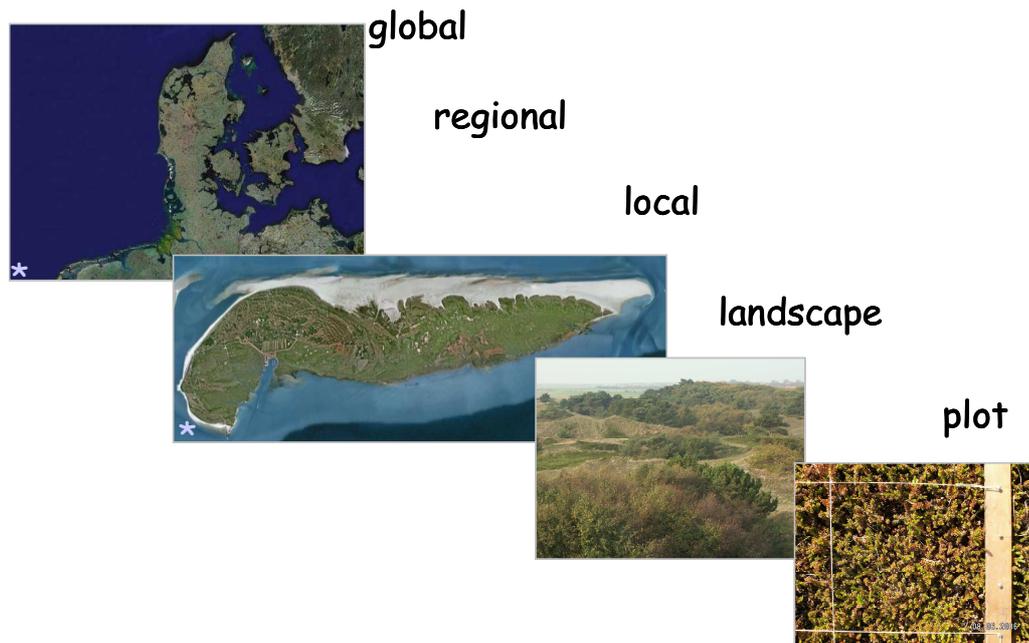


# Phytodiversity in Relation to Scale



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## Contents

<b>0 Acknowledgements</b> .....	<b>1</b>
<b>1 List of Included Publications</b> .....	<b>2</b>
<b>2 Summary</b> .....	<b>3</b>
<b>3 Introduction</b> .....	<b>5</b>
3.1 Terms and Definitions .....	6
<b>4 Quantity of Plant Species Richness</b> .....	<b>7</b>
4.1 How Many Species? .....	7
4.2 Geographic Distribution, Hotspots and Endemism .....	8
<b>5 Scales: Taxonomic, Spatial and Temporal Scale</b> .....	<b>13</b>
<b>6 Measuring Biodiversity</b> .....	<b>17</b>
6.1 Species Richness, Equitability, Abundance, Functional Diversity .....	17
6.2 Spatial Levels of Species Diversity .....	22
6.3 Monitoring and Field Measurements.....	25
6.4 Sampling.....	27
6.4.1 Random vs. Non-Random Sampling (Example I).....	28
<b>7 Species Richness and Sampling Area</b> .....	<b>31</b>
7.1 Island Biogeography.....	31
7.1.1 Species-Area Effects (Example II).....	33
7.1.2 Species Richness and Islands Size (Example III).....	36
7.2 Landscape Heterogeneity .....	37
7.2.1 Bryophytes and Landscape Heterogeneity (Example IV).....	39
<b>8 Species Diversity and Environment at Different Spatial Scales</b> .....	<b>42</b>
8.1 Large Gradients Complexes: Latitude and Altitude.....	44
8.2 Regional Scale .....	49
8.2.1 Macroclimate (Example V) .....	49
8.3 Local Scale .....	51
8.3.1 Soil pH (Example VI).....	51
8.3.2 Disturbance.....	59
8.3.2.1 Human Trampling (Example VII) .....	63
8.3.2.2 Grazing (Example VIII).....	65
8.3.2.3 Shrub Expansion and Grazing (Example IX).....	70
8.3.3 Resource Availability, Competition and Productivity.....	72
8.3.3.1 Light Effects (Examples X, XI, XII, XIII) .....	74
8.3.3.2 Productivity (Examples XIV, XV) .....	80
<b>9 Species Diversity in Time</b> .....	<b>86</b>
9.1 Historical Development.....	86
9.1.1 Time of Isolation of the German Frisian Islands (Example XVI).....	87
9.2 Succession .....	90
9.2.1 Coastal Dune Succession (Example XVII) .....	93
9.3 Biological Invasions .....	97
9.3.1 Native Species Richness and Biological Invasion (Example XVIII).....	98
<b>10 Short Conclusion</b> .....	<b>101</b>
<b>11 References</b> .....	<b>102</b>

