.

Schaetzl R.J., Thompson M.I. 2015. Soils – Genesis and Geomorphology, second edn. Cambridge University Press: Cambridge 795 pp.

Schoeneberger P.J., Wysicki D.A., Benham E.C., Broderson W.D. 1998. Field Book for Describing and Sampling Soils. Natural Resources Conservation Service, USDA, National Soil Survey Center: Lincoln, NE.

Šebková B., Šamonil P., Janík D., Adam D., Král K., Vrška T., Hort L., Unar P. 2011. Spatial and volume patterns of an unmanaged submontane mixed forest in Central Europe: 160 years of spontaneous dynamics. *Forest Ecology and Management* 262: 873–885.

Šebková B., Šamonil P., Valtera M., Adam D., Janík D. 2012. Interaction between tree species populations and windthrow dynamics in natural beech-dominated forest, Czech Republic. *Forest Ecology and Management* 280: 9–19.

Shouse M.L., Phillips J.D. 2016. Soil deepening by trees and the effects of parent material. *Geomorphology* 269: 1–7.

Sobhani V.M., Barrett M., Peterson C.J. 2014. Robust prediction of treefall pit and mound sizes from tree size across 10 forest blowdowns in eastern North America. *Ecosystems* 17: 837–850.

Stevens V. 1997. The Ecological Role of Coarse Woody Debris: An Overview of the Ecological Importance of CWD in B.C. Forests, Working paper 30. Ministry of Forests Research Program: Victoria, BC.

Stokes A., Ghani M.A., Salin F., Danjon F., Jeannin H., Berthier S., Kokutse A.D., Frochot H. 2007. Root morphology and strain distribution during tree failure on mountain slopes. Eco-and Ground Bio-Engineering: The Use of Vegetation to Improve Slope Stability. *Developments in Plant and Soil Sciences* 103: 165–173.

Summerfield M.A., Hulton N.J. 1994. Natural controls of fluvial denudation rates in major world drainage basins. *Journal of Geophysical Research* 99: 13871–13883.

Welzholz J.C., Johann E. 2007. History of protected forest areas in Europe. In Action E 27 Protected Forest Areas in Europe – Analysis and Harmonisation (PROFOR): Results, Conclusions and Recommendations, Frank G., Parviainen J., Vandekerkhove K., Latham J., Schuck A., Little D. (eds). Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW): Vienna; pp. 17–40.

Paper 5

Breakage or uprooting: How tree death type affects hillslope processes in old-growth temperate forests

Pavel Šamonil
Pavel Daněk
Dušan Adam
Jonathan D. Phillips

Geomorphology 299 (2017), 76–84

Abstract

Tree breakage and uprooting are two possible scenarios of tree death that have differing effects on hillslope processes. In this study we aimed to (i) reveal the long-term structure of the biomechanical effects of trees (BETs) in relation to their radial growth and tree death types in four old-growth temperate forests in four different elevation settings with an altitudinal gradient of 152–1105 m a.s.l., (ii) quantify affected areas and soil volumes associated with the studied BETs in reserves, and (iii) derive a general model of the role of BETs in hillslope processes in central European temperate forests.

We analyzed the individual dynamics of circa 55,000 trees in an area of 161 ha within four old-growth forests over 3–4 decades. Basal tree censuses established in all sites in the 1970s and repeated tree censuses in the 1990s and 2000s provided detailed information about the radial growth of each tree of DBH ≥ 10 cm as well as about types of tree death. We focused on the quantification of: (i) surviving still-living trees, (ii) new recruits, (iii) standing dead trees, (iv) uprooted trees, and (v) broken trees. Frequencies of phenomena were related to affected areas and volumes of soil using individual statistical models.

The elevation contrasts were a significant factor in the structure of BETs. Differences between sites increased from frequencies of events through affected areas to volumes of soil associated with BETs. An average 2.7 $m^3\ ha^{-1}\ year^{-1}$ was associated with all BETs of the living and dying trees in lowlands, while there was an average of 7.8 $m^3\ ha^{-1}\ year^{-1}$ in the highest mountain site. Differences were caused mainly by the effects of dying trees. BETs associated with dead trees were 7–8 times larger in the mountains. Effects of dying trees and particularly treethrows represented about 70% of all BETs at both mountain sites, while it was 58% at the highland site and only 32% at the lowland site. Our results show a more significant role of BETs in hillslope processes including slope denudation in the mountains. We would expect a significant decrease of the biogeomorphic effect of trees in managed forests, but with a greater relative effect in mountains.

P. Šamonil[a,b]*, P. Daněk*[a,c]*, D. Adam*[a]*, J.D. Phillips*[d]

[a] Department of Forest Ecology, The Silva Tarouca Research Institute, Brno, Czech Republic [b] Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic [c] Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic [d] Earth Surface Systems Program, Department of Geography, University of Kentucky, Lexington, KY, USA

1 Introduction

Recent studies have revealed the significant effect of organisms in the dynamics and spatial patterns of hillslope processes (Pawlik et al. 2016). The surprisingly large soil and regolith mass transported annually by organisms (e.g. Phillips 2009) has gradually shifted our view of slope dynamics from the traditional emphasis on pure abiotic factors (geomorphology) to more complex concepts of abiotic-biotic driving mechanisms (biogeomorphology, Viles et al. 2008) and their mutual formation (eco-evolution dynamics, review by Corenblit et al. 2011). In regions with significant biological activity, geomorphic work performed by biota, frequently referred to as a biogenous creep (Lehre 1987), may be larger than that associated with endogenic processes and with the kinetic energy of denudation (Tricart 1972, Phillips 2009).

Forested landscapes may be an example of such highly biologically active regions, where trees are likely a crucial agent of biotic processes. This idea has been recently supported for instance by Šamonil et al. (2018b) in a central European old-growth mountain forest. They found that at least 322 m^3 ha^{-1} were associated with various biomechanical effects of trees (BET) such as bioprotectection, root mounding, stemwashing, baumstaining or tree uprooting. Tree uprooting dynamics were the most important studied phenomenon in terms of mass volume in that mountain forested landscape. The exceptional significance of tree uprooting dynamics in biogeomorphic processes has also been found in different temperate forests, for example by Šamonil et al. (2015) on an outwash in Michigan and by Phillips et al. (2017) on flysch in the Czech Republic. Within these studies, our team found 220 and 263 m^3 of soil per hectare associated with tree uprooting. Tree uprooting displaced about 2.9 m^3 of soil per year and hectare on flysch (Phillips et al. 2017). Šamonil et al. (2009, 2013a) further estimated that approximately 30% of all trees die as a result of uprooting in temperate central European primeval forests, and theoretically, within 500–3000 years every site in such forests is likely to be disturbed by uprooting (see also Skvorcova et al. 1983). So-called rotation periods, showing how often an area equivalent to an entire study area is disturbed (Pickett & White 1985), are comparable or even shorter in other temperate or boreal forests (reviews by Schaetzl et al. 1989, Ulanova 2000, Šamonil et al. 2010a, Pawlik 2013).

However, the uprooting of a tree is only one scenario of tree death. Another possible scenario is associated with the break of the trunk (of a living or standing dead tree) and slow decomposition of the remaining tree stump and unaffected root systems. We consider both processes as a disturbance sensu Pickett & White (1985, disturbance = death of at least one canopy tree). If uprooting affects approximately 30% of all trees in temperate old-growth forests, trunk breakage accompanies death in the remaining circa 70% of trees (Šamonil et al. 2009, Šamonil et al. 2013a).

These two possibilities, which can occur in dying or recently dead trees in any forest type, are naturally associated with completely different biogeomorphic and soil-evolutionary processes. In the case of a tree uprooting, soil and regolith in the form of the root plate are completely mixed or even overturned (Schaetzl 1986, Gabet et al. 2003, Šamonil et al. 2015, Pawlik 2013). Pedogenesis is reset by this soil disturbance and proceeds from the beginning on newly-formed microtopographical treethrow mounds and within the pits, usually along completely different evolutionary trajectories. Soil mixing and post-disturbance pedogenesis associated with treethrows have been described in detail in various climate and geological regions by Skvorcova et al. (1983), Vassenev & Targulian (1995), Bormann et al. (1995), Embleton-Hamann (2004), Kooch et al. (2014), and Šamonil et al. 2010b, Šamonil et al. 2015, Šamonil et al. 2018a. On the other hand, biogeomorphic and soil-evolutionary studies on tree stumps (see 'basket' or 'egg cup' podzols in Bloomfield 1953, Schaetzl 1990, Barrett 1997, Retallack 2001) have provided a totally different picture. Soil and regolith are not disturbed during the trunk breakage, and pedogenesis may continue without resetting. The subsequent gradual decay of the trunk base and root system are followed by infilling of these empty spaces by the surrounding soil (Phillips & Marion 2006).

Tree death affects not only local soil evolutionary trajectories on the pedon scale but, through long-term recurrences of events, also the spatial patterns of soils and forest structure on stand and landscape scales. The occurrence of uprootings or breakages is dependent on local variability of environmental conditions and historical contingency (Mueller & Cline 1959, Fumiko et al. 2006, Peterson 2007, Xi et al. 2008, Harcombe et al. 2009), which makes the appearance of these phenomena in forests nonrandom, and complex spatial pattern of disturbance regimes may arise (Šamonil et al. 2014). Moreover, all these processes seem to be species specific. The natural regeneration of some tree species is strongly dependent on microsites originating from the disturbance of the former generation of trees (e.g. treethrow mounds, see Zeide 1981, Simon et al. 2011, Šebková et al. 2012, Šamonil et al. 2016). The complex tree-soil system in primeval forests with many feedbacks potentially results in the impact of trees, including tree death, being a type of biogeomorphic ecosystem engineering (Wilby 2002, Verboom & Pate 2006, Corenblit et al. 2011, Pawlik et al. 2016).

In this study we focused on the quantification of tree uprootings and breakages on a multidecadal time scale in contrasting altitudinal settings in central European old-growth forests. We hypothesized differences in frequencies, areas, and soil volumes associated with these phenomena, which imply different biogeomorphic and soil evolutionary roles of trees along this gradient. We analyzed the dynamics of > 55,000 trees over 33–38 years in 161 ha of forest area. As far as we know, this study is unique and has the potential to improve our knowledge of forest biogeomorphology, ecology, pedology and ecosystem engineering. We further present implications for forest management.

2 Material and methods

2.1 Study sites

The research took place in four forest reserves in the Czech Republic (Fig. 1, Table 1). The localities occur along an altitudinal gradient from 152 to 1105 m a.s.l. on deep (classification of georelief according to Demek 1987), moderately acidic soils. All these ecosystems are represented by spontaneously developed forests under strict protection at least since 1932. Žofínský prales (hereinafter Zofin) has been protected since 1838 and is the 4th oldest forest reserve in Europe, and belongs to the global network of forest research plots ForestGeo (www.forestgeo.si.edu/). The sizes of the sites ranged from 17 to 74 ha.

2.2 Data collection and processing

The health status (living tree, dead standing tree, dead uprooted tree, breakage etc.), dimensions and species of all standing and lying tree individuals of diameter at breast height (DBH) ≥ 10 cm within all reserves (in total 160.5 ha) was first evaluated in the 1970s (Průša 1985). The precise position of each tree was recorded using a theodolite. A map of trees was subsequently developed from the collected data (e.g. Šebková et al. 2011). The same tree census was repeated in the

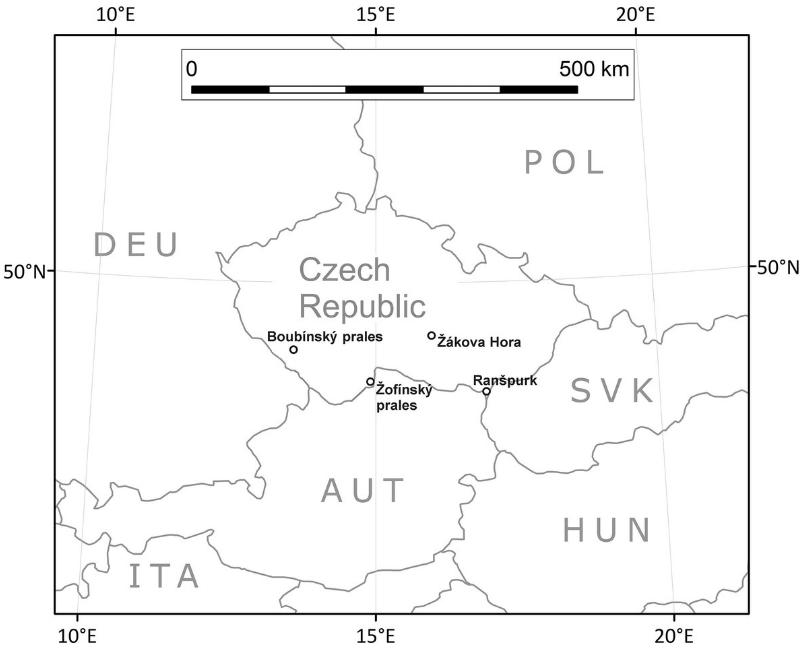


Fig. 1 Study sites location map.

Table 1 Key characteristics of the studied sites relevant to environmental conditions, history, and research data.

Landscape, locality	Lowlands, Ranspurk	Highlands, Zakova Hora	Mountains, Zofin	Mountains, Boubin
Altitude range [m]	152–155	725–800	730–837	925–1105
Latitude	48°40′43″	49°39′20″	48°39′58″	48°58′43″
Longitude	16°56′56″	15°59′39″	14°42′28″	13°48′43″
Mean slope [°]	1.7	8.9	8.6	14.4
Mean annual temperature [°C]	9.9	6.1	6.2	4.9
Mean annual precipitation [mm]	545	781	866	1067
Geology	Fluvial gravels	Gneiss	Granite	Gneiss
Predominant soils	Fluvisols, Gleysols	Cambisols, Podzols	Podzols, Gleysols	Podzols, Gleysols
Strictly protected since	1932	1929	1838	1858
Studied area [ha]	22.25	17.46	74.20	46.62
Initial tree census year	1973	1974	1975	1972
Last tree census year	2006	2011	2008	2010
No. of living trees (in 2000s)	6249	5412	15,221	9798
No. of dead trees (in 2000s)	1110	1183	8890	7629
No. of studied treethrow pit-mound pairs	79	86	456	414
No. of studied tree bases	629	426	248	2346

1990s and in 2000s; in total 55,492 trees were included. These precise tree censuses allowed us to identify each formerly recorded tree and to assess its current status. By comparing data from the 2000s and the 1970s we studied the dynamics of the tree layer. We recorded the number of surviving living trees, number of recruits as well as number of dead trees. We distinguished uprooted, broken or standing dead trees. Because the studies were conducted in protected areas, there were no cut or harvested trees. The census from the 1990s was used to help clarify cases where the fate of individual trees between the 1970s and 2000s was uncertain.

Apart from frequencies of individual events, we studied areas of geomorphic impacts associated with them as well, because this is closely linked to ecosystem engineering and niche construction. Old generations of trees create specific microsites (e.g. treethrow pit-mounds, lying trunks) more or less favorable for tree regeneration. Through these positive or negative feedbacks, one tree species can support or block the regeneration of the same taxon or others. Furthermore, the area of a tree stump represents the potential area of stump hole. Areas of these potential microsites were approximated using basal geometrical shapes such as ellipses (treethrow pit-mound), or circles (living trees, dead standing trees, stumps, etc.). All these forms were measured as horizontal projections on the surface. In total, 3649 diameters of trunks on the surface and 1035 treethrow pit-mounds were measured in the four forest reserves. Subsequently we calculated partial regression models to predict basal areas and treethrow pit-mound areas (R^2 ranged from 0.511 for the relationship between DBH and treethrow volume to 0.991 for the relationship between DBH and trunk base diameter).

We further evaluated the soil volume associated with the studied phenomena. Soil movement due to active (radial growth, treethrow) or passive (root system decomposition) effects of trees may represent important biogeomorphical and soil evolutionary information. Dimensions of 1035 treethrow pit-mounds were measured according to a technique developed by Šamonil et al. (unpublished, and their volumes were approximated by a half of an ellipsoid (Gabet et al. 2003, Pawlik 2013). A regression model between the DBH of trees and volume of treethrow pit-mounds was subsequently applied to all cases that were not directly measured.

The relationship between tree DBH and pit–mound area and volume was modelled using linear regression, with DBH and site as explanatory variables. To assure that the regression lines went through the origin (point (0, 0), i.e. a zero-DBH tree causes a pit–mound of zero dimensions) we only included the terms for DBH (linear or quadratic if significant) and its interaction with site. Because the data exhibited heteroscedasticity, the regression coefficients were tested using the HC4 heteroscedasticity-consistent covariance matrix estimator (Cribari-Neto 2004). To achieve more general results, data from sites that did not differ significantly were merged in a stepwise manner, resulting in several site groups within which the relation between tree DBH and the studied pit–mound property could be considered identical.

The volumes of root systems could not be directly measured in these strictly protected reserves. Therefore, we used standard allometric equations to obtain volumes of root systems based on the known DBH of trees. In the highlands and mountains (Zakova hora, Zofin, Boubin) we applied robust models calculated for *Fagus sylvatica* and *Picea abies* by Bolte et al. (2004). Spruce and beech greatly predominate at these three sites, so the spruce model was also used for the occasional *Abies alba* and the beech model for other rare broadleaves (*Acer* spp., *Ulmus* spp., *Sorbus aucuparia*). In the lowland floodplain forest (Ranspurk) we used an allometric equation calculated directly for this forest type and region (Krejza et al. 2017). Those authors integrated formerly published partial equations for *Quercus* spp. and *Fraxinus* spp. (Vyskot 1976, Tatarinov et al. 2008) into a general model valid in central European floodplain forests.

Differences in the individual effects of trees among localities were tested using bootstrapping. First, 1000 resamples were used to obtain bootstrap distributions of the differences between all pairs of localities. Next, two-sided probabilities of these differences being zero were computed, and pairs significantly different at $\alpha = 0.05$ were identified after correction for multiple testing by controlling the false discovery rate (Benjamini & Hochberg 1995). The alpha level for statistical testing was set to 0.05 and all analyses were performed in R (R Core Team 2016).

3 Results

3.1 Forest size structure and frequencies of tree death types

The size structure of the living tree biomass (survivors + recruits) was congruent in all forest ecosystems (Fig. 2), with the highest frequencies for thin trees and a sharp decrease for larger trees of DBH ≥ 100 cm. This right-skewed diameter distribution of trees is not surprising, and rather demonstrates the old-growth character of these forest ecosystems (Král et al. 2010). During the repeated tree census in the 2000s we found between 210 (Boubin) and 297 (Zakova hora) living trees of DBH ≥ 10 cm per hectare in the studied sites. We observed comparatively faster recruitment in the lowlands and highlands (Ranspurk, Zakova hora). While 4.4 tree individuals were recruited per year and hectare in the lowlands (Ranšpurk), there were only 2.7 and 1.0 trees at mountain sites (Table 2). On the contrary, both mountain sites had higher tree death events. Whereas 2.3–2.5 trees died per year in Ranspurk and Zakova hora, 3.8–4.2 died in Zofin and Boubin. This disproportion in the ratio between tree recruitment and death in these forest ecosystems suggests some differences in the proportion of developmental phases (Král et al. 2010).

Table 2 Mean characteristics of forest dynamics between the 1970s and 2000s at the studied sites. Differences between study sites were tested using bootstrapping (letters).

		Lowlands	Highlands	Mountains		
Property	Unit	Ranspurk	Zakova Hora	Zofin	Boubin	CI for c_v
Frequency						
Survivors	ind. ha^{-1} period^{-1}	130.4^{a}	178.9^{c}	128.1^{a}	172.9^{b}	0.17–0.19
Recruits	ind. ha^{-1} year^{-1}	4.4^{d}	3.2^{c}	2.7^{b}	1.0^{a}	0.49–0.52
Standing dead trees	ind. ha^{-1}	5.3^{a}	6.5^{a}	9.3^{b}	17.1^{c}	0.49–0.62
Broken trees	ind. ha^{-1} year^{-1}	1.6^{a}	1.5^{a}	1.9^{b}	1.9^{b}	0.09–0.14
Uprooted trees	ind. ha^{-1} year^{-1}	0.7^{b}	0.6^{a}	1.6^{c}	1.9^{d}	0.49–0.56
Area						
Surviving basal area	m^{2} ha^{-1} period^{-1}	43.9^{c}	38.9^{b}	44.8^{c}	37.1^{a}	0.08–0.11
Increment of basal area	m^{2} ha^{-1} year^{-1}	1.3^{a}	1.7^{c}	1.3^{a}	1.4^{b}	0.12–0.14
Basal area of standing dead trees	m^{2} ha^{-1}	2.3^{a}	1.6^{a}	3.7^{b}	5.0^{c}	0.39–0.63
Basal area of broken trees	m^{2} ha^{-1} year^{-1}	0.7^{ab}	0.7^{b}	1.1^{c}	0.6^{a}	0.26–0.33
Area of treethrow pit-mounds	m^{2} ha^{-1} year^{-1}	1.5^{a}	2.7^{b}	9.6^{c}	10.3^{d}	0.73–0.79
Volume						
Surviving root systems volume	m^{3} ha^{-1} period^{-1}	53.0^{d}	29.2^{a}	41.2^{b}	46.2^{c}	0.21–0.27
Increment of root systems	m^{3} ha^{-1} year^{-1}	1.5^{a}	1.5^{a}	1.6^{b}	2.3^{c}	0.23–0.26
Root systems of standing dead trees	m^{3} ha^{-1}	3.9^{b}	1.6^{a}	4.6^{b}	8.5^{c}	0.52–0.78
Root systems of broken trees	m^{3} ha^{-1} year^{-1}	0.9^{b}	0.7^{a}	1.4^{c}	1.0^{b}	0.26–0.35
Volume of treethrow root plates	m^{3} ha^{-1} year^{-1}	0.2^{a}	0.6^{b}	4.2^{c}	4.3^{c}	0.94–0.99

ind. = individuals

The inner structure of tree death types differed significantly between sites as well. Whereas 50% of trees that died since 1970s were due to uprooting in Boubin (1.9 tree individual ha^{-1} year^{-1}), only 31% died due to uprooting in Ranspurk (0.7 individual ha^{-1} year^{-1}). In the mountains, tree uprooting prevailed over trunk breakage, particularly in the category of thinner trees of DBH ≤ 40–50 cm. Mountain sites generally had higher occurrences of broken and standing dead trees as well (Table 2).

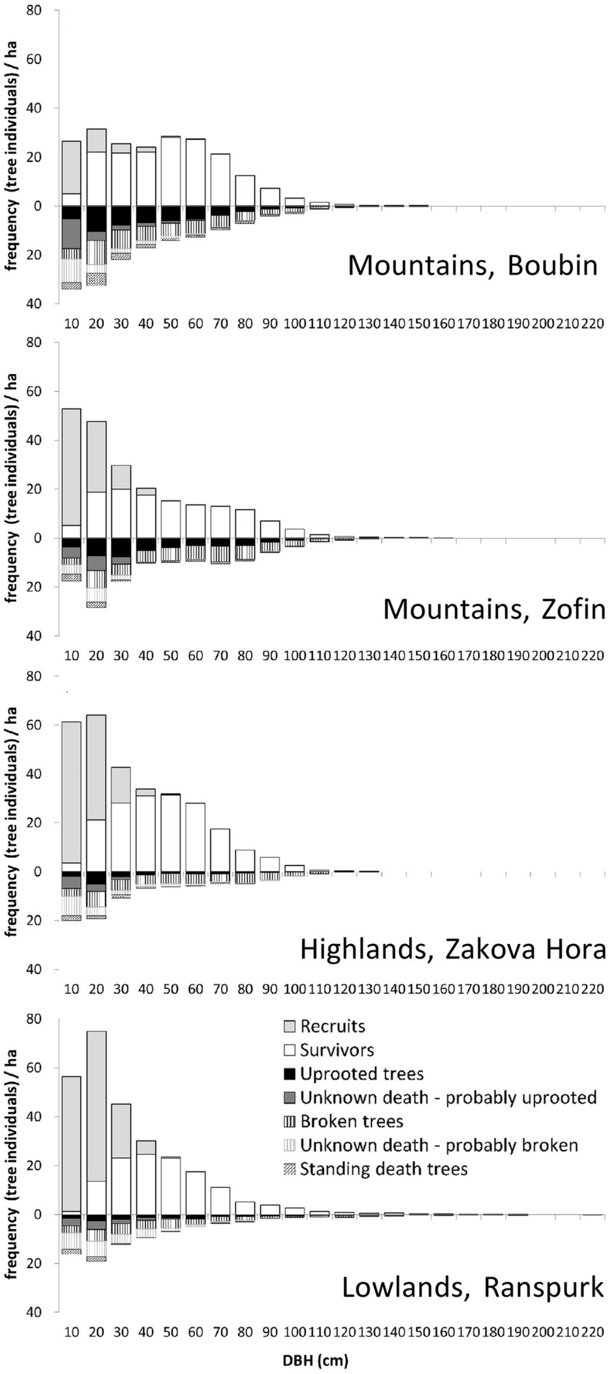


Fig. 2 Development of the tree biomass between the 1970s and 2000s in terms of frequencies of survivors, recruits or various death events in the four strictly protected forest reserves.

3.2 Areas affected by trees

The relationship between trunk DBH (x) and its diameter at surface height (DSH, y) was always best fitted by a linear model in the general form $y = ax$, with the constant (a) between 1.34 (most frequent) and 1.59. Spruce showed more pronounced basal flare ($a = 1.55–1.59$) compared to beech ($a = 1.34–1.49$). The elevation contrast was not a significant variable in the models. Based on these models, we then calculated the total basal areas of living, dead standing and broken trunks. Note that in many previous studies, basal area is computed based on the assumption that ground surface diameter ≈ DBH. Such approach can lead to underestimation of the significance of the studied processes by tens of percent.

Frequencies of uprooting events during 33–38 years (Fig. 2) were correlated to areas affected by uprooting phenomena (z) using simple regression models (Fig. 3). The area of treethrow features in a particular DBH category grew at altitude, but differences between Zakova hora, Zofin, and Boubin, though they existed, were not statistically significant. Finally, the model $z = 0.159305x$ was applied in these 3 sites. Areas affected by uprooted trees were generally much smaller in lowland Ranspurk, where $z = 0.054549x$ was used.

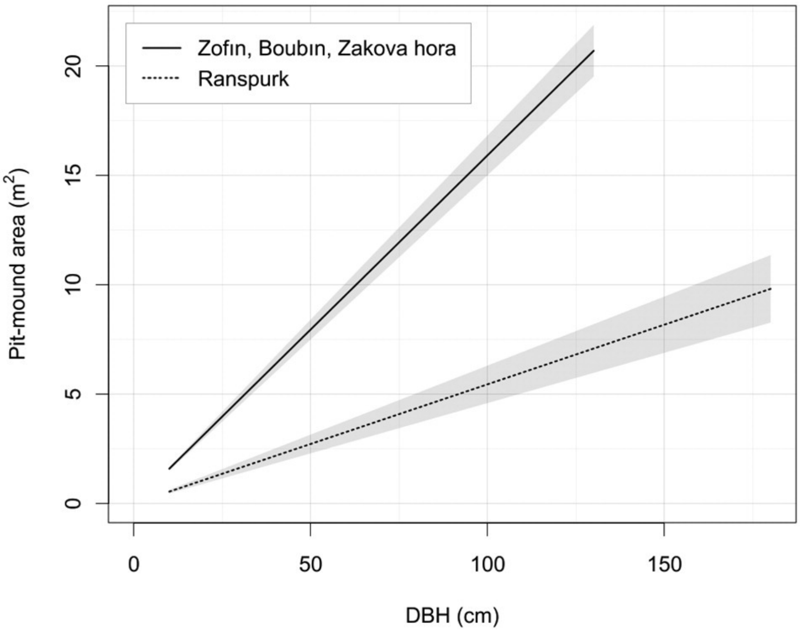


Fig. 3 The best fitting models of the dependence of treethrow area on tree DBH.

Calculations of the areas affected by trees heightened the differences between study sites, and an effect of the altitudinal gradient became apparent (Fig. 4). Only 75 m^2 ha^{-1} were associated with the effect of dying trees in the lowlands (Ranspurk site) in the studied period, whereas nearly six times more, 420 m^2 ha^{-1} were associated in the Boubin mountain site (i.e. an average 1.1% of the area per decade). The area affected by dead trees was not as great as that by living trees (e.g. the process of mass displacement, see Phillips & Marion 2006) in the lowlands, but were clearly more important in the mountains. Areas of treethrow features, where the differences were the most marked, were seven times greater than the relevant areas in lowlands. In the case of living trees, when calculating areas the lower numbers of mountain recruits (Table 2, Fig. 3) were offset by the larger dimensions of these young trees.

As expected, the typical values of calculated areas shifted to the higher DBH categories compared to the frequencies of tree deaths. This was even more significant for living trees. In relation to DBH, the effects of dying trees had a bimodal distribution in Zakova hora and particularly in Zofin. Trees of DBHs between 50 and 80 cm affected the largest area of the sites. Along the gradient of tree thickening, we further observed an increasing proportion of treethrows as opposed to tree stumps. Generally, there was a complete predominance of treethrow areas compared to the other effects of trees.

For any individual tree, the area influenced by mass displacement and other effects while living is of course independent of the mode of tree death. For non-uprooted trees, the area influenced by stumps and stump holes corresponds to the basal area of the tree. However, the area of influence of an uprooted tree is larger–often much more so–than the basal area.

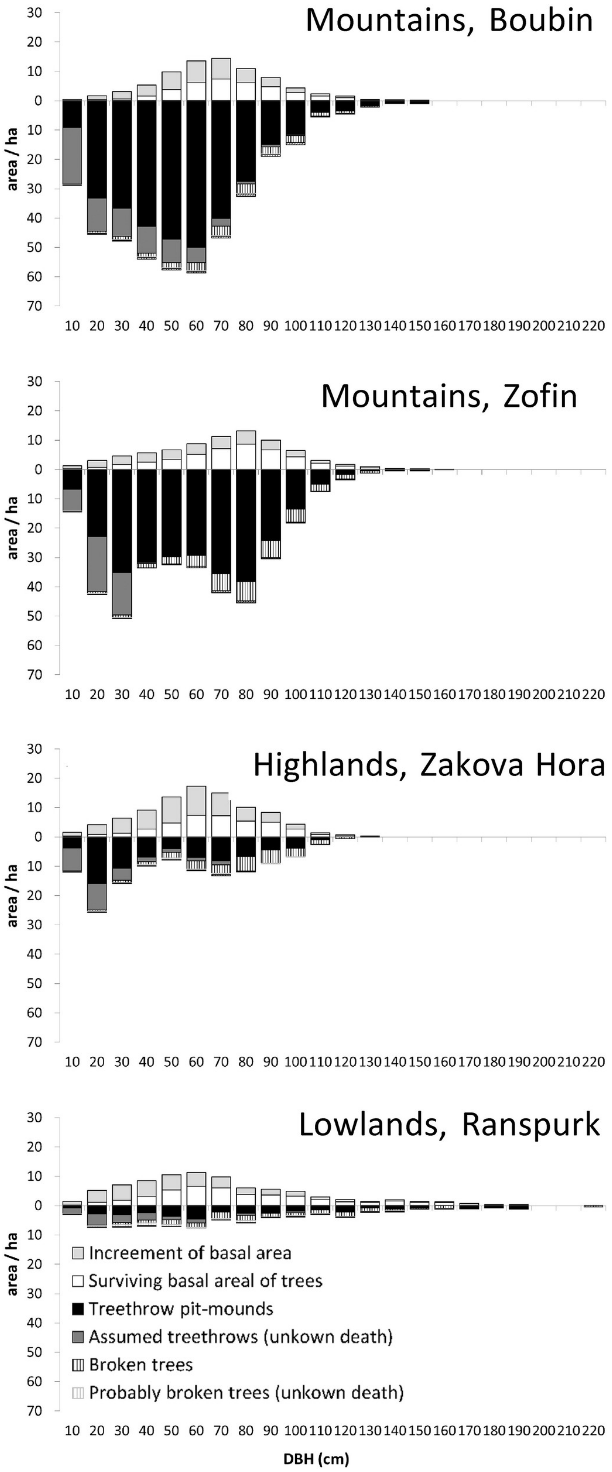


Fig. 4 Development of the tree biomass between the 1970s and 2000s from the viewpoint of basal areas of survivors, recruits or areas affected by various death events in the four forest reserves.

3.3 Volumes of soil affected by trees

In scenarios without soil disturbances, i.e. trees were living, dead standing or broken, standard allometric equations were applied to the root system volume calculations including the volumes of trunk cylinders (see the Material and methods section). On the contrary, volumes of uprooted root plates (v) were calculated according to our own models, and are shown in Fig. 5. The enlargement of the root plates in bigger trees along altitudinal gradient observed in the calculation of areas (see Fig. 3) was much more evident in the calculation of volumes (Fig. 5). A power model in the general form $v = ax^2$ best fitted the treethrow volume data in all sites, with a equal to 0.000768, 0.000129 and 0.00131 in the lowlands (Ranspurk), highlands (Zakova hora), and mountains (Zofin + Boubin), respectively. This power model naturally highlighted the importance of larger trees in the total volume calculation, particularly at mountain sites. This is to be expected, as larger trees of a given species will generally have deeper as well as more areally extensive roots.

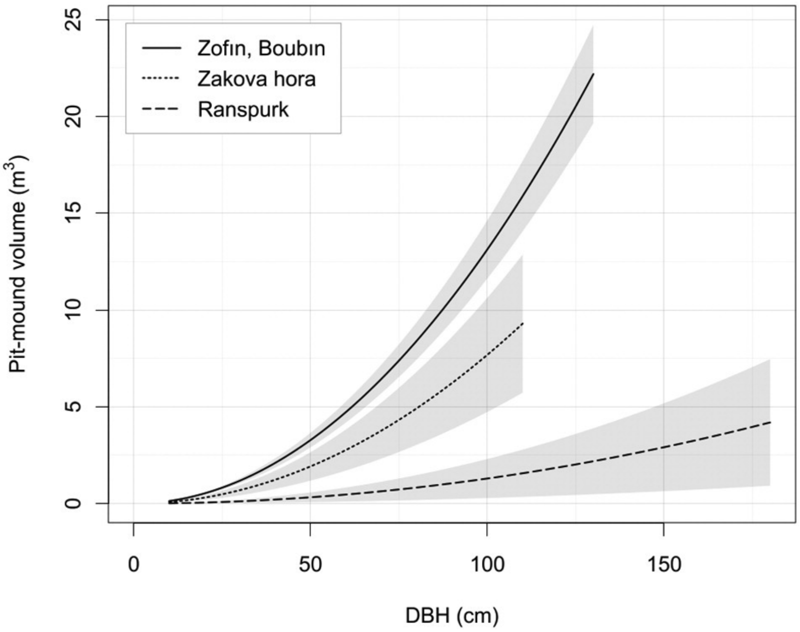


Fig. 5 The best fitting models of the dependence of treethrow volume on tree DBH.

Summary volume graphs (Fig. 6) again express the increasing significance of the BETs from the lowland site (Ranspurk), through the highlands (Zakova hora) to the mountains (Zofin and Boubin). The differences between the lowlands and mountains were even larger than from the viewpoint of areas. An average of 2.7 m^3 ha^{-1} year^{-1} was associated with all studied effects of the living and dying trees in the lowland site, while 7.8 m^3 ha^{-1} year^{-1} was associated at the high elevation Boubin site. This could represent > 7000 kg of dry soil ha^{-1} year^{-1} (the measured average dry bulk density of soil was about 0.9–1.0 g cm^{-1}). Volumes of living root systems ranged between 74 (highland site Zakova hora) and 107 m^3 ha^{-1} (mountain Boubin site) in the census from in the 2000s. The effects of dying trees varied between sites even more, and were the main reason for the observed altitudinal variations in the data. Soil volume associated with the influence of dying trees was only 28 m^3 ha^{-1} in Ranspurk in the studied period, whereas it was 7–8 times higher in the mountains. In Boubin, the soil volume associated with these phenomena was 208 m^3 ha^{-1} per studied period, i.e. 5.5 m^3 ha^{-1} year^{-1}. The effects of dying trees represented only 32% of all biomechanical effects in Ranspurk, but about 70% in both mountain sites.

Analysis of the BETs revealed that tree uprooting had the highest significance. Particularly in mountains, the volumes of root plates were significantly higher than the volumes of the root systems of living and dead trees. Treethrow pit-mounds were responsible for 70% of the volume influenced by effects of dying trees in both mountain sites, which represented nearly 50% of volume of all BETs (living + dying trees). Tree uprootings, which are characteristically directed downslope and therefore a factor in slope denudation, were associated with 3000 to 4000 kg of soil per hectare per year. In the lowland Ranspurk site, the volumes of treethrow forms were only 8.7% of total BET volume. Moreover, treethow pits prevailed over mounds in the lowland site, which resulted

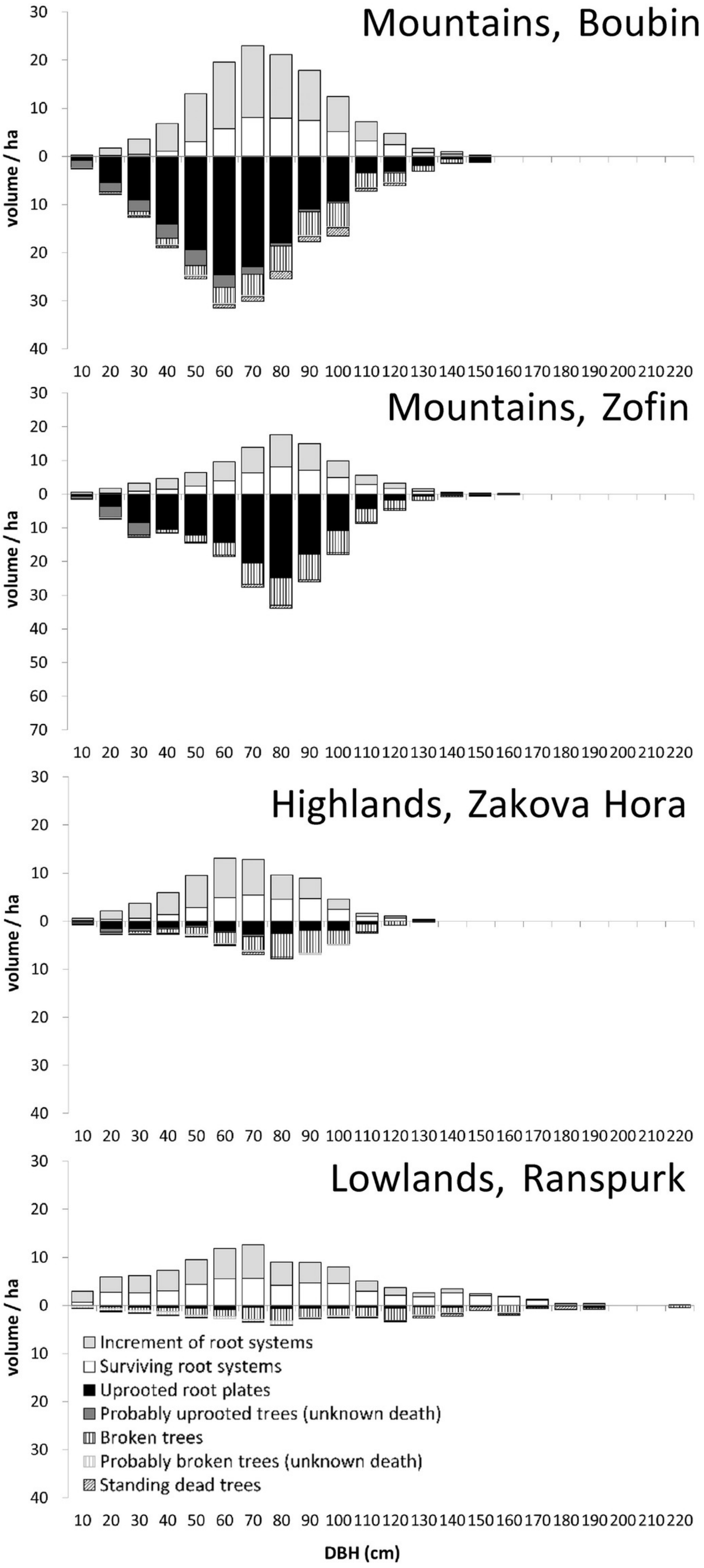


Fig. 6 Development of the tree biomass between the 1970s and 2000s from the viewpoint of the volume of affected soil. The volume of affected soil is expressed as the volume of root systems or uprooting root plates.

from the frequent uprooting of dead standing taproot tree species. In the highlands and mountains, mounds prevailed over pits as a result of our formerly-described mechanism of uprooting and postdisturbance sedimentation (see Šamonil et al. 2015). This predominance of mounds over pits can be considered the usual situation in forested landscapes (see review by Šamonil et al. 2010a). In relation to DBH, the observed bimodal distribution in the area calculations disappeared during the calculations of volumes. The category of intermediate DBH trees between 50 and 80 cm had the highest volumes of soil associated with BETs, especially uprootings.

