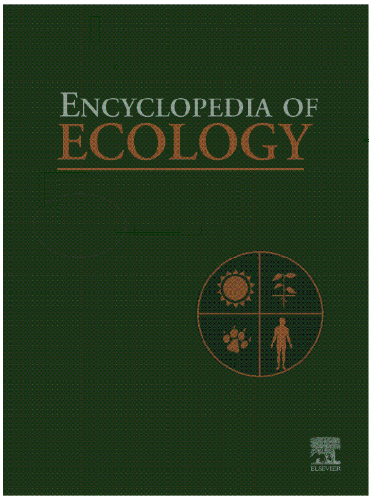

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Phytosociology

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Introduction

Phytosociology is a subset of vegetation science, in which it stands out by focusing on extant (vs. fossil), taxonomic (vs. physiognomic or functional) plant assemblages at the scale of vegetation stands (vs. landscapes or biomes). Its principal goal is the definition and functional characterization of vegetation types based on the total floristic composition of stands. Phytosociology distinguishes between concrete vegetation stand (phytocoenosis), which can be represented by a plot record (relevé), and abstract vegetation type (syntaxon), representing a group of all stands sharing certain attributes. The classification framework (syntaxonomy) is designed in close analogy to plant taxonomy, with association as the basic unit.

The fundamental concepts of phytosociology were developed by Josias Braun-Blanquet in the 1920s. He combined a standardized protocol for plot sampling, sorting of species-by-plot matrices, demarcation of community types, and their hierarchical ordering into a practical and efficient framework for the study of vegetation. In this article, we use the term phytosociology for the Braun-Blanquet approach and its modern extensions.

Phytosociology is the mainstream vegetation classification scheme in Europe, as well as in several countries outside Europe, and has become increasingly popular worldwide from the 1990s onward. Within modern ecology, phytosociology represents the most comprehensive and consistent methodology for vegetation classification. Relevés are the most widely used standardized protocol for sampling plant species co-occurrences at the stand scale. Being derived from the vast body of relevé data, syntaxonomy provides a comprehensive yet open system of vegetation types, which are indispensable in land-use management and nature conservation. Consisting of abundance data on individual plant species, relevés and vegetation types organized in large phytosociological databases are an enormous source of fine-scale biodiversity information. If linked to the growing body of plant trait or indicator value data or environmental information in geographical information systems (GISs), phytosociological data open new avenues for exploring large-scale ecological patterns and processes, and provide spatially explicit information necessary for environmental management.

Phytosociological Data

Data Records

In phytosociology, the data of a single plot are called a relevé (French for record, see **Table 1**), which consists of 'header' and species data. The 'header' comprises plot identification, methodological information, and metric, ordinal, or categorical data on geographic position, environmental conditions, and overall vegetation structure. Some of these data are essential, others optional, depending on the purpose and resources of a project (**Table 2**).

The species data are composed of a list of plant taxa (species and infraspecific taxa; further referred to as 'species') and their attributes. A full relevé lists all plant species occurring in the plot and growing on soil, including bryophytes, lichens, and macroalgae. Additional recording of species growing on substrata other than soil, such as on living plants (epiphytes), rocks (saxicolous plants), or dead wood (lignicolous plants), is desirable, but not standard in phytosociology. Every species observation is assigned to a vertical stratum (e.g., tree layer, shrub layer, herb layer, and cryptogam layer). Woody species occurring in different layers are recorded separately for each layer. For each species observation in a layer, an importance value is estimated and usually expressed on a simplified scale of abundance (number of individuals/ramets) and/or cover (area of the vertical projection of all aerial parts of a species relative to the total plot area) (**Table 3**). As mixed cover-abundance scales pose problems in data analysis, pure cover scales are preferred when precise quantitative estimates are required, for

Table 1 Example of a forest relevé with five vegetation layers distinguished: upper tree layer (T1), lower tree layer (T2), shrub layer (S), herb layer (H), and cryptogam layer (C)

Plot ID/methodology	
Field number	291
Author	J Ewald
Plot size (m^2)	144
Plot shape	square
Sampling date	3 June 1997
Preliminary syntaxon	Galio-Fagetum adenostyletosum
Geographic data	
UTM coordinates	32 U 4434393 E – 5272800 N
Locality	Ettaler Manndl, Höllenstein, 3 km W from Eschenlohe, Garmisch-Partenkirchen, Bavaria, Germany
Environmental data	
Elevation (m a.s.l.)	1300
Slope aspect (°)	35
Slope inclination (°)	32
Soil type	Cambisol
Parent material	Cretaceous sandstone
Management	Protective forest
Stand age (year)	140
Structural data	
Height upper tree layer (m)	30
Height lower tree layer (m)	6
Height shrub layer (m)	3
Cover upper tree layer (%)	75
Cover lower tree layer (%)	3
Cover shrub layer (%)	1
Cover herb layer (%)	20
Cover cryptogam layer (%)	3

Layer	*Species*	*Importance*
T1	*Fagus sylvatica*	3
	Picea abies	3
T2	*Picea abies*	1
S	*Picea abies*	1
H	*Acer pseudoplatanus*	+
	Aconitum vulparia	+
	Adenostyles alliariae	1
	Adoxa moschatellina	+
	Athyrium filix-femina	+
	Cardamine flexuosa	+
	Chaerophyllum hirsutum	+
	Chrysosplenium alternifolium	+
	Cicerbita alpina	+
	Deschampsia cespitosa	+
	Dryopteris dilatata	+
	Dryopteris filix-mas	+
	Epilobium montanum	+
	Galeopsis tetrahit	+
	Galium odoratum	+
	Geranium robertianum	+
	Gymnocarpium dryopteris	+
	Impatiens noli-tangere	+
	Lamiastrum montanum	1
	Luzula sylvatica subsp. *sieberi*	+
	Lysimachia nemorum	1
	Mercurialis perennis	+
	Mycelis muralis	1
	Myosotis sylvatica	+
H	*Oxalis acetosella*	2
	Paris quadrifolia	+
	Polypodium vulgare	+
	Prenanthes purpurea	+
	Primula elatior	+
	Ranunculus lanuginosus	1
	Rumex alpestris	+
	Salvia glutinosa	1
	Sanicula europaea	+
	Saxifraga rotundifolia	1
	Senecio fuchsii	1
	Stellaria nemorum	2
	Thelypteris limbosperma	+
	Veronica urticifolia	+
	Viola biflora	+
C	*Atrichum undulatum*	1
	Brachythecium rutabulum	+
	Conocephalum conicum	+
	Ctenidium molluscum	+
	Dicranella heteromalla	+
	Dicranum scoparium	+
	Fissidens taxifolius	+
	Mnium spinosum	+
	Plagiochila porelloides	+
	Plagiomnium undulatum	+
	Plagiothecium curvifolium	+
	Polytrichum formosum	+
	Rhizomnium punctatum	+
	Thuidium tamariscinum	+