<b>12 Appendix</b> .....	<b>137</b>
12.1 Reprints of Publications .....	137
12.1.1 Coastal dune succession and plant diversity on a German Wadden Sea Island	137
12.1.2 Interactive effects of rabbit grazing and environmental factors on plant species-richness on dunes of Norderney .....	159
12.1.3 Classification and habitat characteristics of plant communities invaded by the non-native <i>Rosa rugosa</i> Thunb. in NW Europe .....	172
12.1.4 Expansion of <i>Rosa rugosa</i> and <i>Hippophaë rhamnoides</i> in coastal grey dunes: effects at different spatial scales.....	191
12.1.5 Effects of <i>Rosa rugosa</i> invasion in different coastal dune vegetation types.....	200
12.1.6 Diversity of bryophytes in an urban area of NW Germany .....	219
12.1.7 Random vs non-random sampling: effects on patterns of species abundance, species richness and vegetation-environment relationships.....	227
12.1.8 Effects of the expansion by <i>Hippophaë rhamnoides</i> on plant species richness in coastal dunes .....	240
12.1.9 Species richness in Sea-Buckthorn scrub.....	251
12.1.10 Soil pH and species diversity in coastal dunes.....	256
12.1.11 Differences in species richness on non-native and native plants between the East and North Frisian Islands .....	267
12.2 Complete Publication List .....	270

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# 1 List of Included Publications

## The habilitation is mainly based on the following articles:

- Isermann M (submitted) Coastal dune succession and plant diversity on a German Wadden Sea Island. submitted. (Chapter 9.2.1)
- Isermann M, Koehler H, Mühl M (2009) Interactive effects of rabbit grazing and environmental factors on plant species richness on dunes of Norderney. *Journal of Coastal Conservation, Planning and Management*, doi: 10.1007/s11852-009-0056-9. (Chapters 8.3.2.2, 8.3.3.2)
- Isermann M (2008a) Classification and habitat characteristics of plant communities invaded by the non-native *Rosa rugosa* Thunb. in NW Europe. *Phytocoenologia* 38, 133-150. (Chapter 9.3.1)
- Isermann M (2008b) Expansion of *Rosa rugosa* and *Hippophaë rhamnoides* in coastal grey dunes: effects at different spatial scales. *Flora* 203, 273-280. (Chapter 8.3.3.1)
- Isermann M (2008c) Effects of *Rosa rugosa* invasion in different coastal dune vegetation types. In: Tokarska-Guzik B, Brock J-H, Brundu G, Child L, Daehler CC, Pyšek P (eds.) *Plant Invasions: Human perception, ecological impacts and management*. Backhuys Publishers, Leiden, The Netherlands, pp. 289-306. (Chapter 8.3.3.1)
- Isermann M (2007) Diversity of bryophytes in an urban area of Bremen, NW Germany. *Lindbergia* 32, 75-81. (Chapters 7.2.1, 8.3.3.1)
- Diekmann M, Kühne A, Isermann M (2007) Random vs non-random sampling: effects on species abundance, species richness and vegetation-environment relationships. *Folia Geobotanica* 42, 179-190. (Chapter 6.4.1)
- Isermann M, Diekmann M, Heemann S (2007) Effects of the expansion by *Hippophaë rhamnoides* on plant species richness in coastal dunes. *Applied Vegetation Science* 10, 33-42. (Chapters 8.3.2.3, 8.3.3.1)
- Isermann M (2005) Soil pH and species diversity in coastal dunes. *Plant Ecology* 178, 111-120. (Chapter 8.3.1)
- Isermann M, Friedrichs L, Grave C, Wagner A (2005) Species richness in Sea-Buckthorn scrub. In: Herrier J-L, Mees J, Salman A, Van Nieuwenhuyse H, Dobbelaere I (eds.) *Dunes and Estuaries. Nature restoration practices in European coastal habitats*. Koksijde, Belgium, pp. 597-600. (Chapter 8.3.3.1)
- Isermann M (2004) Differences in species richness of native and non-native plants between the East and North Frisian Islands. In: Green DR (ed.) *Delivering Sustainable Coasts*. Cambridge Publications, pp. 737-738. (Chapters 7.1.2, 9.1.1)