4 Discussion

4.1 Models of the biomechanical effects of trees in relation to tree size

Our calculated relationships between tree DBH, areas and volumes of root plates correspond to other recent findings of the enormous amount of treethrow features in some temperate old-growth forests. Šamonil et al. (2014) described individual treethrow pit-mound pairs covering > 40 m^2in Novohradské Mts. (Czech Republic), and Phillips et al. (2017) described a treethrow pit-mound that included circa 60 m^3 of soil in Beskydy Mts. (Czech Republic). In a classical study, Lutz (1960) reported the movement of boulders of up to 4 tons due to an uprooting event. It should be mentioned here that mean volumes of root plates can be from 0.1 to 5.6 m^3, depending on the forest type and environmental conditions (review by Pawlik 2013). Exceptional volumes of soil transported by some large uprooted trees are expressed by a nonlinear dependence of root plate volume on DBH. Thick trees may produce higher-order root plates in comparison to thin trees. A nonlinear increase of root plate volumes with DBH gradient was also found by Roering et al. (2010) and by Sobhani et al. (2014), both in northern hardwoods in the USA. Models in this study should be widely valid for central European temperate forests (dimensional considerations alone–relating volume to length–dictate that this relationship should be nonlinear).

4.2 The biomechanical effects of trees on the stand scale

Many teams have studied the biogeomorphic impact of single disturbance events such as hurricanes or bark beetle outbreaks (e.g. Greenberg & McNab 1998, Harrington & Bluhm 2001, Phillips et al. 2008), or quantified existing visible microtopographical features associated with certain current effects of trees, but without the context of time dynamics (e.g. Scatena & Lugo 1995, Šamonil et al. 2016). As far as we know, only a few studies have focused on the frequencies and intensities of BETs based on long-term data, and they have given only partial and inconsistent results, probably due to the various environmental conditions of the forest ecosystems studied. While Brewer & Merritt (1978) found that 0.1–0.2 tree ha^{-1} $year^{-1}$ was uprooted in northern hardwoods in Michigan (USA), Falinski (1978) reported about 2.0–4.5 uprooted tree ha^{-1} $year^{-1}$ in forests sensitive to uprooting on hydromorphic soils in Poland. Our study adds to this incomplete mosaic with an altitudinal gradient, finding 0.7 tree ha^{-1} $year^{-1}$ uprooted in lowlands, but 1.9 tree ha^{-1} $year^{-1}$ uprooted in mountains. Apart from uprooting events, an additional 1.8–2.3 tree ha^{-1} $year^{-1}$ were broken or occurred as standing dead trees. Our data complexity is close to the long-term limit of existing studies, as a majority were focused solely on treethrow dynamics (e.g. Šamonil et al. 2009, Bobrowsky & Loiko 2016), and only a few were focused on BETs other than treethrows (Phillips & Marion 2006). While a few studies have included considerations of mass displacement by trunk growth, stump infilling, and local regolith thickening (e.g., Phillips & Marion 2006, Shouse & Phillips 2016), this is the first to include estimates of total root volume. Although we did not evaluate all the possible biomechanical effects of trees, our study should provide the most complete picture so far of the biomechanical influence of trees on the soil in temperate forests. Because trees also have biochemical effects on soil morphology and weathering (in addition to direct effects on soil chemistry and biology), the biomechanical effects are less than the total biogeomorphic impacts.

The Boubin site, reaching 1100 m a.s.l., may be close to the potential maximum of BETs in central European temperate forests. The height of trees at this site may exceed 60 m (Macar 1988) and they are among the biggest trees in Europe (see Holeksa et al. 2009). At higher altitudes, maximum tree sizes are smaller (e.g. Trotsiuk et al. 2014), their root systems and dimensions of potential root plates are reduced, and the bending moment of trunks on the surface decreases (Mayer et al. 1989). Based on existing studies including our findings (e.g. Valtera et al. 2015), a humped conceptual model likely best represents the biomechanical effects of trees in old-growth central European temperate forests (Fig. 7).

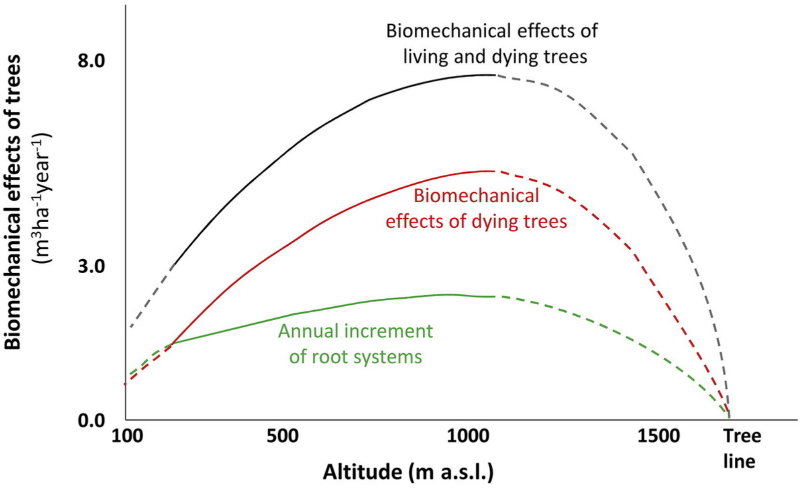


Fig. 7 Conceptual model of the changes of biomechanical effects of trees along an altitudinal gradient. The solid line shows the altitudinal gradient in this study, while the dashed line its extrapolation from former studies.

Geomorphologists usually relate frequencies of events to areas affected, or to volumes and mass of soil and regolith. Panagos et al. (2015) noted that the mean soil loss rate was about 2.46 tons ha^{-1} $year^{-1}$ in the European Union's erosion-prone lands (agricultural, forests and semi-natural areas). Because a majority of treethrows are directed downslope at our studied sites (see Šamonil et al. 2009, Šamonil et al. 2014), and uprooting is followed by the erosion of the unstable edges of mounds and pits, we could simply assumed about 3 tons ha^{-1} $year^{-1}$ associated with treethrows in mountains as an above-average denudation process. However, the effects of trees on soil and hillslope dynamics are a complex system of interactions including many feedbacks, including bioprotection and the spatial concentration of erosion, preventing simple conclusions. Phillips et al. (2017) suggested a potential decreasing activity of abiotic hillslope processes such as continual creep or landsliding due to vegetation succession and the intensification of various BETs in central European old-growth forests. Tree uprooting dynamics may be a key component of biotically driven processes, so-called biogenous creep (Pawlik et al. 2016). Pawlik (2013) found that biogenous creep can globally affect 0.02 to 1.3 t ha^{-1} $year^{-1}$, which does not reach our findings even in the most stable lowlands. Swanson et al. (1982) considered soil and regolith transport driven by BETs to be close in magnitude to soil creep rates (see Clément 1993). Long-term feedbacks between processes driven by biotic and abiotic factors should be among the main issues of future biogeomorphic research.

The relationship between BETs and elevation between the sites is only first-order and needs further investigation. Elevation per se is likely only a small part of the story. Elevation in this region is strongly correlated with slope gradients, soil thickness, temperature, and precipitation. Further, at the lowlands Ranspurk site rooting depth is not inhibited in the alluvial setting, while at the other sites rooting depth is sometimes inhibited by bedrock. Regolith thickness and slope curvature, along with the slope gradient and climate variations already mentioned, may all play a role in the differences.

4.3 Effect of historical land use and strong disturbances

Environmental conditions including altitude represent a relatively predictable group of ecological factors affecting the structure of BETs in forested landscapes. Our research focused on this predictable source of data variability. However, an additional and non-negligible source of data variability is driven by local historical contingency sensu Phillips (2013) (see also Ricklefs et al. 1999). Artificial or natural disturbances represent stochastic variables affecting ecosystem development. The death of the trees themselves, a crucial variable, has stochastic character as well.

All the sites studied here have been strictly protected since at least 1932, and both mountain sites are among the oldest reserves in Europe. The lowland and highland sites also represent the best available examples of relevant old-growth forest ecosystems, and are unique in densely populated central Europe. Unfortunately, these landscapes were more intensively affected by humans in the past, and so historical human impacts in the current forest dynamics are likely minimal but not zero.

Regionally-specific natural disturbance regimes including past strong storms, dry events or insect outbreaks are essential components of the collected data. Although all studied forest ecosystems were driven mainly by fine scale disturbances, occasional intermediate or even stand-replacing events have been documented at both mountain sites (Šamonil et al. 2013b, unpublished). Strong storms may produce dense cohorts of trees (Aakala et al. 2011) affecting the distribution of BETs, and their frequencies, areas and volumes. We assume that strong storm or bark beetle outbreaks caused the bimodal character of the distribution of calculated BET areas. Site specific effects are probably behind the surprisingly large differences between Zakova Hora and Zofin. Both sites are located at similar altitudes, but one of them occurs in more productive mountains and the second in drier highlands. The mass of geomorpological form and associated climate characteristics are still hidden factors in the variability of BETs.

Data from these forest reserves suggests that in unmanaged forests 23–42% of trees are uprooted, as opposed to breaking or standing death. Uprooting is far less common in managed forests, because most trees are cut, and the very large, mature trees most susceptible to uprooting are rare or missing. On the other hand, in many managed forests the growth and death (harvesting) of trees occurs with much greater frequency. What are the net long-term BETs of, say, a mean tree residence time of 80 years (a common rotation or harvesting age for Norway spruce) in the region, almost all of which are cut, vs. a mean tree residence time which is both longer and more variable, and where about 30% of trunks are uprooted? Because of the nonlinear relationship between age and tree growth, and between tree size and BETs, and because these relationships are species and site-specific, this is a complex and as yet unanswered question.

5 Conclusion

Although the size structures of living trees differed only slightly among the four studied reserves, including the tree death dynamics and relating frequencies to affected areas and soil volumes revealed fundamental differences between the sites, frequently along an altitudinal gradient that simultaneously reflects differences in topographic relief and climate. Standing dead tree produces fundamentally different geomorphic impacts with comparison to uprooting tree, which modifies hillslope processes on landscape scale. Only 2.7 $m^3\ ha^{-1}\ year^{-1}$ were associated with all the studied effects of living and dying trees in the lowland site, while 7.8 $m^3\ ha^{-1}\ year^{-1}$ were associated in the mountains. The differences were particularly seen in the biogeomorphic effects of dead trees, and especially in treethrow dynamics. Biomechanical effects caused by dying trees were 7–8 times larger in the mountains compared to the lowlands, and 14.6 times larger in terms of the volumes of uprooted trees. We can conclude that trees are a significant factor in hillslope processes and slope denudation in the mountains, but that this effect decreases in the lowlands.

Our study also has implications for forest management. When changing the tree layer structure through management, BETs are significantly changed as well. Because tree cutting certainly limits uprooting dynamics in managed forests, we can assume that the natural dynamics of forests are more markedly affected in mountain forests than in lowlands.

Acknowledgements

The authors thank their colleagues from the ‘Blue Cat research team’ for field data measurement. Especially, we would like to thank Eduard Průša for the visionary establishment of the tree census research in the 1970s, and Tomáš Vrška and Libor Hort for its continuation in 1990s. We also thank Anička Senecká for help with data processing. Research was supported by the Czech Science Foundation, project No. 16-15319S.

References

Aakala T., Kuuluvainen T., Wallenius T., Kauhanen H. 2011. Tree mortality episodes in the intact *Picea abies*-dominated taiga in the Arkhangelsk region of northern European Russia. *Journal of Vegetation Science* 22: 322–333.

Barrett L.R. 1997. Podzolization under forest and stump prairie vegetation in northern Michigan. *Geoderma* 78: 37–58.

Benjamini Y., Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B (Methodological)* 57: 289–300.

Bloomfield C. 1953. A study of podzolization. Part II. The mobilization of iron and aluminum by the leaves and bark of *Agathis australis* (Kauri). *Journal of Soil Science* 4: 17–23.

Bobrowsky M.V., Loiko S.V. 2016. Patterns of pedoturbation by tree uprooting in forest soils. *Russian Journal of Ecosystem Ecology* 1: 1–22.

Bolte A., Rahmann T., Kuhr M., Pogoda P., Murach D., Gadow K. 2004. Relationships between tree dimension and coarse root biomass in mixed stands of European beech (*Fagus sylvatica* L.)

and Norway spruce (*Picea abies* [L.] Karst.). *Plant and Soil* 264: 1–11.

Bormann B.T., Spaltenstein H., McClellan M.H., Ugolini F.C., Cromack K.Jr., Nay S.M. 1995. Rapid soil development after windthrow disturbance in pristine forests. *Journal of Ecology* 83: 747–757.

Brewer R., Merritt P.G. 1978. Wind throw and tree replacement in a climax beechmaple forest. *Oikos* 30: 149–152.

Clément P. 1993. Erosion balance and slope evolution under continental humid temperate climate: an Appalachian Example (Quebec, Canada). *Catena* 20: 303–315.

Corenblit D., Baas A.C.W., Bornette G., Darrozes J., Delmotte S., Francis R.A., Gurnell A.M., Julien F., Naiman R.J., Steiger J. 2011. Feedbacks between geomorphology and biota controlling earth surface processes and landforms: a review of foundation concepts and current understandings. *Earth-Science Reviews* 106: 307–331.

Cribari-Neto F. 2004. Asymptotic inference under heteroskedasticity of unknown form. *Computational Statistics and Data Analysis* 45: 215–233.

Zeměpisný lexikon ČSR. In: Demek J. (Ed.), Hory a nížiny. Academia, Praha, p. 584.

Embleton-Hamann C. 2004. Processes responsible for the development of a pit and mound microrelief. *Catena* 57: 175–188.

Falinski J.B. 1978. Uprooted trees, their distribution and influence in the primeval biotope. *Vegetatio* 38: 175–183.

Fumiko S., Kiyoshi S., Arevalo J.R., Palmer M.W. 2006. Tornado damage of *Quercus stellata* and *Quercus marilandica* in the Cross Timbers, Oklahoma. USA. *Journal of Vegetation Science* 17: 347–352.

Gabet E.J., Reichman O.J., Seabloom E.W. 2003. The effect of bioturbation on soil processes and sediment transport. *Annual Review of Earth Planetary Science* 31: 249–273.

Greenberg C.H., McNab W.H. 1998. Forest disturbance in hurricane-related downbursts in the Appalachian Mountains of North Carolina. *Forest Ecology and Management* 104: 179–191.

Harcombe P.A., Mann Leipzig L.E., Elsik I.S. 2009. Effects of Hurricane Rita on three long-term forest study plots in east Texas, USA. Wetlands 29: 88–100.

Harrington T.B., Bluhm A.A. 2001. Tree regeneration responses to microsite characteristics following a severe tornado in the Georgia Piedmont. USA. *Forest Ecology and Management* 140: 265–275.

Holeksa J., Saniga M., Szwagrzyk J., Czerniak M., Kapusta P. 2009. A giant tree stand in the West Carpathians—an exception or a relic of formerly widespread mountain European forests? *Forest Ecology and Management* 257: 1577–1585.

Kooch Y., Hosseini S.M., Šamonil P., Hojjati S.M. 2014. The effect of windthrow disturbances on biochemical and chemical soil properties in the northern mountainous forests of Iran. *Catena* 116: 142–148.

Král K., Janík D., Vrška T., Adam D., Hort L., Unar P., Šamonil P. 2010. Local variability of stand structural features in beech dominated natural forests of Central Europe: implications for sampling. *Forest Ecology and Management* 260: 2196–2203.

Krejza J., Svetlík J., Bednár P. 2017. Allometric relationship and biomass expansion factors (BEFs) for above- and below-ground biomass prediction and stem volume estimation for ash (*Fraxinus excelsior* L.) and oak (*Quercus robur* L.). *Trees* 31: 1303–1316.

Lehre A.K. 1987. Rates of soil creep on colluvium-mantled hillslopes in north-central California.

In: Beschta R., Blinn T., Grant C., Ice G., Swanson F. (Eds.), Erosion and sedimentation in the Pacific Rim. IAHS Press, Wallingford, pp. 91–100.

Lutz H.J. 1960. Movement of rocks by uprooting of forest trees. *American Journal of Science* 258: 752–756.

Macar V. 1988. Studie o nejmohutnějších nebo jinak význačných exemplářích smrku a jedle především z areálu horských oblastí Jihočeského kraje. Lesprojekt, Brandýs nad Labem 75.

Mayer H., Raupach M.R., Kohsiek W., Gardiner B., Clarke J.A., Amtmann R., Crowther J.M., Jarvis P.G., Milne R. 1989. Windthrow. *Philosophical Transactions of the Royal Society B* 324: 267–281.

Mueller O.P., Cline G. 1959. Effects of mechanical soil barriers and soil wetness on rooting of trees and soil mixing by blow-down in central New York. *Soil Science* 88: 107–111.

Panagos P., Borrelli P., Poesen J., Ballabio C., Lugato E., Meusburger K., Montanarella L., Alewell C. 2015. The new assessment of soil loss by water erosion in Europe. *Environmental Science Policy* 54: 438–447.

Pawlik, Ł. 2013. The role of trees in the geomorphic system of forested hillslopes — a review. *Earth-Science Reviews* 126: 250–265.

Pawlik, Ł., Phillips J.D., Šamonil P. 2016. roots, rock, and regolith: biomechanical and biochemical weathering by trees and its impact on hillslopes – a critical literature review. *Earth-Science Reviews* 159: 142–159.

Peterson C.J. 2007. Consistent influence of tree diameter and species on damage in nine eastern North America tornado blowdowns. *Forest Ecology and Management* 250: 96–106.

Phillips J.D. 2009. Biological energy in landscape evolution. *American Journal of Science* 309: 271–290.

Phillips J.D. 2013. Networks of historical contingency in Earth surface systems. *Journal of Geology* 121: 1–16.

Phillips J.D., Marion D.A. 2006. Biomechanical effects of trees on soil and regolith: beyond tree-throw. *Annals of the Association of American Geographers* 96: 233–247.

Phillips J.D., Marion D.A., Turkington A.V. 2008. Pedologic and geomorphic impacts of a tornado blowdown event in a mixed pine-hardwood forest. *Catena* 75: 278–287.

Phillips J.D., Šamonil P., Pawlik L., Trochta J., Daněk P. 2017. Domination of hillslope denudation by tree uprooting in an old-growth forest. *Geomorphology* 276: 27–36.

Pickett S.T.A., White P.S. 1985. The ecology of natural disturbance and patch dynamics. California, United States Academic Press, San Diego.

Průša E. 1985. Die böhmischen und mährischen Urwälder—ihre Struktur und Ökologie, Vegetace ČSSR A15. Academia, Praha.

R Core Team 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Austria, Vienna. https://www.R-project.org.

Retallack G.J. 2001. Soils of the past, An Introduction to Paleopedology. 2nd ed. Blackwell, Oxford, UK.

Ricklefs R.E., Latham R.E., Qian H. 1999. Global patterns of tree species richness in moist forests: distinguishing ecological influences and historical contingency. *Oikos* 86: 369–373.

Roering J.J., Marshall J., Booth A.M., Mort M., Jin Q. 2010. Evidence for biotic controls on topography and soil production. *Earth and Planetary Science Letters* 298: 183–190.

Šamonil P., Antolík L., Svoboda M., Adam D. 2009. Dynamics of windthrow events in a natural fir-beech forest in the Carpathian mountains. *Forest Ecology and Management* 257: 1148–1156.

Šamonil P., Daněk P., Schaetzl R.J., Tejnecký V., Drábek O. 2018a. Converse pathways of soil evolution caused by tree uprooting: A synthesis from three regions with varying soil formation processes. *Catena* 161: 122–136.

Šamonil P., Daněk P., Schaetzl R.J., Vašíčková I., Valtera M. 2015. Soil mixing and genesis as affected by tree uprooting in three temperate forests. *European Journal of Soil Science* 66: 598–603.

Šamonil P., Daněk P., Senecká A., Adam D., Phillips J.D. 2018b. The biomechanical effects of trees in a temperate forest: implications for biogeomorphology, soil science, and forest ecology. *Earth Surface Processes and Landforms* 43: 1063–1072.

Šamonil P., Doleželová P., Vašíčková I., Adam D., Valtera M., Král K., Janík D., Šebková B. 2013a. Individual-based approach to the detection of disturbance history through spatial scales in a natural beech-dominated forest. *Journal of Vegetation Science* 24: 1167–1184.

Šamonil P., Král K., Hort L. 2010a. The role of tree uprooting in soil formation: a critical literature review. *Geoderma* 157: 65–79.

Šamonil P., Schaetzl R.J., Valtera M., Goliáš V., Baldrian P., Vašíčková I. 2013b. Crossdating of disturbances by tree uprooting: can treethrow microtopography persist for 6,000 years? *Forest Ecology and Management* 307: 123–135.

Šamonil P., Tejnecký V., Borůvka L., Šebkova B., Janík D., Šebek O. 2010b. The role of tree uprooting in Cambisol development. *Geoderma* 159: 83–98.

Šamonil P., Valtera M., Schaetzl R.J., Adam D., Vašíčková I., Daněk P., Janík D., Tejnecký V. 2016. Impacts of old, comparatively stable, treethrow microtopography on soils and forest dynamics in the northern hardwoods of Michigan, USA. *Catena* 140: 55–65.

Šamonil P., Vašíčková I., Daněk P., Janík D., Adam D. 2014. Disturbances can control fine-scale pedodiversity in old-growth forest: is the soil evolution theory disturbed as well? *Biogeosciences* 11: 5889–5905.

Scatena F.N., Lugo A.E. 1995. Geomorphology, disturbance, and the soil and vegetation of two subtropical wet steepland watersheds of Puerto Rico. *Geomorphology* 13: 199–213.

Schaetzl R.I., Burns S.F., Johnson D.L., Small T.W. 1989. Tree uprooting: review of impacts on forest ecology. *Vegetatio* 79: 165–176.

Schaetzl R.J. 1986. Complete soil profile inversion by tree uprooting. *Physical Geography* 7: 181–189.

Schaetzl R.J. 1990. Effects of treethrow microtopography on the characteristics and genesis of Spodosols, Michigan, USA. *Catena* 17: 111–126.

Šebková B., Šamonil P., Janík D., Adam D., Král K., Vrška T., Hort L., Unar P. 2011. Spatial and volume patterns of an unmanaged submontane mixed forest in Central Europe: 160 years of spontaneous dynamics. *Forest Ecology and Management* 262: 873–885.

Šebková B., Šamonil P., Valtera M., Adam D., Janík D. 2012. Interaction between tree species populations and windthrow dynamics in natural beech-dominated forest. Czech Republic. *Forest Ecology and Management* 280: 9–19.

Shouse M.A., Phillips J.D. 2016. Soil deepening by trees and the effects of parent material. *Geomorphology* 269: 1–7.

Simon A., Gratzer G., Sieghardt M. 2011. The influence of windthrow microsites on tree regeneration and establishment in an old growth mountain forest. *Forest Ecology and Management* 262: 1289–1297.

Skvorcova E.B., Ulanova N.G., Basevic V.F. 1983. Ekologiceskaja rol vetrovalov. Lesnaja Promyslennost. Moskva, Russia.

Sobhani V.M., Barrett M., Peterson C.J. 2014. Robust prediction of treefall pit and mound sizes from tree size across 10 forest blowdowns in Eastern North America. *Ecosystems* 17: 837–850.

Swanson F.J., Fredriksen R.L., McCorison F.M. 1982. Material transfer in a western Oregon forested watershed. In: Edmonds R.L. (Ed.), Analysis of Coniferous Forest Ecosystems in the Western United States. US/IBP Synthesis Series Vol. 14. Hutchinson Ross Publishing Company, Stroudsburg, PA, pp. 233–266.

Tatarinov F., Urban J., Čermák J. 2008. The application of "clump technique" for root system studies of *Quercus robur* and *Fraxinus excelsior*. *Forest Ecology and Management* 255: 495–505.

Tricart J. 1972. Landforms of the humid tropics, forests and savannas. Longman, London, p. 306.

Trotsiuk V., Svoboda M., Janda P., Mikolas M., Bace R., Rejzek J., Samonil P., Chaskovskyy O., Korol M., Myklush S. 2014. A mixed severity disturbance regime in the primary *Picea abies* (L.) Karst. forests of the Ukrainian Carpathians. *Forest Ecology and Management* 334: 144–153.

Ulanova N.G. 2000. The effects of windthrow on forests at different spatial scales: a review. *Forest Ecology and Management* 135: 155–167.

Valtera M., Šamonil P., Svoboda M., Janda P. 2015. Effects of topography and forest dynamics on soil variability in natural *Picea abies* mountain forests. *Plant and Soil* 392: 57–69.

Vassenev I.I., Targulian V.O. 1995. Windtrhrow and Taiga Pedogenesis (Regimes, Processes, Morphogenesis of Soil Successions). Nauka, Moskva.

Verboom W.H., Pate J.S. 2006. Bioengineering of soil profiles in semiarid ecosystems: the 'phytotarium' concept. A review. *Plant and Soil* 289: 71–102.

Viles H.A., Naylor L.A., Carter N.E.A., Chaput D. 2008. Biogeomorphological disturbance regimes: progress in linking ecological and geomorphological systems. *Earth Surface Processes and Landforms* 33: 1419–1435.

Vyskot M. 1976. Tree story biomass in lowland forests in South Moravia. Rozpravy CSAV 86. Academia, Praha.

Wilby A. 2002. Ecosystem engineering: a trivialized concept? *Trends in Ecology and Evolution* 17: 307.

Xi W., Peet R.K., DeCoster J.K., Urban D.L. 2008. Tree damage risk factors associated with large, infrequent wind disturbances of Carolina forests. *Forestry* 81: 317–334.

Zeide B. 1981. Method of mound dating. *Forest Science* 27: 39–41.

Paper 6

Geomorphic controls of soil spatial complexity in a primeval mountain forest in the Czech Republic

Pavel Daněk
Pavel Šamonil
Jonathan D. Phillips

Geomorphology 273 (2016), 280–291

Abstract

Soil diversity and complexity is influenced by a variety of factors, and much recent research has been focused on interpreting or modeling complexity based on soil-topography relationships, and effects of biogeomorphic processes. We aimed to (i) describe local soil diversity in one of the oldest forest reserves in Europe, (ii) employ existing graph theory concepts in pedocomplexity calculation and extend them by a novel approach based on hypothesis testing and an index measuring graph sequentiality (the extent to which soils have gradual vs. abrupt variations in underlying soil factors), and (iii) reveal the main sources of pedocomplexity, with a particular focus on geomorphic controls.

A total of 954 soil profiles were described and classified to soil taxonomic units (STU) within a 46 ha area. We analyzed soil diversity using the Shannon index, and soil complexity using a novel graph theory approach. Pairwise tests of observed adjacencies, spectral radius and a newly proposed sequentiality index were used to describe and quantify the complexity of the spatial pattern of STUs. This was then decomposed into the contributions of three soil factor sequences (SFS), (i) degree of weathering and leaching processes, (ii) hydromorphology, and (iii) proportion of rock fragments.

Six Reference Soil Groups and 37 second-level soil units were found. A significant portion of pedocomplexity occurred at distances shorter than the 22 m spacing of neighbouring soil profiles. The spectral radius (an index of complexity) of the pattern of soil spatial adjacency was 14.73, to which the individual SFS accounted for values of 2.0, 8.0 and 3.5, respectively. Significant sequentiality was found for degree of weathering and hydromorphology. Exceptional overall pedocomplexity was particularly caused by enormous spatial variability of soil wetness, representing a crucial soil factor sequence in the primeval forest. Moreover, the soil wetness gradient was partly spatially correlated with the gradient of soil weathering and leaching, suggesting synergistic influences of topography, climate, (hydro)geology and biomechanical and biochemical effects of individual trees. The pattern of stony soils, random in most respects, resulted probably from local geology and quaternary biogeomorphological processes. Thus, while geomorphology is the primary control over a very locally complex soil pattern, microtopography and local disturbances, mostly related to the effects of individual trees, are also critical. Considerable local pedodiversity seems to be an important component of the dynamics of old-growth mixed temperate mountain forests, with implications for decreasing pedodiversity in managed forests and deforested areas.

P. Daněk[a,b], *P. Šamonil*[b], *J.D. Phillips*[c]

---

[a] Department of Forest Ecology, The Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Brno, Czech Republic [b] Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic [c] Tobacco Road Research Team, Department of Geography, University of Kentucky, Lexington, KY 40506-0027, U.S.A.

1 Introduction

Soil complexity in natural ecosystems represents an area of considerable research with potential implications for soil geomorphology, biogeomorphology, pedology, ecology, and evolutionary biology. Surprisingly high local soil variability and diversity revealed recently in some forest ecosystems (e.g. Šamonil et al. 2011, 2014; Valtera et al. 2013; Carpenter et al. 2014) raises questions about soil forming factors that control or influence spatial patterns of soils.

The digital soil mapping paradigm, which relies heavily on soil-topography relationships identified via analysis of digital elevation models, is at least implicitly based on the idea that topography is a major control over soil spatial patterns (e.g., Thompson et al. 2001; Thompson & Kolka 2005; Smith et al. 2006; Behrens et al. 2010a, 2010b). This control may be direct (the topographic or relief factor in classical pedology, based primarily on gravity-driven moisture and other mass fluxes), or indirect via topographic correlations at a landscape scale with parent geology, microclimate, and ecological habitats. The spatial resolution of topographic data is a key issue in this research, suggesting that if geomorphology has strong influences on soil variability at a local scale then more detailed topographic information could be critical if mapping or modeling this local variation is attempted.

Additionally, several soil and regolith studies have shown that highly localized, pedon-scale biogeomorphic impacts may profoundly increase local soil variability, particularly in forests (Crowther 1987; Phillips & Marion 2005; Phillips et al. 2005; Šamonil et al. 2008, 2011; Estrada-Medina et al. 2013; Shouse & Phillips 2016). These effects are often persistent and result in divergent pedogenesis, rather than being commensurate with the time scale of the biotic effects. These studies show that the biomechanical and biochemical effects of individual trees are particularly important with respect to soil morphology and properties likely to result in taxonomic differences.

At the pedon scale, the impact of abiotic factors such as geology or landscape-scale topography (as opposed to microtopography) is stable; these factors change relatively slowly. On the other hand, dynamic factors such as biotic influences generally develop continuously and rapidly (Johnson et al. 1990). Changing soil forming factors acting synergistically often result in non-linear soil formation. Even in case of podzolization, i.e. an extremely strong weathering and leaching process (Buurman 1984), a regressive component of pedogenesis resulting from change in vegetation (Barrett & Schaetzl 1998; Nikodem et al. 2013) was observed counteracting the predominant progressive pedogenesis. Because of these multidirectional and usually mutually dependent connections, the idea of a single trajectory of soil development from initial to mature climax soils (Buol et al. 1997) has been gradually replaced by a concept of multiple variant trajectories of soil evolution (Johnson et al. 1990; Huggett 1998). As a result, spatial soil variability can gradually decrease in convergent evolution, as traditional pedogenetic theory has supposed (Buol et al. 1997), or increase in recently observed divergent soil evolution (Phillips 2001); both at the landscape (Phillips 2001; Toomanian et al. 2006; Borujeni et al. 2010) and pedon (Šamonil et al. 2015, 2016) scale. Observed complex pattern of soils described in some recent studies was only partly explainable by variability of topography, geology or climate (e.g. Šamonil et al. 2014) which could be partly in accordance with the concept of deterministic chaos in Earth surface systems (Phillips 2006), where historical and spatial contingency are among the driving mechanisms.

In a long-term perspective, soils and landforms may both be generally considered in some cases as extended composite phenotypes (Phillips 2009, 2016). These systems are not only strongly affected by organisms during evolution, but they also have reciprocal effects on biota, and may be integral components of biotic evolution. Moreover, on macroevolutionary level strong feedbacks were found between Darwinian selection of organisms based on heredity and non-Darwinian organization of soils and landscapes (Corenblit et al. 2011). Quantification of local soil complexity in old-growth forests and revealing the structures of soil forming factors laying behind it are important for deeper understanding of mechanisms of biogeomorphic feedbacks in natural ecosystems. Thus the main aims of this study are: (i) to describe local soil diversity in one of the oldest forest reserves in Europe, (ii) to employ existing graph theory concepts in pedocomplexity quantification and extend them by a novel approach based on hypothesis testing and an index measuring graph sequentiality, and (iii) to determine the main sources of pedocomplexity in (fir)-spruce-beech forest ecosystem.

2 Material and methods

2.1 Study site

The research took place in the Boubínský Prales Reserve (hereinafter Boubin) in the Šumava Mts. in the south-west of the Czech Republic (Fig. 1). As the second oldest forest reserve in the Czech Republic and one of the oldest in Europe (Welzholz & Johann 2007), the studied core zone of Boubin has been under strict protection since 1858 and has never been cut. The primeval forest occupies north-eastern slopes built of crystalline rocks of the Bohemian Massif, mainly primary schists, biotic and mica-schist gneisses. At an altitude of 930–1110 m a.s.l. the mean annual temperature is 5 °C and mean annual precipitation is about 1300 mm (Tolasz et al. 2007). Main vegetation types of mesic sites are montane acidophilous or nutrient-rich beech forests (*Calamagrostio villosae-Fagetum sylvaticae*, *Mercuriali perennis-Fagetum sylvaticae*) and montane acidophilous spruce forests (*Calamagrostio villosae-Piceetum abietis*). Wet sites are dominated by wet spruce forests usually with high cover of mosses (*Soldanello montanae-Piceetum abietis*; see Šamonil & Vrška 2008; Chytrý 2013).

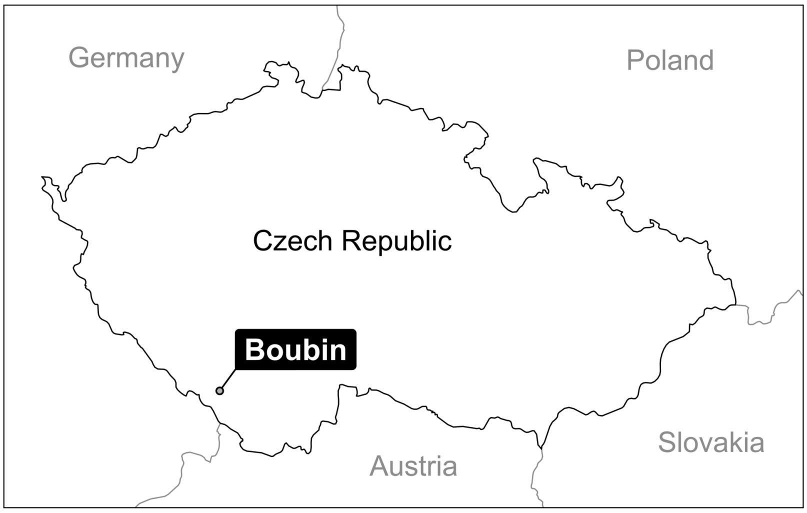


Fig. 1 Map of Central Europe with position of the studied locality.

2.2 Data collection and soil diversity evaluation

Soil survey took place on nodes of a grid with a lateral spacing of 22.125 m (distance derived from the National Forest Inventory in the Czech Republic, www.uhul.cz) within the studied 46 ha area. A fourth of these points (grid of 44.25 m) were located geodetically with an accuracy of ca. 0.05 m and marked by steel rods in the soil. This network of points was used as the basis for all subsequent terrain measurements, including tree census and soil survey. Locations of all trees of DBH ≥ 10 cm within the studied forest ecosystem (e.g. Šebková et al. 2011) helped us to find the remaining unmarked nodes of the denser 22.125 m grid with an accuracy of ca. 1.0 m. Soil survey took place directly on 954 such nodes. If a point was inaccessible, because of standing or lying tree trunks, or was disturbed by a recent tree uprooting event, the position of soil sampling was moved to the nearest available site in a random direction.

On each node position we opened shallow soil profiles up to ca. 0.5 m depth to evaluate forms and thicknesses of the uppermost soil horizons, including organic horizons, and we used a soil corer of diameter 3 cm to evaluate deeper soil horizons up to 1 m depth. Median depth of transition between soil B horizons and C substratum horizons is 103 cm within the locality (SD = 10.6 cm, N = 12; based on 2 m deep soil profiles). Substratum horizons consist of angular weathered gneiss of various sizes. Massive solid rock is usually located at 3 to 5 m depth (measured by ground penetrating radar in 2015). Soil properties were evaluated in detail according to Schoeneberger et al. (1998), including the evaluation of B horizon colors using the Munsell Color Chart. We classified soil taxonomic units (STU) according to the international WRB system (Michéli et al. 2007). During the classification we focused on three crucial gradients of soil properties:

1. *Degree of weathering and leaching processes*, which means in particular the expression of podzolization process in the soils. We focused on the presence of bleached grains of quartz in A horizons; expression of platy structure in A and spherical microaggregate structure in B soil horizons; texture, colour and consistence of A and B horizons, including their transition as well as on the indicators of humus and sesquioxides movement, and E horizon formation. We distinguished three degrees of weathering and leaching processes represented by the predominance of cambic properties in soils (Dystric Cambisols), podzolization without humus or sesquioxides movement (Entic Podzols), and a higher degree of podzolization including the formation of E horizon (Albic Podzols). Morphological criteria were subsequently verified by chemical and physical soil analyses executed in detail in twelve representative soil profiles (Vrška et al. 2012; unpublished).

2. *Water influence in soils,* which are visible as the proportion and forms of hydromorphic features in soil morphology. We distinguished twelve degrees of of soil hydromorphism expression. “Dry” soils with no visible footprints of reduction processes within the profile represented the first step of a chain which then continued through the presence of stagnic and subsequently gleyic properties, followed by the formation of stagnic and then gleyic horizons in terrestrial soils. The rest of the chain contained (semi)hydromorphic soils comprising successively Stagnosols, Gleysols, Histic Gleysols and the final stage represented by Histosols.

3. *Proportion of rock fragments in the soils*. We distinguished Leptosols from other Reference Soil Groups based on the predominance of rock fragments and the absence of spodic, cambic, stagnic or gleyic horizons. At the same time we distinguished Hyperskeletic, Epileptic and

> Lithic second-level soil units within all present Reference Soil Groups. The amount of fine earth decreased along the gradient from soils without a predominance of rock fragments, continuing through Hyperskeletic second-level units, Hyperskeletic Epileptic units, Leptosols, Hyperskeletic Leptosols, and ending with Lithic Leptosols.
>
> Complete chains are depicted in Fig. 9.