Table 2 Essential (*) and selected optional data to be included in the 'header' of a phytosociological relevé

Group	*Data*	*Comment*
ID/methodology	Field number* Author(s)* Plot size* Plot shape Sampling date* Preliminary assignment to a syntaxon	
Geographic data	Geographic coordinates*	For example, Greenwich coordinates, UTM
	Locality in textual form*	including political and/or natural geographic units
Environmental data	Elevation (m a.s.l.)* Slope aspect* Inclination*	
	Soil	For example, type, texture, depth, pH, humus form, humus content, C/N ratio
	Geology (parent material) Management	
Structural data	Height of vegetation layers (m)	For example, tree layer, shrub layer, herb layer, cryptogam layer
	Cover of vegetation layers (%)*	Cover of each layer and total cover
	Cover of other surfaces (%)	For example, bare soil, litter, woody debris, rocks, open water

Table 3 Customary version of an extended Braun-Blanquet cover-abundance scale with ordinal values, which are often used for numerical interpretation. In the original Braun-Blanquet scale, 2m, 2a, and 2b were joined under the symbol '2'

Symbol	*Abundance (number of individuals/ramets)*	*Cover interval (%)*	*Ordinal value*
r	1	0–5	1
+	2–5	0–5	2
1	6–50	0–5	3
2m	More than 50	0–5	4
2a	Any	5–12.5	5
2b	Any	12.5–25	6
3	Any	25–50	7
4	Any	50–75	8
5	Any	75–100	9

example, in studies of vegetation change in permanent plots. Sometimes, additional characteristics of the species – such as sociability (degree of clustering of the individuals), vitality, fertility, age class (e.g., seedling or juvenile), and phenological status – are recorded, but these are of little or no importance for standard analyses.

Selection and Size of Plots

Plot sites in the field are positioned in vegetation stands that are relatively homogeneous in terms of structure, species composition, and environment, so that variation is minimized within and maximized between plots.

The traditional sampling strategy in phytosociology, preferential sampling, in which the researcher selects stands that are considered as representative of some vegetation units, has several disadvantages: it is not repeatable by other researchers, tends to neglect some vegetation types and oversample others, and produces a nonrepresentative sample of vegetation diversity in the study area. In spite of these disadvantages, probabilistic sampling strategies, such as random or systematic sampling, have never received wider acceptance in phytosociology. While providing reliable estimates of vegetation attributes, probabilistic sampling is less suited to phytosociology's goal of representing maximum variation in vegetation diversity across a study area, as it tends to undersample or even miss rare types. GIS and global positioning system (GPS) technology have made stratified-random sampling schemes increasingly popular in phytosociology. Based on the overlay of digital maps in a GIS, the study area can be stratified into patches with certain combinations of land-cover types and environmental variables that are supposed to correlate with plant distribution. Within each of these strata, plot positions are randomly placed and subsequently found in the field with a GPS receiver. A related sampling strategy is a gradient-oriented transect or gradsect, which establishes plot sites along a landscape transect that runs parallel to an important environmental gradient.

Phytosociological plots are usually squares or rectangles, which, as a rule of thumb, are roughly as large in square meters as the vegetation is high in decimeters (e.g., 200 m^2 for a forest of 20 m height). Despite this rule and other suggestions in textbooks, actual plot sizes used may span more than one order of magnitude within the same vegetation type. Standardization of plot sizes is hindered by the vague and misleading concept of 'minimal area', which is thought to be a certain plot size specific for each vegetation type, beyond which any further enlargement has negligible effects on species richness and composition. However, plot size strongly influences estimates of species richness and other vegetation parameters. Joint use of differently sized relevés in a single analysis may thus produce artifacts in classification, ordination, and calculation of fidelity of species to vegetation units. To safeguard data compatibility, standard plot sizes have been proposed for use within certain structural formations, for example, 200 m^2 in forest vegetation; 50 m^2 in scrub vegetation; 16 m^2 in grassland, heathland, and other herbaceous vegetation; and 4 m^2 in aquatic and low-growing herbaceous vegetation.

Vegetation Databanks

Phytosociology has a long tradition of publishing, archiving, and re-analyzing relevés as its basic primary data. Many phytosociological journals print full tables including all relevant relevés, thus making data accessible for future compilation and analysis, which was traditionally performed as synoptic tables on paper. The limitations of manual data management were overcome by using table editing and databank software, which allows seizing, storing, managing, filtering, and analyzing relevé data in multiple ways.

Compilation in a databank requires that all information obeys stringent formal and technical rules laid down in reference lists, meta-data and data models. Databanks of different formats and complexity were established, ranging from simple spreadsheets to relational and object-based data models that allow flexible definitions and comprehensive documentation of meta-data. Simple databanks are able to exchange data freely if the same standards, database formats, definitions, and reference lists are used. The success of phytosociological databanks is so far due to rather simple management software packages such as TURBOVEG, which is currently the most widespread program in Europe and beyond, distributed free of charge or at small cost along with taxonomic reference lists and tools to create, edit, and analyze phytosociological tables.

