

# Classification of Biogeographical and Ecological Phenomena

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## 5.1 INTRODUCTION

Biogeography is a highly interdisciplinary discipline, and one of the fields to which it is strongly linked is ecology. Therefore, the classification approaches of both disciplines should be reconsidered together. According to a commonly accepted definition, biogeography analyzes spatial distributions of organisms in the past, at present, and in the future, taking into account different scales. According to the first definition of ecology, by the zoologist Ernst Haeckel in the year 1866, it is the science of the relations of organisms among themselves and to their surrounding environments, but a modern textbook (Begon et al., 1996) states that ecology deals with 'the distribution and abundance of different types of organism over the face of the earth, and about the physical, chemical but especially the biological features and interactions that determine these distributions and abundances; see also Begon et al. (2006).' As a consequence it is clear that we now consider there to be a broad overlap between biogeographical and ecological topics.

We introduce classification approaches for species, species groups, functional groups, communities, community groups, habitats, biomes, biogeographical realms, ecozones, and ecoregions. We regard classification as a tool for structuring data—in our case, especially data with spatial relevance. The aim of classification is to

obtain groups of objects in discrete classes (often in a hierarchical structure). Within a given group, the objects are homogeneous, allow group-specific generalization, and are distinct from those in other groups. Classification can start from the entity (divisive classification) or the single elements (agglomerative classification). The most common and often most successful approach is the divisive-polythetic one (polythetic = referring to many elements, e.g., species). Ecological and biogeographical data can be compared by univariate procedures (regarding only one factor) or by multivariate procedures with different variables (ordination). The latter are not classification *sensu stricto* but help to understand, for example, different clusters of classification. As biogeographical and ecological elements 'from the community to the biome' often follow gradients, there is no one 'true' and no single classification, but mostly there are several possible ways to typify elements. The same is true for the scale problem: not all classification types are appropriate for all scale levels. In this chapter we concentrate on terrestrial systems and deal with both fine-scale and broad-scale views.

There is no doubt that progress in the area of taxonomic classification is essential for biogeographical and ecological research. The following question arises: how useful is classification, from the level of communities up to the level of the whole geobiosphere, for answering biogeographical questions?

## 5.2 TAXA-BASED CLASSIFICATION

### 5.2.1 Introduction

The diagnosis of the structure of area systems and the evolutionary, historical, and/or ecological reasons for taxa distribution patterns are investigated by the discipline of chorology. The basic elements for classification are taxa and their geographical ranges (areas of distribution) or groups of taxa with similar geographical ranges (area types). Factors limiting geographical ranges are not only floral and faunal history and climate, soil, and topographical boundaries but also dispersal limits and, in the case of plant species, for example, herbivore attacks (Bruehlheide and Scheidel, 1999), or, in the case of animals, for example, the lack of specific food resources. Nowadays, attention is focussed especially on the dynamics of invader-area systems and area dynamics caused by global change.

Taxa-based hierarchical classification systems refer to floral and/or faunal contrasts. The contrast is calculated by summing up the taxa occurring in area A but not in area B, and vice versa. Calculations for sections of 100 km<sup>2</sup> between areas A and B allow a specific gradient to be determined.

The similarities of species composition in specific areas are worked out, for example, by cluster analysis and other numerical classification approaches. Molecular data give new insights into taxa differentiation and distribution (Heywood and Watson, 1995; Cox and Moore, 2005).

### 5.2.2 Historical aspects

Centuries ago, the 'fathers of zoo- and phytogeography', Georges-Louis Leclerc de Buffon, later Comte de Buffon (1707–88), and Gottfried Reinhold Treviranus (1776–1837), described species formations in different parts of the world and tried to classify the distribution and structural pattern (see 'classical papers', compiled by Lomolino et al., 2004; Schroeder, 1998 and references therein). Buffon was the first to recognize the regional biogeographical differentiation of species in what is now referred to as Buffon's law. What is not commonly known is that Treviranus (1803) had already elaborated the first classification of eight main flora types: Nordic (plant species found in the Old and New World north of 50°N); Virginian (North America between 50°N to 35°N); West Indian (Americas between 35°N and 35°S); Orient (Eurasia from the Mediterranean to Japan, but excluding southeast Asia); East Indian (southeast Asia); Africa (Africa); Austroasian

(Australia and the Pacific islands, excluding New Zealand); and Antarctic (South America south of 35°S and New Zealand).

### 5.2.3 Phytogeographic and zoogeographic regions of the world

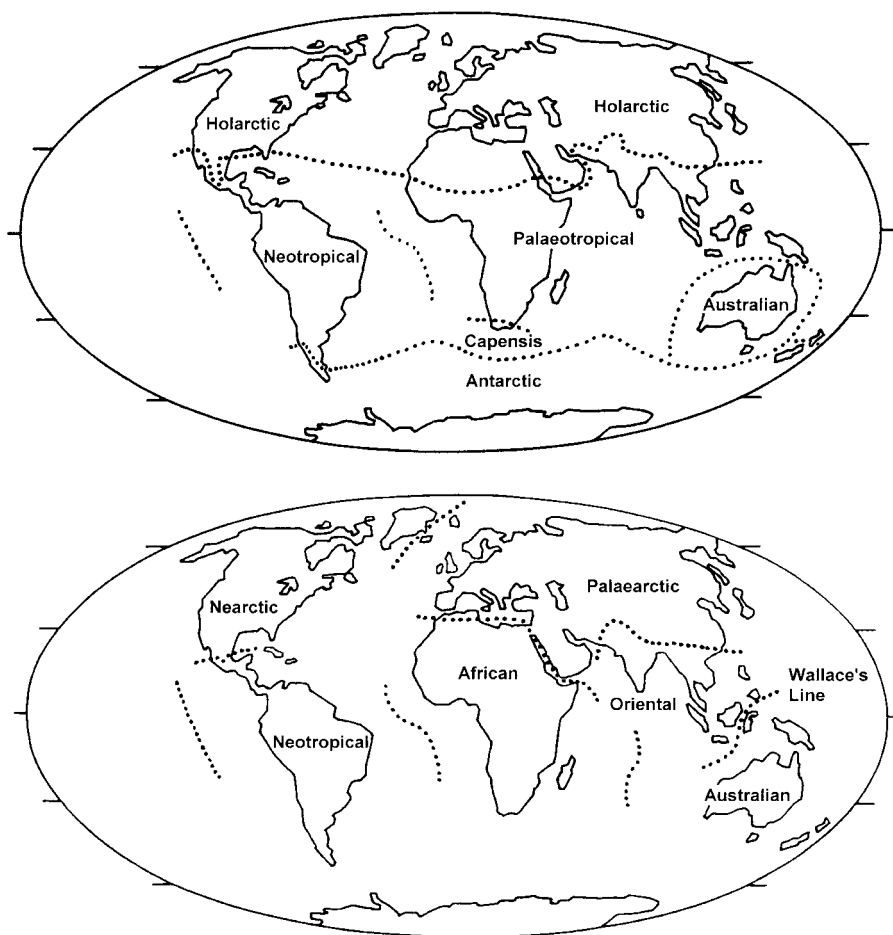
Linking traditional taxa-based phyto- and zoogeographical maps to form one unified biogeographic map of the world is problematic, as the dispersal mechanisms and evolutionary characteristics are different in each taxonomic group. Therefore, we introduce phytogeographic and zoogeographic regions of the world (i.e., for vascular plants and mammals) in two different maps (Figure 5.1). Unified biogeographic maps are possible if mainly structural elements are in focus, as in the case of biomes (see Section 5.6).

### 5.2.4 Phytogeographic classification

As a result of its younger earth history, floral exchange was possible in the northern hemisphere up to the start of the Pleistocene period. The similarities are so strong that North America and northern Eurasia form the Holarctic floral kingdom. The differences between the tropical areas are considerable and there are two distinct Neotropical and Palaeotropical kingdoms. The same is true for the southern part of Africa (Capensis kingdom) as well as for the Australian and Antarctic kingdoms. There are large transition zones, especially between the Holarctic and Neotropical kingdoms. The lines of evidence for this differentiation including the Capensis kingdom refer to Rikli (1913).

The nomenclature for the hierarchically divided subsystems, from broad scale to fine scale, is: kingdoms, regions, subregions, provinces, subprovinces, districts, and subdistricts. The districts are characterized by floral elements. In Europe, for example, the Arctic, Boreal, Atlantic, Central European, Mediterranean, Pontic, and Turanian floral regions can be distinguished. Combinations with orographic characteristics (e.g., boreoalpine) and the use of 'eu-' and 'sub-' prefixes (e.g., eu-, subatlantic) are used for further differentiation. The regions are differentiated with chorological groups of species, which form similar distribution clusters. Many examples of different area types are presented in the classical chorological atlas of Meusel et al. (1965 ff).

Meusel et al. (1965 ff) identified ten floral belts globally, which correspond to latitudinal belts (i.e., arctic, boreal, temperate, submeridional,



**Figure 5.1** Phytogeographic (1a) and zoogeographic regions (1b) of the world; 1b refers mainly to mammals (modified from various authors)

meridional, boreosubtropical, tropical, austrosubtropical, australic, antarctic). They are modified by gradients of continental and maritime climates. Floral kingdoms and floral belts can be combined. In Eurasia, for example, the biogeographical relations between the boreoalpine and the boreal element *sensu stricto* are strong, not only for the flora but for the bird fauna as well, reflecting the shared floral and faunal history. This was, for example, worked out by Mattes (1988), comparing the subalpine *Picea abies*- and *Pinus cembra-Larix decidua* forests of the Central Alps with boreal forests. The forests of the Alps share 72% of its bird species with the boreal zone of northeastern Fennoscandia, but on the level of subspecies the areas are more separated (only 51% shared taxa).