We call these three gradients soil factor sequences (SFS) and most soils in the study area can be differentiated according to these three gradients—that is, some combination of the weathering and leaching (podzolization), wetness, and rock fragment categories is sufficient to distinguish among nearly all soils sampled. A few soil units were not included because determination of key properties in the field was difficult or uncertain.

Soil diversity was evaluated as richness (i.e., number of taxa) of Reference Soil Groups and second-level units within the locality. Moreover, we calculated the Shannon index of soil diversity (H', Shannon & Weaver 1949):

$$H' = -\sum_{i=1}^{n} p_i \ln p_i$$

where p_i is estimated by ratios of n_i/N where n_i represents the area covered by individual i-th soil unit and N is the total studied area. The value of the observed diversity index was than compared with its maximum value $H_{\max}$ (associated with all soils being equally common) to compute evenness (J) (Pielou 1969):

$$J = \frac{H'}{H_{\max}} = \frac{H'}{\ln S}$$

where S represents richness of soil units within the locality. These indices have been commonly used as measures of soil system structural heterogeneity (Ibáñez et al. 1998, 2013).

2.3 Analysis of complexity

2.3.1 Graph representation

The analysis methods we use are based on graph theory, which has been recently applied to soil complexity assessment (Phillips 2013, 2016). A graph consists of a set of n vertices (nodes) which are connected by m edges (links). An edge connecting a node to itself is called a loop and all edges can be assigned a numeric weight. Alternatively, an edge of weight w can be replaced with w unweighted edges in which case the graph is called a multigraph. The number of links connecting a node to other nodes is called node degree and its distribution in the graph is called degree distribution.

To represent the observed spatial adjacency of soil taxa we use a graph whose vertices are STUs and any two of them (or a node with itself in case of loops) are connected if the corresponding STUs were spatially adjacent (neighbouring) in the field. We used both weighted (edges weight equal to the number of such adjacencies) and unweighted versions. The same representation is used for each of the three SFS with graph vertices corresponding to the respective SFS levels.

Only the closest sampling points were considered adjacent which, in case of our square sampling grid, means the typically four neighbouring points in the four cardinal directions. In practice, since the size of the squares was approximately 21 m, to account for some irregularities two points were considered neighbouring if they were within 25 m of each other.

2.3.2 Complexity calculation

Spatial complexity of soils in Boubin was measured based on a set of properties related to complexity of the spatial adjacency graph, and on an assessment of the extent to which adjacent soils vary gradually along gradients of SFS (sequentiality).

Spectral radius, an indicator of many graph properties such as connectivity or number of cycles (Phillips 2013, 2016) is computed as the largest eigenvalue (λ_1) of a graph's adjacency matrix. It is a standard measure of network complexity in algebraic graph theory. For a simple graph with n nodes an adjacency matrix A is a square $n \times n$ matrix with entries a_{ij} of 1 if there is an edge between the i-th and j-th nodes of the graph and 0 otherwise. The spectral radius reaches maximum value $n - 1$ if the graph is complete (each vertex is adjacent to every other vertex) and if we further restrict the number of edges to m, the upper bound for λ_1 is (Hong & Shu 2001)

$$\lambda_1(\max) = \sqrt{2m - n + 1}$$

We also employ the upper bound for a graph with specified degree sequence given by Liu & Weng (2013). To compute the spectral radius we only use a simple representation of a graph, i.e. without weighted (or multiple) edges and loops.

The logarithm of spectral radius is sometimes called graph entropy (Geller et al. 2012) and as such it can be compared to the Shannon diversity index which is an entropy measure itself (see section 2.2). The upper bounds for these two quantities are asymptotically equal, yielding $\ln(n-1)$ for complete graphs in case of graph entropy and $\ln(n)$ for equally frequent soil units in case of Shannon index.

From the definition of spectral radius the properties it reflects can be difficult to understand so we relate it to another measure of graph complexity, the *s*-metric (Li et al. 2005). It measures to what extent high-degree nodes (i.e. those linked to many others) are connected to other high-degree nodes. It was designed to identify so called "scale-free" networks for which it yields high values. For the graphs we will be dealing with the two measures are highly correlated, as evidenced by the Pearson correlation coefficient that is never below 0.95 (Table 2). Given a graph G with a set E of edges the *s*-metric is defined as

$$s(G) = \sum_{(i,j) \in E} d_i d_j$$

where d_i is the degree of node i.

Another aspect of soil complexity we are interested in Boubin is if neighbouring soils are similar in terms of the underlying SFS, a property we call sequentiality. To quantify this we use an index of graph-to-graph coherence to define a *graph sequentiality index* (*GSI*) which measures to what extent edges of a multigraph M follow edges of a reference graph G. Given a multigraph M with vertices V and a multiset E of vertex pairs connected by edges and a simple connected graph G with vertices W (such that $V \subseteq W$) we first compute the mean distance of vertex pairs (MD) in E when the distance is measured in G

$$MD = \sum_{\{x,y\} \in E} d_G(x, y)|E|^{-1}$$

where $d_G(x, y)$ is the distance of vertices x and y in graph G. The index is then defined as

$$GSI = 1 - \frac{MD - 1}{\max(d_G(V) - 1,\ 1)}$$

where $d_G(V)$ is the greatest distance between any pair of vertices in V when measured in graph G and "max" is a function returning the greater of its two arguments used to avoid division by zero when the subgraph of G induced by V is complete. The index reaches values from 0, for multigraphs whose edges connect only the vertices which are the most distant in G, to 1, in cases when all the edges in M exactly follow the edges in G. Both M and G are considered to be undirected but for directed graphs the index works similarly.

In case of a SFS the reference graph G is a linear graph with vertices corresponding to the SFS levels in natural order. For STU G is a lattice (grid) graph constructed as the Cartesian product of the individual SFS G graphs. A graph G based on p SFS can be imagined as a p-dimensional grid with $\prod_{q=1}^{p}(n_q)$ nodes (n_q is the length of the q-th SFS) in which each vertex of a STU is located on coordinates given by its position along the respective SFS. M is the observed spatial adjacency multigraph without loops. Note that although loops could be preserved in M in which case they would increase the index (because the distance of a node to itself is 0) we chose not to include them because we are mainly interested in the adjacency patterns of different soils or SFS levels.

Four examples of landscapes with different sequentiality of a 5-level SFS are shown in Fig. 2. The value of GSI decreases from 1 for absolute sequentiality when neighbouring points differ by no more than one level to 0.54 in case of highly contrasting pattern of adjacency. This change is also visible in the corresponding spatial adjacency graphs as the relative importance of edges connecting distant levels (in the lower half of the graphs) increases.

2.3.3 Randomization tests

To test whether the computed indices are different from what could be observed by chance we used a Monte Carlo approach to derive their null distributions (based on 10,000 resamplings) and check whether the observed values lie within the outer 5% of these null distributions, i.e. below the 2.5th or above the 97.5th percentile. In case of spectral radius we first inspect the observed "wiring" (the specific pattern of connectivity between the nodes; Phillips 2012) by generating the null distribution of λ_1 from random graphs with the same number of nodes and edges (n, m) as the reference graph. A further restriction on the rewiring is set by fixing not only the number of edges but also the observed node degrees. To generate random graphs with prescribed degrees we use an algorithm developed by Blitzstein & Diaconis (2006). Second, to test whether the spatial pattern of soils is responsible for the observed complexity, we derive the null distribution of λ_1 by computing the spectral radii of complexity graphs based on spatially randomized data. The latter approach is also used to test the GSI and weights on edges of STU or SFS complexity graphs.

A significant feature of our data is spatial clustering of identical STU (or SFS levels) in parts of the locality where spatial heterogeneity is lower than the sampling resolution. When spatial randomization is used, these clusters dissolve and the resulting spatial complexity graphs have significantly lower weights of loops on most vertices and subsequently higher weights of edges connecting these. Although this result is a good evidence for spatial clustering, it does mask to some extent the significance of adjacency patterns of different STU. To solve this issue we use reduced data sets from which all points inside clusters were removed. The essence of this approach is to remove from each dataset (STU and the three SFS) a certain portion of sampling points so that

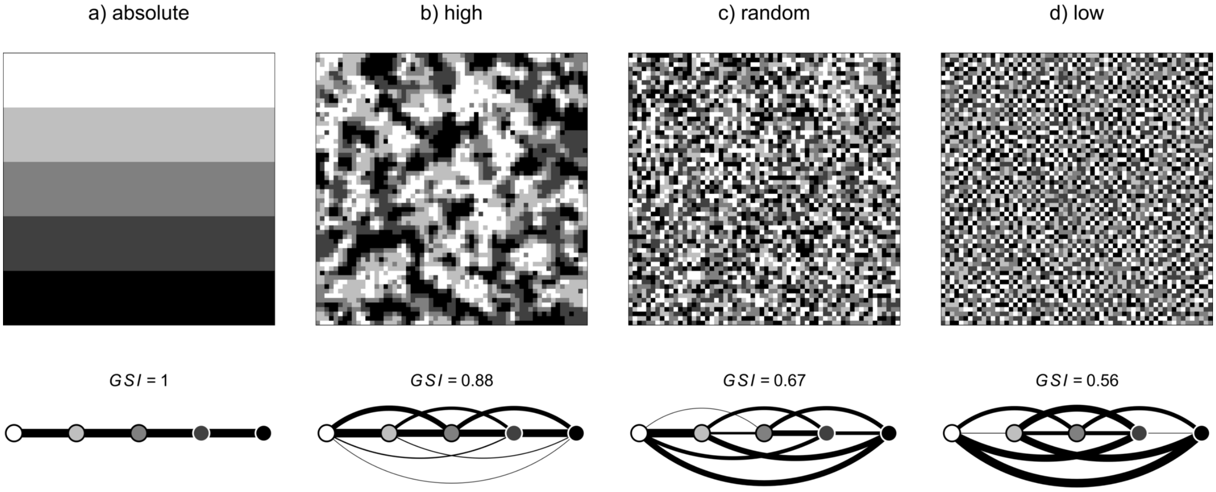


Fig. 2 Sequentiality demonstrated on four spatial arrangements of levels of a gradient of length 5 (e.g. a SFS) in a 60 × 60 area. In a) points are arranged in a perfect gradient so that only levels differing by up to one are neighbouring, in b) points were assigned levels semi-randomly while trying to keep minimum distances along the gradient between neighbours, c) was created by random assignment of levels to the points and d) is a result of semi-random assignment with aim for maximum contrast between neighbouring points. The frequencies of the five levels on each "map" are the same. In the bottom are the sequentiality indices (*GSI*) and spatial adjacency graphs corresponding to the above spatial arrangements. The graphs are multigraphs with numbers of edges connecting two vertices denoted by thickness of the respective links. Loops, representing adjacency of the same levels, are omitted because they do not enter the computation of *GSI*.

after spatial randomization the weights of loops of the associated complexity graph (frequency of self-adjacency) are on average equal to those obtained from non-randomized data. Because of different patterns of clustering of different STU (SFS levels) the portion of data to be removed is determined independently for each of them. The removed points were the most clustered ones and the level of clustering was assessed based on the following criteria:

1. proportion of a point's immediate neighbours that were of the same category as the point itself
2. distance to the closest point of another category
3. proportion of points of the same category within 1.5 times the distance computed in 2)

The points were ordered according to 1) and any ties were then reordered according to 2) and 3) if necessary. A portion of the most clustered points was then removed. These reduced datasets were used for testing when spatial randomization was used.

To avoid alpha inflation when testing the significance of individual edge weights we used a sequential Bonferroni-type procedure (Benjamini & Hochberg 1995) to control the false discovery rate.

All analyses were performed using R (R Core Team 2015).

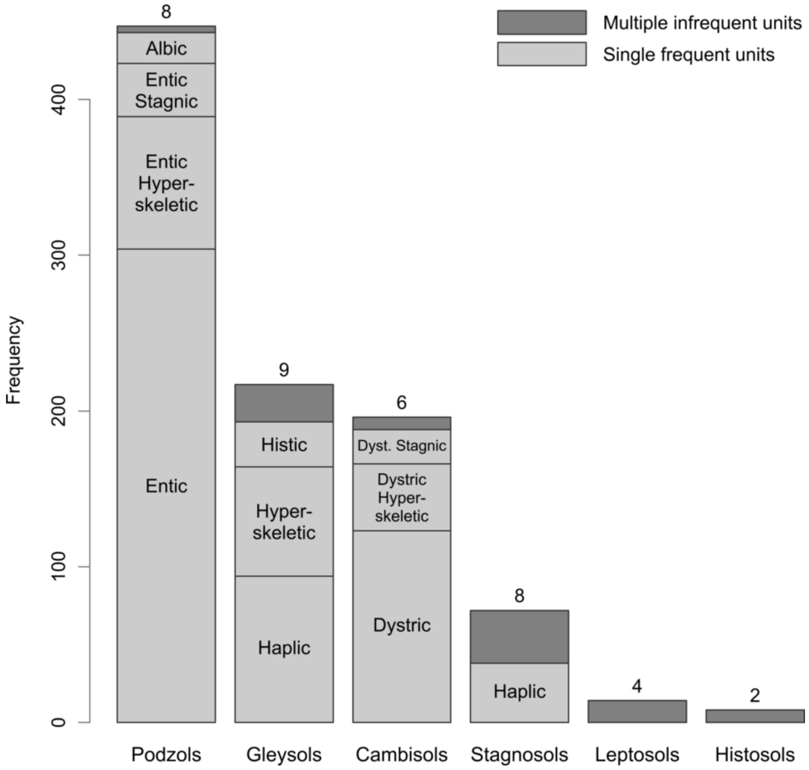


Fig. 3 Frequencies of soil units distinguished on the 954 study plots. Units with more than 15 occurrences are separated and labelled in light parts of the bars, while less frequent units are merged within the dark parts. Numbers above bars give the total number of units distinguished within each soil group.

3 Results and discussion

3.1 Pedodiversity

Within the area of 46 ha we identified 37 second-level soil units belonging to six Reference Soil Groups (Fig. 3). Entic Podzols represented the most frequent soil unit within the site, which means – in terms of the evaluated SFS – moderately podzolized, relatively dry soils with low content of rock fragments. Although these soils can be considered to be a typical soil unit within the study area reflecting the general quality of climate, geology, topography and biota, we found many deviations from this central unit along all studied gradients of SFS. Between terrestrial soil units represented predominantly by Podzols (46%) we found also 20% of Cambisols, where evidence of only initial podzolization occurred. Nearly 8% of the area was occupied by semihydromorphic soils (Stagnosols) and 24% by hydromorphic soils, i.e. Gleysols and Histotosls. Leptosols, soils without other horizon than A and C, occupied 1.5% of area.

Results regarding soil richness in studied (fir)-spruce-beech forest on gneiss complement previous results from various forest types and geology in central Europe. Comparably high local richness of soils including six Reference Soil Groups and tens of lower-level soil units was observed in a mountain beech-dominated forest on granite within an area of 74 ha, in the 4th oldest forest reserve in Europe (Šamonil et al. 2011, 2014). Similar results were obtained in mountain primeval spruce forests on vulcanite as well as phyllite in Romania (Valtera et al. 2013). On the other hand, lower local soil richness was observed in deciduous European forests on sedimentary rocks, especially in lower elevations (e.g. Šamonil et al. 2010a). Similar results originate from forested areas in the US (Phillips & Marion 2005). These results are consistent with generally higher pedodiversity in mountain areas on a global scale (Ibáñez et al. 1998).

High pedodiversity can be caused by higher local variability of some soil forming factors, namely micro- and meso- topography and climate. Additionally, especially in old-growth moun-

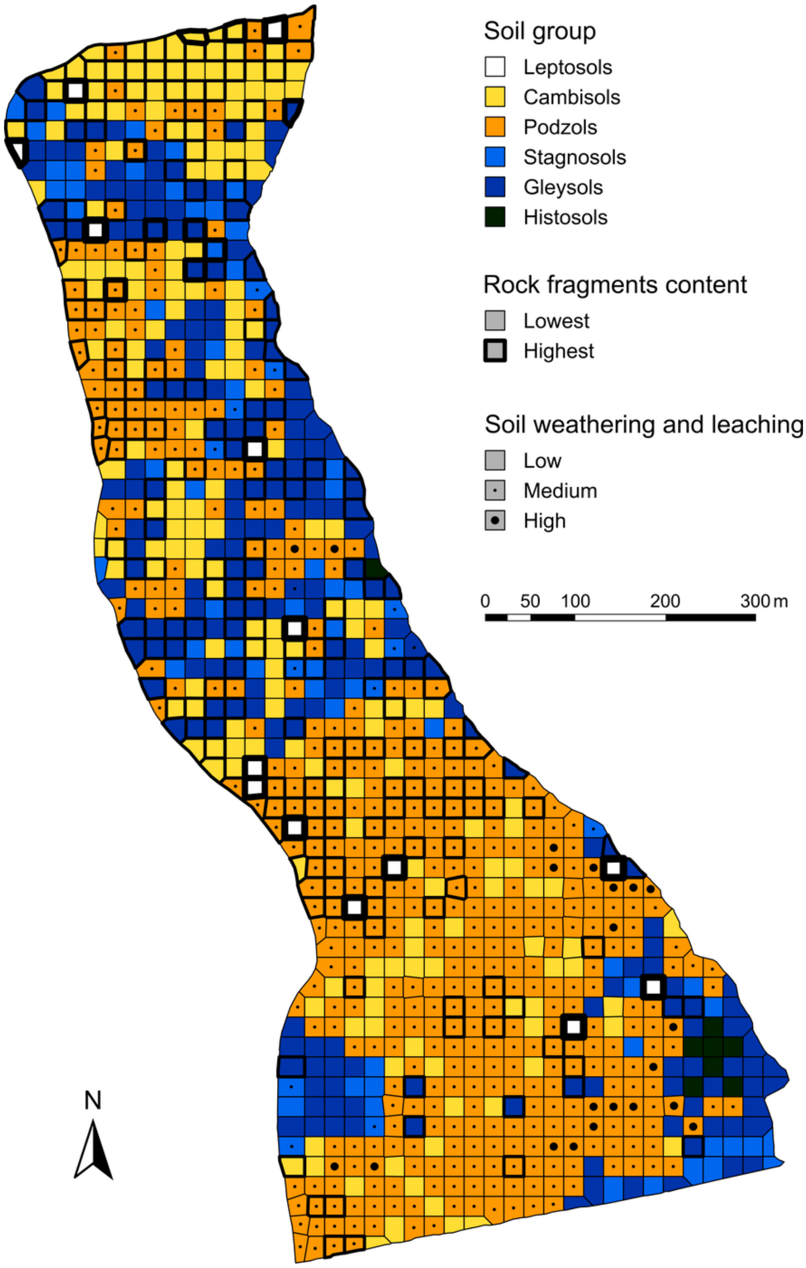


Fig. 4 Map of Boubin showing spatial distribution of the six distinguished soil groups and two of the SFS.

tain forests, as represented by the study site, we have to expect significant influence of individual trees on soil variability and diversity. As recent studies reveal, trees are able – through their biomechanical and biochemical effects – to accelerate or decelerate main soil forming processes such as podzolization in mountain temperate zones (e.g. Binkley & Giardina 1998; Phillips & Marion 2006; Šamonil et al. 2010b, 2015; Pawlik 2013). In light of the very high soil richness in old-growth forest we can speculate about decreasing pedodiversity in managed forests, where the tree layer structure is naturally simplified. For example, relationships between tree DBH and volume of root plate leads to absence of huge treethrow pit-mound pairs of exceptional longevity in managed forests where only younger, smaller trees are uprooted (Roering et al. 2010). Whereas large decaying tree trunks, stumps and root systems locally accelerate or decelerate pedogenesis in old-growth forests (Spears & Lajtha 2004), such processes are limited in managed forests due to deadwood removal and forest cutting. Human impact on soil diversity could be even higher in deforested areas (see Barrett & Schaetzl 1998; Robertson et al. 1993; Bobrovski 2010; Lo Papa et al.

2011) and requires additional research. For example, soil variability and complexity was found to be higher on the forested part of an otherwise similar site than on the cropland portion by Phillips (2013).

The Shannon index of diversity can help to compare managed areas with natural localities. In Boubin old-growth forest, H' calculated for Reference Soil Groups was high relative to the area under evaluation (see Guo et al. 2003; Toomanian et al. 2006; Lo Papa et al. 2011), $H' = 1.32$, and $H' = 2.42$ for second-level soil units. The values of evenness were comparable between the taxonomic levels and reached $J = 0.73$ and $J = 0.67$ for Reference Soil Groups and second-level soil units, respectively.

The mapping of soils revealed their complex spatial pattern. Fig. 4 shows general pattern of the Reference Soil Groups; the spatial pattern of the lower-level soil units is much more complex. Compact blocks of exclusive soil units were rare in Boubin, where only Entic Podzols partly occurred in such blocks. Other soil units were clustered to small, sometimes rather linear (in case of Gleysols connected with stream channels) forms.

3.2 Soil complexity

3.2.1 Overall soil complexity

Fig. 5 shows the soil spatial adjacency graph based on full dataset. From the total number of 191 connections 33 were found statistically significant but from these only the self-loops can be interpreted. They are clearly an evidence of spatial clustering of soil units but to see what is going on between different soils it is necessary to examine the complexity graph based on the reduced dataset (Fig. 6). It is worth noting that although the reduction of dataset by removing clusters resulted in a strong decrease of self-adjacency of clustered soil units (as intended), the numbers of between-soil adjacencies was reduced much less, preserving the complexity pattern of interest.

Most significant connections representing substantially frequent adjacencies remained significant after cluster removal and some new connections appeared (most visibly the connection between Entic Podzols and Dystric Cambisols). Of course, this was not the case of self-loops that were all, by definition, within random variation after the clusters were removed. On the other hand, the number of significant links between less-than-expected adjacent soil units decreased more than twice. Proportions of data removed from each category (STU or SFS level) to reduce clustering are given in Table 1.

Table 1 Proportions of data removed from spatially clustered categories in each dataset.

Dataset	Proportion of data removed from a category
Soil units	CM.dy: 0.15, CM.dy.jk: 0.45, CM.dy.jk.st: 0.20, CM.dy.st: 0.20, GL.ha: 0.19, GL.hi: 0.25, GL.jk: 0.22, GL.st: 0.20, HS.sa+hm: 0.20, LP.cm.jk: 0.20, PZ.ab: 0.28, PZ.et: 0.31, PZ.jk.et:0.23, PZ.st.et: 0.27, ST.gl: 0.10, ST.ha: 0.18
Water influence	1: 0.60, 2: 0.13, 5: 0.10, 8: 0.10, 9: 0.13, 10: 0.20, 12: 0.20
Rock fragments content	1: 0.24, 2: 0.13, 5: 0.20
Soil weathering and leaching	1: 0.29, 2: 0.23, 3: 0.23

We found significantly low adjacency of several types of Stagnosols and Gleysols with certain Cambisols and Podzols which means that the distance of 22 m between two neighbouring

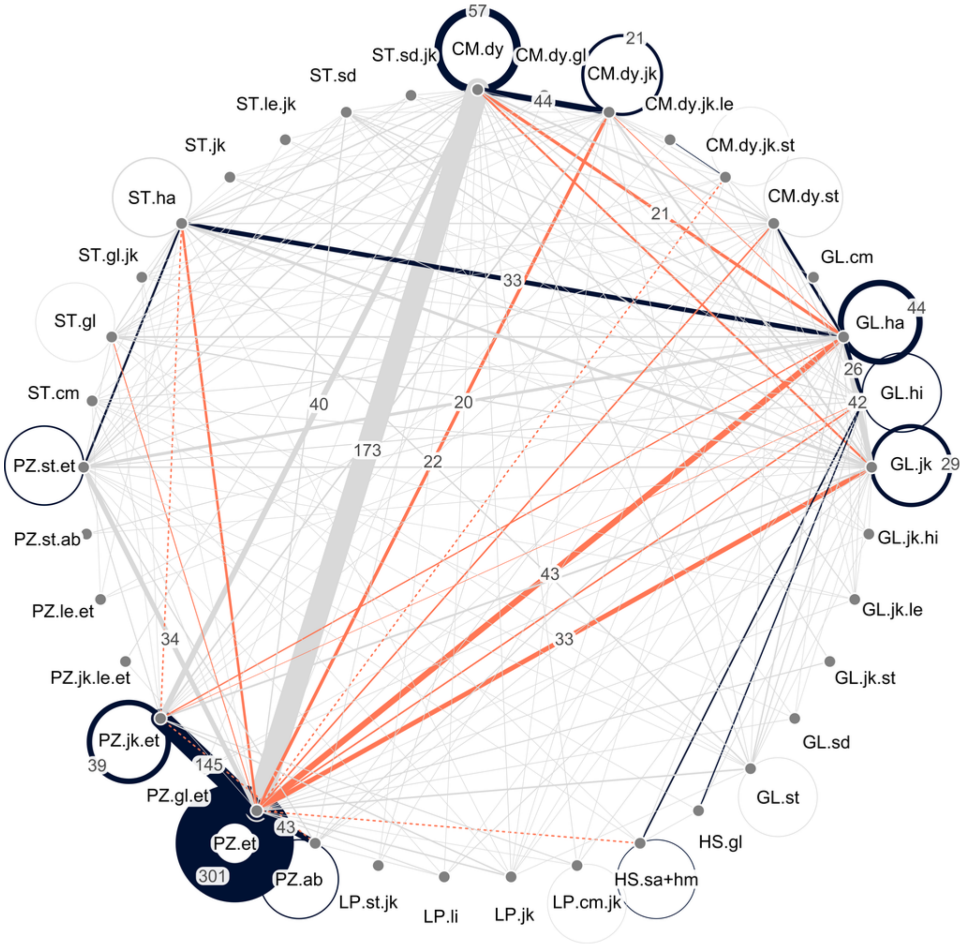


Fig. 5 Spatial adjacency graph for soil taxonomical units (STU). STUs found adjacent in the field are connected by lines of varying thickness proportional to the number of such adjacencies with frequencies of more than 20 labelled. The circles on STU nodes represent loops, i.e. the adjacency of an STU to itself. The links are coloured according to the statistical significance of the respective observed frequencies when compared to their expected null distributions. The three colours represent adjacencies more frequent than expected (dark blue), less frequent (orange) and within random variation (light grey). A special case are unobserved adjacencies expected to occur by chance (dashed orange). CM.dy, Dystric Cambisols; CM.dy.gl, Gleyic Dystric Cambisols; CM.dy.jk, Hyperskeletic Dystric Cambisols; CM.dy.jk.le, Epileptic Hyperskeletic Dystric Cambisols; CM.dy.jk.st, Stagnic Hyperskeletic Dystric Cambisols; CM.dy.st, Stagnic Dystric Cambisols; GL.cm, Cambic Gleysols; GL.ha, Haplic Gleysols; GL.hi, Histic Gleysols; GL.jk, Hyperskeletic Gleysols; GL.jk.hi, Histic Hyperskeletic Gleysols; GL.jk.le, Epileptic Hyperskeletic Gleysols; GL.jk.st, Stagnic Hyperskeletic Gleysols; GL.sd, Spodic Gleysols; GL.st, Stagnic Gleysols; HS.gl, Gleyic Histosols; HS.sa+hm, Hemic or Sapric Histosols; LP.cm.jk, Hyperskeletic Cambic Leptosols; LP.jk, Hyperskeletic Leptosols; LP.li, Lithic Leptosols; LP.st.jk, Hyperskeletic Stagnic Leptosols; PZ.ab, Albic Podzols; PZ.et, Entic Podzols; PZ.gl.et, Entic Gleyic Podzols; PZ.jk.et, Entic Hyperskeletic Podzols; PZ.jk.le.et, Entic Epileptic Hyperskeletic Podzols; PZ.le.et, Entic Epileptic Podzols; PZ.st.ab, Albic Stagnic Podzols; PZ.st.et, Entic Stagnic Podzols; ST.cm, Cambic Stagnosols; ST.gl, Gleyic Stagnosols; ST.gl.jk, Hyperskeletic Gleyic Stagnosols; ST.ha, Haplic Stagnosols; ST.jk, Hyperskeletic Stagnosols; ST.le.jk, Hyperskeletic Epileptic Stagnosols; ST.sd, Spodic Stagnosols; ST.sd.jk, Hyperskeletic Spodic Stagnosols.

sampling points was generally not large enough for these contrasting soil units to meet in the field. On the other hand, certain more related soil units occurred contiguously significantly of-

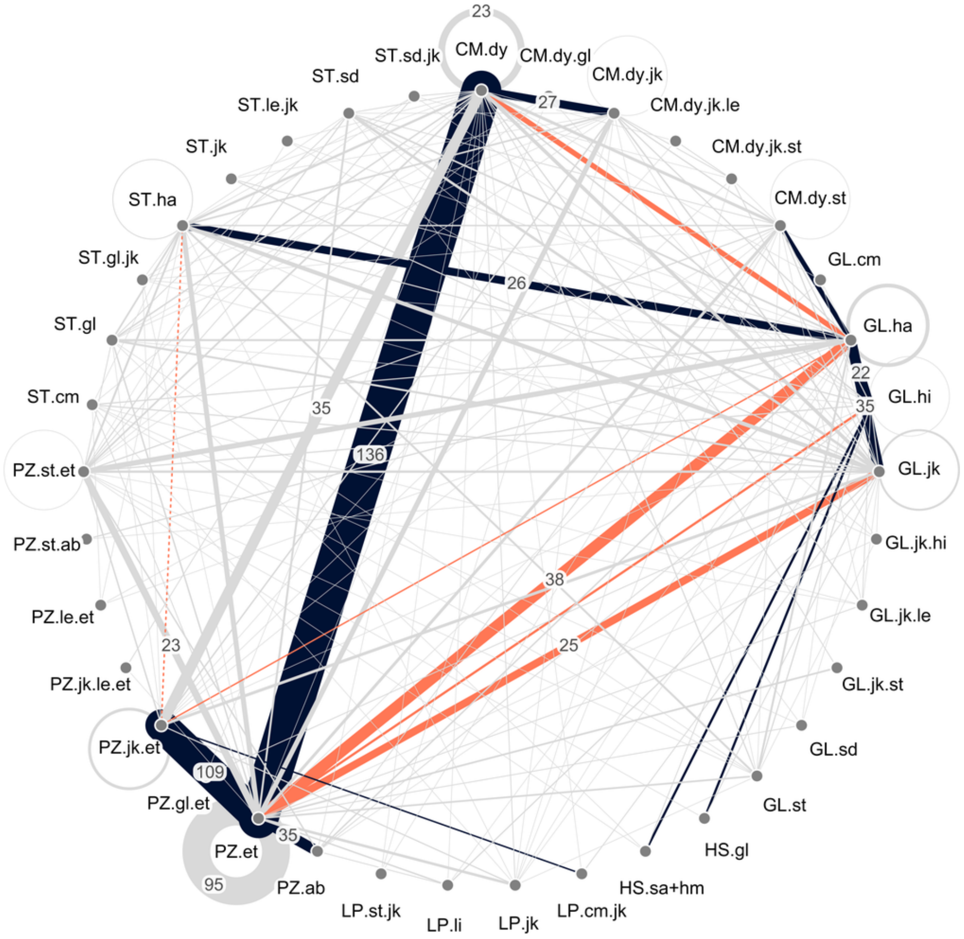


Fig. 6 Spatial adjacency graph of STUs based on the data set with clusters removed. See Fig. 5 for explanation.

ten. Soils within one taxonomic group tended to occur adjacent to mainly their hyperskeletic variants (Dystric Cambisols, Entic Podzols and Haplic Gleysols), or less often soil units differing along SFS other than rock fragment content (Haplic and Histic Gleysols, Entic and Albic Podzols). If significantly adjacent soils belong to different taxonomic groups they are typically influenced by water, as evidenced by the affinity of Stagnic Dystric Cambisols and Haplic Stagnosols for Haplic Gleysols or the affinity of Histic Gleysols for Histosols.

The soil complexity graph has a spectral radius of 14.73 (Table 2) which is significantly more than that of a random graph with the same number of vertices and edges. This is a consequence of non-uniform (right-skewed) distribution (Fig. 7a) of node degrees with many low-degree nodes corresponding to rare soils (e.g. Hyperskeletic Stagnic Gleysols) and few high-degree nodes representing abundant soil units (Entic Podzols, Hyperskeletic Gleysols or Dystric Cambisols). On the other hand, the observed spectral radius is actually lower than the spectral radius of a random graph with the same degree distribution. Considering the fact that we found spectral radius to be highly correlated with *s*-metric (Table 2), this indicates that the nodes tend to be connected with nodes of contrasting degrees rather than with those of similar number of neighbours. The soil complexity in Boubin is much higher than that observed by Phillips (2013, 2016) who reported spectral radius values between 5.5 and 7.6. However, direct comparison of these results with ours is not possible due to differences in data collection and soil taxonomic detail.

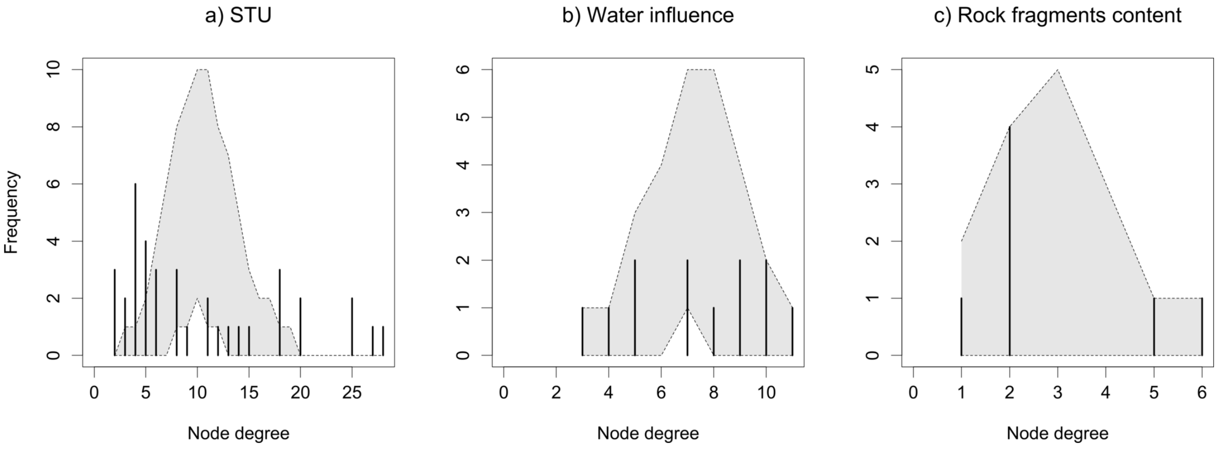


Fig. 7 Node degree distributions for spatial adjacency graphs of STU and first two SFS. Vertical lines are the observed node degree frequencies and the gray area gives the 95% confidence interval for degree distribution based on 10,000 random graphs with the same number of nodes and edges as the reference graph.

Table 2 Properties of spatial adjacency graphs for STU and the three SFS based on the original data set. Reference values are computed for graphs with the same number of nodes and edges (rewired) or with the same degree distribution (rewired degrees). Statistically significant values of spectral radii are in bold as well as the percentiles they exceed.

			Spectral radius								
				Rewired				Rewired degrees			
				NDP				NDP			
Factor	*n*	*m*	Obs.	2.5th	97.5th	Max.	r_s	2.5th	97.5th	Max.	r_s
Soil unit	37	191	**14.73**	10.73	**11.34**	18.60	0.991	**14.97**	15.28	18.11	0.953
Water influence	12	44	**8.03**	7.43	**7.78**	8.77	0.996	8.00	8.06	8.48	0.981
Rock fragments content	7	10	**3.46**	2.96	**3.45**	3.74	0.983	3.46	3.46	3.74	–
Soil weathering and leaching	3	3	2.00	2.00	2.00	2.00	–	2.00	2.00	2.00	–

NDP = null distribution percentile
r_s = correlation between spectral radius and *s*-metric

The spectral radius computed from the reduced data set is, as expected, slightly lower (14.13, Table 3) and lies within the random variation derived from spatial randomization. This suggests that the observed soil spatial complexity emerges as a consequence of uneven frequencies of individual soil units. Fig. 8 shows that neighbouring soils can differ by several levels along the SFS but still, as indicated by the significantly high sequentiality, the adjacency pattern is not random and taxonomically related soils generally tend to be neighbouring (Table 3).

3.2.2 Complexity of individual SFS

Similarly to the STU the spatial adjacency graphs for the three SFS (Fig. 9), when computed from full data set, have significantly high weights on certain self-loops indicating spatial clustering of abundant SFS levels. Also here the reduction of the data set resulted in some originally significant edges becoming non-significant (Fig. 10). Fig. 11 shows the differences along the SFS between neighbouring points within the locality.

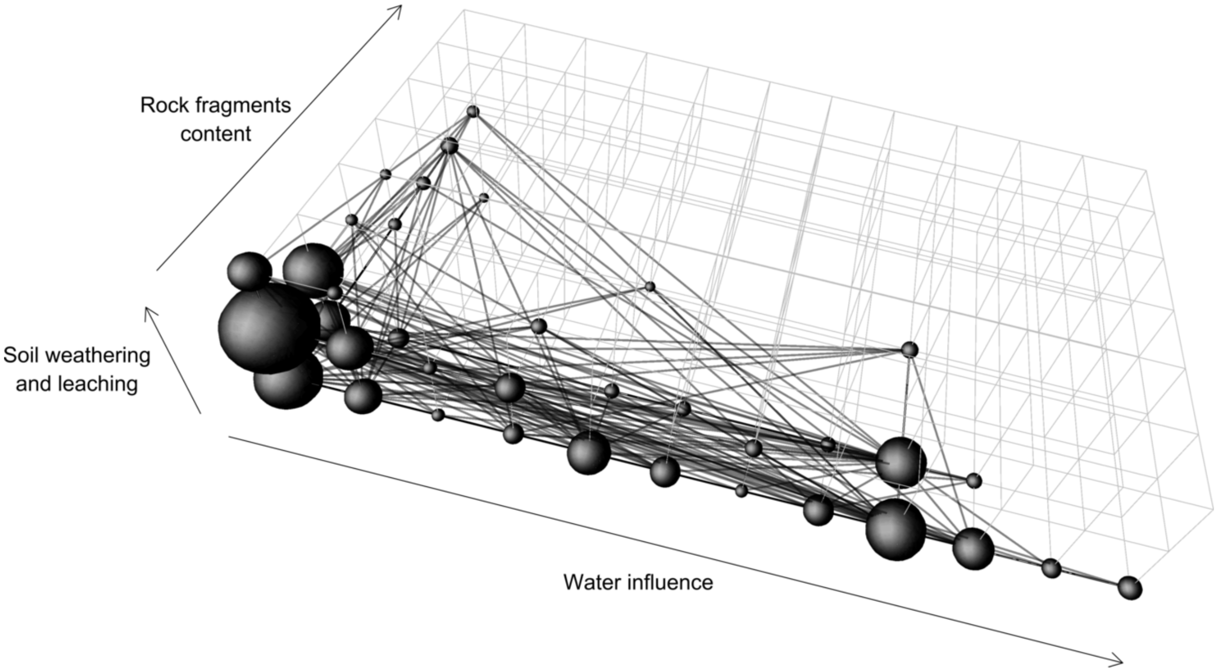


Fig. 8 A 3-dimensional grid representing the combination (Cartesian product) of the three SFS with individual STUs as spheres within it. Volumes of the spheres are proportional to the respective STU frequencies and spatially adjacent STUs are connected by lines.

Table 3 Properties of spatial adjacency graphs, derived from the reduced data sets, for STU and the three SFS and percentiles of their null distributions based on spatial randomizations. Statistically significant values are in bold as well as the percentiles they exceed.