While early databank development revolved around fixing standards for data types and references for plant taxon concepts and names, modern ecoinformatics provides tools to exchange data of different formats and taxonomic reference and, ultimately, link up databanks of any format in networks. Rather than enforcing standard formats, these systems require that data are recovered and stored with as much original information as possible, including meta-data on sampling design and methods, cover-abundance scales, definition of layers, taxonomic references, and original data sources.

Classification of Vegetation

Aims and Criteria

Vegetation classifications are performed with three fundamental goals: (1) delimiting and naming parts of the vegetation continuum to enable communication about them; (2) predicting a multitude of ecosystem attributes (e.g., species composition, site conditions, and ecological processes) from the assignment of a particular stand to a vegetation unit; and (3) making multispecies co-occurrence patterns representable by verbal descriptions, tables, diagrams, and maps. Floristically defined vegetation types are thus suitable reference entities for ecological research, bioindication, and nature conservation.

Reaching these aims requires of the classification approach:

1. coherence of units with respect to major ecosystem properties;
2. simple and clear discernability of units;
3. completeness of the system (i.e., coverage of all vegetation types of the given area);
4. robustness (i.e., minor changes of the data should not considerably change the classification);
5. tolerance against varying data quality;
6. supra-regional applicability;
7. applicability for a range of different purposes;
8. hierarchical structure, allowing for different degrees of generalization;
9. equivalence of units of the same hierarchical level; and
10. adequate number of units with respect to practical use.

As no single classification can ideally meet all of these criteria at the same time, and their relative importance depends on the purposes, competing classifications of the same objects and data are a reality. Thus, the interpretation of local data will change with scaling up from local to regional and supra-regional context. However, there is also a practical requirement to have a unified supra-regional classification to enable communication among scientists, managers, and authorities between regions.

Braun-Blanquet Approach

The 'Braun-Blanquet approach' provides a methodological framework for vegetation classification that seeks an optimal combination of the above criteria and that reconciles conflicting requirements of different scales and purposes. However, it is not an unambiguous and uniform set of recipes, and it has been subject to diverse modifications. Despite the variety of different versions, practitioners agree on certain fundamentals, which distinguish the Braun-Blanquet approach from most other ways of vegetation classification: (1) The classification is based on the (total) species composition of the sample plots (floristic–sociological method), whereas structural or environmental criteria play a subordinate role. (2) The classification units called syntaxa (singular: syntaxon) are arranged into a hierarchical system according to their floristic similarity. The principal ranks of this system are, from bottom up, association, alliance, order, and class. (3) There are generally accepted rules for the scientific naming of syntaxa (see the section entitled 'Phytosociological ranks and nomenclature').

Within the Braun-Blanquet approach, the concept of character and differential species is important for the recognition of previously defined syntaxa. Differential species are those that positively differentiate, by their occurrence, the target syntaxon from other syntaxa. Character species are a special case of differential species: they positively differentiate the target syntaxon from all other syntaxa. The differential and character species combined are called diagnostic species. The validity of diagnostic species may be restricted to comparisons within the syntaxon of the next higher rank or within a physiognomic vegetation type. Diagnostic species are based on the concept of fidelity, that is, concentration of their occurrence or abundance within the given syntaxon. Traditionally, arbitrary measures of fidelity were used, such as constancy in the target syntaxon had to be at least twice as high as in any other syntaxon. Nowadays, statistical fidelity measures are increasingly used (see the section entitled 'Numerical approaches'). However, in spite of several attempts at a formal definition of differential and character species, no widely accepted agreement in this respect has been reached so far.

Phytosociology faces difficulties in the classification of vegetation types that lack species of narrow ecological amplitude which could be used as character species of the respective syntaxa. This problem led early practitioners to avoid stands without specialist species as 'atypical' and 'fragmentary' and oversample those containing presumed character species. Even when sampled and recognized, such poorly characterized vegetation types were often excluded from the syntaxonomic system. Vegetation types poor in diagnostic species may be incorporated into the system in several ways, for example: (1) Deductive classification affiliates such units as so-called basal or derivative communities to higher syntaxa of the system, from which their formal names are derived (e.g., *Elymus repens* [*Artemisietea vulgaris*] derivative community). (2) According to the concept of central syntaxon, there can be one negatively differentiated syntaxon within the next superior syntaxon of the hierarchy; central syntaxa have the same ranks (e.g., association) and nomenclature as normal syntaxa.

This diversity of approaches within the Braun-Blanquet system must be unified where all vegetation types of a large area are to be placed in a single coherent system, such as in modern projects of national vegetation classifications. These projects have usually developed consistent systems of standardized and operational methodology of vegetation classification based on the Braun-Blanquet approach.

Numerical Approaches

Traditional phytosociological work was based on the subjective delimitation of vegetation units, made either already during the field reconnaissance and sampling or in the process of manual sorting of relevés and species within tables. The need for more formal, transparent, efficient, and repeatable classification procedures led to the introduction of numerical classification methods in phytosociology since the 1960s. They can be either agglomerative or divisive. Agglomerative methods start with linking individual relevés based on the similarity of their species composition, forming relevé clusters and subsequently linking these clusters to form a hierarchical classification, usually presented as a dendrogram. Divisive methods start with dividing the set of relevés into subsets, which are further divided into subsets on a lower hierarchical level, thus eventually proceeding to the single relevés. The most popular divisive method is two-way indicator species analysis (TWINSPAN), which uses the ordination method of correspondence analysis to divide the relevés into subsets. Simultaneously with the classification of relevés, TWINSPAN classifies species, and produces an ordered species-by-relevé table similar to that used in traditional phytosociology (see the section entitled 'Phytosociological tables'). The classifications of the same data sets produced by agglomarative clustering and TWINSPAN usually roughly correspond but differ in details. Agglomerative clustering is the method of choice when cluster homogeneity is the principal goal, while TWINSPAN better reflects the main gradients in species composition of the input data set. An important choice in any numerical procedure is the transformation of cover-abundance data, which determines to what degree species cover-abundance will be accounted for in the analysis.

