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FORUM

A critique for phytosociology

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Abstract. Phytosociology is a subdiscipline of plant ecology that describes the co-occurrence of plant species in communities. Gradient analysis and classification are its complementary tools. Various peculiarities and anachronisms of Central European phytosociology conceal its similarity with Anglo-American approaches. Phytosociology deserves to be updated as a part of modern vegetation science that can build on a vast heritage of high-quality data and the tools to store and analyse them in ways that go beyond syntaxonomy. By providing a context to more specialized pure and applied research, it has a crucial role to play in understanding community structure, ecosystem functioning and biological evolution.

Keywords: Braun-Blanquet approach; Classification; Ordination; Plant community ecology.

Abbreviations: AAPE = Anglo-American plant ecology; CEPS = Central European phytosociology; PS = Phytosociology.

Introduction

I recently received a review of an analysis based on a large phytosociological database suggesting that I expunged the term ‘phytosociological’ as being reserved for Central European hierarchical classification. On the verge of following the editor’s advice, I had second thoughts about phytosociology: is it a natural history tradition, a regional vegetation classification, a genuine subdiscipline of plant ecology, or a synonym for plant community ecology? Do we still need the term and its content in vegetation science? A forum discussion on phytosociology may make clear that these questions are far from personal, as many plant ecologists move from ‘descriptive’ phytosociology to ‘causal’ explanation, and others yet find themselves turning back to description. Instead of writing a history of phytosociology and its varied schools, which has been done in earlier reviews (e.g. Whittaker 1973; van der Maarel 1975; Mucina & van der Maarel 1989), I shall reflect on some assumptions, aims and flaws of its traditional Central European form and explain why phytosociology in the broad sense remains a useful and important discipline. I hope the fine line between criticism and critique, as a constructive mode of inquiry, remains discernible throughout this contribution.

What is phytosociology?

Phytosociology (PS) deals with plant species co-occurrences, or, in other words, compositional patterns and gradients at the ‘grain’ of the plant community. As a subdiscipline of plant community ecology and vegetation science, PS works with a set of assumptions and techniques to compare floristic composition among communities. PS data are analysed by gradient analysis, classification and other multivariate methods. Hence PS is broader than the restricted view of the editor of my paper and others suggest, restricting PS to a particular school of classification. Both classification and ordination have a place in vegetation science (Kent & Coker 1992) and modern statistical ecology texts stress the common numerical basis of both approaches (Legendre & Legendre 1998). Just as ANOVA and linear regression are closely related bivariate procedures, multivariate clustering and gradient analysis can be seen as poles in a common body of methods. There is no reason not to call this genuine approach to the study of plant communities phytosociology even if many ecologists would rather avoid the term because of its identification with Central European phytosociology.

What is Central European phytosociology (CEPS)?

I view CEPS as typical complementary analysis. Describing its logic as an algorithm should encourage the numerically-minded ecologist to take CEPS as a method seriously. Typically, CEPS starts with local studies of relatively small areas (e.g. a valley, a nature reserve), where preliminary classifications are carried out and translated into local descriptions and maps (Fig. 1, left column). Visually discernible vegetation types are sampled by recording plant species composition and

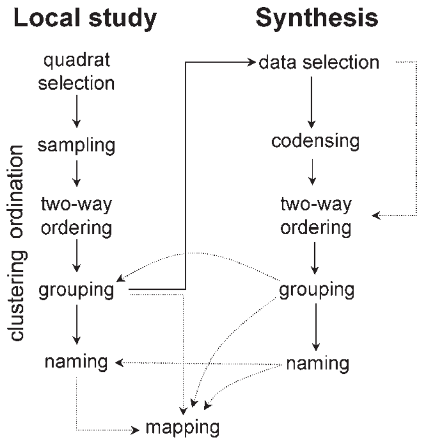

Fig. 1. Structure of Central European phytosociological research and its analogy to multivariate statistics; dashed lines show optional pathways including the feedback from synthetic to subsequent local work.

dominance in plots (quadrats or relevés). A subset of CEPS studies uses transects or permanent plots to measure particular temporal or spatial sequences, which are also analysed by delimiting vegetation types.

The crucial step of data analysis is the so-called table work: plot data are assembled in a rectangular species-by-plot matrix, in which species and plots are sorted, until an optimal diagonal arrangement of species incidences is reached (e.g. Dierschke 1994). The matrix is then partitioned into plot groups (community types) and species groups (differential species) that can be used to discriminate between the former.