			Spectral radius			Sequentiality		
				NDP			NDP	
Factor	n	m	Observed	2.5th	97.5th	Observed	2.5th	97.5th
Soil unit	37	179	14.13	13.97	15.21	**0.82**	0.73	**0.75**
Water influence	12	42	7.84	7.31	8.46	**0.63**	0.54	**0.58**
Rock fragments content	7	10	3.46	3.38	4.14	0.92	0.91	0.93
Soil weathering and leaching	3	3	2.00	2.00	2.00	**0.97**	0.94	**0.97**

NDP = null distribution percentile

The spatial adjacency graph for water influence (Fig. 9a, Fig. 10, Fig. 10a) appears to explain most of the significant relationships found in the STU graph (Fig. 6). Over the sampling distance of 22 m soils can differ by up to 10 levels which means that only the soils from opposite ends of the water influence gradient (e.g. Entic Podzols and Hemic Histosols) were never found neighbouring. Transition zones between upland and hydromorphic soils are sharp and short within the locality being sometimes as narrow as 1 m. Occurrence of small stream and spring areas together with terrain meso- and micro-topography (including pit-mound pairs and lying trunks damming water outflow; Šamonil et al. 2010b; Pawlik 2013) seem to be crucial factors of the observed exceptional spatial heterogeneity. However, as evidenced by the significantly low adjacency between levels 1 and 9, a tendency for separation can be found already between soils differing by 8 levels which is actually the cause of the significantly low adjacencies between certain STU in Fig. 6. Significant mutual affinity was found between soils with histic properties (levels 10–12) and be-

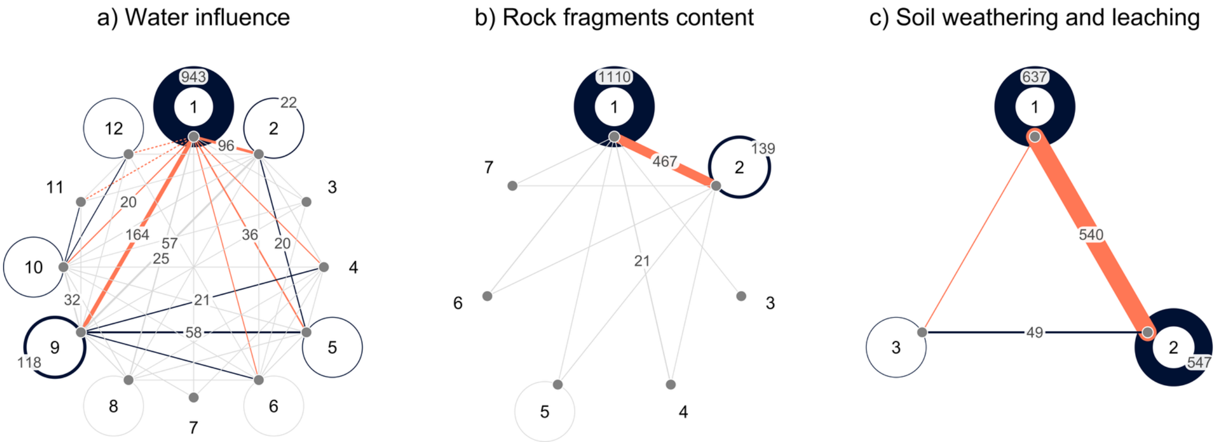


Fig. 9 Spatial adjacency graphs for the three SFS. See Fig. 5 for explanation.

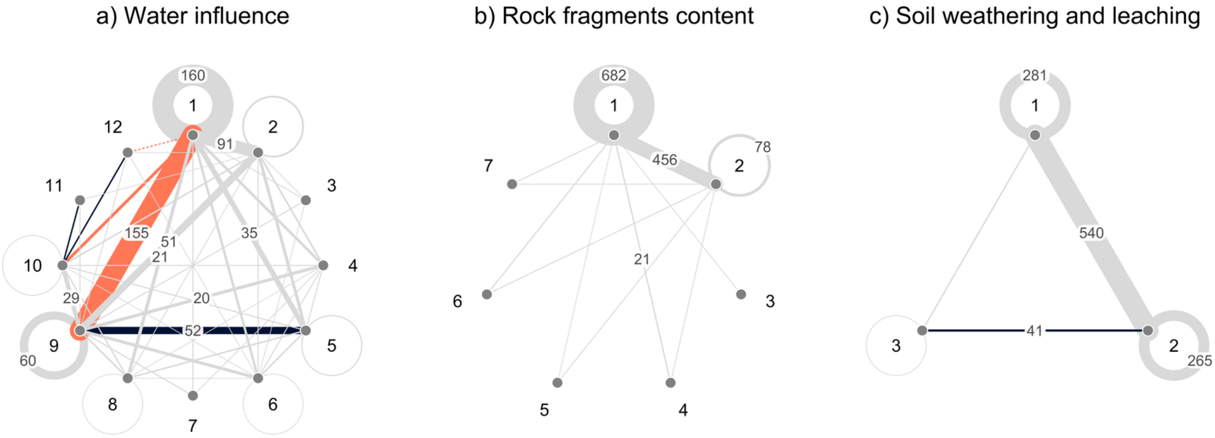


Fig. 10 Spatial adjacency graphs for the three SFS based on data sets with clusters removed. See Fig. 5 for explanation.

tween Gleysols and Stagnosols (levels 5 and 9), again explaining some of the patterns in Fig. 6. The spectral radius associated with water influence is 8.03 (Table 2) which is still more than that of a random graph with the same n and m, again being mainly a consequence of the degree distribution of the graph which is not skewed as in the case of STU but is wider and flatter than in most random graphs (Fig. 7b). In all other aspects the spectral radius appears to be within random variation expected for graphs with given degree distribution or based on spatial categorical data with observed frequencies of categories (Table 2, Table 3). The significantly high sequentiality index (Table 3) gives further, global, evidence that soils with similar degree of water influence were neighbouring more often than soils differing in this regard.

Because macroclimate is constant over 46 ha, differences in soil hydromorphology must be primarily due to topographically controlled (at the ground surface or at the bedrock weathering front) variations in moisture flux and storage, or topographically determined microclimate variation, or the influence of individual plants or woody debris on water movement.

The spatial arrangement of rock fragments content exhibits strong clustering of the first two levels corresponding to the least stony soils (Fig. 9b), a pattern resulting probably particularly from the lithological structure of the gneiss, and Quaternary (bio-)geomorphological processes. Also here the complexity as measured by spectral radius is relatively high given the number of nodes and edges of the spatial adjacency graph (SAG, Table 2), which is a consequence of the

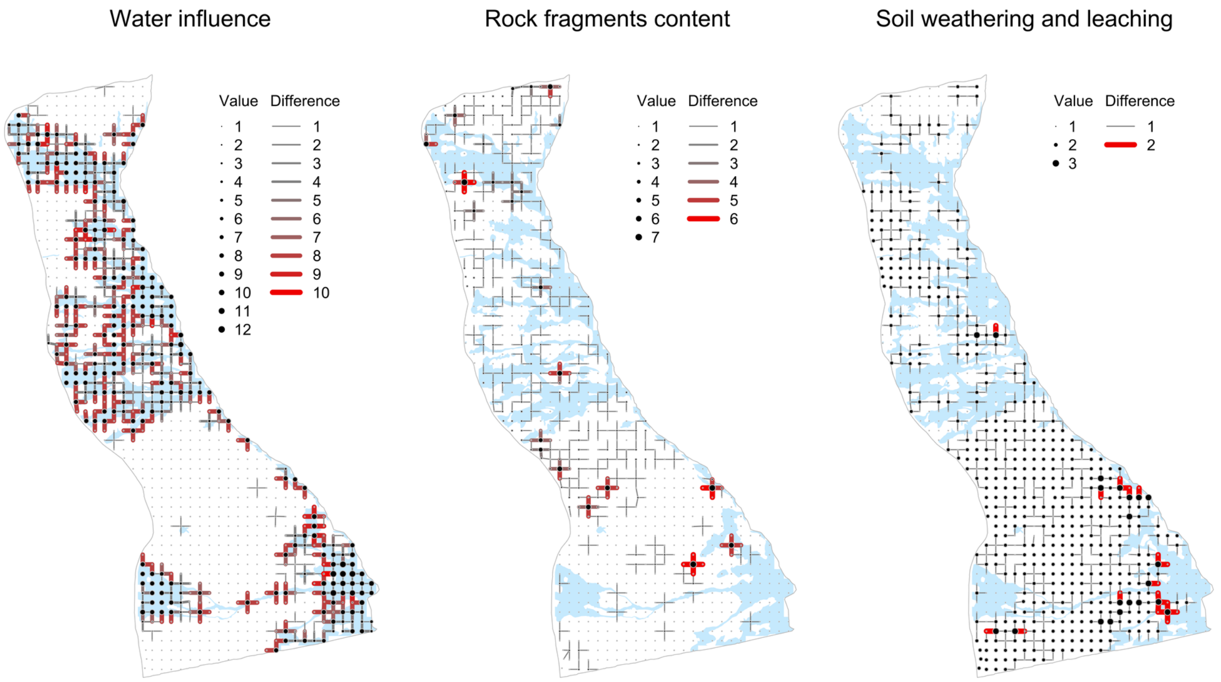


Fig. 11 Differences between neighbouring sampling points along the three SFS. Size of the points represents their position along a SFS (SFS level). Neighbouring points of the same level are not connected, points differing by one level are connected by a gray line and more different neighbours are connected by lines of colour ranging from yellow to red. Areas affected by water are in blue.

skewed node degree distribution (Fig. 7c). In every other respect the spatial pattern appears random (Fig. 10b, Table 2, Table 3) so, evidently, the changes in this property are too abrupt to be captured as gradual at the spatial resolution we used.

Although all the links in spatial adjacency graph for soil weathering and leaching were significant when full data set was used (Fig. 9c) only the one connecting levels 2 and 3 remained significant after cluster removal (Fig. 10c). However, when only upland, non-hydromorphic soil units were kept in level 1, its adjacency with level 3 became significantly low. This illustrates the fact that soils of the highest degree of podzolization, i.e. Albic Podzols, were found predominantly in the vicinity of moderately podzolized upland soils (Entic Podzols) as well as (semi-) hydromorphic soils (Spodic Gleysols, Spodic Stagnosols), but only rarely close to the least podzolized upland soils (Cambisols). Gradual changes in SFS in space are also documented by the significantly high value of the sequentiality index (Table 3). Because the spatial adjacency graph is complete (all possible edges are present), the observed spectral radius is maximum possible and all the benchmark values are equal to 2 (Table 2, Table 3). Within the study area Albic Podzols behaved surprisingly as intrazonal soils, exhibiting affinity to wet areas from which they never occurred farther than 50 m, which is significantly less than could be expected by chance. This is probably supported by (i) more flat topography and hence lower erosion rates in the vicinity of stream areas, (ii) higher proportion of the acidifier *Picea abies* close to the sites affected highly by water, and (iii) colder and more humid microclimate conditions in such areas.

Given that Albic Podzols showed affinity for wet sites but were only rarely adjacent to Cambisols, it would be expected that Cambisols would not occur in the vicinity of wet sites. Surprisingly, a positive relationship was found between Stagnic Dystric Cambisols and Haplic Gleysols (Fig. 6). This tendency was not observed in case of hydromorphic variants of Podzols, which can be explained by lower permeability of Cambisols, caused by higher clay content. Clay particles are destroyed during podzolization (Buurman 1984; Lundström et al. 2000; Buurman & Jongmans 2005) which increases permeability and decreases expression of hydromorphic properties. Indeed, the proportion of soils with hydromorphic properties decreased along the podzolization gradient, reaching 14, 8 and 5% for Cambisols, Entic Podzols and Albic Podzols, respectively. However, it must be said that soil wetness is probably driven mainly by meso- and micro-topography (surface and at the bedrock interface), and clay content in soils has only secondary importance.

All the inspected SAGs (apart from the one for soil weathering and leaching which is complete) share the property that their spectral radius is relatively high given their number of nodes and edges but appears random when frequencies of the categories are taken into account in spatial randomizations. This means that the complexity of the observed spatial pattern is mostly driven by the specific frequencies of the STUs or SFS levels. Abundant and rare categories generate high-degree and low-degree nodes, respectively, and this discrepancy results in relatively high values of spectral radius. However, the significant values of sequentiality indices indicate that this is not the only driver of observed spatial complexity. Apparently, the spatial adjacency of STUs and SFS is not completely random and related categories tend to be adjacent in most cases but this trend is not strong enough to be captured in the simple SAG where only reduced information, whether two nodes are connected or not (but not how often), is retained. Generally, high sequentiality should prevent spatial adjacency of dissimilar categories and thus lower the spectral radius.

3.2.3 Connecting diversity and complexity

The entropy of the STU spatial adjacency graph is 2.69, which is more than the value of the Shannon index for STU diversity (2.42). This means that the uncertainty associated with the frequencies of the STUs is lower than that associated with their spatial adjacency. In other words, the “wiring” of the SAG introduces uncertainty beyond that associated with the relative abundance of STUs. Our simulations (not presented in this study) showed that this happens under three conditions: 1) the distribution of STU frequencies is not uniform, 2) the STUs do not exhibit strong sequentiality, and 3) the studied area is large enough for most STU adjacencies to occur. It appears that while diversity and complexity are closely related, diversity is only one aspect of complexity. However, the nature of the relation between these two characteristics is still an open question that needs further research.

3.3 Implications for geomorphic controls

The SAGs for the three SFS can be considered as subgraphs G' of the STU SAG G. Because $\lambda_1(G) < \lambda_1(G'_k)$ where there are $k = 1, 2, \ldots, n$ subgraphs of G, the sum of the spectral radii for the three identified SFS (13.46) accounts for a large measure of the total complexity of the spatial pattern of STUs ($\lambda_1 = 14.13$). Most of this is attributable to the pattern of water influence, which is controlled within the study area by topography and mass fluxes. Rock fragment content is strongly influenced by biogeomorphic effects, and the third SFS (intensity of podzolization) is strongly correlated in the study area with wetness.

Thus, geomorphology is the primary control over a very locally complex soil pattern. However, rather than (or more properly, in addition to) the broad scale landscape correlations and catenary relationships typically considered in soil geomorphology, the complex pattern of spatial adjaceny of both soils and SFS indicates that microtopography and local disturbances (mostly related to biomechanical and biochemical effects of individual trees) are critical. The sequentiality calculations also support this finding.

This suggests that DEM resolutions finer than what is practical for mapping of extensive area is necessary to capture these geomorphic controls. However, it also suggests that very detailed topographic mapping at the local scale (using, for example, terrestrial laser scanning or ground-based LiDAR, or structure-from-motion photogrammetry) holds great promise capturing local soil complexity.

4 Conclusions

Soil diversity and complexity were analyzed in one of the oldest nature reserves in Europe. Existing graph theory approaches of complexity calculation were upgraded to make better use of spatially explicit data. The hypothesis testing approach allowed assessment of the significance of individual adjacencies in a graph and discovery of important spatial patterns. The newly proposed sequentiality index can be used for comparison of two graphs, measuring to what extent a (multi-) graph follows structure of another graph. The index was applied to find out if spatial arrangement of soils respected the identified gradients of soil factors. An essential step ensuring interpretability of the randomization tests was the removal of highly clustered data so that the results truly reflected the observed adjacency pattern of different soils.

An extensive dataset of 954 soil profiles revealed exceptional local soil diversity and complexity in a primeval forest with six Reference Soil Groups and 37 second-level soil units within a 46 ha area. The sampling distance of ~22 m between neighbouring soil profiles was often too long to capture gradual change in STUs. Among three studied soil forming sequences soil wetness represented the most important component of the overall soil complexity, followed by rock fragment content and intensity of weathering and leaching processes. Spatial correlation between intensity of podzolization and soil wetness suggests synergistic influence of meso- and microtopography, climate, (hydro)geology and effect of individual trees in soil complexity formation. The coevolution of vegetation communities, landforms, and soils is an important factor in the dynamics of primeval mixed mountain forests. The enormous observed local pedodiversity and pedocomplexity raises concerns about possible decreasing pedodiversity in managed forests and deforested areas where certain processes are absent (e.g., effects of long-lasting large pit-m ound pairs or decaying tree trunks and stumps).

Acknowledgements The authors thank their colleagues from the ‘Blue Cat research team’ for field data measurement and Jaroslav Škulavík and Kateřina Drábková for assistance in the field. The research was supported by the Czech Science Foundation (project No. GACR 16-15319S) and partly funded by institutional support of Silva Tarouca Research Institute for Landscape and Ornamental Gardening (VUKOZ IP-00027073).

Supplementary data These include R scripts used to perform the key analysis. Supplementary data to this paper can be found online at http://dx.doi.org/10.1016/j.geomorph.2016.08.023

References

Barrett L.R., Schaetzl R.J. 1998. Regressive pedogenesis following a century of deforestation: evidence for depodzolization. *Soil Science* 163: 482–497.

Behrens T., Schmidt K., Zhu A.X., Scholten T. 2010a. The ConMap approach for terrain-based soil mapping. *European Journal of Soil Science* 61: 133–143.

Behrens T., Zhu A.X., Schmidt K., Scholten T. 2010b. Multi-scale digital terrain analysis and feature selection for digital soil mapping. *Geoderma* 155: 175–185.

Benjamini Y., Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)* 57: 289–300.

Binkley D., Giardina C. 1998. Why do tree species affect soil? The Warp and Woof of tree soil interactions. *Biogeochemistry* 42: 89–106.

Blitzstein J., Diaconis P. 2011. A sequential importance sampling algorithm for generating random graphs with prescribed degrees. *Internet Mathematics* 6: 489–522.

Bobrovski M.V. 2010. Effect of the historical land use on the structure of forest soils in European Russia. *Eurasian Soil Science* 43: 1458–1466.

Borujeni I.E., Mohammadi J., Salehi M.H., Toomanian N., Poch R.M. 2010. Assessing geopedological soil mapping approach by statistical and geostatistical methods: a case study in the Borujen region, Central Iran. *Catena* 82: 1–14.

Buol S.W., Southard R.J., Graham R.C., McDaniel P.A. 2003. Soil Genesis and Classification, 5th edition. Iowa State Press, Ames.

Buurman P. (Ed.) 1984. Podzols. Van Nostrand Reinhold Soil Science Series. New York.

Buurman P., Jongmans A.G. 2005. Podzolisation and soil organic matter dynamics. *Geoderma* 125: 71–83.

Carpenter D.N., Bockheim J.G., Reich P.F. 2014. Soils of temperate rainforests of the North American Pacific Coast. *Geoderma* 230: 250–264.

Chytrý M. (Ed.) 2013. Vegetace České republiky 4. Lesní a křovinná vegetace. Academia, Prague.

Corenblit D., Baas A.C., Bornette G., Darrozes J., Delmotte S., Francis R.A., Gurnell A.M., Julien F., Naiman R.J., Steiger J. 2011. Feedbacks between geomorphology and biota controlling Earth surface processes and landforms: A review of foundation concepts and current understandings. *Earth-Science Reviews* 106: 307–331.

Crowther J. 1987. Ecological observations in tropical karst terrain, West Malaysia. III. Dynamics of the vegetation-soil-bedrock system. *Journal of Biogeography* 14: 157–164.

Estrada-Medina H., Graham R.C., Allen M.F., Jiménez-Osornio J.J., Robles-Casoico S. 2013. The importance of limestone bedrock and dissolution karst features on tree root distribution in northern Yucatán, México. *Plant and Soil* 362: 37–50.

Geller W., Kitchens B., Misiurewicz M., Rams M. 2012. A spectral radius estimate and entropy of hypercubes. *International Journal of Bifurcation and Chaos* 22: 1250096.

Guo Y., Gong P., Amundson R. 2003. Pedodiversity in the United States of America. *Geoderma* 117: 99–115.

Hong Y., Shu J.-L. 2001. A sharp upper bound of the spectral radius of graphs. *Journal of Combinatorial Theory: Series B* 81, 177–183.

Huggett R.J. 1998. Soil chronosequences, soil development, and soil evolution: a critical review. *Catena* 32: 155–172.

Hurlbert S.H. 1971. The non-concept of species diversity: a critique and alternative parameters.

Ecology 52: 577–586.

Ibáñez J.J, De-Alba S., Lobo A., Zucarello V. 1998. Pedodiversity and global soil patterns at coarse scales (with Discussion). *Geoderma* 83: 171–214.

Ibáñez J.J, Zinck J.A., Dazzi C. 2013. Soil geography and diversity of the European biogeographical regions. *Geoderma* 83: 142–153.

Johnson D.L., Keller E.A., Rockwell T.K. 1990. Dynamic pedogenesis: new views on some key soil concepts, and a model for interpreting quaternary soils. *Quaternary Research* 33: 306–319.

Li L., Alderson D., Doyle J.C., Willinger W. 2005. Towards a theory of scale-free graphs: definition, properties, and implications. *Internet Mathematics* 2: 431–523.

Liu C.-a., Weng C.-w. 2013. Spectral radius and degree sequence of a graph. *Linear Algebra and its Applications* 438: 3511–3515.

Lo Papa G., Palermo V., Dazzi C. 2011. Is land-use change a cause of loss of pedodiversity? The case of the Mazzarrone study area, Sicily. *Geomorphology* 135: 332–342.

Lundström U.S., van Breemen N., Bain D. 2000. The podzolization process. A review. *Geoderma* 94: 91–107.

Michéli E., Schad P., Spaargaren O. (Eds.) 2007. World Reference Base for Soil Resources 2006, First Update 2007. World Soil Resources Reports No 103, FAO, Rome.

Nikodem A., Pavlů L., Kodešová R., Borůvka L., Drábek O. 2013. Study of podzolization process under different vegetation cover in the Jizerské hory Mts. region. *Soil and Water Research* 8: 1–12.

Pawlik, Ł. 2013. The role of trees in the geomorphic system of forested hillslopes — A review. *Earth-Science Reviews* 126: 250-265.

Phillips J.D. 2001. Divergent evolution and the spatial structure of soil landscape variability. *Catena* 43: 101–113.

Phillips J.D. 2006. Deterministic chaos and historical geomorphology: a review and look forward. *Geomorphology* 76: 109–121.

Phillips J.D. 2009. Soils as extended composite phenotypes. *Geoderma* 149: 143–151.

Phillips J.D. 2012. Synchronization and scale in geomorphic systems. *Geomorphology* 137: 150–158.

Phillips J.D. 2013. Sources of spatial complexity in two coastal plain soil landscapes. *Catena* 111: 98–103.

Phillips J.D. 2016. Landforms as extended composite phenotypes. *Earth Surface Processes and Landforms* 41: 16–26.

Phillips J.D., Marion D.A. 2005. Biomechanical effects, lithological variations, and local pedodiversity in some forest soils of Arkansas. *Geoderma* 124: 73–89.

Phillips J.D., Marion D.A. 2006. Biomechanical effects of trees on soil and regolith: beyond treethrow. *Annals of the Association of American Geographers* 96: 233–247.

Phillips J.D., Marion D.A., Luckow K., Adams K.R. 2005. Nonequilibrium regolith thickness in the Ouachita Mountains. *The Journal of Geology* 113: 325–340.

Phillips J.D., Schwanghart W., Heckmann T. 2015. Graph theory in geosciences. *Earth-Science Reviews* 143: 147–160.

Pielou E.C. 1969. An introduction to mathematical ecology. Wiley, New York.

Robertson G.P., Crum J.R., Ellis B.G. 1993. The spatial variability of soil resources following long-term disturbance. *Oecologia* 96: 451–456.

Roering J.J., Marshall J., Booth A.M., Mort M., Jin Q. 2010. Evidence for biotic controls on topography and soil production. *Earth and Planetary Science Letters* 298: 183–190.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Šamonil P., Vrška T. 2008. Long-term vegetation dynamics in the Šumava Mts. natural spruce-fir-beech forests. *Plant Ecology* 196: 197–214.

Šamonil P., Král K., Douda J., Šebková B. 2008. Variability in forest floor at different spatial scales in a natural forest in the Carpathians: effect of windthrows and mesorelief. *Canadian Journal of Forest Research* 38: 2596–2606.

Šamonil P., Tejnecký V., Borůvka L., Šebková B., Janík D., Šebek O. 2010a. The role of tree uprooting in Cambisol development. *Geoderma* 159: 83–98.

Šamonil P., Král K., Hort L. 2010b. The role of tree uprooting in soil formation: a critical literature review. *Geoderma* 157: 65–79.

Šamonil P., Valtera M., Bek S., Šebková B., Vrška T., Houška J. 2011. Soil variability through spatial scales in a permanently disturbed natural spruce-fir-beech forest. *European Journal of Forest Research* 130: 1075–1091.

Šamonil P., Vašíčková I., Daněk P., Janík D., Adam D. 2014. Disturbances can control fine-scale pedodiversity in old-growth forest: is the soil evolution theory disturbed as well? *Biogeosciences* 11: 5471–5509.

Šamonil P., Daněk P., Schaetzl R.J., Vašíčková I., Valtera M. 2015. Soil mixing and genesis as affected by tree uprooting in three temperate forests. *European Journal of Soil Science* 66: 589–603.

Šamonil P., Valtera M., Schaetzl R.J., Adam D., Vašíčková I., Daněk P., Janík D., Tejnecký V. 2016. Impacts of old, comparatively stable, treethrow microtopography on soils and forest dynamics in the northern hardwoods of Michigan, USA. *Catena* 140: 55–65.

Schoeneberger P.J., Wysicki D.A., Benham E.C., Broderson W.D. 1998. Field book for describing and sampling soils. Natural Resources Conservation Service, USDA, National Soil Survey Center, Lincoln, NE.

Šebková B., Šamonil P., Valtera M., Adam D., Janík D. 2012. Interaction between tree species populations and windthrow dynamics in natural beech-dominated forest, Czech Republic. *Forest Ecology and Management* 280: 9–19.

Shannon C., Weaver W. 1949. The mathematical theory of communication. University of Illinois Press, Urbana.

Shouse M.A., Phillips J.D. 2016. Soil deepening by trees and the effects of parent material. *Geomorphology* 269: 1–7.

Smith M.P., Zhu, A-X., Burt J.E., Stiles C. 2006. The effects of DEM resolution and neighborhood size on digital soil survey. *Geoderma* 137: 58–69.

Spears J.D.H., Lajtha K. 2004. The imprint of coarse woody debris on soil chemistry in the western Oregon Cascades. *Biogeochemistry* 71: 163–175.

Thompson J.A., Kolka R.K. 2005. Soil carbon storage estimation in a forested watershed using quantitative soil-landscape modeling. *Soil Science Society of America Journal* 69: 1086–1093.

Thompson J.A., Bell J.C., Butler C.A. 2001. Digital elevation model resolution: effects on terrain attribute calculation and quantitative soil-landscape modeling. *Geoderma* 100: 67–89.

Tolasz R., Míková T., Valeriánová A., Voženílek V. (Eds.) 2007. Climate Atlas of Czechia. Český hydrometeorologický ústav and Univerzita Palackého v Olomouci, Prague, Olomouc.

Toomanian N., Jalalian A., Khademi H., Eghbal M.K., Papritz A. 2006. Pedodiversity and pedogenesis in Zayandeh-rud Valley, Central Iran. *Geomorphology* 81: 376–393.

Valtera M., Šamonil P., Boublík K. 2013. Soil variability in naturally disturbed Norway spruce forests in the Carpathians: bridging spatial scales. *Forest Ecology and Management* 310: 134–146.

Vrška T., Šamonil P., Unar P., Hort L., Adam D., Král K., Janík D. 2012. Developmental dynamics of virgin forest reserves in the Czech Republic III – Šumava Mts. and Český les Mts. (Diana, Stožec, Boubín virgin forest, Milešice virgin forest). Academia, Prague.

Watts D.J., Strogatz S.H. 1998. Collective dynamics of 'small-world' networks. *Nature* 393: 440–442.

Welzholz J.C., Johann E. 2007. History of protected forest areas in Europe. In: Frank G., Parviainen J., Vandekerkhove K., Latham J., Schuck A., Little D. (Eds.), COST Action E27 Protected Forest Areas in Europe – Analysis and Harmonisation (PROFOR): Results, Conclusions and Recommendations. Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW), Vienna, AU, pp. 17–40.

Paper 7

Four decades of the coexistence of beech and spruce in a Central European old-growth forest. Which succeeds on what soils and why?

Pavel Daněk
Pavel Šamonil
Tomáš Vrška

Plant and Soil 437 (2019), 257–272

Abstract

Aims

The dynamics of forests dominated by European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) have been studied intensively. However, mainly due to a lack of long-term data, little is known about how these dynamics interact with soil conditions. In an old-growth spruce-beech forest with high soil diversity we studied how the development of tree populations differs among different soils.

Methods

Data from tree censuses carried out in 1972, 1996 and 2010 in the Boubín Primeval Forest in the Czech Republic were combined with detailed soil sampling to assess the relative abundance of beech and spruce and the role of the main drivers of population dynamics (tree growth, mortality and recruitment) in changes with respect to soils.

Results

The spatial distribution of populations of the two species primarily reflected a gradient of soil hydromorphism, with beech dominating drier soils and spruce dominating wetter soils. Over the 38 years, beech expanded on all major soils, yet the most important drivers differed. The only driver acting in favor of spruce on certain terrestrial soils was its faster radial growth. However, the effect was weaker than the effect of drivers that prioritized beech, mainly tree mortality. Fine-scale mortality (deaths of individual trees) was more significant on terrestrial soils, while the effect of coarse-scale mortality (deaths from a single severe windstorm event) increased towards hydromorphic soils. Certain soils (Histosols and Albic Podzols) diverged from the general trends because of their different disturbance regimes and specific tree-soil interactions.

Conclusions

Soils play an important role in the dynamics of an old-growth spruce-beech forest. Their physical and chemical properties together with specific disturbance regimes determine fine-scale differences in tree species composition. At the same time, soils themselves are affected by trees, e.g. through acidification. The current expansion of beech is expected to continue on terrestrial soils but will probably slow down with increasing soil wetness.

P. Daněk[a,b], *P. Šamonil*[a,c], *T. Vrška*[a]

[a] Department of Forest Ecology, The Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Brno, Czech Republic [b] Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic [c] Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic

1 Introduction

European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) are the two most important tree species of Central European submontane and montane regions (Leuschner & Ellenberg 2017), and understanding the long-term dynamics of their coexistence is highly relevant from the perspective of forest ecology, management and nature conservation.

Beech and spruce share a significant part of their ecological niches and often grow together, but at the same time the two species differ in their life strategies and impact on their environment. The necessity to completely refoliate every spring makes beech susceptible to late frosts (Dittmar et al. 2006) and limits its distribution towards higher altitudes and latitudes (Bolte et al. 2010; Körner et al. 2016) where spruce, an evergreen conifer, becomes more successful (Kraus et al. 2016; Leuschner & Ellenberg 2017). Compared to beech, spruce has a shallower root system (Schmid & Kazda 2001; Schume et al. 2004), which makes it more prone to drought (Pretzsch et al. 2014b), but on the other hand allows it to tolerate higher groundwater levels (Leuschner & Ellenberg 2017).

An important factor shaping the species composition of forest stands are direct interactions between tree individuals. These can take various forms, depending on environmental conditions and species identity or the age of the individuals, ranging from competition to facilitation, including also mechanical interactions, such as e.g. crown shyness (Hajek et al. 2015). Beech is a highly competitive shade-tolerant and shade-casting species (Packham et al. 2012) whose growth under the low light conditions of a closed forest canopy is superior to that of spruce (Grundmann et al. 2011; Dobrovolny 2016). However, when no shading from adult trees occurs, both spruce (Grams et al. 2002; Kozovits et al. 2005) and beech (Rolo et al. 2015) seedlings have been shown to have a competitive advantage over the other species in different settings. In addition, competition patterns may differ for trees of different life stages, depending on site properties (Fichtner et al. 2012). In the case of adult beech and spruce stands, the productivity of mixed stands is often higher than that of monocultures (Pretzsch et al. 2012, 2014b). Admixtures of spruce in beech stands generally foster beech through decreased intraspecific competition (Pretzsch et al. 2010; Bolte et al. 2013; Metz et al. 2016). Spruce, when growing together with beech, can benefit from decreased shading in spring and autumn when beech has no leaves (Pretzsch et al. 2014b) or, on poor sites, from nutrient inputs from beech litter (Pretzsch et al. 2010). On fertile sites, however, the high competitive potential of beech is rather detrimental to spruce (Pretzsch et al. 2010; Bolte et al. 2013).

In natural settings, forest dynamics are largely driven by disturbances (Pickett & White 1985; Turner 2010; Kulakowski et al. 2017), which in Europe are represented mainly by windstorms (Schelhaas et al. 2003). In Central Europe, the most damaging windstorms are associated with severe extratropical cyclones that typically occur from late autumn till early spring, when deciduous species are leafless (Fischer et al. 2013; Mitchell 2013). This, together with its more shallow root system, makes spruce more susceptible to windthrow than beech (Jactel et al. 2017). Accordingly, pure spruce stands have repeatedly been shown to be less resistant to wind than mixed stands (Schütz et al. 2006; Knoke et al. 2008; Valinger & Fridman 2011). The risk of wind damage can also be increased by certain soil conditions, e.g. water logging (Dobbertin 2002), and sites with different soils can have different disturbance regimes (Šamonil et al. 2014). Not only are tree populations determined by their environment, but, in the long term, trees are also able to alter the environment, especially soil conditions (Binkley & Giardina 1998). Beech and spruce markedly differ in their effects on soil. Spruce is a strong acidifier and can cause the depletion of base cations from the topsoil (Augusto et al. 2002; Berger et al. 2004), while beech is able to act as a Ca-pump, transporting Ca from deeper soil horizons to the forest floor via the tree litter (Berger et al. 2006). Both species can affect soil via treethrows, not only by physically disrupting it, but also by subsequently causing a different progression of pedogenesis within the resulting microtopographies compared to undisturbed soil (Šamonil et al. 2015, 2018). Trees can thus be viewed as ecosystem engineers (sensu Corenblit et al. 2011), and through specific feedbacks with the soil environment can influence the future vegetation composition.

These processes of environmental filtering, competition, disturbances and feedbacks with the soil environment shape the long-term dynamics of beech and spruce populations, and they determine if one of the species will dominate the other one. Recently, an increasing dominance of beech has been observed in old-growth forests across Europe (Vrška et al. 2009; Bolte et al. 2014; Petritan et al. 2014; Janík et al. 2016b), sometimes after a long period of spruce dominance (Bobek et al. under review). However, if and how the pattern of such an expansion differs with soil conditions and, generally, what is the role of pedodiversity in forest dynamics, are still poorly understood.

In this study, we focus on the dynamics of tree populations in the Boubín Primeval Forest in the Czech Republic, an old-growth beech-spruce mountain forest with high soil diversity (Daněk et al. 2016). Long-term data on forest development allow us to address the following questions: 1) What are the patterns in the distribution of the two focal species with respect to soils? 2) Is there a temporal shift in these patterns? 3) What is the relative importance of tree growth, mortality (fine-scale or disturbance-related) and recruitment in these shifts? 4) Is there evidence of long-term tree–soil feedbacks?

2 Materials and methods

2.1 Study site

This research took place in the Boubínský Prales Reserve (hereinafter Boubín), located in the Šumava Mts. in the southwest of the Czech Republic. Protected since 1858, it is the second oldest forest reserve in the Czech Republic and one of the oldest forest reserves in Europe (Welzholz & Johann 2007). As far as we know its 46 ha core zone has never been cut (Vrška et al. 2001) and provides an excellent site for studying long-term interactions between trees and soils. Boubín occupies north-eastern slopes built of crystalline rocks of the Bohemian Massif, mainly primary schists and biotic and mica-schist gneisses. At an altitude of 930–1110 m a.s.l. the mean annual temperature is 4.9 °C and mean annual precipitation is 1067 mm. Forest stands are mainly formed by European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*), with an admixture of silver fir (*Abies alba* Mill.). On 1 March 2008 Boubín was hit by the Emma windstorm (Šebková et al. 2011), an important disturbance event associated with a significantly high tree mortality. Based on dendrochronological data (Šamonil, unpublished), such events occur approximately once every 100 years.

2.2 Datasets

2.2.1 *Soils*

Soils were investigated in 2015 on 954 points of a regular square grid with a lateral spacing of 22.125 m. At each point we inspected a shallow excavated soil profile coupled with a profile from a soil corer of 3 cm diameter that covered depths up to 1 m. Diagnostic horizons and other features of the profiles were used to determine the soil taxonomical unit (STU) according to the WRB system (IUSS Working Group WRB 2007), and a high number of 37 low-level STUs were identified (see Daněk et al. 2016 for details on the soil survey). In the present study we worked with the broadest STUs, Reference Soil Groups, except for Podzols. We discriminated between Albic and Entic Podzols due to differences in their nutrient status associated with the specific stratigraphy of soil horizons, their relation to topography, and because they are generally considered as distinct stages of the pedogenetic trajectory (Schaetzl & Thompson 2015). This resulted in a total of 7 STUs, hereafter referred to as soils. Two main gradients can be identified in these soils: 1) water influence, and 2) the degree of weathering and leaching processes (Daněk et al. 2016). Along the gradient of water influence the soils can be divided between "drier" terrestrial soils (Leptosols, Cambisols, Entic and Albic Podzols) and "wetter" hydromorphic soils that comprise, with increasing wetness, Stagnosols, Gleysols and Histosols. Weathering and leaching is mainly related to podzolization and its intensification can be observed from Cambisols to Entic Podzols and is most pronounced in Albic Podzols. Leptosols represent specific soils with a high amount of rock content with no additional diagnostic horizons.

2.2.2 *Trees and regeneration*

For quantification of changes in tree populations we used extensive data from tree censuses carried out in 1972, 1996 and 2010 (Šebková et al. 2011). During these censuses, the positions of all standing and lying trees of DBH (diameter at breast height) ≥ 10 cm) inside the 46 ha core zone were recorded together with several tree characteristics, including species, DBH, tree status (alive/dead) and type of death.

To represent the potential for future development, regeneration, i.e. trees with DBH < 10 cm, was investigated during 2015 and 2016 on 118 circular plots of diameter 10 m with centers on the locations of the soil survey. This subset of plots was selected so that it reflected soil diversity and covered the forest evenly. In each circle all tree individuals of DBH ≥ 1 cm that were not already recorded in the 2010 census (i.e., mainly those under the 10 cm threshold of the tree censuses) were counted, distinguishing tree species and three DBH classes (1–3 cm, 3–7 cm and 7+ cm). See the table in Appendix 1 for a regeneration data summary.

2.3 Data processing and analyses

2.3.1 *Tree data processing*

To connect the soils and tree populations we considered the trees growing within 10 m of each soil survey point as representative for the particular soil unit. Our previous results from Boubín (Daněk et al. 2016) showed that even at distances more than two times greater (22 m) soils in most cases do not differ, and soils within these 10 m buffers can be generally considered homogeneous. Our final dataset included about 10,335 living tree individuals recorded between 1972 and 2010.

Because we were interested in the interaction of beech and spruce, we further filtered the tree dataset to only contain these two species. The proportions of other tree species (in terms of basal area) were very low (about 4% of fir and less than 1% of others in 2010) and the total number of analyzed tree individuals thus dropped only slightly, to 9897 (see the table in Appendix 2 for more detailed information).

To compare abundances of the two species on different soils we used the proportion of beech basal area relative to total basal area (p_{beech}). Working with beech and spruce only, the proportion of spruce was then equal to $1 - p_{\text{beech}}$.

2.3.2 Impact of the Emma windstorm

During the 2010 census, whether a tree died during the Emma windstorm was recorded on about one fifth of the study site. We modeled this information for the rest of the site using random forest classification models (Breiman 2001), considering only the trees that died between 1996 and 2010. The variables used as predictors were tree species, DBH, death type (uprooting or breakage), the decay stage of lying trunks and the deviation of the tree's orientation from the average orientation of trees known to have fallen during the storm.

