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Formalized classification of species-poor vegetation: a proposal of a consistent protocol for aquatic vegetation

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Aquatic vegetation; Assignment rules; Association; Cocktail method; Consistency; Functional species group; Physiognomy; Relevé; Supervised classification; Vegetation classification; Vegetation database

Nomenclature
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Abstract

Aims: Most vegetation classification systems developed for large areas include various inconsistencies. Therefore, we (1) propose a new consistent Cocktail-based approach to redefine the traditional phytosociological classification of species-poor vegetation; (2) apply it to create a classification protocol for aquatic vegetation; (3) implement this protocol in a computer expert system; and (4) test it with a data set previously classified using an older version of the Cocktail method.

Methods: The new approach uses formal logic to provide formal definitions of vegetation units. In the classification protocol for aquatic vegetation we defined consistent criteria for delimitation of associations according to the concepts that are predominantly used in phytosociology, based on species cover, dominance patterns and functional species groups. We applied these criteria in a computer expert system running in the JUICE 7.0 program, and applied them to a test data set of 12 171 vegetation plots from the Czech Republic containing at least one aquatic species. The new classification was compared with (1) the previous national Cocktail classification based on species cover values and in few cases on sociological species groups, and (2) a non-formalized expert-based classification.

Results: Thirteen functional species groups were created to build logical formulas of 64 aquatic associations and 5297 (44% of the total data set) vegetation plots were assigned to these associations, i.e. by 4% and 12% more than in the previous Cocktail and expert-based classifications, respectively. There was 94% and 83% classification agreement with the previous Cocktail and expert-based classification.

Conclusions: The new approach produces a formal, consistent and unequivocal classification of species-poor vegetation with several advantages over similar approaches. It provides not only a set of formal definitions of vegetation units, but also a set of rules for building such definitions. All associations with common characteristics are defined by structurally identical formulas, ensuring consistency of the classification. While similar approaches for species-rich vegetation use sociological species groups, which are not applicable to species-poor vegetation, the new approach introduces the use of functional species groups, which reflect vegetation physiognomy and spatial structure and, in combination with species dominance, enable the classification of species-poor vegetation in a similar manner as in traditional phytosociology.

Introduction

Many different approaches, methods and tools are used to classify vegetation, and new ones continue to be proposed (e.g. Kent 2012; Peet & Roberts 2013; Wildi 2013). Although methodological innovations have multiple positive effects (Mucina 1997; Ewald 2003), communication between scientists and users of vegetation classification

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(e.g. nature conservationists) requires that vegetation classifications follow uniform, formally described criteria consistently applied across regions and vegetation types (Jennings et al. 2009; Chytrý et al. 2011).

Consistency in vegetation classification can be achieved by applying rigorously defined concepts, classification protocols and sets of formal rules (De Cáceres & Wiser 2012). These are often applied in single classification exercises; however, variability in the methods, criteria and data sets result in inconsistent comprehensive classification systems that combine the results of separate classification exercises. A considerable degree of consistency in large-scale vegetation classification can be achieved using the Cocktail method (Bruelheide 1997, 2000; Kočí et al. 2003), as demonstrated by its recent application to national vegetation classifications of some European countries (Chytrý 2007–2013; Janišová 2007; Šilc & Čarni 2007; Landucci et al. 2013) and Taiwan (Li et al. 2013). In this method, formalization is achieved by creating logical formulas to define individual vegetation types. These formulas combine occurrences of sociological species groups or cover values of individual species using the logical operators AND, OR and AND NOT. The Cocktail method achieves consistency in the sense that logical formulas are applied in the same way to all the vegetation plots analysed irrespective of the context of the data sets in which they are included. This is a significant advantage over other (unsupervised) classification methods such as cluster analysis, which can classify the same plot to different units if this plot is considered in the context of different data sets (Tichý et al. 2014). However, logical definitions of vegetation units established by Cocktail depend on the concepts and criteria used to define the assignment rules, which may differ among broad vegetation types and persons who create the rules. This means that vegetation units carrying the same name can be defined in different ways in different classification systems, which is the case of the current Cocktail-based national vegetation classifications. Therefore, we argue that more consistency and transparency is also desirable in the phase of establishing the classification rules and formal definitions of the vegetation units (De Cáceres & Wiser 2012).

A universal consistency of vegetation classification is difficult to achieve due to the absence of a single concept and unequivocal definition of the association (or alliance, order or class) that would be broadly accepted and equally applicable to all vegetation types (e.g. Willner 2006; Jennings et al. 2009; Biondi 2011). However, consistency can be reached at least for specific vegetation types. Here, we try to contribute to consistency of vegetation classification by proposing a general approach for formalized classification of species-poor vegetation, and a specific protocol including criteria and rules for aquatic vegetation, based on an extension of the Cocktail method.

Although aquatic vegetation seems to be easy to classify due to the limited number of species in each stand, there are at least three major classification approaches (Chepinoga et al. 2013) and none of these has reached universal acceptance. The first approach establishes broad associations that include stands dominated by different species, which share similar ecology and in some cases also similar sets of subordinate species (e.g. Berg et al. 2004). Using this approach, very species-poor or monospecific stands with no shared species can be classified to the same association. The second approach differentiates the associations based on dominant species and species combinations, and it considers even different growth forms of the same species as separate 'taxa' for the purpose of the classification, e.g. aquatic vs terrestrial growth forms, or stream vs still-water morphotypes (e.g. Pott 1995; Buchwald et al. 2000; Dubyna 2006; Sburlino et al. 2008). The third approach, and currently perhaps the most common, defines associations based on the dominant species of the stands, assuming that the dominance of a particular species reflects specific ecological conditions (e.g. Valachovič et al. 1995; Coldea 1997; Šumberová 2011a,b; Felzines 2012; Chepinoga et al. 2013). Despite the clear differences among these three approaches, many classification schemes of European aquatic vegetation do not consistently apply a single approach across all associations (e.g. Rodwell 1995; Schaminée et al. 1995; Trinajstić 2008).

