

How cyclical and predictable are Central European temperate forest dynamics in terms of development phases?

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Abstract

Questions: Recently there have been vital discussions about the validity of the European patch-mosaic conceptual model of forest dynamics – the traditional concept of a shifting patch-mosaic of development stages and phases, also known as the forest cycle concept. Here we try to answer the fundamental questions of this debate: (1) how much do forest dynamics proceed along a predictable path (in a chronological sequence: growth–optimum–breakdown); or (2) vice versa, are the patches rather a result of disturbances and/or other stochastic growth and mortality patterns?

Location: Five long-term research plots in four different study sites of Central European natural temperate forests.

Methods: The long-term evolution of forest development phases was analysed with a GIS-based, spatially explicit, fully reproducible method enabling accurate verification of the functionality of the model forest cycle. We analysed long-term transitions among forest development phases from the 1970s through the 1990s to 2000s. Observed phase-to-phase transitions were compared to a random transition model. We identified preferential pathways within the forest cycle model as well as the proportion of cyclic/acyclic transitions.

Results: In total, across all sites and observation periods, about 65% of all observed phase-to-phase transitions were realized through preferential pathways, about 28% of observed transitions went along pathways of random frequency and only about 7% of observed transitions were realized through uncommon development pathways. On the other hand, less than 40% of all observed transitions might be classified as cyclic (following the model cycle), and thus more than 60% of the transitions were acyclic (moving across or backward in the model cycle). The overall pattern of all observed transitions resembled a complex web rather than a simple repeating cycle.

Conclusions: Although in all sites we documented signs of the cyclic and predictable development anticipated by the forest cycle concept, the predominance and stochastic nature of multiple acyclic development pathways gave rise to reasonable doubts on the legitimacy and usability of the concept for descriptions of forest dynamics. On the other hand, the verification of the concept may contribute significantly to our understanding of the complexity of forest dynamics.

KEYWORDS

development stages, forest cycle, forest dynamics, long-term observations, model verification, patch dynamics, permanent research plots, transitions, tree census

1 | INTRODUCTION

Recently there has been a vital scientific debate about the validity of the European conceptual model of forest dynamics – the traditional concept of a sequentially shifting mosaic of patches in different phases of forest development (Korpel, 1982, 1995; Leibundgut, 1959, 1982; Mayer & Neumann, 1981; Mayer, Zukrigl, Schrempf, & Schlager, 1989; Zukrigl, Eckhardt, & Nather, 1963), also known as the forest cycle concept (e.g. Christensen & Emborg, 1996; Emborg, Christensen, & Heilmann-Clausen, 2000; Huber, 2011b). The temporal sequence of phases is assumed to go through a development cycle from regeneration and growth, through maturity and senescence, to breakdown and back to regeneration. The patch mosaics of forest development phases have been widely used for various applications (e.g. Bobiec et al., 2000; Boncina, 2000; Winter & Brambach, 2011) and the concept itself is still the subject of research and development (e.g. Begehold, Rzanny, & Winter, 2016; Huber, 2011a,b; Podlaski, 2006, 2008; Winter & Brambach, 2011; Zenner, Peck, Hobi, & Commarmot, 2016). On the other hand, the forest cycle concept has been criticized as being too simplistic (Christensen, Emborg, & Nielsen, 2007; Gratzner et al., 2004) and has been questioned several times using quantitative spatial analyses, abortively looking for non-random ‘patchy’ arrangements of growth and mortality processes (Szwagrzyk & Szweczyk, 2001), or by finding close-to-random stand characteristics on the finest spatial scales in natural spruce–fir–beech forests (Paluch, 2007; Paluch, Kolodziej, Pach, & Jastrzebski, 2015). The latter arguments were rebutted by our previous work (Král, Valtera, Janík, Šamonil, & Vrška, 2014), finding a patch pattern of basic stand characteristics in natural beech-dominated forests through multi-scale spatial analyses: what appeared to be random at the fine scale of individual trees was revealed as a periodic patchy pattern at larger scales (patches usually 400–1100 m² in size). This is a well-known natural phenomenon described e.g. by Levin (1992): by enlarging the scale of sampling we move from unpredictable, unrepeatably individual cases to a collection of cases whose behaviour is non-random enough to reveal significant pattern.

However, as aptly pointed out by Paluch (2007), to date, little attention has been paid to the fundamental difference between ‘patchiness’ as a general forest pattern feature resulting from the spatial and temporal correlation of ecological processes, and the ‘accidental occurrence of less or more homogenous patches’, which may be the effect of quite random natural phenomena. In other words, the fundamental question is: is there spatio-temporal coherence in the development of forest development phases assumed by the patch-mosaic cycle concept? Probably the best way to truly prove or disprove the concept and validity of the patch-mosaic cycle is to perform rigorous multi-temporal analyses and examine the behaviour of the system through phase-to-phase transitions observed in the long term. As a first such attempt may be considered the work of Christensen et al. (2007), who repeated the mapping of forest development phases in Suserup Skov (Emborg et al., 2000) and quantified transitions from phase-to-phase over 10 years. The results were rather surprising, as nearly half of the stand changed the phase during the period and important

deviations from the basic forest cycle appeared: some phases were almost skipped and regressive phase shifts were unexceptional. Such findings might largely be explained by the guestimate field mapping of development phases with limited reproducibility, as well as by the simplified approach of phase definitions (all phases were defined only by the uppermost canopy layer of the patch).

Obviously, a necessary condition for a rigorous multi-temporal comparison of forest development stages is their objective and reproducible distinction and delineation. For that purpose we used spatially explicit rule-based classification, which transforms historical and recent stem position data sets into maps of forest development stages and phases (Král et al., 2016). This method is based on previous works on objectified mapping of forest development stages and phases (Král, McMahon, Janík, Adam, & Vrška, 2014; Král et al., 2010) and ensures that the same stand structures (observed through the local presence of living and dead trees of given breast height diameter (DBH)) will always be classified and delineated in the same way.

The overall aim of our study was thus straightforward: to validate the forest cycle concept by a rigorous examination of spatio-temporal development patterns observed over more than three decades. The two following hypotheses were tested, both of which should be confirmed to validate (authenticate) the patch-mosaic cycle concept: (1) forest dynamics proceed along non-random, predictable paths; and (2) phase-to-phase transitions are predominantly sequential along the model sequence of forest development phases. Both hypotheses were tested at five extensive permanent research plots, representing four different Central European temperate forest types distributed along an altitudinal vegetation gradient.