Other authors use 'centers of plant species endemism' for a subdivision of areas (phytochoria); this approach has been used in South America, Africa, Asia, and New Zealand by various authors (see references in Jäger, 1995).

### 5.2.5 Zoogeographic classification

In comparison with the floral kingdoms, the zoogeographical regions are more differentiated in the case of the Holarctic (Nearctic and Palaeartic are specified as distinct regions by different authors, for example, de Lattin, 1967; Morrone, 2002; Cox and Moore, 2005) and the palaeotropical region (African and Oriental), but there is no separate zoogeographical region

corresponding to the Capensis floral kingdom. Wallace's Line between the Australian-Oriental region corresponds to a remarkable faunal boundary. The differentiation was mainly worked out by Philip Lutley Sclater in the year 1858 and Alfred Russel Wallace in 1876 (see Lomolino et al., 2004 and references therein). In general the differentiation of the two regions on either side of Wallace's Line is strongly taxa-based (in this case, mammal taxa).

If so-called wandering families of mammals (i.e., those with mainly worldwide distribution, e.g., sciurids and leporids) are excluded from the analysis, the interrelationships of the terrestrial mammal families show that especially high specificity characterises the African, Neotropical, and Australian regions, in which 16, 15, and 10 families, respectively, are not shared with any other region (Cox and Moore, 2005: Figure 9.3). The nomenclature of the hierarchically ordered classification from broad-scale to fine-scale is similar to phytogeography: for instance, subregions and provinces are subdivided. However, the term 'district' is not used in a uniform manner.

The nomenclature of faunal elements follows on the one hand the actual area types, an approach that is widely accepted. On the other hand, and often hypothetically, historical-genetic analysis is used (de Lattin, 1967; subsequently adapted by Müller, 1974). 'Centers of taxa dispersal' (i.e., centers of taxa origin and/or differentiation) are distinguished (e.g., holomediterranean faunal element, including refuge areas). This is confusing and criticized by some authors (Cox and Moore, 2005). The assumption that present-day biodiversity hot spots of certain taxa have been the cores for radiation of wider areas is problematic (see, for example, the discussion of the 'New Zealand school of panbiogeography' summarized in Cox and Moore, 2005).

### 5.3 STRUCTURE-BASED CLASSIFICATION AND FUNCTIONAL-ECOLOGICAL APPROACHES

#### 5.3.1 Plant growth forms, life-form types, and functional types

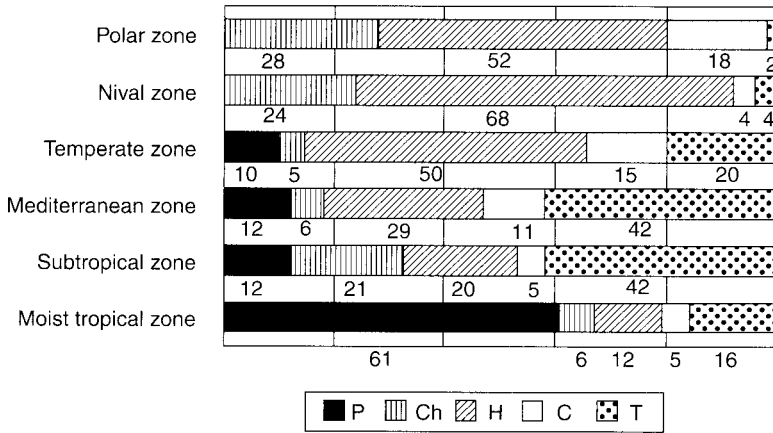
The physiognomy of plants, their specific growth form, had been recognized early as a classification feature, which makes it possible to describe structural types without identifying the specific taxa and therefore to work out global comparisons, for example, of neo- and palaeotropical rain forests with markedly different taxa. Alexander von

Humboldt (1769–1859) in 1805 had already differentiated growth forms such as palms, banana form, malvaceous form, bombaceous form, mimosa form, heather, cactus form, orchids, casuarinas, conifer, arum form, lianas, aloe form, grass form, ferns, lilies, willow form, myrtle form, Melastoma form, and laurel form (see Lomolino et al., 2004).

Growth forms can hardly be regarded without considering functional aspects of adaptation—for instance, to water or salt stresses, extreme temperatures, and wind. Such adaptation strategies lead to similarities of growth forms in different plant taxa. In 1855 Alphonse de Candolle proposed, in his *Géographie botanique raisonnée*, that the main factors influencing the distribution of plant growth forms are heat and drought tolerances of plant species; he had already differentiated types according to temperature and moisture requirements (e.g., Megatherms in the case of high temperature and sufficient moisture, and Mesotherms in the case of moderate temperature and moisture; see Archibold, 1995 and references therein). In retrospect he was the first person who identified physiologically adapted plant forms, which we now call plant functional types (PFTs).

The understanding of growth forms and their ecological significance was reinforced in particular by Eugen Warming from 1895 onwards, and by Andreas F.W. Schimper (1898). Warming (1909) wrote "the greatest advance, not only in biology in its wider sense, but also in oecological phytogeography, will be the oecological interpretation of the various growth forms."

Christen Raunkiaer drew up a system of plant life-form types in 1904, which considered in particular plants' strategies to survive cold or dry periods during a year. This system was later supplemented by Ellenberg and Mueller-Dombois (1974, see references therein). Raunkiaer divided plants into phanerophytes (trees and shrubs), chamaephytes (dwarf shrubs), hemicryptophytes (buds are protected by the litter layer), cryptophytes (storage organs persist in the soil), therophytes (regenerate from seeds), and helo-/hydrophytes (storage organs persist in swamp or water); phanerophytes may be subdivided into phanerophytes *sensu stricto* (trees) and nanophanerophytes (shrubs). Therophytes are often seed-bank species. There are remarkable relations between climatic types and life-form spectra; for example, therophytes are favoured not only in (semi)-deserts with episodic precipitation but also by mediterranean climates with a seasonal change between the wet west-wind and dry trade-wind zone (Figure 5.2). The plant life-form types already bridge structural and functional aspects. In their functional characteristics communities are



**Figure 5.2** Raunkiaer’s plant life-form spectra from different regions of the world (from Kratochwil and Schwabe, 2001). P, Phanerophytes; Ch, Chamaephytes; H, Hemicryptophytes; C, Cryptophytes; T, Therophytes.

comparable, which are floristically dissimilar but have the same traits and trade-offs.

In plant and vegetation ecology, the importance of functional aspects of classification has been discussed extensively since the 1970s, having mainly been inspired by Grime’s (1974) proposed triangular model of competitors, stress-tolerant species and ruderal-strategists (the C-S-R-model), the latter occurring in open, disturbed habitats. Many authors have discussed this model, and there is some agreement that only three and some combined strategies: C-R, S-R, C-S (see Grime, 1979) is a simplification of the reality (e.g., Ellenberg, 1996; Wilson and Lee, 2000 and references therein). Nevertheless, the C-S-R-model had stimulating results for vegetation classification and, especially, in understanding the effects of grazing (intermediate levels of C-S-R) and spontaneous succession (increase of competitors).

To identify the type of function it is useful to differentiate between two types of functional groups:

1. guilds *sensu* Root (1967), which are linked to resource use (see below),
2. PFTs, which in a wider sense are groups of plants with similar structural and functional characteristics.

Meanwhile, extensive trait bases for plant species with functional characteristics were worked out in some parts of the world (e.g., LEDA trait base for the northwest European flora; Walker et al., 2005

for the Arctic vegetation map). Genome sizes may be important characteristics for PFTs, for example, in the total angiosperm sample woody growth form is characterized by a smaller genome size compared with the herbaceous growth form (Ohri, 2005). Life-form types and other different traits can be used for classification, if the data are linked, for example, with relevés (see below). Box (1996) proposed a system of 15 dominant plant structural-functional types, which explains the main global vegetation pattern of mature ecosystems and is compatible with the biome classification by Walter and Breckle (1999) (see below). Plant functional types may be linked to climate change processes (Woodward and Cramer, 1996). In general, there is a need for a unified global framework for PFTs.

### 5.3.2 Animal life-form types, functional groups, and guilds

Adapted to specific environmental conditions and with similar structural, physiological, developmental, and/or ethological features, different organization types (structural types) of animals are characterized as life-form types. Species of the same life-form type—in many cases with no phylogenetic or systematical relationship—have evolved convergences (convergent evolution) and, analogously, adaptations according to a corresponding similarity in environmental selection pressures (adaptive syndrome).

Animal life-form types may be specified according to the following:

1. different locomotion: for example, sessile, hemisessile, and vagile animals; the latter can be burrowing, climbing, creeping, jumping, running, or flying with many subtypes;
2. different foraging or feeding mode: for example, particle feeder: suspension feeder, filterer, tentacle feeder; substrate feeder; sap feeder: licker, piercer-and-sucker; macrophageous animals: 'swallower', comminutor, decomposer; collector, grazer, predator; and
3. different substrate: 'pedo-, geo- and phytophilous animals'; for example, limicolous animals (mud), terricolous a. (ground/soil: epi-, endo-, mesogaion), arenicolous a. (sand: epi-, endo-, mesopsammon), herbicolous a. (on plants: epiphytobios, in plant tissue: endophytobios), lignicolous a. (on dry trunks: epidendrobios, in woody tissue: endodendrobios).

Hundreds of different life-form types are present, for example, in forests (including soils), with the key importance of invertebrates. Therefore, it is not possible to give a scientifically satisfying worldwide overview in a table or figure.