2.3.3 Driving factors of the change in proportions of beech and spruce

We identified and compared five possible drivers of the change in proportions of the two species, based on three main drivers of tree population dynamics – growth, mortality and recruitment. To quantify the absolute effect of a driving factor we computed an alternative proportion of beech, based on a hypothetic scenario in which the factor in question was excluded. This means we kept the initial 1972 census as a fixed starting point and modified only the final 2010 data set. We computed the absolute change in the proportions attributable to each of the five factors by subtracting the hypothetical proportion of beech (after the exclusion of a driving factor) from that actually observed in 2010. These differences were subsequently relativized so that their absolute values summed to 100%.

The modified data sets were constructed as follows. In the case of tree growth we were primarily interested in the ability of one species to grow faster than the other one, i.e. radial growth rate. To assess this, we first fitted a GAM to the relation between tree DBH in 1972 and DBH increment from 1972 to 2010 for each species separately (see Appendix 6 for summary of these models). Then, we computed the modified 2010 DBH of each tree as the DBH in 1972 plus the smaller increment of those predicted by the two species-specific models. This way, any ability of one species to grow faster than the other was eliminated.

For mortality we distinguish fine-scale disturbance and coarse-scale disturbance mortality. The former represents mainly temporally independent deaths of single (or small groups of) trees over the study period, and the latter reflects the effect of a single rare severe disturbance event – i.e. the Emma windstorm. When constructing the modified data set, both types of mortality were treated similarly – trees that died between 1972 and 2010 were added to those that survived, and their expected 2010 DBH was computed using species-specific GAMs, based on their latest recorded DBH.

In the case of recruitment, all recruits (individuals not present in the initial census) were simply removed in the modified data set.

In addition to these four factors we identified another that we did not initially consider – population structure. It turns out that if individuals of one of the two compared species are generally smaller (as is the case for beech), as the trees grow the proportion of the species increases even if none of the aforementioned factors is acting. To exclude this factor, trees in the modified data set were not allowed to exhibit the growth that was common to both species. This factor is reciprocal to radial growth rate and the basal area increment between 1972 and 2010 for trees in the modified data set and it was computed as the observed increment during this period minus the increment considered for the exclusion of radial growth rate.

2.3.4 Statistical analyses

To compare population structure of the two species we assessed their dominance along the DBH gradient. We first computed basal areas of beech and spruce for trees in 10-cm DBH classes. Based on 10,000 bootstrap resamples we derived 95% confidence intervals (CI) for the ratios of beech basal area to spruce basal area for these classes and interpolated them to span the whole studied DBH range (10–150 cm). Then, beech was considered dominant in DBH intervals where the lower bound of the ratio's CI was greater than 1, and spruce in intervals where the upper bound of the CI was lower than 1.

We used a standard approach for calculating fine-scale mortality rates over the 38 year period (Condit et al. 1999) from $m = (\ln n_0 - S_t)/t$, where n_0 is the initial population size and S_t the number of survivors after time t. The effect of coarse-scale disturbance mortality, as a one-time event, was evaluated simply as the percentage of lost basal area. Recruitment was calculated as the number of recruits (individuals not recorded in the initial census) per unit area and time.

The relation between beech proportion in trees or regeneration and soil gradients was fitted using GAMs with binomial distribution corrected for overdispersion. In the case of soil wetness, a soil wetness index (SWI) was used as an explanatory variable. SWI is essentially the position of a soil unit along the soil wetness gradient (see Daněk et al. 2016). The values of SWI used for the terrestrial soils, Stagnosols, Gleysols and Histosols were 0, 1/3, 2/3 and 1, respectively. In the case of the other gradient (weathering and leaching) we used only data from terrestrial soils (excluding Leptosols) and the order of a soil unit along the gradient (Cambisols – Entic Podzols – Albic Podzols) was used as a continuous explanatory variable.

For GAMs the 10 m diameter circles (see above) were taken as individual units and confidence intervals were derived from standard error estimates. In other cases, tree individuals from all circles of one soil unit were treated as one metapopulation, and confidence intervals for means were computed based on 10,000 bootstrap resamples of these populations. Bootstrapping should be capable of handling the heterogeneity in the size and variation of our samples (most markedly the contrast in representation of Histosols and Entic Podzols). When the significance of differences between groups was tested, pairwise p values were computed from bootstrap distributions of differences in means for all pairs of groups. These p values were subsequently corrected for multiple testing using a sequential Bonferroni-type procedure (Benjamini & Hochberg 1995). In the rare cases when due to absence of the studied phenomenon (beech coarse-scale mortality and spruce recruitment on Histosols) all bootstrap means for a group were zero, statistical significance of the difference between this group and the others was not assessed. All analyses were performed using R (R Core Team 2016) with the packages *randomForest* (Liaw & Wiener 2002) used for random forests classification and *mgcv* (Wood 2011) for GAMs.

3 Results

3.1 Current differences between populations of beech and spruce with respect to soils

There were substantial differences in the distribution of the two focal species between the studied soils. These differences were consistent between the censuses and can be demonstrated using the 2010 census (Fig. 1, Table 1). Beech was least abundant on Histosols (present on 50% of plots with an average population density of 29 ha^{-1}) and most on Albic Podzols (100% of plots and 154 ha^{-1}). It also had the lowest basal areas on Histosols (0.9 m^2ha^{-1}) but the highest on Entic Podzols (23.5 m^2ha^{-1}). Reciprocally, spruce was least abundant on Entic Podzols (69 ha^{-1}) and most on Histosols (234 ha^{-1}), and also reached minimum and maximum basal areas on these two soils (16.0 and 55.2 m^2ha^{-1}, respectively). It was least abundant on Leptosols (79% of plots) and was present on all plots of Histosols and Albic Podzols.

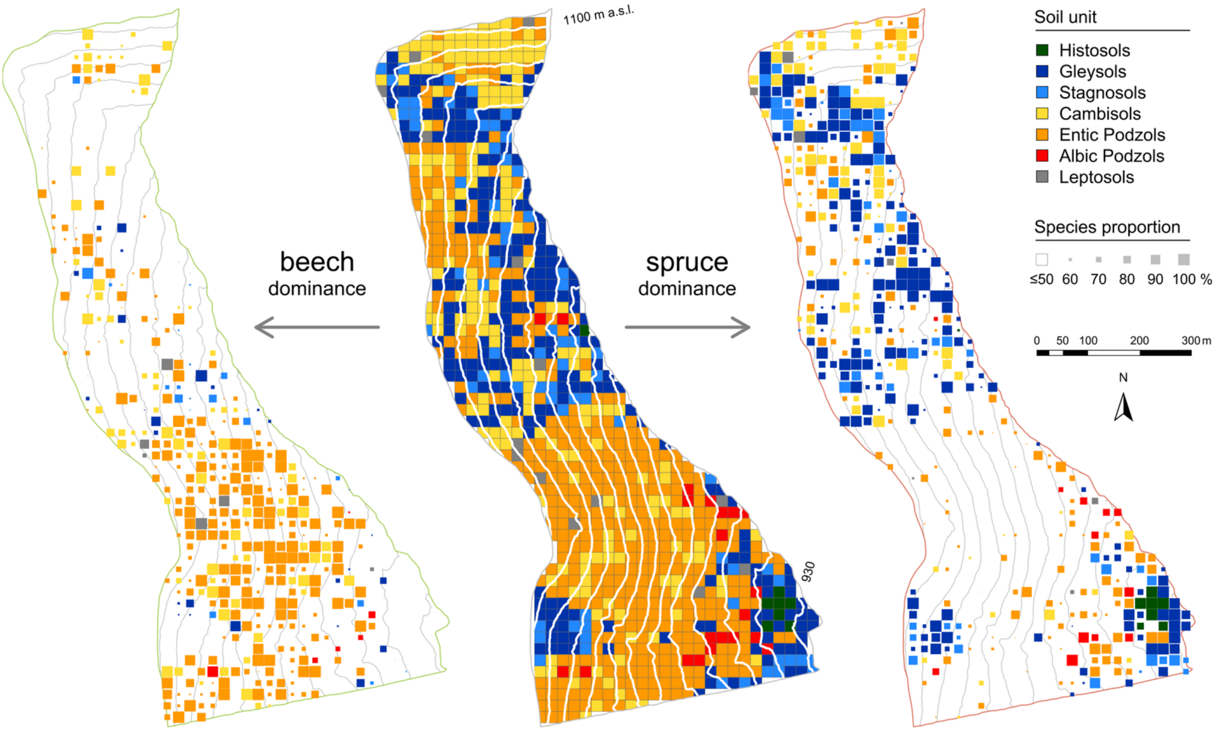


Fig. 1 Map of soils in Boubín (middle; grid size 22.125 m). To the left and the right are maps with only those squares where either beech or spruce, respectively, dominate. The size of the squares is proportional to the degree of dominance in 2010.

The main trends could thus be observed along the gradient of soil wetness. In general, and according to our expectations, spruce dominated on hydromorphic soils and beech on terrestrial soils. While the dominance of spruce on hydromorphic soils was significant both in terms of numbers of individuals and basal area, the beech dominance on terrestrial soils was less pronounced. Numbers of beech individuals (compared to spruce) were higher on all terrestrial soils except for Leptosols; however, this difference was only significant for Entic and Albic Podzols. In terms of basal area, Entic Podzols were the only terrestrial soils where beech dominated over spruce, with spruce being dominant on both Cambisols and Albic Podzols.

Table 1 Selected characteristics of the study area and tree populations. Mean values are given with their 95% confidence intervals in parentheses. For maximum DBH a value comparable between all soils is given instead. This value was computed based on bootstrap resamples of size equal to the smallest sample size among all soils (i.e. 5, the number of beech individuals on Histosols). Letters indicate differences between soils within species – if two values have no common letter, they differ significantly ($\alpha = 0.05$). Asterisks/pluses denote a significant difference between species (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). Asterisks indicate that the mean value for spruce is higher than that for beech, pluses the opposite. Numbers of stems and basal areas are computed for the whole population, median and maximum DBHs are mean values of medians or maxima from individual plots where the species is present

		Hydromorphic soils			Terrestrial soils			
Quantity	Species	Histosols	Gleysols	Stagnosols	Cambisols	Entic Podzols	Albic Podzols	Leptosols
Soil characteristics	—	•⟶	decreasing water impact ⟶		•⟶	intensification of weathering and leaching processes (e.g. podzolization)	⟶	stony soils with low amount of earth fraction[†]
Studied area (ha)	—	0.17	6.51	2.22	6.04	13.24	0.65	0.43
Number of plots	—	6	214	72	196	426	21	14
Plots occupied (%)	beech	50	60	78	92	98	100	79
	spruce	100	94	89	86	82	100	79
No. stems (ha^{-1})	beech	29 (6–53)^{a}	56 (51–60)^{a}	82 (72–92)^{b}	104 (99–110)^{c}	138 (134–142)^{d}	154 (136–174)^{d}	107 (86–128)^{c}
	spruce	234 (205–258)^{d}	139 (134–144)^{c}	147 (137–156)^{c}	91 (86–96)^{b}	69 (65–73)^{a}	96 (76–116)^{b}	105 (84–125)^{b}
		***	***	***	+	+++	+++	
Basal area (m^{2} ha^{-1})	beech	0.9 (0.1–2.2)^{a}	5.8 (4.9–6.8)^{b}	9.5 (7.8–11.4)^{c}	19.2 (17.7–20.8)^{d}	23.5 (22.4–24.7)^{e}	18.0 (14.0–22.7)^{d}	14.8 (9.7–20.2)^{cd}
	spruce	55.2 (42.6–67.7)^{e}	33.1 (30.9–35.3)^{cd}	36.6 (32.6–40.9)^{d}	23.6 (21.4–26.0)^{b}	16.0 (14.5–17.5)^{a}	32.2 (23.3–41.7)^{bcd}	23.6 (15.3–32.4)^{abc}
		***	***	***	**	+++	*	
Median DBH (cm)	beech	14 (10–32)^{ab}	20 (18–24)^{a}	28 (22–34)^{b}	47 (44–48)^{d}	42 (40–44)^{c}	33 (20–40)^{ab}	32 (22–44)^{abc}
	spruce	50 (42–58)^{b}	51 (49–53)^{b}	51 (47–54)^{b}	51 (47–55)^{b}	39 (36–43)^{a}	59 (50–69)^{b}	45 (32–52)^{ab}
		***	***	***	*		***	
Max. DBH (cm)	beech	32 (29)	93 (57)	90 (58)	97 (67)	95 (67)	80 (57)	81 (63)
	spruce	92 (72)^{a}	127 (78)	145 (79)	117 (83)	129 (82)	127 (93)^{b}	104 (80)
		***	***	***	***	***	***	**

[†] intensification of weathering and leaching processes nod considered on Leptosols

This disproportion between differences in the numbers of individuals and basal area was a consequence of the distribution of tree diameters in populations of the two species (Fig. 2). While on hydromorphic soils the predominance of spruce was apparent in trees of almost all diameters, on terrestrial soils beech predominated up to DBHs of approx. 80 cm, above which spruce was more common, thus reaching higher basal areas even with lower numbers of individuals (Table 1). The change to spruce dominance in trees of large diameters could be explained by the ability of spruce to grow to larger dimensions than beech. The largest spruce DBH recorded in Boubín was 145 cm as compared to only 102 cm for beech, and this difference between the species was significant on all soils (Table 1).

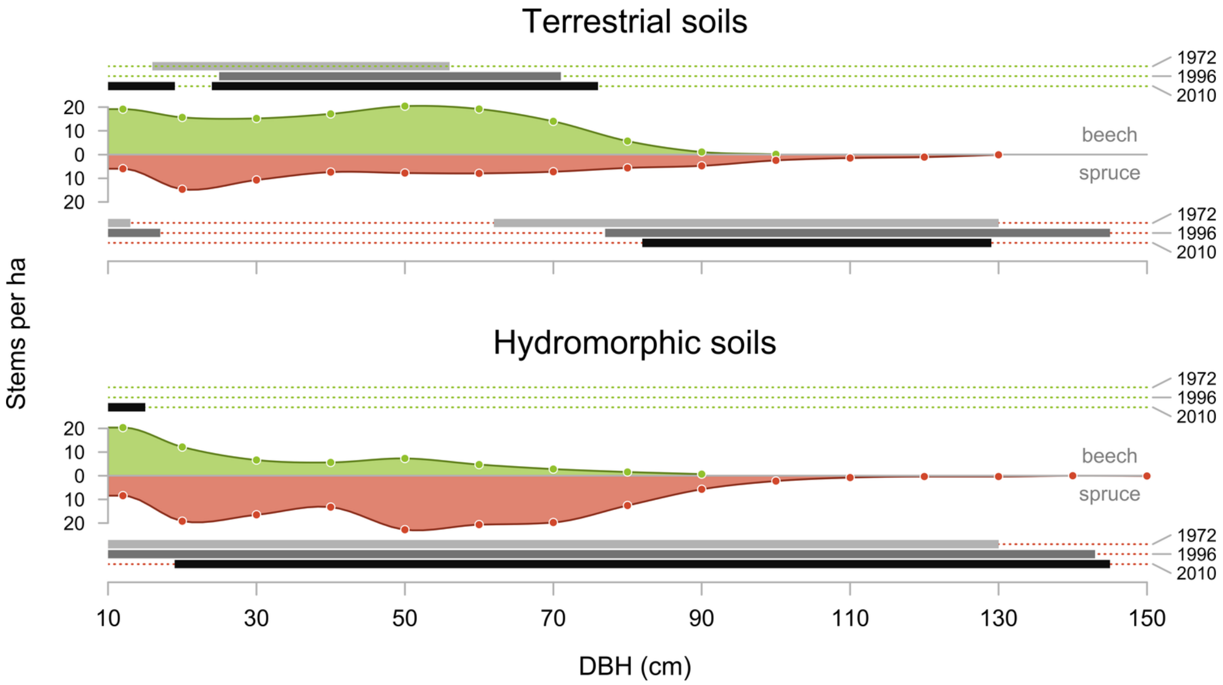


Fig. 2 Population structure and DBH ranges of dominance on different soils. Upper parts of the graphs (green) describe beech, lower parts (red) spruce. Filled areas show average numbers of individuals of different diameters in 2010. Thick line segments in shades of grey indicate DBH intervals in which a species significantly ($\alpha = 0.05$) dominated, with census years 1972, 1996 and 2010 displayed in light gray, middle gray and black, respectively.

Besides abundance and dominance, the two species also differed in the diversification of tree sizes. The population structure of beech varied significantly among the soils, with median DBH ranging from 14 cm on Histosols to 47 cm on Cambisols (Table 1), i.e. increasing with an increasing abundance of beech. On the contrary, populations of spruce on different soils were less diversified, with median DBH ranging from 39 to 59 cm on Leptosols and Albic Podzols, respectively; only the value for Entic Pozdols was significantly lower than those for most other soils. Maximum DBHs generally increased with decreasing wetness in both tree species. For beech, this trend was weak and there was no statistically significant difference between any soils despite a twofold difference between Histosols (standardized maximum DBH 32 cm) and all terrestrial soils (>60 cm). In spruce, the largest trees on Histosols were significantly smaller than those on Albic Podzols.

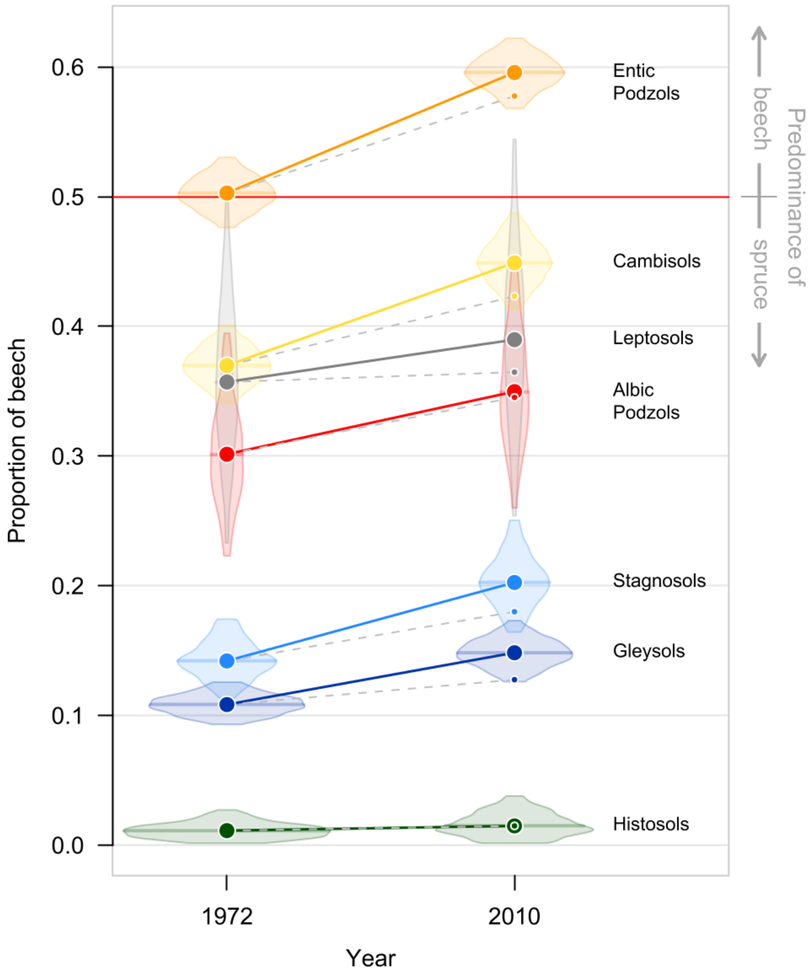


Fig. 3 Change of proportions of beech on different soils between 1972 and 2010. Large colored circles, connected by solid colored lines, represent means for individual soils in two censuses. Surrounding colored areas show 95% confidence intervals (vertically) together with bootstrapped distribution of means (horizontally). Small colored circles in 2010, connected to 1972 values by gray dashed lines, give mean proportions in the case where the effect of the Emma windstorm is excluded.

The transition from spruce to beech dominance was gradual, following the trajectory Histosols–Gleysols–Stagnosols–Cambisols–Entic Podzols (Fig. 3). Leptosols and Albic Podzols were between Stagnosols and Cambisols and exhibited the highest variability of all soils, partly attributable to their relative rareness. A distinctive feature of Albic Podzols was that they were never dominated exclusively by either of the two species (Table 1).

3.2 Temporal changes in tree populations and their drivers

During the studied period, beech, relative to spruce, expanded on all soils (Fig. 3; a version of the figure with 1996 census included can be found in Appendix 3). However, this general trend differed in significance as well as in the driving factors behind it. Statistically significant increases in the proportion of beech between 1972 and 2010 were observed on Gleysols, Stagnosols, Cambisols and Entic Podzols (Fig. 4a). The absolute change in proportion on these soils ranged approximately from 0.04 (Gleysols) to 0.1 (Entic Podzols), increasing from hydromorphic to terrestrial soils. Albic Podzols were also within this range, but the change on these soils was not significant due to high variability. The relative change (Fig. 4b) exhibited the opposite trend, with no significant differences between individual soil units but a noticeable difference between terrestrial and hydromorphic soils. Absolute differences were to a large extent driven by the proportion of beech, being greater when beech was more abundant. On the other hand, there was a greater potential for relative change on soils with smaller populations of beech composed of thinner trees.

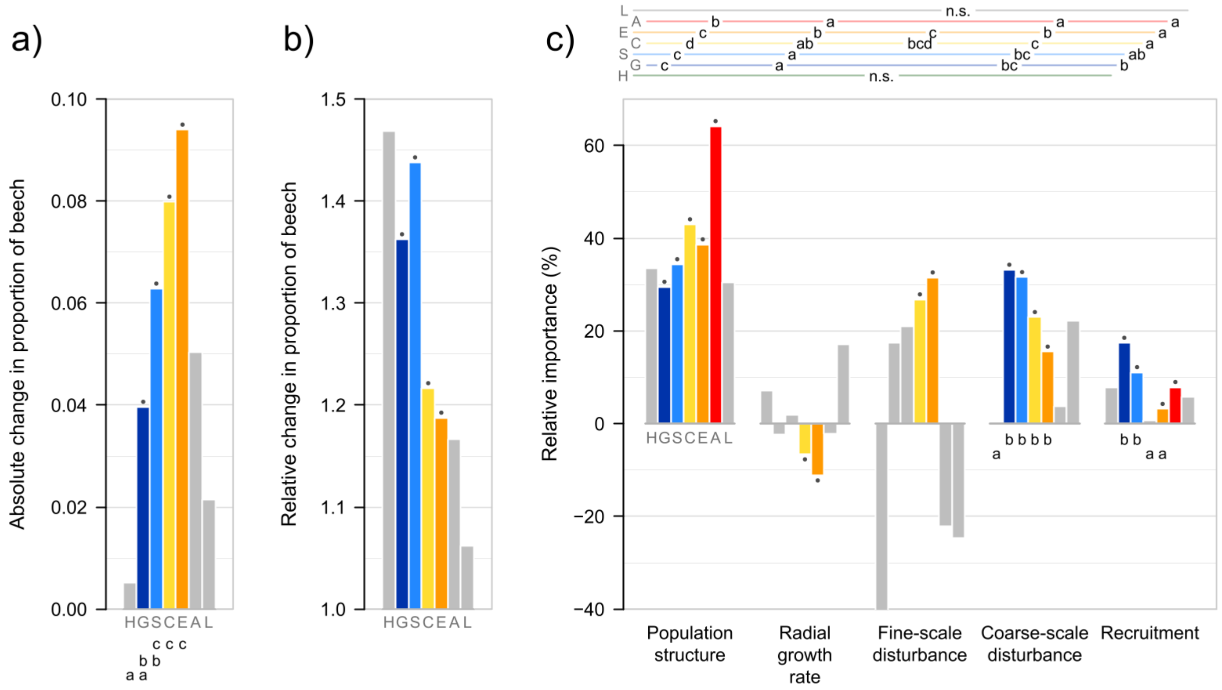


Fig. 4 Changes in the proportion of beech between 1972 and 2010 on different soils and the importance of driving factors: a) absolute changes in proportion; b) relative changes in proportion (the ratio between the two proportions, i.e. 1 means no change); c) relative importance of five possible driving factors; in each group the bars correspond to the 7 distinguished soils that are indicated by upper case one-letter abbreviations H, Histosols; G, Gleysols; S, Stagnosols; C, Cambisols; E, Entic Podzols; A, Albic Podzols; L, Leptosols. Bars representing values significantly different from zero (or one, in the case of relative change) are marked by dots and colored using the same soil color scheme as in Fig. 1 and Fig. 3. Significant differences between soils are indicated by lower case letters under bars, and in c significant differences between factors within one soil are coded by letters above the plot. If two bars share a letter, then there is not a significant difference between the values. When there is no letter, the value does not differ from any other (equivalent to all letters being present); n.s. indicates no significant differences.

All of the driving factors considered were important at least on some soils, acting mostly in favor of beech (Fig. 4c). The difference in population structures of the species played a major role on all soils and on average was responsible for 39% of the change in proportion. This illustrates that even if the two species grew at equal rates, the proportion of beech increased. This was a consequence of the disproportion between numbers of individuals and basal areas, which was caused by generally smaller dimensions of beech trees compared to spruce (see above). Hypothetically, if the trees were to continue to grow infinitely at a common rate and no other factors were involved, the ratio based on basal areas would approach an asymptotic value determined only by the numbers of individuals. Thus, the proportion of beech tended to increase on soils where beech trees had on average lower DBH than spruce trees, even when the growth rates of both species were assumed to be equal.

Contrastingly, radial growth rate reflects the actual difference in growth rates of beech and spruce. This was the only factor that significantly (on Cambisols and Entic Podzols) decreased the proportion of beech. The reason for this was the faster growth of spruce compared to beech. However, this factor was the weakest, with an average importance of only 6.9%.

Fine-scale mortality changed the proportion of beech in both directions, depending on soil. However, a significant relative importance of more than 20% was only observed on terrestrial soils (Cambisols and Entic Podzols) where it resulted in increased proportions of beech. Indeed, the beech mortality rate was significantly lower than that of spruce on Entic Podzols (Fig. 5a). Other than that, mortality did not differ between any pair of soils or between species, although there was a decreasing trend in beech mortality on the gradient from Histosols to Entic Podzols.

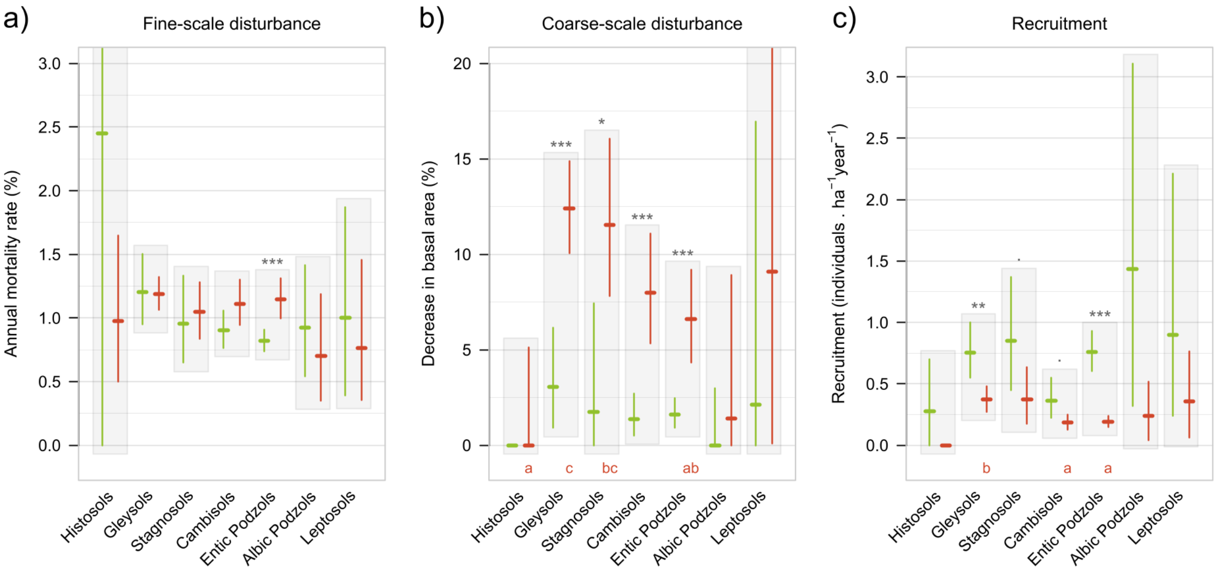


Fig. 5 Mortality related to two types of disturbance and recruitment on different soils: a) fine-scale disturbance (death of single trees); b) coarse-scale disturbance (a singular severe event, the Emma windstorm); c) annual recruitment; horizontal bars show mean values and corresponding vertical lines expand over their 95% confidence intervals. Within each soil unit beech is on the left (green) and spruce on the right (red) and the statistical significance of difference between the species is given above (., $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). Significant differences between soils within each species are indicated by letters in the bottom of the plot. When two soils share a letter, then there is not a significant difference in mortality between them. When there is no letter, mortality or recruitment does not differ from any other (equivalent to all letters being present). Some confidence intervals were cut to increase plot clarity; they can be considered roughly symmetric around the mean.

The coarse-scale disturbance caused significant changes on all abundant soils, shifting the ratio towards beech dominance (Fig. 4c). For Gleysols it was the most important factor (33%), and its importance decreased towards Entic Podzols (16%). The coarse-scale disturbance-related mortality also declined along this gradient for both species (Fig. 5b). It was on average five times higher for spruce, and on Gleysols caused a 12% decline in the basal area of spruce as opposed to only about a 3% decline in beech. On Entic Podzols it was responsible for a 6.6% and 1.6% basal area loss in spruce and beech, respectively. The Emma windstorm had practically no effect on Histosols (Fig. 4c, 5b), which is most likely because these soils were located in a valley where they were protected from severe winds.

Recruitment is another process favoring beech on most soils (Fig. 4c). Its effect was most pronounced on Gleysols (17% importance) but the highest numbers of recruits were recorded on Albic Podzols (1.4 ha^{-1}year^{-1}; Fig. 5c). Beech, as a stronger competitor, exceeded spruce in numbers of recruits everywhere, on average by a factor of 2.5.

One consequence of beech being more successful in recruitment than spruce was the switch from spruce to beech dominance in trees of the lowest diameters (ca. 10–15 cm) on both hydromorphic and terrestrial soils (Fig. 2). On terrestrial soils only, beech increased its upper DBH limit of dominance from 56 cm in 1972 to 76 cm in 2010, which reduced the range of DBH where spruce dominated (its lower limit increased from 62 to 82 cm).

3.3 Regeneration

The proportion of beech in regeneration, just as in trees, was related (regeneration: adjusted $R^2 = 0.458$, $p < 0.001$; trees: adj. $R^2 = 0.248$, $p < 0.001$) to the main gradient in soils, i.e. soil wetness (Fig. 6a). But while in trees beech predominated only marginally and just at the very dry end of the gradient, in regeneration it dominated the driest soils almost absolutely, slowly retreating towards hydromorphic soils. Regeneration of the two species was balanced only in the wettest conditions (Gleysols and Histosols). The large range of the confidence interval on hydromorphic soils is partly caused by the small sample size on Histosols but even more so by the high variability on Gleysols, where either of the species could predominate.

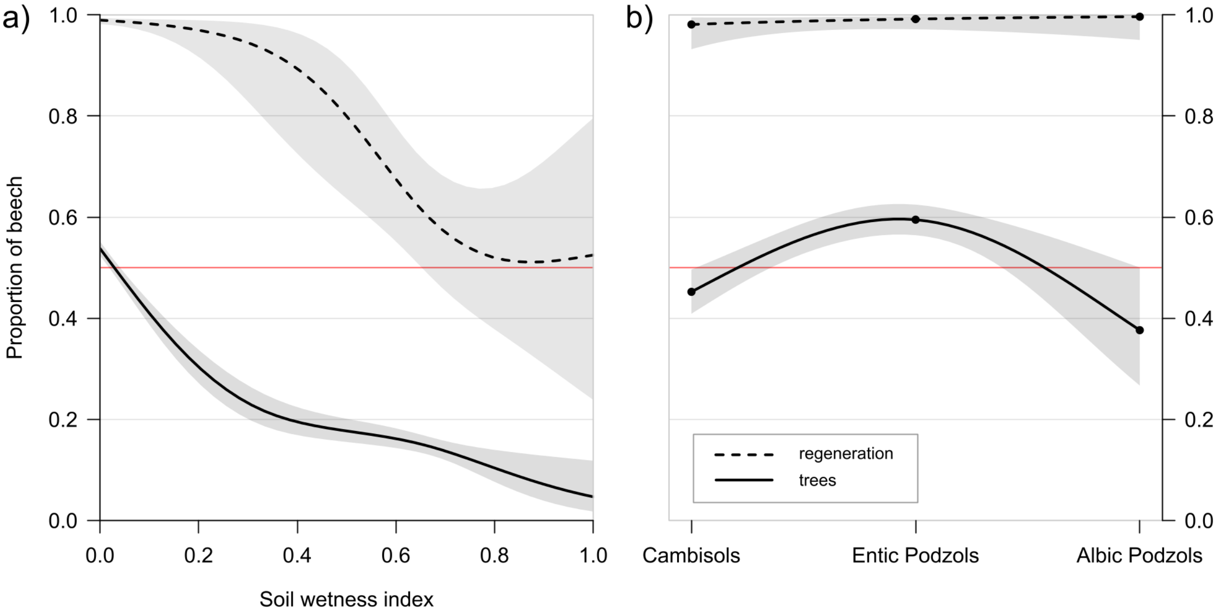


Fig. 6 Proportions of beech in regeneration (DBH < 10 cm, dashed lines) and adult trees (DBH ≥ 10 cm, solid lines) along two main soil gradients: a) the proportion of beech along the gradient of soil wetness; b) the proportion of beech on soils of different degrees of weathering and leaching; gray areas represent 95% confidence intervals. Proportions are based on basal areas.

No significant differences (adj. $R^2 = 0$, $p = 0.3$) in regeneration were observed along the gradient of soil weathering and leaching on terrestrial soils (Fig. 6b). Beech highly dominated in regeneration on all three soil units, which was in contrast with the situation in populations of adult trees, where beech dominance was only observed on Entic Podzols and overall there was a significant unimodal trend (adj. $R^2 = 0.045$, $p < 0.001$).

4 Discussion

4.1 Differences in tree populations across soils

The strongest pattern in the distribution of beech and spruce we observed was the transition from almost pure spruce stands on the wettest soils to almost balanced or even beech-dominated stands on terrestrial soils, following the sequence Histosols–Gleysols–Stagnosols–terrestrial soils. This was expected, given the ecological requirements of the two species (Leuschner & Ellenberg 2017). Spruce should be able to tolerate all soil conditions in our studied forest, and in the past probably dominated everywhere (Bobek et al. under review). On the other hand, the growth of beech on the wettest sites is known to be limited (Langshausen et al. 2001). This main pattern was manifested in all three main indicators: the proportions of occupied plots, numbers of individuals and basal areas.

While the response of tree species to the main soil gradient of wetness was clear, the relation to the other soil gradient, weathering and leaching, was more complicated. Here, soils in the middle of the gradient (Entic Podzols) were dominated by beech, whereas soils on both ends of the gradient (Cambisols and Albic Podzols) were dominated by spruce. The reasons for this are complex. Albic Podzols in Boubín are always found close to wet areas (see Daněk et al. 2016) in relatively flat lower parts of slopes, where a more cold and humid microclimate as well as slower erosion rates can be expected, both supporting the process of podzolization. Podzolization is also intensified by the acidifying effect of spruce (Sohet et al. 1988; Augusto et al. 1998), whose dominance on Albic Podzols is probably caused by a mass effect mechanism (Holyoak et al. 2005), realized through the supply of seeds from strong spruce populations on the nearby hydromorphic soils. It thus appears that unlike other soil units, for Albic Podzols it is the soil development that is determined by the tree species composition, rather than the other way around. These soils can thus be viewed as extended phenotypes (Corenblit et al. 2011) of the trees they host. On the contrary, Entic Podzols are usually located on steeper slopes farther from the wettest, spruce-dominated, sites, so the abundance of spruce is relatively low and its effects on soil are also less pronounced. On Cambisols, the relatively high proportion of spruce, compared to Entic Podzols, can be at least partly attributed to their higher clay content and related more frequent hydromorphic properties or even soil horizons (Daněk et al. 2016). This hydromorphism can, in turn, hinder podzolization or its morphological manifestation. However, assuming that Entic Podzols are the next step in the development of Cambisols, it is not clear what actually controls whether or not this step will be taken.

4.2 Temporal changes in tree populations

A significant expansion of beech was observed on most soils but its drivers differed. The generally most important factor turned out to be the least intuitive one: population structure. Although this factor could be viewed as a sort of artifact, the fact that in certain situations it can be responsible for a change in the proportion of a species is interesting. In a situation like this, where two species of inherently different stem diameters coexist, in order to keep basal area proportions stable through time the species with larger individuals must either exhibit faster growth, lower mortality or higher recruitment rates.

The only factor found to significantly act in favor of spruce was radial growth rate. This is a result of the faster radial growth of spruce compared to beech, as has been described previously

(Bolte et al. 2010; Pretzsch et al. 2014b). The only soils in Boubín where this effect was significant were Cambisols and Entic Podzols, where, on the other hand, fine-scale mortality supported an increase in the proportion of beech. These two seemingly contradicting patterns are in fact complementary, and come from individuals of different sizes and life history. Among smaller trees mortality is higher in spruce (see Appendix 4), probably because of its lower shade-tolerance compared to beech. However, if spruce trees survive and manage to become established within the canopy they can exert their faster growth and even profit from reduced shading during the early spring and late autumn when beech trees have no foliage (Pretzsch et al. 2014b; Ding et al. 2017). The overall fine-scale mortality rates (1.00 for beech and 1.58 for spruce, Appendix 5) are comparable to those reported from Žákova hora, another Czech old-growth forest by Janík et al. (2016a) but rather lower than those observed by Pretzsch et al. (2014a) in even-aged forests in Germany. The coarse-scale disturbance clearly favored beech over spruce, and this effect increased with increasing soil wetness. This is a pattern similar to that observed in the Žofín forest after the Kyrill storm of 18 January 2007 (Šamonil et al. 2013). Spruce, with its shallow root system (Schmid & Kazda 2001), is generally more susceptible to uprooting than beech (Knoke et al. 2008; Brázdil et al. 2017) and in a winter storm, such as the Emma windstorm, the difference between the wind-driven mortality of evergreen spruce and deciduous beech, leafless at the time of the storm, is even greater (Schütz et al. 2006; Valinger & Fridman 2011; Bolte et al. 2014). The intensification of the storm's effect towards hydromorphic soils is likely a consequence of two phenomena. Firstly, with increasing levels of the soil water table the root system of spruce becomes even shallower and trees are even more prone to uprooting (Ray & Nicoll 1998; Dobbertin 2002; Ilisson et al. 2005). Secondly, an admixture of broadleaves is known to mitigate the impact of storms (Schütz et al. 2006; Knoke et al. 2008), so their decreasing abundance towards wetter sites may result in positive feedbacks leading to increasing spruce mortality rates. It would be expected that these processes would lead to the greatest effect of coarse-scale disturbances on the wettest soils with the highest abundance of spruce, which in the case of Boubín are Histosols. Surprisingly, for both tree species Histosols exhibited the lowest coarse-scale disturbance mortality of all soils. This is likely a result of the different disturbance regime (Šamonil et al. 2014) of these soils, which are situated at the bottom of a N–S oriented valley where the effects of strong westerly winds associated with the Emma storm were likely reduced (Ruel et al. 1998). A similar pattern is visible also in Albic Podzols, which are located in similar topographical positions. Another factor that could be responsible for the lower wind-driven mortality of spruce on Histosols is its previously reported higher resistance to overturning on peats compared to both mineral and gleyic soils (Nicoll et al. 2006).