2 | METHODS

2.1 | Data sets

A multi-temporal comparison of forest development stages and phases was performed on five permanent research plots located in four study sites dispersed along altitudinal and related climate and vegetation gradients ranging from 150 to 1110 m a.s.l. The sites represent four Central European forest types, Pannonian alluvial hardwood forests (Cahnov and Raňšpurk plots), Carpathian fir–beech forests (Salajka plot), Hercynian sub-montane beech-dominated forests (Žofín plot) and mixed mountain beech–spruce forests (Boubín plot). All research plots are located in strict forest reserves left to spontaneous development in the long term; their main characteristics are listed in Table 1, for extended description of research sites see Appendix S1. At all plots (in total covering almost 180 ha) detailed tree censuses including stem mapping were carried out in the 1970s, 1990s and 2000s (Vrška, Hort, Odehnalová, Adam, & Horal, 2001; Vrška et al., 2006, 2012). In the 1970s and 1990s the stem positions were measured with a tripod-based theodolite. In the 2000s the Field-Map technology (<http://www.fieldmap.cz>) was employed. The censuses included all standing and downed trees with a minimum DBH of 10 cm. For the purposes of this paper, we used data sets that contain tree position coordinates (X, Y), species, DBH, basal area (BA) and tree status (live/dead). For lying

TABLE 1 Characteristics of research plots and stem position data sets

| Research plot | GPS northing [φ] | GPS easting [λ] | Census area [ha] | Elevation range [m a.s.l.] | Mean annual temp ^a [°C] | Mean annual prec. totals ^a [mm] | Years of census | Number of living woody stems ^b | Prevailing soil types | Primary species ^c | References to plots and datasets |
|---------------|------------------|-----------------|------------------|----------------------------|------------------------------------|--|----------------------|---|---------------------------------------|--|---|
| Cahnov | 48°39′ | 16°56′ | 17.3 | 150–153 | 9.9 | 545 | 1973 1994 2006 | 3,718 | Endogleyic and Epigleyic Fluvisols | <i>Fraxinus angustifolia</i> <i>Acer campestre</i> <i>Carpinus betulus</i> | Vrška et al. (2006) Janík et al. (2008) Janík et al. (2011) |
| Ranšpurk | 48°40′ | 16°56′ | 22.3 | 152–155 | 9.9 | 545 | 1973 1994 2006 | 6,250 | Endogleyic and Epigleyic Fluvisols | <i>Carpinus betulus</i> <i>Acer campestre</i> <i>Fraxinus angustifolia</i> | Vrška et al. (2006) Janík et al. (2008) Janík et al. (2011) |
| Salajka | 49°24′ | 18°25′ | 19.0 | 710–820 | 6.2 | 1142 | 1974 1994 2007 | 8,782 | Haplic Cambisols | <i>Fagus sylvatica</i> <i>Abies alba</i> <i>Picea abies</i> | Vrška, (1998) Janík et al. (2014); Král, McMahon, et al. (2014) |
| Žofín | 48°40′ | 14°42′ | 70.6 | 735–830 | 6.2 | 866 | 1975 1997 2008 | 15,221 | Entic Podzols Haplic Cambisols | <i>Fagus sylvatica</i> <i>Picea abies</i> <i>Abies alba</i> | Trochta, Král, Janík, & Adam, (2013) Král, Valtera, et al. (2014) |
| Boubín | 48°58′ | 13°48′ | 46.6 | 925–1110 | 4.9 | 1067 | 1972 1996 2010 | 9,798 | Entic Podzols GleysolsCambisols | <i>Picea abies</i> <i>Fagus sylvatica</i> <i>Abies alba</i> | Šebková et al. (2011) Vrška et al. (2012) |

^aSite specific interpolation of Czech Hydrometeorological Institute based on 1981–2010 data.

^bLiving woody stems of DBH ≥ 10 cm in the last census.

^cThe most frequent woody stems of DBH ≥ 10 cm.

deadwood, only distinguishable stems were recorded; woody debris of tree branches was neglected (analogous to living trees, where only stem positions are recorded).

2.2 | Rule-based spatially explicit classification of development phases

The classification used here employs the stem position maps of living and dead trees of $DBH \geq 10$ cm as input data, and therefore can be applied to corresponding data sets. The stem maps were spatially filtered by the moving widow approach in GIS. Through this focal filtering, the local tree counts and basal areas of both live and dead trees in different DBH classes were calculated separately for every square meter in the stand and its circular surroundings (diameter of the calculation window was 21 m; shifting step 1 m). This information was consequently classified with a rule-based classification; the complete method is available as a ready-to-use ArcGIS Toolbox published as the Supplementary Material of Král et al. (2016). The DBH bins used in different forest types were defined and justified in Král, McMahon, et al. (2014). In accordance with Král et al. (2016) this classification distinguishes ten development phases described in the following section and portrayed by respective local DBH distributions characteristic for individual development phases (Appendix S2).

2.3 | Characterization of forest development phases

Individual forest development phases may be defined as follows (see also Appendix S2): 'Treeless areas' are distinguished on patches where no trees (either live or dead) are present, usually because of extreme edaphic conditions (e.g. standing surface water or bare rock). 'Live tree gaps' characterize places where only dead trees occur (e.g. after severe disturbance but prior to subsequent regeneration). The 'Growth initial' phase is characterized by the local predominance of recruits and juvenile trees in terms of stem numbers and also basal areas. The DBH distribution of living trees is thus characterized by a reverse J-shaped curve. The presence of dead trees (either thin – an indication of stem exclusion, or thick – a mark of previous breakdown) is quite common; however, it is not a determinant feature. The 'Growth advanced' phase has a similar pattern, but the tree size distribution is shifted to larger DBHs, which means that the distribution of basal area (BA) starts to follow a bell-shaped pattern in the range from small to mid-sized trees. The phase of 'Optimum typical' is characterized by the bell-shaped DBH distribution of living trees (both in terms of counts and the BA of trees), sub-canopy regeneration is typically missing; although in the 'Optimum ageing' phase numerous recruits (small understorey trees) may occur. In both cases, mid-sized and thick trees strongly predominate in the BA of living trees. Similarly, thick dead trees are missing in Optimum typical, but in Optimum ageing a limited amount of the BA of mature dead trees may be present. When the local BA of mature dead trees exceeds half of the BA of mature living trees, the patch is classified as 'Breakdown initial' (without the presence of living recruits/juveniles) or 'Breakdown/regeneration' (with the

presence of natural regeneration). If the BA of juvenile/thin trees exceeds the BA of remaining thick trees, the patch is classified as the 'Growth/expiration' phase. Last, but not least, the 'Steady State' phase is defined by the coinciding presence of trees of various sizes; smaller trees are more frequent, but the BA of mature trees predominates. The basal area of mature dead trees is limited to half of the BA of living trees. Exact complex decision rules defining all development phases are explicated in the ArcGIS Toolbox published as electronic Supplementary Material in Král et al. (2016).