In animal ecology a functional group refers to species groups with similar structural and functional characteristics; they may be grouped, for example, according to similar locomotion mode (see above). This definition corresponds to the PFTs in the wider sense (see above).

Guilds *sensu* Root (1967) are composed of species with similar resource utilization (e.g., phytophageous animals with the subtypes sap feeder, ectophageous leaf-eater, or miner). Guild classifications were elaborated, for example, for soil predators, for flower-visiting insects, for different groups of birds and mammals (see Kratochwil and Schwabe, 2001 and references therein). Especially the guild concept *sensu* Root (1967) leads to structural and functional insights and—in view of the enormous species richness—it is mostly linked to taxonomic groups, such as ungulate browsers versus grazers in the savanna biome, semiaquatic herbivore mammals, flower-visiting bees feeding on nectar and pollen, and so forth. Unfortunately, for many existing guild classifications it is unclear what concept the classification is based on (Wilson, 1999).

### 5.3.3 Formations

Heinrich August Grisebach was the first to differentiate the vegetation of the earth according to physiognomic types, which he called 'formations'. In 1838 he defined a phytogeographical

formation as a group of plants that built up a physiognomic type, for example, a meadow or deciduous woodland. These formations are characterized either by only one dominant species or by different species of the same physiognomic type. There are numerous formation classifications of the Earth, for example, those elaborated by Schimper (1898); Rübél (1930); Whittaker (1970, 1973); and others. These formation types are integrated in the biome approach (Section 5.6).

## 5.4 COMMUNITY-BASED CLASSIFICATION

### 5.4.1 Clarifying terminology

Groups of different species or species-groups that occur regularly together in a spatially limited area are defined as coenosis or community; both terms do not imply any hierarchical rank. Most of the species interact and form the biotic part of an ecosystem. As a general term for the occurrence of different species in a certain spatial unit—either with or without interspecific relations—the word 'assemblage' is proposed. Some authors use 'community' and 'assemblage' synonymously (e.g., Cox and Moore, 2005). Other authors suppose that plant communities have no fixed boundaries (see discussion in van der Maarel, 2005).

The term 'biocoenosis' was first described by Karl August Möbius in 1877, including the specification that all organisms in a biocoenosis require one another. Since then a biocoenosis has come to be seen as a species composite in which the individuals have similar requirements for abiotic and biotic conditions at a site. Interactions occur, at least for some of the species. Trophic relations between the individuals are concentrated in the biocoenosis, but not fully restricted to it. In particular, most of the animals of a biocoenosis, as well as the cryptogams and microorganisms found in it, depend on the structure built up by the plants (Kratochwil and Schwabe, 2001). Corresponding to this definition, a phytocoenosis is characterized by a definable and repeated grouping of plant species, which reflects the abiotic and biotic site conditions (including anthropogenic factors such as grass mowing, management of forests, harvesting or anthropo-zoogenic factors as livestock grazing). A classification for the phytocoenosis-part of a biocoenosis is possible, and we will introduce some approaches. The zoocoenosis has to be divided into different zootaxocoenoses with reference to the phytocoenosis, to parts of the phytocoenosis or to vegetation complexes. Such parts may be different strata (e.g., litter layer,

components of woodland and forest structure such as canopy, understorey) or minor habitats (choritope = biochorion, e.g., tree stumps).

Ten years before Tansley (1935) introduced the term 'ecosystem', Sukatschew (1926) combined the biocoenosis and the abiotic site conditions (clima-, hydro-, pedo-, and edaphotope) in the term 'biogeocoenosis'. A biogeocoenosis is defined as the complex of homogeneous natural environmental factors covering a distinct part of the Earth's surface (atmosphere, rock, soil, hydrological conditions, vegetation, animals, and microorganisms). According to Sukatschew, the 'biogeocoenosis' represents, as a classification unit, the result of biotic and abiotic interaction emphasizing climatological, hydrological, pedological, and geological factors. In contrast, the ecosystem describes a functional and dimensionless unit consisting of biotic and abiotic characteristics and processes. Flows of energy in food webs with producers, consumers, and decomposers and cycling of carbon, mineral nutrients, and water characterize the open systems and should guarantee ecosystem functioning. In principle, ecosystems are not objects for classification.

### 5.4.2 Classification of plant communities

#### Historical aspects

Theophrastus (372–287 BC) in his *Historia Plantarum* had already described the regular occurrence of different plant species at particular sites. The first steps toward the modern investigation of plant communities were made especially by Warming in 1895; Schroeter and Kirchner in 1902 (see Westhoff and van der Maarel, 1973), Sukatschew (1926), and Braun-Blanquet (1928). In the 1920s a controversy was initiated between the approaches of Clements (1916) and Gleason (1926). Clements was convinced that communities are so strictly organized that they act like a 'superorganism' and can only survive if the specific organisms coexist. Gleason (1926) believed just the opposite with his individualistic concept. The superorganism-concept has been fully rejected (first by Tansley, 1939; see Austin, 2005 for a modern view), but there is evidence—documented by many research results—that community structures exist (see, e.g., Westhoff and van der Maarel, 1973; Ellenberg, 1996; Rodwell et al., 2002; van der Maarel, 2005). However, there are assemblages without community structure, for example, pioneer stages on disturbed sites as road margins or debris accumulations with a lot of stochastic dispersal processes in the course of recovery by

plant and animal species. Another example for such assemblages without community structure is insects, flying in the night close to a lighting system.

In continental Europe and Russia in particular, plant community-based classification systems had been elaborated as early as the first half of the twentieth century, based on relevé samples with exact floristic census and cover-abundance scales (e.g., the Braun-Blanquet method with character plant species; see, e.g., Knapp, 1984 and references therein). The latter method has now become widely used globally.

#### Different classification approaches for plant communities

There are differences in classification systems with respect to the importance of the analytical characteristics 'dominance' and 'character species', which had been compiled, for example, by Whittaker (1973) and Westhoff and van der Maarel (1973). The vegetation classification based on dominant species was established by Ragnar Hult, Rutger Semander, and Einar Du Rietz between 1881 and 1921 and used in the Scandinavian and Baltic areas. It is mostly applied to communities that contain few species but have extensive layers of dominant species, and hence are differentiated according to the dominant plant species. The basic unit is the 'sociation', defined by a homogeneous species composition with dominant species in each stratum of the vegetation (e.g., *Pinus sylvestris-Vaccinium myrtillus-Cladonia alpestris*-Sociation). Aimo Cajander in Finland developed a system from the year 1909 onwards by using the field layer in a forest as the indicator for abiotic conditions. The vegetation types of the 'Russian School' of Sukatschew (1926) and other authors are also defined by the dominance of species: the term 'association' corresponds here to the Scandinavian sociation (see Westhoff and van der Maarel, 1973 and references therein). From 1980 onwards the floristic association concept has been widely adopted in the (former) Soviet Union (Korotkov et al., 1991).

The floristic association concept, with its first representatives being Schröter and Flahault (see Westhoff and van der Maarel, 1973 and references therein), was mainly established by Josias Braun-Blanquet and was later called the 'Zürich-Montpellier school'. Already Flahault and Schröter (1910) defined the association "as a plant community type of definite floristic composition, uniform habitat conditions, and uniform physiognomy." The Braun-Blanquet approach was elaborated in species-rich communities, especially in the Alps, and is based on floristic similarities between plot areas, which are sampled by relevés

(all occurring plant species and macroscopic cryptogams). Relevés are made in the field in homogeneous plots, which differ in size according to the structure (richness in strata) and species richness of a community type, using the Braun-Blanquet cover-abundance scale (Braun-Blanquet, 1928, 1964). For vascular plant communities the minimal areas range from 0.5 l m<sup>2</sup> (Lemnetea communities) to about 10,000 m<sup>2</sup> in tropical rain forests (further data are given by Braun-Blanquet, 1964; van der Maarel, 2005). The relevés are grouped according to their floristic similarity (today by polythetic-divisive approaches, such as TWINSPLAN, or by multivariate ordination, see below).

A hierarchical system of character and differential species is the fundamental principle of the Braun-Blanquet approach. The basic unit is the association: the lowest-level unit in a hierarchical system that still has its own character species. A character species should be restricted to a particular, defined phytosociological unit, whereas differential species indicate special, for example, abiotic factors, such as soil moisture and nutrient supply. The highest-level phytosociological unit is the class (ending -etea), followed by the order (-etalia), the alliance (-ion), and the association (-etum). Subassociations and the lowest-level unit (variant) only have differential species (see Pignatti et al., 1994). All levels from class to association have their specific character species. The general term for types at all hierarchical levels is 'syntaxon'. As an example from the vegetation of eastern Siberia, the following syntaxa have been identified or described: Festuco-Brometea, Thymetalia gobici, Festuco-Thymion gobici, and Hemerocalletum minoris (Korotkov et al., 1991).

