

REVIEWS

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EcoVeg: a new approach to vegetation description and classification

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Abstract. A vegetation classification approach is needed that can describe the diversity of terrestrial ecosystems and their transformations over large time frames, span the full range of spatial and geographic scales across the globe, and provide knowledge of reference conditions and current states of ecosystems required to make decisions about conservation and resource management. We summarize the scientific basis for EcoVeg, a physiognomic-floristic-ecological classification approach that applies to existing vegetation, both cultural (planted and dominated by human processes) and natural (spontaneously formed and dominated by nonhuman ecological processes). The classification is based on a set of vegetation criteria, including physiognomy (growth forms, structure) and floristics (compositional similarity and characteristic species combinations), in conjunction with ecological characteristics, including site factors, disturbance, bioclimate, and biogeography. For natural vegetation, the rationale for the upper levels (formation types) is based on the relation between global-scale vegetation patterns and macroclimate, hydrology, and substrate. The rationale for the middle levels is based on scaling from regional formations (divisions) to regional floristic-physiognomic types (macrogroup and group) that respond to meso-scale biogeographic, climatic, disturbance, and site factors. Finally, the lower levels (alliance and association) are defined by detailed floristic composition that responds to local to regional topo-edaphic and disturbance gradients. For cultural vegetation, the rationale is similar, but types are based on distinctive vegetation physiognomy and floristics that reflect human activities. The hierarchy provides a structure that organizes regional/continental vegetation patterns in the context of global patterns. A formal nomenclature is provided, along with a descriptive template that provides the differentiating criteria for each type at all levels of the hierarchy. Formation types have been described for the globe; divisions and macrogroups for North America, Latin America and Africa; groups, alliances and associations for the United States, parts of Canada, Latin America and, in partnership with other classifications that share these levels, many other parts of the globe.

Key words: *biogeography; Canadian National Vegetation Classification; cultural vegetation; ecosystem; floristics; growth form; International Vegetation Classification; natural vegetation; novel ecosystem; ruderal vegetation; U.S. National Vegetation Classification; vegetation type.*

INTRODUCTION

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There never has been greater need than now to systematically inventory, classify, and map the incredible diversity of vegetation and ecosystems on Earth as land managers, conservationists, and policy makers are facing ever intensifying land uses and degraded land-

scapes. The implications of global change for biodiversity, ecological processes, and ecosystem services are profound, even as historic natural systems are replaced by new or novel ecosystems. A paramount need for assessing these alterations is a system of vegetation classification that is operable at multiple spatial and temporal scales of resolution. Although vegetation-based classifications are often eschewed because of the heterogeneous and dynamic nature of vegetation, modelers of both climate and land-cover changes also recognize the merits of describing the dynamics of vegetation types (Leemans 1997, Williams et al. 2000, Mitchell 2005, Willis and Birks 2006, Beckage et al. 2008, Chiarucci et al. 2010, Williams and Baker 2011). In addition, ecologists and conservation scientists need real-time knowledge of ecosystem structure and composition in order to characterize reference conditions and natural disturbance dynamics across the landscape (Swetnam et al. 1999, Scott et al. 2002, Stoddard et al. 2006, Leu et al. 2008, Keene et al. 2009, Tierney et al. 2009, Thompson et al. 2013).

Vegetation ecologists acknowledge the need for more comprehensive systematic approaches to both vegetation survey and classification (e.g., Chytrý et al. 2011). Although vegetation classifications are a priority in many parts of the world, the systems devised cater to national or subcontinental interests and scale (e.g., Curtis 1959, Rodwell 1991–2000, Sawyer et al. 2009, Navarro 2011, Chytrý 2012), thereby limiting the need for the classifiers to account for the worldwide diversity of vegetation patterns. A globally applicable classification system is lacking.

We present a hierarchical classification that integrates biogeography, bioclimatology, and land-cover data into a scientifically based global vegetation classification for the interpretation of vegetation pattern at all scales. Our methodology, which we term the EcoVeg approach, provides a repeatable scientific system for the development and description of vegetation types. The goal is to systematically classify existing vegetation, reflecting both ecological and human processes and applicable from the global to local scale. While we do not argue that this is the only vegetation classification approach to use, we will show that it does address an important set of current needs and solves other classification shortcomings.

The EcoVeg approach builds on the traditional physiognomic-floristic-ecological classifications that have been developed over many years (e.g., Rùbel 1930, as cited in Shimwell 1971, Whittaker 1962, Westhoff 1967, Webb et al. 1970, Beard 1973, Werger and Sprangers 1982, Borhidi 1991, Adam 1992). These classifications suggested ways in which multiple criteria for vegetation classification could be used to organize vegetation patterns along ecological lines. Common to these authors' perspectives is that both floristic and physiognomic units should be constructed in the context of ecological relationships. As Warming stated early in

the last century (1909:142), "Why not use each growth form [lichen, moss, herb, dwarf-shrub, shrub, tree] as a foundation upon which to build a special class? The following classes could then be distinguished: that of forest formations, of bush-formations, of shrub-formations, of dwarf-shrub formations, of perennial-herb formations, of moss-formations, and of alga-formations . . . from a morphological standpoint this would possess a certain interest, *but from a phytogeographical one it must be dismissed, because it would involve the separation of formations that are oecologically closely allied.*" (Emphasis added.)

Similarly, Daubenmire (1968:252) observed that ". . . a 'needle-leaved coniferous forest' category would embrace the *Pinus elliottii* forests of Cuba, the *Pinus ponderosa* forests of Colorado, the *Sequoia sempervirens* forests of California, the *Picea glauca* forests of Yukon Territory, etc. Collectively these share nothing in common from the synecologic standpoint . . . thus it is clear that physiognomy by itself lumps vegetation types that are vastly different in their ecological relations, and so results in an artificial classification. Then the opposite difficulty is illustrated by Warming's placement of salt marshes dominated by shrubby *Salicornia* in a different category from salt marshes dominated by herbaceous species of the same genus . . . all this is not to deny that physiognomy can serve a useful purpose in defining major plant groupings, but it is useful only when ecologic and other considerations are allowed to govern its application."

Floristic approaches, such as those of Braun-Blanquet or Daubenmire, often give strong consideration to ecological relationships when assessing vegetation types (Westhoff and van der Maarel 1973:619). In fact, the historic association concept typically includes habitat conditions (Mueller-Dombois and Ellenberg 1974, Willner 2006, Jennings et al. 2009). Thus, both physiognomic and floristic characteristics can provide the biotic information needed for defining vegetation classification units, and the organization of their relationships can be assessed by their ecological, dynamic, and geographic (chorology) relevance (see also Pignatti et al. [1994]).

There are other vegetation characteristics that are still being explored for their role in vegetation classification. For example, inductive approaches to characterizing plant functional traits are now being gathered at the same scale as floristic data, such that classifications may benefit from considering these traits for classification (Box 1981, Cramer 1997, Gillison 2013). Although these fine-scale traits can be used to characterize environmentally adaptive aspects of plants, more research is needed to understand how they might be incorporated with physiognomic and floristic criteria for classification purposes. We note how information on functional traits could be used to extend our approach.

One of the challenges of a global classification is to provide guidance for type recognition across all scales. An accurate, concise definition for a global-scale

tropical dry forest formation may be difficult, given the enormous diversity of tropical forests across the globe. Because the principles of the EcoVeg hierarchy ultimately bring global and local scales together, there is the opportunity for ongoing refinement and improvement of type definitions using both top-down and bottom-up methods (e.g., Miles et al. 2006).

No other global vegetation classification approach that we know of is based on an integration of physiognomy and floristics across all vegetation types at multiple scales. Perhaps the closest in scope to our approach is that of Di Gregorio and Jansen (1996), but theirs is a comprehensive descriptive method with multiple attributes organized around a few core categories. There are also a number of important continental or subcontinental physiognomic-floristic classifications, though they differ from our approach in a variety of ways, including in North America (Brown et al. 1979, Brown 1982), the former USSR (Komarov Botanical Institute; Aleksandrova 1973), in Australia (Specht et al. 1974, Specht and Specht 2001), in Europe, the physiognomic-floristic classification that guides the Natural Vegetation Map of Europe (Bohn et al. 2000–2003) and EUNIS (European Nature Information System; see Davies et al. [2004]), with its various predecessors (e.g., Devillers et al. 1991 [CORINE biotopes manual] and Devillers and Devillers-Terschuren 1996). Apart from Brown et al. (1979), the units and hierarchy neither attempt to represent global patterns of vegetation nor contain multiple scales of global to local types. We therefore developed the EcoVeg approach to address this need.

METHODS

Working group

The classification approach presented here is the product of numerous efforts that began in the 1970s and 1980s to establish global ecological classification frameworks (see Grossman et al. [1998] for a brief overview of various physiognomic, floristic, and physiognomic-floristic approaches). At that time, any effort to develop a systematic vegetation classification in the United States had to first respond to challenges to community-unit concepts raised by continuum-based theories (Austin 1985), disenchantment with strongly floristic approaches based on the character species concepts of the Braun-Blanquet method (Mueller-Dombois and Ellenberg 1974:208–209), which led to a greater emphasis on the characteristic species combination (Chytrý and Tichý 2003), and a desire to explore more bio-geo-ecosystem approaches (Driscoll et al. 1984, Pojar et al. 1987, Bailey 1989a, Rowe and Barnes 1994). Concurrently, however, improvements in remote sensing technology and spatial modeling tools created a demand for a classification system that was consistent, repeatable, and operable at multiple spatial scales for characterization of vegetation-ecosystem patterns from both the ground and the air (Lowry et al. 2007).

In 2003, the Vegetation Subcommittee of the United States Federal Geographic Data Committee (FGDC 2008) sponsored the Hierarchy Revisions Working Group (HRWG) to address shortcomings in the UNESCO (1973) physiognomic-ecologic classification that formed the basis for the first iteration of the United States National Vegetation Classification (USNVC; see Grossman et al. [1998]). UNESCO (1973) was intended to facilitate global vegetation classification and mapping using remote sensing imagery. Because of an FGDC requisite that international standards for vegetation classification be considered during development of the USNVC, the HRWG was composed of vegetation ecologists from across the western hemisphere (see Appendix A for a list of members), and it sought peer review from international experts. The HRWG focused on the conceptual development of the upper and middle level units of the hierarchy to complement the lower level (alliance and association) units already put in place by Grossman et al. (1998). The FGDC (2008) and Jennings et al. (2009) provided guidance for the collection of vegetation field data from plots and for the description and analysis of lower level units of the classification, guidance that is relevant to the descriptions of all levels of the hierarchy presented here. They also provided a glossary of terms. A brief introduction to the USNVC was given in Faber-Langendoen et al. (2009), Franklin et al. (2012), and Kent (2012). An introduction and systematic description of the global formation types is provided in Faber-Langendoen et al. (2012).

The terrestrial vegetation focus of EcoVeg is based on assumptions that vegetation represents the majority of primary production of terrestrial ecosystems, is readily observable, and to a large degree integrates the biotic response to a variety of abiotic and disturbance factors at local, regional, and global scales. Thus, the approach adopts a bio-ecosystems (Walter 1985), as opposed to a geo-ecosystems (Rowe and Barnes 1994) approach, and is largely synonymous with the natural or ecological community concept used by a variety of state agencies and organizations within the United States (Grossman et al. 1998).

The conceptual development and description of EcoVeg units draws on important ecological products from bioclimatic (e.g., Holdridge 1947, Pojar et al. 1987, Rivas-Martínez 1996–2011, Metzger et al. 2012), biogeographic (e.g., Takhtajan 1986, Rivas-Martínez et al. 2011), and soils classifications (USDA 1999, Eswaran et al. 2003) to facilitate the understanding of vegetation patterns. In addition, the multiscale structure of the EcoVeg approach is compatible with existing land cover classifications that are utilized at national, continental, and global scales (see USGS National Land Cover Database [*data available online*];¹³ Loveland et al. 1991,

¹³ <http://landcover.usgs.gov/natl/landcover.php>

2000, Di Gregorio and Jansen 1996, USGS 2001, Bontemps et al. 2009, Fry et al. 2011).

Methodological principles

We contend that an operable vegetation classification scheme must have the capacity to describe existing vegetation patterns, including both cultural (planted and dominated by human processes) and natural (spontaneously formed and dominated by ecological processes, cf. van der Maarel 2005); describe vegetation types at multiple thematic scales, from thematically coarse formations (biomes) to fine-scale associations (biotopes); provide a readily interpretable inventory of vegetation and ecosystem patterns within and across landscape/ecoregional/watershed units; document status and trends of vegetation and ecosystems (e.g., trends in extent, such as range shifts, or trends in condition); facilitate interpretation of long-term (even paleoecological) change in vegetation with short-term change of existing vegetation, based on multiple vegetation criteria (growth forms, structure, floristics, etc.); and document the real-time shifts in ecosystem states caused by invasive species, land use, and climate change.

Based on these contentions, the EcoVeg approach contains nine core principles.

- 1) The classification is based on existing vegetation types, defined as the plant cover, including both floristic composition and vegetation structure, documented at a specific location and time, under specified ecological conditions, and preferably described at an optimal time during the growing season (Tart et al. 2005, FGDC 2008, Jennings et al. 2009). This is in contrast to potential vegetation concepts (Küchler 1964, Daubenmire 1968, Loidi and Fernández-González 2012), which rely on assumptions regarding vegetation successional stages, the presence of selected late successional plant species, and ecological species groups related to soils, topography, and climatic factors in the description of vegetation types. The two concepts are related in that mature examples of existing vegetation may represent expected states of potential vegetation types (Loidi and Fernández-González 2012).
- 2) Vegetation types are characterized by full floristic and growth form (physiognomic) composition, which together express ecological and biogeographical relations. Floristic data can provide joint species responses to environment and disturbance, both in the short and long term. These responses can be indicators of environmental change, disturbance regime shifts, and anthropogenic alterations. Growth forms reflect ecological and evolutionary pressures and processes; thus the composition of growth forms expresses both the long-term and immediate set of abiotic variables influencing vegetation structure (Whittaker 1975, Werger and Sprangers 1982, Adam 1992). For example, Box (1981) defined 90 plant growth-forms based on structural types (e.g., tree, shrub, etc.), leaf form (e.g., broad-leaved macrophyll), relative plant and leaf size, and seasonal activity pattern (e.g., summer green) for predictively mapping world biomes or vegetation formations. Thus, regional patterns of growth forms and species constitute distinctive patterns that can be used to define regional biomes, reflecting a long-term adjustment of vegetation to sites (Williams et al. 2000). At the same time, natural disturbances and human activities can rapidly alter the growth forms and species composition.
- 3) Vegetation characteristics are the product of natural and cultural processes. Cultural processes are human activities with purposeful, direct vegetation management objectives that produce distinct suites of species and growth forms (e.g., orchards, vineyards, row crops, gardens, forest plantations). Natural processes are ecologically driven and lead to more or less spontaneous vegetation patterns (Küchler 1969, Westhoff and van der Maarel 1973, Di Gregorio and Jansen 1996, van der Maarel 2005). See also *Basic categories of the EcoVeg approach: Natural and cultural vegetation*.
- 4) Characterizing and describing vegetation types is best accomplished using plot data, including both vegetation and other ecological data, which is collected and compiled using systematic protocols and survey techniques. Data management tools, including botanical databases, vegetation plot databases, and vegetation classification databases (Westhoff and van der Maarel 1973, Dengler et al. 2011, Peet et al. 2012), are essential for these activities.
- 5) Vegetation types can be defined using a number of differentiating criteria, including diagnostic, constant and dominant species, dominant and diagnostic growth forms, and compositional similarity. The most useful criteria are those that express ecological and biogeographical relationships and that clearly distinguish types (Warming 1909, Curtis 1959, Westhoff and van der Maarel 1973, Pignatti et al. 1994, Dierschke 1997, Willner 2006). These criteria should be defined for application in the field or lab, so that recognizable field characteristics are provided to ensure consistent identification using keys and other tools (De Cáceres and Wiser 2012). To that end, types are preferably defined as extensive concepts (the class concepts of Whittaker [1962:114–118]). Extensive concepts describe the full membership or range of variation of a type in relation to other types (e.g., as shown in Austin [2013: Fig. 3.4]), as compared to intensive or nodal concepts, where the membership or range of variation in the type is based on selected typical plots, but such variation may exclude intermediate plots. Intensive concepts may provide a first approximation of a type, which can be later expanded with increased knowledge of the type. There will always be

difficulties in assigning stands to a type as one type transitions to another along a gradient, even when differentiating criteria are well understood.

- 6) Classification and field recognition of vegetation types is a distinct process that differs from vegetation mapping in that all vegetation maps are constrained by issues related to scale and technical limitations of mapping, which may restrict the ability of the map legend to show all vegetation types in a mapped area. Conversely, mapping units can describe spatial relationships among types not described by the classification (e.g., dry-dune-wet-swale type relationships). Because vegetation maps are often developed to study the geographic distribution, extent, and landscape patterns of vegetation, the linkages between recognizable field characteristics of vegetation classification and vegetation mapping should be established (Tart et al. 2005).
- 7) Differentiating criteria for vegetation types can be arranged hierarchically from upper levels primarily based on general growth forms to middle levels based on specific growth form and floristics that includes suites of general and regional combinations of characteristic species, and lower levels based primarily on regional to local floristics. At all levels, vegetation provides the primary criteria for descriptions within the hierarchy, but the organization may be based on the ecological and biogeographical relations expressed by the vegetation (Rübel 1930 as cited in Shimwell 1971, Whittaker 1962, Westhoff 1967, Pignatti et al. 1994, Brown et al. 1998).
- 8) An integrated hierarchy of vegetation types is best established by considering each level as both independent and interconnected in a nested relationship; that is, criteria selected to differentiate levels in the hierarchy are sufficient to define and distinguish types of a particular level, thereby preventing it from being arbitrarily defined by the level immediately above or below in the hierarchy. Thus, the EcoVeg method is both top-down and bottom-up. It is largely an inductive method, in so far as it rarely poses formal hypotheses, and the method of induction can be appropriately applied at any level (Mentis 1988). Opportunities for hypothesis testing (e.g., how relationships among vegetation types are established based on their physiognomy, floristics, and ecology) may emerge as the hierarchy is further developed.
- 9) A coordinating body should be established to oversee the recognition and integration of new classification units. A coordinating body is needed, given the more or less continuous nature of vegetation patterns and the potential for both multiple overlapping or uneven concepts. Even when such concepts are published, they may be difficult to reconcile with other independently published types. Proposed vegetation types, whether previously published or not, should undergo a peer review process specific to the classification standard conducted by a coordinating

body. The coordinating body can review types published in independent publications to determine their relation to the standard set of vegetation types to ensure that all scientific contributions to the classification are considered, but the coordinating body provides the critical role of ensuring that published types are clearly distinguished from each other as much as possible. This assures that an authoritative version of the classification is maintained at all times, and it prevents potential confusion over duplication, overlap, and uneven scaling among types. A coordinated approach makes a standardized classification system readily available to practitioners, policy makers, and others (e.g., Rodwell 1991–2000, Grossman et al. 1998, Davies et al. 2004, Mucina and Rutherford 2006, Jennings et al. 2009).

These principles are essential when a consistent and comprehensive set of vegetation types is needed that are organized by vegetation and ecological relationships within a global framework. We encourage local or regional inventories and classifications to retain the core methodological principles 1–5 on defining types, even if their classification hierarchy is structured differently, in order to permit linking these local and regional inventories with this global approach because these inventories are an important source of information for any global classification effort.

Related classification methods

The philosophy guiding the EcoVeg methodology reflects, to varying degrees, the physiognomic-floristic-ecological systems noted in the *Introduction* (e.g., see Mueller-Dombois and Ellenberg [1974] for a general presentation of such systems). Those systems have typically not developed the kind of formal principles and methods presented here, so comparisons are difficult to make (but see the basic postulates of vegetation classification and mapping for southern Africa presented in Mucina and Rutherford [2006]). One system deserves special comparison: the Braun-Blanquet approach, as the HRWG learned much from it. Excellent summaries of that approach are available in Westhoff and van der Maarel (1973) and Dengler et al. (2008). First, both approaches share many aspects of principles 1–6. In particular, it is worth noting that principle 4, collecting plot-based (relevé) vegetation data for classification purposes, a core feature of the Braun-Blanquet approach, has become embedded in most formal vegetation classification approaches, including this one. But there also some noteworthy differences. The Braun-Blanquet approach strongly emphasizes floristic-diagnostic features at all levels (cf. EcoVeg principle 2), restricts the scope of vegetation to natural and seminatural or spontaneous (not planted) vegetation (cf. EcoVeg principle 3), arranges the hierarchy based strongly on floristic-ecological criteria, with less empha-

TABLE 1. Conceptual categories and level 1 of the hierarchy.