At a higher level, published data from many local studies are included in a meta-analysis (Fig. 1, right column) in which broad-scale compositional patterns emerge and are forged into new classifications and a hierarchy of higher syntaxa. In the days of manual table work aggregated data, namely the constancy of species in locally defined clusters ('operational syntaxonomic units'), formed the starting point of such higher level analysis (Dierschke 1994). The synoptic species-by-community type matrix was then subjected to a sorting process equivalent to that in local analysis, yielding a diagonal structure partitioned by groups of community types and corresponding differential species. Contrary to the traditional method, modern computerized algorithms permit the processing of virtually unlimited numbers of single plots from many locations.

Being based on the same data, local and synthetic CEPS classifications (Fig. 1) are mutually related in non-trivial ways. Being built from the bottom (locally defined units) to the top (synthetic units), the traditional system is often called 'inductive'. Contrary to this, numerical algorithms assign every individual plot according to its relative position in the chosen universe of investigation, with the consequence that plot groups found in local studies may be divided during higher level analysis. Thus, methodological choices conceal different hierarchies of scale, that account for the different outcomes of traditional CEPS and numerical syntaxonomy. Conversely, even where it was built in a bottom-up process, synthetic classification may inspire subsequent local CEPS work by imposing its definition and naming of vegetation types in a top-down fashion.

Regardless of its scale, CEPS tabular classification is a two-way matrix ordering process, that involves the extraction of a gradient in rows and columns and its division into groups of vegetation types and differential species. Lower-order gradients orthogonal to the main diagonal in a table are expressed by nesting the table in a way that points to recurring groups of differential species.

In summary, CEPS does not differ fundamentally from other approaches of analysing compositional vegetation patterns (Fig. 1). In fact, it has been repeatedly attempted to mimic CEPS numerically (e.g. Hill 1979; Wildi 1989; Bruelheide 1995).

What is special about CEPS?

Idiographic science

Trepl (1994) explained the tension between CEPS and Anglo-American plant ecology (AAPE) by juxtaposing idiographic and nomothetic science – the former dedicated to describing unique structures, the latter to finding a-historic universal laws (Windelband 1901). Rooted in local natural history, CEPS dwells on an intimate knowledge of flora, vegetation and landscape, which deserve preservation as special historical phenomena. Description, comparison and classification of plant communities serve the purpose of putting their uniqueness in perspective. Until very recently, a monograph about the vegetation of a particular area would have been a standard academic CEPS thesis and CEPS periodicals would print tabulated plot data in full. It adds to the impressiveness of CEPS work to describe new community types. In AAPE this is considered natural history and not science, which is about reducing complexity to simple equations and testable predictions (McIntosh 1985; Peters 1991). Dismissing plot data as merely descriptive, AAPE modernists may ignore the importance of natural history collections for biodiversity research (Berendsohn et al. 1999).

Appeals to pragmatism

CEPS seeks *ad hoc* solutions applicable in land use and conservation, in which there appears to be little room for theory and methodology. Consequently, some practitioners openly consider personal experience and subjectivity in placing, arranging and classifying plots as necessary (e.g. Dierßen 1990; Dierschke 1994). Data collection is often preceded by subjective pattern recognition, which is not only informed by individual experience but also by the collective knowledge of existing classifications (Fig. 1). Such bias can lead to an overrepresentation of certain 'typical' stands at the expense of poorly characterized, but common 'transitional' community types and to skewed estimates of species richness (Chytrý 2001). The preconceived pattern is once again enforced when a diagonalized table is cleaned of plots that are considered transitional, which artificially increases the fidelity of diagnostic species towards the emerging vegetation types. Such subjectivity may amount to sacrificing unprejudiced research in favour of satisfying a compulsion for neatness in the end product: in the worst case, data are merely collected to confirm a predefined classification. Quite contrary to this, AAPE strives to base its very applicability on repeatable sampling designs and modes of analysis.

Hierarchical formalism

CEPS's answer to scaling phenomena is a hierarchy of discrete scales for classification (patches/synusiae, stands/community types, landscapes/sigmeta etc., Gillet & Gallandat 1996; Wilmanns 1998). Species-area relationships are perceived as saturation curves (indicating a 'minimum area' for sampling) and step-shaped curves are expected in heterogeneous environments (Barkman 1968; Dierßen 1991). In other words, heterogeneity is thought of as a mosaic of homogeneous units that are waiting to be classified. Just as the vegetation types, these discrete levels are most often preconceived by experience and convention rather than based on objective pattern analysis (see Schmidtlein 1998 for an exception). Contrary to this, AAPE recognizes species-area curves as a fundamental scaling property, in which effects of sampling, heterogeneity and autocorrelation are superposed and often confounded (Rosenzweig 1995). Attention is focused on the range of underlying processes, which more often than not create individualistic spatial patterns of species and communities (Tilman & Kareiva 1997).