In addition to numerical classification, phytosociology frequently uses various ordination methods, such as correspondence analysis (CA), detrended correspondence analysis (DCA), or principal components analysis (PCA). Sometimes, ordination and classification are perceived as antagonistic approaches, representing the Gleasonian continuum concept and the Clementsian concept of superorganism, respectively. However, phytosociologists never engaged in that ideological debate, and nowadays both approaches seem to be reconciled: classification studies often use ordination to visualize the position of vegetation units along gradients, and ordination patterns are used to propose the delimitation of relevé groups for certain purposes.

Applicability of an established classification crucially depends on finding those species that are typical of relevé groups (vegetation units) and make them recognizable by simple floristic criteria. Such species may include the most frequent species, dominant species, or diagnostic species. The former two groups of species can be easily defined by setting some threshold of constancy or cover-abundance values that a species must exceed to be considered as frequent (constant) or dominant, respectively. Diagnostic species are determined based on the concept of fidelity, which quantifies the degree of concentration of a species' occurrence or abundance in the relevés of the target vegetation unit. If a species occurs mainly in the relevés of the target vegetation unit while it is largely absent elsewhere, it is considered as faithful to this vegetation unit. Fidelity can be quantified by various statistical measures. If it is based on species presence/absence, various measures of association between categorical variables can be used, for example, chi-square, *G* statistic, or phi coefficient of association. Some fidelity measures have also been proposed to deal with cover-abundances, for example, the Dufrêne–Legendre indicator value. The properties of different fidelity measures vary slightly, for example, with respect to the weight given to rare or common species. Statistical significance of fidelity can be either derived directly from the values of some of these measures or determined by a separate procedure such as permutation test. Apart from the selection of the appropriate fidelity measure, fidelity can be measured in two different ways. First, species occurrence in the target group of relevés can be compared with all the relevés in the data set that do not belong to the target group, irrespective of the divisions of the rest of the data set. Second, species frequency in that group of relevés where it is most common is compared with its frequency in the group where this species is the second most common. In both cases, some arbitrary threshold fidelity value is selected and species that exceed this value are considered as diagnostic. The first approach is not affected by the divisions of the data set outside the target vegetation unit, thus yielding a more general result, whereas the latter approach is only valid in the context of a given table or classification, but it provides a clearer separation of vegetation units through diagnostic species within this table or classification. The results of both approaches depend on the geographical extent, sampling design, and delimitation of the available set of relevés, the 'universe of investigation'.

Integrating the Different Approaches

While having the basic aims in common, the traditional Braun-Blanquet approach and numerical approaches differ in some respects. Indeed, no approach produces an objective or 'the correct' classification. In spite of the high degree of formalization involved in numerical classification, the numerous choices concerning the data set composition, cover-abundance transformation, numerical coefficients, classification algorithms, or number of vegetation units to be accepted result in the fact that numerical methods, like the traditional expert-based approaches, may suggest many different partitions of the same data.

Unlike the expert-based classifications, which often use unclear classification criteria, numerical classification methods consistently use explicit information on species occurrence and cover-abundance and apply it consistently across vegetation types. However, while experts often implicitly incorporate in the classification process knowledge of species behavior in a broad geographical and environmental range, numerical methods only use information contained in the particular data set, which often results in rather idiosyncratic classifications. It is therefore difficult to combine different numerical classifications into a single system of syntaxa, which would be valid over large areas and different habitats, without relying on expert judgment.

To avoid these problems, supervised classification methods have gained importance recently. They take traditional syntaxa that are widely recognized by phytosociologists as given and assign new relevés to these syntaxa by numerical procedures. Such an approach supports both the stability of the traditional phytosociological system, which has already received wide acceptance, and the application of formal, unequivocal classification procedures. A simple approach is to calculate an index of similarity of species composition between new relevés and constancy columns of synoptic tables (see the section entitled 'Phytosociological tables') that summarize the traditional classification and subsequent matching of each new relevé to the vegetation unit to which it has the highest similarity. More sophisticated methods of supervised classification include quadratic discriminant analysis, multinomial log-linear regression, classification trees, and artificial neural networks. The latter, for example, can establish a classifier based on the previous knowledge of what the relevés belonging to a certain vegetation unit look like. When new relevés are submitted, the classifier assigns them, with some degree of uncertainty, to the correct vegetation unit.

Another method of supervised classification is COCKTAIL, which was specifically designed to imitate traditional Braun-Blanquet classification. It uses the external information on species behavior, extracted from large phytosociological databases, and forms sociological groups of species with statistical tendency of co-occurrence in the relevés of the database. Then, unequivocal definitions of syntaxa are created that involve decision rules, postulating which of the sociological species groups must be present or absent for a particular relevé to be assigned to the target syntaxon. COCKTAIL definitions can be created to fit the meaning of the syntaxa of traditional phytosociology. In such a way, traditional syntaxa can be defined formally and applied in the computer expert systems, which automatically assign newly encountered relevés to syntaxa.

Phytosociological Tables

In phytosociology, original data and classification results are presented as tables of species by relevés or community types. There are two types of phytosociological tables, relevé tables (**Table 4(a)**) and synoptic tables (**Table 4(b)**). In both cases, species are listed in the lines and relevés (in relevé tables) or combined groups of relevés (in synoptic tables) in the columns.

Both types of tables are normally presented in a structured manner. Lines and columns are arranged in such a way that 'species blocks' (i.e., groups of nonempty table cells) form more or less a diagonal from the top left to the bottom right. Therefore, the diagnostic species corresponding to the syntaxa ordered from left to right are to be found from top downward (except for the negatively differentiated syntaxa). In tables representing multi-layered woody vegetation, plant species of upper layers are normally listed at the top of the table to give an impression of stand structure. At the bottom of the table, those species are listed that have no diagnostic value within the respective table. These may be diagnostic species of superior syntaxa or 'companions', that is, species that have no diagnostic value for any syntaxon included in the table. Within blocks, species are sorted by decreasing constancy or decreasing fidelity. Species blocks or individual diagnostic species can be highlighted by frames or shadings in the tables; the criteria for doing so are related to species fidelity to syntaxa and should be clearly defined in particular studies.