Category and level 1	Scientific name
Vegetated	
Natural vegetation	
Forest and Woodland	Mesomorphic Tree Vegetation
Shrub and Herb Vegetation	Mesomorphic Shrub and Herb Vegetation
Desert and Semi-Desert	Xeromorphic Woodland, Scrub and Herb Vegetation
Polar and High Montane Scrub and Grassland	Cryomorphic Vegetation
Aquatic Vegetation	Hydromorphic Vegetation
Open Rock Vegetation	Mesomorphic Vegetation
Cultural vegetation	
Agricultural and developed vegetation	Anthromorphic Vegetation
Nonvegetated	excluded from classification, per se

sis on physiognomy (cf. EcoVeg principle 7), specifies one level, the association, as the fundamental unit, thereby placing other levels in a more dependent relation (cf. EcoVeg principle 8), and relies on the accumulation of literature-based, peer-reviewed publications to establish types, with no official coordinating body (cf. EcoVeg principle 9). Another difference is that the primary top Braun-Blanquet level, the class, contains many hundreds of units, e.g., 80 classes are reported for Europe alone by Rodwell et al. (2002), with no formal higher levels. In principle, the Braun-Blanquet method does have one higher level, division (Hadač 1967), but it is rarely used. The aggregation of classes is typically accomplished using ad hoc formations, but there has been no interest in the development of a formalized procedure for those units (Mucina 1997). This leaves the global patterns of vegetation unaccounted for by the Braun-Blanquet approach. Third, lack of specified class criteria for both physiognomy and floristics at the upper levels of the Braun-Blanquet approach has led to fewer range-wide standardized publications and applications, except through occasional synoptic publications. To some degree, the lack of systematic criteria for these units within Europe led to the creation of alternative European classifications, such as EUNIS (European Nature Information System). That system provides a comprehensive and specific set of criteria at the highest levels of the classification for all European vegetation (Davies et al. 2004), though revisions are under way to make it a more consistent framework (M. Chytrý, *personal communication*). Because of these differences, we believe the EcoVeg approach can better serve as a global vegetation classification framework.

Although there are other components of the Braun-Blanquet system that bear further consideration (nomenclature, requirements for a type relevé when describing a new type, etc.), they are beyond the scope of this paper. Instead, we emphasize that there also is great compatibility between the two approaches, as is apparent in the natural vegetation map of Europe (Bohn et al. 2000–2003), which incorporates Braun-Blanquet types to describe European vegetation (Rodwell et al.

2002). We discuss these similarities when presenting the levels of the hierarchy.

BASIC CATEGORIES OF THE ECOVEG APPROACH

We introduce two basic dichotomies that guide the overall hierarchy: the distinction between (1) vegetated and nonvegetated and (2) natural and cultural vegetation (cf. Di Gregorio and Jansen 1996). These categories explicitly demonstrate how the approach systematically classifies the enormous variation in terrestrial vegetation and how the classification units produced by the approach can be part of a larger set of categories that cover all ecosystems on the globe (freshwater, marine, subterranean; see Table 1).

Vegetated and nonvegetated

All terrestrial areas are classified as vegetated that have $\geq 1\%$ surface coverage with live vascular and nonvascular plant species, including wetland vegetation (rooted emergent, submergent, and floating aquatic vegetation). For guidance on classifying nonvegetated terrestrial habitats, users should consult units provided by the Food and Agriculture Organization of the United Nations (FAO) Land Cover Classification System (Di Gregorio and Jansen 1996) and the United States National Land Cover Database (see footnote 13). For classifying freshwater and marine habitats, users should consult Cowardin et al. (1979), Higgins et al. (2005), and the Coastal and Marine Ecological Classification System (FGDC 2012), among others.

Natural and cultural vegetation

Although the term vegetation is often explicitly or implicitly (as in many texts that describe regional vegetation) restricted to natural vegetation (e.g., Westhoff and van der Maarel 1973, Barbour and Billings 2000, van der Maarel 2005), here we extend it to include cultural vegetation. The EcoVeg approach adopts this inclusive view because of the distinctive and ever-growing quantity of human-dominated/derived land-cover types, whether cultural vegetation (Küchler 1969, Di Gregorio and Jansen 1996, Davies et al. 2004),



FIG. 1. Asian elephant passing through a tea plantation (cultural vegetation) in the Valparai plateau in Anamalai Hills of the western Ghats, India, on its way from one natural forest patch to another. Classifying the type of cultural vegetation is important to the overall assessment of elephant habitat because, although the elephants are able to use the tea plantations as part of a migratory corridor, they are also likely to run into conflict with humans as they pass through (Sukumar and Easa 2006). Photo Kalyan Varma. Used with permission.

cultural soils (i.e., the proposed Anthroisol order [Bryant and Galbraith 2003; International Committee for Anthropogenic Soils, *available online*]),¹⁴ or cultural biomes (Ellis and Ramankutty 2008). Describing cultural vegetation is also important within state and transition models that characterize the successional relationships among types on ecological sites (Bestmeyer et al. 2004). Thus, including cultural vegetation in the EcoVeg approach is vital to characterizing the full range of variation in terrestrial ecosystems and in wildlife habitats (Di Gregorio and Jansen 1996). That variation will include challenging areas of transition between the two, such as sites where former industrial plantations have been partially cut and abandoned and acquire an increasingly native or naturalized flora, or where native grasslands are grazed and managed so intensively they take on many characteristics of seeded pastures. The roles of natural and cultural processes are not mutually exclusive. For example, although cultural vegetation can provide a degree of connectivity between natural habitats that wildlife depend on, knowledge of the type of cultural vegetation is important to understanding potential conflicts with human activities (Fig. 1). Thus, we incorporate human and natural processes into our high-level distinctions of types, recognizing that

these influences form a continuum of human and ecological interactions.

Cultural vegetation possesses a distinctive structure and composition that is determined by the response to human intervention (cultural vegetation *sensu stricto* Kùchler 1969, Di Gregorio and Jansen 1996). Characteristics of cultural vegetation are (1) regularly spaced herbaceous vegetation with substantial cover of bare soil for significant periods of the year (usually determined by tillage, chemical treatment, or agricultural flooding), (2) vegetation consisting of highly manipulated growth forms or structures rarely found under natural plant development (usually determined by mechanical pruning, mowing, clipping, etc.), and (3) vegetation composed of species not native to the area that have been intentionally introduced to the site by humans and that would not persist without active management by humans (e.g., arboretums).

Natural (including seminatural, ruderal, or weed) vegetation is composed predominantly of spontaneously growing sets of plant species with composition shaped by both abiotic (site) and biotic processes; these are vegetation types whose species composition is primarily determined by nonhuman ecological processes (Kùchler 1969, Westhoff and van der Maarel 1973, van der Maarel 2005). Although natural vegetation is variously affected by human activities (e.g., logging, livestock

¹⁴ <http://clic.cses.vt.edu/ICOMANTH>

grazing, fire, introduced pathogens), it retains a distinctive set of spontaneous vegetation and ecological characteristics (Westhoff and van der Maarel 1973, Di Gregorio and Jansen 1996).

Natural vegetation is sometimes restricted to historic, native vegetation or vegetation with analogs to potential natural vegetation (e.g., Barbour and Billings 2000, van der Maarel 2005). Here, we follow the Braun-Blanquet tradition and others in extending it to include the full range of natural vegetation from what Ellenberg (1988) called near-natural to seminatural. Thus, just as cultural vegetation is not devoid of some natural influences, so too within natural vegetation there is a range of both ecological and human processes affecting the vegetation. Ellenberg's near-natural vegetation of central Europe includes native, historic vegetation primarily shaped by ecological processes, such as the forests, wetlands, dunes, and alpine vegetation. His seminatural vegetation includes modified, ruderal, or weedy vegetation that had been moderately to substantially altered by anthropogenic disturbances, such as central European grasslands and dwarf-shrub heaths with relatively moderate human influences, as well as ruderal and weed communities found on heavily soil disturbed sites, and even the more intensively manipulated vegetation of forest plantations, hay, and litter meadows. Apart from our treatment of the more intensively manipulated vegetation as cultural vegetation, we agree with Ellenberg on the full scope of what is termed natural vegetation. We leave it to the classification process to determine how distinctive the vegetation may be as it relates to the varying degrees of human vs. ecological processes. Inclusion of both native and weedy vegetation within natural vegetation is perhaps akin to many botanical manuals that treat both native and naturalized species within their scope, but exclude the multitude of cultivated species found in lawns and farm fields.

That said, there has been growing interest in the more distinctive ruderal, invasive, and weedy vegetation types; that is, those with no apparent historical natural analogs, sometimes referred to as novel or emerging ecosystems (Hobbs et al. 2006, Belnap et al. 2012). These systems are often composed of invasive species, whether exotic or native, that have expanded in extent and abundance due to human disturbances, whether from abandonment of sites with cultural vegetation or from extensive alteration and degradation of more natural vegetation. For example, old fields in eastern North America that form on abandoned farm lands contain a mix of weedy natives and exotic shrubs, such as *Rhamnus cathartica* and *Lonicera* spp. (Wright and Fridley 2010). These fields have no analog to surrounding historic native vegetation in the regions. Similarly, vegetation that forms after tropical forests are cleared and burned may differ from any native vegetation in the area. For example, when sites with *cerrado* seasonally dry forest are extensively cleared and frequently burned, they may subsequently contain a floristically distinct

derived savanna, comprised of invasive cogon grasses (*Imperata cylindrica*, *Imperata brasiliensis*) mixed with other weedy native and exotic grasses, herbs, and palms, rather than a natural *cerrado* savanna (Veldman and Putz 2011). In the southwestern United States and Mexico, a native invasive, *Prosopis glandulosa*, expanded into more natural vegetation because of strongly altered fire and grazing regimes, leading to the formation of dense stands with an understory of *Opuntia* spp. and *Bromus* spp. (Belnap et al. 2012). *P. glandulosa* is also an exotic invader in parts of South African and Australia. These kinds of seminatural vegetation types reflect a fairly strong role of anthropogenic processes alongside successional ecological processes leading to a set of characteristic species with distinctive growth forms, ecology, and biogeography. For that reason, we add a ruderal label to the name of the type to indicate their placement in the classification (see *Natural Vegetation: Hierarchy levels for natural vegetation: 3. Macrogrouper and ruderal vegetation*). We define ruderal vegetation as "vegetation found on human-disturbed sites, with no apparent recent historical natural analogs and whose current composition and structure is not a function of continuous cultivation by humans and includes a broadly distinctive characteristic species combination, whether tree, shrub, or herb dominated. The vegetation is often composed of invasive species, whether exotic or native, that have expanded in extent and abundance due to the human disturbances" (Curtis 1959, Ellenberg 1988, Lincoln et al. 1998). Our term is more restrictive than that of Grime (2001), who uses the term for any vegetation that forms after regular and severe disturbances, whether natural or human caused. By cataloguing these ruderal ecosystems, we seek to capture the full dynamics of existing vegetation on the landscape.

NATURAL VEGETATION

Criteria for the description of natural vegetation

Growth forms and floristic characteristics that reflect ecological and biogeographical variables (Faber-Langendoen et al. 2009) are the primary properties of natural vegetation and are used to define all units of the hierarchy (cf. Mueller-Dombois and Ellenberg 1974). Further research is needed to determine whether the approach can be extended to include plant functional types (Gillison 2013).

Growth forms and structure.—Growth form criteria include (1) diagnostic combinations of growth forms, (2) dominant growth forms, singly or in combination, and (3) vertical and horizontal structure of growth forms. Growth forms are defined as the shape or appearance (physiognomy and structure) of a plant reflecting growing conditions and genetics (FGDC 2008). We use the term growth form in preference to life form, sensu Raunkier (1934), who defined forms into types based on environmental condition, specifically based on the position of the bud or perennating organ during the

most unfavorable season. Growth forms describe a variety of types that reflect multiple ecological conditions. Growth forms are based on structural types (e.g., tree), leaf form (e.g., broad-leaved macrophyll), relative plant and leaf size, and seasonal activity pattern (e.g., summer green; see Mueller-Dombois and Ellenberg [1974], Whittaker [1975:359], Box [1981], Box and Fujiwara [2005], Mucina and Rutherford [2006: Table 2.1]). A growth form is usually consistent within a species, but may vary under extremes of environment.

The growth forms provided in Appendix B are a first approximation for defining upper level formation types (FGDC 2008) and for characterizing global vegetation patterns. The list consists of both general (Appendix B: Table B.1) and specific (Appendix B: Table B.2) growth forms. Morphological, anatomical, and physiological adaptations can be used to derive additional growth forms, but the use of species in combination with growth forms at middle levels of the hierarchy will alleviate this need. Nevertheless, the list in Appendix B can be amended to include, for example, the growth forms suggested by Box (1981) and Box and Fujiwara (2005) or some of the characteristics of plant functional types (e.g., the VegClass elements of Gillison 2013).

Because the growth forms used in the EcoVeg approach emphasize morphological adaptations, the suffix morphic is applied to vegetation types: hydromorphic, mesomorphic, xeromorphic (see also Ellenberg [1988: Table 4]). Although comparable to the use of hydrophyte, mesophyte, thermophyte, or xerophyte in other classification systems (e.g., Warming 1909, Rodwell et al. 2002, Huber and Riina 2003), we contend those terms are more aptly applied to species. In addition, the term hydrophyte in North America is applied to species occupying wetland habitats, irrespective of any obvious morphologic or anatomical adaptations. For example, Tiner (2006) defines hydrophytes as “plants growing in water or on a substrate that is at least periodically deficient in oxygen due to excessive wetness.” By contrast, hydromorphic vegetation is defined by rooted and floating aquatic growth forms with anatomical features such as aerenchyma.

By identifying the growth forms on a site or in a vegetation plot, it is possible to empirically characterize the growth forms of a vegetation type and relate them to ecological factors. Thus, we can assess the diagnostic and dominant types of general growth forms that define a formation class, such as xeromorphic (desert) vegetation. At finer scales of formations, additional specific growth forms may be needed. For example, in distinguishing the tropical lowland rain forest from the tropical montane forest formation, Whitmore (1984: Table 18.1) noted differences in canopy height, leaf type, and flowering phenology among the growth forms of dominant trees, and he included a variety of minor diagnostic growth forms, such as vascular and nonvascular epiphytes and climbers. In other cases, growth forms, such as flowering forb, do not show particularly

strong ecological relationships, at least not as currently defined, in which case, they may still be identified as constant growth forms (i.e., found in a high percentage of the plots sampled for a type, cf. *Natural vegetation: Criteria for the description of natural vegetation: Floristics*).

Growth forms also are closely related to plant functional types (PFTs), defined as a group of organisms with a shared response to environmental factors (Gitay and Noble 1997). For example, regeneration strategies of woody plant species subject to recurrent fire vary between regions, but many share the primary functional traits of resprouting following a crown fire and the retention of a viable postfire seed bank (Gillison 2013). The PFTs used for global-scale ecological assessments closely resemble the growth forms in the EcoVeg approach. Thus, PFTs can be concatenated with growth forms within a formation (Leemans 1997) for modeling the response of formations to disturbances and to climate change, following Box (1981), Cramer (1997) and Box and Fujiwara (2005).

In the EcoVeg approach, the following definitions are applied to growth forms.

Dominant growth form has a high percent cover (typically >10%), usually in the uppermost vegetation layer.

Diagnostic growth form is the presence, abundance, or vigor of growth forms that help differentiate one vegetation type from another. Diagnostic growth forms also reflect certain climatic and site conditions and can be identified using conceptual and analytical techniques, including their relation to global climatic factors (e.g., Cramer 1997, Box 2002, Wang et al. 2003).

Structural features, such as the canopy height of each vegetation stratum and canopy spacing, may be utilized for description of vegetation types. Cultural types (e.g., apple orchards) often differ fundamentally in both the growth form and the structural characteristic from natural types. Structural features may also serve a descriptive role within or between types, such as early, mid, or late seral forests, or open and closed shrublands.

Floristics.—Given that species are a fundamental unit of biodiversity, floristic composition is important in characterizing vegetation types. The definition of a vegetation type is summarized by characteristic species combinations, including (1) diagnostic combinations of species (character and differential species), (2) constant species, (3) dominant species, which reflect similar ecology and dynamic significance, and (4) vertical and horizontal structure of species. The terminology for characteristic species combinations largely follows the Braun-Blanquet tradition (Westhoff and van der Maarel 1973, Chytrý and Tichý 2003), with the inclusion of dominant species, which is also an expression of the dominant growth form. The characteristic species combination is considered a strong indicator of bioclimatic, biogeographic, geodaphic, and successional conditions. We use the term species broadly to mean

taxa, as the diagnostic value of taxa are occasionally made at the genus or subspecies level.

1. *Diagnostic species*.—Diagnostic species exhibit a relative constancy or abundance that clearly differentiates vegetation types and includes character and differential species (dominant and constant species may or may not be diagnostic).

Character species show a distinct maximum concentration, either in constancy and/or abundance, in one well-defined vegetation type, as compared to all others, and are recognizable at local, regional, and larger geographic scales (see Mueller-Dombois and Ellenberg [1974:178, 208], Bruehlheide [2000]). Character species are often determined by comparison of vegetation types within the same physiognomic unit of a climatic or biogeographic region (Dengler et al. 2008).

Differential species are distinctly more widespread or abundant in a pair or closely related sets of plant communities than in the other(s), though they may still be more abundant in other communities not under consideration (Curtis 1959, Bruehlheide 2000). The more limited a species is to one or a few plant community types under consideration, the stronger its differential value. Character species are a special case of differential species, since they differentiate a type from all other vegetation types, whereas differential species differentiate one closely related type from another (Dengler et al. 2008). In both cases, there is a “continuum in fidelity (diagnostic capacity) of species to vegetation types” (Chytrý and Tichý 2003, Chytrý 2007).

Constant species are present in a high percentage of the vegetation plots sampled to define a type. Threshold constancy values vary from lower to middle levels of the hierarchy because of increasing vegetation heterogeneity between levels, i.e., 40–60% for association, 40% for alliance, and 25% for group and macrogroup (Mueller-Dombois and Ellenberg 1974, Chytrý and Tichý 2003, Chytrý 2007). The lower levels of constancy for mid-level types means that they are often defined by partially overlapping combinations of species. Constancy is influenced by plot size; thus, a fairly constrained range of plot sizes is recommended for vegetation studies (Dengler et al. 2009).

The term diagnostic species may overlap with the terms indicator species and ecological species groups (“species whose presence, abundance, or vigor is considered to indicate certain ecological conditions” [Gabriel and Talbot 1984]), particularly when the indicated ecological condition is known. In some classification methods, diagnostic species identified through data analysis receive more weight in determining a vegetation type, particularly when they have well understood relationships to specific environmental variables (soil moisture, soil pH, nutrient regime, disturbance regime). However, diagnostic species may not always indicate a clear ecological relationship nor will all indicator species be diagnostic of a particular vegetation type.

Diagnostic species may be identified through analytical techniques, such as tabular sorting based on fidelity criteria (Westhoff and van der Maarel 1973), and numerical analyses, such as two-way indicator species analysis (e.g., Roleček et al. 2009), indicator value index (Dufrière and Legendre 1997), phi coefficient (e.g., Chytrý et al. 2002), and hybrid approaches that optimize clustering for diagnostic species values (e.g., Tichý et al. 2010).

2. *Dominant species*.—Dominant species have the highest percent cover (the standard abundance measure for vegetation classification), biomass, or density. Species dominance is often assessed by strata, because taller statured species have greater volume or biomass. At the stand- or plot-level, the average cover of a dominant species is >10%, including codominant species. At the type-level, a dominant species is defined as a constant species with at least 10% average cover (adapted from Pojar et al. [1987]). In habitats where the vegetation is rather sparse, relative dominance may be a more helpful criterion.

Compositional similarity.—Compositional similarity is defined as a measure of the similarity in the presence and/or abundance of plant species between two or more plots or types. Numerical indices (e.g., Sorenson, Bray-Curtis, Euclidean distance), ordination, and cluster analyses can be used to assess the degree of compositional similarity (Mueller-Dombois and Ellenberg 1974, Peet and Roberts 2013). At middle scales of vegetation pattern, where plots increasingly lack overlap in species composition but occupy similar ecological and biogeographical space, compositional similarity is assessed using suites of diagnostic species and growth forms related to biogeographic patterns (Pignatti et al. 1994).

Ecological context.—Criteria for ecological context include (1) biogeography (from large-scale biogeographic regions to regional biogeographic and biogeoclimatic zones), (2) climate (macro, meso, and microclimates), (3) disturbances (natural and cultural disturbances, and successional patterns), and (4) topo-edaphic factors, including the topographic features of elevation, slope, and aspect, as well as edaphic factors, such as pH, moisture, nutrients, and texture.

Box and Fujiwara (2005) note the role of two ecological perspectives in interpreting vegetation patterns: “a historical-floristic perspective concerned with migration, dispersal and the historical development of regional floras; and the environmental perspective concerned with environmental constraints and ecological relations influencing distributions.”

1. *Biogeography*.—Biogeography enters the hierarchy mostly at the middle levels to facilitate the identification of vegetation types that have very distinct floristic patterns. The province level of Takhtajan (1986) was very helpful for the EcoVeg approach, because it expresses the limited overlap in floristic composition between the dominant vegetation types across regions, and it accounts for the area effect (small provinces

require more distinctive species than larger provinces). Thus, physiognomically based formation types that cross biogeographic provinces are typically distinct floristically, which points the way to division-level distinctions within the formation. The role of biogeography at lower levels (L6–L8) is less explicitly tied to biogeographic units per se; rather, greater emphasis is given to the interaction between ecological and biogeographic gradients.