The power of names

Mimicking the rules of Linnean plant taxonomy and nomenclature, CEPS has formalized the standards for the description and naming of plant community types. With its codified hierarchical levels and naming and priority rules (Weber et al. 2000), syntaxonomy is meant to organize community classification as a decentralized and open-ended endeavour. However, the implied analogy between taxonomy and syntaxonomy is a superficial one, as syntaxonomy has no genealogy to reconstruct and community types are much harder to circumscribe than the vast majority of plant species. The fuzziness of vegetation types also makes it hard to operationalize their identification: very few syntaxonomical revisions give explicit keys or assignment algorithms for placing new plots into the system (e.g. Keller 1979; Bruelheide 1995). In contrast, academic AAPE does not appear to regard floristic vegetation classification as a scientific goal in itself, no matter how badly conservation may need it (e.g. Scott et al. 1993). If performed at all, classifications are less formal and their validity is constrained to a particular purpose of data analysis or mapping.

Contesting the essence of the community

CEPS takes the species analogy even further, when postulating a basic rank in the syntaxonomical hierarchy called association, which is thought of as an entity with emergent properties lending itself particularly well to typification (von Glahn 1968). Meanwhile, divergent interpretations of this concept have led to the separation of several schools of CEPS and their respective syntaxonomies. While some stress structural homogeneity as a key criterion (e.g. tree species dominance in forests, Passarge & Hofmann 1967), others have invoked the formal and qualitative criterion of 'character species' (absolute diagnostic or differential species) as necessary to preclude an inflation of associations (Dierschke 1994). Somewhat tautologically, character species define the very association that defines their status (Willner 2001). Furthermore, the status of character species depends strongly on the extent of an analysis, which has been addressed by designating arbitrary geographical (Mucina 1993) or conceptual limits to their validity (Bergmeier et al. 1990). All these attempts to ground the association are based on formal arguments rather than theory. Despite their regular appeal to practicality, the debates around them are as opaque to the average user of syntaxonomy as they are to scientists outside CEPS.

A relic?

Alone or in combination, these idiosyncrasies can be perceived as philosophical and methodological anachronisms. Less benevolent contemporaries will, therefore, either ignore CEPS or look at it as a relic outside the community of plant ecologists. They are unaware that failure to incorporate the essential aspects of CEPS into modern community ecology deprives the field of empirical knowledge that is critical for understanding community structure and for providing the broader context in which particular ecological phenomena occur.

Infusing vegetation science with CEPS ideas requires adaptation to modern standards of exposing one's concepts and methods of sampling and data analysis. Perhaps more critically, CEPS is in danger of betraying its own goals, when practical goals of conservation and landscape ecology are compromised by poor methodology and vague or even inconsistent rules of implementation. CEPS classifications seem to work reasonably well for relatively small regions (e.g. Oberdorfer 1978: Southern Germany; Schaminée et al. 1995: The Netherlands) and for well-defined purposes, e.g. forest typology (Keller et al. 1998), provided they are based on thorough analyses of large phytosociological databases. Unfortunately, this does not prevent the mismatch of community definitions among adjacent or overlapping regional systems, which haunts international implementation as in the European Union's Natura 2000 network (Anon. 1992). The task of joining existing classifications is often reduced to problems of priority and nomenclature at the expense of empirical substance and operability. The heat of many a nomenclatural discourse may in fact overplay the absence of proper data analysis (as in Rennwald 2000). CEPS becomes counterproductive when classifications are based on small and selective datasets, or when data analysis is omitted altogether and subjective systems are proclaimed *ex cathedra*. This will make it difficult for later users to distinguish operational from formal, and thorough from superficial solutions in CEPS.

The future

How can the two goals of (1) merging the core concepts of CEPS with related strains in AAPE to form a modern science of plant species co-occurrence and of (2) safeguarding good practice in its application and implementation in the survey and conservation of natural resources be tackled? And do these tasks justify retention of the discipline of PS?