4.3 Outlook for the future

An expansion of beech similar to that we observed in Boubín has also been witnessed in other old-growth forests across Europe. For example, in Romania shade-tolerant beech has expanded at the expense of light-demanding oak (Petritan et al. 2014). At several localities in the Carpathians beech has started to replace fir after changes in forest management (Vrška et al. 2009). Beech outcompeted spruce using its space-occupation strategy in another Czech old-growth forest (Janík et al. 2016b), and Bolte et al. (2014) related the dominance of beech in a formerly spruce-dominated forest in Sweden to its increased productivity in a warming climate and a lower risk of stand failure. The expansion of beech in Boubín is thus not unique but rather fits a wider pattern. Climate-change-related increased temperatures should prolong the growing season and are expected to shift the distribution of beech upward in altitude (Saltré et al. 2015). The future development can to some extent be estimated based on the species composition of young tree individuals. Since we worked with data from just one site, the generalizability of our results is somewhat limited and the following outlooks thus relate primarily to our study site. At Boubín, beech was more successful than spruce in recruitment on all soils, and the same trend was even more visible in regeneration, where beech strongly dominated all but the wettest soils. Although the environmental requirements of young tree individuals may differ from those of adults (Máliš et al. 2016), the differences between species proportions in regeneration and adults on most soils are so strong that a further shift towards beech dominance seems inevitable. This has already happened on Entic Podzols, is currently happening on Cambisols and can be expected on Albic Podzols. Hydromorphic soils exhibit signs of this trend as well, but here the expansion of beech will always be limited by its environmental requirements and is expected to weaken with increasing soil wetness.

Although in the short term the Emma windstorm was clearly advantageous to beech, the newly formed canopy gaps provided new sites for the regeneration of trees, and, if no advance regeneration was present at these sites, spruce may be more successful than beech in direct competition (Grams et al. 2002; Kozovits et al. 2005). However, this process would not yet be visible in our data because 8 years after the storm the regeneration we studied (DBH > 1 cm) likely consisted mainly of advance regeneration (Macek et al. 2017). If disturbance-related regeneration becomes established in the canopy, this windstorm could thus hypothetically be beneficial to spruce in the long term.

Acknowledgements We would like to thank our colleagues Dušan Adam and Ivana Vašíčková from the 'Blue Cat' research team for technical and field support, David Hardekopf for English proofreading and three anonymous reviewers for their valuable comments. The research was supported by Grantová Agentura České Republiky (the Czech Science Foundation), project No. 16-15319S and partly funded by non-project institutional support of The Silva Tarouca Research Institute for Landscape and Ornamental Gardening (VUKOZ IP-00027073).

References

Augusto L., Bonnaud P., Ranger J. 1998. Impact of tree species on forest soil acidification. *Forest Ecology and Management* 105: 67–78.

Augusto L., Ranger J., Binkley D., Rothe A. 2002. Impact of several common tree species of European temperate forests on soil fertility. *Annals of Forest Science* 59: 233–253.

Benjamini Y., Hochberg Y. 1995. Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *Journal of the Royal Statistical Society. Series B (Methodological)* 57: 289–300.

Berger T.W., Köllensperger G., Wimmer R. 2004. Plant-soil feedback in spruce (*Picea abies*) and mixed spruce-beech (*Fagus sylvatica*) stands as indicated by dendrochemistry. *Plant and Soil* 264: 69–83.

Berger T.W., Swoboda S., Prohaska T., Glatzel G. 2006. The role of calcium uptake from deep soils for spruce (*Picea abies*) and beech (*Fagus sylvatica*). *Forest Ecology and Management* 229: 234–246.

Binkley D., Giardina C. 1998. Why do tree species affect soils? The Warp and Woof of tree–soil interactions. *Biogeochemistry* 42: 89–106.

Bolte A., Hilbrig L., Grundmann B., Kampf F., Brunet J., Roloff A. 2010. Climate change impacts on stand structure and competitive interactions in a southern Swedish spruce-beech forest. *European Journal of Forest Research* 129: 261–276.

Bolte A., Hilbrig L., Grundmann B.M., Roloff A. 2014. Understory dynamics after disturbance accelerate succession from spruce to beech-dominated forest—The Siggaboda case study. *Annals of Forest Science* 71: 139–147.

Bolte A., Kampf F., Hilbrig L. 2013. Space sequestration below ground in old-growth spruce-beech forests—signs for facilitation? *Frontiers in Plant Science* 4: 1–11.

Brázdil R., Szabó P., Stucki P., Dobrovolný P., Řezníčková L., Kotyza O., Valášek H., Melo M., Suchánková S., Dolák L., Chromá K. 2017. The extraordinary windstorm of 7 December 1868 in the Czech Lands and its central European context. *International Journal of Climatology* 37(March 1990): 14–29.

Breiman L. 2001. Random Forests. *Machine Learning* 45: 5–32.

Condit R., Ashton P.S., Manokaran N., LaFrankie J.V., Hubbell S.P., Foster R.B. 1999. Dynamics of the forest communities at Pasoh and Barro Colorado: comparing two 50-ha plots. *Philosophical Transactions of the Royal Society B: Biological Sciences* 354: 1739–1748.

Corenblit D., Baas A.C.W., Bornette G., Darrozes J., Delmotte S., Francis R.A., Gurnell A.M., Julien F., Naiman R.J., Steiger J. 2011. Feedbacks between geomorphology and biota controlling Earth surface processes and landforms: A review of foundation concepts and current understandings. *Earth-Science Reviews* 106: 307–331.

Daněk P., Šamonil P., Phillips J.D. 2016. Geomorphic controls of soil spatial complexity in a primeval mountain forest in the Czech Republic. *Geomorphology* 273: 280–291.

Ding H., Pretzsch H., Schütze G., Rötzer T. 2017. Size-dependence of tree growth response to drought for Norway spruce and European beech individuals in monospecific and mixed-species stands. *Plant Biology* 19: 709–719.

Dittmar C., Fricke W., Elling W. 2006. Impact of late frost events on radial growth of common beech (*Fagus sylvatica* L.) in Southern Germany. *European Journal of Forest Research* 125: 249–259.

Dobbertin M. 2002. Influence of stand structure and site factors on wind damage comparing the storms Vivian and Lothar. *Forest Snow and Landscape Research* 77: 187–205.

Dobrovolny L. 2016. Density and spatial distribution of beech (*Fagus sylvatica* L.) regeneration in Norway spruce (*Picea abies* (L.) Karsten) stands in the central part of the Czech Republic. *IForest* 9: 666–672.

Fichtner A., Sturm K., Rickert C., Härdtle W., Schrautzer J. 2012. Competition response of European beech *Fagus sylvatica* L. varies with tree size and abiotic stress: Minimizing anthropogenic disturbances in forests. *Journal of Applied Ecology* 49: 1306–1315.

Fischer A., Marshall P., Camp A. 2013. Disturbances in deciduous temperate forest ecosystems of the northern hemisphere: Their effects on both recent and future forest development. *Biodiversity and Conservation* 22: 1863–1893.

Grams T.E.E., Kozovits A.R., Reiter I.M., Barbro Winkler J., Sommerkorn M., Blaschke H., Häberle, K.-H., Matyssek R. 2002. Quantifying Competitiveness in Woody Plants. *Plant Biology* 4: 153–158.

Grundmann B.M., Bolte A., Bonn S., Roloff A. 2011. Impact of climatic variation on growth of *Fagus sylvatica* and *Picea abies* in Southern Sweden. *Scandinavian Journal of Forest Research* 26(SUPPL. 11): 64–71.

Hajek P., Seidel D., Leuschner C. 2015. Mechanical abrasion, and not competition for light, is the dominant canopy interaction in a temperate mixed forest. *Forest Ecology and Management* 348: 108–116.

Holyoak M., Leibold M.A., Holt R.D. 2005. Metacommunities: spatial dynamics and ecological communities. University of Chicago Press.

Ilisson T., Metslaid M., Vodde F., Jõgiste K., Kurm M. 2005. Storm disturbance in forest ecosystems in Estonia. *Scandinavian Journal of Forest Research* 20(Suppl 6): 88–93.

IUSS Working Group WRB. 2007. World Reference Base for Soil Resources 2006, first update 2007. World Soil Resources Reports No. 103. FAO, Rome.

Jactel H., Bauhus J., Boberg J., Bonal D., Castagneyrol B., Gardiner B., Gonzalez-Olabarria J.R., Koricheva J., Meurisse N., Brockerhoff E.G. 2017. Tree Diversity Drives Forest Stand Resistance to Natural Disturbances. *Current Forestry Reports* 3: 223–243.

Janík D., Adam D., Hort L., Král K., Samonil P., Unar P., Vrska T. 2016. Breaking through beech: A three-decade rise of sycamore in old-growth European forest. *Forest Ecology and Management* 366: 106–117.

Janík D., Král K., Adam D., Hort L., Samonil P., Unar P., Vrska T., McMahon S. 2016. Tree spatial patterns of *Fagus sylvatica* expansion over 37 years. *Forest Ecology and Management* 375: 134–145.

Knoke T., Ammer C., Stimm B., Mosandl R. 2008. Admixing broadleaved to coniferous tree species: A review on yield, ecological stability and economics. *European Journal of Forest Research* 127: 89–101.

Körner C., Basler D., Hoch G., Kollas C., Lenz A., Randin C.F., Vitasse Y., Zimmermann N.E. 2016. Where, why and how? Explaining the low-temperature range limits of temperate tree species. *Journal of Ecology* 104: 1076–1088.

Kozovits A.R., Matyssek R., Barbro Winkler J., Göttlein A., Blaschke H., Grams T.E.E. 2005. Aboveground space sequestration determines competitive success in juvenile beech and spruce trees. *New Phytologist* 167: 181–196.

Kraus C., Zang C., Menzel A. 2016. Elevational response in leaf and xylem phenology reveals different prolongation of growing period of common beech and Norway spruce under warming conditions in the Bavarian Alps. *European Journal of Forest Research* 135: 1011–1023.

Kulakowski D., Seidl R., Holeksa J., Kuuluvainen T., Nagel T.A., Panayotov M., Svoboda M., Thorn S., Vacchiano G., Whitlock C., Wohlgemuth T., Bebi P. 2017. A walk on the wild side: Disturbance dynamics and the conservation and management of European mountain forest ecosystems. *Forest Ecology and Management* 388: 120–131.

Langshausen J., Kolb E., Ewald J., Rehfuess K.E. 2001. Über die Eignung von Flyschstandorten der Bayerischen Voralpen für die Buche (*Fagus sylvatica* L.). *Forstwissenschaftliches Centralblatt* 120: 363–374.

Leuschner C., Ellenberg H. 2017. Ecology of Central European Forests. Vegetation Ecology of Central Europe, Volume I. Springer International Publishing, Switzerland.

Liaw A., Wiener M. 2002. Classification and Regression by randomForest. *R News* 2: 18–22.

Macek M., Wild J., Kopecký M., Červenka J., Svoboda M., Zenáhlíková J., Brůna J., Mosandl R., Fischer A. 2017. Life and death of *Picea abies* after bark-beetle outbreak: Ecological processes driving seedling recruitment. *Ecological Applications* 27: 156–167.

Máliš F., Kopecký M., Petřík P., Vladovič J., Merganič J., Vida T. 2016. Life stage, not climate change, explains observed tree range shifts. *Global Change Biology* 22: 1904–1914.

Metz J., Annighöfer P., Schall P., Zimmermann J., Kahl T., Schulze E.D., Ammer C. 2016. Site-adapted admixed tree species reduce drought susceptibility of mature European beech. *Global Change Biology* 22: 903–920.

Mitchell S.J. 2013. Wind as a natural disturbance agent in forests: A synthesis. *Forestry* 86: 147–157.

Nicoll B.C., Gardiner B.A., Rayner B., Peace A.J. 2006. Anchorage of coniferous trees in relation to species, soil type, and rooting depth. *Canadian Journal of Forest Research* 36: 1871–1883.

Packham J.R., Thomas P.A., Atkinson M.D., Degen T. 2012. Biological Flora of the British Isles: *Fagus sylvatica*. *Journal of Ecology* 100: 1557–1608.

Petritan I.C., Marzano R., Petritan A.M., Lingua E. 2014. Overstory succession in a mixed *Quercus petraea-Fagus sylvatica* old growth forest revealed through the spatial pattern of competition and mortality. *Forest Ecology and Management* 326: 9–17.

Pickett S.T.A., White P.S. 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Inc, San Diego.

Pretzsch H., Biber P., Schütze G., Uhl E., Rötzer T. 2014. Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nature Communications* 5: 4967.

Pretzsch H., Block J., Dieler J., Dong P.H., Kohnle U., Nagel J., Spellmann H., Zingg A. 2010. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. *Annals of Forest Science* 67: 712–712.

Pretzsch H., Dieler J., Seifert T., Rötzer T. 2012. Climate effects on productivity and resource-use efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in stands with different spatial mixing patterns. *Trees* 26: 1343–1360.

Pretzsch H., Rötzer T., Matyssek R., Grams T.E.E., Häberle K.-H., Pritsch K., Kerner R., Munch J.-C. 2014. Mixed Norway spruce (*Picea abies* [L.] Karst) and European beech (*Fagus sylvatica* [L.]) stands under drought: from reaction pattern to mechanism. *Trees* 28: 1305–1321.

R Core Team. 2016. R: A Language and Environment for Statistical Computing. Vienna, Austria.

Ray D., Nicoll B.C. 1998. The effect of soil water-table depth on root plate development and stability of Sitka spruce. *Forestry* 71: 169–182.

Rolo V., Andivia E., Pokorný R. 2015. Response of *Fagus sylvatica* and *Picea abies* to the interactive effect of neighbor identity and enhanced CO2 levels. *Trees* 29: 1459–1469.

Ruel J.-C., Pin D., Cooper K. 1998. Effect of topography on wind behaviour in a complex terrain. *Forestry* 71: 261–265.

Saltré F., Duputié A., Gaucherel C., Chuine I. 2015. How climate, migration ability and habitat fragmentation affect the projected future distribution of European beech. *Global Change Biology* 21: 897–910.

Šamonil P., Daněk P., Schaetzl R.J., Tejnecký V., Drábek O. 2018. Converse pathways of soil evolution caused by tree uprooting: A synthesis from three regions with varying soil formation processes. *Catena* 161: 122–136.

Šamonil P., Daněk P., Schaetzl R.J., Vašíčková I., Valtera M. 2015. Soil mixing and genesis as affected by tree uprooting in three temperate forests. *European Journal of Soil Science* 66: 589–603.

Šamonil P., Doleželová P., Vašíčková I., Adam D., Valtera M., Král K., Janík D., Šebková B. 2013. Individual-based approach to the detection of disturbance history through spatial scales in a natural beech-dominated forest. *Journal of Vegetation Science* 24: 1167–1184.

Šamonil P., Vašíčková I., Daněk P., Janík D., Adam D. 2014. Disturbances can control fine-scale pedodiversity in old-growth forests: is the soil evolution theory disturbed as well? *Biogeosciences* 11: 5889–5905.

Schaetzl R.J., Thompson M.L. 2015. Soils: Genesis and Geomorphology, (2nd ed.). Cambridge University Press, New York.

Schelhaas M.-J., Nabuurs G.-J., Schuck A. 2003. Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology* 9: 1620–1633.

Schmid I., Kazda M. 2001. Vertical distribution and radial growth of coarse roots in pure and mixed stands of *Fagus sylvatica* and *Picea abies*. *Canadian Journal of Forest Research* 31: 539–548.

Schume H., Jost G., Hager H. 2004. Soil water depletion and recharge patterns in mixed and pure forest stands of European beech and Norway spruce. *Journal of Hydrology* 289: 258–274.

Schütz J.P., Götz M., Schmid W., Mandallaz D. 2006. Vulnerability of spruce (*Picea abies*) and beech (*Fagus sylvatica*) forest stands to storms and consequences for silviculture. *European Journal of Forest Research* 125: 291–302.

Šebková B., Šamonil P., Janík D., Adam D., Král K., Vrška T., Hort L., Unar P. 2011. Spatial and volume patterns of an unmanaged submontane mixed forest in Central Europe: 160 years of spontaneous dynamics. *Forest Ecology and Management* 262: 873–885.

Sohet K., Herbauts J., Gruber W. 1988. Changes caused by Norway spruce in an ochreous brown earth, assessed by the isoquartz method. *Journal of Soil Science* 39: 549–561.

Turner M.G. 2010. Disturbance and landscape dynamics in a changing world 1. *Ecology* 91: 2833–2849.

Valinger E., Fridman J. 2011. Factors affecting the probability of windthrow at stand level as a result of Gudrun winter storm in southern Sweden. *Forest Ecology and Management* 262: 398–403.

Vrška T., Adam D., Hort L., Kolář T., Janík D. 2009. European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) rotation in the Carpathians-A developmental cycle or a linear trend induced by man? *Forest Ecology and Management* 258: 347–356.

Vrška T., Hort L., Odehnalová P., Horal D., Adam D. 2001. The Boubín virgin forest after 24 years (1972–1996) – development of tree layer. *Journal of Forest Science* 47: 439–459.

Welzholz J., Johann E. 2007. History of protected forest areas in Europe. In Frank G., Parviainen J., Vandekerkhove K., Latham J., Schuck A., Little D. (Eds.), COST Action E27 Protected Forest Areas in Europe – Analysis and Harmonisation (PROFOR): Results, Conclusions and Recommendations (pp. 17–40). Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW), Vienna.

Wood S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 73: 3–36.

Paper 8

Canopy trees drive regeneration of a spruce-beech forest through forest floor alteration

Pavel Daněk
Pavel Šamonil
Libor Hort

submitted to Forest Ecology and Management

Abstract

Natural regeneration of European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) is an important process that may affect the future composition of many European mountain forests, but its dynamics in mixed stands of these two species are still not well understood.

In a mixed old-growth forest (Boubín, Czech Republic) we sampled all beech and spruce regeneration in 563 plots from different microsite types (deadwood, intact soil, treethrow pits and mounds), distinguishing three seedbeds (mosses, beech litter, bare substrate) for seedlings. We used soil survey and tree census data with generalized linear mixed models to identify the main factors driving tree regeneration, focusing in particular on canopy tree-induced changes in the forest floor.

Although beech was less abundant in the canopy than spruce, it strongly outnumbered spruce in regeneration. Beech showed an affinity for beech litter-rich microsites and drier soils, while spruce was more common on deadwood and moister soils and its response to the seedbed was microsite-specific. The regeneration of both species was positively related to the proportion of their own species in the canopy, but more so in seedlings than in older regeneration cohorts, where soil wetness was more important.

Where beech regeneration is not suppressed by excess soil wetness, it is much more successful than spruce due to its shade tolerance and ability to be established in the beech litter that dominates the forest floor. Spruce regeneration is mostly restricted to elevated microsites with lower litter accumulation, such as deadwood and treethrow mounds. Both species exhibit an ability to modify their environment in favor of their own regeneration, but without significant disturbances, beech is expected to become even more dominant in the future.

P. Daněk[a,b], *P. Šamonil*[a], *L. Hort*[a]

[a] Department of Forest Ecology, The Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Brno, Czech Republic [b] Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic

1 Introduction

Mountain forests of Central Europe are mostly dominated by two tree species, the evergreen conifer Norway spruce (*Picea abies*) and the deciduous broadleaf European beech (*Fagus sylvatica*). Beech is considered to be the strongest competitor among European trees (Leuschner & Ellenberg 2017). Its dense canopy creates deep shade in the understorey, where the regenerating seedlings of only a few shade-tolerant species (particularly beech itself) can survive (Wagner et al. 2010). Furthermore, its slowly decomposing litter accumulates on the forest floor to create a thick layer, which can act as a barrier to the establishment of tree seedlings (Dzwonko & Gawroński 2002; Sayer 2006). This can also play to beech's advantage, since beech produces large seeds (Wagner et al. 2010) with enough reserves to supply the growth of a long radicle that can penetrate the litter and reach the mineral soil underneath (Sayer 2006). Compared to spruce, beech is less capable of growing in cold environments, such as at higher altitudes, mainly due to its susceptibility to late frosts (Dittmar et al. 2006; Wagner et al. 2010). It also forms a comparatively deeper root system, which prevents it from occurring in places with a high water table (Schmid & Kazda 2001; Leuschner & Ellenberg 2017).

Spruce, while also being rather shade-tolerant, tends to form natural stands with more light in the understory, and its seedlings are also more light-demanding (Leuschner & Ellenberg 2017; Asplund et al. 2018). Although its rooting depth is comparable to other tree species, it can tolerate a high water table by developing a shallow root system (Puhe 2003). Spruce litter is also persistent, similarly to that of beech (Berger & Berger 2012), and causes stronger topsoil acidification (Augusto et al. 2015). However, compared to the broadleaf's litter, it presents less of a barrier to the establishment of small-seeded species, including spruce itself (Asplund et al. 2018).

Mixed stands of beech and spruce form where soils are not too wet for beech and not too dry for spruce, and where the climate is not too cold for beech. In such stands, both competition and facilitation between the species can be observed. In the presence of spruce, beech can benefit from decreased intraspecific competition (Pretzsch et al. 2010; Bolte et al. 2013), while an admixture of beech can decrease shading of spruce when beech trees are leafless (Pretzsch et al. 2014). However, beech often tends to dominate the stands, using a space occupation strategy (Pretzsch & Schütze 2005). In recent decades, beech has been repeatedly observed to increase its abundance at the expense of spruce (Bolte et al. 2014; Janík et al. 2016; Daněk et al. 2019). Although the underlying drivers of this process are complex and likely external, including changes in forest management (Vrška et al. 2009) and climate (Bolte et al. 2014; Kašpar et al. 2021), the actual species turnover in mixed stands is still realized through direct competition between the species, and begins in their regeneration phase.

There are several factors that can drive the regeneration of a mixed beech-spruce forest. Stand composition, i.e. the abundance of beech and spruce, determines seed supply, the prevailing type of litter and to some extent also light conditions (Leuchner et al. 2011). High soil wetness can prevent the occurrence of adult beech trees (Daněk et al. 2019), but this need not be true for young individuals. Disturbances (sensu Pickett and White (1985) defined as the death of at least one canopy tree) can modify the forest environment in several ways. Newly formed canopy gaps increase light levels in the understorey, and the trunks of dead trees physically alter the forest floor in two important ways. First, decaying tree trunks themselves form a unique microsite that can be important for spruce regeneration (Bače et al. 2012; Orman & Szewczyk 2015; Orman et al. 2016). Second, if a tree is uprooted (typically by strong winds), the distinct microtopographical features of pits and mounds are formed. These alternative microsites differ from the forest floor in many properties, such as moisture content (Simon et al. 2011), temperature (Beatty 1984), microbial community composition (Šamonil et al. 2020) and the amount of accumulated litter, which can be both lower (deadwood, mounds) and higher (pits; Dwyer and Merriam 1981, Simon et al. 2011). Where litter is absent, the bare substrate (wood or soil) can be exposed or covered with mosses, which also affects the probability of a tree seedling becoming established. For spruce seedlings, both positive (Hörnberg et al. 1997; Hunziker & Brang 2005; Kathke & Bruelheide 2010) and negative (Harmon & Franklin 1989; Bače et al. 2012) effects of moss cover on seedling establishment has been observed.

These factors exhibit different levels of biotic components. They may be negligible for topographically and hydrogeologically driven soil wetness, but may already play a role in disturbances. Even if a disturbance agent such as wind is external, the final outcome can be dependent on the different susceptibilities of tree species to uprooting (Knoke et al. 2008; Jactel et al. 2017). The effect of stand composition is an example of a strictly biotically driven factor, controlled by tree species' characteristics. The ability of trees to modify their environment, potentially in favor of their own regeneration, is typical of ecosystem engineers (Jones et al. 1994; Corenblit et al. 2011).

Although a lot of research has been conducted in both beech and spruce forests, studies from mixed stands of these two species are relatively scarce and usually only deal with a limited number of factors. An important feature is the inherent correlation between some of these factors (e.g. stand composition and soil wetness). To separate a factor's unique effect, this correlation has to be addressed, which has not been done so far. Thus, we focus here on the roles of canopy composition, soil wetness, disturbances and microsite in the regeneration of beech and spruce in an old-growth forest with balanced populations of these two species in the canopy. We ask the following questions. 1) What is the importance of these factors and how much of their effect is unique to each of them? 2) How does the importance of a factor change with the size of the regeneration? 3) Does the suitability of a microsite depend on the seedbed (litter, mosses or bare substrate)? 4) How do canopy trees effect regeneration through these factors?

2 Materials and methods

2.1 Study site

This study was conducted in the Boubín Primeval Forest (hereinafter Boubín), Czech Republic. This forest reserve has been under strict protection since 1858, and to our knowledge its core zone (46 ha) has never been cut (Vrška et al. 2001). The reserve is located at an altitude of 930–1100 m a.s.l. on the northeastern slope of Boubín mountain (1364 m), one of the highest peaks in the Šumava Mts. Its bedrock is built of crystalline rocks (migmatite) and in some places covered with fluvial sediments. The climate is relatively humid and cold, with an annual precipitation of 1067 mm and mean annual temperature of 4.9 °C. Boubín has high soil diversity (Daněk et al. 2016), with most of its area (ca. 70%) covered by terrestrial soils (Entic Podzols, Cambisols, Albic Podzols) but also a significant proportion of hydromorphic soils (Gleysols, Stagnosols, Histosols). The specific combination of climatic and edaphic conditions is optimal for the coexistence of European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*). Total populations of these two tree species are almost balanced within the reserve, but the local species composition reflects the gradient of soil wetness. There are almost pure spruce stands on soils with highest water content

(Histosols), and the proportion of beech increases with decreasing soil wetness. Beech reaches its maximum abundance on Entic Podzols, where it accounts for 60% of the total basal area (Daněk et al. 2019).

2.2 Data collection

Data sampling took place within the reserve's 46 ha core area, where all standing and lying trees have been repeatedly censused since the 1970s. Along with other parameters, the position, DBH and species of each standing or lying tree with DBH > 10 cm was recorded in 1972, 1996 and 2010 (Šebková et al. 2011). Soils were investigated in detail at 954 points of a permanent regular square grid with a lateral spacing of 22.125 m (Daněk et al. 2016).

Regeneration and microsite data were collected on two types of plots with different levels of sampling detail (Fig. 1). 1) 116 circular plots (10 m radius) centered at points of the permanent grid (sampled during 2016 and 2017), and 2) detailed single-microsite plots located within a subset of 46 of the circular plots (in 2018). Circular plots were selected using a stratified random approach that considered plot homogeneity, soil unit and distances between plots.

2.2.1 Microsite types

We distinguished five main microsites present on the forest floor. Woody microsites included 1) stumps, i.e., the still-rooted remnants of broken trees, up to 130 cm high, and 2) deadwood (DW), lying tree logs at least 10 cm in diameter. Soil microsites comprised two treethrow-related microtopographies: 3) pits and 4) mounds, at least 10 cm deep or high, respectively, and 5) intact soil, i.e., soil without no visible signs of disturbance during the last decades.

2.2.2 Data collection within circular plots

Within each circle (10 m radius) we identified all present microsites and measured their area and other properties. The area of woody microsites was calculated as their projected area, i.e., for stumps the area of an ellipsis defined by the stump's two perpendicular diameters at ground level, and for deadwood the area of an isosceles trapezoid based on the deadwood's start and end diameters and length. The area of treethrow pits and mounds was approximated by ellipses based on two perpendicular diameters of each microtopography (Šamonil et al. 2018). The area of intact soil was computed as the total circle area minus the areas of all other identified microsites including the area of cross sections at ground level (base area) of all trees present in the circle, based on tree census data. Tree base area was derived from DBH as $\pi(1.34\,\mathrm{DBH})^2/4$ (Šamonil et al. 2018). Three stages of decay were distinguished for deadwood (Přívětivý et al. 2018): fresh (DW_1), moderately decayed (DW_2) and highly decayed (DW_3). Deadwood decay stages and species identification were adopted from the 2010 census.

Next, we censused all tree regeneration individuals with DBH between 1 and 10 cm. For every identified microsite we counted the number of individuals present, distinguishing two DBH categories (1–3 cm and 3–10 cm) and tree species.

2.2.3 Data collection within microsite plots

Microsite plots were placed inside a subset of 46 circular plots. In each circle at least 3 (but no more than 6) plots were sampled for each microsite, when available (Fig. 1). In the case of woody microsites, the whole stump or the maximum part of deadwood that was still within the 10-m

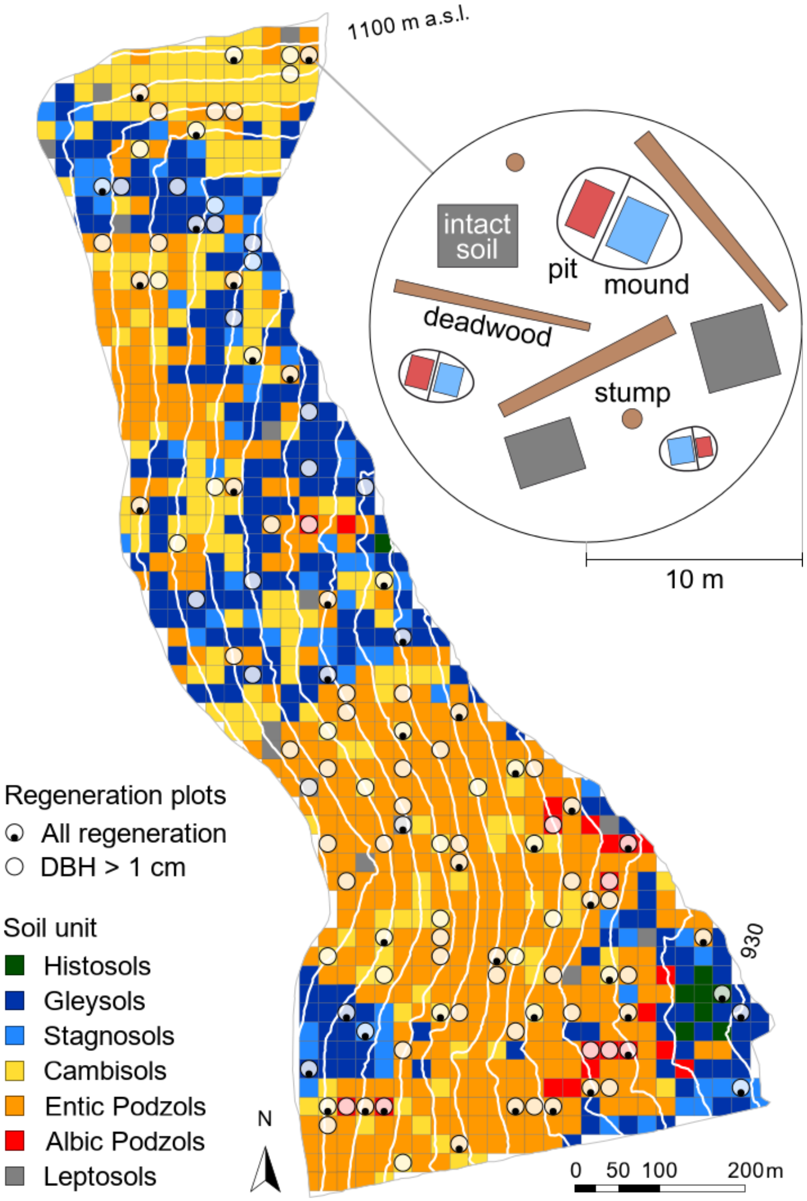


Fig. 1 a) Soil map of Boubín with positions of 116 circular plots where all regeneration (DBH < 10 cm) was sampled, and a subset of 46 plots where detailed sampling within single-microsite plots was carried out. b) A schematic depiction of the placement of 14 single-microsite plots within a circular plot.

circle was sampled. The area of these microsites was again computed as their projected area (see above). In the case of soil microsites, rectangular plots of maximum possible size were sampled. First, plots for microsites other than intact soil were placed at the microsite's closest occurrences to the circle's center. Then, intact soil plots were placed between them so as to reflect the microsite's variability, including the regeneration structure. Within each plot we estimated the proportions of all present seedbeds, distinguishing eight seedbed types: bare substrate (bare wood or soil), stones, water (standing or flowing), mosses, lichens, beech litter and mixed litter (any other litter than beech, e.g., conifer, mixed beech and conifer or herb litter). Additionally, the percent of herb cover was recorded for each plot.

In microsite plots, we considered all regeneration with DBH below 10 cm, distinguishing five size classes: individuals less than 15 cm high, 15–50 cm high, more than 50 cm high but less than 1 cm in DBH, DBH 1–3 cm and DBH 3–10 cm. Individuals were counted separately based on their species and size class, and for the smallest class also based on the seedbed they grew on. We only considered the seedbed in the case of the smallest regeneration class because we were interested in the role the seedbed may play in seedling establishment. The seedbed under older individuals is more likely to differ from the seedbed on which a seedling initially became established.

The smallest regeneration class (< 15 cm) was used individually only when seedbeds were considered. Otherwise, it was merged with the next size class (15–50 cm). Within the following text, the regeneration classes are referred to as “seedlings” (height < 50 cm), “small saplings” (height > 50 cm, DBH < 1 cm), “large saplings” (1 cm < DBH < 3 cm) and “small trees” (3 cm < DBH < 10 cm).

2.3 Statistical analyses

Mean regeneration densities and the corresponding beech/spruce ratios were computed from the most extensive data set available, i.e., using microsite plots for seedlings and small saplings and circular plots for individuals with DBH > 1 cm. We weighted values for different soil units, microsites and seedbeds (or their combinations) based on the actual areal proportions of these entities within the study area. For example, if we knew from our data that the area of intact soil was, e.g., five times that of treethrow pits, regeneration numbers from intact soil would get (on average) five times higher weights than those from pits when computing the mean values.

2.3.1 Modeling

To assess the importance of different variables on the presence of regeneration we used generalized linear mixed-effects models (GLMM) with binomial distribution, converting the count data from individual plots into presence/absence. We chose this approach instead of modeling counts explicitly (e.g., with negative binomial distribution) mainly because of the large proportion of zeros in the data.

We used several explanatory variables in our models. The dominance of either beech or spruce in the canopy was represented by the proportion of beech in the total basal area of these two species within a circle of 30 m in radius. We called this variable **beech dominance**, and computed it for the centers of all circular plots, which means that all microsite plots within one circular plot share the same value. Soil conditions were represented by their most important gradient, soil hydromorphism (Daněk et al. 2016). This is a complex of various soil properties that develop under different levels of water influence, and for the sake of simplicity we refer to it as **soil wetness**. This was coded as a numeric variable with a minimum value of 1 for terrestrial soils (Leptosols, Cambisols, Entic and Albic Podzols) and a maximum of 4 for Histosols. Intermediate soil units Stagnosols and Gleysols were given values 2 and 3, respectively. We also tried coding the eight soil units as a categorical explanatory variable, but this led to similar results in terms of the variance explained by the models, so we decided to use the simpler and more easy to interpret wetness. **Microsite** type was used as a categorical variable with deadwood split into the three decay classes ($DW_{1–3}$). We also distinguished young treethrow pits and mounds from old ones, based on the presence or absence of the originally uprooted tree. Local **disturbance** intensity was determined as the total basal area of trees that died inside the 10 m radius circles between censuses. Therefore, we used two variables for disturbance intensity, one for each intercensus period (1972–1996 and 1996–2010). **Deadwood decay** class was treated as a continuous explanatory variable, and **deadwood species** as a categorical variable with two levels – beech and conifer (spruce and fir). When working with seedbeds we also used **seedbed type** and its interaction with microsite type. To obtain sufficient observations for all microsite-seedbed combinations, we only used data from the three most common seedbed types (beech litter, mosses and bare wood/soil), that together accounted for about 93% of the total sampled microsite area.

We used the circular plot as a random factor when modeling microsite-level data, and the microsite plot nested within a circular plot when working on the level of seedbeds.

To quantify the importance of each variable, we used an analogue of the coefficient of determination (R^2) used for linear models. Although there is not a perfect equivalent for GLMMs that would retain all properties of the classical R^2, several alternatives exist (Nakagawa & Schielzeth 2013; Nakagawa et al. 2017; Zhang 2017). We first computed the explained variances of all variables and their combinations of interest (including the full model) following Zhang (2017), using the *rsq* R package (Zhang 2020). Next, we rescaled these values based on the full model marginal (excluding the variance explained by random effects) R^2 obtained via the delta method (Nakagawa et al. 2017) using the *r.squaredGLMM* function from the *MuMIn* package (Bartoń 2020). That is, we multiplied each (partial) R^2 by the R_d/R_Z ratio, where R_d and R_Z are the full model R^2 computed by the delta method and following Zhang (2017), respectively.

As some of the variables were correlated (e.g. beech dominance with soil wetness), we were interested in how much of the variance a variable explains can be attributed uniquely to that variable and how much is shared with others. According to the principles of commonality analysis (Ray-Mukherjee et al. 2014), the total R^2 for variable X was adopted from a model with X as the only explanatory variable. The unique effect of X was computed as the difference between the R^2 of a full model (all explanatory variables included) and the R^2 of a model with all explanatory variables except X.

We also had to account for the effect of sampling area that differed between plots. We did this by virtually splitting the plots with area exceeding a certain threshold T into the smallest set of equally sized subplots whose area did not exceed T. This threshold was set to a value at which the subplot area included as an explanatory variable in the GLMMs did not remain significant; this was 0.7 m^2 and 0.3 m^2 when working with microsite and seedbed plots, respectively. The individuals recorded in the original plot were then randomly distributed between the virtual subplots. To account for the dependence between subplots, we used the original plot identity as another level of nesting in the random effect structure (Table 1).

If a model with young and old pits/mounds kept as separate microsites was not significantly better than a model with these age categories merged, the separation of young and old treethrow microtopographies was not retained. The separation had to result in AIC drop of at least 4 units (Burnham & Anderson 2004) to be considered significant. Similarly, when using deadwood decay as an explanatory variable, we started with a model with both linear and quadratic terms of decay included, but if the quadratic term was not significant, it was dropped.

With certain models we had to deal with the problem of perfect separation, which in our case appeared in situations when seedlings were completely missing from one or more microsites. In such cases, the respective model coefficients (which would theoretically be infinite) could not be properly estimated and the model-fitting algorithm failed to converge. We solved this problem by changing one randomly selected absence into a presence within every microsite where perfect separation occurred. This is a rather conservative approach that may somewhat decrease the importance of microsite as a variable, but only marginally. To minimize possible side effects this solution might have on other variables, we repeated this procedure 100 times and used averaged estimates from the resulting 100 models.

Table 1 Overview of fitted GLMM models.

Models	Reg. species	Reg. classes	Sampling unit	Data subset	Explanatory variables	Random effect	Presented in
1–8	*FS, PA*	all	microsite	everything	beech, wet, micro, disturb$_1$, disturb$_2$	circle/plot$_M$	Fig. 3–4, S4
9–12	*FS*	”	”	microsites: IS, M, P	”	”	Fig. 5a, S5–6
13–16	*PA*	”	”	”	”	”	Fig. S5–6
17–20	*FS*	”	”	microsites: DW$_{1-3}$	beech, wet, disturb$_1$, disturb$_2$, DW decay(^{2}), DW species	”	Fig. S7
21–24	*PA*	”	”	”	”	”	Fig. 5b, S7
25–26	*FS, PA*	< 15 cm	seedbed	seedbeds: moss, beech litter, bare substrate	beech, wet, micro, disturb$_2$, seedbed, micro × seedbed	circle/plot$_M$/plot$_S$	Fig. 8, Tab. 2

Reg., Regeneration; FS, *Fagus sylvatica*; PA, *Picea abies*; ”, ditto; IS, intact soil; M, mounds; P, pits; DW, deadwood; explanatory variables: beech, beech dominance in canopy; wet, wetness; micro, microsite; disturb$_1$, disturbance 1972–1996; disturb$_2$, disturbance 1996–2010; plot$_M$, microsite sampling plot; plot$_S$, seedbed sampling plot

3 Results

3.1 Species densities by soils and microsites

Overall, beech was more abundant than spruce in all regeneration classes, and this disproportion grew stronger with the increasing size of individuals (Fig. 2a). While the density of beech seedlings was about four times that of spruce (2.6 m^{-2} and 0.6 m^{-2}, respectively; Fig. 2b), in the largest regeneration class, beech outnumbered spruce by a factor of more than 50 (0.08 m^{-2} and 0.002 m^{-2}). However, the pattern was clearly not universal and differed between soils and microsites.