In this paper we (1) propose a new Cocktail-based approach to formalize the traditional classification of species-poor vegetation, in which definitions of vegetation units are based on the consistent application of a single set of general concepts and rules; (2) create a specific protocol for the classification of aquatic vegetation; (3) implement this protocol in a computer expert system; and (4) test it with a data set of Czech aquatic vegetation plots, which were previously classified using a set of partially inconsistent Cocktail-based definitions. We do not attempt to build a completely new classification system; we rather aim at redefining the traditional phytosociological classification in a formalized and consistent way.

Methods

For the purpose of the present study, we define vegetation classification as grouping vegetation plots into units and establishing unequivocal boundaries between them. The new approach for classification of species-poor vegetation proposed here is a broad extension of the Cocktail method (Bruelheide 1997, 2000). It uses logical formulas to define

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units of species-poor vegetation for which no sociological species groups (Doing 1969; Bruelheide 2000; Kočí et al. 2003) can be established, and it introduces a consistent approach to defining these formulas. To do this we propose a new kind of formulas, which use the concept of functional species groups instead of (or in addition to) the sociological species groups. By functional species groups we mean groups of species that share the same characteristics (e.g. traits) useful (or commonly used) for the purpose of vegetation classification. The objective of our new approach is to redefine the existing phytosociological classification systems in a consistent way but following the traditional concepts of vegetation types and their delimitations whenever possible. Therefore, we first identify the most commonly used concepts in the classification of our target vegetation; second, we formulate general classification criteria and suitable functional species groups; and third, we use them to create formal definitions of units in the form of logical formulas to be used for the classification of our target vegetation.

The classification protocol for aquatic vegetation was developed based on the recent Cocktail-based national classification of the Czech Republic (Chytrý 2011). In this national classification, simple rules were used to create logical formulas of aquatic vegetation associations, namely that the cover of selected individual species had to exceed a subjectively selected threshold value, while the cover of other species could not exceed the same or different cover value. In the new protocol we tried to follow, and at the same time to make explicit, the concepts used in this national classification system and in the traditional expert-based phytosociological classifications. However, in order to introduce consistency, slight adjustments of the boundaries between some associations of the previous classification system were necessary because the previous Cocktail-based vegetation units were inconsistently defined.

We first tried to identify the most commonly used concepts in the classification of aquatic vegetation based on the review of the main European literature, including national and regional overviews (e.g. Rodwell 1995; Schaminée et al. 1995; Valachovič et al. 1995; Coldea 1997; Berg et al. 2004; Dubyna 2006; Chytrý 2011; Felzines 2012) and thematic papers (e.g. Buchwald 1992; Buchwald et al. 2000; Sburlino et al. 2008; Chepinoga et al. 2013). This review indicated that the most commonly adopted concept of association for aquatic vegetation, but also for species-poor vegetation in general, uses species dominance as the main classification criterion. In addition, physiognomy of vegetation stands and the occurrence or dominance of functional species groups (groups of species with similar traits) have been recognized as important for the classification by several authors, particularly for aquatic vegetation and its higher syntaxa such as alliance, order and class (Den Hartog & Segal 1964; Den Hartog 1981; Den Hartog & van der Valde 1988; Willby et al. 2000). Vegetation scientists generally accept that species differ in their importance for classification depending on the functional groups they belong to. In an aquatic environment, the cover of species belonging to particular functional groups reflecting species morphology, size or occurrence in a specific layer of the aquatic environment, is a good indicator of habitat conditions, competition or successional status (Den Hartog & Segal 1964; Den Hartog 1981; Alahuhta et al. 2014). Therefore, a threshold abundance value of one or collectively all species belonging to certain functional groups can be assumed as an appropriate criterion to define vegetation units.

Considering these generally recognized concepts, we formulated a set of criteria for the construction of the logical formulas to define units of aquatic vegetation. All the functions needed for applying these criteria and the new protocol to the vegetation-plot data have been provided in the freeware program JUICE 7.0 (Tichý 2002; www.sci.muni.cz/botany/juice).

Functional species groups and priority degrees

The species occurring in the aquatic environment were assigned to 13 functional species groups according to their life form, morphology and position occupied in the water column. We considered several existing functional species classifications (Den Hartog & Segal 1964; Hutchinson 1975; Wiegleb 1991; Boutin & Keddy 1993; Willby et al. 2000), but did not strictly adhere to any of these, as they were not completely suitable for our purpose. In general, we only used the functional species groups that are used for vegetation classification in the main European phytosociological literature.

The functional species groups were organized on three hierarchical levels. The first (highest) level distinguished 'aquatic species' and 'non-aquatic species'. The subsequent levels were applied only to aquatic species, because further divisions of the latter group were not needed for classification of aquatic vegetation. The second and third levels of division grouped aquatic species according to their size, life form and broad taxa (vascular plants, bryophytes and algae) as an expression of overall morphology. A priority degree from I (low priority) to V (high priority) was assigned to each functional group of level 2 and to 'non-aquatic species', based on the vegetation layer, the overall size and the population stability of the species belonging to the functional groups (Fig. 1). For example, small pleustonic species floating on the water surface (such as *Lemna minor*) have a lower priority degree than pleustonic species floating under the surface (such as *L. trisulca*). This reflects a lower functional and structural importance of *L. minor*.