In synoptic tables, all relevés assigned to the same vegetation unit are represented by a single column with constancy values (i.e., the percentage proportion of relevés in which the species is present). Constancy values are often presented as classes indicated by Roman numerals (I: 1–20%; II: 21–40%; . . .; V: 81–100%), but the use of percentages has several advantages, for example, it does allow the application of modern fidelity concepts and merging of different synoptic tables without loss of accuracy. In addition to the constancy values, medians or ranges of the cover-abundance values or fidelity levels may be indicated. It is important to note (though long-neglected in phytosociology) that the calculation and comparison of constancy values does only make sense for plots of the same or similar size, because constancy values are strongly influenced by plot size.

Phytosociological Ranks and Nomenclature

Abstract vegetation units defined by floristic–sociological criteria are termed syntaxa. They are positioned in a hierarchy of different ranks (**Table 5**), which is meant to make the multitude of units manageable and offers the opportunity to vary the conceptual resolution of analysis, maps, and graphs. The association is considered as the basic unit, comparable to species in taxonomy. Ranks below the association level are often used to express edaphic (subassociations and variants), climatic (altitudinal forms), geographic (vicariants or races), structural (facies of dominant species), and successional variation (phases).

Like other fields of biological systematics, syntaxonomy is an open-ended process that is carried out by a large community of independent researchers and requires unequivocal rules for naming classification units. Therefore, the Nomenclature Commission of the International Association for Vegetation Science (IAVS) and the Féderation Internationale de Phytosociologie (FIP) have established the International Code of Phytosociological Nomenclature (ICPN), similar to the nomenclature codes used in botanical and zoological taxonomy.

The ICPN regulates the scientific nomenclature of four principal and four supplementary ranks of syntaxa. Neither synusial nor symphytosociological units (see the section entitled 'Symphytosociological approaches'), nor informally named syntaxa (e.g., *Elymus repens* community) fall under the ICPN. The ICPN provides precise instructions for the formation of syntaxon names, their valid publication, and the decision about which of several available names from the earlier literature to apply. According to the ICPN, every syntaxon of a certain circumscription and rank has only one correct name. However, the ICPN only regulates the nomenclature and does not define rules for proper delimitation and classification of syntaxa. Aiming to provide unambiguity and stability of syntaxon names, the ICPN is based on two major principles: (1) among several names for a syntaxon, the oldest valid (published) name is the correct one (priority); (2) each syntaxon name is connected to a nomenclatural type (a single relevé for associations, a validly described lower-rank syntaxon for higher syntaxa), which determines the usage of the name when this syntaxon is split off, merged with others, or otherwise changed in its delimitation.

Syntaxon names are formed of the scientific names of one or two (in the case of subassociations, up to three) plant species or infraspecific taxa, which usually are, but

Table 4 (a) Worked example (I): Relevé table containing three associations of three alliances and two classes of the subalpine heathland and grassland vegetation of the Czech Republic (see Table 6 for their position in the syntaxonomic hierarchy). Species of the cryptogam layer are marked with 'C', the other species belong to the herb layer. Blocks of diagnostic species are shaded. Within blocks, diagnostic species are ranked by decreasing fidelity to the given syntaxon. Fidelity was measured with the phi coefficient of association and was based on the comparison of species occurrences within the syntaxa of this table only; species with $\phi > 0.25$ were considered as diagnostic. As each association belongs to a different alliance, diagnostic species of the associations can be partly considered as diagnostic of the alliances. Companion species are ranked by decreasing constancy within the entire table. Data were taken from the Czech National Phytosociological Database. Species occurring in a single relevé are not shown. (b) Worked example (II): Synoptic table based on the same data as Table 4a. The numbers in the table are percentage constancies

	(a) Relevé table																													*(b) Synoptic table*		
Association	*Junco trifidi-Empetretum hermaphroditi*													*Cetrario-Festucetum supinae*										*Carici-Nardetum*						*J-E*	*C-F*	*C-N*
Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	*n* = 13	*n* = 10	*n* = 6
Diagnostic species of the association *Junco trifidi-Empetretum hermaphroditi*																																
Empetrum hermaphroditum	5	3	3	3	5	4	3	3	3	3	4	4	4	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	100	10	.
Hylocomium splendens (C)	.	.	1	r	.	2	.	.	1	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	38	.	.
Vaccinium myrtillus	1	1	2	2	1	2	1	1	2	2	1	2	2	1	+	.	.	+	1	.	.	.	+	.	.	+	+	+	.	100	50	50
Melampyrum sylvaticum	.	.	+	.	.	+	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	31	.	.
Pleurozium schreberi (C)	.	.	1	r	.	2	.	.	3	r	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	46	.	17
Polytrichum piliferum (C)	2	+	.	.	.	.	2	+	.	.	2	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	38	10	.
Diagnostic species of the association *Cetrario-Festucetum supinae*																																
Cladonia bellidiflora (C)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	30	.
Thamnolia vermicularis (C)	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	+	+	.	.	.	+	.	.	.	.	.	.	8	40	.
Diagnostic species of the association *Carici bigelowii-Nardetum strictae*																																
Nardus stricta	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	.	+	1	3	4	4	4	4	5	.	40	100
Galium saxatile	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	+	.	2	.	.	.	50
Anthoxanthum alpinum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	r	.	1	2	.	.	10	50
Deschampsia cespitosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	1	.	.	.	.	33
Festuca rubra agg.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.	33
Luzula campestris agg.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.	33
Potentilla erecta	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.	33
Diagnostic species of the class *Juncetea trifidi*																																
Calluna vulgaris	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	+	1	1	+	2	.	+	2	.	+	1	r	.	.	.	90	50
Bistorta major	.	.	.	.	.	.	+	.	.	.	.	.	.	1	+	1	+	+	+	1	.	1	+	+	.	+	+	.	.	8	90	50
Agrostis rupestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	+	.	1	1	.	.	+	.	.	.	.	.	40	17
Carex bigelowii	.	.	.	.	.	.	.	.	.	.	.	.	.	4	+	.	3	+	.	1	1	1	.	1	+	.	+	.	+	.	70	67
Hieracium alpinum agg.	.	.	.	.	.	.	1	.	.	.	+	.	.	.	+	2	.	+	+	1	2	1	+	+	1	+	+	+	.	15	80	83
Companion species																																
Avenella flexuosa	+	+	+	1	1	1	2	1	1	+	1	1	1	1	+	1	3	+	.	3	1	2	2	4	+	3	2	.	2	100	90	83
Vaccinium vitis-idaea	.	2	1	2	.	2	.	1	2	1	+	1	2	1	1	.	.	.	+	.	.	.	.	.	+	+	+	2	.	77	30	67
Cetraria islandica (C)	.	+	1	r	.	1	.	+	2	r	2	.	r	.	+	2	.	+	.	.	2	3	+	.	.	.	.	.	.	69	60	.
Festuca supina	.	.	.	1	.	.	.	.	1	.	1	.	.	2	2	3	1	.	3	.	2	+	.	.	.	+	.	1	+	23	70	50

