

The whole and its parts: why and how to disentangle plant communities and synusiae in vegetation classification

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Abstract

Most plant communities consist of different structural and ecological subsets, ranging from cryptogams to different tree layers. The completeness and approach with which these subsets are sampled have implications for vegetation classification. Non-vascular plants are often omitted or sometimes treated separately, referring to their assemblages as “synusiae” (e.g. epiphytes on bark, saxicolous species on rocks). The distinction of complete plant communities (phytocoenoses or holocoenoses) from their parts (synusiae or merocoenoses) is crucial to avoid logical problems and inconsistencies in the resulting classification systems. We here describe theoretical differences between the phytocoenosis as a whole and its parts, and outline consequences of this distinction for practice and terminology in vegetation classification. To implement a clearer separation, we call for modifications of the International Code of Phytosociological Nomenclature and the EuroVegChecklist. We believe that these steps will make vegetation classification systems better applicable and raise recognition of the importance of non-vascular plants in the vegetation as well as their interplay with vascular plants.

KEYWORDS

cryptogam, epiphyte, EuroVegChecklist, holocoenosis, International Code of Phytosociological Nomenclature (ICPN), merocoenosis, phytocoenosis, phytosociology, plant community, spatial scale, synusia, vegetation classification system

1 | INTRODUCTION

Vegetation classification, and specifically phytosociology, was developed as a method to describe plant communities and to analyse their environmental and dynamic relationships at different levels of generalisation (Braun-Blanquet, 1964; Dierschke, 1994; Ewald, 2003; Dengler, Chytrý, & Ewald, 2008; Guarino, Willner, Pignatti, Attorre, & Loidi, 2018). For better communication, especially in applied fields like forestry, landscape planning, vegetation mapping, or nature conservation, plant communities are classified and ordered in

hierarchical classification systems. The study of plant communities and specifically their classification consider macroscopic plants of widely varying size and stature, ranging from bryophytes, lichens and macro-algae (further called “non-vascular plants”) to forbs, grasses, shrubs and trees. Based on life form and canopy height, plant species are usually assigned to vegetation layers. In records of plant communities, often only a subset of these layers is sampled (e.g. only trees in forest inventories, only vascular plants, only soil-dwelling plants). Non-vascular plants are often omitted or sometimes treated separately in a system of microhabitats or “synusiae” (epiphytes on bark,

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saxicolous species on rocks, epiphytic species on dead wood). Both approaches forego the potential of non-vascular plants as diagnostic species of plant community types (Berg & Dengler, 2005). Jointly analysing vegetation plots from studies with and without treatment of the non-vascular components, which is inevitable in broad-scale classifications, biases the determination of diagnostic species (Chytrý, Tichý, Holt, & Botta-Dukát, 2002; Dengler et al., 2008) and hence classification results.

There is a wide range of ways how non-vascular plants are considered in vegetation plot records, if they are considered at all:

- a. Several of the recent broad-scale, data-driven vegetation classifications consider terricolous non-vascular plants as diagnostic species of equal value to vascular plants and use them for the discrimination of their vegetation types (syntaxa) at any rank (Schaminée et al., 1995 et seq., Berg et al., 2001; Berg et al., 2004; Chytrý, 2007 et seq.). In these classification systems, non-vascular plants figure as prominent diagnostic species in the moss-dominated vegetation of raised bogs (*Oxycocco-Sphagneteta*) and springs (*Montio-Cardamineteta*) as well as benthic stonewort-lawns (*Charetea*). However, at the same time, most of these classification systems “ignore” other community types such as moss- and lichen-dominated rocks and screes as well as many macro-algal stands in marine environments
- b. Other authors study bryophyte- or lichen-dominated communities (very rarely also vegetation of macro-algae other than *Charetea*) in isolation and describe them as formal “syntaxa” (associations, alliances and so forth) in the normal syntaxonomic system, irrespective of whether the species grow on soil, bark, rock or other substrata and whether or not they are part of a vascular-plant-dominated plant community or not. Often, there are even two separate classification systems, one for bryophyte (von Hübschmann, 1986; Dierßen, 2001; Marsteller, 2006) and one for lichen communities (Klement, 1955; Wirth, 1995). Although these “cryptogam communities” are formally described according to the same nomenclatural rules (International Code of Phytosociological Nomenclature [ICPN]; Weber, Moravec, & Theurillat, 2000), the majority of phytosociological surveys and textbooks simply ignore them
- c. Several authors have highlighted that it is illogical if, for example, an epiphytic lichen assemblage is treated in the same system as the forest community of which it is part (Wilmanns, 1970; Barkman, 1973; Hobohm, 1998; Dengler, 2003). Accordingly, there have been some proposals for two separate classification systems, one for complete plant communities and one for partial communities (merocoenoses or synusiae; Barkman, 1973; Dengler, 2003; and see below), but they hitherto have not been adopted widely
- d. Lastly, the “integrated synusial approach” (Gillet & Julve, 2018) resolves the logical problems by extending synusial classification to the layers of vascular plants. In this approach, vegetation is disintegrated into mono-layered synusial components

as the basic objects of classification. In explicit contradiction to ICPN rules (Weber et al., 2000), these synusial communities are classified as “associations” (and higher ranks of the Braun-Blanquet system). In this view, a forest consists of separate tree, shrub, herb and cryptogam communities instead of individual plant species. The combinations of such synusial “associations” in one vegetation stand are used to describe “coenassociations” (equivalent to the associations of the Braun-Blanquet system) and then grouped into higher “coenotaxa”, the coenotaxa having different terminology and ending from the one-layer “syntaxa” of the integrated synusial system. Elaboration of this solution has largely remained restricted to a few studies, mainly in France and Switzerland