Beyond classification

CEPS (and its scattered counterparts worldwide) must replace its fixation on classification and formal hierarchies by appreciating gradient analysis as inherent in its own methodology and as complementary to its proximate goal. The question 'how is vegetation classified?' must be replaced by the more fundamental 'how can plant species co-occurrence be understood?' The latter question will include the first as a legitimate subset. This widening of horizons is greatly furthered by putting certain textbooks (e.g. Kent & Coker 1992; Legendre & Legendre 1998) and software packages (McCune & Mefford 1998; ter Braak & Šmilauer 1998) on the shelves of CEPS students, who must learn to ask questions beyond classification and frame their questions in a language that will also be understood in the AAPE community. Very likely, this will make the far-reaching equivalence of concepts such as sociological behaviour and niche apparent (Lawesson & Oksanen 2002) and prove the power of CEPS to contribute to the solution of problems like the definition of species pools (Zobel 1997; Dupré 2000).

The plot legacy

CEPS and AAPE should continue and revive their appreciation of vegetation plot data. Recording all visible plant species in a plot of defined size and position is the smallest methodological denominator in vegetation science (Mucina et al. 2000) and has produced immense amounts of compatible data. This field method is fundamental in the training of students in plant biodiversity research and conservation biology. Its neglect cuts off ecology's natural history roots and promotes an unhealthy detachment of theory and practice (Weiner 1995). CEPS's tradition of placing plot data in public archives is a precursor of biodiversity informatics (Berendsohn et al. 1999). The provision of a worldwide pool of plot data through electronic databanks (Hennekens & Schaminée 2001; Ewald 2001) has the potential of stimulating all kinds of meta-analyses, ranging from classical synthetic classifications to predictive mapping (Brzeziecki et al. 1993) and tests of hypotheses on functional traits (Bakker et al. 2000) and biodiversity (Austin 1999).

Biodiversity informatics

Increased data availability brings new chances and challenges. Multiple taxonomies must be managed on the levels of plant taxa (Berendsohn et al. 1999) and vegetation types (Anon. 2001). Data must be screened for quality and bias (Chytrý 2001) and stratified and subsampled prior to the analysis proper (Ewald 2002). Developing and evaluating data models and routines for these purposes is becoming a new field of research. Well-established procedures will subsequently be implemented and distributed in standard software packages (McCune & Mefford 1999; Tichý 2002). Shifting the current focus of phytosociological databanking from producing regional or national vegetation classifications to methodological and conceptual issues could initiate a worldwide exchange among phytosociologists and lead us to a much deeper understanding of community assembly.

Scaling revisited

Large databanks of spatially and temporally explicit plot data allow novel analyses of scaling phenomena in vegetation. Besides revealing the significance of sampling, filtering and aggregating data for the classification process, this could finally give classics such as Walter's (1954) law of relative site specificity and Oberdorfer's (1968) three-dimensional partitioning of community types a numerical underpinning (Diekmann

& Lawesson 1999). Databanks can also be used to estimate the parameters of species-accumulation curves, which can be linked up to biogeographic data like floristic atlases, giving access to ecological patterns at the mesoscale (Holt 1993).

Continued classification

Without doubt classification will remain an important field of applied PS where meaningful units for recognizing and mapping vegetation and habitats are needed on various levels of abstraction, scale and administration (Anon. 1992; Scott et al. 1993). We must take this task very seriously, but at the same time we should abandon the illusion of the ultimate all-purpose classification. We have to learn to treat classifications as conjectural models, that must be judged by explicit criteria of purpose, internal consistency, external validity and predictive capacity. Properly managed phytosociological databanks linked to data on landscape structure, environmental variables and plant traits provide the tool for this daunting task. Before a new classification is delivered to the users, it must undergo thorough checks of operability. Assignment rules must be made explicit, the potential for predictive mapping must be evaluated, and acceptance by the intended users must be secured. Accepting multiple classifications as a reality, that will not vanish even with the strictest application of the code of nomenclature, we must develop and apply algorithms for comparing, correlating and merging com&-peting and overlapping syntaxonomies (Bruelheide & Chytrý 2000).

There is little doubt that PS can continue to be a significant, central element within plant ecology, vegetation science, landscape ecology and conservation biology. Field-based phytosociologists should not be frustrated by the fact that their work is often intrinsically regional in character and is unlikely to lead to exciting general discoveries. They may remain ecologists with a particularly strong rooting in natural history and floristic botany, which does not imply a rejection of objective and quantitative methods. At the same time, ecologists in general need to realize the largely untapped wealth of co-occurrence information that lies in the legacy of generations of phytosociological research. Well-organized large databanks of co-occurrence data are indispensable in a field like plant community ecology, where experiments have been frustratingly specific to context and study organisms, and general truths are often obscured by the importance of marginal conditions. By providing an empirical context to our understanding of the biology of legions of wild plant species and of their assembly into communities, PS contributes to the predictive capacity of ecology.

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