2. *Climate*.—Climate is considered in all levels of the hierarchy. Macroclimate is used to describe vegetation types at the continental scale and is mostly independent of landform and vegetation (e.g., Köppen and Trewartha climate types, in Bailey [1996], macrobioclimates of Rivas-Martínez et al. [1999]). Mesoclimate (ecoregional climate) describes large geographic areas and is modified by continental position, landform, and elevation (Bailey 1989a, b, Ecoregions Working Group 1989). Mesoclimates are often inferred from vegetation formation patterns (Bailey 1996). Microclimate (or site climate) is modified by local topo-edaphic position.

The bioclimatic approach is helpful here because it describes the relationship between temperature and precipitation and the geographic distributions of species and ecosystems (e.g., Holdridge 1947, Thornthwaite 1948, Rivas-Martínez et al. 1999). The system of Rivas-Martínez et al. (1999) recognizes five macrobioclimates based on variation in rainfall, elevation and temperature, and bioclimate variants at the continental scale (tropical, mediterranean, temperate, boreal, and polar). These, along with the desert climate category of other eco-geographers (Walter 1985, Bailey 1989a, b, Schulz 1995) are reflected in the global formation types.

3. *Disturbance regimes*.—Disturbance regimes are used in descriptions at all levels of the hierarchy, from cultural or anthropogenic disturbances to flooding, fires, grazing, pathogen outbreaks, and windthrows. For our purposes, a disturbance occurs when the floristic or physiognomic characteristics of the vegetation are disrupted. Thus, disturbances may include both presence and absence of certain ecological or human processes that maintain a type. Disturbance regimes describe the types, frequency, severity, and size of disturbance on a given landscape and the interactions among disturbance types (Frelich 2002). The description of disturbance regimes is a function of the spatial and temporal scale of observation. In natural vegetation, humans have little to moderate influence on the frequency or severity of spontaneous ecological disturbance processes, whereas in cultural vegetation, humans largely determine the disturbance processes and those processes are tied to human activities.

4. *Topo-edaphic factors*.—Topo-edaphic factors are applied at mid to low levels of the hierarchy, but factors such as consolidated or unconsolidated rock, mountain ranges, peat, or other waterlogged soils can be utilized in the upper levels of the hierarchy. At finer scales, the relation of vegetation to topography and soils can be

summarized by environmental gradients or a topo-edaphic classification based on the primary gradients that determine vegetation patterns (e.g., moisture and nutrients, moisture and elevation; Curtis 1959, Whittaker 1975, Beckingham et al. 1996, Peet 2000).

Hierarchy levels for natural vegetation

The classification hierarchy consists of eight levels that are aggregated into three groupings: upper levels (L1–L3), middle levels (L4–L6), and lower levels (L7–L8; see Table 2). The criteria outlined in *Natural Vegetation: Criteria for the description of natural vegetation* are used to develop descriptions of each unit in the hierarchy, but recall that the utility and relevance of the criteria vary with the level in the hierarchy. We provide the name, definition, and description for each level.

Upper levels (L1–L3).—The upper levels were developed based on the formation, a prominent concept throughout the history of vegetation classification (Shimwell 1971, Beard 1973, Mueller-Dombois and Ellenberg 1974, Faber-Langendoen et al. 2012). The formation as defined by UNESCO (1973) is “basically physiognomic-structural in character with supplementary ecological information integrated into its various categories and applicable to natural and semi-natural vegetation” and by Whittaker (1962:150) is “a community type defined by dominance of a given growth form in the uppermost stratum (or the uppermost closed stratum) of the community, or by a combination of dominant growth forms.”

Formations are treated primarily as physiognomic units with descriptions based on ecological considerations. However, at the formation (L3) level, limited use of floristic (and biogeographic) descriptors from lower levels of the hierarchy can be applied. The comprehensive set of formation types for all three levels is provided in Appendix C. A detailed description of each formation type is available in Faber-Langendoen et al. (2012), along with guidance and comments over the precise boundaries of these classes. Practical applications of the classification suggest that clearly specified criteria for what constitutes forests and woodlands as compared to various grasslands and shrublands is important for conservationists, land managers, and policy makers. Here, we summarize the criteria for the three levels and compare them with the division level (Table 3).

1. *Formation class (L1)*.—The formation class is “defined by broad combinations of dominant general growth forms adapted to basic moisture, temperature, and/or substrate or aquatic conditions” (FGDC 2008; cf. Beard 1973, cf. major physiognomic types of Whittaker [1975]). The formation class is the level at which users typically enter the classification; thus, a relatively small set of clearly defined types is helpful.

2. *Formation subclass (L2)*.—The formation subclass is “defined by combinations of general dominant and diagnostic growth forms that reflect global macro-

TABLE 2. Levels, definition, and example of the hierarchy for natural vegetation.

Natural hierarchy	Definition	Example names	
		Scientific	Colloquial
Upper levels			
L1: Formation class	A broad combination of dominant general growth forms adapted to basic moisture, temperature, and/or substrate or aquatic conditions.	Mesomorphic Shrub and Herb Vegetation	Shrub and Herb Vegetation
L2: Formation subclass	A combination of general dominant and diagnostic growth forms that reflect global mega- or macroclimatic factors driven primarily by latitude and continental position or that reflect overriding substrate or aquatic conditions.	Temperate and Boreal Shrub and Herb Vegetation	Temperate and Boreal Grassland and Shrubland
L3: Formation	A combination of dominant and diagnostic growth forms that reflect global macroclimatic conditions as modified by altitude, seasonality of precipitation, substrates, and hydrologic conditions.	Temperate Shrub and Herb Vegetation	Temperate Grassland and Shrubland
Mid levels			
L4: Division	A combination of dominant and diagnostic growth forms and a broad set of diagnostic plant species that reflect biogeographic differences in composition and continental differences in mesoclimate, geology, substrates, hydrology, and disturbance regimes.	<i>Andropogon–Stipa–Bouteloua</i> Grassland and Shrubland	Great Plains Grassland and Shrubland
L5: Macrogroup	A moderate set of diagnostic plant species and diagnostic growth forms that reflect biogeographic differences in composition and subcontinental to regional differences in mesoclimate, geology, substrates, hydrology, and disturbance regimes.	<i>Andropogon gerardii–Schizachyrium scoparium–Sorghastrum nutans</i> Grassland and Shrubland	Great Plains Tallgrass Prairie
L6: Group	A relatively narrow set of diagnostic plant species (including dominants and codominants), broadly similar composition, and diagnostic growth forms that reflect regional mesoclimate, geology, substrates, hydrology, and disturbance regimes.	<i>Andropogon gerardii–Heterostipa spartea–Muhlenbergia richardsonis</i> Grassland	Northern Great Plains Tallgrass Prairie
Lower levels			
L7: Alliance	A characteristic range of species composition, habitat conditions, physiognomy, and diagnostic species, typically at least one of which is found in the uppermost or dominant stratum of the vegetation. Alliances reflect regional to subregional climate, substrates, hydrology, moisture/nutrient factors, and disturbance regimes.	<i>Andropogon gerardii–Sporobolus heterolepis</i> Grassland	Northern Mesic Tallgrass Prairie
L8: Association	A characteristic range of species composition, diagnostic species occurrence, habitat conditions, and physiognomy. Associations reflect topo-edaphic climate, substrates, hydrology, and disturbance regimes.	<i>Andropogon gerardii–Heterostipa spartea–Sporobolus heterolepis</i> Grassland	Northern Mesic Big Bluestem Prairie

Note: The name of the level can be added to the type name for clarity, where needed.

climatic factors driven primarily by latitude and continental position, or that reflect overriding substrate or aquatic conditions” (FGDC 2008; cf. Whittaker 1975). Macroclimatic factors largely determine vegetation patterns.

3. *Formation (L3)*.—Formation is “defined by combinations of dominant and diagnostic growth forms that reflect global macroclimatic conditions as modified by altitude, seasonality of precipitation, substrates, and hydrologic conditions” (FGDC 2008; cf. formation-type

and biome-type of Whittaker [1975], Lincoln et al. [1998]). Here the vegetation patterns typically reflect the combination of major climates and substrate and topography.

4. *Other applications of the formation concept*.—A number of physiognomic or formation systems (Whittaker 1975, Brown et al. 1998, NLWRA 2001, Olson et al. 2001, Specht and Specht 2001, Rodwell et al. 2002) were reviewed when developing the EcoVeg approach (Appendix D). Most of these classification systems

TABLE 3. Interpretive guidelines for vegetation and ecologic criteria for upper formation levels.

Guideline	Level			
	Formation class	Formation subclass	Formation	Division
Growth forms	Broad combinations of dominant general growth forms and specific growth forms. Overlapping general growth forms (e.g., shrub, herb), but combinations of diagnostic growth forms generally nonoverlapping (e.g., xeromorphic forms in desert vegetation).	Combinations of general and specific dominant and diagnostic growth forms. Some growth forms partially nonoverlapping among subclasses (e.g., broadleaf evergreen trees in warm temperate forests and tropical forests).	Combinations of dominant and diagnostic growth forms based on either individual diagnostic growth forms (e.g., mangrove, seagrass beds), or combinations (e.g., warm temperate sclerophyll evergreen broadleaf, cool temperate broad-leaf cold-deciduous). Relative abundances in relation to ecological factors important.	Broadly uniform sets of growth forms and canopy closure (same as formation, but variant expressions; e.g., conifer-dominated Rocky Mountain forest division, compared to broadleaf deciduous hardwood dominated Eastern North American forest division). Essentially nonoverlapping floristics.
Ecological factors (climate, disturbance, and edaphic/hydrology)	Basic moisture, temperature, and/or substrate or aquatic conditions.	Global macroclimatic factors driven primarily by latitude and continental position, or that reflect overriding substrate or aquatic conditions.	Global macroclimatic conditions as modified by altitude, seasonality of precipitation, substrates, and hydrologic conditions.	Continental macroclimate separates formations by continental or major inter-continental climatic patterns. Broad range of conditions consistent with continental expression of formation (e.g., the division spans floodplain and swamp conditions). Divisions within a formation are often geographically separated.
Diagnostic species				One or more sets of strongly diagnostic (character) species among the diagnostic species; species have high fidelity but variable constancy.

Notes: The division level is included for comparison. Empty cells signify no data possible. See also Table 4.

develop a large set of general physiognomic units within one or two levels (about 40 world formation units) rather than having multiple physiognomic levels. Similarly, the EcoVeg formation units are based on multiple criteria at each level, reflecting global-scale ecological factors rather than a single major vegetation criterion at each level (Faber-Langendoen et al. 2012). The objective was to ensure that the EcoVeg formations were truly global in scope and contained a range of growth forms (Appendix B) that together reflected major ecological factors.

Middle level units (L4–L6).—The middle level units are based on regional species pools that have been sorted through biogeographic and ecological drivers (regional climate, topo-edaphic factors, and geologic substrates) of species composition and growth forms. EcoVeg can take a bottom-up approach to classification, which

results in the resolution of floristic affinities at middle levels. Nevertheless, as noted in *Methods: Methodological principles*, middle-level types and descriptions can be drafted independently of or prior to the establishment of units lower in the hierarchy, drawing on the large body of knowledge on the response of species and growth forms to regional ecological factors. Thus, the biogeographical and ecological relationships structuring vegetation patterns can be described within the regionally scaled level of the division (regional formation) and the finely scaled alliances and associations. Criteria for the development of middle-level descriptions are summarized in Table 4.

1. *Division (L4).*—Division is defined as “combinations of dominant and diagnostic growth forms and a broad set of diagnostic plant species that reflect biogeographic differences in composition and continen-

TABLE 4. Interpretive guidelines for vegetation and ecology criteria, from division to association.

Guideline	Level	
	Division	Macrogroup
Definition (FGDC 2008)	A vegetation unit with broadly uniform growth forms and a broad set of diagnostic plant species at large biogeographic scales that reflect continental distinctions in climate, geology, substrates, hydrology, and disturbance regimes.	A vegetation unit that contains moderate sets of diagnostic plant species and diagnostic growth forms that reflect subcontinental to regional biogeographic composition and subcontinental to regional mesoclimate, geology, substrates, hydrology, and disturbance regimes.
Biogeography/floristics	Large scale, continental, biogeography with largely nonoverlapping floristics (i.e., most species ranges fully contained), species heterogeneity high. Global formations separated by continental-intercontinental patterns of species into divisions.	Subcontinental to regional ecological gradient segment (often mesoclimatic), reflected by sets of strongly diagnostic species (many species ranges fully contained); overall composition very distinct from other units.
Diagnostic species	A large suite of strongly diagnostic species (large number of character species among the diagnostic species; species have high fidelity but variable constancy).	Multiple sets of strong diagnostic species, including many strong differential and character species. Constant species become more important; at least 25% constancy expected.
Growth forms	Broadly uniform sets of growth forms and canopy closure (same as formation level, but variant expressions; e.g., conifer-dominated Rocky Mountain forest division vs. broad-leaf deciduous hardwood forests of Eastern North American forest division).	Broadly uniform sets of growth forms and canopy closure. May be specific growth form variants that support floristic patterns, e.g., herb vs. shrub, coastal soft-leaved chaparral vs. inland sclerophyll chaparral.
Climate	Continental macroclimate. Separates formations by continental or major intercontinental climatic patterns.	Subcontinental mesoclimate. Indicative of primary regional gradients in vegetation, e.g., latitudinal, altitudinal, continentality (major zonal or strong azonal gradients).
Disturbance regime/succession	Variable range of disturbance regimes consistent with continental expression of formation.	Broadly consistent, but variable disturbance regimes indicative of subcontinental climate (e.g., floods, large-scale fires).
Edaphic/hydrology	Broad range of conditions consistent with continental expression of formation (e.g., the divisions span floodplain and swamp conditions).	Broad range of conditions, sometimes reflective of broad topo-edaphic interactions with climate (e.g., large-scale droughty soils with or without fires) or broad-scale specialized geological substrates.

Notes: These are typical criteria, and the role of factors may differ for some types. The role of ecological factors at each level may also differ depending on the site conditions, e.g., at the macrogroup and group levels, the substrate factors on atypical or azonal wet or dry sites may more strongly influence on vegetation patterns than do mesoclimates, which may more strongly influence vegetation on typical or zonal or characteristic mesic upland sites. See also Table 3.

tal differences in mesoclimate, geology, substrates, hydrology, and disturbance regimes” (FGDC 2008). Whereas the formation level (L3) is more strictly physiognomic, the division level includes both physiognomic and floristic criteria. The term division was adopted from the Braun-Blanquet approach, which proposed it as a level above the class (Hadač 1967, Westhoff and van der Maarel 1973, Pignatti et al. 1994). For example, Westhoff and van der Maarel (1973:665) define the division as follows:

“A [vegetation type] above the class level that unites related classes within a floristic region (or province) on the basis of common division character-taxa. The character taxa may be species, or genera or both ...

the definition of the division is not physiognomic. We suggest that, the difference in definition notwithstanding, divisions may converge in practice with the formations of the Anglo-American ecology as broad physiognomic units limited to a given region or continent.”

As the EcoVeg approach explicitly defines the division using both physiognomic and floristic criteria, it should largely be compatible with their definition of division.

The term division is sometimes referred to as a regional formation (Richards 1952, Beard 1973, Whittaker 1975). For example, Richards divides his tropical rain forest-type into the American rain-forest formation, African rain-forest formation, and the Indo-Malayan

TABLE 4. Extended

Level		
Group	Alliance	Association
A vegetation unit that is defined by a relatively small set of diagnostic plant species (including dominants and codominants), broadly similar composition, and diagnostic growth forms that reflect regional mesoclimate, geology, substrates, hydrology, and disturbance regimes.	A vegetation classification unit containing one or more associations and defined by a characteristic range of species composition, habitat conditions, physiognomy, and diagnostic species, typically at least one of which is found in the uppermost or dominant stratum of the vegetation. Alliances reflect regional to subregional climate, substrates, hydrology, moisture/nutrient factors, and disturbance regimes.	A vegetation classification unit defined on the basis of a characteristic range of species composition, diagnostic species occurrence, habitat conditions and physiognomy. Associations reflect subregional to local topo-edaphic factors of substrates, hydrology, disturbance regimes, and climate.
Regional ecological gradient segment (often broadly topo-edaphic) reflected by a set of moderately diagnostic species (at least a few species ranges fully contained); overall composition broadly distinct from other units.	Regional to subregional gradient segment (often more narrowly topo-edaphic or biogeographic), reflected by at least several moderate diagnostic species, including from the dominant strata; overall composition moderately distinct from other units.	Subregional to local ecological gradient segment reflected in several diagnostic species, including differential species and constant dominants across strata; overall composition not well separated from other units.
A set of moderately strong diagnostic species, preferably with one or more strong differentials or character species. Constancy of at least 25% expected for some species.	Several or more moderate diagnostic species, preferably including at least one strong differential (character species may be absent). Constant species more important for defining type, with at least 40% constancy expected.	At least a few diagnostic species, preferably including at least one moderate differential. Constancy 40–60% for a suite of species.
Moderately uniform growth forms and canopy closure, (e.g., varying from evergreen to deciduous and open to closed canopy).	Moderately uniform growth forms and canopy closure, at least in the dominant layer (e.g., conifer and mixed hardwood, other layers may vary from shrub to herb or moss-dominated ground layers with either open or closed canopy).	Strongly uniform growth forms, in both dominant and other layers and degree of canopy closure (e.g., closed canopy evergreen dominated shrubland with a primary understory growth form dominant (sedge forb).
Regional mesoclimate. Could indicate secondary regional gradients (depends upon selected primary gradient for macrogroup).	Regional to subregional topo-edaphic factors, sometimes reflective of biogeography and climate.	Climate rarely a driver; rather a narrow range of topo-edaphically related influences.
Moderately consistent disturbance regime; may incorporate successional stages that are otherwise floristically similar.	Moderately specific disturbance regime; may group successional related associations.	Narrow range of disturbance regime; may have disturbance or successional relationships to other local associations.
Moderate range of variation in specific topo-edaphic or hydrologic conditions.	Moderately specific edaphic or hydrologic conditions, e.g., dry, dry-mesic, mesic, wet-mesic, or wet moisture conditions and poor, moderate, moderately rich, or rich nutrient conditions.	Narrow range of edaphic or hydrologic conditions, indicative of locally significant factors, e.g., soil moisture/nutrient regimes, soil depth and texture. Site-scale drivers of structural variation (e.g., dry woodlands).

rain-forest formation. We retain the term formation for the more strictly growth-form-based global type. The division concept also overlaps with the term biome. For example, Rutherford et al. (2006:32) note that, strictly speaking, the term biome includes both plant and animal communities on a continent, but because of the dominant nature of vegetation cover in (nearly) all terrestrial ecosystems, biomes have been based only on vegetation characteristics (see also Ladle and Whittaker [2011]). Thus, the Rutherford et al. Nama Karoo biome (or subcontinental formation) of South Africa is largely equivalent to a division.

With the introduction of the division concept and floristic criteria, the upper-level formation units can be subdivided on the basis of biogeographically distinct regional species pools. Thus the tropical lowland humid forest formation can be divided into Amazonian

lowland humid forest, Brazilian-Parana lowland humid forest, Guineo-Congolian evergreen and semievergreen rainforest, and Malagasy evergreen and semievergreen rain forest. Typically, suites of diagnostic (character) species are selected that are restricted to a particular division type, along with the dominant species that express the dominant growth forms. In turn, from the bottom-up, it is the shared growth forms among division types reflecting a set of shared climatic and edaphic factors that leads to their placement within the same formation.

When developing global division units, we consulted Takhtajan (1986), as well as regional biogeographic studies, such as Greller (2000) for North America, Rivas-Martinez et al. (2011) for Latin America, and White (1983) for Africa. These provide useful guides to the scope of biogeographic regions relevant to describing

division level concepts. These biogeographic classifications are not used to introduce a formal phytogeographic regionalization into the hierarchy (as done by Brown et al. [1998]); rather, they inform us of the likelihood that, for example, Mongolian grasslands share species in common with either European or North American grasslands. Not all formations have patterns relevant to Takhtajan's biogeographic units. For example, whereas the biogeography reflected in the dozen or so divisions for the temperate grassland and shrubland formation correspond closely to Takhtajan's provinces, the two divisions of the mangrove formation do not. Below the division level, large-scale, biogeographic-scale descriptors typically yield to other factors.

By emphasizing the diagnostic value of species or suites of species, the division level facilitates the establishment of lower-level classification units, thus minimizing the need to search for universally valid diagnostic species or genera for those units. The value of diagnostic species groups is clearer among similar habitats within a biogeographic region (Mueller-Dombois and Ellenberg 1974). Species that are widespread and occur across multiple biogeographic regions may have potentially different ecological niches, and thus different diagnostic characteristics among the regions, as discussed by Damman (1979) and Wells (1996) for bog and fen species shared between eastern Canada and Western Europe.

2. *Macrogroup (L5)*.—Macrogroup is defined by “moderate sets of diagnostic plant species and diagnostic growth forms that reflect biogeographic differences in composition and subcontinental to regional differences in mesoclimate, geology, substrates, hydrology, and disturbance regimes” (FGDC 2008; cf. Brown 1982, Pignatti et al. 1994).