Recently, the first comprehensive overview of the vegetation types (syntaxa) of Europe has been published (EuroVegChecklist; Mucina et al., 2016), as a milestone in harmonising syntaxonomic classification schemes at a continental scale. This work includes, side by side, three syntaxonomic systems: EVC1 for “syntaxa dominated by vascular plants”, EVC2 for “syntaxa dominated by bryophytes and lichens” and EVC3 for “syntaxa dominated by algae”. Thus, it applies partially way (a) and partially way (b) mentioned before, while the concerns of the proponents of ways (c) and (d) are not addressed. Using the same nomenclature and the title “Vegetation of Europe” suggests that EVC1, EVC2 and EVC3 provide an equivalent basis for the description of European vegetation and represent the same conceptual levels, just in independent vegetation classification systems (VCSs) in the sense of De Cáceres et al. (2015). It is a major merit of Mucina et al. (2016) to present rock- and scree-dwelling moss- and lichen communities (e.g. *Racomitrietea heterostichi*) as well as marine macro-algal communities (e.g. *Cystoseiretea*) as separate vegetation classes alongside with and equivalent to the “normal” vascular-plant-dominated vegetation classes. In EVC2 and EVC3 the authors exclusively list bryophytes and lichens or “algae” as diagnostic species. By contrast, EVC1, apart from 95.8% vascular plants, also includes 3.5% bryophytes, 0.7% lichens and 0.1% macro-algae as diagnostic species of classes “dominated by vascular plants”, although the listing is rather inconsistent and incomplete for the non-vascular plants. While these aspects could potentially raise the interest in studying cryptogam-dominated vegetation types, there is a major drawback to the presentation of EVC2 and EVC3 in Mucina et al. (2016): both systems comprise an intricate mixture of units that occur as independent vegetation units and others that can only be found as elements of other plant communities. One example is the class *Hypogymnietea physodis* (exclusively comprising epiphytic lichen communities) considered as equivalent to the classes of forest vegetation.

The evident lack of a generally accepted and consistent way how to treat non-vascular plants in phytosociological classification inspired this Forum contribution. In the following we summarise the main arguments of the discussion, then propose a general way forward and finally make suggestions how such a more consistent approach could be reflected in future revisions of (a) the ICPN and (b) the EuroVegChecklist.

TABLE 1 Suggestions for the terminology of phytocoenoses and cryptogam synusia following Barkman (1969, 1973) Hobohm (1998) and Dengler (2003: p. 179). If desired, the nomenclature of synusia could be regulated in its own code, separate from the ICPN, and developed by the specialists of the field

	System of phytocoenoses		System of synusia		
	Name	Suffix	Name	Suffix	Example
Concrete stand/ relevé	Phytocoenosis/Holocoenosis		Plant synusia/Merocoenosis		
Abstract unit	Syntaxon		Plant synusia/Merocoenon		
Main ranks of the hierarchical classification	Class	-etea	Meroclass	-uletea	<i>Neckeruletea complanatae</i>
	Order	-etalia	Meroorder	-uletalia	<i>Antitrichuletalia curtispindulae</i>
	Alliance	-ion	Federation	-ulion	<i>Lobarulion pulmonariae</i>
	Association	-etum	Union	-uletum	<i>Fabroniuletum pusillae</i>

2 | CHALLENGES AND POSSIBLE SOLUTIONS

2.1 | The whole and its parts

There is a long discussion in different sciences about the "part-whole theory", sets and subsets, and "mereology" (see Husserl, 1901; Whitehead, 1929; Grattan-Guinness, 2000).

Already during the 6th International Botanical Congress in Amsterdam in 1935, different schools of vegetation science suggested a clear separation between whole plant communities or associations on the one hand (Braun-Blanquet's approach) and their parts, called synusia or unions (Lippmaa's approach and the Scandinavian school), on the other hand (see Cain, 1936; Du Rietz, 1936; Pavillard, 1936; Lippmaa, 1939). However, the problem already faced back in 1935 was largely neglected afterwards. In any case we think that it is important to describe and analyse the whole and its parts separately, and to clarify which parts were intentionally not considered in vegetation plot records. It is crucial to know whether a species not occurring in the relevé was absent in the plot or was just not recorded for methodological reasons.

In the following, we refer to concrete plant assemblages with all their floristic elements as plant communities (phytocoenoses = holocoenoses, from Greek: *hólos* = whole), while concrete partial communities here are named synusia (= merocoenoses; from Greek: *méros* = part, portion). The term synusia (plural synusia) was originally introduced in a lecture by E. Rübél in 1917 to denote units within a plant association growing on different substrates, for instance a layer community or an epiphytic community (Barkman, 1973). Historically, "synusia" has been used by different authors in varying, sometimes narrower, sometimes wider senses, with concrete as well as abstract meaning (see review by Barkman, 1973). Here we use the term synusia in a wide sense and thus equivalent to merocoenosis, which, according to Barkman (1973), refers to any partial community delimited within a phytocoenosis based on taxonomic, functional, horizontal, vertical or temporal criteria or a combination thereof. For the sake of simplicity, we use synusia both in the concrete and in the abstract sense; if a distinction is desired, the terms merocoenosis (concrete) and merocoenon (abstract) might be

used (see Table 1). In this paper, we focus on the distinction between phytocoenoses and smaller cryptogam assemblages within these.

There are good reasons to study both synusia and phytocoenoses. However, for the sake of logical consistency and practical application one should not equalise these two categories, nor use the same terminology for both systems (Barkman, 1973; Gillet, 1986; Hobohm, 1998; Dengler, 2003). To use an analogy: mixing synusia and phytocoenoses in the same system (as in Mucina et al., 2016) is like building a classification of trees (e.g. a functional one) and including in the same system a classification of bark types at the same hierarchical levels.