Functional species groups			Species belonging to the groups	Priority degree and explanation	Threshold cover value
A. Aquatic species. Vascular plant, macroalgae and bryophyte species growing in water bodies from the bottom to the water surface. They can have leaves or branches completely submerged or floating on the water surface. They produce flowers/spores in water or a few centimetres above the water surface. Occasionally these species can grow and complete their life-cycle outside water, but always in very wet conditions.	**A.A. Small pleustonic species floating on the water surface.** Free-floating plant and bryophyte species on the water surface, with small leaves (usually much smaller than 5 cm). The overall size of the individuals is generally smaller than 8 cm (occasionally slightly larger, e.g., *Salvinia* sp.).		*Lemna minor, L. gibba, L. turionifera, Spirodela polyrhiza, Azolla filiculoides, Ricciocarpos natans, Salvinia natans, Wolffia arrhiza*	**Priority degree I.** Despite the capability of these species to reach high cover values, the lowest priority degree of this group is due to the small size of the plant individuals, the two-dimensional structure of their populations on the water surface (rather than three-dimensional in the water column) and their high probability of being moved away from the sites by water or wind.	
	A.B. Submerged species. Free-floating plant and bryophyte species on the water surface, with small leaves (usually much smaller than 5 cm). The overall size of the individuals is generally smaller than 8 cm (occasionally slightly larger, e.g., *Salvinia* sp.).	**A.B.1. Small pleustonic species floating under the water surface.** Species free-floating under the water surface, characterized by an overall size of the individuals smaller than 5 cm.	*Lemna trisulca, R. fluitans, R. rhenana*	**Priority degree II.** The priority degree of this group is determined by the position of the species in the water column and by a low probability of their populations being moved away by water or wind. Even though the groups A.B.1 and A.B.2 include species characterized by a small size or absence of an anchorage to the bottom, they are given the same priority degree as submerged rooted species of a similar size. The species of these groups develop three-dimensional populations in the water column, often anchoring to the individuals of other submerged species, forming mixed stands that are often difficult to separate.	50%
		A.B.2. Large pleustonic species floating under the water surface. Species free-floating under the water surface, characterized by an overall size of the plants larger than 10 cm. Occasionally they have rhizoids with an anchor but not a trophic function.	*Ceratophyllum demersum, C. submersum, Utricularia australis, U. bremii, U. intermedia, U. minor agg., U. ochroleuca* s.l., *U. vulgaris*		
		A.B.3. Submerged bryophytes anchored to the bottom. Aquatic and sub-aquatic bryophytes anchored to the bottom.	*Amblystegium fluviatile, Dichelyma falcatum, Fontinalis antipyretica, F. hypnoides, F. squamosa, Hygrohypnum molle, H. luridum, H. ochraceum, H. smithii, Rhynchostegium riparioides, Amblystegium tenax , Aneura pinguis, Brachythecium rivulare, Calliergonella cuspidata, Calliergon giganteum, Chiloscyphus polyanthos, Drepanocladus aduncus, D. fluitans, Leptodictyum riparium, Sphagnum cuspidatum*		
		A.B.4. Macroalgae. Large algae morphologically similar to submerged vascular plants, permanently attached to the bottom through rhizoids.	*Chara aspera, C. braunii, C. delicatula, C. globularis, C. hispida, C. vulgaris, Nitella flexilis, N. mucronata, N. opaca, Tolypella glomerata, T. intricata*		
		A.B.5. Rooting vascular plant species with only submerged leaves. Vascular plants rooted in the bottom and producing only submerged leaves. This group also includes species that can produce both submerged and floating leaves, but more often they have only submerged leaves, e.g., *Batrachium penicillatum*.	*Callitriche hermaphroditica, Hottonia palustris, Myriophyllum alterniflorum, M. spicatum, M. verticillatum, Najas marina, N. minor , Potamogeton acutifolius, P. crispus, P. friesii, P. lucens, P. obtusifolius, P. pectinatus, P. perfoliatus, P. praelongus, P. pusillus* s.l., *P.trichoides, Batrachium circinatum, B. fluitans, B. penicillatum, B. rionii, B. trichophyllum, Elodea nuttallii , E. canadensis, Groenlandia densa, Zannichellia palustris* s.l.		
	A.C. Middle-sized species with floating leaves on the water surface. Species free-floating or attached to the bottom characterized by relatively large leaves (usually smaller than 10 cm) floating on the water surface. The overall size of the plants is larger than 10 cm.	**A.C.1. Middle-sized rooting vascular plant species with floating leaves on the water surface.** Species rooted in the bottom and producing two types of leaves (floating and submerged) or only floating leaves. When only floating leaves occur, they are oblong and shorter than 15 cm (e.g. *Persicaria amphibia, Potamogeton natans*). When two types of leaves occur, floating leaves usually have different shape and are broader than submerged leaves. Sometimes these species can occur, especially in rivers, in submerged growth forms characterized by submerged leaves only. By contrast, in stagnant turbid water they sometimes occur with only floating leaves.	*Batrachium aquatile* s.l., *B. baudotii, Callitriche hamulata, C. palustris* s.l., *Potamogeton alpinus, P. x angustifolius, P. gramineus, P. lucens* x *natans, P. natans, P. nodosus, P. polygonifolius, Persicaria amphibia*	**Priority degree III.** This priority degree reflects the capability of the species to develop three-dimensional populations in the water column and to form a carpet of leaves on the water surface that acts as a barrier for the light, thus limiting the development of the submerged species. Even though the species of the group A.C.2 are not rooted in the bottom, they are rarely moved away from the sites due to the large dimension of their individuals.	50%
		A.C.2. Large pleustonic species floating on the water surface. Species free-floating on the water surface, characterized by relatively large leaves. The overall size of the plants is generally much larger than 10 cm.	*Hydrocharis morsus-ranae, Pistia stratiotes, Stratiotes aloides*		
	A.D. Nymphaeoid species. Species rooted in the bottom producing only broad floating leaves or both broad floating and submerged leaves. The size of the plants is usually between 20 and 300 cm.		*Nuphar lutea, N. pumila, Nymphaea alba, N. candida, Nymphoides peltata, Trapa natans*	**Priority degree IV.** Similarly to the previous group, these species develop throughout the water column and form leaf carpets on the water surface. However, these species occupy a larger space in the water column and are stronger competitors. The persistence of their populations on particular sites is very high due to the large size of the individuals and because they are mostly rooted in the bottom.	25%
N. Non-aquatic species. Vascular plant species and bryophytes growing in dry or wet habitats, but able to complete their life-cycle only when emerging from water or in terrestrial conditions. Amphibian species producing both emergent and submerged growth forms but with optimum as emergent plants are also included in this group.			See Appendix S1	**Priority degree V.** The priority degree of this group is the highest due to the high persistence of its species on the site and occurrence in successional stages of advanced terrestrialization.	25%