The macrogroup is similar to the class level of the Braun-Blanquet approach, which uses the definition of “the common ecological space of the included associations, and recognizable by the occurrence of a common set of characteristic taxa, which are by preference chorologically [biogeographically] homogeneous” (Pignatti et al. 1994:150). According to Pignatti et al. (1994), three primary conditions must be met for the recognition of a Braun-Blanquet class: characteristic taxa, ecology, and biogeography; and one secondary condition, physiognomy. A vegetation class should therefore have a wide geographic distribution. These same conditions appear in the macrogroup definition, but, as with the division, the physiognomic condition plays a more explicit role.

A macrogroup definition should typically contain a moderately large set (dozens) of strongly diagnostic species that share a broadly similar physiognomy and ecology in response to continental, subcontinental, or regional differences in ecological factors (Table 4). Thus, the macrogroup expresses the floristic, growth form, and regional ecological factors that separate vegetation within a division. For example, the Amazonian Lowland

Humid Forest contains a number of macrogroups based on species changes that reflect regional climate and elevational gradients, including Central Amazon Humid Forest, Northern Amazon Humid Forest, Southern Amazon Humid Forest, Southwestern Amazon Lowland Humid Forest, Southwestern Amazon Subandean Humid Forest, Western Amazon Lowland Humid Forest, Western Amazon Subandean Humid Forest. The California Scrub division is based on both a variety of distinct species and distinct growth form patterns, e.g., California Chaparral and the California Coastal Scrub.

When assessing compositional similarity, presence/absence data (as measured by constancy) may work reasonably well to distinguish the wide diversity of species and growth forms found within and between related macrogroups, though dominance should not be ignored. Analytical tools such as shortest path or step-across similarity (Boyce and Ellison 2009) can address compositional similarity. Constant species are defined based on a 25% threshold, given the higher level of heterogeneity among stands at this level, as compared to lower levels (Chytrý and Tichý 2003; and see Pojar et al. [1987], who refer to these as important companion species).

3. *Macrogroups and ruderal vegetation*.—For the EcoVeg approach, the macrogroup level appears to be a very appropriate level for recognizing ruderal (weedy, invasive, or novel) vegetation, that is, vegetation found on human-disturbed sites (abandoned farmland, quarries, roadsides, or vegetation dominated by invasives; see *Basic Categories of the EcoVeg Approach: Natural and cultural vegetation*). Ruderal types often contain remnants of the larger regional species pool, as reflected by the division level, but otherwise have a very distinctive species composition. For that reason, macrogroups of ruderal vegetation are labelled as such. For example, within the Eastern North American Cool Temperate Forest division, there are seven native forest macrogroups (e.g., Northern Pine and Oak Hardwood Forest) and one ruderal forest macrogroup (Eastern North American Ruderal Forest). The latter group is typically found on abandoned farm fields that contain both weedy native and invasive exotic forests species (e.g., *Acer platanoides* Ruderal Forest, *Robinia pseudo-acacia* Ruderal Forest, and the old field *Pinus strobus* Ruderal Forest, dominated by *Pinus strobus* and *Acer rubrum*, with various invasives shrubs and herbs [e.g., *Rhamnus cathartica*, *Alliaria petiolata*]).

The Braun-Blanquet approach also recognizes distinct classes (equivalent to macrogroups) of invasive or weed vegetation, both forested and nonforested (see Rodwell et al. [2002]). The *Robinietaea* of central European vegetation (Chytrý and Tichý 2003) contains anthropogenic tree communities dominated by *Robinia pseudo-acacia*, *Acer negundo*, and *Ailanthus altissima* that colonize disturbed habitats, such as deforested lands, cleared forest edges, and agricultural and industrial

fallows. The *Molinio-Arrhenatheretea* (anthropogenic pastures and meadows) is an example of a more complicated mix of natural and ruderal vegetation, reflecting the long history of agricultural use on both originally natural and extensively human-created meadows. In Rodwell et al. (2002), this class is treated alongside other native European grassland types. In Hungary, a grid-based vegetation mapping project explicitly distinguished habitats strongly dominated by perennial alien species from habitats containing native species, with or without some proportion of perennial aliens (Botta-Dukát 2008). The former category parallels our ruderal macrogroup.

For a new type to be defined based on invasive plant species, it must contain a new set of diagnostic species in the region and have essentially removed the diagnostic species of existing native types. That is, when invasive species overwhelmingly dominate a stand (e.g., >90% cover, but this may vary by type) and native diagnostic species are largely to completely absent, or replaced by new, often “weedy” native species, that stand is placed within a ruderal macrogroup. Setting a high threshold minimizes the creation of new types until it is certain that a new characteristic combination of species has been formed. Such is the case for abandoned exotic tree plantations and post agricultural forests in Europe and the United States; these exhibit some characteristics of more natural vegetation, but differ from a near-natural analog for at least a full generation of trees, during which time native diagnostic species establish (Ellenberg 1988, Flinn and Marks 2007). The same is true of many secondary tropical forests (Zanini et al. 2014).

By expanding the category of natural vegetation to include historic, native, and recent naturalizing and altered vegetation, we provide ecologists with a method that goes beyond a simple dichotomy of pristine nature or not and allows us to document types that reflect the range of influences on natural vegetation. We can then begin to assess the proportion of landscapes that contain native vs. invasive vs. cultural vegetation (Botta-Dukát 2008). There is a long history of interactions between natural and human processes in some regions of the world, and we recognize that it will not always be easy to make these distinctions.

4. *Group (L6)*.—A vegetation unit defined by “a relatively narrow set of diagnostic plant species (including dominants and codominants), broadly similar composition, and diagnostic growth forms that reflect regional mesoclimate, geology, substrates, hydrology, and disturbance regimes” (FGDC 2008; cf. Brown 1982). As with the macrogroup, meeting this definition requires four conditions: characteristic taxa, physiognomy, ecology, and biogeography (see Table 4). It is similar to the order level of the Braun-Blanquet hierarchy (Pignatti et al. 1994).

A group description should contain several to many diagnostic species that share a similar structure and ecology, responding to regional ecological factors, with

many moderately differential species or two or more strongly differential (character) species. There should be several diagnostic species in the dominant stratum or growth form, but the diagnostic value is typically that of constancy and dominance. Several dominant growth forms are consistent throughout the type. There may be some variation in dominant overstory species, where overall floristics and ecology are otherwise quite similar (e.g., subalpine larch and Engelmann spruce–subalpine fir with similar site factors and disturbance regimes).

The criterion of compositional similarity addresses the overall range of composition, rather than specific diagnostic species or dominants. Whereas for the macrogroup, presence/absence may play a strong role in discriminating among types (given the large number of species that are expected for macrogroup discrimination), for the group, the abundance of a set of dominant species along with other diagnostic species together play a stronger role in the characteristic species combination. As with macrogroups, a constant species could be as low as 25% (Chytrý and Tichý 2003).

5. *Comparison of middle level units to other classifications*.—A number of classifications have parallels to the middle levels of the EcoVeg approach (see also Franklin et al. [2012]). Comparable units have been developed at the class and order level in the Braun-Blanquet classification (Walker et al. 1994, Peinado et al. 1997, 2011, Rivas-Martinez et al. 1999, Spribille 2002, Barbour et al. 2005, Talbot et al. 2005). In British Columbia, a comprehensive set of classes and orders has been described for most vegetation types based on a modification of the Braun-Blanquet approach (Meidinger et al. 2003).

Brown et al. (1998) published an impressively comprehensive list of biotic communities for North America (including Central America). Biotic communities are defined as “regional [biogeographic] plant formations characterized by particular species of plants and animals,” that express the multivariate effects of environmental factors and are identified using both dominant and diagnostic species (Brown et al. 1998). The scale of their units is comparable to the macrogroup or group. Although descriptions are only available for the American Southwest, Brown et al. (1998) also produced a list and map for all North American types.

The terrestrial ecological system classification was recently completed by NatureServe for both the United States (Comer et al. 2003) and Latin America (Josse et al. 2003, Sayre et al. 2008). Terrestrial ecological systems are defined as “a group of plant community types that tend to naturally co-occur within similar environmental settings, ecological dynamics, and/or environmental gradients” (Comer and Schulz 2007). Although developed as a single, nonhierarchical set of types, they have a fairly strong correspondence to the EcoVeg group level. Indeed, their concepts were consulted when developing group concepts in North America because, as with groups, system units are derived by a bio-ecosystems

approach that includes vegetation and ecological factors. Whereas groups rely more strongly on vegetation criteria correlated to ecological factors, systems more directly use ecological factors and landscape pattern together with vegetation to define types. Both systems and EcoVeg groups consist of aggregations of associations (data available online).¹⁵ Systems guide the mapping legends and successional models of natural ecosystems for the USGS LANDFIRE program (data available online)¹⁶ and for wildlife habitat characterization of the USGS Gap Analysis Program (Comer and Schulz 2007, Lowry et al. 2007).

Lower levels (L7–L8).—Although not our focus, these levels are briefly defined so that the reader can see how they integrate with L1–L6. For complete descriptions of the lower level units, see FGDC (2008) and Jennings et al. (2009).

1. *Alliance.*—A classification unit containing one or more associations and defined by a characteristic range of species composition, habitat conditions, physiognomy, and diagnostic species, typically at least one of which is found in the uppermost or dominant stratum of the vegetation. Alliances reflect regional to subregional climate, substrates, hydrology, moisture/nutrient factors, and disturbance regimes. Additional information on the alliance concept is provided in Appendix E, including guidelines, literature review, and glossary of terms.

2. *Association.*—A classification unit defined on the basis of a characteristic range of species composition, diagnostic species occurrence, habitat conditions, and physiognomy. Associations typically reflect topo-edaphic climate, substrates, hydrology, and disturbance regimes.

The alliance and association concepts have been used widely by various vegetation classification systems (see discussion in Jennings et al. [2009] and Franklin et al. [2012]) but are most fully developed in the Braun-Blanquet approach. As outlined in Jennings et al. (2009), the concepts for these two levels has close similarities to that approach (more so than for other levels of the hierarchy) and builds on decades of work applying those terms within North America (Grossman et al. 1998).

3. *Subassociations, variants, and phases.*—Additional lower levels, such as subassociation, variant, and phases may be developed, if desired. For example, in the USNVC hierarchy, these levels are noted, but not formally included (FGDC 2008). Westhoff and van der Maarel (1973) provide guidance on the definitions and applications of the subassociation and variant levels, and Boublik et al. (2007) provide a contemporary application. The phase level is an optional level that may be used to track levels of alteration caused by human impacts. That is, the phase level can be used to describe the range of variation from minimally disturbed to

strongly altered stands, where overall composition, diagnostic species, and invasive species change along that gradient. It then becomes possible to define a limit of alteration, after which the type is so altered that it becomes a ruderal type (see *Natural Vegetation: Hierarchy levels for natural vegetation: 3. Macrogroup and ruderal vegetation*). Analyses of types may benefit from initially removing altered phases when characterizing floristic and growth form patterns, then adding these phases back in to determine their relationship to minimally disturbed types. The phase level may also be useful at multiple levels of the hierarchy. That is, as the composition of a natural association is altered by human impacts, and invasives and weedy natives increasingly dominate a stand, it may only be possible to assign a stand to an alliance, and as the composition across the alliance is altered, it may only be possible to assign a stand to a group. Very strong alteration could lead to a novel type and placement in a ruderal category.

Type description and review

Many aspects of type description are discussed in FGDC (2008) and Jennings et al. (2009), including plot data preparation and analysis, interpretation, documentation, and archiving, and type description, nomenclature, and peer review. Those publications focused on the alliances and associations. We focus on the middle and upper levels of the hierarchy.

Vegetation field plots and analyses

Field plot data collection methods described in FGDC (2008) and Jennings et al. (2009) are suitable for all levels of the hierarchy, since collection methods for physiognomic, floristic, and relevant ecological information are included. A hybrid, nested plot design method for data collection is recommended (Jennings et al. 2009). In particular, we recommend the nested 0.1-ha design with core plot sizes between 100 m² and 1000 m² because almost all vegetation can be adequately characterized within these size ranges (Peet et al. 1998, Dengler et al. 2009), though many studies still sample open grass and low shrub vegetation at between 10 m² and 100 m² (Dengler et al. 2008, Peet and Roberts 2013). For vegetation that is very species rich and physiognomically complex (e.g., tropical rainforests) or very sparse (e.g., deserts), additional plot sizes of between 0.25 and 1.0 ha may be needed to accurately describe floristics and physiognomy. By using these plot methods, the physiognomy, floristics, and ecology of a wider range of vegetation types can be consistently characterized at multiple spatial scales.

Choosing a nested design, with a relatively narrow range of plot sizes, also increases the compatibility with other plot data and the consistency of the overall data. There is no good ecological reason, apart from differences in stature, to change plot sizes between types with different dominant growth form (e.g., grasslands and forests) in terms of composition, diversity, and

¹⁵ <http://explorer.natureserve.org/servlet/NatureServe?init=Ecol>

¹⁶ <http://landfire.cr.usgs.gov/viewer/>

ecological responses. Studies in Europe have found that vegetation classification analyses are confounded when plots of different sizes are included, because measures of richness and constancy are not comparable (Chytrý 2001, Chytrý and Otýpková 2003, Otýpková and Chytrý 2006, Dengler et al. 2009). Thus careful consideration should be given to the merits of retaining as uniform a plot sampling design as possible within and across vegetation types, anywhere in the world.

The increasing trend toward standardizing vegetation data collection methods and online database repositories is encouraging. In North America, VegBank has helped set standards for plot databases and data collection and can help aggregate the diverse set of plots from across North America (Peet et al. 2012). Additional vegetation databases are documented in the global index of vegetation databases (Dengler et al. 2011). Access to this quantity of global data will allow for large scale analysis of vegetation patterns and clarification of the hierarchy at multiple levels.

Nomenclatural rules

We continue the approach taken in Jennings et al. (2009), whereby a scientific name, a translated scientific name (based on the vernacular plant names available from widely accepted standard taxonomic references), and a common name are all provided. Translated names and common names are provided in English and other languages. The names can include both physiognomic terms (forest, grassland, bog, tundra) and plant species names, and may also include a biogeographic term. Nomenclatural terms from other classifications can be noted in the field for synonymy.

Upper level nomenclature.—Formation types (L1–L3) are named, defined, and organized by structure and physiognomy to reflect global climatic and site factors. Naming the formations is aided by the use of common terminology (FGDC 2008) reflecting the habitats occupied by a unit (Whitmore 1984:155). A one-sentence descriptive summary is provided for each type. The result is an easily recognizable set of formations with readily memorable names that describe concisely the ecological characteristics of the formation unit. While not developed here, formal Latinized names could be developed for these three levels, as proposed by Rübél (1930–1931, as cited in Shimwell 1971: Appendix II). For example, *Deserta* for the desert and semidesert class, *Siccadeserta* for the warm semidesert subclass or *Frigorideserta* for the cool semidesert subclass.

1. *Formation class (L1).*—Class names are based on the general growth forms that correspond to global moisture/temperature regimes. The single name identifies the typical growth forms that correspond to particular moisture/temperature conditions, and a parenthetical set of names can be included to inform users as to the main vegetation types included. Given overlapping usage of terms such as forest and woodland, both terms are combined (Forest and Woodland) to

indicate that the class definition encompasses all stands dominated by mesomorphic (i.e., broad-leaved or needle-leaved) trees of varying height and canopy spacing. The term grassland is broadly applied to include upland herbaceous (forb and graminoid) dominated vegetation. Formation class names include: Mesomorphic Tree Vegetation (Forest and Woodland), Mesomorphic Shrub and Herb Vegetation (Shrub and Herb Vegetation), Cryomorphic Scrub and Herb Vegetation (Polar and High Montane Scrub and Grassland), Xeromorphic Woodland, Scrub and Herb Vegetation (desert and semidesert), Hydromorphic Vegetation (Aquatic Vegetation), and Rock Vegetation.

2. *Formation subclass (L2).*—The subclass name reflects the structure, physiognomy, and environmental factors that characterize the unit. The primary environmental factor is macroclimate. Physiognomic terms are sometimes more specific than the formation class name (e.g., scrub vs. shrubland, where the vegetation may include tall, xeromorphic, tree-like plants such as tall cacti or microphyllous-leaved shrubs). All such terms, if used, should be defined. Examples include: Tropical Forest, Temperate and Boreal Grassland and Shrubland, Cool Semidesert Scrub and Grassland, and Saltwater Aquatic Vegetation.

3. *Formation (L3).*—The formation name reflects the structure, physiognomy, and environmental factors that characterize the formation. The primary environmental factors are soil moisture and elevation. Physiognomic terms are sometimes more specific than the formation class or subclass name. All physiognomic terms should be defined in the vegetation type description. Examples include: Tropical Lowland Humid Forest, Mediterranean Scrub and Grassland, Cool Semidesert Scrub and Grassland, and Marine and Estuarine Saltwater Aquatic Vegetation.

Mid- and lower-level nomenclature.—Lower level nomenclature for alliances and associations is described in Jennings et al. (2009). For mid levels, many of the same guidelines apply. These include:

- 1) Nomenclature shall contain scientific and colloquial names.
- 2) Combinations of floristic and physiognomic terms are always used in the name, and biogeographic and ecological terms may be used.
- 3) Among the taxa that are chosen to name the type (up to three species for mid levels), those occurring in the same stratum or growth form (tree, shrub, herb, nonvascular, floating, submerged) are separated by a hyphen (-) with a space on each side, and those occurring in different strata are separated by a slash (/). Diagnostic taxa occurring in the uppermost stratum are listed first, followed successively by those in lower strata. The order of taxon names within a stratum or growth form generally reflects a dominant of high constancy (whether or not strongly diagnostic), a dominant of moderate to strong diagnostic

TABLE 5. Example names for macrogroup and group.

Scientific name	Colloquial name
Macrogroup	
<i>Juniperus coahuilensis</i> , <i>Pinus cembroides</i> , <i>Quercus arizonica</i> Woodland	Madrean Lowland Evergreen Woodland
Macrogroup	
Great Basin and Intermountain <i>Chrysothamnus viscidiflorus</i> , <i>Coleogyne ramosissima</i> / <i>Achnatherum hymenoides</i> Shrubland and Grassland	Great Basin and Intermountain Dry Shrubland and Grassland
Macrogroup	
<i>Acer saccharum</i> , <i>Betula alleghaniensis</i> , <i>Pinus strobus</i> , <i>Tsuga canadensis</i> Forest Macrogroup	Northern Mesic Hardwood and Conifer Forest
<i>Acer saccharum</i> , <i>Betula lenta</i> , <i>Quercus rubra</i> Forest Group	Southern and Central Appalachian Northern Hardwoods–Hemlock Forest
Group	
<i>Acer rubrum</i> , <i>Acer platanoides</i> / <i>Rhamnus cathartica</i> Ruderal Forest	Eastern North American Ruderal Forest
Macrogroup	
northern and Central <i>Juniperus virginiana</i> , <i>Liriodendron tulipifera</i> / <i>Lonicera tatarica</i> Ruderal Forest Group	Northern and Central Old Field Forest

value, and a strong diagnostic species, whether or not dominant. Species may meet one or more of these criteria.

- 4) Physiognomic terms used for middle levels should be as consistent and specific as possible within formations. For example, various mid or lower level units may use physiognomic terms such as grassland, marsh, bog, and woodland. A catalogue of terms and their usage should be maintained to ensure consistency (see *Natural Vegetation: Peer review*). For example, the term scrub is used to describe vegetation where shrub and tree-like growth forms are hard to distinguish, as in desert and alpine regions, whereas shrubland refers to more typical multistemmed, weakly canopied, mesomorphic-dominated vegetation.
- 5) Types that fall under the category of natural vegetation but are dominated by invasive species or found on strongly human disturbed habitats, such as old fields on abandoned farm sites or invasive grass-dominated rangelands, and which clearly have no analog to historic native vegetation, should be placed in a distinct macrogroup with the term ruderal in the name.
- 6) Nomenclature for vascular plant taxa should follow the name in an accepted botanical reference (e.g., in the United States, USDA PLANTS database (data available online)).¹⁷ Each plant taxon used in a scientific name shall have only one common name that shall form the basis for the common name of types (e.g., quaking aspen, not aspen or trembling aspen).

At the division level, the names are expected to include biogeographic terms, as large-scale biogeographic patterns play a large role in their concepts. Because it is difficult to choose a few typical species at this scale, scientific and colloquial names may initially be the same. For example, within the Tropical Lowland Grassland,

Savanna and Shrubland, appropriate division names (both scientific and colloquial) include Caribbeo-Mesoamerican Lowland Shrubland, Grassland and Savanna; Brazilian-Parana Lowland Shrubland, Grassland and Savanna; Mopane Savanna; Indo-Malayan Mesic Savanna and Grassland; and Australian Tropical Savanna. See Table 5 for examples of names for macrogroup and group.

Although our nomenclatural approach allows for somewhat lengthy scientific names, it is concerned with clarity, and provides a concise common name accessible to many users, as is typical of biological nomenclature for at least larger sized organisms, such as plants, insects, birds, and fish.