2.2 | Recording all plants or subsets?

To restrict sampling of plants to a certain stratum or taxonomic group is legitimate, and such a choice depends on the particular objectives (Nimis, 1991). However, this methodological decision should be clearly declared in the corresponding methods section! Many relevés of bryophyte "communities" ignore lichens and vascular plants that grow intermingled with them, and vice versa; relevés of *Lemnetea* communities often ignore the submerged macrophytes below the floating duckweeds; and, as indicated above, many phytosociologists generally ignore the terricolous bryophytes and lichens in their plots. According to our understanding, by contrast, only microscopic algae, (cyano-)bacteria and non-lichenised fungi should, normally, not be considered in vegetation classification as a field-based method (Berg, Ewald, Berg, & Hobohm, 2018).

To be as informative as possible, phytosociological classifications should be principally based on complete plant communities, i.e., all plants and other macroscopic photoautotrophic organisms of a section of the Earth's surface (see Dengler et al., 2008). This means that, in principle, all species should be considered that occur in the vertical projection above a certain ground area, which includes also epiphytic species as well as those growing on specific substrata within the plot, such as rocks and wood debris. Evidently, not in all cases all components of a phytocoenosis can be recorded completely due to methodological constraints (e.g. it would be very challenging to achieve a complete record of the epiphytes on branches), and this is also not needed for the majority of purposes, including classification.

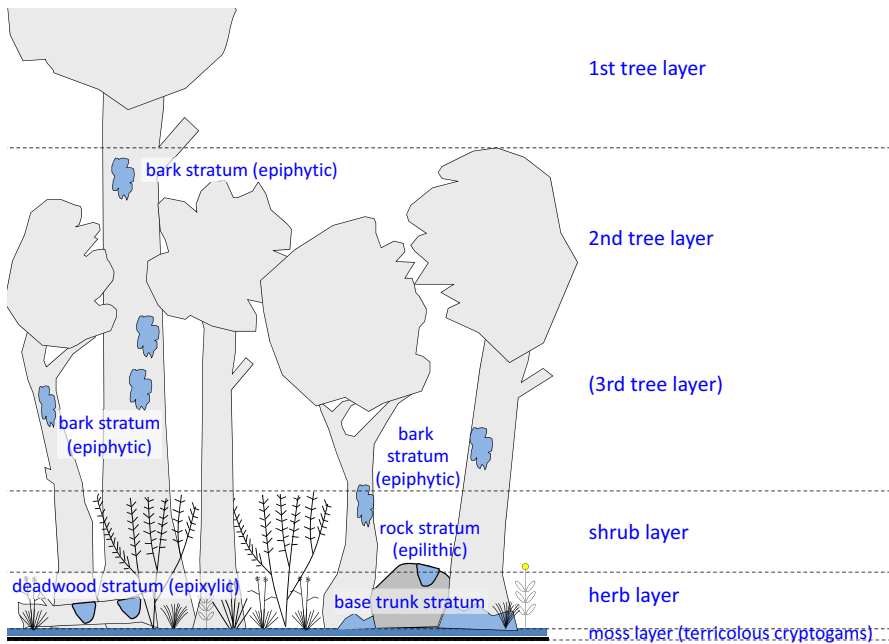


FIGURE 1 Example of a forest phytocoenosis composed of several different synusiae. They comprise on the one hand the vertical strata (layers), on the other hand the substrate strata. If needed, the main strata can be further subdivided, e.g. the tree layer into an upper (1st) and a lower (2nd) tree layer and the epiphytic stratum into a stem stratum and a base trunk stratum. For a possible comprehensive system of strata and substrata, see the proposal of Dengler (2003: p. 136)

We believe that terricolous non-vascular plants are needed for a sound classification of community types in which they constitute, in some cases, a major part of the biodiversity and biomass (e.g. in mires and rocky outcrops). On the other hand, classification results will hardly be affected by the omission of non-vascular plants in vegetation types in which these species play a subordinate role (e.g. mesic grasslands and ruderal communities). Thus, while emphasising that conceptually bryophytes, lichens and macro-algal assemblages are elements of the phytocoenoses in which they occur, we do not suggest that they need to be recorded for all possible purposes. Likewise, large phytosociological databases such as EVA (Chytrý et al., 2016) and sPlot (Bruehlheide et al., 2019) are invaluable tools for numerous studies even though the majority of their data contain only records of the vascular plant component or, in some sPlot datasets, even only of the woody component. For proper handling of the different degrees of completeness of vegetation-plot records, it is crucial to document precisely which elements were considered. Only then it is possible to distinguish whether the absence of cryptogams in a relevé means absence in the stand or only intentional non-recording.

2.3 | The dependency argument

Some authors (Barkman, 1973; Hobohm, 1998; Dengler, 2003) claim that a cryptogam synusia inside a plant community depends on the latter in the sense that it would not have the same composition if the vegetation structures were absent. Mucina et al. (2016) and Bültmann (2012), by contrast, argue that the dependency does not provide sufficiently clear and manageable evidence to distinguish plant communities and cryptogam-rich merocoenoses. Indeed, while nobody seriously can question the dependence of epiphytic cryptogam assemblages from the trees they grow on, the situation is less clear-cut for, e.g., rock-dwelling (saxicolous) assemblages. To

consider all cryptogam assemblages (for example on rocks) as dependent on surrounding vascular plant communities seems to be as wrong as the statement “[lichen] communities on rock are indisputable independent” (Bültmann, 2012: p. 11). Both situations can occur, cryptogams on rocks can be part of forests rich in montane blocks as well as of rocky grassland (e.g. *Sedo-Scleranthetea*, *Halacsyetalia sendtneri*), or specialised rock, talus and stonewall vegetation types (e.g. *Schistidieta apocarpis*, *Rhizocarpetea geographici*).