Beech was generally more common on terrestrial than on hydromorphic soils, whereas the opposite was true for spruce. The only soils that did not completely fit this pattern were Albic Podzols, with an average beech seedling density of about 0.5 m^{-2}, as opposed to at least 2.7 m^{-2} on other terrestrial soils. However, spruce seedling densities on Albic Podzols were low as well (0.02 m^{-2}). Thanks to its higher abundance, spruce outnumbered beech on hydromorphic soils, but only in seedlings and small saplings. In larger regeneration classes beech was again the more abundant species but much less so than on terrestrial soils.

There was also an apparent distinction between woody and soil microsites. Most strikingly, no beech individuals higher than 50 cm were found on either stumps or deadwood. On the contrary, these microsites hosted the highest numbers of spruce regeneration (4.1 m^{-2} seedlings on fresh deadwood and 0.02 m^{-2} of the largest regeneration class on moderately decayed deadwood). On soil microsites, the situation was the opposite. Densities of beech exceeded those of spruce in all regeneration classes, and spruce individuals of DBH 1 cm or more were completely missing from treethrow pits.

3.2 Factors responsible for patterns in regeneration occurrence

The total explained variance (R^2) in regeneration occurrence ranged from 2% to 44% (Fig. 3, S4). For beech, the relationship between explained variance and the size of the regeneration was uni-

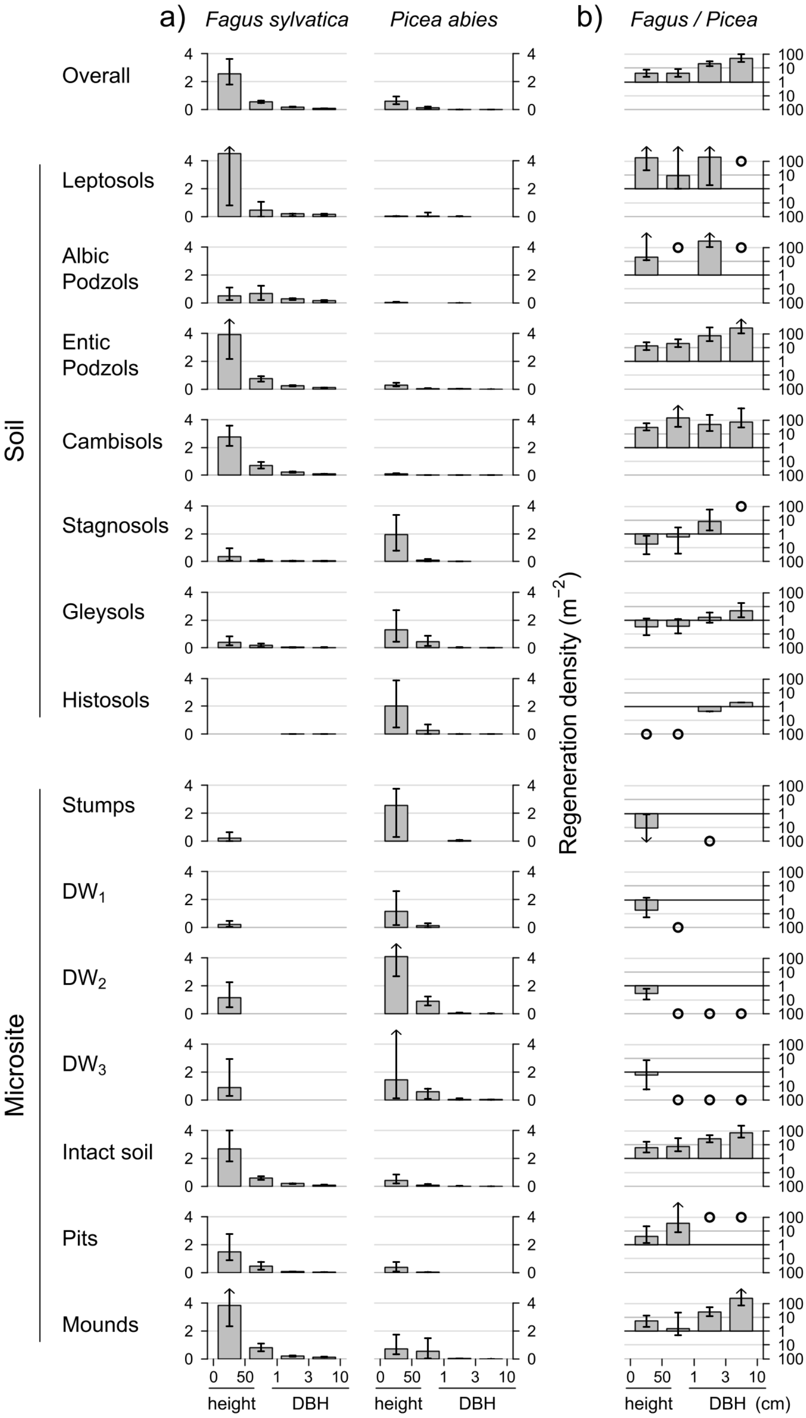


Fig. 2 Regeneration densities of beech and spruce (a) and the ratio between these densities (b) for the whole study site and different soil units and microsites. Bars show mean values and vertical whiskers represent the corresponding 95% confidence intervals (CI) based on 1000 bootstrap resamples (CIs exceeding Y axis range are marked by arrows). In b), upper and lower halves of the plots correspond to beech and spruce dominance, respectively, i.e., a value in the upper part is computed as *Fagus*/*Picea*, while in the lower part the ratio *Picea*/*Fagus* is used. Empty circles in b) indicate cases where one of the species was missing, i.e., the ratio was infinite.

modal, with peak explained variance for small saplings (44%), whereas for spruce this relationship was decreasing, with a maximum value for seedlings (19%).

In terms of quality, beech and spruce exhibited exactly opposite responses to beech dominance in the canopy and soil wetness. Beech showed an affinity for beech-dominated stands and drier soils, while spruce was more common under a spruce-dominated canopy and on moister soils. However, regarding the importance of these factors for different regeneration classes, patterns in the two species were similar. The importance of beech dominance in the canopy was highest for seedlings and decreased towards older regeneration, while the importance of soil wetness was highest for small saplings. The inherent correlation between soil wetness and canopy

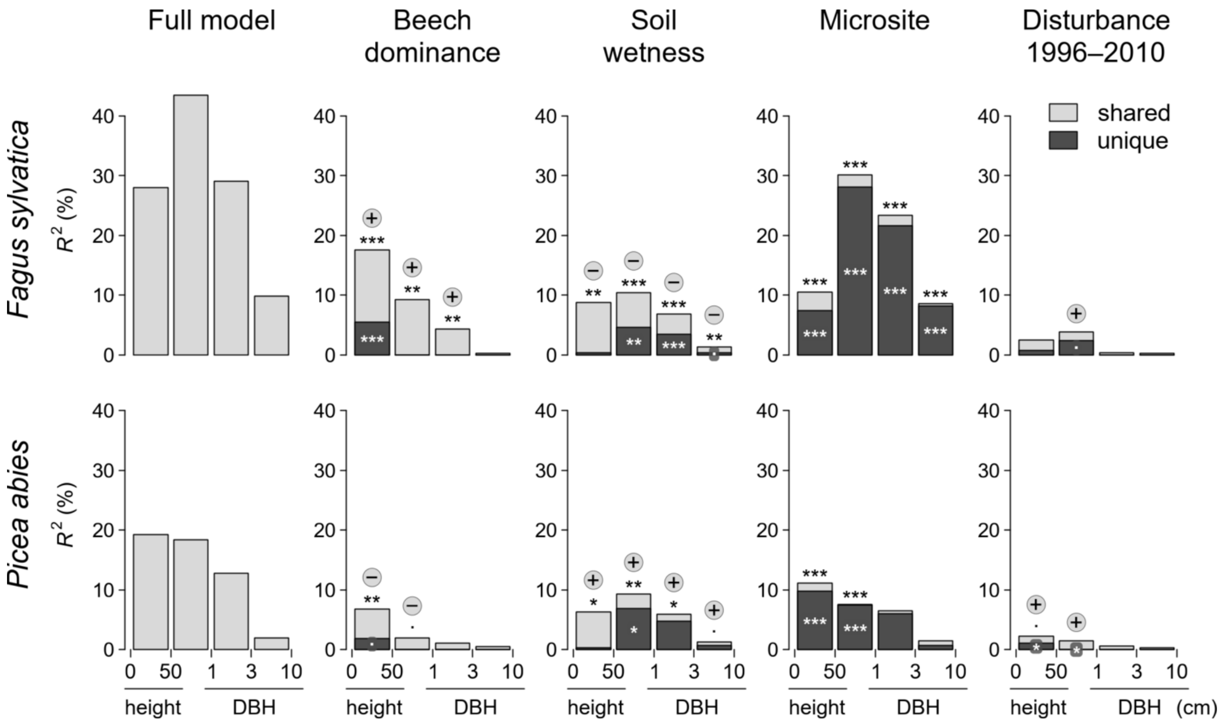


Fig. 3 The importance of studied factors for the occurrence of beech and spruce regeneration, measured by their explained variance (R^2). The first bar chart in a row shows the total variance explained by all variables, and the contributions of individual variables follow. Dark and light parts of bars mark the unique variance explained by each variable, and the explained variance it shares with other variable(s), respectively. Stars inside the dark areas denote the statistical significance of the unique effects of variables, while stars above bars mark the significance of total effects of variables (., $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). For significant continuous variables, the sign of their effect (+/−) is displayed above bars.

composition resulted in large parts of the explained variance being shared between the two variables. Consequently, the unique effect of beech dominance was only significant in the case of beech seedlings ($p < 0.001$, total $R^2 = 18\%$) and soil wetness in the case of older regeneration.

Microsite was clearly more important for beech than for spruce, especially for regeneration higher than 50 cm. The high variance explained by this factor in beech (up to 30% for small saplings) was mainly caused by the complete absence of larger regeneration of this species from woody microsites (Fig. 2a). For spruce, the R^2 related to microsite did not exceed 11%, but in terms of unique explained variance, microsite was the best explanatory variable for both seedlings and small saplings. The suitability of individual microsites differed markedly between beech and spruce (Fig. 4). For beech, soil microsites were generally more suitable than woody ones. While intact soil and old treethrow mounds were practically indiscernible in this respect, treethrow pits appeared to be a less preferred microsite than these two. The probability of the occurrence of beech regeneration on young mounds decreased with the increasing size of regeneration. This was likely not caused by the low suitability of this microsite, but rather by its implicit short time of existence. Contrastingly, spruce showed the highest affinity for moderately and more decayed deadwood, and the lowest for fresh deadwood, intact soil and treethrow pits. There was no statistical support for distinguishing between young and old treethrow mounds, and these two microsites together were moderately suitable for spruce regeneration.

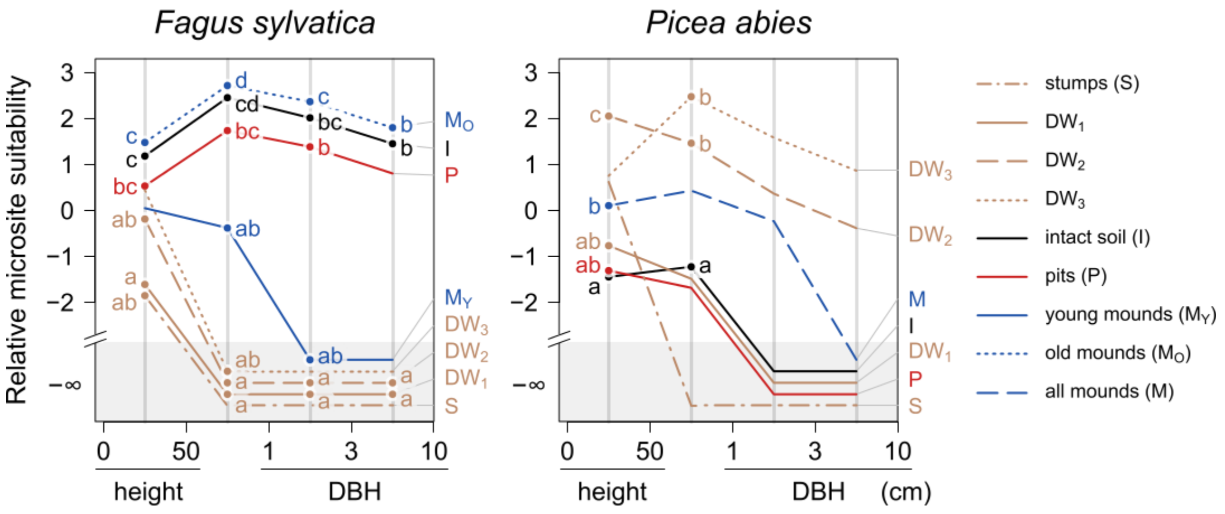


Fig. 4 Relative effects of microsites on the occurrence of beech and spruce regeneration. Plotted values are microsite-specific coefficients from the fitted GLMMs centered around zero, i.e., higher values mean higher probabilities of occurrence. Lowercase letters indicate significant differences ($p < 0.05$) between microsites within regeneration classes. The bottom gray parts of graphs contain cases where no occurrence of a species was recorded on a microsite, and thus the corresponding coefficient would theoretically be negative infinity. When two microsites share a letter, their effects do not differ significantly. No letter is displayed for microsites that are not significantly different from any other.

The lowest explained variances were generally related to disturbances. The more recent disturbance (between 1996 and 2010) had a positive effect on spruce regeneration below 1 cm DBH, but only weak effects ware found in the case of the older disturbance or for the regeneration of beech.

When focusing on soil microsites only, the explanatory power of the models for beech dropped substantially (Fig. 5a). This was mainly driven by the reduced importance of microsite (7% explained variance at most) when woody microsites, avoided by larger beech regeneration, were not considered. Changes in the importance of other variables were generally negligible. For spruce, the drop in microsite importance was also visible, but not as dramatic as for beech. The effect of disturbances became weaker for spruce, but, on the other hand, was more pronounced for beech. A weak ($p < 0.1$) negative and positive effect of the older disturbance was identified for small beech saplings and small beech trees, respectively. At the same time, small beech saplings showed a weak positive relation to the more recent disturbance. (see Fig. S5 for complete results).

Focusing on deadwood only resulted in an increase in explained variance for spruce seedlings (19%, Fig. 5b). The factor responsible for the increase was mainly deadwood decay stage, whose role differed between seedlings and older individuals. For spruce seedlings ($R^2 = 12\%$, $p < 0.001$), there was a unimodal response with an occurrence peak on moderately decayed wood, while for small saplings ($R^2 = 5\%$, $p < 0.001$) and larger regeneration classes the response was strictly positive, with the probability of occurrence increasing with advanced log decay. For beech seedlings, the deadwood decay stage was less important than for spruce ($R^2 = 4\%$, $p < 0.01$), and unlike spruce, the occurrence of beech seedlings exhibited a positive relation to deadwood decay stage (Fig. S7). Spruce seedlings showed a tendency to prefer conifer deadwood (total $R^2 = 5\%$), but most of the variance explained by deadwood species was shared with other variables, and although the respective p value was rather low, it was not strongly convincing ($p = 0.054$). Accordingly, all logs with spruce regeneration of DBH ≥ 1 cm were conifers ($\chi^2 = 2.96$; $p = 0.09$).

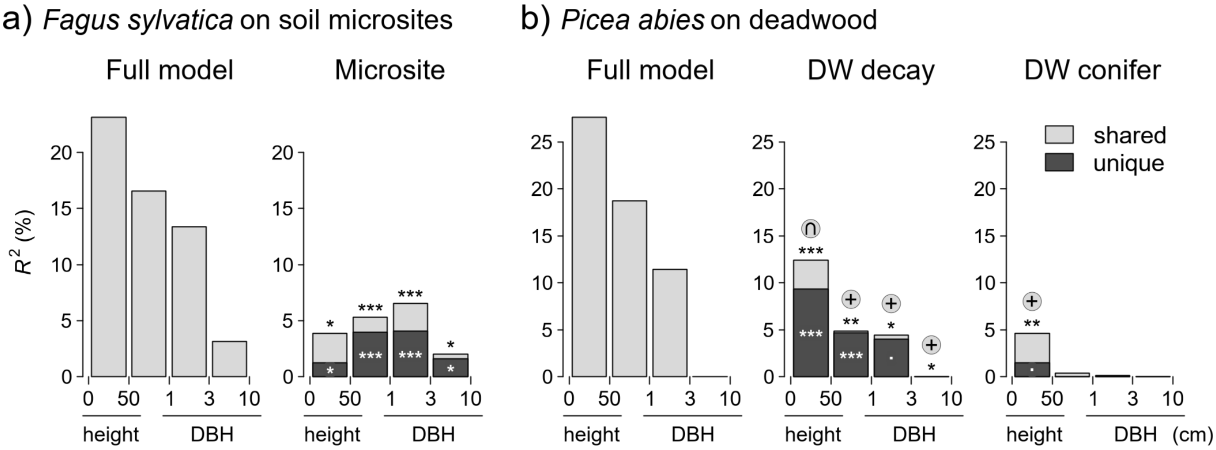


Fig. 5 Variance explained (R^2) by selected factors in the occurrence of a) beech on soil microsites (intact soil, pits and mounds) and b) spruce on deadwood. In a), a model with the same variables as in Fig. 2 was fitted while in b) microsite was substituted by DW decay and whether DW was a conifer (beech otherwise), compared to the model in Fig. 2. See Fig. 2 for explanations. The ∩ symbol above a bar marks a concave quadratic (unimodal) relationship. Only selected variables are shown; complete results for both species can be found in Fig. S5 and S7.

3.3 Differences in the proportions of seedbeds and the importance of seedbeds for seedlings

Overall, most of the forest area was covered by beech litter but this changed substantially on certain microsites and soil units (Fig. 6). Beech litter mainly dominated established soil microsites (intact soil and old pits and mounds), but was less abundant on woody microsites and young pits and mounds. These microsites were instead mostly covered by mosses, bare wood/soil and stones. Lichens were only found on woody microsites, and were the only seedbed reaching a maximum abundance on stumps. Among soils, beech litter clearly dominated on terrestrial soils, but its proportion gradually decreased towards wetter soils until it practically disappeared on Histosols. It was replaced mainly by mosses and other types of litter (herb, conifer). The herb cover also increased with increasing soil wetness.

Seedbeds had a significant influence on the occurrence of both beech and spruce seedlings, but observed patterns differed between the species. Highest beech seedling densities were generally found in beech litter, while spruce was most common in mosses and beech litter on woody substrates and in mosses on mounds (Fig. 7). However, these overall patterns could partly be driven by other factors (mainly stand composition), so to determine the net effect of seedbeds it is necessary to interpret the results from GLMMs, where all factors were considered (Fig. 8, Table 2). The total variance explained by the seedbed-based models was similar to that of the microsite-based models (26% and 23% for beech and spruce, respectively). However, the seedbed-based models ascribed more importance to beech dominance, so that its unique R^2 increased to 9% in the case of beech and became highly significant in the case of spruce (6%, $p < 0.001$). These increases in importance were caused mainly by the different seedling height thresholds in the two analyses (50 cm for microsites vs. 15 cm for seedbeds), and the difference in increase between species reflected the number of individuals that fell between the two thresholds. In beech, individuals between 15 and 50 cm of height were quite rare (ca. 6% of all seedlings below 50 cm), and consequently the difference in stand composition importance was small. In spruce, however,

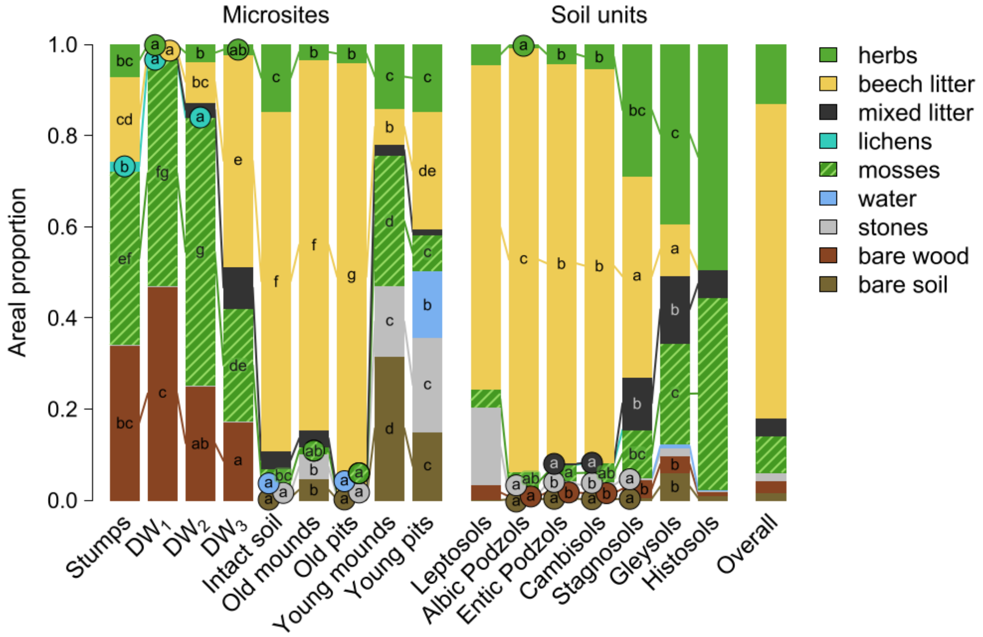


Fig. 6 Average areal proportions of seedbeds by microsites, soil units and overall. Different lowercase letters indicate differences in a seedbed's areal proportion between microsites or soils. Two microsites/soils do not differ significantly if they share a common letter, and no letter means no difference from any other microsite/soil. Note that here, herbs were considered together with seedbeds, i.e., the proportion of seedbeds was decreased according to herb cover.

the 15–50 cm cohort was much stronger (43%), and leaving it out resulted in a significant increase in stand composition importance. Other factors generally became slightly less important (the effect of the recent disturbance on spruce seedlings was only weakly significant), and the variance explained by microsite in the microsite-based models split into the effects of microsite, seedbed and their interaction.

Table 2 The importance and role of the interaction between microsite and seedbed for beech and spruce seedlings. The same models as in Fig. 6 were fitted, and ΔAIC is the change in model's AIC following the addition of the microsite × seedbed interaction to a no-interaction model. Significant differences in the probability of seedling occurrence on different microsites/seedbeds (based on post hoc tests) are given as inequalities. The last (bottom right) inequality, e.g., means that the probability of occurrence of spruce seedlings on moss was higher on moderately decayed deadwood than on fresh deadwood. Statistical significance is indicated as *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

	Microsite × seedbed interaction			Differences in species' occurrence			
				Between seedbeds (within microsites)		Between microsites (within seedbeds)	
Species	R^2 (%)	ΔAIC	p	Microsite	Differences	Seedbed	Differences
Fagus sylvatica	0.24	−1.4	0.027	overall	litter > moss, bare substrate (***)	overall	mound > pit (*)
Picea abies	3.46	−29.9	< 0.001	intact soil, mound	moss > litter (*)	litter	DW_1 (*), DW_2 (**) > mound
				DW_1	litter > moss (**), wood (***)		DW_1 (**), DW_2 (***) > pit
				DW_2	litter, moss > wood (*)		DW_1, DW_2 > intact soil (***)
						moss	DW_2 > DW_1 (**)

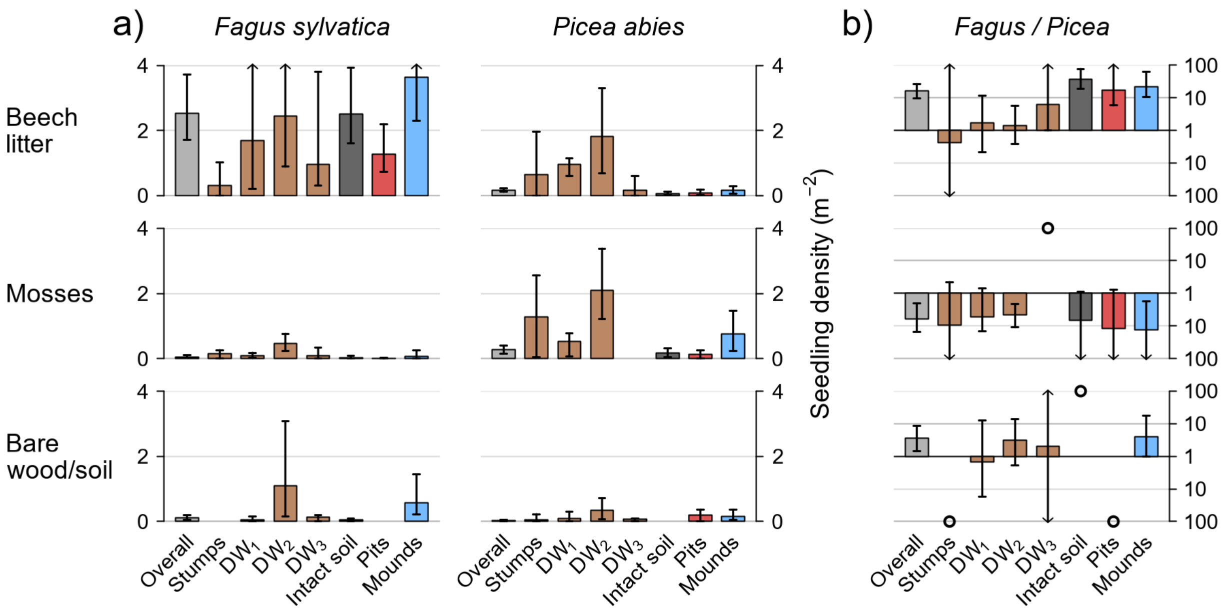


Fig. 7 Densities of beech and spruce seedlings (a) and the ratio between these densities (b) for seedbeds on different microsites. See Fig. 1 for explanations. Bar colors correspond to colors for microsites used in Fig. 1, 3.

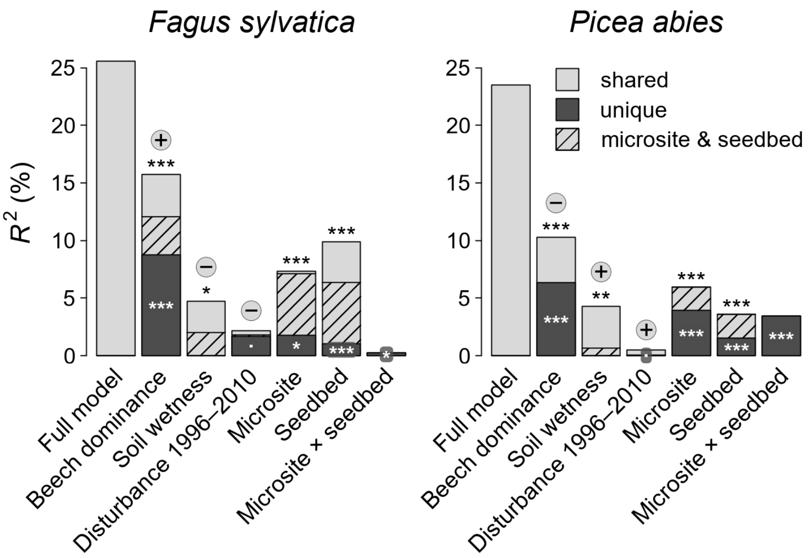


Fig. 8 Variance explained (R^2) in the occurrence of beech and spruce seedlings ($h < 15$ cm) when the seedbed and its interaction with a microsite were considered. See Fig. 2 for explanations. Hatched parts of bars show the variance explained by microsite and seedbed together.

In the case of beech, both microsite and seedbed showed significant unique effects, but the effect of their interaction was inconclusive. Its importance was, on the one hand, supported by a slightly significant p value of 0.027, but inclusion of the interaction in the model caused only a minor decrease in AIC (−1.4). On the other hand, this suggests that the interaction did not considerably improve the model. Moreover, the associated R^2 was quite low (0.2%), and post hoc tests showed no significant differences between any of the interaction-related coefficients, which further indicates that the interaction's effect was rather negligible. The effect of seedbed was stronger than that of microsite (in terms of total R^2 and unique effect p value), and the two variables shared a large part of the variance they explained. Beech seedlings clearly occurred more frequently in beech litter than on moss or bare substrate (Table 2).

In spruce, the first noticeable difference from beech is that there was much less explained variance shared between microsite and seedbed. Secondly, unlike beech, the interaction between microsite and seedbed had a significant effect. Its R^2 (3.5%) was not comparable to or higher than the unique R^2 of both microsite and seedbed, but it was highly significant ($p < 0.001$) and its inclusion in the model caused a substantial drop in AIC (ΔAIC = −29.9). This indicates that the role of the seedbed was not universal, but rather microsite-dependent. While on soil microsites the occurrence of spruce was more likely on moss than in beech litter, on fresh deadwood this pattern was reversed. This was complemented by the result that in beech litter, spruce seedlings were more likely to occur on deadwood than on soil microsites. Furthermore, mosses were more likely to host spruce seedlings on moderately decayed deadwood than on fresh deadwood.

4 Discussion

4.1 Role of stand composition, soil wetness and disturbances

Stand composition was the most important factor for seedlings of both species. This was most clear when seedbeds and only individuals below 15 cm were considered (Fig. 8). Stand composition is the most complex variable (in terms of how many phenomena influence it) among those we used. Naturally, it determines the relative supply of beech and spruce seeds, but also reflects certain environmental factors. These factors either determine the stand composition in the first place, or subsequently, result from the effects of adult trees. In the case of beech and spruce in Boubín, the former includes mainly soil wetness, while the latter are represented by lighter conditions in stands with a higher proportion of spruce (Leuchner et al. 2011; Asplund et al. 2018) or the ratio of broadleaf to conifer litter. All these factors can be important for seedling establishment and growth. Some were accounted for by specific variables (soil wetness, seedbed), so the unique effect of stand composition can be considered free of these, and reflects mostly seed supply and also partly light availability. However, since light conditions become more important as seedlings grow higher (Iijima et al. 2007; Kathke & Bruelheide 2010), seed rain is likely the dominant factor when interpreting the unique effect of stand composition in the smallest seedling category. For regeneration higher than 50 cm, stand composition bore no unique information and gradually lost importance with the increasing size of the regeneration in the case of beech and became insignificant in the case of spruce. This illustrates the fact that as regeneration gets older, factors other than seed supply become important. In beech-dominated stands, the relatively light-demanding spruce regeneration can be limited by shady conditions or outcompeted by the more competitive beech regeneration (Rolo et al. 2015).

There was a large part of explained variance shared between soil wetness and stand composition. This would be expected, since soil hydromorphism is the main environmental gradient along which canopy species composition changes from beech to spruce dominance (Daněk et al. 2019). However, the part of the explained variance that was unique to soil wetness increased with the increasing size of the regeneration. This shows that soil wetness itself (rather than stand composition or other correlated properties) becomes more important for the occurrence of older beech and spruce regeneration along the gradient of soil hydromorphism. Beech is a species that does not tolerate waterlogging (Dreyer 1994; Schmull & Thomas 2000) and has a relatively deep root system (Schmid & Kazda 2001), which is likely why it avoids strongly hydromorphic soils. Such conditions are not ideal for spruce either, but it can better tolerate them by developing shallow root systems (Puhe 2003). The positive effect of soil wetness on the regeneration of spruce is thus probably a consequence of reduced competition from beech.

We found rather weak evidence of the effect of canopy tree mortality on regeneration, mainly concerning the more recent disturbance. The older disturbance (1972–1996) appears to have had a positive effect on beech regeneration, and was reflected in recent occurrence of small beech trees. Consequently, increased shading by these individuals is probably responsible for the observed lower occurrence of small beech saplings. The effect of the recent disturbance (1996–2010) was visible in individuals below 1 cm DBH, and was more pronounced and consistently positive in spruce. The two periods differed in the nature of the canopy disturbance. During the first, small-scale disturbance driven by the spatially scattered mortality of individual trees was typical. On the contrary, the second was dominated by the 2008 Emma windstorm, a coarse-scale disturbance event (Daněk et al. 2019). It thus appears that the moderate increase in light levels following the small-scale disturbance was more beneficial to beech, while spruce regeneration reacted to the stronger changes in light regime after the coarse-scale disturbance, which is in line with the previously described behavior of these two species with respect to light (Stancioiu & O'Hara 2006; Barna & Bosela 2015; Dobrovolny 2016). In a study from the same region, Kašpar et al. (2020) showed that historically, beech tended to regenerate under the canopy.

4.2 Importance of the seedbed and microsite for seedlings

The seedbed was important for seedlings of both species, but the species' responses differed, especially with respect to beech litter. Beech seedlings showed affinity for beech litter in two ways: directly, i.e. by preferring it to the two other seedbeds within the same microsite, and indirectly, by occupying beech litter-rich microsites (intact soil, mounds and pits). Unless too deep, litter is not a barrier for the establishment of beech seedlings as beech seeds are relatively large (average seed mass 0.26 g, compared to 0.007 g in spruce; Szwagrzyk et al. 2015) and can support the growth of a long radicle (Dzwonko & Gawroński 2002; Sayer 2006). Litter can also act positively by protecting seeds from dessication or predation (Beatty & Sholes 1988; Sayer 2006).

Spruce seedlings showed affinity to beech litter only on deadwood, but not on soil microsites. This contrasting behavior is likely caused by the different qualities of litter on the two types of microsites. Only a limited amount of litter can accumulate on raised surfaces such as deadwood, as opposed to the forest floor, where a much deeper litter layer can develop over time. Although we did not specifically measure litter depth, the differences between microsites with respect to this variable can be inferred from the microsite-specific areal proportions of litter. As would be expected, the amount of litter increased from highly convex surfaces (deadwood) to concave forms (treethrow pits). This topographical forcing works in interaction with time. On the one hand, time is necessary for the accumulation of a deep litter layer, but on the other hand, the microsites gradually flatten out with time due to wood decay (deadwood) or soil erosion/accumulation (treethrow features). The full decomposition of a large log (diameter > 55 cm) takes on average between 40 and 80 years in Boubín, depending on the log species and other factors, e.g. mortality mode (Přívětivý et al. 2016; Přívětivý et al. 2018). Treethrow microtopographies have a much higher longevity of hundreds or even thousands of years (Šamonil et al. 2013). The thin beech litter layer on deadwood is thus not a barrier in the small-seeded conifer's establishment, unlike the deeper litter on soil (Simard et al. 1998; Asplund et al. 2018). Another reason for a positive relation between litter and seedlings on a raised surface such as a decaying log is that both litter and seeds are likely to get trapped in similar spots that are locally flat or even concave. The occurrence of pure spruce litter was quite rare (< 2% of total microsite area) so we could not test whether it might be a better seedbed for the establishment of spruce seedlings than beech litter. However, Asplund et al. (2018) showed that in a beech forest, spruce seedling emergence was significantly higher in spruce than in beech litter.

The relationship of spruce seedlings to mosses was also ambiguous. On fresh deadwood mosses were rather avoided, while on more decayed deadwood, the occurrence of seedlings on mosses was comparable to that on beech litter. This likely relates to the changes in structure and species composition of bryophyte communities as deadwood decays. Initial, less developed bryophyte communities composed mostly of epiphytic species (Táborská et al. 2015) are probably less suitable for seedling establishment than thicker cushions of epixylic bryophytes on logs of advanced decay stages with better water holding and seed trapping capacity. On intact soil and mounds, we found mosses to be generally suitable for spruce seedlings. On these microsites, where beech litter prevents the successful establishment of spruce, the occurrence of mosses may indicate spots where litter accumulation is impeded for some reason (e.g. topographically). Our results are thus rather in accordance with studies that found a positive effect of mosses on spruce regeneration (Hörnberg et al. 1997; Hunziker & Brang 2005; Kathke & Bruelheide 2010), than with those that reported a negative effect (Harmon & Franklin 1989; Iijima & Shibuya 2010). Mosses can act negatively when their biomass is too high, which was probably not common in Boubín.

4.3 Differences in suitability between microsites

The main trends in the occurrence of regeneration on different microsites were generally visible already in the seedling stage and became clearer as the regeneration grew larger. At the same time, since the numbers of individuals decreased with larger regeneration sizes, the differences between microsites became less statistically significant, especially for spruce.

Soil microsites were the only ones with successful beech regeneration, but its densities at those sites were relatively high and much higher than those of spruce, especially in larger size classes. Given that soil microsites cover the vast majority of forest floor, this disproportion also translates to overall beech dominance in regeneration. Treethrow pits were less suitable for beech than mounds, and partly also less than intact soil. This has been observed before both for beech regeneration (Simon et al. 2011; Barker Plotkin et al. 2017) and older trees (Šebková et al. 2012). Although beech can generally become established well in its own litter, the thick litter accumulations in treethrow pits may be a problem. Contrastingly, for spruce regeneration only mounds appeared to be a somewhat suitable soil microsite, but still less so than certain deadwood. Microtopography can have different effects on spruce regeneration, depending on environmental conditions and stand composition. Higher moisture in depressions can be beneficial on well drained soils (Hanssen 2003), but it becomes limiting on hydromorphic soils (Hörnberg et al. 1997; Vodde et al. 2015). The effect of the generally drier mounds is then inverse to that of pits. In Boubín, soil moisture on mounds is likely sufficient, and their main advantage over intact soil and pits is that they accumulate less beech litter, especially when younger.

On woody microsites, beech regeneration densities were lower than on soil, and only seedlings but no individuals above 50 cm were present. This pattern is in line with other studies that did not report beech regeneration classes taller than 80 cm from decaying logs (Szewczyk & Szwagrzyk 1996; Orman & Szewczyk 2015). This suggests that beech seedlings can be established on deadwood but cannot survive there. A similar pattern was observed for *Acer saccharum* in hemlock–hardwood forests, where no *Acer* seedlings more than 9 years old were present on deadwood (Marx & Walters 2008). Spruce, on the other hand, is known for its ability to successfully regenerate on deadwood, and this behavior is also visible in our results. Compared to other studies (Hofgaard 1993; Hörnberg et al. 1997; Bace et al. 2011), we did not identify an important role for stumps. In Boubín, stumps often form by the gradual disintegration of standing dead trees (contrary to e.g. stumps formed by tree felling), which makes them an unstable substrate with low chances for seedling survival. Once a stump becomes more stable near ground level, it starts accumulating litter, which may hamper spruce establishment. The best microsites for spruce regeneration were logs of advanced decay stage (DW_2 and DW_3). Similar to other authors (Bače et al. 2012; Orman et al. 2016), we found a unimodal response of spruce seedlings to deadwood decay stage (with a peak occurrence on moderately decayed logs), but a positive response in the case of older regeneration. Logs in the initial stages of decay show lower rates of seedling establishment and survival due to e.g. high mechanical resistance, low moisture content or few seed trapping crevices (Bače et al. 2012; Orman & Szewczyk 2015; Orman et al. 2016). The relatively small number of spruce seedlings on highly decayed logs was probably due to their thicker litter layers and occupation by older spruce cohorts. We also found some indication that conifer deadwood is more suitable for spruce regeneration than beech logs. The role of deadwood species in tree regeneration is still poorly understood, but interspecific differences in deadwood suitability were reported also by Marx & Walters (2008), who found disproportionately more seedlings >3 years-old on *Tsuga* and *Betula*, compared to *Acer* deadwood. This could be caused by differences in wood decay patterns or fungal community composition (Arnstadt et al. 2016; Purahong et al. 2018).