Solidago virgaurea	.	+	+	.	.	.	.	.	.	+	+	.	.	.	.	.	.	+	r	+	.	.	1	+	.	.	+	.	r	31	40	50
Homogyne alpina	.	.	r	.	.	.	.	.	.	r	.	.	.	.	.	+	.	+	.	.	.	+	1	+	.	.	2	1	.	15	40	50
Huperzia selago	.	+	.	.	.	.	1	+	.	.	.	.	.	.	.	+	.	+	+	.	.	1	+	.	.	.	.	.	.	23	50	.
Calamagrostis villosa	.	.	.	.	+	.	.	.	.	.	+	+	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	r	+	23	10	50
Juncus trifidus	1	2	.	.	.	.	.	3	.	.	.	.	.	.	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	23	20	.
Trientalis europaea	.	.	+	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	31	.	17
Vaccinium uliginosum	.	.	.	+	.	+	.	.	+	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	31	10	.
Racomitrium lanuginosum (C)	.	2	.	.	.	.	.	2	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	15	20	.
Cladonia arbuscula (C)	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	+	.	.	.	+	.	.	.	.	.	.	.	8	30	.
Cladonia rangiferina (C)	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	+	.	.	.	.	.	.	.	.	.	.	.	8	30	.
Dicranum fuscescens (C)	.	1	.	.	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	23	.	.
Polytrichastrum alpinum (C)	.	+	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	15	10	.
Alectoria ochroleuca (C)	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	2	.	+	.	.	.	.	.	.	8	20	.
Campanula bohemica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	1	.	.	.	20	17
Pulsatilla alpina ssp. *austriaca*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	1	.	.	20	17
Pohlia nutans (C)	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	8	.	17
Polytrichum strictum (C)	.	.	2	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15	.	.
Silene vulgaris	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	10	17
Cetraria cucullata (C)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	20	.
Diphasiastrum alpinum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	20	.
Polytrichum juniperinum (C)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	20	.
Cladonia pyxidata (C)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	10	17
Veratrum album subsp. *lobelianum*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	+	.	.	.	.	.	10	17

Table 5 Syntaxonomic ranks whose names are regulated by the International Code of Phytosociological Nomenclature (ICPN)

Rank	*Termination*	*Example (without author citation)*
Class[a]	*-etea*	*Koelerio-Corynephoretea*
Subclass[b]	*-enea*	*Koelerio-Corynephorenea*
Order[a]	*-etalia*	*Phragmitetalia australis*
Suborder[b]	*-enalia*	*Oenanthenalia aquaticae*
Alliance[a]	*-ion*	*Fagion sylvaticae*
Suballiance[b]	*-enion*	*Cephalanthero-Fagenion*
Association[a]	*-etum*	*Corniculario aculeatae-Corynephoretum canescentis*
Subassociation[b]	*-etosum* or ‘*typicum*’ or ‘*inops*’	*Corniculario aculeatae-Corynephoretum canescentis cladonietosum*

[a] Principal rank (obligatory).
[b] Supplementary rank (optional).

Table 6 Worked example (III): Syntaxonomic hierarchy including all principal ranks and full syntaxon names with author citations for the syntaxa presented in **Table 4**

- Class: *Loiseleurio-Vaccinietea* Eggler ex Schubert 1960
  - Order: *Rhododendro-Vaccinietalia* Braun-Blanquet in Braun-Blanquet et Jenny 1926
    - Alliance: *Loiseleurio procumbentis-Vaccinion* Braun-Blanquet in Braun-Blanquet et Jenny 1926
      - Association: *Junco trifidi-Empetretum hermaphroditi* Šmarda 1950

- Class: *Juncetea trifidi* Hadač in Klika et Hadač 1944
  - Order: *Caricetalia curvulae* Braun-Blanquet in Braun-Blanquet et Jenny 1926
    - Alliance: *Juncion trifidi* Krajina 1933
      - Association: *Cetrario-Festucetum supinae* Jeník 1961
    - Alliance: *Nardo strictae-Caricion bigelowii* Nordhagen 1943
      - Association: *Carici bigelowii-Nardetum strictae* (Zlatník 1928) Jeník 1961

Table 7 Levels of classification from synusial phytosociology to sigmasociology

Concrete object	*Elements recorded in relevés*	*Abstract type*
Partial vegetation stand (e.g., layer)	Species	Synusia
Vegetation stand (phytocoenosis)	Species	Syntaxon
Vegetation stand (phytocoenosis)	Synusiae	Coenotaxon
Vegetation mosaic (tesela)	Syntaxa or coenotaxa	Sigmataxon
Landscape mosaic (catena)	Sigmataxa	Geosigmataxon

need not be, characteristic in the respective vegetation type. The formation of the scientific syntaxon names involves connecting vowels, the declination of the taxon epithets, and addition of terminations indicating syntaxonomic rank (**Table 5**). An ‘author citation’ (i.e., the author(s) and year of the first valid publication) also forms part of the complete syntaxon name (see **Table 6**).