2.4 | Empirical classification of transitions

All phase-to-phase transitions were quantified between the 1970s and 1990s, 1990s and 2000s and 1970s and 2000s. The nature of the transition was arbitrarily classified into one of the following descriptive categories: Stable – the development phase remained unchanged between censuses; Progressive – the phase was shifted forward in the cycle; Regressive – the phase was shifted backward in the cycle; Disturbance – a shortcut to early development phases likely caused by a disturbance; No trend – development with no clear direction along the forest cycle; Unlikely – unlikely development (a possible misclassification of the phase in either of the observations).

Because some transitions could in theory be classified in more than one of the descriptive categories (e.g. in both Disturbance and Regressive), they were consequently regrouped into mutually exclusive summary categories evaluating the nature of transitions from the dichotomous viewpoint of cyclic/acyclic development essential for testing the validity of the model forest cycle: the Stable category was further marked as No transition, the Progressive as Cyclic transition and all other categories were merged into Acyclic transition (for more see Appendix S3).

2.5 | Quantitative evaluation of transitions

The statistical significance of the observed frequencies of transitions between phases, i.e. whether they were lower or higher than could be expected by chance, was assessed using bootstrapping. From 10,000 bootstrap samples we derived null distributions for all transition frequencies under the assumption that a transition to any phase is equally likely. To tackle the spatial autocorrelation present in the 1-m resolution classification of development phases, for each research plot we used a bootstrap sample size equal to the number of non-overlapping moving windows (see the section Rule-based classification) necessary to cover the whole area of the plot. The null distributions were then used to compute two-sided *p*-values for the observed transition frequencies. The significance level was set at 0.05 and to avoid alpha inflation associated with multiple testing we used a sequential Bonferroni-type procedure (Benjamini & Hochberg, 1995), which controls for a false discovery rate.

For interpretation and visualization of relative sources and sinks of phase-to-phase transitions the transitions were standardized by scaling either all sources and/or all targets of one phase to sum up to one. The standardized transitions then give the relative importance of



particular pathways relative to the source and/or the target development phase (see Appendix S3).

3 | RESULTS

3.1 | General behaviour of the system

Although development on individual sites was largely specific, there was a considerable consistency in the overall pattern of observed transitions. In the period from the 1990s to 2000s (i.e. in ca 12 years) usually almost half of the area ($47 \pm 1.5\%$; mean \pm SEM) remained in the same development phase. From the 1970s to 1990s (i.e. in a ca 22-year period) it was usually about one third ($32 \pm 2.5\%$) of the forest, and from the 1970s to 2000s (i.e. in ca 34 years) only about one fifth ($21 \pm 0.8\%$) of the forest remained in the same phase. The rest of the stand passed from one phase into another (Table 2). In total (across all plots and observation periods) only about $39 \pm 2.8\%$ of these realized transitions (i.e. omitting No transition) might be classified as cyclic (along the model cycle), and thus more than $61 \pm 2.8\%$ of these transitions were acyclic (moving across or backward in the model cycle). While the proportion of the stand remaining in a phase naturally decreases with the length of the observation period, the mean ratio of cyclic/acyclic transitions (2:3) was more or less stable throughout time. However, there were some differences among individual plots, e.g. while for Salajka the proportion of cyclic/acyclic transitions was consistently about 1:1, for Boubín it was rather 1:3 (Table 2).

A different way to evaluate phase-to-phase development is according to their observed frequency compared to a completely random development (Table 3). In total about $65 \pm 2.3\%$ of all observed phase-to-phase transitions (including cases when the phase remained unchanged) proceeded along pathways that were

significantly more frequent than random switches between phases (hereafter also called 'preferential pathways' of forest development). About $28 \pm 3.1\%$ of observed transitions proceeded along pathways of random frequency, and only about $7 \pm 1.3\%$ of observed transitions were realized through pathways significantly less frequent than random switches between phases (hereafter also called 'uncommon pathways' of forest development). These proportions were similar across different observation periods; the proportion of significantly more and less frequent transitions only slightly decreased with the length of the observation period, while the percentage of randomly frequent transitions slightly increased (Table 3). These values confirm the existence of a significant non-random component in the forest dynamics.

A more complex evaluation of phase-to-phase transitions and the functionality of the conceptual model of forest cycle in general are provided through a combination of the two approaches used above (Table 4). We can see that even if only a minority of the forest remained in the development phase during the observation period (on average 47%, 32% and 21% in ca 12, 22 and 34 years, respectively; Table 2), this was essentially non-random behaviour, because from 90% to 100% of this 'stable' development (depending on the length of the observation period) was realized through the preferential pathways (Table 4). In contrast, practically none of this kind of forest development was classified as an uncommon pathway. The persistence of development phases in time is thus clearly predictable, spatio-temporally autocorrelated behaviour of the forest, providing evidence for some of the assumptions of the forest cycle concept.