Fig. 1. Functional species groups, their descriptions, species from the Czech vegetation-plot data set included to these groups, priority degrees and threshold cover values of the functional groups or of the 'dominant character species' used in the logical formulas (formal definitions) of associations. The functional species groups are organized hierarchically. Species included in the group 'non-aquatic species' are reported in App. S1.

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This species can be more easily moved away from the site, which makes its presence and cover a rather unstable feature of the vegetation unit. Moreover, its populations are developed in two dimensions only, resulting in a smaller space occupancy in comparison with three-dimensional populations of *L. trisulca* despite the same cover value of both species. The priority degrees are used in the classification process to resolve situations when different species (or species groups) have the same cover.

Assignment criteria

After the establishment of the functional species groups and priority degrees, we formulated general criteria for the assignment of vegetation plots to the vegetation units. We distinguished two groups of criteria. First, the physiognomic criteria, related to the functional species groups, help assign plots to the main groups of associations (associations characterized by 'nymphaeoid species', 'middle-sized species with floating leaves on the water surface', 'submerged species', 'small pleustonic species floating on the water surface' and 'non-aquatic' associations). Second, species dominance criteria guide the assignment of vegetation plots to specific associations within these main groups.

1 Physiognomic criteria

a) If the total cover of 'non-aquatic species' (code N; see Fig. 1) (including emergent wetland species) is >25%, the plot does not belong to aquatic vegetation association, irrespective of the cover of aquatic species.
b) If (a) is not true and the total cover of 'nymphaeoid species' (A.D) is >25%, the plot is assigned to a nymphaeoid association, irrespective of the cover value of any other aquatic species.
c) If (b) is not true and the total cover of any functional group within the superior group 'middle-sized species with floating leaves on the water surface' (A.C) is >50%, the plot is assigned to an association defined by species belonging to these groups, irrespective of the cover value of other aquatic species.
d) If (c) is not true and the total cover of any functional group within the superior group 'submerged species' (A.B) is >50%, the plot is assigned to an association defined by species belonging to these groups, irrespective of the cover value of other aquatic species.
e) If (d) is not true and the group 'small pleustonic species floating on the water surface' (A.A) is dominant (i.e. it has a higher cover than all the others), the plot is assigned to an association defined by species belonging to this group.

2 Species dominance criteria (valid if the physiognomic criteria are met)

f) If a species is dominant (i.e. it has the highest cover value in the plot), the plot is assigned to the association characterized by that species.
g) If the cover of a particular 'nymphaeoid species' (A.D) is >25%, the plot is assigned to the association characterized by that species.
h) If the cover of a particular species from the groups of 'submerged species' (A.B) or 'middle-sized species with floating leaves on the water surface' (A.C) is >50%, the plot is assigned to the association characterized by that species.
i) If two or more species co-dominate (i.e. have identical cover values), the assignment of the plot is based on the priority degrees. For example, if a pleustonic species floating on the water surface (e.g. *Lemna minor*) is co-dominant with another pleustonic species growing in the water column (e.g. *L. trisulca*), the plot is assigned to the association defined by the dominance of the latter because of its higher priority degree.

Formal definitions of associations

Following the assignment criteria described above, we created formal definitions of phytosociological associations of aquatic vegetation. These formal definitions are expressed in logical formulas, which can be used for the assignment of specific vegetation plots to the associations. Each formula consists of membership conditions combined using the logical operators AND, OR and AND NOT. The terms used in the membership conditions are species names, threshold cover values and functional species groups. Each membership condition contains different terms related by relational operators GR (greater than) and GE (greater than or equal to). Any membership condition can have positive or negative meaning. It has a positive meaning if placed, separately or in combination with other membership conditions, before the logical operator AND NOT. It has a negative meaning if placed after AND NOT (Appendix S2).