We conclude that the dependency argument is too theoretical and the term “dependence” is used too differently to provide a good criterion for differentiation in practice. What remains is that some bryophyte and lichen assemblages are obviously parts of plant communities, in the sense that they share the same space on the Earth’s surface. At least these represent a different conceptual category than “normal” phytocoenoses.

2.4 | The layer argument

Du Rietz (1966) distinguished synusiae from plant communities by their multi-layer structure. This sounds easy and practicable. However, Bültmann (2012) argued that even lichen communities could consist of a crustaceous lichen layer and a foliose lichen layer. If we break down the scale further, lichens themselves consist of different layers, and finally lichens can be considered as ecosystems of their own, harbouring various functionally different microbial communities (Grube, Cardinale, Castro, Müller, & Berg, 2009). Whatever we do, without definition of a scale, many arguments fail.

On the other hand, many parts of the vegetation cover on Earth consist of single layers only, e.g. the herbs in a salt marsh, where there is neither a moss nor a shrub layer, or rock vegetation, comprises non-vascular plants only. Not considering such assemblages as phytocoenoses (and thus not to classify them as syntaxa) would make no sense from either a theoretical or a practical point-of-view.

2.5 | The role of grain size

It is generally accepted that spatial scale, in particular the grain size used for analyses, influences the perception of ecological patterns (Shmida & Wilson, 1985; Levin, 1992; Chiarucci, 2007). It has been shown that species richness (Crawley & Harral, 2001; Wilson, Peet, Dengler, & Pärtel, 2012), biodiversity patterns along gradients (Siefert et al., 2012; Turtureanu et al., 2014), vegetation–environment relationships (Reed, Peet, Palmer, & White, 1993; Otýpková & Chytrý, 2006) and plant–plant interactions (Herben, Mandák, Bímová, & Münzbergová, 2004) are all strongly dependent on grain size. While it appears evident that these strong relationships must influence vegetation classification, effects of different plot sizes have only very rarely been taken into account in this field. Chytrý and Otýpková (2003) illustrate this in their Figure 1: while based on a 200-m² plot their stand would be classified in the class *Quercetea pubescentis*, a 16-m² plot within the same stand could belong to the *Festucion valesiacae* (*Festuco-Brometea*), a 4-m² plot to the *Alyssoidis-Sedion* (*Sedo-Scleranthetea*), and we might add that at even smaller grain size of perhaps 0.1 m² one could find the cryptogam class *Psoretea decipiens*. Chytrý and Otýpková (2003) concluded that relevés of different plot size should not be classified in the same system. In a more formal way, Dengler, Löbel, and Dolnik (2009) demonstrated that species constancies depend on plot size. Since the large majority of current classification approaches is based on species presences (rather than cover), and diagnostic species are determined by constancies in different groups, it is evident that classification outcomes must be influenced by plot sizes. Dengler et al. (2009) also conclude that if very different plot sizes are used, separate VCSs are required and comparisons (e.g. determination of diagnostic species) are only possible within but not across these.

However, common practice in phytosociology still is to choose plot sizes based on the vague ideas of *minimum area*, *representativeness* and *homogeneity* of the vegetation (Braun-Blanquet, 1964; Dierschke, 1994). All these criteria depend themselves on scale. Dengler (2003) demonstrated that there is no objective way to determine minimum areas, and thus the whole concept is flawed and should be abandoned. With regard to representativeness, Chytrý and Otýpková (2003) argue that this term inevitably involves circular reasoning because how representative a plot is can only be tested after sampling, not before. Levels of homogeneity, finally, can change several times when altering the plot size (Fryday, 2001; Berg, Schwager, Pörtl, & Dengler, 2016).

The only solution seems to be to define plot size a priori through methodological agreement. Accordingly, Chytrý and Otýpková (2003), Dengler (2003) and Berg et al. (2016) suggested standard plot sizes. Then, plot size could be a simple and practicable criterion to separate synusiae from phytocoenoses. For example, following Berg et al. (2016), any plant assemblage recorded on <1 m² would automatically be considered as a synusia.

There is also an upper threshold, perhaps not for plant communities themselves, but certainly for recording them. We suggest that this could be 1,000 m², an area beyond which it gets more and more impossible to record a complete species list or to estimate cover

values. In fact, plot sizes of above 1,000 m² have extremely rarely been used in phytosociology (Chytrý & Otýpková, 2003). We agree with Chiarucci (2007) that plant communities are operational units and thus the proper size of recording them cannot be defined by their properties, but only by convention.

2.6 | Cover of taxonomic groups as criterion for supra-classification?

Mucina et al. (2016) used a new supra-classification criterion to separate their three VCSs: the dominance of certain plant groups (vascular plants, “bryophytes and lichens”, “algae” including cyanobacteria). These groups, except the first, however, comprise phylogenetically unrelated taxa, and each of them is extremely heterogeneous in functional and ecological terms. Moreover, spermatophytes, clubmosses, ferns, mosses, liverworts, thallose and crustose lichens, charophytes and other macro-algae co-occur in different proportions in different ecological situations and at different scales. Such an approach is also undermined by situations where the dominance of cryptogams can change at the lowest level within a single plant association. For example, the *Corniculario aculeatae-Corynephorum canescentis* can be dominated by lichens, bryophytes or grasses at the smallest space; likewise, dominance in the *Sphagnetum magellanici* can vary between *Sphagnum* and *Eriophorum*. Nobody would subordinate *Sphagnum*-dominated bog vegetation (*Oxycocco-Sphagnetea*), freshwater springs dominated by *Palustriella commutata* or *Philonotis fontana* (*Montio-Cardaminetea*), or duckweed vegetation dominated by *Ricciocarpos natans* or *Riccia fluitans* (*Lemnetea*) to some bryophyte and lichen classes, not even Mucina et al. (2016). We argue that the dominance of bryophytes, lichens or algae alone does not provide ecological or functional information that would justify their use for the separation of different VCSs.