Description template

The template provided in Jennings et al. (2009: Box 2) is appropriate for describing units at all levels of the hierarchy (see also FGDC [2008: Section 3.2.3]). The specifications for describing a type including: (1) a standard template is used, supplemented with a few additional fields for data management purposes. (2) A standard set of growth forms is used, as provided in Appendix C. These should be consulted to maintain consistent concepts. Growth form types are placed in italics to remind the reader that the terms have specific meanings. Additional growth forms will be added as needed. Over time, biogeographic terms and scientific sources for species names will be added. (3) The descriptions can be submitted to a coordinating body established for a country or regions.

Peer review

The approach to peer review described by Jennings et al. (2009) is applicable for those adopting the EcoVeg approach. The process is based on a dynamic classification standard, where peer review is an open process conducted by professional organizations in collaboration with other interested parties. It is administered by a peer review board under the aegis of an institution or institutions capable of providing independent reviewers

¹⁷ <http://plants.usda.gov>

with experience in vegetation classification. Currently, NatureServe manages the data content for the International Vegetation Classification, working in collaboration with international partners, such as International Union for Conservation of Nature, World Wildlife Fund, The Nature Conservancy, International Association of Vegetation Science, a variety of agencies, organizations and academic scientists, and with national projects, such as the USNVC and Canadian National Vegetation Classification (CNVC). Whether a more formal international body can be developed will depend on the interests of vegetation ecologists around the world (see also *Implementing the EcoVeg Approach*).

CULTURAL VEGETATION

Criteria for the description of cultural vegetation

Vegetation criteria are the primary properties used to define all units of cultural vegetation, but the role of human management processes is often much stronger than ecological or biogeographic processes. Excluded from the vegetation criteria are explicit habitat factors (e.g., climate, soil type) or land use practices (e.g., grazed pasture vs. ungrazed pasture), except as these are expressed in the vegetation. Some types are difficult to place in terms of natural vs. cultural vegetation (e.g., some intensively managed forests, some pastures), and the user may need to look in both parts of the hierarchy to determine the type's location.

The criteria for classifying cultural vegetation include growth forms, floristics, and ecological setting (Di Gregorio and Jansen 1996). The definition of terms used for cultural vegetation criteria largely correspond to that of natural vegetation (see *Natural Vegetation: Criteria for the description of natural vegetation*), but compositional similarity is not a primary criterion, given the monodominance of many cultural vegetation types. Some common characteristics of cultural vegetation include (1) regularly spaced vegetation with substantial cover of bare soil for significant periods of the year (e.g., tillage, chemical treatment, or agricultural flooding), (2) dominant growth forms or structure are highly manipulated and rarely found in natural vegetation (e.g., mechanical pruning, mowing, clipping, etc.), and (3) dominant vegetation comprised of planted, nonnative species.

Growth forms.—As with the natural vegetation, growth form criteria include (1) diagnostic patterns of growth forms, (2) dominant growth forms, singly or in combination, and (3) vertical and horizontal structure of growth forms (Di Gregorio and Jansen 1996). Distinctive sets of cultural growth forms are not currently described, but will be needed (orchard tree, vineyard grape, row crop, etc.).

Floristics.—Floristic (crop or managed species) criteria include (1) diagnostic combinations of species/crop or managed types, (2) dominant species, reflecting similar agricultural or developed vegetation patterns, and (3) vertical and horizontal structure of species.

Together these criteria are evaluated in a human management context.

Ecological context.—Criteria for ecological context include (1) climate (macro, meso, and microclimate), though human management activities often overcompensate for many of the climatic effects, except at the extremes (frost free climates, extreme cold or drought climates), (2) effects of human activities (e.g., plowing, mowing), and (3) topo-edaphic factors, including creation of ponds, plowing, modifications of pH, moisture, nutrients, and texture. Because many crop species are planted and maintained outside their provenance, biogeography is rarely considered in the description of cultural types.

All type concepts based on these criteria should be derived from field observations, in which the crops or managed species, growth forms, and their abundances, along with the field observation record, overall vegetation structure, management activities, and habitat setting are described. These field data provide the fundamental information for the description of types. All types at all levels should be described and characterized.

Hierarchy levels for cultural vegetation

As with natural vegetation, the hierarchy consists of eight levels that are aggregated into three sets, but physiognomy plays a greater role for classifying cultural vegetation. The criteria outlined in *Cultural Vegetation: Criteria for the description of cultural vegetation* are used to develop descriptions of each unit in the hierarchy, with the utility and relevance of the criteria varying by level. In this section, we provide the names, definition, and descriptions for each of the levels (see also Table 6), following FGDC (2008).

Cultural upper levels (L1–L4).—As with natural vegetation, physiognomic criteria are the primary properties of cultural vegetation used to define the four upper levels. The formation concept, as discussed for natural vegetation, is relevant to cultural vegetation too, but units are assessed in light of human activities that govern their properties.

1. *Cultural class (L1).*—Cultural class is defined by a broad and characteristic combination of dominant growth forms adapted to relatively intensive human management, as reflected in relatively rapid changes in structure and/or composition. Relatively intensive human management refers to activities affecting vegetation composition and/or structure that occur from multiple times in a year (haying, mowing) to decadal (thinning of forest structure, orchard pruning, swidden slash and burn cycles).

2. *Cultural subclass (L2).*—Cultural subclass is defined by a broad combination and degree of herbaceous vs. woody growth forms that reflect widespread human management activities. The types are based on broadly distinct growth form combinations, including herbaceous vs. woody vs. aquatic cultural vegetation types.

TABLE 6. Levels, definitions, and examples of the hierarchy for cultural vegetation (see FGDC 2008).

Cultural hierarchy	Definition (FGDC 2008)	Example 1 names		Example 2 names	
		Scientific	Colloquial	Scientific	Colloquial
Upper levels					
L1: Cultural class	defined by a broad and characteristic combination of dominant growth forms adapted to relatively intensive human manipulations, as reflected in relatively rapid changes in structure and/or composition	Anthromorphic Vegetation	Agricultural and Developed Vegetation	Anthromorphic Vegetation	Agricultural and Developed Vegetation
L2: Cultural subclass	defined by broad combinations and degree of herbaceous versus woody growth forms that reflects global human management activities	Herbaceous Agricultural Vegetation	Herbaceous Agricultural Vegetation	Woody Agricultural Vegetation	Woody Agricultural Vegetation
L3: Cultural formation	defined by the degree to which canopy structure of dominant growth forms is annually converted or heavily manipulated/harvested	Row and Close Grain Crop	Row and Close Grain Crop	Forest Plantation and Agroforestry	Forest Plantation and Agroforestry
L4: Cultural subformation	defined by the spatial structure of the Vegetation, including whether in swards, rows, and degree of manipulation to the canopy	Graminoid Row Crop	Graminoid Row Crop	Forest Plantation	Forest Plantation
Mid levels					
L5: Cultural group	defined by a common set of growth forms and many diagnostic plant taxa sharing a broadly similar region and climate, and disturbance factors	Tropical and Temperate Corn Crop	Tropical and Temperate Corn Crop	Temperate and Boreal Conifer and Hardwood Plantation	Temperate and Boreal Conifer and Hardwood Plantation
L6: Cultural subgroup	defined by a common set of growth forms and diagnostic species (taxa) preferentially sharing a similar set of regional edaphic, topographic, and disturbance factors	Temperate Corn Crop	Temperate Corn Crop	Native Eastern North American Conifer and Hardwood Plantation	Native Eastern North American Conifer and Hardwood Plantation
Lower levels					
L7: Cultural type	defined by one or more dominant or codominant species, as well as habitat conditions and physiognomy	<i>Zea mays</i> Crop	Maize Corn Crop	<i>Pinus strobus</i> – <i>Pinus resinosa</i> – <i>Pinus banksiana</i> Native Plantation	Native White-Red-Jack Pine Plantation
L8: Cultural subtype	defined by one or more dominant or codominant species, in conjunction with a characteristic set of associated species, habitat conditions, and physiognomy	<i>Zea mays</i> var. <i>saccharata</i> – <i>Zea mays</i> var. <i>rugosa</i> Crop	Sweet Corn Crop	<i>Pinus strobus</i> Plantation	White Pine Plantation

Notes: The name of the level can be added to the type name for clarity, where needed. Scientific names are not well developed for all levels of the cultural hierarchy.

3. *Cultural formation (L3)*.—Cultural formation is defined by the degree to which canopy structure of dominant growth forms is annually converted or heavily manipulated/harvested.

4. *Cultural subformation (L4)*.—Cultural subformation is defined by the spatial structure and specific growth form dominance of the vegetation, including whether in swards, rows, and degree of manipulation to the canopy.

The comprehensive set of cultural formation types for the top three levels is provided in Appendix C.

Cultural mid-levels (L5–L6).—For the mid-level units, the combination of criteria based on the specific dominant growth forms, genera, and species that comprise cultural vegetation are applied.

1. *Cultural group (L5)*.—Cultural group is defined by a common set of growth forms and many diagnostic plant taxa sharing a broadly similar region and climate, and disturbance factors.

2. *Cultural subgroup (L6)*.—Cultural subgroup is defined by a common set of growth forms and diagnostic species (taxa) preferentially sharing a similar set of regional edaphic, topographic, and disturbance factors.

Cultural lower levels (L7–L8).—For the cultural type level, emphasis is given to the assemblage of dominant or codominant species, along with the associated species, habitat conditions, and physiognomy. At the subtype level, species compositional variation can be recognized within a dominant crop type, reflecting different soils or different treatments.

1. *Cultural type (L7)*.—Cultural type is defined by one or more dominant or codominant species, as well as habitat conditions and physiognomy.

2. *Cultural subtype (L8)*.—Cultural subtype is defined on the basis one or more dominant or codominant species, in conjunction with a characteristic set of associated species, habitat conditions, and physiognomy.

Examples of cultural types for all levels are provided in Table 6.

The development of a global cultural vegetation hierarchy is relatively novel and has no parallels in other global vegetation classifications. By the same token, it needs further testing and review, including in the name of the levels. For the United States, a comprehensive set of cultural vegetation types is available in pilot form for most levels, based on the Natural Resources Conservation Service's National Resources Inventory (NRI; see FGDC [2008: Appendix I]). These may prove valuable as a global set of cultural types, pending further review.

Type description, peer review, and analyses

Guidelines for the classification of cultural vegetation needs further development and will be developed in the future with interested parties. In the meantime, standards for natural vegetation may be followed, as desired (see *Natural Vegetation: Type description and review;*

Natural Vegetation: Peer review; and Natural Vegetation: Vegetation field plots and analyses).

Nomenclatural rules

As with natural vegetation, the EcoVeg approach includes a scientific name, a translated scientific name (from the vernacular plant names available from widely accepted standard taxonomic references), and a common name (Table 6). Translated names and common names are provided in English and in a variety of other common languages. The names can include both physiognomic terms (forest, grassland, bog, tundra) and species names and may also include a human management term. Nomenclatural terms from other classifications can also be noted in synonymy fields. The guidelines for naming cultural vegetation needs further development and will be developed in the future with interested parties. Examples are provided in Table 6.

IMPLEMENTING THE ECOVEG APPROACH

Development of the EcoVeg approach has spanned 12 years, during which time we have had the opportunity to work with state, regional, and national partners to test and refine the approach. At the national level, the USNVC partnership catalyzed our initial efforts (FGDC 2008, Peet 2008, Faber-Langendoen et al. 2009, Jennings et al. 2009, Franklin et al. 2012), assisted by partnerships with the CNVC (Alvo and Ponomarenko 2003, Baldwin and Meades 2008), and the Bolivian vegetation classification (Navarro 2011). Partnerships in the United States and Canada have also been strong at the provincial and state level, allowing for rigorous applications of fine-scaled concepts (e.g., Hoagland [2000] and Sawyer et al. [2009], among many, as documented in Grossman et al. [1998] and Alvo and Ponomarenko [2003]). Development of the EcoVeg approach across the western hemisphere has been greatly assisted by the prior development of the NatureServe terrestrial ecological systems classification (Comer et al. 2003, Josse et al. 2003), which provided midscale units comparable to group units. Subsequently, various multijurisdictional collaborations emerged, including in the Andes (Josse et al. 2009) and Africa (Sayre et al. 2013). Collaboration with IUCN and WWF on a global grasslands classification has helped refine our approach (Faber-Langendoen and Josse 2010, Dixon et al. 2014). Discussions with European colleagues have produced a better understanding of the relationship between this approach and both the Braun-Blanquet approach (Rodwell et al. 2002) and the European Nature Information System (EUNIS; Davies et al. 2004).

Thus, our system is now well-developed for application across large parts of the globe. NatureServe maintains all International Vegetation Classification units in an institutional database, posts North American units online, and is working to make all units across the globe available publicly.¹⁸ The comprehensive and multiscale

¹⁸ natureserve.org/explorer

set of types documented by the EcoVeg approach will aid in documenting at-risk status of ecosystems under IUCN's emerging red list of ecosystems (see Rodríguez et al. [2011] and Keith et al. [2013]). IUCN and partner ecologists require ecological classifications, including terrestrial, freshwater, marine, and subterranean, to guide red listing efforts, both nationally and internationally. Although these classifications may take a variety of forms at national or subnational levels, their contribution to a global ecosystem red list would be greatly facilitated by the multilevel hierarchy such as that provided here and through the IVC. The IVC could serve as a reporting framework for integrating national information relevant to various levels of terrestrial ecosystem types, in much the same way that the WWF ecoregions have provided one source of standardized units for reporting ecoregional conservation status (Olson et al. 2001). The IVC is already strongly compatible at the formation level with the terrestrial component of IUCN's species habitat classification scheme (version 3.0 2007; *available online*).¹⁹ Improving the IUCN habitats to IVC compatibility could greatly facilitate reporting of both the ecosystem red lists and the description of the species-habitat relations for species red lists.

In conclusion, the EcoVeg approach is now able to address many core needs for vegetation description and classification, and sets the stage for further research. It can describe existing vegetation patterns, including both cultural (planted and dominated by human processes) and natural (spontaneously formed and dominated by ecological processes). By providing a set of hierarchical units for both cultural and natural vegetation (including ruderal or novel vegetation), the EcoVeg approach is able to describe the full range of anthropogenic and ecological influences on vegetation patterns. The approach to description and classification of cultural vegetation types requires more research.

EcoVeg describes vegetation types at multiple thematic-scales, from thematically coarse formations (biomes) to fine-scale associations (biotopes). The eight-level hierarchy for both cultural and natural vegetation draws on well-established traditions of classification in vegetation ecology, compiling both the existing information on vegetation types and providing a peer-review based process for improving and documenting new types.

EcoVeg can inventory vegetation and ecosystem patterns within and across landscape/ecoregional units. In combination with the terrestrial ecological systems classification, the EcoVeg approach provides maps of units at the group or macrogroup level and above for the United States, South America, and Africa. The geographic distribution of all major grassland divisions around the globe is now available (Dixon et al. 2014).

¹⁹ www.iucnredlist.org/technical-documents/classification-schemes/habitats-classification-scheme-ver3

It can support the documentation of status and trends of vegetation and ecosystems (e.g., trends in extends, trends in condition). The current conservation status of macrogroups and systems in the western hemisphere is being assessed as part of the IUCN red list of ecosystems project (Keith et al. 2013; Comer et al., *unpublished manuscript*) and complements the global and state/provincial assessments of at-risk associations in the United States and Canada (Grossman et al. 1998).

EcoVeg facilitates the interpretation of long-term change in vegetation with short-term change of existing vegetation, based on multiple vegetation criteria (growth forms, structure, floristics, etc.). Short-term changes can now be examined at multiple thematic scales to assess types from association to formation scales. Long-term changes can be examined using mid-level types documented in the paleoecological record. Delcourt and Delcourt (1987) used multiple thematic scales, including a level corresponding to the division, to show how vegetation and environmental change varies from dynamic equilibrium to disequilibrium over the last 60 000 years, in contrast to a simple transitory view of vegetation at one level, the community, and a stable physical template on the other (Hunter et al. 1988). Similarly, the late quaternary biomes documented by Williams et al. (2000) in the eastern United States have parallels to current existing biomes at the division and macrogroup level of the EcoVeg approach. The slower rates of historical change for these units, i.e., their persistence over longer periods of time, as compared to the lower level units of alliance and association, opens up new avenues of discussion on vegetation change and conservation applications (Delcourt 2002).

The EcoVeg approach can provide a structure to track real-time ecosystem responses to invasive species, land use, and climate change. The EcoVeg approach treats invasives both at the level of variants within natural types, for example, where they can be an indication of degradation of types characterized by native species, and ultimately, should native species disappear from stands, as a basis for describing new types. For all these reasons, we encourage the use of the EcoVeg approach to describe and classify vegetation.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–E are available online: <http://dx.doi.org/10.1890/13-2334.1.sm>

ERRATUM

The editorial office omitted a sentence in the Review by Faber-Langendoen et al., published in the November 2014 issue.

At the end of the first paragraph on *Nomenclature rules* on p. 551, it should read: “All first letters of English words in a vegetation type name are capitalized and separated, as needed, by either a hyphen with spaces (-), a comma and space (,), or the “and” symbol with spaces (&).” These rules should be applied to Tables 1, 2, 5, and 6, and Appendix C, and wherever formal vegetation type names are used in the text. E.g., in Table 1 “Forest and Woodland” should be “Forest & Woodland,” et cetera.

We apologize for any inconvenience this has caused.

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APPENDICES

Appendix A. Hierarchy Revisions Working Group

Appendix B. Growth Form Names, Codes, and Definitions

Appendix C. Formation Units - Level 1 to Level 3

Appendix D. Examples of Other Formation-Level Classifications

Appendix E. Alliance Concept, Guidelines and Literature Review

Appendix A. Hierarchy Revisions Working Group

Members shown below have been active on the working group since 2003-2004, unless otherwise indicated.

CANADA

Del Meidinger	(British Columbia Ministry of Forests/ Private Consultant)
Serguei Ponomarenko	(Parks Canada)
Jean-Pierre Saucier	(Ministère des Ressources naturelles et de la Faune, Québec)

UNITED STATES

Don Faber-Langendoen	(NatureServe) (co-chair)
Eileen Helmer*	(U.S. Forest Service, Puerto Rico)
Gene Fults*	(U.S. Natural Resource Conservation Service)
Andy Gray††	(U.S. Forest Service, Forest Inventory and Analysis)
Bruce Hoagland	(University of Oklahoma)
Sherm Karl†	(U.S. Bureau of Land Management)
Todd Keeler-Wolf	(California Department of Fish and Game)
David Tart	(U.S. Forest Service) (co-chair)
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* 2010ff

† 2003 - 2006

†† 2003 - 2010

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Don Faber-Langendoen, Todd Keeler-Wolf, Del Meidinger, Dave Tart, Bruce Hoagland, Carmen Josse, Gonzalo Navarro, Serguei Ponomarenko, Jean-Pierre Saucier, Alan Weakley, and Patrick Comer. 2014. EcoVeg: a new approach to vegetation description and classification. *Ecological Monographs* 84:533–561. <http://dx.doi.org/10.1890/13-2334.1>

APPENDIX B. Growth form names, codes, and definitions.

Names, definitions and codes for growth forms for use in collecting vegetation plot data (from Table E.1 of FGDC (2008) (see also Whittaker 1975:359, Tart et al. 2005, Box and Fujiwara 2005).

TABLE B1. General growth forms.

Growth Form Code	Name and Definition
T	Tree - A woody plant that generally has a single main stem and a more or less definite crown. In instances where growth form cannot be readily determined, woody plants equal to or greater than 5 m in height at maturity are to be considered trees (adapted from FGDC 1997). Excludes krummholz (wind-stunted trees), but includes small trees or "treelets" (Box 1981). Tall multistemmed woody plants with strong canopy structure and which well exceed 5 m would be included here (e.g., mature, multi-stemmed <i>Quercus ellipsoidalis</i> in the United States or some Australian mallee eucalypts). ;
S	Shrub - A woody plant that generally has several erect, spreading, or prostrate stems which give it a bushy appearance. In instances where growth form cannot be readily determined, woody plants less than 5 m in height at maturity are to be considered shrubs [even if monopodial?] (adapted from FGDC 1997). Includes krummholz (wind-stunted trees), but excludes small trees (Box 1981). Includes dwarf-shrubs (less than 30 cm), low or short woody vines, and arborescents (woody plants that branch at or near ground-level but grow to low tree heights). (Box 1981). Some multi-stemmed, bushy woody species ("scrub") that reach up to 10m may be included here, such as Australian mallee comprised of <i>Eucalyptus viridis</i> and <i>Eucalyptus dumosa</i>).
H	Herb - A vascular, non-woody plant without perennial aboveground woody stems, with perennating buds borne at or below the ground surface. (Whittaker 1975, FGDC 1997). Includes forbs (both flowering forbs and spore-bearing vascular plants), graminoids, and herbaceous vines.
N	Nonvascular - A plant or plant-like organism without specialized water or fluid conductive tissue (xylem and phloem). Includes mosses, liverworts,

	hornworts, lichens, and algae (adapted from FGDC 1997). Also called thallophytes or "nonvascular cryptogams," (that is, excluding the vascular cryptogams; see Herb) (Box 1981).
E	Epiphyte - A vascular or nonvascular plant that grows by germinating and rooting on other plants or other perched structures, and does not root in the ground (adapted from FGDC 1997).
L	Liana - A woody, climbing plant that begins life as terrestrial seedlings but relies on external structural support for height growth during some part of its life (Gerwing 2004), typically exceeding 5 m in height or length at maturity. Non-woody climbers are treated as "Herb."