The definitions of associations were constructed using five general formula models. Because we follow the concept of associations based on the dominance of single species and stand structure, each association is defined by one species that is dominant (reaching the highest cover value in the vegetation plot) or has a cover value greater than the thresholds of 25% or 50%. This species is also the character species of the given association (hereafter termed the 'dominant character species'). All formulas are listed in Appendix S3, while here we only describe the five general formula models (see Fig. 2):

Priority degree			I	II					III		IV	V
			A aquatic									N non-aquatic
Functional groups			A.A pleustonic on water small	A.B submerged					A.C leaves on water middle		A.D nymphaeoid	
				A.B.1 pleustonic in water small	A.B.2 pleustonic in water large	A.B.3 submerged bryophytes	A.B.4 macroalgae	A.B.5 rooting vascular leaves submerged	A.C.1 rooting leaves on water	A.C.2 pleustonic on water large		
	1. Associations of small pleustonic species floating on the water surface		DCS	> TC	> TC TC ≤ 50%	> TC TC ≤ 50%	> TC TC ≤ 50%	> TC TC ≤ 50%	> TC TC ≤ 50%	> TC TC ≤ 50%	> TC TC ≤ 25%	> TC TC ≤ 25%
	2. Associations of small pleustonic species floating under the water surface		≥ TC	DCS	≥ TC	≥ TC	≥ TC	≥ TC	> TC TC ≤ 50%	> TC TC ≤ 50%	> TC TC ≤ 25%	> TC TC ≤ 25%
	3. Associations of large pleustonic species, macroalgae and rooting vascular plants floating in the water column	Ass. dom. by pleust. species in water large		≥ TC	DCS	≥ TC	≥ TC	≥ TC	> TC TC ≤ 50%	> TC TC ≤ 50%	> TC TC ≤ 25%	> TC TC ≤ 25%
						DCS > 50% SC ≤ 50%			TC ≤ 50%	TC ≤ 50%	TC ≤ 25%	TC ≤ 25%
Formula models		Macroalgae ass.		≥ TC	≥ TC	≥ TC	DCS	≥ TC	> TC TC ≤ 50%	> TC TC ≤ 50%	> TC TC ≤ 25%	> TC TC ≤ 25%
						DCS > 50% SC ≤ 50%			TC ≤ 50%	TC ≤ 50%	TC ≤ 25%	TC ≤ 25%
		Ass. dom. by rooting vascular plant species submerged		≥ TC	≥ TC	≥ TC	≥ TC	DCS	> TC TC ≤ 50%	> TC TC ≤ 50%	> TC TC ≤ 25%	> TC TC ≤ 25%
						DCS > 50% SC ≤ 50%			TC ≤ 50%	TC ≤ 50%	TC ≤ 25%	TC ≤ 25%
	4. Associations with middle size floating leaves on the water surface	Ass. dom. by rooting species with two types of leaves							DCS	≥ TC	> TC TC ≤ 25%	> TC TC ≤ 25%
									DCS > 50% SC ≤ 50%		TC ≤ 25%	TC ≤ 25%
		Ass. dom. by pleust. species on water large							≥ TC	DCS	> TC TC ≤ 25%	> TC TC ≤ 25%
									DCS > 50% SC < 50%		TC ≤ 25%	TC ≤ 25%
	5. Associations of nymphaeoid species										DCS	> TC TC ≤ 25%
											DCS > 25% SC ≤ 25%	TC ≤ 25%

Fig. 2. Summary of the membership conditions that compose the logical formulas of the aquatic vegetation associations. Some formulas contain two alternative combinations of membership conditions, which are respectively shown in the light grey and white rows. Dark grey cells contain the 'dominant character species' (DCS). The symbols >TC (or ≥ TC) mean that the cover of the 'dominant character species' must be greater than (or greater than or equal to) the total cover of the functional species group in the column. TC <25% (or TC <50%) indicates that the total cover of the species of the functional group must not exceed 25% (or 50%). SC <25% (or SC <50%) means that the cover value of any other species in the functional species group must not exceed 25% (or 50%). DCS >25% (or DCS >50%) indicates that the 'dominant character species' must have a cover >25% (or >50%). An example is shown in the framed cells: *Stratiotetum aloidis* (an association of a 'species with middle-sized floating leaves on the water surface') must have the cover of its 'dominant character species', *Stratiotes aloides*, (1) greater than or equal to the cover of any other species in the plot (this membership condition is not shown in the table, but it is valid for all formulas), (2) greater than or equal to the total cover of the functional species group A.C.1 and (3) greater than the total cover of the functional species groups A.D and N. Alternatively, *S. aloides* (1) must have a cover >50% and (2) any other species of the same functional species group (A.C, including A.C.1 and A.C.2) must not have a cover >50%. In both alternatives, the total cover of the groups A.D or N must not be >25% (compare the formula of the association *Stratiotetum aloidis* in Appendix S3).

1 Associations of small pleustonic species floating on the water surface

must have the cover of the 'dominant character species':

- greater than or equal to the cover of any other species and
- greater than the total cover of any other functional group at the lowest level of division applied (A.B.1, A.B.2, A.B.3, A.B.4, A.B.5, A.C.1, A.C.2, A.D and N).

must not have the total cover of:

- any functional group within the superior group of 'submerged species' (A.B) except A.B.1 or any group within 'middle-sized species with floating leaves on

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the water surface' (A.C, including A.C.1 and A.C.2) >50%,
- 'nymphaeoid' (A.D) or 'non-aquatic species' (N) >25%.