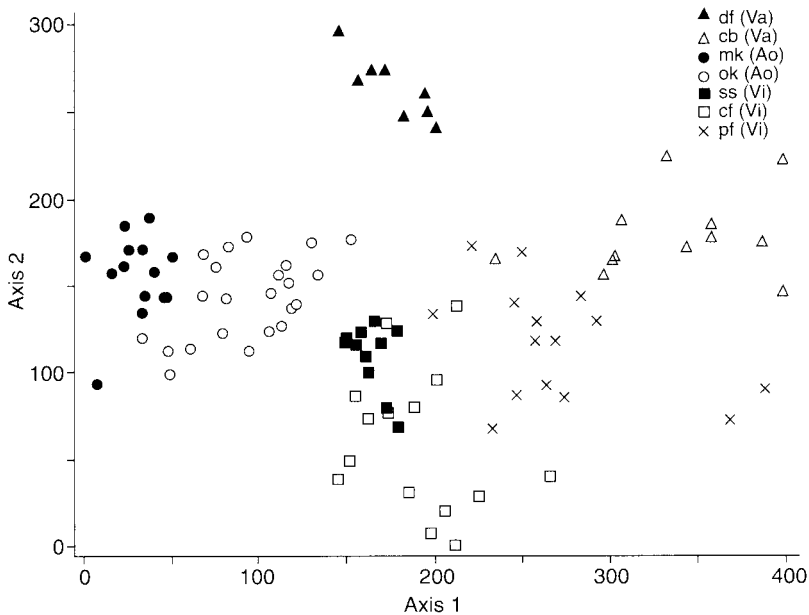
In handbooks of phytosociology (e.g., Ellenberg, 1963, 1996; Wilmanns 1973, 1998) the order of plant communities in the books follows the 'sociological progression': from simply structured types with one stratum (e.g., Lemnetea) to structurally diverse woodland types. Ellenberg (1963, 1966) and Wilmanns (1973, 1998) combined the sociological progression with formations in the course of their books, which are both excellent examples for a combination of the Braun-Blanquet classification approach and the functional-ecological aspects.

Ellenberg (1974, 1992) developed a system of 'indicator values for vascular plants' based on the large central European phytosociological databases and the relative abundance of species in specific communities in the field. For the parameters that follow here, moisture, light, temperature, continentality, soil reaction, salts, and nitrogen, there are relative values (mostly on 9- to 12-part scales: higher numbers indicate the higher intensity of the factor) for each plant species. In phytosociological relevés it is possible to calcu-

late the quantitative or qualitative value of the whole relevé (according to either cover/abundance or presence/absence data of each plant species). In the case of moisture and soil reaction values in particular, the approach reflects quite well the abiotic conditions. Meanwhile, such indicator values are available for different countries in Europe: for example, Italy (Pignatti et al., 2005), the southern Aegean region (Böhling et al., 2002), Hungary (Borhidi, 1993), Switzerland (Landolt et al., 2010), Poland (Zarzycky, 1984), Great Britain and Eire (Hill et al., 2004), and the Faröe Islands (Lawesson et al., 2003). There is also some criticism, for example, concerning the nitrogen values (which are values for soil fertility according to Hill et al., 1997, 2004; or in some systems for phosphorus, Chytrý et al., 2009) and the empirical data for nutrient values are often insufficient. Further, there are pitfalls that indicator values may interact and certain processes cannot be separated (Schwabe et al., 2007). On the other side many authors have shown that the pH-gradient correlates well with the R-values (e.g., reviewed by Diekmann, 2003; see also Schaffers and Sýkora, 2000). Nevertheless, the approach helps to develop generalizations (van der Maarel, 1993) and is especially useful to interpret ordinations and to use the values as benchmarks (Hill et al., 2004). In Figure 5.3 we present an example of dry grassland from three separated valleys in the southern inner Alps in Italy. According to macroclimatological data (Schwabe and Kratochwil, 2004) gradients of moisture, temperature, and continentality in particular should be reflected by the indicator values. A Detrended Correspondence Analysis (DCA) of about 90 Braun-Blanquet relevés of 50 square-meter-plots is shown in Figure 5.3a. The net diagrams of the average indicator values of the plots and communities underline the xero-mesothermic gradient on axis one. The upper parts of axis two are characterized by more mesohygic conditions. The net diagrams (Figure 5.3b) explain decisive factors for the position of the communities (Pignatti et al., 2005; Schwabe et al., 2007). This data set was also applied to compare relevés from 1990 to 1995 with older ones of Braun-Blanquet, sampled from 1930 to 1950 (Schwabe et al., 2007), and has shown high stability of the dry grassland communities; it is useful not only for spatial but also for temporal approaches.

Criticisms of the Braun-Blanquet method refer mainly to possible observer bias in sampling and classification (Westfall et al., 1997). This can be excluded by improved objectivity (e.g., by representative sampling, no selection of plot areas with specific species) and by polythetic-divisive classification methods. Nonetheless, in the case of rare types (e.g., rock-fissure vegetation), preferential sampling is necessary and objectivity is



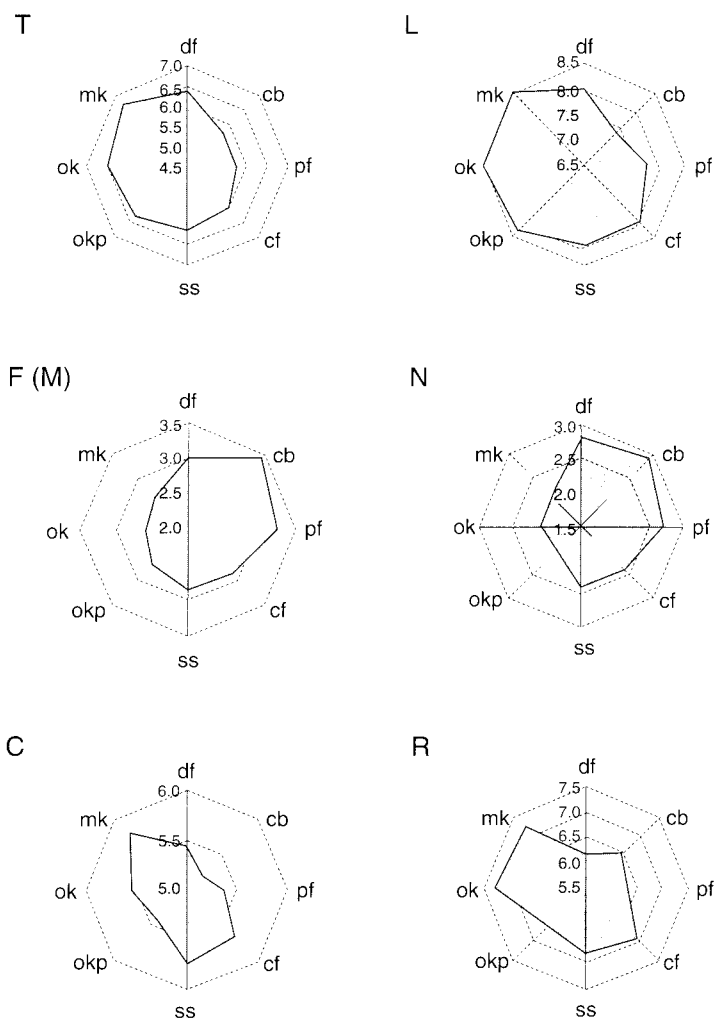


**Figure 5.3a** DCA of dry grassland communities in a climatical gradient of the inner Alps. Valleys: Va Valtellina, Ao Valle d'Aosta, Vi Vinschgau, Valle Venosta. Small letters refer to distinct plant communities: mk, *Melico-Kochietum prostratae*; ok, *Onosmo-Koelerietum vallesianae* (okp acidophytic subassociation); ss, *Stipo-Seselietum variae*; df, *Diplachno-Festucetum valesiaca*; pf, *Poo-Festucetum valesiaca*; cb, *Centaureo-Brachypodietum*. Eigenvalues axis 1: 0.53, axis 2: 0.28 (from Schwabe et al., 2007)

compromised. Because of this difficulty, the method had not been widely adopted in Britain and the United States up to the 1980s. Heywood and Watson (1995: 97) stated, "Outside continental Europe, phytosociology has attracted less interest and as a result much less is known about the types of vegetation." Nevertheless, various phytosociological publications originated from Great Britain as early as 1955 (Poore, 1955a, 1955b) and later (e.g., Shimwell, 1968 and others). Since then an elaborated classification system has been developed by Rodwell (1991–2000), covering all British plant communities in five volumes according to a National Vegetation Classification (NVC) summarizing 35,000 relevés. This classification is used in, for instance, the journals of the British Ecological Society. The plot areas are chosen solely on the basis of homogeneity. The communities are grouped into 12 differentiated formations: woodland and scrub, mires, heaths, and so forth, and are named according to diagnostic species, for example, *Fraxinus excelsior*–*Acer campestre*–*Mercurialis perennis* woodland.

In the United States, meanwhile, a Vegetation Classification Panel was set up by the Ecological

Society of America and adapted by the Federal Geographic Data Committee (National Vegetation Classification, see also Grossman et al., 1998). The classification is based on a system with higher-level floristic-physiognomic units (alliances) and lower-level floristic units (associations). The definition for association used here combines floristic and physiognomic aspects: "A vegetation classification unit defined on the bases of a characteristic range of species composition, diagnostic species occurrence, habitat conditions and physiognomy." In general the Braun-Blanquet approach is more floristically defined than the U.S. system, but the two approaches overlap to a considerable extent regarding the associations and alliances, with the exception that there are no fixed endings in the U.S. system. Here is an example for the U.S. system: Formation: Temperate Grassland, Meadow and Shrubland, Alliance: *Sporobolus heterolepis*–(*Deschampsia caespitosa*, *Schizachyrium scoparium*) herbaceous alliance, Association: *Sporobolus heterolepis*–*Schizachyrium scoparium*–(*Carex scirpoidea*)(*Juniperus horizontalis*) herbaceous association.