3 | CONCLUSIONS FOR FUTURE VEGETATION SURVEYS

3.1 | Definitions of phytocoenoses and synusiae

Phytocoenoses (holocoenoses, plant communities) are assemblages of all macroscopic photoautotrophic organisms (vascular plants, bryophytes, lichens, macro-algae) that cover a contiguous part of the Earth's surface of at least of 1 m² and at maximum 1,000 m² across a vegetation period (year). For practical reasons, phytocoenoses might be represented by subsets that contain at least the dominant layer(s) and possibly only those present at one point of time.

Synusia (merocoenoses) are (a) taxonomical, structural, functional or within-year temporal subsets of phytocoenoses that are recorded on any plot size under intentional omission of other macroscopic plants of a phytocoenosis, or (b) any such complete or partial plant assemblage recorded on <1 m² of soil, rock, live or dead plant material. They can be considered as parts of phytocoenoses, describing the internal structure and heterogeneity of these.

3.2 | Phytocoenoses and synusiae should be classified in different systems and named according to different nomenclature rules

Since synusiae are conceptually different from phytocoenoses and are usually recorded on different spatial scales, they should be classified in two separate systems. To avoid confusion, the suffixes used for the respective hierarchical levels of classification should be different (for a possible solution, see Table 1). Appendix S1 lists the required changes to make the ICPN the ruling code for phytocoenoses, while researchers dealing with synusiae can easily develop a similar set of rules for their purposes if desired.

3.3 | Additional strata for non-terricolous species

As suggested by Wilmanns and Bibinger (1966), Schuhwerk (1986), Hobohm (1998) and Dengler (2003), it is both possible and advantageous to record non-terricolous merocoenoses, such as epiphytes, in normal vegetation relevés. The straightforward solution for doing so is to define in addition to the usual four *vertical strata* – tree, shrub, herb and “moss” (terricolous cryptogam) layer – additional *substrate strata*. Dengler (2003: p. 136) proposed four such substrate strata: water, other plants (epiphytic species), wood debris (lignicolous species) and stones and rocks (saxicolous species). Similar to the subdivision of the tree layer into several sublayers, each of the substrate strata can be further subdivided. The epiphytic stratum, for example, can be divided into species growing on trunk bases, stems, branches and leaves (epiphyllic) or into vascular and non-vascular epiphytes (Figure 1). In these additional layers, species are then comprehensively recorded for the whole extent of the plot of the phytocoenosis, just as is done in the vertical strata. There are not many examples of this approach, but Boch and Dengler (2006) did it for the classification of dry grasslands on Saaremaa, Estonia, with their very rich non-terricolous components. Another way to proceed would be to sample only subsets of each stratum, classify them to synusiae and describe the phytocoenosis as the combination of these synusiae instead of the combination of species (Schuhwerk, 1986; Hobohm, 1998; Gillet & Julve, 2018). This approach has two disadvantages, however: (a) it requires a formal classification of the synusiae, which is time-consuming and introduces additional fuzziness, and (b) it does not provide a complete species list for the phytocoenosis.

4 | IMPLICATIONS FOR PHYTOSOCIOLOGICAL NOMENCLATURE

A main reason for the confusion around the distinction of phytocoenoses vs synusiae is the International Code for Phytosociological Nomenclature (Weber et al., 2000) itself. While the first sentence of definition 1 defines syntaxa within ICPN as abstract units of phytocoenoses, i.e., holocoenoses, which would be consistent with our

suggestion, the second sentence in this definition directly contradicts the first when stating: “*The abstract units of bryophyte, lichen or other cryptogamic communities are also considered as syntaxa when they are treated as particular communities defined by floristic-sociological criteria despite the fact that they do not always correspond to phytocoenoses.*” The fundamental change required in the forthcoming fourth edition of the ICPN to ensure both more logic and more practicability thus would be to remove/change this contradictory statement. While the understanding of the meaning of phytocoenosis by the ICPN seems to be similar to ours (i.e., their second sentence essentially acknowledges that cryptogam synusiae are something different from phytocoenoses), the ICPN would benefit from including a definition of the term “phytocoenosis”, on which much of its rules build. In future editions of the ICPN it should be clarified that synusiae, whether cryptogamic as discussed here, or composed of isolated vascular tree, shrub or herb layers (as e.g. the *Anemone nemorosae-Caricetea sylvaticae* proposed by Julve, 1993), cannot be valid syntaxa. Further, a mechanism should be introduced to remove and formally rename those types of merocoenoses described in the past as regular syntaxa. Notwithstanding a few borderline cases, this issue can be solved by slightly adjusting Articles 3 (*Causes of invalid publication of names*) and 37 (*Rejection of a nomen dubium*) of the ICPN. We present all the proposed changes of the ICPN in Appendix S1 in a way that could be used directly to create the future ICPN edition.