Other Levels of Classification

Synusial approaches

While phytosociological classifications are usually based on all plant species occurring in vegetation stands, for some purposes sampling may be restricted to certain taxonomic, functional, or structural parts of these. Abstract types of such partial communities are called synusiae (singular: synusia) in order to differentiate them from normal community types (syntaxa) (**Table 7**). Synusiae include plant assemblages of horizontally differentiated microhabitats within larger vegetation stands, of vertical vegetation layers, and of seasonally separated phenological phases. Epiphytic cryptogams inhabiting tree bark are a typical example of a synusia, which is recorded in small plots with cover projection estimated perpendicular to the substrate surface. Synusiae should be placed in a separate hierarchical system with ranks of their own and the union as its basic unit. However, many studies of partial communities place their units in the system of syntaxa, leading to the ambiguous situation that the same name can refer to both a synusia and a syntaxon.

Symphytosociological approaches

While plant communities and partial communities are assemblages of plant species and their individuals, symphytosociological units are assembled of synusiae or syntaxa (**Table 7**) and represent a coarser view of community diversity. Sampling and classification basically follow the phytosociological method, but use synusiae or syntaxa (fine-scale vegetation types) instead of plant species as objects of observation. Two major concepts fall in this category and may be combined: (1) ‘Integrated synusial phytosociology’ of some French authors classifies separate ‘associations’ for tree, shrub, herb, and cryptogam layers, which in the normal terminology would be synusiae. These ‘associations’ are recorded in relevés of entire stands, analyzed like species in normal phytosociological tables, and such relevés are then classified to form so-called coenotaxa. (2) Sigmasociology records syntaxa (or coenotaxa) in large relevés of uniform macrotopography, substrate, and climate (tesela), which are tabulated and classified to form sigmataxa, which at a yet coarser scale (catena) become the elements of landscape units called geosigmataxa.

Applied Phytosociology

Ecological Assessment

The study of species–environment and community–environment relations is the key to the functional interpretation of plant communities and to applications of phytosociology in bioindication and predictive modeling. Since the time of Braun-Blanquet, many relevés have been made in conjunction with measurements of soil, topographic, and climate variables. If relevé coordinates are known, environmental variables can also be *post hoc* read from maps or modeled from geodata. Environmental data are of multivariate nature, which requires condensing their information content and choosing the most meaningful variables. As in species-by-relevé matrices, the dimensions of environmental variation can be reduced by extracting continuous gradients (ecological factors) or by forming clusters (site types). Relationships with the environment can be established for community types or species.

While often restricted to verbal descriptions and simple outlines of schematic correspondences (e.g., vegetation type–soil type) in early phytosociology, vegetation type–environment relationships are nowadays studied based on measured variables. These data enable to establish environmental envelopes, which define the possible occurrence of each vegetation type in ecological space. The overall significance of environmental differentiation between types can be tested, for example, by nonparametric permutation procedures (MRPPs).

There is a long tradition in phytosociology of defining ecological groups of species that exhibit similar behavior along gradients and represent species of similar realized niche ('ecological amplitude') rather than fundamental niche ('physiological amplitude'). Such groups are mainly based on expert knowledge and are only partly calibrated on independent measurements of environmental variables. Also, the derivation of ecological indicator values of plant species strongly relies on phytosociological descriptions of vegetation patterns, from which the principal ecological gradients are extracted. While separate species group systems and indicator value systems have been devised for vegetation of arable fields, grasslands, and forests, Heinz Ellenberg created a general, semiquantitative system of indicator values for the central European flora, in which most species of vascular plants, bryophytes, and lichens are assigned a value on an ordinal scale, ranging from 1 to 9 and representing the estimated ecological optimum with respect to the principal factors light, temperature, continentality, moisture, soil reaction, nutrient availability, and salinity. Being unique in summarizing the niches of an entire flora, Ellenberg values are widely used for calibrating ecological conditions based on plant communities. The concept of plant indicator values has been recently adapted for use beyond central Europe.

Vegetation Maps

Information on spatial distribution of syntaxa is often summarized in vegetation maps. Maps of actual vegetation show the current distribution of vegetation types in a given area, usually in small areas of particular interest, such as nature reserves. Fine-scale mapping of actual vegetation requires operational definitions of syntaxon boundaries and their differential floristic and structural features, which are laid down in detailed mapping keys.

For mapping larger areas, the concept of potential natural vegetation (PNV) is often used. PNV is hypothetical vegetation that would exist at certain sites under current site conditions and current climate, provided the vegetation is not disturbed by humans and is allowed to develop into equilibrium with the prevailing site conditions. Being based on the knowledge of the relationship between habitat and natural vegetation, PNV maps implicitly or explicitly rely on models, which can take different forms. Traditional phytosociology establishes the correspondence between actual (e.g., certain meadow or weed communities) and natural vegetation (e.g., certain forest types), and maps PNV units by interpreting actual vegetation. More modern PNV models are calibrated from joint descriptions of vegetation and site conditions of remnant natural stands, and use combinations of site conditions to extrapolate natural vegetation for any point in the landscape. Process-based models predict the outcome of competition between the dominant plant species, but have so far rarely been used to construct PNV maps.

While maps of actual or potential vegetation provide full coverage of a study area and its vegetation units, selective maps show the distribution of certain syntaxa, based on the available relevés. They can be presented as dot maps of exact plot positions or as grid maps, indicating presence or absence of the syntaxon in grid cells. As, however, information on distribution of syntaxa is often less comprehensive than on plant species, the potential range of a syntaxon can be modeled by superimposing distribution maps of its diagnostic species. The more the number of these co-occur in a certain area, the higher the probability to find the respective community type there. Models of potential syntaxon ranges can be based on outline or grid maps and on simple or weighted sums of species, but the prediction value is best for high-resolution grid maps where the contribution of diagnostic species to the prediction of a syntaxon is weighted by their fidelity to the latter.