## 2 Summary

Species diversity has been of particular interest e.g. for nature conservation as well as human well-being, since the Convention on Biological Diversity (CBD) in Rio de Janeiro (1992). This study demonstrates the complex relationships between environmental conditions and species diversity. Against a theoretical background, it is the first study that represents various, partly interrelated phytodiversity relationships, in particular, in the context of coastal dune systems. Species diversity relationships are scale-dependent e.g. from global across regional to local scales, and in a hierarchical approach, various patterns and processes are highlighted. In many cases, patterns and processes of each higher level affect species diversity at the lower scale, and partly vice versa. Factors shown in this study consider the temporal and the spatial scale that can be classified into three groups: methodical factors, abiotic and biotic factors (Table 1).

**Table 1. Patterns and processes affecting species diversity at spatial and temporal scales.**

<b>spatial scale</b>		
<b>methodical factors</b>	<b>abiotic factors</b>	<b>biotic factors</b>
sampling area <i>per se</i> diversity indices functional groups	latitude and altitude historical factors island size landscape heterogeneity habitat heterogeneity resource availability macroclimate	disturbance competition productivity biological invasions
<b>temporal scale</b>		
	historical development, succession, biological invasions	

General hypotheses discussed in relation to **methodical factors** are:

Species richness reflects sampling effects (Chapter 6.4) e.g. random or non-randomly selected plots.

Area *per se* effect (Chapter 7.1.1), the larger the area, the more space occur for more species.

Comparing species richness and species diversity indices (Chapter 6.1), there might be differences (e.g. Chapter 8.3.1).

Species richness relationships are different using single species and functional groups, respectively.

Considering **abiotic factors**, the study discussed:

Species richness in large gradients complexes (Chapter 8), for example, increases with decrease in latitude and altitude.

Historical factors, e.g. the time of isolation in relation to the origin of islands (Chapter 9.1), are of interest. It is shown, that unsaturated island flora contains more neophytes than islands formerly belonging to mainland, because of the prevented species establishment on islands.

Independent of the origin, species richness increased with island size (Chapter 7.1.2). Landscape heterogeneity, the number of habitats maintains species richness, for example, of bryophytes in urban areas (Chapter 7.2.1). Macroclimate, transition areas at landscape scale enhance the vegetation heterogeneity as well as dune species richness (Chapter 8.2). Habitat heterogeneity, the variability of available resources (Chapter 8.3), for example, the variation of soil pH, enhances species richness, furnishing more ecological niches, facilitating the coexistence of species. This is related to diversity patterns of the vegetation. Resource availability (Chapter 8.3.3), for example, light conditions and soil pH, are in a humped-back manner related to species richness.

In relation to **biotic patterns** and processes, the study demonstrates:

Disturbances (Chapter 8.3.2) such as trampling and rabbit grazing prevent competitive exclusion, for example, by shrub expansion. Moreover, species diversity reached highest values at intermediate disturbances.

Ecological interactions such as competition (Chapter 8.3.3.1) in relation to resources, like space, light and nutrients, affect species diversity. Species diversity declined in accordance to the competitor linear or regarding various functional groups in a humped-back relation. Effects of various factors such as resource availability and competition are combined e.g. in the productivity approach (Chapter 8.3.3.2). It was shown, that species richness in dunes was highest at intermediate levels of biomass. Moreover, biomass and disturbances are connected, so with increasing biomass floristic similarity between grazed and ungrazed sites decreases.

Similar to productivity, different factors especially competition due to dispersal and growth are merged in pattern and processes of biological invasions (Chapter 9.3). The study shows, amongst others, that invasions by shrubs like *Rosa rugosa*, causes native species richness to decline and the percentage of neophytes to increase.

Abiotic and biotic factors are related to **temporal aspects**:

Species richness is higher in areas less isolated by distance as well as by time from source areas (Chapter 9.1).

During succession, species richness and species diversity changes (Chapter 9.2).