**Figure 5.3b** Net diagrams of the average of Pignatti-Ellenberg indicator values of the data set of Figure 5.3a. T, Temperature; L, Light; F(M), Moisture; N, Nutrients; C, Continentality; R, Reaction. The T values of mk, ok, df reflect the top position of the summer hot valleys, additionally df (near Lago di Como with insubric climate) shows higher F (M) values. The highest L values are present in the very open communities of mk and ok. The intrinsic parts of Ao and Vi show the highest C values. Reaction values reflect quite well the acidity of the substrate. Communities with higher soil moisture show higher N values (interaction of two types of indicator values) (from Schwabe et al., 2007)

National vegetation classifications using the Braun-Blanquet approach are available for different countries. For example, in the Netherlands there is a nearly complete census of all plant communities and their distribution with an excellent phytosociological database of more than 300,000 relevés and a permanent plot system (*De Vegetatie van Nederland* 1995 ff.). Large amounts of

summarized data also exist, for example, for Japan (e.g. Miyawaki, 1980–1989), Austria (e.g., Willner and Grabherr, 2007), the Czech Republic (Chytrý, 2007), Hungary (Borhidi, 1996), Germany (Oberdorfer, 1977 ff.; Dierschke et al., 1996 ff.), France (e.g. Géhu, 1973; Julve, 1993), Italy (Biondi et al., 1997), Romania (e.g., Coldea et al., 1997) Spain and Portugal (e.g., Rivas-Martínez

et al., 2001), and South Africa (Mucina et al., 2000; Mucina and Rutherford, 2006).

The 'European Vegetation Survey' (Rodwell et al., 2002) summarizes the phytosociological alliances for Europe; and the Prodrromus of Korotkov et al. (1991) summarizes the syntaxa for the territory of the former Soviet Union.

Numerical and multivariate methods have become available for the ordination and classification of vegetation relevés. As ordination methods, principal components and correspondence analysis are used as well as multidimensional scaling (MDS) and nonmetric MDS (NMDS). An example for a DCA for species-rich communities with a clear gradient is given in Figure 5.3a; further examples for different ordination methods are introduced by Quinn and Keough (2007). There is still discussion about the best ordination method; often DCA ordinations produce results that can be ecologically interpreted very well (see Figure 5.3a) but are from a theoretical approach not as elegant as NMDS. But even NMDS produces in some cases, for example, horseshoe effects (see Leyer and Wesche, 2007). A classification method with an agglomerative approach is the cluster analysis. TWINSpan is a polythetic-divisive classification method. It is widely used in classification approaches, because relevés and species are classified. Nevertheless, there is a lot of criticism, especially concerning the transparency of the TWINSpan approach (van Groenewoud, 1992; Bruelheide and Chytrý, 2000). An example of a classification for a large area using TWINSpan was worked out in Australia, where 5,000 relevés were sampled in the major plant communities. Presence/absence data were classified by TWINSpan into 338 overstorey and 60 understorey floristic groups. The types belong to eight biogeographical regions with 45 subdivisions. Furthermore, this is an excellent basis for correlations with animal communities: in this case, species richness of nonarboreal vertebrates correlates with the plant species richness of the understorey stratum (Specht and Specht, 2001).

### *Classification of plant communities as a basis for vegetation mapping*

Classified data with differentiation of species-groups are the bases for community-based vegetation maps. Extensive map material is available, for example, for Japan, France, Spain, Italy, Germany, Poland, whole Europe, the Arctic region, and others. The abiotic-biotic potential of a site is often assessed by using a map of potential natural vegetation; this is defined as the vegetation that would become established if succession processes were to be completed abruptly under the present

abiotic and biotic conditions (Tüxen, 1956). Geobotanical mapping approaches are summarized in Pedrotti (2004). Maps of the actual vegetation and the potential natural vegetation have been elaborated, for example, by Miyawaki (1980–1989), for all provinces in Japan. This has proven to be an excellent basis for planning purposes. For the *Map of the Natural Vegetation of Europe* (2004; scale 1:2,500,000), spatial data are based on the exact classification of 700 mapping units. In Europe the data are essential for the per se protected areas 'Fauna-Flora-Habitat' of the European Union. The vegetation map for the whole Arctic region 1:7,500,000 is an excellent example of the combined mapping of vegetation, plant functional types, and an abiotic template (Raynolds et al., 2005; Walker et al., 2005). From tropical regions there are only few maps available (e.g., Hueck and Seibert, 1981 for South America; Navarro and Ferreira, 2004 for Bolivia).

By linking the results of community mapping with the biome approach (see below), plant communities may have a zonal, an extrazonal, an azonal, or an intrazonal distribution. 'Zonal' applies to the large biomes ordered according to the latitudinal belts, such as the boreal zone. If there are plant communities, for example, dominated by *Picea abies* in the nemoral zone on mesoclimatically cold sites, they occur extrazonally. When extreme edaphic conditions are indicated, for example, by salt marsh vegetation, they are always termed azonal. Intrazonal distribution of communities occurs only scattered in one zone (e.g., specific Central European dry grassland types in the temperate zone).

### **5.4.3 Is it possible to classify animal communities?**

There is a long tradition of describing animal communities as units characterized by the similarity of typical and/or dominant species. The pioneers in the nineteenth century (see references in Kratochwil and Schwabe, 2001) focussed primarily on marine systems. For terrestrial systems, for example, Shelford (1913) proposed a comprehensive characterization of animal communities of the temperate-zone Americas.

A classification of animal communities is in principle difficult: the species and life-form diversity is much higher than in plants, there is high variation of body sizes between species, animals exhibit high mobility, there is a high diversity of habitat preferences, often there are different life-history stages with different habitats, and many species are short-lived or characterized by small population sizes.

A pragmatic approach is to focus on zootaxocoenoses and guilds. Specific coincidences and affinities exist between plant formations (e.g., savannas, steppes, boreal coniferous forests) and the species composition of animal communities. But fluctuations in animal guilds between different years may be high even in relatively stable vegetation types, as was shown for the subcontinental sand vegetation (class *Koelerio-Corynephoretea*) and the wild bee pollinator community (Kratochwil et al., 2009). Almost all terrestrial animal species prefer (at least in one developmental stage) habitats dominated by vegetation. Therefore the classification of vegetation can serve as a matrix to work out coincidences and noncoincidences between different zootaxocoenoses, guilds, and vegetation. This approach has been successfully applied, for example, to soil fauna, nematodes, annelids, spiders, mollusks, millipedes, insects (e.g., flower-visiting insects), birds, and mammals (there are many examples, see Kratochwil and Schwabe, 2001). However, classification of the whole biocoenosis is unfeasible.

#### 5.4.4 *Microhabitats and micro-communities*

Especially when plant communities are rich in different structures they compose sub-communities, which belong to the same life-form type and which inhabit certain microhabitats—for instance, tree stumps with their bryophyte layer, which are called ‘synusiae’, ‘microcoena’, or ‘microcommunity’. These are ‘dependent communities’. There are different approaches to the ranking of synusial units (summarized, for example, by Barkman, 1973), especially for lichen and bryophyte communities. Animal synusiae are in most cases characterised by guilds. Biological crusts are often good examples of microorganism-dominated microcoena built up by Cyanobacteria, green algae and macro-cryptogams. Phanerogams and cryptogams interact: for example, cyanobacteria provide nitrogen by fixation. Especially in cold and/or very arid regions there are extensive crusts without phanerogams. Often biological crusts are classified according to floristic similarity (Belnap and Lange, 2001).

Bültmann (2005) studied lichen-dominated microcoena in southeast Greenland. These often only extend a few square centimetres but occur over vast areas. Fine-scale abiotic factors such as snow-cover duration and wind exposure are reflected in their occurrence. There are specific correlations between phytocoena and microcoena: for example, *Solorinon* croceae communities are mainly restricted to *Salicetea* herbaceae communities.

In this case, as in others, the biogeographer gains deeper insights into the ecology of phanerogam communities by understanding the types of microcoena and how they indicate environmental variables and vice versa.

### 5.5 COMMUNITY COMPLEX-BASED CLASSIFICATION

Repeated combinations of plant communities in landscape sections form vegetation complexes, which constitute a bridge between the community level and the landscape level. Groups of vegetation complexes link the level of the landscape (topic level) to the choric level.

A systematic registration and analysis of the vegetation complexes by mainly inductive methods began around 1970. The first concepts for inductive recording and analysis were developed by Reinhold Tüxen, following suggestions made by the vegetation geographer Josef Schmithüsen (Schwabe, 1997 and references therein).

The young scientific field of vegetation complex research (or sigmasociology, sigma = sum of communities) has been applied in different countries and regions. Examples include Japan (e.g., Miyawaki, 1978); Canada (Béguin et al., 1994; Thannheiser, 1989); Bolivia (Navarro, 2003); Poland (Matuszkiewicz, 1979; Wojterski et al., 1994); France (e.g., Géhu, 1977); Italy (e.g., Pignatti, 1980); Spain (e.g., Rivas-Martínez, 1987, 1994); Scandinavia (e.g., Dierssen and Dierssen, 1980); Germany (e.g., Tüxen, 1978; Schwabe, 1989, 1991); and Switzerland (e.g., Theurillat, 1992; Zoller et al., 1978). Important applications of sigmasociology to vegetation complexes and biogeography so far have been the differentiation of animal habitats (e.g., Béguin et al., 1977; Schwabe and Mann, 1990), the comparison of different cultural landscapes (e.g., southern Spain and northern Morocco: Deil, 1997, 2003), as a component of multi-layer models in landscape ecology (Navarro, 2003; Thannheiser, 1988), and in identifying and explaining altitudinal gradients (Theurillat, 1992; Schmidlein, 2003) (see Schwabe, 1997 and further references therein).

It is generally impossible to determine ecosystem boundaries at the landscape level. Such an ecosystem “should be uniform regarding the biogeochemical turnover, and contain all fluxes above and below the ground area under consideration” (Schulze et al., 2005). Certain vegetation complexes occur in a regular order: for example, complexes around springs, along the margins of running water, in fens or bogs, and on *Calluna*-heathland. To study the plant communities of such complexes, methods have been elaborated that use

definable spatial units. These are relatively homogeneous geotopes (= physiotoypes), specified as plot areas. Physiotoypes, such as rock complexes with steep slopes, designate a unit having an approximate homogeneity, which can be defined geomorphologically and topographically. Physiotoypes are built up by ever-repeated combinations of (micro)-habitats, which is reflected in the occurrence of plant communities that often have indicator value. Forman and Godron (1981) call them "clusters of interacting stands which are repeated in similar form in a landscape." In anthropogenically influenced landscapes, different types of land use mark the boundaries of plot areas in addition to the physiotope factors.