2 Associations of small pleustonic species floating under the water surface

must have the cover of the 'dominant character species':

- greater than or equal to the cover of any other species,
- greater than or equal to the total cover of 'small pleustonic species floating on the water surface' (A.A),
- greater than or equal to the total cover of any functional group other than that of the 'dominant character species' within the superior group of 'submerged species' (A.B),
- greater than the total cover of any functional group within 'middle-sized species with floating leaves on the water surface' (A.C, including A.C.1 and A.C.2), 'nymphaeoid' (A.D) and 'non-aquatic species' (N).

must not have the total cover of:

- any functional group within 'middle-sized species with floating leaves on the water surface' (A.C, including A.C.1 and A.C.2) >50%,
- 'nymphaeoid' (A.D) or 'non-aquatic species' (N) >25%.

3 Associations of large pleustonic species, macroalgae and rooting vascular plants floating in the water column:

must have the cover of the 'dominant character species':

- greater than or equal to the cover of any other species,
- greater than or equal to the total cover of any functional group other than that of the 'dominant character species' within the superior group 'submerged species' (A.B),
- greater than the total cover of any functional group within 'middle size species with floating leaves on the water surface' (A.C, including A.C.1 and A.C.2), 'nymphaeoid' (A.D) and 'non-aquatic species' (N).

alternatively must have

- the cover of the 'dominant character species' >50%
- the cover of any other species included in the group 'submerged species' (A.B) not >50%,

must not have the total cover of 'nymphaeoid' (A.D) or 'non-aquatic species' (N) >25%.

4 Associations of species with middle-sized floating leaves on the water surface:

must have the cover of the 'dominant character species':

- greater than or equal to the cover of any other species,
- greater than or equal to the total cover of the functional group other than that of the 'dominant character species' within the superior group of 'middle-sized species with floating leaves on the water surface' (A.C) and
- greater than the total cover of 'nymphaeoid' (A.D) and 'non-aquatic species' (N).

alternatively must have

- the cover of the 'dominant character species' >50%,
- the cover of any other species within the group of 'middle-sized species with floating leaves on the water surface' (A.C) not >50%,

must not have the total cover of 'nymphaeoid' (A.D) or 'non-aquatic species' (N) >25%.

5 Associations of nymphaeoid species:

must have the cover of the 'dominant character species':

- greater than or equal to the cover of any other species,
- greater than the total cover of the functional group 'non-aquatic species' (N).

alternatively must have

- the cover of the 'dominant character species' >25%,
- the cover of any other species within the group of 'nymphaeoid species' (A.D) not >25%,

must not have the total cover of the functional group of 'non-aquatic species' (N) >25%.

Data set and the expert system

We applied the new Cocktail-based protocol on a data set of 12 171 vegetation plots containing at least one aquatic species, extracted from the Czech National Phytosociological Database (Chytrý & Rafajová 2003). Species taxonomy and nomenclature were unified using species aggregates (indicated with 's.l.' or 'agg.') when necessary, and records of the same species in different layers were merged. All the species groups except the 'aquatic species' group were used in the logical formulas to define associations. The associations defined were the same as those recognized in the monograph 'Vegetation of the Czech Republic' (Šumberová 2011a,b; Šumberová et al. 2011) with some adjustments of the association boundaries. To make the classification reproducible for the same data set and applicable to new data sets, we created an expert system running in the program JUICE 7.0 (Appendix S4, S5).

Comparison with previous classifications

To show the efficiency of the new protocol we compared the results of the new classification with the already

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Table 1. Numbers of classified and unclassified vegetation plots of the complete set of 12 171 plots from the Czech Republic that contain at least one aquatic species. The previous Cocktail classification was developed in the project *Vegetation of the Czech Republic*, the expert-based classification was mostly done by the authors of the plot records, and the new Cocktail classification follows the protocol proposed in this paper.

	No. of vegetation plots (% of the total data set)		
	New Cocktail classification	Previous Cocktail classification	Expert-based classification
Plots classified to an aquatic vegetation association	5297 (44)	4785 (39)	3862 (32)
Unclassified plots or those classified as non-aquatic vegetation types	6750 (55)	7153 (59)	8309 (68)
Plots with double/multiple classification	124 (1)	233 (2)	0 (0)

existing Cocktail classification of the same vegetation plots (Šumberová 2011a,b; Šumberová et al. 2011). In order to realize this comparison we classified our data set using the expert system based on the previous Cocktail classification (Chytrý 2011; Appendix S6, S7) and the expert system developed in the current study (Appendix S4, S5). We also compared the results of the new classification with the original assignment of plots to the associations by experts (usually the authors of the plot records), provided this information was available in the Czech National Phytosociological Database (Appendix S8, S9).

Results

The new protocol unequivocally assigned 5297 vegetation plots (44% of the total data set) to 17, 40 and 7 aquatic vegetation associations included, respectively, in the classes *Lemnetea*, *Potametea* and *Charetea* (Appendix S10), whereas 6750 plots (55%) remained unclassified because they belonged to other vegetation types, especially to non-aquatic vegetation, and 124 (1%) were classified to more than one association (Table 1). The number of plots classified to aquatic associations by the new Cocktail protocol was by 512 (4%) higher than in the previous Cocktail classification, and by 1435 plots (12%) higher than in the expert-based classification.

The comparison of the new classification with the previous Cocktail and expert-based classifications showed a good correspondence. The new protocol respected the assignment performed by experts better than the previous Cocktail classification. The number of plots classified using the new protocol and not assigned by the previous Cocktail classification was 573 (5%) (Appendix S11). Of the plots not assigned by the new protocol but assigned by the previous Cocktail classification, 49 (75%) are assignable, according the criteria established, to a non-aquatic association or to associations not considered in this study (e.g. aquatic bryophyte-dominated associations). The remaining 16 (25%) plots have transitional characteristics and do not fit any definition.