The probability of invasions and the strength of ecosystem effects increase with time since the first introduction (Chapter 9.3).

In summary, the presented study gives an overview of the manifold patterns and processes affecting species diversity at various spatial and temporal scales. The interrelations between factors and across hierarchical structured scales demonstrate the importance of their consideration for both scientific and management approaches.

### 3 Introduction

The term biodiversity has been used since the 1960s, and was assessed as an environmental issue since the early 1980s, culminating in the Convention on Biological Diversity (CBD) in Rio de Janeiro (1992). Direct and indirect human activities, such as global warming, agriculture, and landscape alteration represent an existential problem between nature and society in relation to ecosystem services, such as human well-being and human health (Solbrig 2000). Biodiversity might reflect the condition of nature and ecosystem functioning, and probably reflects the condition of complex ecological webs. Considerable attention has been given to biological diversity over the last fifteen years, since the term was adopted into human society, the political world and popularised by the media. The effect of human activities upon natural environments such as overexploitation and destruction of habitats threatens future biological diversity. The Convention on Biological Diversity mandates the preservation, exploration, and sustainable use of biodiversity, and requires its protection at all levels from the genome to the ecosystem (Gaston & Spicer 2004, Lévêque & Mounolou 2004).

The **global decline in biodiversity** and the loss of species and habitats is enormous (Myers 1990). Global models estimate that changes in land use and climate, as well as anthropogenic disturbances with subsequent habitat decline, will result in a loss of vascular plant species of around 25 % in the next few hundreds of years in comparison to 1995 (Cowling & Samways 1995, Magurran 2006, Van Vuuren et al. 2006).

Biodiversity loss no longer represents just the extinction of single species, but rather the modification of entire ecosystems (Lévêque & Mounolou 2004). Threats to biodiversity are linked e.g. with global change, introduced species, pollution, unsustainable use of native species (Caldecott et al. 1996), and include the loss of genetic variability within a population, which can reduce its flexibility to adjust to a changing environment. The addition or deletion of a species can have a considerable effect on an ecosystem's ability to provide services, and in turn, a reduction in the capacity of an ecosystem to resist changing environmental conditions, could negatively affect the number of species (Mooney et al. 1996).

Biodiversity along with phytodiversity are products of dynamic interactions among different levels of integration within the living world. They are controlled by various factors, such as the abiotic environment, structural complexity of the landscape and habitat, the history of the area, ecological interactions amongst species, such as competition, and past biogeographic events. This integrated approach towards biodiversity has led to new concepts such as functional ecology, biocomplexity, and ecosystem services (Gaston & Spicer 2004, Lévêque & Mounolou 2004).

The Convention on Biological Diversity addresses the role of biological diversity in the biosphere and human responsibility for decreasing biological diversity. The, still common, lack of knowledge needed to undertake suitable measures for its sustainable conservation, results in greater emphasis being placed on the protection of species, ecosystems and natural habitats, rather than resorting to ex situ measures (Lévêque & Mounolou 2004).

Biodiversity of coastal systems represents an important value for humans in **ecosystem services** (species richness, functional groups), in the provision of services e.g. genetic resources, in regulating services e.g. climate and erosion regulation, in cultural services, e.g. knowledge systems, educational values, aesthetic values, and especially in recreation and health, furthermore it includes supporting services, such as primary production and nutrient cycling.

The presented study contributes to the understanding of conditions and causes affecting phytodiversity, to the mechanisms explaining species richness and species diversity, and to the relationship with the abiotic and biotic environment. Complex interactions between parameters change the visible expression of biodiversity. One of the most important factors of biodiversity considers the scale-dependent variation of patterns and processes determining biodiversity. Because of the different relationships between species diversity and scale, scientific approaches as well as management measures supporting biodiversity should consider this phenomenon.

### **3.1 Terms and Definitions**

The term **biodiversity**, the variety of life in all its expressions, is subject to various definitions (Allem 2000). The linguistic use of the term diversity began in the 18<sup>th</sup> century, but the use of biodiversity started much later, around 1980 (Barthlott et al. 1996). Biodiversity is roughly differentiated into three components: **genetic diversity** (within-species diversity), **species diversity** (number of species), and **ecological diversity** (diversity of communities). Thus, biodiversity is much more than species diversity, in its broadest sense it encompasses nested hierarchies, and includes molecular, gene, phylogenetic, organismal, population, community, habitat, ecosystem, landscape, bioregion, biome diversity, as well as the diversity of the entire world. As such, research on biodiversity in its supreme form requires a multifaceted approach from a variety of fields and is related to the three primary ecosystem attributes, composition, structure, and function (Wilson & Peter 1988, Solbrig 1994, Whittaker 1998, Ward et al. 1999, Mumby 2001, Gaston & Spicer 2004).