Analogously, although on average less than 40% of transitions between different development phases were classified as cyclic (following the model cycle), the majority of these transitions were realized through significantly frequent preferential pathways. The mean

| Research plots: | Boubín | Žofín | Salajka | Cahnov - Ranšpurk | Mean | SEM |
|-------------------------|--------|-------|---------|-------------------|------|-----|
| 1990s–2000s | | | | | | |
| Period (years) | 14 | 11 | 13 | 12 | 12.5 | 0.6 |
| No transitions (%) | 46.6 | 45.0 | 46.0 | 51.7 | 47.4 | 1.5 |
| Cyclic transitions (%) | 14.7 | 22.0 | 27.4 | 15.7 | 20.0 | 3.0 |
| Acyclic transitions (%) | 38.6 | 33.0 | 26.5 | 32.5 | 32.7 | 2.5 |
| 1970s–1990s | | | | | | |
| Period (years) | 24 | 22 | 20 | 21 | 21.8 | 0.9 |
| No transitions (%) | 30.0 | 37.4 | 26.2 | 34.2 | 31.9 | 2.5 |
| Cyclic transitions (%) | 16.7 | 23.4 | 37.0 | 27.8 | 26.2 | 4.3 |
| Acyclic transitions (%) | 53.4 | 39.2 | 36.8 | 38.0 | 41.8 | 3.9 |
| 1970s–2000 | | | | | | |
| Period (years) | 38 | 33 | 33 | 33 | 34.3 | 1.3 |
| No transitions (%) | 19.2 | 22.5 | 20.5 | 22.2 | 21.1 | 0.8 |
| Cyclic transitions (%) | 20.1 | 31.0 | 40.8 | 34.8 | 31.7 | 4.4 |
| Acyclic transitions (%) | 60.8 | 46.4 | 38.6 | 43.0 | 47.2 | 4.8 |

TABLE 2 The proportion of the three major transition categories in all observations; SEM, standard error of the mean

TABLE 3 The proportion of transitions following preferential, randomly frequent and uncommon pathways defined by the comparison of observed transitions with bootstrapped random development (significance $\alpha = 0.05$); SEM, standard error of the mean

| Research plots | Boubín | Žofín | Salajka | Cahnov - Ranšpurk | Mean | SEM |
|--------------------------------|--------|-------|---------|-------------------|------|-----|
| 90s–00s | | | | | | |
| Period (years) | 14 | 11 | 13 | 12 | 12.5 | 0.6 |
| Preferential pathways (%) | 70.4 | 66.1 | 70.2 | 63.0 | 67.4 | 1.8 |
| Randomly frequent pathways (%) | 21.1 | 18.8 | 27.8 | 29.5 | 24.3 | 2.6 |
| Uncommon pathways (%) | 8.5 | 15.1 | 2.0 | 7.5 | 8.3 | 2.7 |
| 1970s–1990s | | | | | | |
| Period (years) | 24 | 22 | 20 | 21 | 21.8 | 0.9 |
| Preferential pathways (%) | 76.5 | 75.1 | 49.6 | 57.6 | 64.7 | 6.6 |
| Randomly frequent pathways (%) | 13.5 | 12.5 | 48.4 | 37.7 | 28.0 | 9.0 |
| Uncommon pathways (%) | 10.0 | 12.4 | 2.0 | 4.6 | 7.2 | 2.4 |
| 1970s–2000s | | | | | | |
| Period (years) | 38 | 33 | 33 | 33 | 34.3 | 1.3 |
| Preferential pathways (%) | 69.7 | 61.8 | 60.9 | 59.7 | 63.0 | 2.3 |
| Randomly frequent pathways (%) | 23.0 | 28.3 | 38.3 | 35.5 | 31.3 | 3.5 |
| Uncommon pathways (%) | 7.3 | 9.8 | 0.9 | 4.8 | 5.7 | 1.9 |

proportion of 'preferential' cyclic transitions increased with the length of the observation period, from $63 \pm 3.5\%$ in 22 years to $68 \pm 2.6\%$ in 34 years, as the proportion of the stand retaining the phase decreased. In addition, only about 7% to 8% of these transitions were realized through uncommon pathways; the rest proceeded along pathways of random frequency (Table 4). The cyclic transitions thus usually represented a predictable component of forest dynamics, consistent with the conceptual model of the forest cycle.

Rather the opposite was true of acyclic transitions. Although on average they formed more than 60% of realized transitions, the frequency of individual acyclic transitions was largely not significantly different from random switches between phases (on average from $53 \pm 9.0\%$ in a 12-year period to $46 \pm 8.0\%$ in a 34-year period). The proportion of acyclic transitions of preferential pathways was generally lower but still significant, and gradually increased with the length of the observation period (from $27 \pm 5.8\%$ in 12 years to $46 \pm 7.7\%$ in 34 years). The proportion of acyclic transitions that followed uncommon pathways was also not inconsiderable – i.e. about $21 \pm 7.0\%$ in 12 years and $13 \pm 4.5\%$ in 22 years. The acyclic transitions thus usually represent stochastic and accidental components of forest dynamics; however, many of the acyclic transitions also proceed through preferential pathways.

3.2 | Specific development pathways

The complex patterns of phase-to-phase transitions in all sites and observation periods are illustrated in Figure 1. The importance of individual phase-to-phase transitions relative to their source or target phases is illustrated in standardized versions of these charts (Appendix S4). The development phases – Growth advanced, Optimum ageing, Breakdown/regeneration and Steady

State – proved to be more stable than the others. In both observation periods over 20 years (i.e. from the 1970s to 1990s and from the 1970s to 2000s), only these four phases remained stable as a preferred way of development in all (or at least in three) study sites. Other development phases proved to be much shorter lasting and could be ordered from shorter to longer as follows: Live tree gap, Growth/expiration, Breakdown initial, Optimum typical, Treeless area and Growth initial. As a consequence, the short phases were generally less abundant in all sites and observations (see Appendix S5). It is no accident that all but one of these short phases (except Growth/expiration) are of simple stand structure, where the living trees are either entirely missing (Treeless area, Live tree gap) or form unimodal (either right-skewed or bell-shaped) DBH distributions of tree counts and their BA (see Appendix S2). These 'simple' phases (Optimum typical, Breakdown initial), and especially the early development phases (Live tree gap, Growth initial) were frequently skipped (see Figure 1), because during forest development the living biomass drops to zero only exceptionally, even at local scales. The initial part of the model forest cycle is thus rarely followed, because advanced sub-canopy regeneration or multi-layered stand structures are developed in most of the stands. If the early phases were not bypassed, they mostly originated from phases other than the Breakdown (on average in >75%), indicating that they are the result of unexpected (impulsive) disturbances rather than the gradual breakdown anticipated by the forest cycle.