The method for making vegetation complex relevés is relatively similar to the Braun-Blanquet approach (cf. Section 5.4.2). Homogeneous plot areas are determined and all vegetation units (which must carefully be studied beforehand) are sampled on a scale adapted to the Braun-Blanquet scale (but referring to communities, not to species). In open communities (e.g., extensively grazed grassland) also, single individuals or groups of shrubs or trees may be added. The relevés are classified afterwards by using a divisive-polythetic approach such as TWINSPAN, by cluster analysis, and/or ordinated by correspondence analysis (see, e.g., Schwabe and Kratochwil, 2004 for inneralpine vegetation complexes). The denomination of the complexes is based on the communities that characterize them most. For near-natural site complexes, a unit of the natural vegetation is used by preference.

After studying large landscape sections it is possible to work out landscape-typical distribution patterns (e.g., community complexes showing different levels of eutrophication). The method was applied, for example, to large transects in the driest parts of the Alps, reflecting the indicator value of community complexes influenced by humidity and temperature (Schwabe and Kratochwil, 2004).

Biogeographers in Europe used the sigmasociological approach for mapping purposes (Sigmachorology, see the review by Schwabe, 1997 and references therein). Rivas-Martínez (1987) includes, apart from the potential natural vegetation, all substitute communities to describe a sigmetum. The next spatial level is to regard whole geoserries (geosigmetum) (e.g., Rivas-Martínez, 1987).

In Switzerland an approach has been elaborated that employs areas of a certain prespecified size as a base unit, and therefore includes a deductive element to sampling. These areas are characterized by phytosociological units (e.g., associations/communities or alliances). On the level of phytosociological alliances, this procedure was

applied to draw up a remarkable atlas of the whole of Switzerland (Hegg et al., 1993).

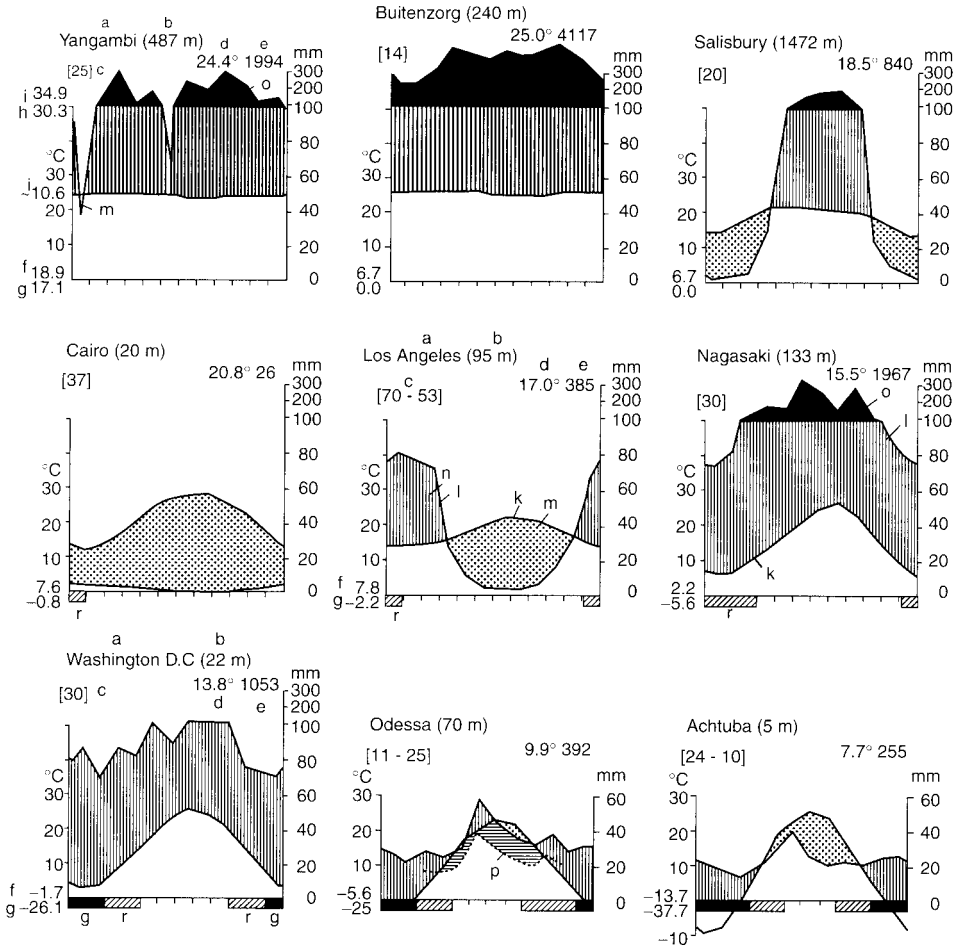
## 5.6 COMBINED PLANT STRUCTURAL, ABIOTIC, AND PARTLY TAXA-BASED APPROACHES: BIOMES AND BIOGEOGRAPHIC REALMS

Regarding higher levels of complexity, Clements (1916) proposed a classification approach for the whole geobiosphere, including phyto- and zoogeographical aspects—biomes. The biome approach is the key concept of the global work of Heinrich Walter (1898–1989). According to Walter and Breckle (1970 ff, 1983 ff) biomes are characterized by similar plant formations that include their animals and microorganisms. Decisive is the plant formation that occurs as the terminal stage in the macroclimate in question. The biome differentiation published by Walter and Breckle is based on the pattern of aridity, humidity, and extreme temperatures, which are essential for the ecophysiological conditions of plant growth and correspond to plant formations and soil types. The most important information for plant growth is depicted in the 'Ecological climate diagrams', the 'Walter diagrams' (Walter and Breckle 1970 ff, 1983 ff), which show very clearly the humid and arid periods in a year (Figure 5.4).

The authors differentiate 'zonobiomes' ('ecological climatic zones' with sub-zonobiomes), which are large and climatically uniform zones within the geobiosphere. Additionally there are orobiomes (OB X) with altitudinal belts in the different zonobiomes and extreme types of soil with azonal vegetation such as swamp soils (pedobiomes). All sharp borderlines are often artificial, and therefore transitional zones occur (zonocotones). The nine main zonobiomes (ZB) are presented in Figure 5.5.

The most important PFTs of the biomes are described in Table 5.1. In some biomes large herbivore mammals with high browsing or grazing impact are common (e.g., ZB IIa, VII, IX, orobiomes). In others, small mammals such as *Dipodomys* sp. (ZB III: neotropical), *Marmota* species (ZB VII, orobiomes), or invertebrates such as termites (ZB II, III and others) influence biome structures.

Physiognomic similarities are often high between ecological-equivalent types in different continents as a result of convergent evolution and adaptive syndromes. For instance, striking floristic differences and structural similarities are present in the five mediterranean areas of the world: the Mediterranean proper, California,



**Figure 5.4 Ecological climate diagrams of the main zonobiomes according to Breckle (Walter and Breckle, 1999), slightly modified. Horizontal axis: northern hemisphere January to December, southern hemisphere July to June. Vertical axis: Temperature in °C, precipitation in mm. Letters indicate a, station; b, height above sea level; c, number of years of observation (first temperature, second precipitation); d, mean annual precipitation; e, mean daily maximum temperature of the warmest month; f, mean daily temperature of the coldest month; g, absolute minimum temperature; h, mean daily maximum temperature of the warmest month; i, absolute maximum temperature; j, mean daily temperature fluctuation (h, i, j only for tropical stations); k, curve of mean monthly temperature; l, curve of mean monthly precipitation; m, arid period (dotted); n, humid period (vertical hatching); o, mean monthly precipitation >100 (scale reduced, dark areas indicate perhumid season; p, supplementary precipitation curve, reduced to 10°C = 30 mm, horizontal area above = relative dry period (only for steppe stations); q, month with a mean daily minimum below 0°C (black) = cold season; r, months with absolute minimum below 0°C (diagonally hatched), i.e., late or early frosts possible; s, number of days with mean temperature above +10°C (duration of vegetation period); t, number of days with mean temperature above -10°C. Zonobiomes according to Figure 5.5: ZB I, Yangambi (Congo), Buitenzorg (Java); ZB II, Salisbury (Zimbabwe); ZB III, Cairo (lower Nile); ZB IV, Los Angeles (California); ZB V, Nagasaki (Japan); Washington D.C.; ZB VII, Odessa (Black Sea); ZB VIIa, Ach tuba (lower Volga); ZB VII (rIII) (extreme arid desert with cold winters), Nukuss (Central Asia); ZB VIII, Archangelsk (Siberian boreal zone); ZB IX, Karskije Vorota (Island Vaigatsch, Russian tundra)**