TABLE B2. Specific growth forms.

General Growth Form Code	Specific Growth Form Code	Name and Definition
T	TBD	Broad-leaved deciduous tree - <i>A tree with a branching crown, leaves that have well-defined leaf blades that are generally of at least microphyll size ($\geq 225 \text{ mm}^2$, or 0.35 in^2)* and which seasonally loses all of its leaves and becomes temporarily bare-stemmed</i> (adapted from FGDC 1997, Box 1981; Includes monopodial and sympodial growth forms.
	TBE	Broad-leaved evergreen tree - <i>A tree with a branching crown, leaves that have well-defined leaf blades that are generally of at least microphyll sized ($\geq 225 \text{ mm}^2$ or 0.35 in^2) and which has green leaves all year round.</i> (FGDC 1997, Box 1981). Includes monopodial and sympodial growth forms, and woody-like bananas (<i>Musa</i> spp.).
	TBES	Sclerophyllous tree - <i>A type of broad-leaved evergreen tree with leaves that are stiff and firm, and retain their stiffness even when wilted.</i> The leaves are typically relatively small (microphyll to small mesophyll in size) and sometimes rather linear , (FGDC 1997, Whittaker 1975, Box 1981)
	TN	Needle-leaved tree - <i>A tree with slender, often cylindrical, elongated leaves or with small overlapping leaves.</i> Includes scale-leaved and needle-leaved trees, deciduous and evergreen, needle-leaved trees. such as <i>Abies</i> , <i>Larix</i> , <i>Picea</i> ,

		<i>Pinus, Thuja.</i> (FGDC 1997, Box 1981).
	TU	Succulent tree – <i>A tree or arborescent plant with fleshy stems or leaves with specialized tissue for the conservation of water</i> (FGDC 1997). Includes Cactaceae, <i>Yucca brevifolia</i> (Joshua trees), euphorbias, and others over 5 meters in height at maturity. An "arborescent stem-succulent" (Box 1981) Some Dracaenaceae may fit here.
	TM	Small-leaved tree - <i>A tree with very small leaves (<225 mm², or 0.35 in²)*, or even leafless, sometimes armed with spines.</i> Includes both evergreen and deciduous small-leaved trees, such as <i>Acacia greggii</i> , <i>Mimosa</i> spp. (adapted from "thorn tree" by Whittaker 1975)
	TP	Palm tree - <i>An evergreen, broad-leaved, flowering, (non-sporing, tree, typically with a simple, unbranched stem and terminal, rosulate crown of large, pinnate or fan-shaped leaves. A type of rosette tree.</i> Palms are the primary taxa, but see Dracaenaceae, some Pandanaceae, etc. (Box 1981). <i>Hyphaene thebaica</i> is an example of a branched palm tree
	TF	Tree fern - <i>An evergreen, broad-leaved, spore-bearing tree (or arborescent fern) with a simple, unbranched stem and terminal, rosulate crown of large fronds. A type of rosette tree, including taxa from Cyatheaceae</i> (Box 1981).
	TG	Bamboo tree - <i>A woody-stemmed, arborescent grass that is equal to or greater than 5 m in height at maturity. Only applies to woody-stemmed bamboos. Includes the "Arborescent grasses" (Box 1981). Other more typically woody grasses, such as <i>Arundo</i>, <i>Saccharum</i>, currently excluded, and treated as Herb-graminoid.</i>
S	SD	Dwarf-shrub – <i>A mature caespitose, creeping, matted, or cushion-forming shrub that is generally small-leaved and is typically less than 30 cm tall at maturity due to genetic and/or environmental constraints</i> (adapted from Mueller-Dombois and Ellenberg 1974).
	SBD	Broad-leaved deciduous shrub - <i>A shrub that is typically more than 30 cm tall at maturity with leaves that have well-defined leaf blades that are generally of at least microphyll size (≥ 225 mm², or 0.35 in²* and seasonally loses all of its leaves and becomes temporarily bare-stemmed</i> (FGDC

	1997).
SBE	Broad-leaved evergreen shrub - <i>A shrub that is typically more than 30 cm tall at maturity with leaves that are generally of at least microphyll sized ($\geq 225 \text{ mm}^2$, or 0.35 in^2)* and has green leaves all year round</i> (adapted from FGDC 1997, Box 1981).
SBES	Sclerophyllous shrub - <i>A type of broad-leaved evergreen shrub, typically with relatively small, leaves that are stiff and firm, and retain their stiffness even when wilted</i> (FGDC 1997, Whittaker 1975).
SN	Needle-leaved shrub - <i>A shrub that is typically more than 30 cm tall at maturity with slender, elongated leaves or with small overlapping leaves that usually lie flat on the stem</i> (FGDC 1997). Includes scale-leaved as well as needle-leaved shrubs, and deciduous as well as evergreen.
SU	Succulent shrub – <i>A fleshy shrub that is typically more than 30 cm tall at maturity with specialized tissue for the conservation of water</i> (adapted from FGDC 1997 and the Thorn shrub of Whittaker 1975). Includes cacti less than 5 meters in height at maturity. Includes both the "Typical Stem succulents" and "Bush succulents" (Box 1981). Includes Aloe, Agave.
SM	Small-leaved shrub - <i>A shrub that is typically more than 30 cm tall at maturity with very small leaves ($< 225 \text{ mm}^2$, or 0.35 in^2)*, or even leafless, sometimes armed with spines, usually having compound, deciduous leaves that are often reduced in size. Includes <i>Larrea tridentata</i>, <i>Prosopis glandulosa</i>, <i>Acacia neovernicosa</i>, <i>Senna</i>, <i>Calliandra</i> (Whittaker 1975)</i>
	Bamboo shrub - <i>A woody-stemmed, shrubby grass that is less than 5 m in height at maturity. Only applies to woody-stemmed bamboos. Includes <i>Arundo</i>, <i>Saccharum</i>, <i>Sinarundinaria</i> spp (=Yushania spp.).</i>
SP	Palm shrub - <i>An evergreen, broad-leaved, typically unbranched shrub that is typically more than 30 cm tall at maturity with a simple stem and terminal, rosulate crown of large, pinnate or fan-shaped leaves. Includes palms and palm-like plants, such as espeletia.</i>

H	HA	Aquatic herb - <i>A flowering or non-flowering herb structurally adapted to live floating or submerged in an aquatic environment.</i> Does not include emergent plants such as cattails and sedges. (FGDC 1997). Includes flowering and non-flowering, and forb and graminoid aquatic herbs. Further subdivision may be warranted if ecologically meaningful.
	HF	Forb - <i>A non-aquatic, flowering or spore-bearing, non-graminoid herb.</i>
	HFF	Flowering forb - <i>A forb with relatively broad leaves and showy flowers.</i> Does not include graminoids, ferns, or fern-allies. Includes herbaceous vines.
	HFE	Spore-bearing forb - <i>A non-flowering, spore-bearing forb.</i> Includes non-aquatic, non-woody ferns, clubmosses, spikemosses, horsetails, and quillworts.
	HFS	Succulent forb - <i>A flowering forb with a fleshy stem and often with reduced leaves.</i> Includes <i>Salicornia</i> and others.
	HG	Graminoid - <i>A non-aquatic, flowering herb with relatively long, narrow leaves and inconspicuous, reduced flowers.</i> Includes grasses, sedges, rushes, and arrow-grasses. Aquatic graminoids are treated with aquatic herbs.
N	NB	Bryophyte - <i>A nonvascular, non-flowering, photosynthetic plant that bears leaf-like appendages or lobes and attaches to substrates by rhizoids.</i> Includes mosses, liverworts, and hornworts (Abercrombie et al. 1966).
	NA	Alga - <i>A nonvascular, photosynthetic plant with a simple form ranging from single- or multi-celled to a filamentous or ribbon-like thallus with relatively complex internal organization</i> (Abercrombie et al. 1966).
	NL	Lichen - <i>An organism generally recognized as a single plant that consists of a fungus and an alga or cyanobacterium living in symbiotic association</i> (FGDC 1997). Technically, lichen is not a plant, but is often treated together with moss as a type of nonvascular growth form.

E	E	Epiphyte - <i>A vascular or nonvascular plant that grows by germinating and rooting on other plants or other perched structures, and does not root in the ground</i> (adapted from FGDC 1997). This growth form may be used as a modifier of other growth forms. For example, HFF(Flowering forb) - -E
L	L	Liana - <i>A woody, climbing plant that begins life as terrestrial seedlings but relies on external structural support for height growth during some part of its life</i> (Gerwing 2004), typically exceeding 5 m in height or length at maturity. Non-woody climbers are treated as a type of "Herb."

cf. Gillison (2013, Table 12.3), who defines microphylls as 225–2025 mm², and nanophylls as 25–225 mm²

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Appendix C. Formation Units - Level 1 to Level 3

	LEVEL 1 – FORMATION CLASS	LEVEL 2 – FORMATION SUBCLASS	LEVEL 3 – FORMATION Wetland and aquatic formations marked with *
	1. Forest & Woodland [Mesomorphic Tree Vegetation]	1.A. Tropical Forest & Woodland	1.A.1. Tropical Dry Forest & Woodland
			1.A.2. Tropical Lowland Humid Forest
			1.A.3. Tropical Montane Humid Forest
			1.A.4. Tropical Flooded & Swamp Forest *
			1.A.5. Mangrove*
		1.B. Temperate & Boreal Forest & Woodland	1.B.1. Warm Temperate Forest & Woodland
			1.B.2. Cool Temperate Forest & Woodland
			1.B.3. Temperate Flooded & Swamp Forest *
			1.B.4. Boreal Forest & Woodland
			1.B.5. Boreal Flooded & Swamp Forest *
	2. Shrub & Herb Vegetation [Mesomorphic Shrub & Herb Vegetation]	2.A. Tropical Grassland, Savanna & Shrubland	2.A.1. Tropical Lowland Grassland, Savanna & Shrubland
			2.A.2. Tropical Montane Grassland & Shrubland
			2.A.3. Tropical Scrub & Herb Coastal Vegetation

	2.B. Temperate & Boreal Grassland & Shrubland	2.B.1. Mediterranean Scrub & Grassland	
		2.B.2. Temperate Grassland & Shrubland	
		2.B.3. Boreal Grassland & Shrubland	
		2.B.4. Temperate to Polar Scrub & Herb Coastal Vegetation	
		2.C. Shrub & Herb Wetland	2.C.1. Tropical Bog & Fen *
			2.C.2. Temperate to Polar Bog & Fen*
			2.C.3. Tropical Freshwater Marsh, Wet Meadow & Shrubland*
			2.C.4. Temperate to Polar Freshwater Marsh, Wet Meadow & Shrubland*
			2.C.5. Salt Marsh*
		3. Desert & Semi-Desert [Xeromorphic Woodland, Scrub & Herb Vegetation]	3.A. Warm Desert & Semi-Desert Woodland, Scrub & Grassland
	3.A.2. Warm Desert & Semi-Desert Scrub & Grassland		
	3.B. Cool Semi-Desert Scrub & Grassland		3.B.1. Cool Semi-Desert Scrub & Grassland
	4. Polar & High Montane Scrub, Grassland & Barrens [Cryomorphic Scrub, Herb & Cryptogam Vegetation]	4.A. Tropical High Montane Scrub & Grassland	4.A.1. Tropical High Montane Scrub & Grassland
		4.B. Temperate to Polar Alpine & Tundra Vegetation	4.B.1. Temperate & Boreal Alpine Dwarf-shrub & Grassland
		-	4.B.2. Polar Tundra & Barrens
5. Aquatic Vegetation [Hydromorphic Vegetation]	5.A. Saltwater Aquatic Vegetation	5.A.1. Floating & Suspended Macroalgae Saltwater Vegetation*	
		5.A.2. Benthic Macroalgae Saltwater Vegetation*	
		5.A.3. Benthic Vascular Saltwater Vegetation*	
		5.A.4. Benthic Lichen Saltwater Vegetation*	
	5.B. Freshwater Aquatic Vegetation	5.B.1. Tropical Freshwater Aquatic Vegetation*	
		5.B.2. Temperate to Polar Freshwater Aquatic Vegetation*	

Non-vegetated Classes (non - NVC)	6. Open Rock Vegetation [Cryptogam - Open Mesomorphic Vegetation]	6.A. Tropical Open Rock Vegetation	6.A.1. Tropical Cliff, Scree & Other Rock Vegetation
		6.B. Temperate & Boreal Open Rock Vegetation	6.B.1. Temperate & Boreal Cliff, Scree & Other Rock Vegetation
	7. Agricultural & Developed Vegetation [Anthromorphic Vegetation]	7.A. Woody Agricultural Vegetation	7.A.1. Woody Horticultural Crop
			7.A.2. Forest Plantation & Agroforestry Crop
			7.A.3. Woody Wetland Horticultural Crop*
		7.B. Herbaceous Agricultural Vegetation	7.B.1. Row & Close Grain Crop
			7.B.2. Pasture & Hay Field Crop
			7.B.3. Herbaceous Horticultural Crop
			7.B.4. Fallow Field & Weed Vegetation
			7.B.5. Herbaceous Wetland Agricultural Crop*
		7.C Herbaceous & Woody Developed Vegetation	7.C.1. Lawn, Garden & Recreational Vegetation
			7.C.2. Other Developed Vegetation
			7.C.3. Developed Wetland Vegetation*
		7.D. Agricultural & Developed Aquatic Vegetation	7.D.1. Agricultural Pond Vegetation*
			7.D.2. Urban & Recreational Pond Vegetation*
	<i>6 natural classes</i>	<i>13 natural subclasses</i>	<i>37 natural formations</i>
	<i>1 cultural subclass</i>	<i>4 cultural subclasses</i>	<i>13 cultural formations</i>
	8. Natural Open Fresh Water	Lake	
		River	
Subterranean Freshwater			
9. Natural Open Salt Water	Estuary and Ocean		
10. Cultural Open Water	Reservoir and Canal (etc.)		

	11. Perennial Snow/Ice	Perennial Snowfield
		Ice Sheet
		Glacier
	12. Natural Surface Bare Area	Consolidated Bare Area (Rock, etc)
		Unconsolidated Bare Area (Sand, Gravel, etc)
	13. Natural Subterranean	Cave (etc).
	14. Cultural Surface Bare Area	Developed, Low Intensity
		Developed, Medium Intensity
		Developed, High Intensity
15. Cultural Subterranean	Mine Shaft (etc.)	

APPENDIX D. EXAMPLES OF OTHER FORMATION-LEVEL CLASSIFICATIONS

Main World Terrestrial Biome Types (Box and Fujiwara 2005, Table 4.4,)

The authors provide 18 major biome types recognized by most modern treatments of world vegetation. For example, they recognize the following forest biomes:

Tropical rain forest (including montane and cloud forests)
Tropical deciduous forest, woodland, and thorn scrub
Temperate forests
Deciduous broad-leaved forest
Evergreen broad-leaved forest (incl. laurel forest, warm-temperate mixed forest)
Temperate rain forest
Conifer forests
Boreal (including deciduous)
Montane conifer forest (temperate montane and subalpine)

From. Box, E. O., and K. Fujiwara. 2005. Vegetation types and their broad-scale distribution. Pp. 106–128 in van der Maarel, E. Vegetation ecology. Blackwell Publishing. Malden, Massachusetts, USA.

World Wildlife Fund Major Habitat Types (Olson 2001)

MAJOR HABITAT TYPES
Tropical & Subtropical Moist Broadleaf Forests
Tropical & Subtropical Dry Broadleaf Forests
Tropical & Subtropical Coniferous Forests
Temperate Broadleaf & Mixed Forests
Temperate Coniferous Forests
Boreal Forests/Taiga
Tropical & Subtropical Grasslands, Savannas, & Shrublands
Temperate Grasslands, Savannas, & Shrublands
Flooded Grassland and Savannas [temperate and tropical]
Montane Grassland and Savannas [temperate and tropical]
Polar
Mediterranean Forests, Woodlands, & Shrub
Deserts & Xeric Shrublands
Mangroves
Lake
Rock and Ice

David M. Olson, Eric Dinerstein, Eric D. Wikramanayake, et al. 2001. Terrestrial ecoregions of the world: a new map of life on earth. *BioScience* 51(11):933–938.

Formations (Biomes) - (Whittaker 1975)

FORMATIONS (BIOMES)	
FORESTS AND WOODLANDS	
1.	Tropical rain forest
2.	Tropical seasonal forest
3.	Temperate rain forest
4.	Temperate deciduous forest
5a.	Temperate evergreen forest --broadleaf
5b.	Temp. evergreen forest--needleleaf
5c.	Temperate evergreen forest--sclerophyll [Mediterranean]
6	Taiga & subarctic-subalpine needle-leaved forest
7.	Elfin woodland
8.	Tropical broadleaf woodland
9a.	Thornwood--woodland
9b.	Thornwood--scrub
10a.	Temperate woodland --needleleaf
10b.	Temperate woodland--sclerophyll
10c.	Temperate woodland--deciduous broadleaf
SHRUBLANDS	
11a.	Temperate shrubland--deciduous
11b.	Temperate shrubland--heath
11c.	Temperate shrubland--sclerophyll [Mediterranean]
11d.	Temperate shrubland--subalpine, needleleaf
11e.	Temperate shrubland--subalpine, broadleaf
GRASSLANDS AND ALPINE VEGETATION	
12.	Savanna [tropical grassland]
13.	Temperate grassland
14.	Alpine shrubland
15.	Alpine grassland
COLD AND WARM DESERTS and TUNDRA	
16.	Tundra
17.	Warm semidesert scrub
18a.	Cool semidesert--open scrub
18b.	Cool semidesert--dry grassland
19.	Arctic-alpine semidesert

20. True desert
21. Arctic-alpine desert
SWAMPS, MARSHES AND BOGS
22. Cool temperate bog
23. Tropical freshwater swamp forest
24. Temperate freshwater swamp forest
25. Mangrove swamp
25. Saltmarsh
MARINE AND AQUATIC
[26-29 are aquatic]
29. Marine rocky shores
30. Marine sandy beaches
31. Marine mudflats

Whittaker, R. H. 1975. Communities and ecosystems. Second edition. MacMillan, New York. (pp. 135–161).

Formations of Australia (Specht and Specht 2001)

FORMATIONS^{1,2}
Closed forests (rainforests) - tropical north-eastern Australia
Closed forests (rainforests) - subtropical eastern Australia
Closed forests (rainforests) - temperate south-eastern Australia
Semi-deciduous closed forests - monsoonal northern Australia
Semi-deciduous closed forests - subtropical eastern Australia
Eucalypt open forests and woodlands - monsoonal northern Australia
Eucalypt open forests and woodlands - subtropical eastern Australia
Eucalypt open forests and woodlands - temperate south-eastern Australia
Eucalypt open forests and woodlands - montane south-eastern Australia
Eucalypt open forests and woodlands - temperate south-western Australia
Eucalypt open forests and woodlands - Australia wetland forests
Mallee eucalypt open-scrubs - monsoonal northern Australia
Mallee eucalypt open-scrubs - subtropical eastern Australia
Mallee eucalypt open-scrubs - temperate south-eastern Australia
Mallee eucalypt open-scrubs - temperate south-western Australia
Heathlands and related shrublands - monsoonal northern Australia
Heathlands and related shrublands - subtropical eastern Australia
Heathlands and related shrublands - temperate south-eastern Australia
Heathlands and related shrublands - montane south-eastern Australia
Heathlands and related shrublands - temperate south-western Australia
Tussock grasslands
<i>Acacia</i> vegetation - subhumid, subtropical eastern Australia
<i>Acacia</i> vegetation - Australian Arid Zone
Hummock grasslands - Australian Arid Zone
Chenopod low shrublands - southern Australia Arid Zone

Aquatic vegetation - tropical and subtropical northern Australia
Aquatic vegetation - temperate southern Australia
Coastal dune vegetation
Coastal wetland vegetation (mangroves, salt marshes, and brackish wetlands)

1. Specht, R. L., and A. Specht. 2001. Australia, ecosystems of. Pp. 307–324, *in* S. A. Levin, editor. Encyclopedia of Biodiversity, Vol. 1. Academic Press, New York, New York, USA.
2. Within each formation, Specht and Specht (2001) also provide a set of Floristic Groups.

Australian Native Vegetation (NWLRA 2001)

Vegetation profile fact sheets were developed for each type listed below:

MAJOR VEGETATION GROUP
Rain forest and vine thickets
Eucalypt and tall open forests
Eucalypt open forests
Eucalypt low open forests
Eucalypt woodlands
<i>Acacia</i> forests and woodlands
<i>Callitris</i> forests and woodlands
<i>Casuarina</i> forests and woodlands
<i>Melaleuca</i> forests and woodlands
Other forests and woodlands
Eucalypt open woodlands
Tropical Eucalypt woodlands/grasslands
<i>Acacia</i> open woodlands
Mallee woodlands and shrublands
Low closed forests and closed shrublands
<i>Acacia</i> shrublands
Other shrublands
Heath
Tussock grasslands
Hummock grasslands
Other grasslands, herblands, sedgelands and rushlands
Chenopod shrublands, samphire shrubs and forblands
Mangroves, tidal mudflats, samphires, claypans, sand, rock, salt lakes, lagoons and freshwater lakes

NWLRA (National Land and Water Resources Audit). 2001. Australian Native Vegetation Assessment 2001. National Land And Water Resources Audit. Canberra, Australia.