On the other hand, transitions following the early development phases were cyclical in more than 80% of cases, and transitions from Optimum typical and Breakdown initial were usually cyclical in more than 70% and 60% of cases, respectively. The early and simple structure development phases are thus the forerunners of cyclic development.

TABLE 4 The proportion of preferential, randomly frequent and uncommon pathways within the three major transition categories: No transition, Cyclic transitions, Acyclic transitions; SEM, standard error of the mean

| Research plots: | Boubín | Žofín | Salajka | Cahnov - Ranšpurk | Mean | SEM |
|-----------------------|--------|-------|---------|-------------------|------|------|
| 1990s – 2000s | | | | | | |
| Period (years) | 14 | 11 | 13 | 12 | 12.5 | 0.6 |
| No transitions | | | | | | |
| Preferential (%) | 100.0 | 99.4 | 99.8 | 99.6 | 99.7 | 0.1 |
| Randomly frequent (%) | 0.0 | 0.6 | 0.1 | 0.4 | 0.3 | 0.1 |
| Uncommon (%) | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 |
| Cyclic transitions | | | | | | |
| Preferential (%) | 47.5 | 60.1 | 66.8 | 37.7 | 53.0 | 6.5 |
| Randomly frequent (%) | 43.3 | 28.5 | 30.4 | 57.7 | 40.0 | 6.8 |
| Uncommon (%) | 9.2 | 11.4 | 2.8 | 4.6 | 7.0 | 2.0 |
| Acyclic transitions | | | | | | |
| Preferential (%) | 43.4 | 24.4 | 22.3 | 17.0 | 26.8 | 5.8 |
| Randomly frequent (%) | 38.1 | 37.2 | 73.3 | 62.1 | 52.7 | 9.0 |
| Uncommon (%) | 18.5 | 38.3 | 4.4 | 20.9 | 20.5 | 7.0 |
| 1970s–1990s | | | | | | |
| Period (years) | 24 | 22 | 20 | 21 | 21.8 | 0.9 |
| No transitions | | | | | | |
| Preferential (%) | 95.9 | 99.8 | 82.6 | 96.6 | 93.8 | 3.8 |
| Randomly frequent (%) | 4.1 | 0.2 | 17.4 | 3.4 | 6.2 | 3.8 |
| Uncommon (%) | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Cyclic transitions | | | | | | |
| Preferential (%) | 66.8 | 66.0 | 65.1 | 52.2 | 62.5 | 3.5 |
| Randomly frequent (%) | 15.5 | 22.6 | 32.7 | 45.4 | 29.1 | 6.5 |
| Uncommon (%) | 17.7 | 11.5 | 2.2 | 2.4 | 8.4 | 3.8 |
| Acyclic transitions | | | | | | |
| Preferential (%) | 68.6 | 57.0 | 10.5 | 26.5 | 40.7 | 13.4 |
| Randomly frequent (%) | 18.2 | 18.2 | 86.3 | 63.0 | 46.4 | 17.0 |
| Uncommon (%) | 13.2 | 24.7 | 3.2 | 10.5 | 12.9 | 4.5 |
| 1970s–2000s | | | | | | |
| Period (years) | 38 | 33 | 33 | 33 | 34.3 | 1.3 |
| No transitions | | | | | | |
| Preferential (%) | 77.2 | 88.0 | 99.0 | 93.9 | 89.5 | 4.7 |
| Randomly frequent (%) | 21.6 | 12.0 | 1.0 | 6.1 | 10.2 | 4.4 |
| Uncommon (%) | 1.2 | 0.0 | 0.0 | 0.0 | 0.3 | 0.3 |
| Cyclic transitions | | | | | | |
| Preferential (%) | 66.3 | 74.6 | 66.8 | 62.3 | 67.5 | 2.6 |
| Randomly frequent (%) | 18.8 | 15.3 | 32.9 | 36.8 | 26.0 | 5.3 |
| Uncommon (%) | 14.9 | 10.1 | 0.2 | 0.8 | 6.5 | 3.6 |
| Acyclic transitions | | | | | | |
| Preferential (%) | 68.4 | 40.6 | 34.3 | 39.9 | 45.8 | 7.7 |
| Randomly frequent (%) | 24.9 | 45.0 | 63.7 | 49.7 | 45.8 | 8.0 |
| Uncommon (%) | 6.7 | 14.4 | 2.0 | 10.4 | 8.4 | 2.6 |

In contrast, more advanced and multi-layered phases, such as Growth advanced, Optimum ageing, Breakdown/regeneration and Steady State, were not only generally more abundant (see Appendix

S5) and longer lasting, but often served as crossroads where the stand development might be redirected into different pathways (Figure 1). Most of these pathways were preferential, but acyclic; i.e. either

substantial shortcuts within the cycle or pathways going through the Steady State, which is the acyclic phase by definition (Král et al., 2010).

Appendix S5 also shows some differences in the site conditions and disturbance history of the plots. The Kirill windstorm in Jan 2007 gave rise to significant Live tree gaps in the Žofín plot in the 2008 census. Permanent Treeless areas in floodplain forests (Cahnov - Ranšpurk bi-plot) are formed in lagoons of standing surface water. Note also the fact that in most of the plots and thus also in total, the proportion of Breakdown phases substantially increased over more than the 30 years of observations (Appendix S5).

4 | DISCUSSION

Our results clearly demonstrate that the forest cycle concept traditionally used in European forestry research has been generally too simplistic. The mean proportion of cyclic/acyclic development was about 2:3 over the long term. Cyclic transitions, which also usually proceeded along preferential pathways, were thus significantly less frequent than acyclic development. Moreover, some of the cyclic transitions (more than one third) were still realized through pathways classified as random and/or uncommon. And although on average about 65% of phase-to-phase transitions proceeded along preferential pathways, many of these pathways were branched in multiple ways. Such preferential pathways are in effect hardly predictable. The most predictable component of forest patch dynamics thus appeared to be temporal stability of certain phases. As soon as there was some development, its direction (pathway) was largely unpredictable at the local observation scale. Further use of this traditional, intrinsically phenomenological concept for descriptions of forest dynamics is thus clearly limited. The incorporation of truly quantitative concepts and methods in European forest dynamics research, e.g. 'A general quantitative theory of forest structure and dynamics' (Enquist, West, & Brown, 2009; West, Enquist, & Brown, 2009), is thus highly desirable.