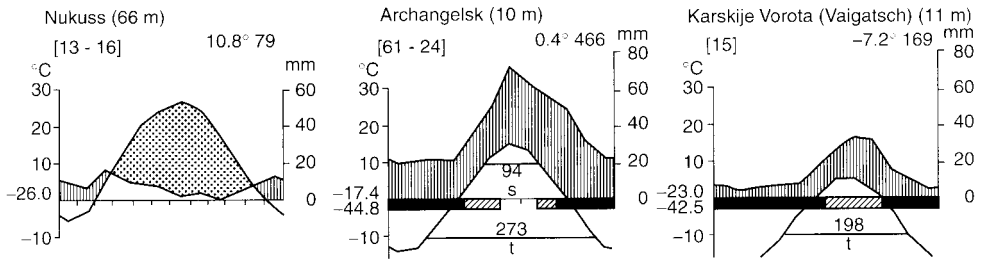


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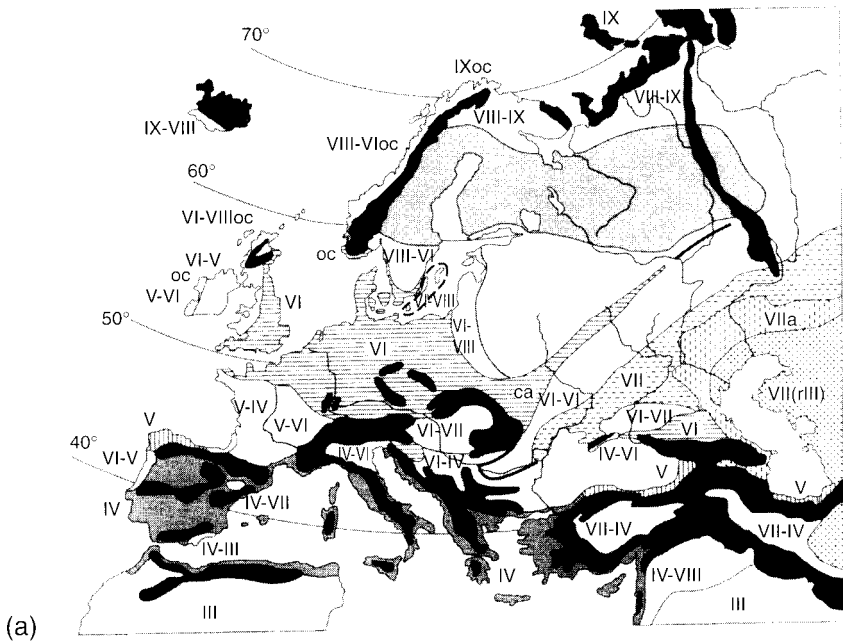


Figure 5.5 Main zoniomes of the earth (after Breckle, from Walter and Breckle 1999; slightly modified); a, Europe; b, Asia; c, Australia, New Zealand; d, Africa; e, North and Central America; f, South America: ZB I, evergreen tropical rain forest: equatorial humid diurnal climate; ZB II, tropical semi-evergreen and wet-season green forests and (IIa) savannas, grassland, dry woodlands: humido-arid tropical summer rain region; ZB III, warm deserts and semi-deserts: subtropical arid climates; ZB IV, sclerophyllic mediterranean woodlands: arido-humid winter rain region, Mediterranean regions; ZB V, temperate rain forests, evergreen broad-leaved laurophyll forests: warm-temperate, humid climate; ZB V, deciduous nemoral forests: temperate climate; ZB VII, steppes and (VIIa) (semi)-deserts with cold winters: arid-temperate climate; ZB VIII, boreal forest (evergreen or deciduous coniferous): cold-temperature boreal climate; ZB IX, tundra and polar deserts: arctic climate. OB X Orobionies, mountains. White spaces between zoniomes (ZB) are zoocotones. Further abbr.: a/h, relatively arid or humid for a specific ZB; oc/co, climate with oceanic or continental tendency; fr, frequent frost in tropical mountain regions; wr/sr, prevailing winter or summer rain; swr, two rainy seasons; ep, episodic rain; nm, dew or fog precipitation (nonmeasurable); (rIII), rain as sparse as in ZB III; (tl), temperature curve as in ZB I





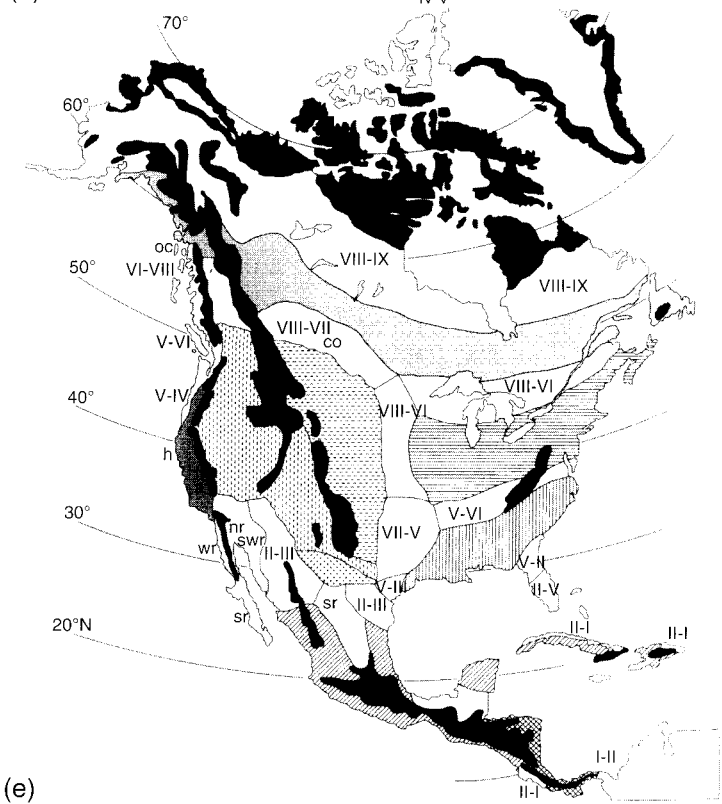
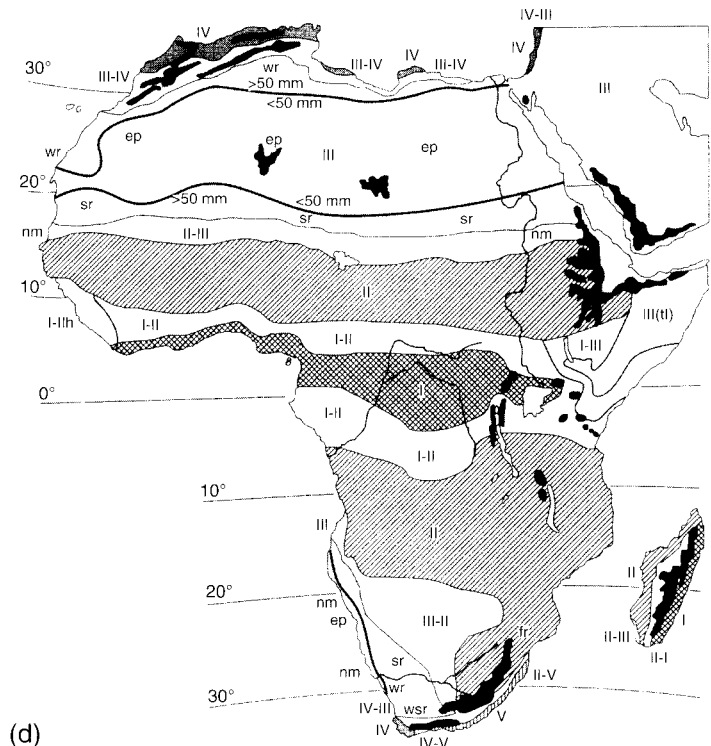
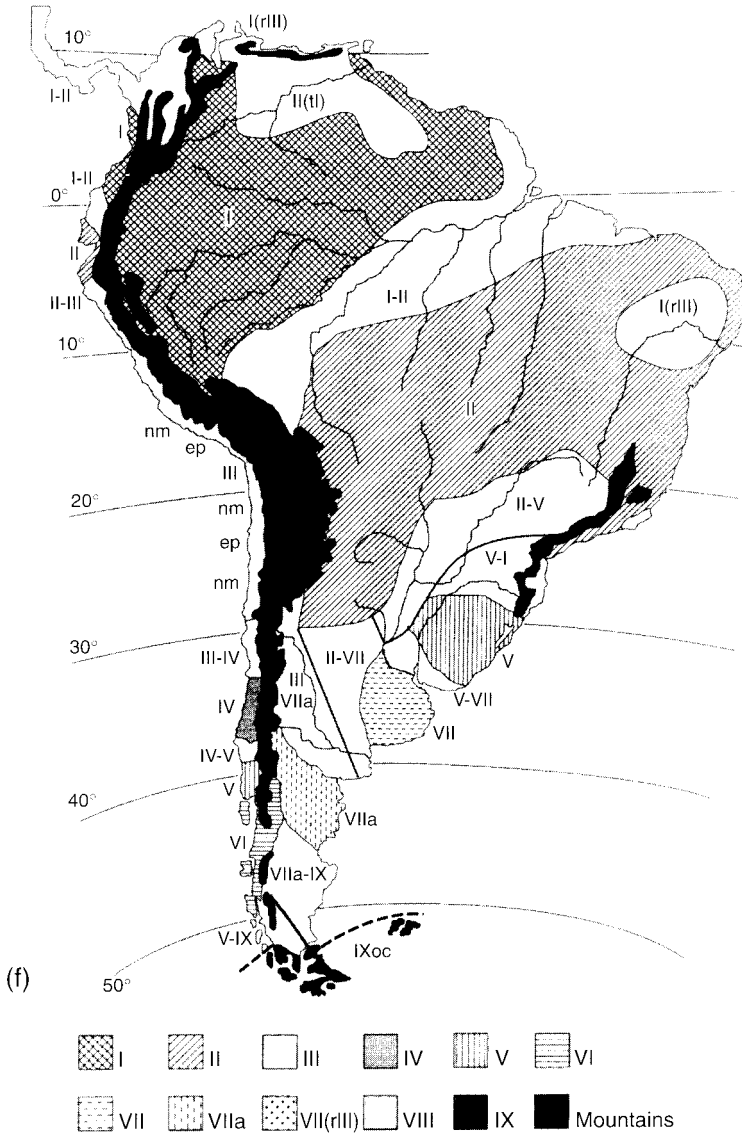


Figure 5.5 Cont'd



**Figure 5.5** Cont'd

central Chile, the Cape Province of South Africa, and southwest Australia. This is also true for the guild of nectar-feeding birds and mammals.