EUROPEAN VEGETATION SURVEY (2002)

FORMATIONS

A. Coastal mud-flats and brackish waters
B. Saltmarsh, sand-dune and sea-cliff vegetation
C. Rock crevice, scree and boulderfield vegetation
D. Freshwater aquatic vegetation
E. Springs, shoreline, and swamp [marsh] vegetation
F. Bogs and fens
G. Temperate grasslands, heaths, and fringe vegetation
H. Dry grasslands and semi-deserts
I. Oromediterranean grasslands and scrub
J. Montane tall-herb, grassland, fell-field and snowbed vegetation
K. Mediterranean garrigue, maquis, matorral, tomillar and phrygna
L. Temperate broadleaved forests and scrub
M. Montane heaths and coniferous forests
N. Weed communities

Rodwell, J. S., J. H. J. Schamineé, L. Mucian, S. Pignatti, J. Dring, and D. Moss. 2002. The diversity of European vegetation. An overview of phytosociological alliances and their relationships to EUNIS habitats. Wageningen, NL. EC-LNV. Report EC-LNV nr. 2002/054. 168 p.

APPENDIX E. ALLIANCE CONCEPT, GUIDELINES AND LITERATURE REVIEW

1. ALLIANCE DEFINITION

The alliance is “A vegetation classification unit containing one or more associations, and defined by a characteristic range of species composition, habitat conditions, physiognomy, and diagnostic species, typically at least one of which is found in the uppermost or dominant stratum of the vegetation. Alliances reflect regional to subregional climate, substrate, hydrology, and moisture/nutrient factors, and disturbance regimes. (FGDC 2008, Jennings et al. 2009).

2. ALLIANCE CONCEPT

[words in bold are defined in the glossary]

The **alliance** is a classification unit defined primarily by **floristic composition** (including **diagnostic**, **constant** and **dominant** species) and **physiognomy**, with consideration given to the relation of these vegetation parameters to ecological (**habitat and biogeographic**) factors. The alliance is placed between the **association** and **group** levels in EcoVeg and the association and order levels of Braun-Blanquet.

The alliance is a more inclusive (or taxonomically higher scaled) concept than the association; as such, it should be well separated floristically from other alliances by multiple diagnostic species (either by one or more **character** species or many **differential** species) that have diagnostic value over **large geographic areas** (Mueller-Dombois and Ellenberg 1974). The alliance aggregates vegetation and habitat factors at somewhat broader biogeographic and ecologic scales than the association. That is, whereas the association contains vegetation characteristics that emphasize more local and narrowly defined environmental and biotic relationships, the alliance emphasizes somewhat larger environmental gradients and biogeographic regions (Table 5 in Faber-Langendoen et al. 2014).

In EcoVeg, the alliance concept is constrained by some moderate level of both floristic and physiognomic variation, in the context of ecologic and biogeographic factors. For example, alliances do not (or only rarely) span woodland and shrub physiognomy, or shrub and herb physiognomy (unless shrubs are creeping or share the dominant layer with herbs), or even purely evergreen and purely deciduous tree physiognomy. Moreover, floristic composition includes recognition of the importance of dominants and diagnostic species. That is, rarely are associations united if they do not share similar or overlapping dominants. In this way, an integration of floristics with physiognomy, as typically expressed through the dominants species, is maintained.

Assessing the acceptable range of floristic variation in a vegetation unit proposed as an alliance is judged both by diagnostic and dominant species and by overall composition. It is a challenge

to analytically balance these criteria, but at minimum both should be considered. In some applications, diagnostic species identified through vegetation analyses receive more 'weight' in determining a type when they also have clearly understood site **indicator** interpretations with respect to specific ranges of soil moisture and/or nutrient regimes, or to disturbance regimes (e.g., frequent flooding). Overall composition is often assessed through ordination and cluster analyses. These analyses may be used as either the primary tools to identify types, from which the number of diagnostic species can be extracted, or as secondary tools that provide important insights into the degree to which types identified through diagnostic and dominant species methods are reflective of overall composition and environmental factors. A hybrid of the two methods may also be used (e.g., cluster criteria are partly judged by the number of diagnostic species present in those clusters).

3. GUIDELINES

- a) *Plot data*: alliances are best characterized through floristically comprehensive **plot** data that provide the basis for identifying diagnostic species, dominants and overall compositional similarity. Incomplete plot data, literature and expert judgment may still be helpful for initial development of concepts, e.g., plot data that include only species from the dominant layer or of the dominant growth forms (i.e., tree/sapling data in forests and woodlands, grass/forb data in grasslands), or species from the dominant layer along with environmental factors.
- b) *Compositional Similarity*: the alliance concept is assessed by overall floristic composition - a measure of the similarity in the presence and abundance of plant species (and sometimes subspecies) among alliances.
- c) *Characteristic Species Combination*: Typically, alliances are identified by a combination of **diagnostic (differential, character), constant** and **dominant** species, including from the uppermost or dominant stratum, and reflective of overall **compositional similarity**. Diagnostic species should include at least one character species or multiple strong differential species (by "species" we mean taxa, thus subspecies could be used as well), sometimes referred to as ecological species groups. Where such diagnostics are lacking, but there are meaningful ecological or successional groupings of associations, consideration can be given to recognizing these as suballiances, or, more informally as subtypes¹. Not all diagnostic species are found in all stands, but stands may still be identified as a particular alliance using overall composition and ecology.
- d) *Invasive/Exotic Species*: Invasive species (typically invasive exotics) are treated as degrading elements within a native alliance or association, and documented as informal "**phases**" of a type, as long as some portion of the native composition remains (perhaps >10% native species cover). When invasive species overwhelmingly dominate the stand, and native diagnostics are largely to completely absent (a rough guide may be when invasives have >90% cover, but this may vary by type), they define ruderal alliances and are placed within a

¹ Sub-alliances have not been considered a formal (or even informal) part of the USNVC hierarchy. They are occasionally used by the Braun-Blanquet tradition. They are discussed here for completeness in light of their use by others. See Chytrý (2007), who recommends against using formal sub-level units, preferring instead to use "subtypes" to express internal variability within a type.

ruderal Macrogroup, separate from other natural vegetation alliances. See extended presentation in Appendix 2: "Alliance Concepts and Ruderal Vegetation (Novel Ecosystems)."

- e) *Physiognomy*: alliances are typically moderately uniform in physiognomy, with consistent **layers**. For example, tree-dominated alliances will typically be primarily either: forest or woodland, evergreen- mixed or deciduous–mixed. There may be considerable range in height within an alliance and variable dominance of other layers (e.g., an alliance may contain associations that have either a dominant shrub or herb layer, where these otherwise have strongly overlapping composition.
- f) *Ecology*: alliances reflect regional to subregional climate, substrate, hydrology and moisture/nutrient factors, and disturbance regimes. These patterns may also be reflective of regional biogeographic patterns.
- g) *Successional status* : alliances may include some successional stages that are floristically similar. For example, blow-downs of red spruce – fir (*Picea rubens* – *Abies balsamea*) stands may lead to a distinct successional stage defined as an association, with *Prunus serotina*, *Acer rubrum*, *Betula papyrifera* and other light demanding species dominating the stand, along with these conifers. The more mature / old growth stage may be a separate successional stage. But the overall floristic similarity of these two associations may be such that they are placed in the same alliance. By contrast, a recently burned stand of spruce-fir, where spruce and fir are virtually absent, may be so distinctive that it is placed in a separate early successional aspen-birch *Populus tremuloides* – *Betula papyrifera* alliance.
- h) *Wetland/upland*. Alliances contains associations that are typically either 'wetland' or 'upland.' But some transitional wetland types may be placed in an upland alliance (e.g., flatwoods post oak (*Quercus stellata*) stands that exhibit xero-hydric hydrologies may be in the same alliance as other upland stands), depending on the strength of overall compositional or diagnostic features. Some species may occur in both upland and wetland types (e.g., *Thuja occidentalis*, *Acer rubrum*).

4. LITERATURE REVIEW OF ALLIANCE CONCEPT

Below are a number of articles and books that discuss the alliance concept. The goal of presenting these is both to highlight the range of views on the alliance concept (as captured through the summary observations), and from among these views, to provide some support for the guidelines presented above. Sections in quotations are direct quotes.

A. Ellenberg, H. 1988. Vegetation Ecology of Central Europe

"Down as far as the alliances in section E III 1 the character species have been included. These are the species which appear almost exclusively, or at least preferentially, in a particular unit. In many of the alliances and some orders, and even in a few classes, the number of such species is in each case restricted. Thus a greater subdivision of the higher units is hardly possible if one is not to dispense entirely with Braun-Blanquet's 'character species principle' and work only with 'differential species' or other devices. This principle prevents the confusing splitting up of units and so should be accepted unconditionally, at least down to the level of alliance. "

“There is some uncertainty about the classification of the Birch woods which replace Alder in wet sites where the soil is very acid (section B V 2c). Their species composition has so many similarities with the acid-soil coniferous woods (*Vaccinio-Piceetea*) that they are usually included in this class although, at least in the west of Central Europe, they rarely contain any conifers. One could include them in the unit *Vaccinio-Piceion* as a special suballiance (*Betulion pubescentis*), although their systematic classification is of little significance for the understanding of Central European vegetation since they occupy a decreasing number of small areas. We will deal with the systematic arrangement of the coniferous woodland after we have discussed the classes *Querco-Fagetea* and *Quercetea robori-petraeae*.”

Observation 1: For Ellenberg, alliance concept relies on character species, in combination with differential and constant species, whereas the association may be defined solely by differential and constant species.

Observation 2: For Ellenberg, the alliance concept, historically, could include both deciduous and evergreen acid (nutrient poor) swamp woodland associations; with a suballiance used to distinguish the different dominants and physiognomy. More recently Rodwell et al. (2002) recognized separate birch-dominated swamp woodlands (*Betulion pubescentis*) and pine-dominated swamp woodlands (*Ledo-Pinion*) as separate alliances within a *Sphagno-Betuletalia* order (birch and pine open bog woodlands) (see also Solomeshch et al. 1997).

B. Diekmann 1997. The Differentiation of Alliances in South Sweden

Folia Geobot. Phytotax. 32: 193-205, 1997

Martin Diekmann

[In deciding which level of the Braun-Blanquet hierarchy to organize the Swedish vegetation, the] “two higher-ranking units “order” and “class” were ...unsuitable. Both usually have a wide geographic distribution over large parts of Europe, and both are ecologically and floristically (often also structurally) quite heterogeneous, such as *Phragmito-Magnocaricetea/Phragmitetalia*, *Molinio-Arrhenatheretea/Arrhenatheretalia*, *Vaccinio-Piceetea/Piceetalia* and *Quercu-Fagetea/Fagetalia*. On this level, differences between Sweden and Central Europe would not become evident. The alliance therefore emerged as the most appropriate unit for our purposes. In contrast to the association, the alliance is often well delimited by character and differential species; unlike the higher units, it shows fairly homogeneous ecological conditions. Alliances usually also have a more restricted geographic extension than orders and classes and are therefore better suited for comparing the vegetation of different regions (ELLENBERG 1956, BRAUN-BLANQUET 1964, DIERSCHKE 1994). Orders can sometimes be split up into corresponding alliances occurring in different geographic regions, e.g., the *Androsacetalia alpinae* on siliceous screes in comprising the *Androsacion alpinae* of the mountains in Central Europe (DIERSCHKE 1994, POTT 1995) and the *Saxifrago stellaris-Oxyrion digynae* of the Scandinavian mountains (DIERSSEN 1996), or the *Thlaspietalia rotundifolii*, the equivalent order on calcareous ground, comprising the *Thlaspion rotundifolii* (POTT 1995) and *Arenarion norvegicae* (DIERSSEN 1996), respectively. “

Observation: For Diekmann, in contrast to the association, the alliance is often well delimited by character and differential species. In contrast to higher levels (Braun-Blanquet class and order), it shows fairly homogeneous ecological and physiognomic conditions, and it usually has a more restricted geographic range.

Table 1. [from Diekmann 1997]. Some South Swedish vegetation classes and orders and their syntaxonomical differentiation. Orders are listed only if they include at least two alliances. For the alliances recognized the following is given: a brief description on their vegetation and ecological conditions, geographic distribution and diagnostic species (if not otherwise indicated – character species; d – differential species; N – exclusively or mainly boreal species).

Alliance	Description	Distribution	Diagnostic species
a) Zonal vegetation			
Coniferous forest communities (<i>Vaccinio-Piceetea</i>, <i>Piceetalia</i>)			
<i>Piceion excelsae</i>	spruce forests on mesic to moist soils	widely dominant	<i>Bazzania trilobata</i> , <i>Dicranum majus</i> , <i>Picea abies</i> , <i>Ptilium crista-castrensis</i> , <i>Barbilophozia lycopodioides</i> (N), <i>Listera cordata</i> (N), <i>Stellaria longifolia</i> (N), etc.
<i>Dicrano-Pinion</i>	pine forests on dry soils	common, particularly in the E	<i>Chimaphila umbellata</i> , <i>Cladonia</i> spp. (d), <i>Dicranum fuscescens</i> (d), <i>D. polysetum</i> , <i>Leucobryum glaucum</i> (d), <i>Monotropa hypopitys</i> , <i>Pyrola chlorantha</i> , <i>Astragalus penduliflorus</i> (N), <i>Diphysium complanatum</i> (N), <i>Pulsatilla vernalis</i> (N)

b) Selection of azonal vegetation types

Swamp communities (Phragmito-Magnocariceta, Phragmitetalia)

<i>Phragmition</i>	reed swamps at eutrophic lakes	widespread, particularly in the S	<i>Acorus calamus</i> , <i>Butomus umbellatus</i> , <i>Glyceria maxima</i> , <i>Phragmites australis</i> (d), <i>Ranunculus lingua</i> , <i>Schoenoplectus lacustris</i> , <i>Typha latifolia</i> , etc.
<i>Bolboschoenion maritimi</i>	swamps at brackish water	common along the coast	<i>Bolboschoenus maritimus</i> , <i>Schoenoplectus tabernaemontani</i>
<i>Magnocaricion elatae</i>	sedge swamps at mesotrophic to eutrophic lakes	widespread	<i>Carex elata</i> , <i>C. gracilis</i> , <i>C. paniculata</i> , <i>C. riparia</i> , <i>C. vesicaria</i> , <i>Cladium mariscus</i> , <i>Peucedanum palustre</i> , etc.

Flushes and spring communities (Montio-Cardaminetea, Montio-Cardaminetalia)

<i>Cardamino-Montion</i>	springs on siliceous substrates	common	<i>Bryum schleicheri</i> , <i>Epilobium obscurum</i> , <i>Montia</i> spp., <i>Philonotis fontana</i> , <i>Stellaria alsine</i> , etc.
<i>Cratoneurion commutati</i>	springs on calcareous substrates	scattered	<i>Catocopium nigritum</i> (d), <i>Cratoneurum</i> spp., <i>Eucladium verticillatum</i> , <i>Philonotis calcarea</i> , <i>Saxifraga aizoides</i> (N), etc.

Mire communities (Scheuchzerio-Caricetea nigrae) (Scheuchzerietalia palustris)

<i>Rhynchosporion albae</i>	bog margins and hollows; wet, peaty, places	widespread except in SE Sweden	<i>Carex limosa</i> , <i>Drosera intermedia</i> , <i>Lycopodiella inundata</i> , <i>Rhynchospora alba</i> , <i>R. fusca</i> , <i>Sphagnum cuspidatum</i> , <i>S. majus</i> , <i>Dactylorhiza sphagnicola</i> (N), <i>Hammarbya paludosa</i> (N), <i>Sphagnum annulatum</i> (N), etc.
<i>Caricion lasiocarpae</i>	oligotrophic to mestrophic mires	widespread	<i>Carex chordorrhiza</i> , <i>C. diandra</i> , <i>C. heleonastes</i> , <i>C. lasiocarpa</i> , <i>Cinclidium stygium</i> , <i>Eriophorum gracile</i> , <i>Meesia triquetra</i> , <i>Sphagnum obtusum</i> , <i>Juncus stygius</i> (N), etc.
(<i>Caricetalia davallianae</i>) <i>Caricion davallianae</i>	calcareous fens	scattered in lowland areas with calcareous bedrock	<i>Carex dioica</i> , <i>C. hostiana</i> , <i>Eriophorum latifolium</i> , <i>Gymnadenia odoratissima</i> , <i>Liparis loeselii</i> , <i>Orchis palustris</i> , <i>Primula farinosa</i> , <i>Schoenus ferrugineus</i> , <i>S. nigricans</i> , <i>Tofieldia calyculata</i> , <i>Campylium elodes</i> (N), etc.

Salt marsh communities (Asteretea tripolii, Glauco-Puccinellietalia)

<i>Puccinellion maritimae</i>	salt marshes at the lower geolittoral, high salinity	common along the W-coast	<i>Halimione pedunculata</i> , <i>Puccinellia maritima</i> , <i>Salicornia</i> spp. (d), <i>Spergularia media</i> , <i>Carex paleacea</i> (N), <i>C. vacillans</i> (N)
<i>Armerion maritimae</i>	salt marshes at the upper geolittoral, low salinity	common at the W-coast and Baltic coast	<i>Armeria maritima</i> , <i>Artemisia maritima</i> , <i>Blysmus rufus</i> , <i>Carex extensa</i> , <i>Festuca rubra</i> subsp. <i>litoralis</i> , <i>Juncus gerardi</i> , <i>Limonium vulgare</i> , <i>Odontites litoralis</i> , <i>Deschampsia bottnica</i> (N)

Deciduous forest communities (Quercu-Fagetea, Fagetalia sylvaticae)

<i>Alnion</i>	alder-ash forest	widespread	<i>Alnus incana</i> , <i>Carex remota</i> , <i>Circaea intermedia</i> , <i>Festuca</i>
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<i>incanae</i>	on moist or wet soils	but absent in the Scandes	<i>gigantea</i> , <i>Matteuccia struthiopteris</i> , <i>Poa remota</i> , <i>Stellaria nemorum</i> , <i>Cinna latifolia</i> (N), <i>Equisetum pratense</i> (N), <i>Glyceria lithuanica</i> (N), etc.
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C. Dierschke 1990

Dierschke, H. 1990. Species-rich beech woods in mesic habitats in central and western Europe: a regional classification into suballiances. *Vegetatio* 87:1-10.

“In this contribution for the first time an attempt is made to present a regional classification of beech woods by means of a synthetic table. The review is restricted to species-rich communities on mesic site (mesophile) beech woods....Only relevés with *Fagus sylvatica* dominant were chosen....

The Fagion is the most extensive alliance of deciduous woodland in Europe due to the broad ecological range of *Fagus sylvatica*. All described beech woods of central and western Europe are combined by a high number of widespread character species of Fagion, *Fagetalia*, and *Quercus-Fagetea*.... As a good Fagion character species for the total area, only *Galium odoratum* can be named. “

Dierschke presents 5 suballiances for central and western Europe. 1. *Endymio-Fagenion*, 2. *Scillo-Fagenion*, 3. *Galio odorati-Fagenion*, 4. *Lonicero alpigenae-Fagenion*, and 5. a transitional type of western Carpathians, Sedetic and Bohemian mountains. In discussing the “*Scillo-Fagenion*” he notes that it shows the clearest floristic differentiation of all suballiances, and includes both character and differential species.

“Observation 1. Dierschke uses dominance to guide the overall selection of plots, and differential species to guide the suballiance distinctions, which correspond to both ecological and biogeographic patterns.

Observation 2. All 5 suballiances were raised to the level of alliance in Rodwell et al. 2002. See also Dierschke 1997 (below).

D. Dierschke 1997

Dierschke, H. 1997. Syntaxonomical survey of European beech forests: Some general conclusions. *Annali di Botanica* 55:17–26

“A short overview is given about the historical development of syntaxonomy of European beech forests. Different solutions of classification have been proposed, following more or less two main approaches: Division of alliances and suballiances by ecologically or geographically orientated species groups.”

“A new classification of European beech forests is proposed with 8 (or more) geographically orientated alliances, which can be further divided into suballiances by ecological species groups. For each alliance character and differential species, nomenclatural type and the area is mentioned, based on a (non published) synthetic table, including 10.006 relevés from all parts of Europe. From this table also some overlapping species groups (a–n) are given.”

Different approaches : ecological versus geographical species groups

The history of higher syntaxa of beech forests shows different approaches and many different solutions, resulting in a series of names. In the bibliography of *Quercus-Fagetea* by Tüxen *et al.* (1981) 68 names for alliances and suballiances for beech forests are mentioned. However, all syntaxonomical solutions can be reduced more or less to two main approaches:

1. Division by ecological species groups in three clusters of associations:
 - a- species-rich forests in mesic habitats (floristic center of beech woods).
 - b- species-rich forests in rather dry and warm habitats (with transitions to thermophilous forests of *Quercetalia pubescenti-petraeae*).
 - c- species-poor forests in acid habitats (with transitions to acido-tolerant forests of *Quercetalia robori-petraeae*).