4.1 | Specific development patterns

The development pathways of early development phases appeared to be fairly straightforward, because these phases are less susceptible to disturbances, and their growth, thinning and aging is mostly inevitable. However, homogenous patches of smaller trees (i.e. without the simultaneous presence of mature trees) are rather rare in Central European temperate old-growth forests. The long-term predominance of trees established in the understorey compared to gap origin trees found by Šamonil et al. (2013) in the Žofín forest testifies to this. Gap origin trees predominated only rarely during the dendrochronologically analysed disturbance history of the stand (ca 350 years), only following major and rather exceptional disturbance events. In consequence, straightforward initial development pathways were also encountered only rarely. In other words, tree recruitment and the survival of shade-tolerant species in temperate forests are either not directly linked to gap forming processes (Manabe, Shimatani, Kawarasaki, Aikawa, & Yamamoto, 2009), or the canopy gaps are usually very fine-scale, with

mean gap sizes of about 100 m² (Holeksa & Cybulski, 2001; Kenderes, Král, Vrška, & Standovar, 2009; McCarthy, 2001), and thus might be 'dissolved' in the scale of our mapping moving window (ca 346 m²). Substantially larger gaps detectable by our method are much less frequent, given the reverse J-shaped gap size frequency distribution repeatedly documented in European temperate forests (Kathke & Bruelheide, 2010; Kucbel, Jaloviar, Saniga, Vencurik, & Klimas, 2010; Nagel & Svoboda, 2008). Gap forming processes thus might be slightly underestimated in our results.

Advanced development phases with unimodal DBH distribution (Optimum typical and Breakdown initial in our nomenclature) are similarly rare. These phases are quite unstable (see also Lorimer & Halpin, 2014) and usually quickly convert to the next development phase with established sub-canopy trees. On the contrary, advanced multi-layered phases usually form most of the stands and essentially act as splitters among several preferential pathways. This is only logical, since complex stand structures do offer more possibilities for further development. For instance, Optimum ageing with first dying canopy tree and emerging regeneration may either proceed forward in the model cycle to the Breakdown/regeneration by the further dieback of canopy trees, or the residual canopy trees may be released from competition and respond with increased radial and lateral canopy growth. The sub-canopy regeneration is consequently suppressed and withers away, and the phase returns to the Optimum typical. Backward transitions from Breakdown regeneration to Breakdown initial/Optimum ageing or from Optimum ageing to Optimum typical were the most common documented cases of regressive development. Several such back and forth development pulses may follow in sequence – about 6% of observations having the same development phase in the 1970s and 2000s 'bounced' in between into a different phase in the 1990s. Such repetitive development pulses in mature stands were also evidenced with dendrochronology. Multiple releases (up to nine) of canopy trees followed by periods of suppression were frequently found in their life history (Šamonil, Vašíčková, Daněk, Janík, & Adam, 2014), even at DBH large enough to form advanced development phases.

Alternatively, the dieback of canopy trees may be very gradual, with the sub-canopy regeneration steadily proceeding from understorey to mid-storey and the phase moving from Optimum ageing to Steady State (Figure 1). In total, the transitions to and from the Steady State formed about one third of all transitions. This confirms our earlier assumption (Král, McMahon, et al., 2014) that the Steady State phase characterized by complex fine-scale stand structure plays an important role in the dynamics of Central European temperate forests and may persist in stands over the long term. This is in contrast to the traditional view of this phase (Plenter phase in traditional terminology) as a temporary transitional phase of limited duration (Mayer, 1976; Schütz, 2001). This 'all in one' phase more closely follows the recent perception of forest dynamics that shifts from the dynamics of discrete patches to interactions among individual trees – so-called 'neighbourhood dynamics' (Gratzer et al., 2004). Also, the latest results of Drössler et al. (2016) indicate that neighbouring trees of different sizes dominate the heterogeneous stand structure of European natural forests, and even an initially homogenous large single cohort of small



trees can in the course of forest development be divided into different tree groups, with formerly distinct patchiness thus gradually subsiding in the long term. A similar development pattern was found by Heiri, Wolf, Rohrer, and Bugmann (2009), who documented a long-term broadening of local diameter distributions of shade-tolerant tree species, which means that the trees increased radial increment and regenerated continuously (i.e. exhibited a pattern conforming to the Steady State). Of course, the partial incompatibility of research methods, terminology and observation scales used by different authors should be taken into account. Yet, even considering all such differences, the main message of more recent studies is noticeably similar.

4.2 | The effect of disturbance regime

Specific development patterns are inevitably linked to the respective disturbance regime. The occurrence of larger-scale stand-replacing disturbances unavoidably increases the formation of initial development phases (documented on the Žofín plot after the Kyrill windstorm in 2007; see Appendix S5). Similarly, disturbances of intermediate severity and/or a synergy of frequent fine-scale disturbances likely promote the formation of Breakdown, while less frequent fine-scale disturbances rather allow the formation of the Steady State. This might be one explanation for the fact that the complex patterns of phase-to-phase transitions are rather similar across the three (sub-)montane plots that are exposed to occasional strong winds, and where multiple preferential pathways to Breakdown/regeneration phase are common (Figure 1a–c). On the contrary, the pattern of transitions in alluvial lowland plots (Cahnov-Ranšpurk), where average annual and seasonal wind speeds are generally lower and severe winds are rather rare (Tolasz, Míková, Valeriánová, & Voženilek, 2007) is clearly different, almost lacking preferential pathways to Breakdown while pathways going to the Steady State are very significant (Figure 1d).