Spatial models of syntaxon distribution can also be based on the knowledge of the relationships between environmental variables (including land use) and syntaxon occurrence. If digital maps of environmental factors and landscape structures relevant to plant distribution are available, the model can be made with the probability of syntaxon occurrence as a response variable and a set of landscape variables as predictors. The relevant environmental maps are then overlaid in a GIS and the probabilities of syntaxon occurrence predicted by the model are mapped.

Monitoring Temporal Change

As spatially and temporally explicit, detailed representations of vegetation, phytosociological relevés and maps are appropriate tools for monitoring change in plant species composition and the underlying environmental conditions. Thus, fine-scale monitoring systems in agriculture, forestry, nature conservation, and civil engineering have used repeated phytosociological relevés at permanently marked locations over many decades, which allow us to analyze trends in diversity of species and species groups (such as Ellenberg indicators or plant functional types). Besides detecting gradual changes, phytosociology expresses succession as a change of community types. Where many permanent plots conform to the same rules, succession can be generalized into temporal gradients and/or sequences of community types (seres). However, many phytosociological succession models have been based on comparative observation (space-for-time substitution) rather than real time series. Larger groups of old relevés without permanent marking are sometimes used to detect succesional trends by making new relevés in the supposed old positions ('quasi-permanent plots') and by detecting systematic differences between old and new data.

Repeated mapping may reveal changes in the spatial delimitation of vegetation units and allow representation of succession in a transition matrix. However, its validity crucially depends on fully operational mapping keys that unequivocally define the criteria for drawing boundaries between types.

Nature Conservation

The conservation of species depends on the maintenance of their habitats. Habitat classifications can be founded on structural or abiotic features, but they are often based on syntaxa, conveying a summary of ecosystem properties that are difficult to measure or model. Preserving the diversity of extant plant communities is thought to safeguard the survival of typical species not only of plants, but also of animals, fungi, and microorganisms, and the maintenance of current ecosystem processes.

In Europe, phytosociological units were important in defining habitats (biotopes) in the CORINE and EUNIS systems, which contain a comprehensive classification of European habitats. The CORINE classification provided the basis for inclusion of habitat types under the Habitats Directive of the European Union, the most powerful legislative instrument for nature conservation in Europe. In the Union-wide conservation network Natura 2000, phytosociologically defined habitat types are crucial for the delimitation, inventory, monitoring, and management of protected areas.

In landscape planning and policy making, phytosociological units are used to underpin normative judgments and set conservation priorities by evaluating their naturalness and endangerment. Naturalness, or its reciprocal concept, hemeroby, ranks communities by the strength of human influence and consequent alterations of species composition, structure, and ecological processes. Methodologies range from assigning community types to classes of naturalness to complex evaluation schemes taking detailed account of community features.

Reporting the degree of threat to the habitats of a region, red lists of plant communities are another potentially powerful policy tool in nature conservation. Compilation of red lists presupposes a comprehensive and well-established phytosociological classification for the target region, including detailed knowledge about distribution, commonness, and temporal trends of syntaxa. With the advent of phytosociological databanks and GIS, red list compilation is moving from pure expert judgment to a process driven by relevé data and rule-based decisions on the vulnerability and conservation value of plant communities. While vulnerability considers current distribution, quantitative development in the past, and foreseeable threats in the future, conservation value may be based on the frequency and status of component red-listed plant species, naturalness of the inhabited sites, and responsibility of the target region for the global preservation of a syntaxon. The combination of vulnerability and conservation value may be used to set reasonable priorities for conservation measures.

See also: Application of Ecological Informatics; Artificial Neural Networks: Temporal Networks; Association; Biodiversity; Biotopes; Community; Dominance; Ecological Niche; Ecosystem Ecology; Ecosystems; Environmental Protection and Ecology; History of Ecology; Intertidal Zonation; Ordination; Plant Demography; Plant Ecology; Principal Components Analysis; Scale; Seasonality; Spatial Models and Geographic Information Systems; Statistical Prediction; Succession; Synecology.

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Pioneer Species

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Introduction

In early ecological literature, the term pioneer was used to describe those plant species that initiate community development on bare substrate (primary succession). More recently, usage of the term has included microbial and invertebrate taxa, and describes the first colonists of sites affected by less extreme disturbance which undergo secondary succession. Pioneers of primary and secondary successions share some traits; in both cases colonization of new habitat depends on effective dispersal, which generally selects for high reproductive output and small propagule size. However, differences in resource availability between these habitat types result in different opportunities for growth and reproduction. Few species can be successful on both primary and secondary successions.

Pioneers in Primary Succession

Primary succession occurs when extreme disturbances, such as landslides and volcanic eruptions, create new habitats by removing or covering existing vegetation and soil. Pioneers that initiate primary succession must be able to establish and grow on substrates that are nutrient poor and that often have unfavorable moisture conditions. The most extreme sites are exposed unweathered rock surfaces. Here, colonization may be limited to cyanobacteria ('blue-green algae'), lichens, and bryophytes, with no further vegetation development. Somewhat more nutrient-rich conditions associated with weathered or fragmented bedrock surfaces, such as the scree slopes of landslides, are often dominated by tree species. Sites still richer in mineral nutrients, which may contain some residual organic soil, such as the depositional zones of glacial moraines, in turn are often colonized by herbaceous species and grasses with faster growth rates (**Figure 1**).

For pioneers in primary successions, nitrogen is often the most limiting resource. Unlike other mineral nutrients that can be released through weathering of underlying rock, nitrogen must either be transported to primary successions through leaching and deposition, or fixed *in situ*. Some of the most inconspicuous pioneers on exposed rock faces are nitrogen-fixing cyanobacteria. Rates of nitrogen fixation by cyanobacterial 'biofilms' on rock surfaces may be considerable; thus, nitrogen-rich leachate from these surfaces may affect community development at down-slope sites. Cyanobacteria may also form symbiotic associations with lichens (e.g., *Stereocaulon* spp.).