The plots with double or multiple classifications obtained by the previous Cocktail classification and the new classification corresponded only marginally (eight plots) because of different principles of formula construction. According to the previous Cocktail classification, plots with a cover value of non-aquatic species >25% were considered transitional between aquatic and non-aquatic vegetation (and classified to more than one association), whereas in the new protocol they were not considered as belonging to the aquatic vegetation. The new protocol considers as transitional only those plots that have two or more co-dominant species belonging to the functional groups of the same priority degree.

Discussion

Advantages of the new classification approach

The new Cocktail-based approach yields a consistent, formalized and unequivocal classification of plot records of species-poor vegetation. It uses the rules of formal logic to define phytosociological associations (Bruelheide 1997), but it has several advantages over previous approaches of this kind. The two main innovations are: (1) a set of explicit and consistent concepts to create formal definitions of vegetation units, and (2) new terms introduced to the Cocktail formulas, which help to create more precise definitions of vegetation units, especially (but not only) for species-poor vegetation, in which sociological species groups cannot be defined or their content varies considerably among regions (Šumberová & Hrivnák 2013).

Unlike the previous approaches based on logical formulas, the new approach defines all the associations with similar characteristics by structurally identical formulas. Although the results of the new classification largely correspond to those of the expert-based and previous Cocktail classifications, there are some differences in the assignment of vegetation plots due to different concepts and criteria used to define the associations. Most of these changes in the association definitions were made to overcome the lack of consistency in the expert-based classifi-

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cation. An example is the associations *Lemnetum minoris* and *Lemno-Spirodeletum polyrhizae* (Appendix S11). Many vegetation plots assigned by the previous classifications to *Lemno-Spirodeletum* (because they contained *Spirodela polyrhiza* even if it was not dominant) were classified to *Lemnetum minoris* by the new protocol, following the criterion of species dominance. The main reason for a different definition of *Lemno-Spirodeletum* in the previous classifications was a slightly narrower niche and less common occurrence of *Spirodela* than *Lemna minor*; therefore, *Spirodela* was often given a higher weight in the association definition than *L. minor*. To ensure the consistency of the classification, we did not accept classification criteria involving different species' weights, because once introduced, they would have to be applied to many similar cases, which would dramatically change the commonly accepted boundaries of many associations. Moreover, ecological niche width and rarity of species vary among regions and are difficult to quantify, even in relative terms. Therefore, their use in the classification process would lead to inconsistencies among the classifications established in different regions and by different authors.

The new Cocktail approach formally recognizes physiognomy as a classification criterion, which was not the case in the previous approaches. It introduces the use of the functional species groups in addition to, or instead of, the sociological species groups used in the original Cocktail version (Bruelheide 1997, 2000). The use of the functional species groups in the Cocktail formulas also contributes to more accurate definitions of the target vegetation units. For example, we could easily exclude all the vegetation plots of non-aquatic vegetation using the new definitions.

The new membership conditions introduced to the Cocktail formulas enable the assignment of larger proportions of plots to vegetation units. The new formulas can use, in addition to the threshold cover values, the relative abundance of species, making it also possible to classify plots with a low total cover of the most abundant species. This is advantageous if the users of the classification require all plots to be assigned to units, such as in fine-scale vegetation mapping.

Šumberová & Hrivnák (2013) stressed that applying the Cocktail formulas produced in one country to another often requires considerable modifications of the formulas and, if used, also of the sociological species groups. This is due to different occurrence and co-occurrence patterns of the same species in different countries. In the new Cocktail formulas for aquatic vegetation, this problem is significantly reduced because all species, except for the dominant character species that appears directly in the formulas, are contained in the functional species groups. Therefore, the validity of the formulas remains unchanged provided that all the species of the data set have been assigned to the proper functional species group. In other words, for transferring the classification of aquatic vegetation now developed for the Czech Republic to other countries, the only requirements are matching the taxonomic concepts and nomenclature of the species that appear in the formulas to those used in the new data set, assignment of all the species in the data set to the functional species groups and, if necessary, defining new associations not occurring in the Czech Republic using the general models of the formulas proposed here. Adjustments of the existing formulas are not needed.

An additional practical advantage is that the formulas structured according to the models proposed here cannot become very long. It is no longer necessary to list a large number of species in the formulas, because they are included in a limited number of functional species groups and listing these groups is sufficient. For example, in the previous Cocktail classification for the Czech Republic (Šumberová 2011a) the negative part of the definition of the association *Lemnetum minoris* included 64 membership conditions corresponding to 64 species. The selection of these membership conditions depended on the Czech data set used, and it would probably have to be extended if applied to a new area. The formula created by the new protocol for the same association comprises only 18 membership conditions (including *Lemna minor* repeated ten times and nine functional species groups, of which eight are repeated twice).

Although the new formulas never become very long, they are never very short. In particular, for rare associations they are generally longer than those in the previous Cocktail classification. However, most of the previous definitions were short because they only defined boundaries with the vegetation types contained in the specific data set used. The new definitions contain boundaries against all possible vegetation types, which makes them longer and more complex, but also universally applicable to any data and any new region. The length and complexity of the formulas make them less useful for assigning vegetation plots to units directly in the field. However, the general classification concepts and assignment criteria underlying the formal definitions can be used for this purpose.

Application of the new approach beyond aquatic vegetation

The same approach as applied here to aquatic vegetation can be used to create a formalized classification of other species-poor vegetation types, which can be difficult to formalize based on the sociological species groups, such as some types of wetland, ruderal, rock or scree vegetation.