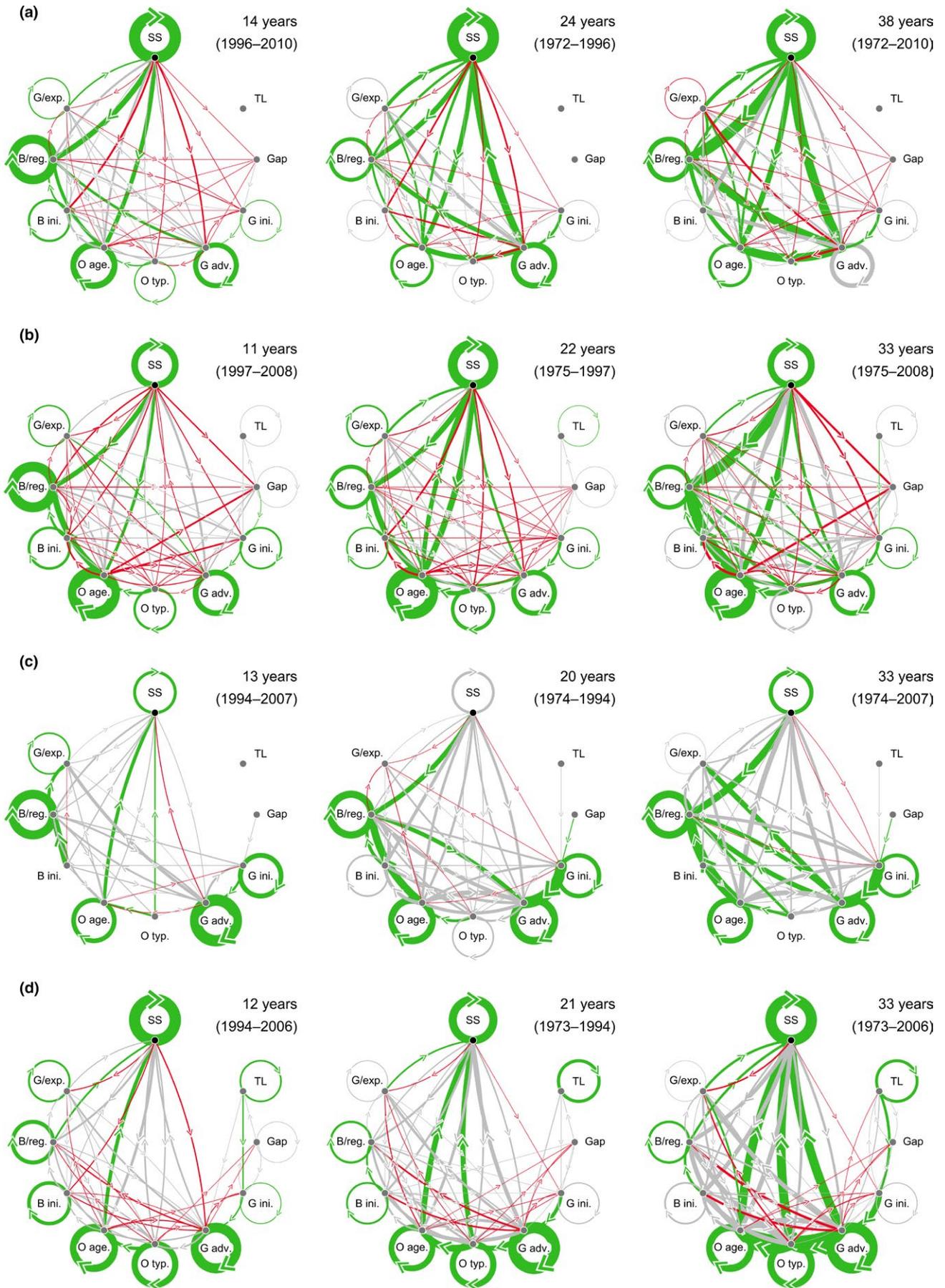
4.3 | Is the mosaic cycle resource- or consumer-controlled?

In recent years there has been an on-going debate on the importance of resource (bottom-up) vs. consumer (top-down) control in forming the structure and dynamics of vegetation communities. The prevailing paradigm in temperate forest ecology is that forest structures and dynamics are predominately bottom-up, controlled by the availability of resources such as light, water and soil nutrients (Gratzer et al., 2004; Gravel, Canham, Beaudet, & Messier, 2010; Janík et al., 2011, 2016; Rademacher, Neuert, Grundmann, Wissel, & Grimm, 2004); i.e. they are resource-controlled. On the other hand, large-bodied animals in general and apex consumers in particular have been increasingly

portrayed as key drivers of global ecosystems through their top-down effects on lower trophic levels; many ecosystems are thus largely consumer-controlled (Bond, 2005; Estes et al., 2011). The top-down control hypothesis has also been applied to European temperate, especially lowland, forests (Churski, Bubnicki, Jedrzejewska, Kuijper, & Cromsigt, 2017; Kuijper et al., 2010; Vera, 2000), advocating an alternative shifting mosaic (Olf et al., 1999) to Watt's (1947) original conceptual model of forest dynamics. For that reason we would like to put our results into the context of this on-going debate.

First, we need to point out that four out of the five research plots employed in this study have been fenced as protection against high ungulate game levels, especially red deer and roe deer (the first of which having the largest impact on most of our research plots). The lowland hardwood Cahnov-Ranšpurk bi-plot is located within a large commercial game preserve for red deer, where browsing is extremely high, with hardly any tree regeneration outside of game exclosures. The game preserve was established in 1971 (till present), while the research plots were fenced much later: Ranšpurk in 1992 and Cahnov in 2005 (Vrška et al., 2006). The situation was similar in the Boubín forest, which was part of a hunting game preserve from 1874 until World War II, although it was fenced no sooner than in 1966 (Šebková et al., 2011) because of persistently high numbers of ungulates in the area free of large predators. The Žofín plot was also fenced (from 1991 till present) because this isolated island of beech-dominated old-growth forest within the surrounding extensive even-aged spruce monoculture attracted much of the local population of ungulates (especially red deer) by providing exceptional quiet, shelter and forage. Only the Salajka plot has not been fenced, although the situation can be analogous to Žofín (Vrška, Adam, Hort, Kolář, & Janík, 2009). Therefore, all the plots experienced varying periods of increased consumer control by large browsers in their recent history, which inherently left long-term footprints in the structure and dynamics of the stands. Recent significant transitions to the Steady State (e.g. Figure 1d) thus might to some extent have originated from fencing – a broadening of local DBH distributions by successful sub-canopy regeneration and growth recently allowed by the elimination of consumer control. In contrast, the cyclic development anticipated by the model might in some parts be supported by the impact of large browsers limiting natural regeneration in the Optimum stage, which is highly visible and easily accessible for large ungulates (and saplings grow slowly in these conditions because of limited light resources). Stand regeneration would then be largely confined to canopy openings of the Breakdown stage, where advance regeneration grows faster (Čátek & Diaci, 2017) and seedlings and saplings are protected against browsing by numerous lying logs and branches (Olf et al., 1999). In the presence of large carnivores such places are perceived as 'patches of fear', where browsing intensity