The eight 'biogeographical realms' of Udvardy (1975, updated 1982) are principally based on floral kingdoms of the world: Nearctic, Western and Eastern Palaearctic, Afrotropical, Indomalaya, Australian, Neotropical, Oceania, and Antarctica are differentiated (the Capensis region is integrated into the Afrotropical realm). In a second step, 14 biomes are differentiated, including some mixed mountain and island

systems and lakes; the other types correlate to a large extent with the Walter-Breckle biome approach introduced above, with the exception that boreal forests are classified as temperate needle-leaf forests. The 14 biomes are subdivided into biogeographical provinces. This approach bridges taxic- and structure-based classifications. The classification is used by the International Union for Conservation of Nature (e.g., for the World Heritage Areas) and was prepared as part of the UNESCO 'Man and the Biosphere Programme (MAB)'; see also Lomolino et al. (2005).

**Table 5.1 Dominant plant structural-functional types of the world, related to the biome types of Figure 5.5; ZB zonobiomes, OB orobiomes (after Box, 1996; slightly modified)**

	<i>Dominant plant type</i>	<i>Biome type(s)</i>	<i>Structure, life-form</i>	<i>Other characteristics</i>
a	Tropical evergreen/ broad-leaved trees	Tropical rain forests ZB I	Tall woody, evergrowing	Mesomorphic
b	Tropical deciduous broad-leaved trees, arborescents	Raingreen forests, woodlands, scrub ZB II	Woody (p.p. facultative deciduous)	
c	Extra-tropical evergreen broad-leaved trees (mainly laurophyll)	Evergreen broad-leaved forests, temp. rain forests ZB V	Woody, evergreen	Mesomorphic, shade-tolerant
d	Temperate deciduous broad-leaved trees	Summergreen broad-leaved forests and woodlands ZB VI	Woody, obligate deciduous	Winter-dormant
e	Temperate/boreal needle-leaved evergreen trees	Needle-leaved evergreen forest/open woodlands ZB (VI) VIII	Woody, evergreen	Winter-dormant (cold-tolerant)
f	Boreal/cool-temperate deciduous needle-leaved trees	Deciduous boreal needle-leaved forest/ open woods ZB VIII	Woody, obligate deciduous	Winter-dormant (cold-tolerant)
g	Sclerophyll trees/arborescents	Arido-humid woodlands, scrub ZB IV	Short woody, (semi-) evergreen	Xeromorphic, light-demanding
h	Sclerophyll/coriaceous shrubs/dwarf shrubs	Shrublands, krummholz, semi-deserts ZB III, OB X	Basally determinate, (semi-) evergreen	Xeromorphic, light-demanding
i	Deciduous shrubs/ dwarf shrubs	Shrublands, krummholz, semi-deserts ZB VIIa, OB X	Basally determinate, deciduous	Rapid growth, seasonally dormant
k	Short-season broad-leaved dwarf shrubs	Tundra: dwarf shrub, graminoid, etc. ZB IX	Basally ramifying, evergreen/deciduous	Winter-dormant (cold-tolerant)
l	Diurnally active tuft- arborescents/frutescents/ forbs	Tropical alpine scrub OB X	Rosettes (diurnal), evergreen	Tolerant to diurnal frost, high UV, etc.
m	Grasses and related graminoids	Savannas and grasslands ZB II, VII	Herbaceous, opportunistic	Rapid growth, spreading
n	Stress-tolerant succulents	Semi-desert scrub ZB III	Stem/leaf/root-succulents, evergreen	Slow growth, water storage in tissue
o	Ephemeral herbs	Semi-desert scrub ZB III	Annual, perennial, ephemeral	Short life cycle/growing season
p	Stress-tolerant cryptogams	Tundra, deserts ZB III, VIIa, IX	Cryptogams	Slow growth

Biome types were chosen as reference areas for experimental-ecological research in the International Biological Program (IBP); see, for example, Archibold (1995) and examples in Goodall (1977 ff). For some biomes, therefore, ecosystem studies with a great deal of flux- and other ecosystem-based data are available; nevertheless, these data are never sufficient to enable an extrapolation to the whole biome.

## 5.7 CLASSIFICATIONS WITH PREDOMINANCE OF ABIOTIC FACTORS

Climate and vegetation as a basis for classification of the world's vegetation were already used in the classification system drawn up by Wladimir Köppen (1846–1940). Köppen (1931) referred to

the plant groups of Alphonse de Candolle (see Section 3.1) and classified five major climate zones, using annual and monthly precipitation and temperature: A (tropical/megathermal) climates, B dry (arid and semiarid) climates, C (temperate/mesothermal) climates, D (continental/microthermal) climates, and E polar climates. Further subgroups are differentiated (climate types and subtypes).

The life-zone system of Holdridge (1947) uses annual precipitation and 'biotemperature' (average days/year without temperatures  $<0^{\circ}\text{C}$  and  $>30^{\circ}\text{C}$  and potential evapotranspiration ratio, combining precipitation and biotemperature in an index). The life-zone system differentiates 38 life-zone types referring to 'terminal communities'. As average data are used, the regions characterized by seasonal pattern are not depicted in an appropriate way. The ecoregions of Bailey and Hogg (1986) integrate landform, soil, drainage system, and altitude. The global differentiation of four domains (polar, humid temperate, humid tropical, and dry), 30 divisions, and 98 provinces is based on the macroclimate.

Ecozones are characterized by climatic factors, morphodynamics, soil-forming processes, production, and potential for agriculture and forestry. Different plant formations, biomes, and land-use systems reflect these characteristics (Schultz, 1988, 2000). The borderlines of the ecozones refer to the climatic differentiation of Troll and Paffen (1964), focusing especially on the climate to vegetation impact. The ecozone map elaborated by Schultz (1988, 2000) has overlaps to a great extent with the Walter-Breckle biome map (Figure 5.5).

Lauer et al. (1996) worked out a global classification that focusses on the heat and water budget, especially on the lengths of wet and dry seasons. Four principal zones, marked by day-length variation of irradiation: tropics, subtropics, mid-latitudes, and polar regions, are differentiated, which is problematic, for example, when winter-cold steppe areas are characterized as being subtropical. The aim is to classify the climates of the earth by ecophysiological characteristics of the real vegetation.

## 5.8 OUTLOOK: THE IMPORTANCE OF CLASSIFICATION FOR BIOGEOGRAPHERS AND ECOLOGISTS

As discussed above, there are taxa-, structure-, community/community complex-, and biome/ecoregion-based classification approaches to classification. Vegetation analysis at the landscape level can be carried out by traditional vegetation

mapping, by analysis of transects and gradients (see Mutke, this volume) or by studying vegetation complexes. It can be hypothesized that the understanding of vegetation complexes as spatial units will lead to new insights on a high complexity level. Three main levels of spatial vegetation classification lead from communities to vegetation-complexes in landscapes and to biomes.

Though the antecedents for classification go back in some cases over two centuries, there are three compelling reasons why we still need classification:

1. Classified data are essential as reference units for questions concerning subjects such as global environmental change, environmental impact assessment, in the context of nature conservation and resource management (especially of threatened habitat types, for example, the 'Flora-Fauna-Habitat-directive' of the European Union), for planning purposes, in restoration ecology, and also as a reference framework for expensive experimental research.
2. Many research results demonstrate that 'ecological rules' are dependent on the type of ecosystem investigated. An example would be biodiversity-productivity rules. Often a unimodal, hump-shaped relationship with a diversity maximum at medium productivity level is proposed (e.g. Garcia et al., 1993 for a Mediterranean saltmarsh; Süß et al., 2007 for temperate sand ecosystems). For different grassland communities some authors described positive relationships (e.g., Pfisterer et al., 2004; Huston and DeAngelis, 1994) and others negative ones (e.g., Goldberg and Miller, 1990). It is important to classify the system in question, with the aim of producing transferable results.
3. Using classification, new relationships have been worked out (e.g., by correlation of indicator species- or indicator community groups and plot-based abiotic or biotic data, nowadays with the help of cluster analysis and multivariate data analysis). The example of the 'Elenberg' indicator values shows that most of these values, which had been worked out by analysing phytosociological databases, are very useful (Figure 5.3).

A number of plant and vegetation ecologists are interested in 'how vegetation works' and not in distinguishing plant communities (Rodwell, 1991–2000). Nonetheless a large, worldwide system of GIS-referenced permanent plots in classified communities, which are repeated for each community type, are essential for the identification of effects of climate change, atmospheric pollution, species invasions, and other disturbance factors. Meanwhile large parts of the world use

floristically based classifications, which are relatively similar. A goal for the future is to standardize national vegetation classification systems by developing a system that is acceptable worldwide. The integration of zoological and functional-ecological data will be easier if such a database were established and homogeneous.

The first period of classification can be defined between the eighteenth and early twentieth centuries. A second period can be identified in the second half of the twentieth century in which the study of ecological and biogeographical processes has dominated biogeography and ecology leading to the idea that, to some extent, classification is not essential. Now its importance is again becoming generally accepted, especially in the context of long-term studies, global change, and applied biogeography and ecology. In the future the combination of classification and functional aspects has to be developed. Functional aspects should have a macroecological scale in order to be useful for prediction and modelling.

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