From many areas of Europe this differentiation is described with varying associations and partly also with own alliances or suballiances. Often we find the a. *Asperulo- (=Galio odorati)-Fagion*, b. *Cephalanthero-Fagion* and c. *Luzulo-Fagion*.

2. Especially in species-rich areas with many own characteristic plant species, geographically orientated units have been established, e.g., the *Scillo-* and *Aremonio-Fagion* in southwestern and southeastern Europe, with further differentiation into association groups or suballiances by ecological species groups. Sometimes both approaches are mixed, e.g., geographically and ecologically orientated suballiances within the *Fagion sylvaticae*.

“Now, I would suggest to classify the beech forests in Europe on the level of alliances on the basis of one criterion: ecological or geographical. Török *et al.* (1989) have analyzed this question for Illyrian beech forests by multivariate methods and have found a clear prevalence of geographical species groups. First my own opinion was more the ecological solution with three main alliances and geographically orientated suballiances. However, after the study of more literature, especially of southeastern areas of Europe, the geographical version seems to be more appropriate, though not all geographically orientated alliances have good character species. But in this way syntaxonomical treatment in the area of each alliance is open for more individual differentiation in an ecological sense. Also the *Abies alba* forests can be easier incorporated.”

“In the meantime there is another discussion about the acidotolerant beech forests: more and more authors agree with their position within the *Quercetalia robori-petraeae*, as Müller (1991) proposed for the *Luzulo-Fagion* of central Europe. In this case the *Fagion* contains only species-rich beech forests of mesic to warmer habitats.”

Observation 1. Dierschke develops geographically oriented alliances, within which ecologically-based suballiances are considered. In some cases, these more geographic alliances may lack good character species. Dierschke points to the work of Torok *et al.* (1989) as shaping his view (see below).

Observation 2. Acid-tolerant beech forests are treated in a different order than the mesic to somewhat dry, calcareous beech forests.

E. Török *et al.* 1989

Török, K., Podani, J. and Borhidi, A., 1989 - *Numerical revision of the Fagion illyricum*

alliance. Vegetatio 81: 169-180.

“Another problem concerns the selection of species groups to be used in the classification. The question is whether ecological species groups of geographically distinct groups of character- and differential species should receive more emphasis in syntaxonomy. Moor (1952, 1960) and Tüxen (1960) are of the opinion that higher syntaxonomic units must be delimited using ecological species rather than geographically ‘significant’ species. However, it has been suggested over and over again that species with similar ecological requirements but occurring in different geographical regions are equally applicable, and the classifications thus obtained are of more general purpose than those considering ecological differences only. It is implicitly emphasized in numerical approaches to syntaxonomy in which no arbitrary species weights are useful in the analysis.”

“The dendrogram obtained by SSQ [Sums of Square Agglomeration] (Fig. 1) provides an answer with respect to the controversy over ecologic vs geographic species groups. The four main clusters recognized on the dendrogram are formed according to geographic separation, i.e., associations from different vegetation zones of the same area rather than the vicarious associations became clustered (see the positions of OSUs [Operational Syntaxonomic Unit] 2 and 13, 3 and 14, 4 and 15, 5 and 16, 29 and 32, and 17, 27 and 31). It must be noted, however, that this is not necessarily the case in other high-level syntaxa. In the explanation of this result one must consider that the Balkan Peninsula is a relic-preserving centre with a high tendency to develop diverse floras and that the local diversity of these floras is much higher than in the central European beechwood zone. Therefore, it is not surprising that species shared by vicarious associations are apparently outnumbered by locally distributed species.”

Observation 1. Overall composition similarity, as assessed by cluster analyses and ordinations, is a criterion in deciding how to aggregate associations into suballiances and alliances, and is used in combination with diagnostic species to characterize these units.

F. Dzwonko and Loster 2000.

Dzwonko, Z. & Loster, S. 2000. Syntaxonomy and phytogeographical differentiation of the *Fagus* woods in the Southwest Balkan Peninsula. *Journal of Vegetation Science* 11: 667-678

“In consequence, the local diversity of the Balkan flora is much higher than in the central European *Fagus* wood zone, and strong floristic-geographical differentiation of the *Fagus* woodland communities in the Balkan Peninsula is observed. This creates the need to classify them also in regional high-rank syntaxa, on the basis of geographically different groups of characteristic and differential species. That is also true of the *Fagus* woods of the Apennine Peninsula (Feoli & Lagonegro 1982; Nimis & Bolognini 1993). The authors of earlier syntaxonomic surveys believed that the higher syntaxonomic units should be delimited using ecological rather than geographical groups of species (Moor 1960; Tüxen 1960; Zoller et al. 1977). However, a comparative survey has shown that even the associations of mesophilous *Fagus* woods of central and western Europe combine into regional suballiances (raised to alliances recently) following a climatic gradient from oceanic to subcontinental, and a floristic gradient from south to north (Dierschke 1990, 1997). Various broad comparative studies suggest that classifications based on both ecological and geographical species groups are more generally useful than those considering ecological differences only. In the classification presented here, the associations and most of their subassociations and variants within the *Doronico columnae-Fagenion* and *Doronico orientalis-Fagenion* – geographically orientated suballiances – are clearly determined ecologically by altitude and soil conditions (Bergmeier 1990; Habeck & Reif 1994; Dzwonko et al. 1999; Dzwonko & Loster 2000). The *Epimedio-Fagenion* and

Ostrya-Fagenion are ecologically orientated suballiances which comprise submontane and thermophilous woods, respectively.”

Observation: For Dzwonko and Loster, geographically different groups of character and differential species define alliances, based in part on how these geographic regions reflect changing meso-climatic gradients.

G. Marinsek et al. 2013

Marinšek, A., U. Šilc & A.Čarni. 2012 Geographical and ecological differentiation of *Fagus* forest vegetation in SE Europe. *Applied Vegetation Science* 16:131-147

“In general, differences among *Fagus* forests are due to broad scale (historic, phytogeographic, macroclimatic and macroecological) and regional (edaphic, meso-climatic and ecological) factors (Bergmeier & Dimopoulos 2001). Soil ecology is usually considered to be the principle factor on a regional scale (Ellenberg 1996), while on a broader scale macroecological (geography and climate) differentiation has precedence (Dierschke 1990; Dierschke & Bohn 2004). Dierschke & Bohn (2004) proposed a differentiation of European Beech Forest into nine regional, geographically based alliances, with subsequent partition towards various suballiances, based on the combination and gradual disappearance of several groups of plants species, due to changed ecological factors. “

“Which factors should be considered more important for classification is an ongoing topic among syntaxonomists dealing with the classification of European *Fagus* forests (Soo 1964; Horvat et al. 1974; Torok et al. 1989; Dierschke 1990; Dierschke & Bohn 2004). Willner (2002) and Tzonev et al. (2006) follow an approach based on ecological factors, while Dierschke (1990), Dierschke & Bohn (2004), Dzwonko & Loster (2000) and Bergmeier & Dimopoulos (2001) emphasize geographical differentiation. Various comparative studies suggest that classifications based on both ecological and geographical differentiation are generally more adequate than those that consider ecological or geographical differences alone (e.g. Dzwonko & Loster 2000). “

Observation 1: For Marinsek et al., alliance concepts should consider both ecological and geographic considerations.

H. Boublik et al. 2007

Boublík, K., Petřík, P., Sádlo, J., Hédli, R., Willner, W., Černý, T. & Kolbek, J. (2007): Calcicolous beech forests in the Czech Republic and related vegetation – a comparison of formalized classifications. – *Preslia* 79: 141–161.

Methods

“Relevés dominated by *Fagus sylvatica* (at least 25% cover in tree layer).. were accepted regardless of the original assignment to vegetation units by the authors of these relevés (stored in the header data field ‘Syntaxon code’ in the database). Second, a diagnostic species group was formed of calcicolous and/or xerothermophilous species, which have high values according to Ellenberg et al. (2001) for soil reaction (most of them with values higher than 7), light, or temperature. The diagnostic species group consisted of 38 species.... At least two of the 38-species diagnostic group had to be present in a relevé in order for it to be selected as calcicolous beech forest.”

Discussion

“As for uniqueness (i.e. whether there are other similar vegetation units in a classification system), the calcicolous beech forests were similar to oak-hornbeam forests of the *Carpinion* alliance...The floristic affinities between *Cephalanthero-Fagenion*¹ and *Carpinion*² have also been discussed in the German literature (e.g. Oberdorfer 1992). However, most authors agree that *Cephalanthero-Fagenion* should be included into *Fagenion*, and not *Carpinion*, because of the dominance of *Fagus sylvatica*.”

¹*Cephalanthero-Fagenion* (suballiance) or full alliance (*Cephalanthero –Fagenion*: Rodwell et al. 2002): warm (thermophilous) beech forests mostly on limestone.

²*Carpinion betuli*: broadleaved woodlands rich in hornbeam on lime-rich and neutral mull soils.

Observation 1: For Boublik et al., dominance in the dominant strata plays a role in the definition of suballiances and alliances, in combination with diagnostic species and their relation to habitat characteristics.

Observation 2: For Boublik et al., the *Fagus* association was defined using a combination of many differential species, combinations of which help define the association.

I. Sawyer et al. 2009.

Sawyer, Todd Keeler-Wolf, Julie Evens. Manual of California Vegetation. 2009.

Definitions follow the USNVC (FGDC 2008, Jennings et al. 2009).

Sawyer et al (2009) also state: “Our emphasis is at the alliance level. This level is best for considering vegetation at a regional and statewide level because it is based on a tangible number of floristic categories, defined by well-known plant species, some of which are widespread throughout the state.”

Another focus of Sawyer et al 2009 is the use of the dominant and diagnostic species of alliances as indicators of fire or natural process stage e.g., (from Appendix 1): “By reviewing these traits and looking at supporting evidence from fire effects tables... and individual alliance treatments), we can begin to assess different strategies that indicator plants use to sustain themselves. These plants, as the most characteristic or indicative of each of the vegetation alliances yet described, can provide useful information on what it takes to be a successful species in the state’s current array of vegetation.”

Regarding ruderal or semi-natural alliances, Sawyer et al. state “... We believe invasive plant types are not equivalent to alliances. That is why we call them “semi-natural stands.” The stands replace native vegetation, and the non-native plants become dominant...In the first edition, we created a few series (alliances) for non-natives. However, we approach these types differently in this edition. In the case of alliances, the descriptions include information on ways to maintain the natives. In cases where the dominants are non-natives that form semi-natural stands, the emphasis is on wildlife/plant habitat qualities with them and on ways to restore native vegetation...we do not list associated species because so many of the naturalized types are widespread in the state and grow with a diverse set of native plants. We provide the invasive species ranking rather than the rarity ranking that is given for the alliances... “

Observation 1: For Sawyer et al., the alliance concept relies strongly on dominant and co-dominant species in the defining layer (tree, shrub or herb layer), sometimes with other characteristic species from that layer.

Observation 2: For Sawyer et al., a clear distinction is made between native alliances and semi-natural (what we call “ruderal”) alliances.

J. Pojar et al. 1987

Pojar, J., K. Klinka, and D.V. Meidinger. 1987. Biogeoclimatic ecosystem classification in British Columbia. *Forest Ecology and Management* 22:119-154.

“Plant subassociations are usually distinguished by differences in one (usually dominant) or several species that indicate relatively minor climatic and/or edaphic variations among ecosystems included in the circumscribing plant association. Plant associations with similarities in floristic composition, life-form, and structure [i.e., dominance by evergreen shrubs, deciduous shrubs, ferns, graminoids, herbs, bryophytes, or lichens in conjunction with a prominent (usually climax tree) species] are grouped into alliances. A plant alliance represents a major segment of the edaphic gradient that occurs in one or several related climates. Plant alliances with physiognomically similar vegetation and general affinities in a dominant stratum are grouped into orders. A plant order signifies a broad segment of the edaphic gradient that usually occurs in many different climates and is represented by one or two prominent climax species.”

(From Table 3). “The ‘diagnostic (characteristic) combination of species’ (DCS) that is *exclusive* to a given vegetation unit is the sole differentia for organizing ecosystems into a floristic hierarchy.”

“Phytosociologists have neither precisely specified nor agreed upon the required composition of the DCS for particular categories (cf. Becking, 1957; Mueller-Dombois and Ellenberg, 1974; Westhoff and Van der Maarel, 1980). In British Columbia, our experience indicates that character-species exist for only a few plant associations, typically those of nonforested ecosystems on environmentally extreme sites. To provide suitable criteria we propose that: (1) character-species (i.e., the species that differentiate in the absolute sense) not be required in the DCS for any vegetation unit at present; (2) units be recognized by an exclusive DCS that must include at least one differential or dominant-differential species; (3) units that represent the central concept of a higher circumscribing unit also be recognized without a DCS, providing they are differentiated by the absence or low occurrence of species that characterize other units of the same category and circumscription; and (4) plant subassociations also be recognized by non-exclusive DCS’s that include at least two differential or dominant-differential species. “

Observation: For Pojar et al, the requirement for character species is dropped for the association, and apparently for alliances and other upper levels of the vegetation hierarchy (which otherwise follows Braun-Banquet). Emphasis is placed on the diagnostic combination of differential and dominant-differential species. And the “central” unit of any level may lack differentials at all.

5. GLOSSARY

alliance—A group of associations with a defined range of species composition, habitat conditions, and physiognomy, and which contains one or more of a set of diagnostic species, typically at least one of

which is found in the uppermost or dominant stratum of the vegetation. Alliances typically reflect regional to subregional climate, substrates, hydrology, moisture/nutrient factors, and disturbance regimes (FGDC 2008, Jennings et al. 2009).

association—A vegetation classification unit defined on the basis of a characteristic range of species composition, diagnostic species occurrence, habitat conditions and physiognomy. Associations typically reflect topo-edaphic climate, substrates, hydrology, and disturbance regimes (FGDC 2008, Jennings et al. 2009).

character species— a species that shows a distinct maximum concentration, by constancy and abundance, in one well-defined vegetation type as compared to all other types; sometimes recognized at local, regional, and general/global geographic scales (Mueller-Dombois and Ellenberg 1974, p. 178, 208; Bruelheide 2000). Character species are often recognized from comparisons of vegetation within the same physiognomic type of a climatic or large biogeographic region, such as the NVC Division or regional formation (Dengler 2008). *cf differential species, diagnostic species, fidelity.*

characteristic species combination —the combination of diagnostic, constant and dominant species that characterize a type.

compositional similarity — a measure of the similarity in the presence and/or abundance of plant species (and sometimes subspecies) between two or more plots or types (*cf.* floristic composition). Similarity can be measured in a variety of ways, including various indices (such as Bray –Curtis, Euclidean distance, etc.)

constancy— percentage of plots in which a species is found.

constancy classes:

- I – 1-20% occurrence
- II – 21-40%
- III – 41-60%
- IV – 61-80%
- V – 81-100%

constant species—“species that are present in a high percentage of the plots that define a type.”

Recommended requirements for constancy at different levels of hierarchy include:

Association:	60%
Alliance:	40%
Group & Macrogroup:	25%

Constancy values change at different hierarchy levels because, as one moves up the hierarchy, the vegetation types are more heterogeneous vegetation units, with partially overlapping sets of species that comprise a meso-scale ecological gradient segment (Mueller-Dombois and Ellenberg 1974, Chytrý and Tichý 2003). Constancy is also influenced by plot size; thus fairly constrained ranges of plot sizes (four to ten-fold range) are recommended for vegetation studies (Dengler et al. 2009, Peet and Roberts 2013).

cover type – a type of community defined solely on the basis of the dominance or co-dominance of one or several species

diagnostic species— any species or group of species whose relative constancy or abundance differentiates one vegetation type from another; includes ‘character’ and ‘differential’ species. Character species can

be viewed as a special case of differential species, in that character species differentiate a type from all other vegetation types, whereas differential species differentiate one closely related type from another (Dengler et al. 2008). Thus, by definition, species indicated as diagnostic for a single vegetation unit can be called character species, while those indicated as diagnostic for more than one vegetation unit should be considered as differential species. However, there is a continuum in fidelity (diagnostic capacity) of species to vegetation units (Chytrý and Tichý 2003). Cf. *differential species, character species*

differential species— plant species that is distinctly more widespread or successful in one of a pair or closely related set of plant communities than in the other(s), although it may be still more successful in other communities not under discussion (Curtis 1959, Bruelheide 2000); the more limited a species is to one or a few plant community types, the stronger its differential value. cf. *character species, diagnostic species*

dominant species— species with the highest percent cover (the standard measure for vegetation classification), biomass, or density. Dominance is often assessed by strata, because taller statured species contain greater volume or biomass. At the stand or plot level a dominant has > 10% cover, thus including what may be called co-dominant species. At the type level, a dominant species is defined as a *constant species* (cf.) with at least 10% average cover, with the requirements for constancy varying by the level of the hierarchy. In sparsely vegetated habitats, such as deserts, dominance may not be a valuable criterion.

fidelity—A measure of the degree to which a species is concentrated more-or-less exclusively within a given vegetation type. cf. *character species*.

floristic composition – the presence and abundance of plant species (and sometimes subspecies) in a plot or type.

group — A vegetation unit defined by a relatively narrow set of diagnostic plant species, dominants and co-dominants, broadly similar composition, and diagnostic growth forms that reflect regional mesoclimate, geology, substrates, hydrology, and disturbance regimes (FGDC 2008).

growth form — the characteristic structural or functional type of plant. Growth form is usually consistent within a species, but may vary under extremes of environment (Mueller-Dombois and Ellenberg 1974). Growth forms determine the visible structure or physiognomy of plant communities (Whittaker 1973).

habitat—the combination of environmental or site conditions and ecological processes influencing a plant community.

indicator species—a species whose constancy or abundance is considered to indicate certain habitat conditions, e.g., climate, soil moisture, soil nutrients, flooding regime, disturbance history, among others.

large geographic area – a region of relatively uniform macroclimate and broadly uniform physiographic features (e.g., Great Plains-Prairie Parkland, Rocky Mountain Region, North American Boreal Region) (Bailey 1989). These areas may be on the scale of the ecoclimatic regions of Canada (Ecoregions Working Group 1989) the Ecoregional Divisions of Bailey (1989, 2009), or the floristic regions and provinces of Takhtajan (1986). As used to define the scope of alliances and associations, these areas do not provide fixed boundaries; rather they indicate the region of concentration for the units.

layer (vegetation)—a structural component of a plant community defined by (a) dominant growth form(s) of approximately the same height (e.g., tree, shrub, herb, and non-vascular layer).

phase— a non-standard level of the hierarchy that describes floristic variation caused by invasive species (typically invasive exotics) or other kinds of degradation to native vegetation types. The phase level may have substantial value in tracking levels of degradation caused by human impacts (see *facies* of Westhoff and van der Maarel 1973), from minimally disturbed to degraded stands. At some point, the limit of degradation of a native type is reached, after which the type is so altered that it becomes a ruderal type. Analyses of types may benefit from initially removing degraded phases when characterizing floristic and growth form patterns, then adding these phases back in to determine their relationship to minimally disturbed types. The USNVC standard (FGDC 2008) notes that additional lower levels may be developed, if desired, but they are not formally part of the USNVC hierarchy. Phases could be developed for various floristic levels of the hierarchy, but perhaps are of most value at the association and alliance levels.

physiognomy—narrowly defined as the outward appearance of a plant community as expressed by the dominant growth forms, such as their leaf appearance or deciduousness (Fosberg 1961); more broadly defined as the outward appearance and structure (i.e., spatial pattern of vegetation cover and layers) of the vegetation (Mueller-Dombois and Ellenberg 1974). See also structure.

plant community— a group of plant species living together and linked together by their effects on one another and their responses to the environment they share (adapted from Whittaker 1975); or more simply “the living plant species present within a defined space at a given time (adapted from Palmer and White 1994).

plot—in the context of vegetation classification, a sampling area of defined size and shape that is intended for characterizing the vegetation and habitat of a stand.

ruderal – vegetation found on human-disturbed sites, with no apparent recent historical natural analogues, and whose current composition and structure includes a broadly distinctive characteristic species combination, whether tree, shrub or herb dominated. The vegetation is often comprised of invasive species, whether exotic or native, that have expanded in extent and abundance due to the human disturbances. (Allaby 2010). Cf. *semi-natural*.

semi-natural - vegetation in which past or present human activities significantly influence composition or structure, but do not eliminate or dominate spontaneous ecological processes (Westhoff and Van der Maarel 1973). Semi-natural vegetation may have historical analogues, even if they are “off-site” (e.g. native grasslands on historically forested sites. Semi-natural sites with strong human influences that have no recent historical analogue in terms of recognizable vegetation characteristics are referred to as *ruderal*.

stand—an uninterrupted unit of vegetation, homogeneous in composition with uniform habitat conditions.

structure (vegetation)—the spatial pattern of growth forms (or life forms) in a plant community, especially with regard to their height, abundance, or coverage within the individual layers (Gabriel and Talbot 1984). Sometimes distinguished from physiognomy, when physiognomy is narrowly defined as the “outward appearance” of the vegetation.

vegetation—(1) the collective plant cover over an area (FGDC 1997), (2) the total of the plant communities of a region (Curtis 1959), (3) the mosaic of plant communities in the landscape (Küchler 1988).

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