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Because traditional phytosociology uses different classification criteria for different vegetation types, a set of specific criteria, rules and functional species groups must be defined before applying the new protocol to other vegetation types beyond aquatic vegetation. For each broad vegetation type, it is necessary to (1) identify or define specific classification criteria (e.g. biogeographical, structural, ecological) and rules applicable to the target vegetation type; (2) define functional species groups and assign the species of the data set to them; (3) construct logical formulas of vegetation units using the available membership conditions; (4) classify the data sets of vegetation plots, and optionally (5) re-assess the classification criteria if needed.

Although the new classification approach can be applied to any species-poor vegetation type, it is not suitable for species-rich types. While species dominance is considered as the main criterion to classify species-poor vegetation, species co-occurrences are usually used as the main criterion to classify species-rich vegetation (e.g. Grabherr & Mucina 1993; Rodwell 1995; Schaminée et al. 1995; Valachovič et al. 1995; Chytrý 2011). Using a similar approach to classify species-rich vegetation would require an integration of other classification criteria and sociological species groups (Bruelheide 2000; Bruelheide & Chytrý 2000) to the general models, which is not an easy task.

Alternative ways to classify species-poor vegetation and overall consistency of classification systems

Some authors suggest that vegetation classification should be carried out using a uniform approach across all vegetation types (e.g. Berg et al. 2004). However, presently there is no consistent method to produce such a formalized and unambiguous classification and it is unclear whether such a classification would be possible at all. Applying a single standard protocol across all vegetation types would likely result in a classification system that would be very different from that accepted in traditional phytosociology, at least for some vegetation types: the number of associations might be extremely reduced in some types and increased in others. For example, Berg et al. (2004) applied the so-called uniform approach to classify the vegetation of Mecklenburg-Vorpommern (Germany), which resulted in a strong reduction of the number of species-poor associations. Although they provided diagnostic species of syntaxa that could be used to assign plots to vegetation units (e.g. van Tongeren et al. 2008; Willner 2011), their approach was not formalized (plots were manually assigned to units, while partially considering the results of numerical classifications); therefore, the underlying concepts, classification decisions and consistency cannot be evaluated. A consistent formalization of such a classification for species-poor vegetation would be very difficult to achieve using either logical formulas or traditional methods such as cluster analysis, because the broadly defined species-poor associations often include plots that share no species. Associations that group together plots with different dominant species and sometimes even with no shared species, do not follow the traditional phytosociological ideas of associations and, therefore, they are not accepted in most phytosociological studies.

In contrast to this lumping approach, some authors prefer refined classification approaches, such as those based on species growth forms (e.g. Buchwald 1992; Buchwald et al. 2000; Sburlino et al. 2008) or geographically restricted species combinations (Raimondo et al. 2011). These approaches recognize different associations based on different growth forms of the same dominant species or small differences in species composition that can be stochastic or locally idiosyncratic. An example is two associations for vegetation dominated by *Potamogeton coloratus* recognized by Buchwald et al. (2000): *Berulo submersae-Potametum oblongi* Buchwald et al. 2000 and *Potametum colorati* Allorge 1921, the former occurring in streams and the latter in still water, although their species composition can be identical. Such associations would be very difficult to identify in vegetation-plot databases, because information on growth form is missing for most historical and current plot records. Although formalization of some of the associations delimited in this way would be theoretically possible based on the dominant species' growth form, such criteria are different from the species occurrence and cover that are applied in most phytosociological studies.

In conclusion, we suggest that a uniform formal vegetation classification approach that would be applicable across all vegetation types is probably impossible to achieve if we want to preserve concepts of vegetation units similar to those defined in traditional phytosociology. In particular, there are fundamental differences in the approaches traditionally used to classify species-poor and species-rich vegetation. Therefore, we believe these contrasting vegetation types require different classification criteria and rules, the former with a stronger focus on cover of individual species and functional species groups, the latter on presence of sociological species groups. At the same time, we argue that within broad vegetation types such as aquatic vegetation, grasslands or forests, or at least within the same classes the same formal approach should be used consistently. In this study, we tried to support the development of consistent classification within broad vegetation types by proposing a set of criteria and rules for the classification of aquatic vegetation. We are aware of the fact that understanding the criteria commonly used to classify

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other vegetation types and creating a common classification protocol can be very difficult due to large differences between classifications developed by different authors or in different countries. Nevertheless, we propose that establishment and explicit description of the classification criteria and rules would be fundamental for starting the integration of different classifications into a single consistent system. We also suggest that the option of a dominance-based classification for species-poor plant communities is most similar to the approaches used in the traditional phytosociology. The example given in this paper suggests that such an approach can be translated into formalized classifications that are consistent and at the same time largely preserve the established vegetation units.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Species included in the functional species group 'non-aquatic species'.

Appendix S2. Structure and syntax of the logical formulas containing formal definitions of associations.

Appendix S3. Logical formulas of the associations of aquatic vegetation of the Czech Republic.

Appendix S4. Description of the expert system in App. S5.

Appendix S5. New electronic expert system running in the JUICE 7.0 program prepared using the new Cocktail-based protocol.

Appendix S6. Description of the expert system in App. S7.

Appendix S7. Previous electronic expert system running in the JUICE 7.0 program developed in the project *Vegetation of the Czech Republic*.

Appendix S8. Description of the files for the JUICE 7.0 program contained in App. S9.

Appendix S9. Data set used. Files for the JUICE 7.0 program.

Appendix S10. Synoptic table of aquatic vegetation of the Czech Republic according to the new Cocktail-based classification.

Appendix S11. Comparative table of the assignments of vegetation plots to the associations by the new Cocktail-based protocol, previous Cocktail classification and by experts.

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