As stated, the study of synusiae is a valid and important aim in vegetation science, which merits a separate system of formal classification. Since only a relatively small number of researchers deals with this topic and this group is only marginally overlapping with the much larger group of people classifying phytocoenoses, we recommend that the former specialists set up their own rules. This will allow them to define principles that suite their purposes best (e.g. whether all synusiae or only cryptogam-dominated ones should be classified). The only critical point is that they should use separate ranks and names clearly distinct from normal phytocoenoses for their units (see Table 1).

5 | IMPLICATIONS FOR THE EUROPEAN SYSTEM OF SYNTAXA

Mucina et al. (2016) should be merited for drawing due attention to the role of bryophytes, lichens and algae for vegetation classification purposes. The fact, however, that they placed the majority of community types with dominant bryophytes, lichens and macroalgae not in their main vegetation classification system (EVC1), but in two separate VCSs (EVC2 and EVC3) will probably achieve the opposite. Most researchers will simply ignore EVC2 and EVC3 and not realise that, among many synusiae, they also contain a considerable number of “real” phytocoenoses. For example, the classification underlying the European Red List of habitats (Janssen et al., 2016) was largely based on higher-rank units of EVC1, while the authors refrained from extracting the relevant entities of EVC2

and EVC3 even in cases where they account for the major part of the respective habitat type as in some rock and scree communities. Therefore, some major vegetation types dominated by cryptogams and covering considerable spatial extent in Europe were excluded from the conservation assessment.

In this respect, the EcoVeg Approach used for the US National Vegetation Classification (USNVC) is a better practice, as it includes all landscape-scale vegetation types irrespective whether they are dominated by vascular plants, bryophytes or lichens (Faber-Langendoen et al., 2014). For example, on their highest classification level, three of the seven units are mainly or completely dominated by cryptogams, 4. *Polar & High Montane Scrub, Grassland & Barren [Cryomorphic Scrub, Herb & Cryptogam Vegetation]*, 5. *Aquatic Vegetation [Hydromorphic Vegetation]* (with 5.A.1. *Floating and Suspended Macroalgae Saltwater Vegetation*, 5.A.2. *Benthic Macroalgae Saltwater Vegetation* and 5.A.4. *Benthic Lichen Saltwater Vegetation*) and 6. *Open Rock Vegetation [Cryptogam – Open Mesomorphic Vegetation]*.

The IAVS Working Group EVS has established a scientific committee (see <http://euroveg.org/evc-committee>) to improve the EuroVegChecklist successively, based on well-founded suggestions from researchers. We recommend thus to revise the EuroVegChecklist in a way that instead of three separate VCSs there is only one, but which exclusively comprises phytocoenoses in the sense of holocoenoses, which are useful for a landscape-scale analysis. By contrast, the remaining purely synusial (merocoenotic) classes might be removed altogether or placed in a separate VCS with different terminology (except the classes based on microorganisms; Berg et al., 2016). We provide a preliminary suggestion which of the classes in the EuroVegChecklist falls into which category (Appendix S2).

6 | CONCLUSIONS AND OUTLOOK

Bryophytes, lichens and macro-algae are ecologically important, but understudied elements of many ecosystems and can make a significant contribution to the delimitation and characterisation of vegetation types (Dierßen, 2001; Berg & Dengler, 2005). They should therefore be treated as equivalent components and potential diagnostic species of plant communities (holocoenoses). The vegetation of partial communities of certain structural, taxonomic or functional components (merocoenoses) should be classified in a separate system of synusiae. We recommend to the committees in charge to make this distinction explicit in the ICPN as well as in further editions of the checklist of European vegetation types (EuroVegChecklist).

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AUTHOR CONTRIBUTIONS

CB conceived the idea for this contribution, which then was drafted by him and afterwards revised by all co-authors.

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REFERENCES

- Barkman, J. J. (1973). Synusial approaches to classification. In R. H. Whittaker (Ed.), *Ordination and classification of communities* (pp. 435–491). The Hague, The Netherlands: Junk.
- Barkman, J. J. (1969). Epiphytengemeinschaften. In V. Westhoff & A. J. Held [Hrsg.] (Eds.), *DEN:Plantengemeinschaften in Nederland* (pp. 272–286). Zutphen, Netherlands: Thieme.
- Berg, C., & Dengler, J. (2005). Moose und Flechten als diagnostische Arten von Pflanzengesellschaften – eine Übersicht aus Mecklenburg-Vorpommern. *Herzogia*, 18, 145–161.
- Berg, C., J. Dengler, & A. Abdank (Eds.) (2001). *Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung – Tabellenband*. Jena, Germany: Weissdorn.
- Berg, C., J. Dengler, A. Abdank, & M. Isermann (Eds.) (2004). *Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung – Textband*. Jena, Germany: Weissdorn.
- Berg, C., Ewald, J., Berg, G., & Hobohm, C. (2018). What are the organic elements of vegetation science? *Applied Vegetation Science*, 21, 341–344. <https://doi.org/10.1111/avsc.12371>
- Berg, C., Schwager, P., Pörtl, M., & Dengler, J. (2016). Plot sizes used for bryophyte and lichen communities in Europe. *Herzogia*, 29, 654–667.
- Boch, S., & Dengler, J. (2006). Floristische und ökologische Charakterisierung sowie Phytodiversität der Trockenrasen auf der Insel Saaremaa (Estland). *Arbeiten Aus Dem Institut Für Landschaftsökologie Münster*, 15, 55–71.
- Braun-Blanquet, J. (1964). *Pflanzensoziologie – Grundzüge der Vegetationskunde*, 3rd ed. Vienna, Austria: Springer.
- Bruehlheide, H., Dengler, J., Jiménez-Alfaro, B., Purschke, O., Hennekens, S. M., Chytrý, M., ... Zverev, A. (2019). sPlot – a new tool for global vegetation analyses. *Journal of Vegetation Science*, 30, 161–186. <https://doi.org/10.1111/jvs.12710>
- Bültmann, H. (2012). The Lichen syntaxa in the checklist of higher syntaxa of Europe – an overview and what we can do with them. *Annali Di Botanica – Coenology and Plant Ecology*, 2, 11–18.
- Cain, S. A. (1936). Synusiae as a basis in plant sociological field work. *The American Midland Naturalist*, 17, 665–672.
- Chiarucci, A. (2007). To sample or not to sample? That is the question ... for the vegetation scientist. *Folia Geobotanica*, 42, 209–216. <https://doi.org/10.1007/BF02893887>
- Chytrý, M. (Ed.) (2007). *Vegetation of the Czech Republic – 1. Grassland and heathland vegetation [in Czech, with English summary]*. Praha, Czech Republic: Academia.
- Chytrý, M., Hennekens, S. M., Jiménez-Alfaro, B., Knollová, I., Dengler, J., Jansen, F., ... Yamalov, S. (2016). European Vegetation Archive (EVA): An integrated database of European vegetation plots. *Applied Vegetation Science*, 19, 173–180. <https://doi.org/10.1111/avsc.12191>
- Chytrý, M., & Otýpková, Z. (2003). Plot sizes used for phytosociological sampling of European vegetation. *Journal of Vegetation Science*, 14, 563–570. <https://doi.org/10.1111/j.1654-1103.2003.tb02183.x>