5 Conclusions

Regeneration of beech and spruce in a temperate mountain forest, while being fundamentally constrained by the soil spatial pattern, is also largely driven by the effects of canopy trees. The mostly topographically and hydrologically determined occurrence of hydromorphic soils defines areas where beech is prevented from growing and only spruce can become established successfully. On terrestrial soils, however, both species are within their ecological niche, and their different traits become important. Beech trees create a shady environment with a broadleaved litter-covered forest floor. As a shade-tolerant and large-seeded species, beech is able to regenerate in such conditions well, but for the more light-demanding small-seeded spruce, such an environment is much less amenable. Spruce regeneration, however, can take advantage of elevated microsites with impeded litter accumulation. These include patches of mosses on treethrow mounds and particularly decaying logs, where spruce regeneration is free from competition with beech, which does not survive there. Interestingly, the availability of these microsites can be dependent on the presence of spruce in the canopy, as our results indicate that spruce deadwood is more suitable than that of beech for spruce regeneration. Furthermore, during windstorms spruce is more susceptible to uprooting than beech (Knoke et al. 2008; Jactel et al. 2017), hence potentially attributing more to mound creation than its competitor. Both species thus modify their environment in ways that can facilitate their own regeneration. While spruce does this directly by creating specific microsites, beech achieves this rather indirectly by suppressing its competitor. Overall, beech comes out of this as a much stronger competitor, which has resulted in its long-term increasing dominance on terrestrial soils in Boubín (Daněk et al. 2019). This increase in beech dominance is likely to continue, or even intensify with the expected climate change-related rise in temperatures, as temperature is an important factor limiting beech in Boubín (Kašpar et al. 2021). However, spruce could potentially benefit from disturbance events, such as infrequent severe windstorms that come usually in winter months (Brázdil & Dobrovolný 2001). Such events typically have an immediate negative effect on mature spruce individuals (Daněk et al. 2019), but in the long term could support spruce regeneration by increasing light levels in the understorey and the availability of suitable mound and deadwood microsites.

Acknowledgements We would like to thank our colleagues from the 'Blue Cat' research team and other collaborators (especially Radka Matějíčková and Christina Bachmannová) for their help with data collection. We are also grateful for the support from the Šumava National Park Administration. The research was supported by the Czech Science Foundation, project No. 19-09427S. Last but not least we would like to thank David Hardekopf for improving the English.

References

Arnstadt T., Hoppe B., Kahl T., Kellner H., Krüger D., Bauhus J., Hofrichter M. 2016. Dynamics of fungal community composition, decomposition and resulting deadwood properties in logs of *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris*. *Forest Ecology and Management* 382: 129–142.

Asplund J., Hustoft E., Nybakken L., Ohlson M., Lie M.H. 2018. Litter impair spruce seedling emergence in beech forests: a litter manipulation experiment. *Scandinavian Journal of Forest Research* 33: 332–337.

Augusto L., De Schrijver A., Vesterdal L., Smolander A., Prescott C., Ranger J. 2015. Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests. *Biological Reviews* 90: 444–466.

Bace R., Svoboda M., Janda P. 2011. Density and height structure of seedlings in subalpine spruce forests of central Europe: Logs vs. stumps as a favourable substrate. *Silva Fennica* 45: 1065–1078.

Bače R., Svoboda M., Pouska V., Janda P., Červenka J. 2012. Natural regeneration in Central-European subalpine spruce forests: Which logs are suitable for seedling recruitment? *Forest Ecology and Management* 266: 254–262.

Barker Plotkin A., Schoonmaker P., Leon B., Foster D. 2017. Microtopography and ecology of pit-mound structures in second-growth versus old-growth forests. *Forest Ecology and Management* 404: 14–23.

Barna M., Bosela M. 2015. Tree species diversity change in natural regeneration of a beech forest under different management. *Forest Ecology and Management* 342: 93–102.

Bartoń K. 2020. MuMIn: Multi-Model Inference.

Beatty S.W. 1984. Influence of Microtopography and Canopy Species on Spatial Patterns of Forest Understory Plants. *Ecology* 65: 1406–1419.

Beatty S.W., Sholes O.D. V. 1988. Leaf litter effect on plant species composition of deciduous forest treefall pits. *Canadian Journal of Forest Research* 18: 553–559.

Berger T.W., Berger P. 2012. Greater accumulation of litter in spruce (*Picea abies*) compared to beech (*Fagus sylvatica*) stands is not a consequence of the inherent recalcitrance of needles. *Plant and Soil* 358: 349–369.

Bolte A., Hilbrig L., Grundmann B.M., Roloff A. 2014. Understory dynamics after disturbance accelerate succession from spruce to beech-dominated forest—The Siggaboda case study. *Annals of Forest Science* 71: 139–147.

Bolte A., Kampf F., Hilbrig L. 2013. Space sequestration below ground in old-growth spruce-beech forests—signs for facilitation? *Frontiers in Plant Science* 4: 1–11.

Brázdil R., Dobrovolný P. 2001. History of strong winds in the Czech lands: causes, fluctuations, impacts. *Geographia Polonica* 74: 11–28.

Burnham K.P., Anderson D.R. 2004. Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research* 33: 261–304.

Corenblit D., Baas A.C.W., Bornette G., Darrozes J., Delmotte S., Francis R.A., Gurnell A.M., Julien F., Naiman R.J., Steiger J. 2011. Feedbacks between geomorphology and biota controlling Earth surface processes and landforms: A review of foundation concepts and current understandings. *Earth-Science Reviews* 106: 307–331.

Daněk P., Šamonil P., Phillips J.D. 2016. Geomorphic controls of soil spatial complexity in a primeval mountain forest in the Czech Republic. *Geomorphology* 273: 280–291.

Daněk P., Šamonil P., Vrška T. 2019. Four decades of the coexistence of beech and spruce in a Central European old-growth forest. Which succeeds on what soils and why? *Plant and Soil* 437: 257–272.

Dittmar C., Fricke W., Elling W. 2006. Impact of late frost events on radial growth of common beech (*Fagus sylvatica* L.) in Southern Germany. *European Journal of Forest Research* 125: 249–259.

Dobrovolny L. 2016. Density and spatial distribution of beech (*Fagus sylvatica* L.) regeneration in Norway spruce (*Picea abies* (L.) Karsten) stands in the central part of the Czech Republic. *iForest* 9: 666–672.

Dreyer E. 1994. Compared sensitivity of seedlings from 3 woody species (*Quercus robur* L, *Quercus rubra* L and *Fagus silvatica* L) to water-logging and associated root hypoxia: effects on water relations and photosynthesis. *Annales des Sciences Forestières* 51: 417–428.

Dwyer L.M., Merriam G. 1981. Influence of Topographic Heterogeneity on Deciduous Litter Decomposition. *Oikos* 37: 228.

Dzwonko Z., Gawroński S. 2002. Influence of litter and weather on seedling recruitment in a mixed oak–pine woodland. *Annals of Botany* 90: 245–251.

Hanssen K.H. 2003. Natural regeneration of *Picea abies* on small clear-cuts in SE Norway. *Forest Ecology and Management* 180: 199–213.

Harmon M.E., Franklin J.F. 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. *Ecology* 70: 48–59.

Hofgaard A. 1993. Structure and regeneration patterns in a virgin *Picea abies* forest in northern Sweden. *Journal of Vegetation Science* 4: 601–608.

Hörnberg G., Ohlson M., Zackrisson O. 1997. Influence of bryophytes and microrelief conditions on *Picea abies* seed regeneration patterns in boreal old-growth swamp forests. *Canadian Journal of Forest Research* 27: 1015–1023.

Hunziker U., Brang P. 2005. Microsite patterns of conifer seedling establishment and growth in a mixed stand in the southern Alps. *Forest Ecology and Management* 210: 67–79.

Iijima H., Shibuya M. 2010. Evaluation of suitable conditions for natural regeneration of *Picea jezoensis* on fallen logs. *Journal of Forest Research* 15: 46–54.

Iijima H., Shibuya M., Saito H. 2007. Effects of surface and light conditions of fallen logs on the emergence and survival of coniferous seedlings and saplings. *Journal of Forest Research* 12: 262–269.

Jactel H., Bauhus J., Boberg J., Bonal D., Castagneyrol B., Gardiner B., Gonzalez-Olabarria J.R., Koricheva J., Meurisse N., Brockerhoff E.G. 2017. Tree Diversity Drives Forest Stand Resistance to Natural Disturbances. *Current Forestry Reports* 223–243.

Janík D., Král K., Adam D., Hort L., Samonil P., Unar P., Vrska T., McMahon S. 2016. Tree spatial patterns of *Fagus sylvatica* expansion over 37 years. *Forest Ecology and Management* 375: 134–145.

Jones C.G., Lawton J.H., Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* 69: 373.

Kašpar J., Šamonil P., Vašíčková I., Adam D., Daněk P. 2020. Woody species-specific disturbance regimes and strategies in mixed mountain temperate forests in the Šumava Mts., Czech Republic. *European Journal of Forest Research* 139: 97–109.

Kašpar J., Tumajer J., Šamonil P., Vašíčková I. 2021. Species-specific climate-growth interactions determine tree species dynamics in mixed Central European mountain forests. *Environmental Research Letters* 16: 034039.

Kathke S., Bruelheide H. 2010. Interaction of gap age and microsite type for the regeneration of *Picea abies*. *Forest Ecology and Management* 259: 1597–1605.

Knoke T., Ammer C., Stimm B., Mosandl R. 2008. Admixing broadleaved to coniferous tree species: A review on yield, ecological stability and economics. *European Journal of Forest Research* 127: 89–101.

Leuchner M., Hertel C., Menzel A. 2011. Spatial variability of photosynthetically active radiation in European beech and Norway spruce. *Agricultural and Forest Meteorology* 151: 1226–1232.

Leuschner C., Ellenberg H. 2017. Ecology of Central European Forests. Vegetation Ecology of Central Europe, Volume I. Springer International Publishing, Switzerland.

Marx L., Walters M.B. 2008. Survival of tree seedlings on different species of decaying wood maintains tree distribution in Michigan hemlock-hardwood forests. *Journal of Ecology* 96: 505–513.

Nakagawa S., Johnson P.C.D., Schielzeth H. 2017. The coefficient of determination R^2 and intraclass correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface* 14: 20170213.

Nakagawa S., Schielzeth H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4: 133–142.

Orman O., Adamus M., Szewczyk J. 2016. Regeneration processes on coarse woody debris in mixed forests: do tree germinants and seedlings have species-specific responses when grown on coarse woody debris? *Journal of Ecology* 104: 1809–1818.

Orman O., Szewczyk J. 2015. European beech, silver fir, and Norway spruce differ in establishment, height growth, and mortality rates on coarse woody debris and forest floor—a study from a mixed beech forest in the Western Carpathians. *Annals of Forest Science* 72: 955–965.

Pickett S.T.A., White P.S. 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Inc., San Diego.

Pretzsch H., Block J., Dieler J., Dong P.H., Kohnle U., Nagel J., Spellmann H., Zingg A. 2010. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. *Annals of Forest Science* 67: 712–712.

Pretzsch H., Rötzer T., Matyssek R., Grams T.E.E., Häberle K.-H., Pritsch K., Kerner R., Munch

J.-C. 2014. Mixed Norway spruce (*Picea abies* [L.] Karst) and European beech (*Fagus sylvatica* [L.]) stands under drought: from reaction pattern to mechanism. *Trees* 28: 1305–1321.

Pretzsch H., Schütze G. 2005. Crown allometry and growing space efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) in pure and mixed stands. *Plant Biology* 7: 628–639.

Přívětivý T., Adam D., Vrška T. 2018. Decay dynamics of *Abies alba* and *Picea abies* deadwood in relation to environmental conditions. *Forest Ecology and Management* 427: 250–259.

Přívětivý T., Janík D., Unar P., Adam D., Král K., Vrška T. 2016. How do environmental conditions affect the deadwood decomposition of European beech (*Fagus sylvatica* L.)? *Forest Ecology and Management* 381: 177–187.

Puhe J. 2003. Growth and development of the root system of Norway spruce (*Picea abies*) in forest stands—a review. *Forest Ecology and Management* 175: 253–273.

Purahong W., Wubet T., Krüger D., Buscot F. 2018. Molecular evidence strongly supports deadwood-inhabiting fungi exhibiting unexpected tree species preferences in temperate forests. *ISME Journal* 12: 289–295.

Ray-Mukherjee J., Nimon K., Mukherjee S., Morris D.W., Slotow R., Hamer M. 2014. Using commonality analysis in multiple regressions: A tool to decompose regression effects in the face of multicollinearity. *Methods in Ecology and Evolution* 5: 320–328.

Rolo V., Andivia E., Pokorný R. 2015. Response of *Fagus sylvatica* and *Picea abies* to the interactive effect of neighbor identity and enhanced CO2 levels. *Trees* 29: 1459–1469.

Šamonil P., Daněk P., Baldrian P., Tláskal V., Tejnecký V., Drábek O. 2020. Convergence, divergence or chaos? Consequences of tree trunk decay for pedogenesis and the soil microbiome in a temperate natural forest. *Geoderma* 376: 114499.

Šamonil P., Daněk P., Senecká A., Adam D., Phillips J.D. 2018. Biomechanical effects of trees in an old-growth temperate forest. *Earth Surface Processes and Landforms* 43: 1063–1072.

Šamonil P., Schaetzl R.J., Valtera M., Goliáš V., Baldrian P., Vašíčková I., Adam D., Janík D., Hort L. 2013. Crossdating of disturbances by tree uprooting: Can treethrow microtopography persist for 6000 years? *Forest Ecology and Management* 307: 123–135.

Sayer E.J. 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological Reviews of the Cambridge Philosophical Society* 81: 1–31.

Schmid I., Kazda M. 2001. Vertical distribution and radial growth of coarse roots in pure and mixed stands of *Fagus sylvatica* and *Picea abies*. *Canadian Journal of Forest Research* 31: 539–548.

Schmull M., Thomas F.M. 2000. Morphological and physiological reactions of young deciduous trees (*Quercus robur* L., *Q. petraea* [Matt.] Liebl., *Fagus sylvatica* L.) to waterlogging. *Plant and Soil* 225: 227–242.

Šebková B., Šamonil P., Janík D., Adam D., Král K., Vrška T., Hort L., Unar P. 2011. Spatial and volume patterns of an unmanaged submontane mixed forest in Central Europe: 160 years of spontaneous dynamics. *Forest Ecology and Management* 262: 873–885.

Šebková B., Šamonil P., Valtera M., Adam D., Janík D. 2012. Interaction between tree species populations and windthrow dynamics in natural beech-dominated forest, Czech Republic. *Forest Ecology and Management* 280: 9–19.

Simard M.-J., Bergeron Y., Sirois L. 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. *Journal of Vegetation Science* 9: 575–582.

Simon A., Gratzer G., Sieghardt M. 2011. The influence of windthrow microsites on tree regeneration and establishment in an old growth mountain forest. *Forest Ecology and Management* 262: 1289–1297.

Stancioiu P.T., O'Hara K.L. 2006. Regeneration growth in different light environments of mixed species, multiaged, mountainous forests of Romania. *European Journal of Forest Research* 125: 151–162.

Szewczyk J., Szwagrzyk J. 1996. Tree regeneration on rotten wood and on soil in old-growth stand. *Vegetatio* 122: 37–46.

Szwagrzyk J., Gratzer G., Stępniewska H., Szewczyk J., Veselinovic B. 2015. High reproductive effort and low recruitment rates of european beech: Is there a limit for the superior competitor? *Polish Journal of Ecology* 63: 198–212.

Táborská M., Přívětivý T., Vrška T., Ódor P. 2015. Bryophytes associated with two tree species and different stages of decay in a natural fir-beech mixed forest in the Czech Republic. *Preslia* 87: 387–401.

Vodde F., Jõgiste K., Engelhart J., Frelich L.E., Moser W.K., Sims A., Metslaid M. 2015. Impact of wind-induced microsites and disturbance severity on tree regeneration patterns: Results from the first post-storm decade. *Forest Ecology and Management* 348: 174–185.

Vrška T., Adam D., Hort L., Kolář T., Janík D. 2009. European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) rotation in the Carpathians-A developmental cycle or a linear trend induced by man? *Forest Ecology and Management* 258: 347–356.

Vrška T., Hort L., Odehnalová P., Horal D., Adam D. 2001. The Boubín virgin forest after 24 years (1972–1996) – development of tree layer. *Journal of Forest Science* 47: 439–459.

Wagner S., Collet C., Madsen P., Nakashizuka T., Nyland R.D., Sagheb-Talebi K. 2010. Beech regeneration research: From ecological to silvicultural aspects. *Forest Ecology and Management* 259: 2172–2182.

Zhang D. 2017. A Coefficient of Determination for Generalized Linear Models. *American Statistician* 71: 310–316.

Zhang D. 2020. rsq: R-Squared and Related Measures.

Table S1 Numbers of studied circles, plots within them and areas they covered on different microsites and soils for the two data sets (all regeneration, regeneration with DBH > 1 cm).

		Microsite							Soil unit							
Regeneration	Sampled	Stumps	DW_1	DW_2	DW_3	Intact soil	Pits	Mounds	Leptosols	Albic Podzols	Entic Podzols	Cambisols	Stagnosols	Gleysols	Histosols
All	circles	21	37	39	12	46	43	44	1	3	20	12	3	6	1
	plots	30	57	79	16	155	105	116	13	34	261	135	39	66	10
	area (m^2)	19	266	325	56	980	148	325	47	114	975	557	120	248	56
DBH > 1 cm	circles	60	101	111	86	116	108	111	2	9	54	28	5	17	1
	plots	110	423	432	166	116	374	434	40	153	935	391	118	401	17
	area (m^2)	70	1173	1223	396	30079	1207	1962	623	2798	16818	8714	1549	5298	310

Table S2 Average regeneration densities (m^{-2}; values shown in Fig. 2a).

		Fagus sylvatica				*Picea abies*			
		H < 50 cm	DBH < 1 cm	DBH < 3 cm	DBH < 10 cm	H < 50 cm	DBH < 1 cm	DBH < 3 cm	DBH < 10 cm
Overall		2.558	0.542	0.178	0.076	0.601	0.132	0.009	0.002
Soil	Leptosols	4.501	0.453	0.194	0.149	0.026	0.051	0.001	
	Albic	0.518	0.687	0.265	0.136	0.024		0.001	
	Entic	3.925	0.729	0.239	0.098	0.286	0.038	0.003	0.000
	Cambisols	2.771	0.703	0.236	0.091	0.091	0.005	0.005	0.001
	Stagnosols	0.366	0.059	0.046	0.041	1.919	0.105	0.006	
	Gleysols	0.414	0.173	0.038	0.022	1.308	0.455	0.024	0.005
	Histosols			0.010	0.007	2.011	0.288	0.023	0.003
Microsite	Stumps	0.200				2.572		0.024	
	DW1	0.196				1.168	0.132		
	DW2	1.142				4.074	0.888	0.047	0.010
	DW3	0.885				1.427	0.575	0.048	0.016
	Intact soil	2.696	0.580	0.199	0.083	0.426	0.079	0.007	0.001
	Pits	1.490	0.440	0.052	0.026	0.364	0.013		
	Mounds	3.834	0.781	0.202	0.113	0.702	0.517	0.009	0.000

Table S3 Average *Fagus*/*Picea* (positive values) or *Picea*/*Fagus* (negative values) ratios (values shown in Fig. 2b).

		H < 50 cm	DBH < 1 cm	DBH < 3 cm	DBH < 10 cm
Overall		4.307	4.143	20.516	51.036
Soil	Leptosols	186.488	8.765	205.075	∞
	Albic	21.059	∞	303.563	∞
	Entic	13.822	19.118	71.452	257.714
	Cambisols	30.718	152.398	48.653	74.725
	Stagnosols	−5.538	−1.694	8.097	∞
	Gleysols	−3.069	−2.608	1.566	5.067
	Histosols	−∞	−∞	−2.333	2.000
Microsite	Stumps	−10.805		−∞	
	DW_1	−5.838	−∞		
	DW_2	−3.639	−∞	−∞	−∞
	DW_3	−1.630	−∞	−∞	−∞
	Intact soil	6.380	7.346	26.633	71.261
	Pits	4.206	36.490	∞	∞
	Mounds	5.391	1.540	23.412	241.342

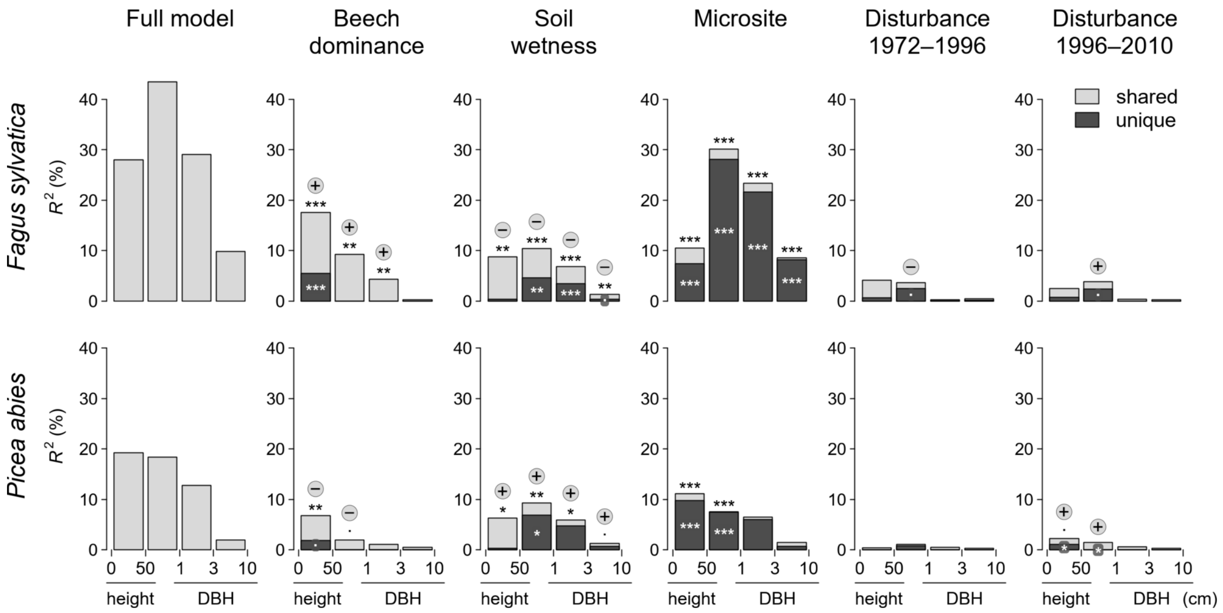


Fig. S4 Variance explained (R^2) in the occurrence of beech and spruce regeneration by different factors on soil microsites only (full version of Fig. 3). The first bar chart in a row shows the total variance explained by all variables and the contributions of individual variables follow. Dark and light parts of bars mark the unique variance explained by each variable, and the explained variance it shares with other variable(s), respectively. Stars inside the dark areas denote statistical significance of the unique effects of variables, while stars above bars mark the significance of total effects of variables (., $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$, ***, $p < 0.001$). For significant continuous variables, the sign of their effect (+/−) is displayed above bars.

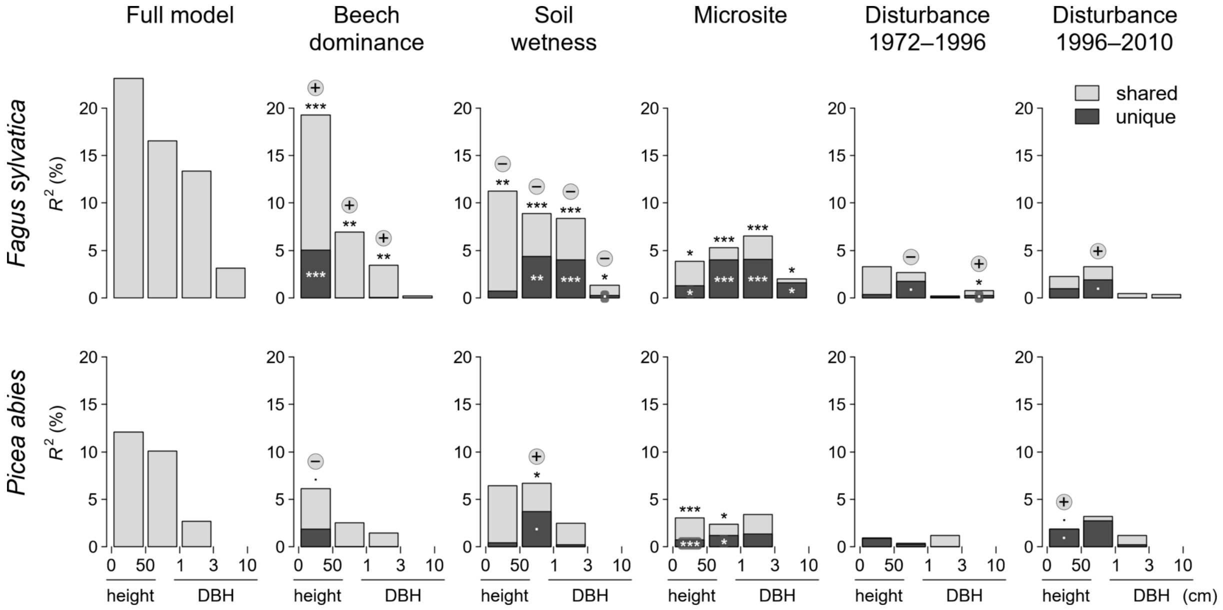


Fig. S5 Variance explained (R^2) in the occurrence of beech and spruce regeneration by different factors on soil microsites only (full version of Fig. 5a). See Fig. S4 for explanations.

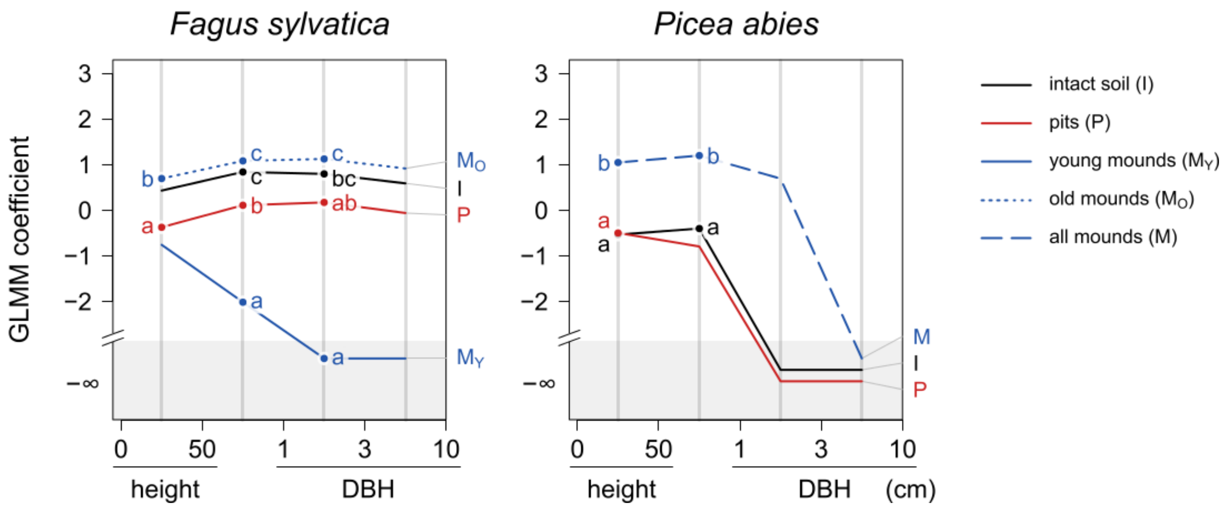


Fig. S6 Relative effects of soil microsites on the occurrence of beech and spruce regeneration. Plotted values are microsite-specific coefficients from the fitted GLMMs centered around zero, i.e. higher values mean higher probabilities of occurrence. Lowercase letters indicate significant differences between microsites within regeneration classes. When two microsites share a letter, their effects do not differ significantly. No letter is displayed for microsites that are not significantly different from any other.

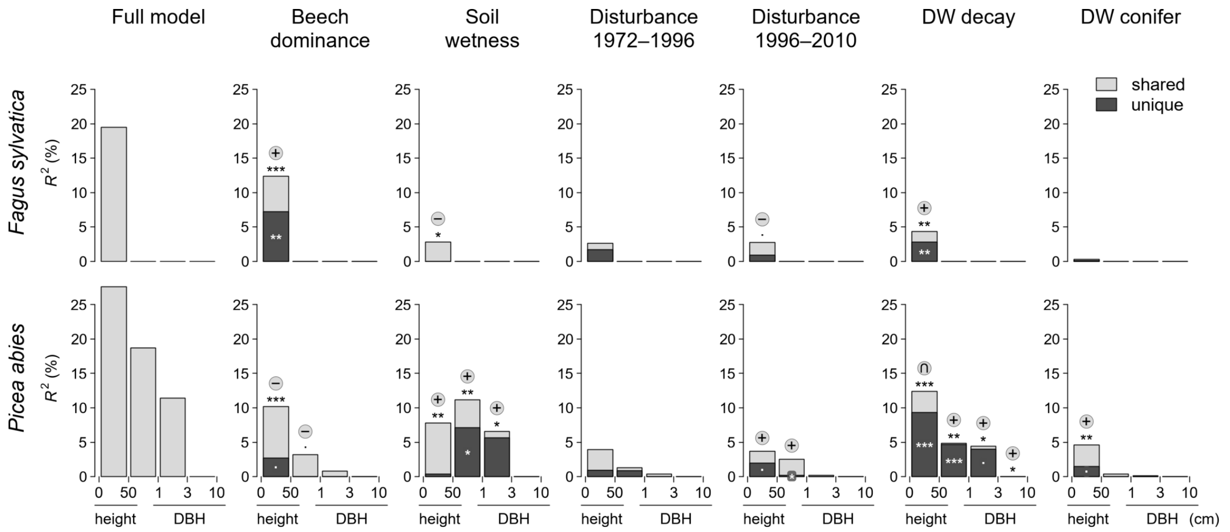


Fig. S7 Variance explained (R^2) in the occurrence of beech and spruce regeneration by different factors on deadwood only (full version of Fig. 5b). See Fig. S4 for explanations. The ∩ symbol above a bar marks a concave quadratic (unimodal) relationship.

Curriculum vitae

Personal details

Pavel Daněk, born 17 May 1985, Zlín, Czech Republic

Education

2013–present	PhD student of *Botany* (Faculty of Science, Masaryk University)
2008–2013	MSc in *Ecological and Evolutionary Biology* (Faculty of Science, Masaryk University)
2004–2011	MSc in *Applied Informatics* (Faculty of Informatics, Masaryk University)

Employment

2013–present	Department of Forest Ecology, The Silva Tarouca Research Institute; researcher

Publications

Articles in international peer-reviewed journals

Šamonil P., Vašíčková I., **Daněk P.**, Janík D., Adam D. 2014. Disturbances can control fine-scale pedodiversity in old-growth forests: is the soil evolution theory disturbed as well? *Biogeosciences* 11: 5889–5905.

Šamonil P., **Daněk P.**, Schaetzl R.J., Vašíčková I., Valtera M. 2015. Soil mixing and genesis as affected by tree uprooting in three temperate forests. *European Journal of Soil Science* 66: 589–603.

Vašíčková I., Šamonil P., Fuentes Ubilla A.E., Král K., **Daněk P.**, Adam D. 2016. The true response of *Fagus sylvatica* L. to disturbances: A basis for the empirical inference of release criteria for temperate forests. *Forest Ecology and Management* 374: 174–185.

Šamonil P., Valtera M., Schaetzl R.J., Adam D., Vašíčková I., **Daněk P.**, Janík D., Tejnecký V. 2016. Impacts of old, comparatively stable, treethrow microtopography on soils and forest dynamics in the northern hardwoods of Michigan, USA. *Catena* 140: 55–65.

Daněk P., Šamonil P., Phillips J.D. 2016. Geomorphic controls of soil spatial complexity in a primeval mountain forest in the Czech Republic. *Geomorphology* 273: 280–291.

Phillips J.D., Šamonil P., Pawlik Ł., Trochta J., **Daněk P.**2017. Domination of hillslope denudation by tree uprooting in an old-growth forest. *Geomorphology* 276: 27–36.

Šamonil P., **Daněk P.**, Adam D., Phillips J.D. 2017. Breakage or uprooting: How tree death type affects hillslope processes in old-growth temperate forests. *Geomorphology* 299: 76–84.

Šamonil P., Moravcová A., Pokorný P., Žáčková P., Kašpar J., Vašíčková I., **Daněk P.**, Novák J., Hájková P., Adam D., Leuschnerg H.H. 2018. The disturbance regime of an Early

Holocene swamp forest in the Czech Republic, as revealed by dendroecological, pollen and macrofossil data. *Palaeogeography, Palaeoclimatology, Palaeoecology* 507: 81–96.

Král K., **Daněk P.**, Janík D., Krůček M., Vrška T. 2018. How cyclical and predictable are Central European temperate forest dynamics in terms of development phases? *Journal of Vegetation Science* 29: 84–97.

Šamonil P., **Daněk P.**, Schaetzl R.J., Tejnecký V., Drábek O. 2018. Converse pathways of soil evolution caused by tree uprooting: A synthesis from three regions with varying soil formation processes. *Catena* 161: 122–136.

Šamonil P., **Daněk P.**, Senecká A., Adam D., Phillips J.D. 2018. Biomechanical effects of trees in an old-growth temperate forest. *Earth Surface Processes and Landforms* 43: 1063–1072.

Roleček J., Hájek M., Dřevojan P., Prokešová H., Fajmon K., Těšitel J., **Daněk P.**, Hájková P., Jongepierová I., Novák P., Poluyanov A.V., Shumska N.V., Chorney I.I. 2019. Gradients, species richness and biogeographical links of steppe grasslands in Western Podolia (Ukraine). *Phytocoenologia* 49: 349–367.

Pawlik Ł., Šamonil P., Malik I., Kroh P., Ślęzak A., **Daněk P.**2019. Geomorphic edge effects in response to abiotic and anthropogenic disturbances in forest ecosystems of the Gorce Mountains, Western Carpathians. *Catena* 177: 134–148.

Daněk P., Šamonil P., Vrška T. 2019. Four decades of the coexistence of beech and spruce in a Central European old-growth forest. Which succeeds on what soils and why? *Plant and Soil* 437: 257–272.

Vašíčková I., Šamonil P., Král K., Ubilla A.E.F., **Daněk P.**, Adam D. 2019. Driving factors of the growth response of *Fagus sylvatica* L. to disturbances: A comprehensive study from Central-European old-growth forests. *Forest Ecology and Management* 444: 96–106.

Kašpar J., Šamonil P., Vašíčková I., Adam D., **Daněk P.**2020. Woody species-specific disturbance regimes and strategies in mixed mountain temperate forests in the Sumava Mts., Czech Republic. *European Journal Of Forest Research* 139: 97–109.

Šamonil P., Phillips J., **Daněk P.**, Beneš V., Pawlik L. 2020. Soil, regolith, and weathered rock: Theoretical concepts and evolution in old-growth temperate forests, Central Europe. *Geoderma* 368: 1–15.

Šamonil P., Egli M., Steinert T., Norton K.P., Abiven S., **Daněk P.**, Hort L., Brandova D., Christl M., Tikhomirov D. 2020. Soil denudation rates in an old-growth mountain temperate forest driven by tree uprooting dynamics, Central Europe. *Land Degradation and Development* 31; 222–239.

Kašpar J., Šamonil P., Krůček M., **Daněk P.**2020. Changes in the radial growth of trees in relation to biogeomorphic processes in an old-growth forest on flysch, Czechia. *Earth Surface Processes and Landforms* 45: 2761–2772.

Šamonil P., **Daněk P.**, Baldrian P., Tláskal V., Tejnecký V., Drábek O. 2020. Convergence, divergence or chaos? Consequences of tree trunk decay for pedogenesis and the soil microbiome in a temperate natural forest. *Geoderma* 376: 1–16.

Daněk P., Šamonil P., Hort L. Canopy trees drive regeneration of a spruce-beech forest through forest floor alteration. Submitted to *Forest Ecology and Management*.

Book chapter

Chytrý M., Danihelka J., Michalcová D., Chytrá M., **Daněk P.**, Grulich V., Hédl R., Jongepier J.W., Jongepierová I., Kočí M., Novák P., Peterka T., Roleček J., Šumberová K., Tichý L. 2015. *Botanical Excursions in Moravia*. Masaryk University, Brno.

Conference presentations

Daněk P. *Tree–soil interactions in natural temperate forests*. Sixth meeting of PhD students in plant ecology and botany, 10–12 October 2014, Karpacz, Poland. (oral presentation)

Daněk P., Šamonil P., Adam. D., Phillips J.D. *Komplexita půd lesů s převahou* Fagus sylvatica. [Soil complexity in forests with *Fagus sylvatica* predominance]. Aktuality šumavského výzkumu, 9.–10. 9. 2015, Ludwigsthal, Germany. (oral presentation)

Daněk P., Šamonil P., Adam D., Phillips J.D. *Zdroje diverzity a prostorové komplexity půd Boubínského pralesa*. [Sources of diversity and spatial complexity of soils of the Boubín Primeval Forest]. Pedologické dni 2016, 7.–9. 9. 2016, Dudince, Slovakia. (oral presentation)

Daněk P. Šamonil P., Vrška T. *Four decades of beech-spruce interactions in a Central European old-growth mountain forest. Who succeeds on which soils and how?*. IAVS 61st Annual Symposium, 22.–27. 7. 2018, Bozeman, Montana, USA. (poster)

Participation in research projects

2013	*The effect of disturbance regime on soil variability and soil formation on a coarse spatial scale in a primeval temperate forest*. Czech Science Foundation GACR P504/11/2135, PI: Pavel Šamonil
2013–2015	*Role of disturbance in soil formation and soil variability in temperate forests: synthesis through soil-formation-processes, spatial and time scales*. American Science Information Center and the Czech Ministry of Education, Youth and Sports AMVIS LH 12039, PI: Pavel Šamonil
2016–2018	*Ecosystem engineering and soil complexity in old-growth temperate forests*. Czech Science Foundation 16-15319S GACR, PI: Pavel Šamonil
2016–2018	*Comprehensive analysis of the biological value of natural forests in the Protected Landscape Area Sumava under administration of the Forests of the Czech Republic, and the proposal of multifunctional management*. Grant Service of the Forests of the Czech Republic, state enterprise, PI: Pavel Šamonil
2019–2021	*The mystery of biogenic soil creep: the biogeomorphic role of trees in temperate and tropical forests and its ecological consequences*. Czech Science Foundation 19-09427S, PI Pavel Šamonil
2020–2022	*Biodiversity, disturbance history and soil memory: testing the Holocene continuity of species-rich forest-steppe ecosystems*. Czech Science Foundation 20-09895S, PI: Jan Roleček
2018–2020	*Role of strong disturbances in Boubínský Primeval Forest: Impact of Herwart Storm in forest stands formed by storms in 1870 and 2008 – phase I*. Šumava National Park Administration – contract research, PI: Pavel Šamonil

2020–2021	*Role of strong disturbances in Boubínský Primeval Forest: Impact of Herwart Storm in forest stands formed by storms in 1870 and 2008 – phase II*. Šumava National Park Administration – contract research, PI: Pavel Šamonil