FIGURE 1 The complex patterns of transitions between development phases observed in different periods at: (a) the Boubín plot, (b) the Žofín plot, (c) the Salajka plot and (d) the Cahnov-Ranšpurk bi-plot. The thickness of an arrow is directly proportional to the observed frequency of the transition; the colours indicate the significance compared to random transitions between phases: green is significantly more frequent than random (preferential pathway) and red is significantly less frequent than random (uncommon pathway), grey is not different from random frequency. TL – Treeless area; Gap – Live tree gap; G ini. – Growth initial; G adv. – Growth advanced; O typ. – Optimum typical; O age. – Optimum ageing; B ini. – Breakdown initial; B/reg. – Breakdown/ regeneration; G/exp. – Growth/ expiration; SS – Steady State [Colour figure can be viewed at wileyonlinelibrary.com]



is strongly reduced and local tree recruitment facilitated (Kuijper, Bubnicki, Churski, Mols, & van Hooft, 2015). The higher consumer control thus might reduce possible shortcuts within the model cycle while encouraging the cyclic development of local stand structures (see the only unfenced Salajka plot in Figure 1c and Table 2 with less shortcuts and highest proportion of cyclic/acyclic transitions (1:1)).

4.4 | Comparison with prior related research

Generally, similar patterns of forest dynamics were found by Frelich and Lorimer (1991) and Halpin and Lorimer (2016) for northern hardwoods through modelling at the landscape scale. Those authors concluded that frequent partial disturbances followed by quick recovery resulted in stand development pathways that resemble a complex web rather than a simple repeating cycle. Without severe stand-replacing disturbances, only transitions among different multi-aged phases dominated the dynamics of the forest landscape (Halpin & Lorimer, 2016). The frequency and importance of partial disturbances resulted in development pathways of those multi-age stands being largely unpredictable. Early development phases were promoted only by large-scale disturbances, and the following recovery was also the only part of the model where the stand development was fairly predictable (Frelich & Lorimer, 1991). Our picture of forest dynamics is incredibly similar, although based on actual long-term observations and describing the dynamics at the much finer scale of patches within individual forest stands: only the development pathways of initial development phases driven by the collective development of juvenile tree cohorts appeared to be fairly straightforward. The development of more advanced and multi-layered phases gradually became stochastic, as their development is increasingly driven by the fate of bigger and bigger individual trees, and the future of individual trees is far less predictable (see also Drössler et al., 2016).

Also, the first indications of Christensen et al. (2007) from the 10-year idiosyncratic field observations of Suserup Skov may be largely confirmed. In particular, our results support their findings on: (1) the release of understorey trees following (partial) canopy breakdown as a common process enabling most patches to bypass the innovation phase; (2) in contrast, the innovation phase mostly originated from phases other than the degradation phase; and (3) the release of canopy trees after partial disturbance leading to the closing of small gaps by the lateral canopy expansion of remaining trees as a kind of regressive development (Christensen et al., 2007). The high complexity of forest development pathways was anticipated even earlier (Bobiec et al., 2000) in the Białowieża primeval forest, although without the support of repeated observations.

4.5 | What happens next?

Because the proportion of the Breakdown phases generally increased significantly over the more than 30 years of observations, numerous transitions went into the Breakdown stage (especially into the Breakdown/regeneration phase), while transitions from the Breakdown stage were rather rare. This indicates that even when

summing all the plots (almost 180 ha in total), the observed transitions were not in 'demographic equilibrium'. This may be somewhat surprising, but might be explained by the fact that all the plots are located in strict forest reserves that were usually established in the 19th and first decades of the 20th centuries in old remnants of ancient forests with significant amounts of large and veteran trees, which in those times were generally perceived as having natural value worth protecting. However, this also means that further long-term observations might reveal another (additional) pattern of transitions describing the recovery of stands from the Breakdown stage.

5 | CONCLUSIONS

Although most traditional forest cycle models accounted for multiple pathways and bypasses of certain phases (e.g. Korpel', 1995; Leibundgut, 1959; Zukrigl et al., 1963), regressive development (backward transitions), multiple back-and-forth transitions between two phases (repetitive pulsation) and the importance of the Steady State were not well incorporated into those models. That is understandable, as the conceptual models were based on patch-level chronosequences and therefore a rather linear development was subjectively anticipated, while other less obvious and/or unexpected transitions were unrecognized due to the lack of quantitative long-term spatio-temporal data in those times. And although at all sites we documented signs of cyclic and predictable development anticipated by the forest cycle concept, the predominance and often stochastic nature of multiway acyclic pathways gives rise to reasonable doubts as to whether it is appropriate to call the model 'the cycle.' Similarly, if the future development of individual patches is largely unpredictable, it is rather questionable to call the phases 'developmental'. Instead, use of the term 'stand structural stages' as provided e.g. by Frelich and Lorimer (1991) and Halpin and Lorimer (2016) might be more appropriate. On the other hand, although the fitness of the traditional concept for descriptions of forest dynamics seems to be limited, its (failed) verification has (somewhat ironically) significantly increased our understanding of forest dynamics complexity.

Therefore, we do not wish to question the overall usefulness of the concept. There is still a heuristic value in recognizing the range of stand structural stages that are commonly encountered and that may be perceived uniformly due to the unifying concept (Franklin et al., 2002). The description of stand structural stages can be still useful as a framework for biodiversity assessments (e.g. Boncina, 2000; Winter & Brambach, 2011); for purposes of nature conservation (e.g. Bobiec et al., 2000); as a model for uneven-aged silviculture (e.g. Schütz, Saniga, Diaci, & Vrška, 2016); or in other forestry and/or environmental applications.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1 Extended description of the four research sites of Table 1.

APPENDIX S2 DBH and basal area distribution in forest development phases.

APPENDIX S3 Empiric classification of phase-to-phase transition types.

APPENDIX S4 Relative sources and sinks of phase-to-phase transitions.

APPENDIX S5 The proportion of individual forest development phases across all study sites and censuses.

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