- Chytrý, M., Tichý, L., Holt, J., & Botta-Dukát, Z. (2002). Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science*, 13, 79–90. <https://doi.org/10.1111/j.1654-1103.2002.tb02025.x>
- Crawley, M. J., & Harral, J. E. (2001). Scale dependence in plant biodiversity. *Science*, 291, 864–868. <https://doi.org/10.1126/science.291.5505.864>
- De Cáceres, M., Chytrý, M., Agrillo, E., Attorre, F., Botta-Dukát, Z., Capelo, J., ... Wiser, S. K. (2015). A comparative framework for broad-scale plot-based vegetation classification. *Applied Vegetation Science*, 18, 543–560. <https://doi.org/10.1111/avsc.12179>
- Dengler, J. (2003). Entwicklung und Bewertung neuer Ansätze in der Pflanzensoziologie unter besonderer Berücksichtigung der Vegetationsklassifikation. *Archiv Naturwissenschaftlicher Dissertationen*, 14, 1–297.
- Dengler, J., Chytrý, M., & Ewald, J. (2008). Phytosociology. In S. E. Jørgensen, & B. D. Fath (Eds.), *Encyclopedia of ecology* (pp. 2767–2779). Oxford, UK: Elsevier.
- Dengler, J., Löbel, S., & Dolnik, C. (2009). Species constancy depends on plot size – A problem for vegetation classification and how it can be solved. *Journal of Vegetation Science*, 20, 754–766. <https://doi.org/10.1111/j.1654-1103.2009.01073.x>
- Dierschke, H. (1994). *Pflanzensoziologie – Grundlagen und Methoden*. Stuttgart, Germany: Ulmer.
- Dierßen, K. (2001). Distribution, ecological amplitude and phytosociological characterization of European bryophytes. *Bryophytorum Bibliotheca*, 56, 1–289.
- Du Rietz, G. E. (1936). Classification and nomenclature of vegetation units 1930–1935. *Svensk Botanisk Tidskrift*, 30, 580–589.
- Du Rietz, G. E. (1966). Biozönosen und Synusien in der Pflanzensoziologie. *Berichte Der Internationalen Symposien Der Internationalen Vereinigung Für Vegetationskunde*, 4, 23–42.
- Ewald, J. (2003). A critique for phytosociology. *Journal of Vegetation Science*, 14, 291–296. <https://doi.org/10.1111/j.1654-1103.2003.tb02154.x>
- Faber-Langendoen, D., Keeler-Wolf, T., Meidinger, D., Tart, D., Hoagland, B., Josse, C., ... Comer, P. (2014). EcoVeg: A new approach to vegetation description and classification. *Ecological Monographs*, 84, 533–561. <https://doi.org/10.1890/13-2334.1>
- Fryday, A. M. (2001). Phytosociology of terricolous lichen vegetation in the Cairngorm Mountains, Scotland. *Lichenologist*, 33, 331–351. <https://doi.org/10.1006/lich.2001.0322>
- Gillet, F. (1986). Analyse concrète et théorique des relations à différents niveaux de perception phytoécologique entre végétation forestière et géomorphologie dans le Jura nord-occidental. *Colloques Phytosociologiques*, 13, 101–131.
- Gillet, F., & Julve, F. (2018). The integrated synusial approach to vegetation classification and analysis. *Phytocoenologia*, 48, 141–152. <https://doi.org/10.1127/phyto/2017/0164>
- Grattan-Guinness, I. (2000). *The search for mathematical roots 1870–1940*. Princeton, NJ: Princeton University Press.
- Grube, M., Cardinale, M., de Castro, J. V., Müller, H., & Berg, G. (2009). Species-specific structural and functional diversity of bacterial communities in lichen symbioses. *The ISME Journal*, 3, 1105–1115. <https://doi.org/10.1038/ismej.2009.63>
- Guarino, R., Willner, W., Pignatti, S., Attorre, F., & Loidi, J. J. (2018). Spatio-temporal variations in the application of the Braun-Blanquet approach in Europe. *Phytocoenologia*, 48, 239–250.
- Herben, T., Mandák, B., Bímová, K., & Münzbergová, Z. (2004). Invasibility and species richness of a community: A neutral model and a survey of published data. *Ecology*, 85, 3223–3233.
- Hobohm, C. (1998). Pflanzensoziologie und die Erforschung der Artenvielfalt – Überarbeitete und erweiterte Fassung der an der Universität Lüneburg eingereichten und angenommenen Habilitationsschrift. *Archiv Naturwissenschaftlicher Dissertationen*, 5, 1–231.
- Husserl, E. (1901). *Logische Untersuchungen. Zweiter Teil: Untersuchungen zur Phänomenologie und Theorie der Erkenntnis*. Halle, Germany: Max Niemeyer.
- Janssen, J. A. M., Rodwell, J. S., Garcia Criado, M., Gubbay, S., Haynes, T., Nieto, A., ... Valachovič, M. (2016). *European Red List of Habitats – Part 2. Terrestrial and freshwater habitats*. Luxembourg, Luxembourg: European Union.
- Julve, P. (1993). Synopsis phytosociologique de la France (communautés de plantes vasculaires). *Lejeunia N. S.*, 140, 1–160.
- Klement, O. (1955). Prodröm der mitteleuropäischen Flechtengesellschaften. *Feddes Repertorium Beihefte*, 135, 1–194.
- Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology*, 73, 1943–1967.
- Lippmaa, T. (1939). The unistratal concept of plant communities (the unions). *The American Midland Naturalist*, 21, 111–145. <https://doi.org/10.2307/2420378>
- Marsteller, R. (2006). Syntaxonomischer Konspekt der Moosgesellschaften Europas und angrenzender Gebiete. *Hausknechtia Beiheft*, 13, 1–192.
- Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Raus, T., Čarni, A., ... Tichý, L. (2016). Vegetation of Europe: Hierarchical floristic classification system of plant, lichen, and algal communities. *Applied Vegetation Science* 19(Suppl. 1), 3–264.
- Nimis, P. L. (1991). Developments in lichen community studies. *Lichenologist*, 23, 215–225. <https://doi.org/10.1017/S0024282991000385>
- Pavillard, J. (1936). La nomenclature phytogéographique devant le Congrès d'Amsterdam. *Station Internationale De Géobotanique Méditerranéenne Et Alpine, Communication*, 46, 1–7.
- Reed, R. A., Peet, R. K., Palmer, M. W., & White, P. S. (1993). Scale dependence of vegetation-environment correlations: A case study of a North Carolina piedmont woodland. *Journal of Vegetation Science*, 4, 329–340. <https://doi.org/10.2307/3235591>
- Schaminée, J. H. J., A. H. F. Stortelder, & V. Weesthoff (Eds.) (1995). *De vegetatie van Nederland – Deel 1. Inleiding tot de plantensociologie – grondslagen, methoden en toepassingen*. Uppsala, Sweden: Opulus.
- Schuhwerk, F. (1986). Kryptogamengemeinschaften in Waldassoziationen – ein methodischer Vorschlag zur Synthese. *Phytocoenologia*, 14, 79–108. <https://doi.org/10.1127/phyto/14/1986/79>
- Shmida, A., & Wilson, M. V. (1985). Biological determinants of species diversity. *Journal of Biogeography*, 12, 1–20. <https://doi.org/10.2307/2845026>
- Siefert, A., Ravenscroft, C., Althoff, D., Alvarez-Yépez, J. C., Carter, B. E., Glennon, K. L., ... Fridley, J. D. (2012). Scale dependence of vegetation-environment relationships: A meta-analysis of multivariate data. *Journal of Vegetation Science*, 23, 942–951. <https://doi.org/10.1111/j.1654-1103.2012.01401.x>
- Turtureanu, P. D., Palpurina, S., Becker, T., Dolnik, C., Ruprecht, E., Sutcliffe, L. M. E., ... Dengler, J. (2014). Scale- and taxon-dependent biodiversity patterns of dry grassland vegetation in Transylvania (Romania). *Agriculture, Ecosystems and Environment*, 182, 15–24. <https://doi.org/10.1016/j.agee.2013.10.028>
- von Hübschmann, A. (1986). Prodröm der Moosgesellschaften Zentraleuropas. *Bryophytorum Bibliotheca*, 32, 1–413.
- Weber, H. E., & Moravec, J. & Theurillat, J.-P. (2000): International Code of Phytosociological Nomenclature. 3rd edition. *Journal of Vegetation Science*, 11(5), 739–768. <https://doi.org/10.2307/3236580>.
- Whitehead, A. N. (1929). *Process and reality: An essay in cosmology*. New York, London: Free Press.
- Wilmanns, O. (1970). Kryptogamen-Gesellschaften oder Kryptogamen-Synusien? *Berichte Der Internationalen Symposien Der Internationalen Vereinigung Für Vegetationskunde*, 10, 1–7.
- Wilmanns, O., & Bibinger, H. (1966). Methoden der Kartierung kleinflächiger Kryptogamengemeinschaften. *Botanische Jahrbücher*, 85, 509–521.



Wilson, J. B., Peet, R. K., Dengler, J., & Pärtel, M. (2012). Plant species richness: The world records. *Journal of Vegetation Science*, 23, 796–802. <https://doi.org/10.1111/j.1654-1103.2012.01400.x>

Wirth, V. (1995). *Die Flechten Baden-Württembergs*, 2nd ed. Stuttgart, Germany: Ulmer.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

APPENDIX S1 Recommended changes for the 4th edition of the

International Code of Phytosociological Nomenclature

APPENDIX S2 Vegetation classes of the EuroVegChecklist (Mucina et al., 2016) that would be partly or fully affected by alteration, if synusia are excluded from the syntaxonomic system of phytocoenoses

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