The framework for biodiversity includes different terms, i.e. **geodiversity** that could be defined as the variety of abiotic factors: the structure, function, and dynamic of the abiotic part of the ecosystems, such as geosphere, climosphere, and hydrosphere (Leser & Nagel 1998). Sometimes the term **landscape diversity** is distinguished, describing different interacting ecosystems, each characterised by a specific geodiversity and biodiversity. It is similar to the term **ecological diversity**, at first defined as the richness and variety of natural ecological communities (Pielou 1975), including both biodiversity and geodiversity (Barthlott et al. 1996). The term ecological diversity is mainly associated with the diversity of communities or ecosystems and considers pattern such as the number of trophic levels, the range of life cycles, the relative abundance of species and the diversity of ecological resources (Tregenza & Butlin 1999, Izsák & Papp 2000).

All aspects of diversity in relation to plants, instead to animals, are represented by **phytodiversity**. This includes all levels of diversity from genes to community. The search for causing effects, often considers abiotic factors, so that phytodiversity is directly connected with ecological diversity.

## 4 Quantity of Plant Species Richness

### 4.1 How Many Species?

This question is also addressed by biodiversity research (May 1988, 1990), but the exact answer is unknown (Barthlott et al. 1996). The number of species worldwide is certainly greater than a million and less than a billion (Wilson 1997), and is estimated at somewhere between 7, 20, 100 and up to 360 million (Barthlott et al. 1996). Roughly, 270000 vascular plant species are described **worldwide**, and about 320000 are estimated (Barthlott et al. 1996, Barthlott & Winiger 1998, Gaston & Spicer 2004). The number of plant species varies with the taxonomic group considered, for example, vascular plants species are composed of about 12000 pteridophytes, 766 gymnosperms, and 250000 angiosperms, in total 263000 species (Whittaker 1998). Worldwide there are about 15000 bryophytes (Mutke & Barthlott 2005, Frahm 2008) and about 25000-30000 lichens (Sipman & Aptroot 2001).



**Figure 1. Vascular plants, bryophytes and fungi of coastal dunes.**

In **Europe**, there are approximately 12000 vascular plant species (Tutin et al. 1980), 3500 of which are restricted to Europe (Lévêque & Mounolou 2004). The number of bryophytes is about 1600 in Europe and about 1000 in Germany (Frahm 2001). **Lower Saxony** and **Bremen** contain about 2500 vascular plant species (Garve 2007).

Dry coastal habitats contain about 5800 vascular plants worldwide; in European dry coastal habitats there are approximately 2400 vascular plants and 350 bryophytes and lichens, examples are shown in Figure 1. Typical coastal plant species represent about 7 % of the total European flora (Van der Maarel & Van der Maarel-Versluys 1997).

(In this manuscript, nomenclature in general according to Wisskirchen & Haeupler (1998) for vascular plants and Koperski et al. (2000) for bryophytes)

## **4.2 Geographic Distribution, Hotspots and Endemism**

### **Biodiversity Hotspots**

In relation to manifold factors, the distribution of species, hence also the geographic distribution of biodiversity varies across the earth. More species occur in some regions than in others, and the distribution is neither random nor uniform over the world (Woodward 1987, Brown 1988, Lévêque & Mounolou 2004). Biogeographic regions with high numbers of endemic species and a dramatic loss of habitats are described as biodiversity hotspots (Myers et al. 2000). Hotspot regions are defined as containing at least 0.5 % or 1500 of the world's 263000 vascular plant species as endemic and having lost at least 70 % of its primary vegetation (Myers et al. 2000). Remarkably about 20 % of the world's human population are living within the recent hotspots. Because of a significantly higher population growth rate in most of these areas, it is suggested that substantial human-induced environmental changes are likely to continue (Cincotta et al. 2000). The hotspot approach considers the original number of species, the recent number of species, and the number of species probably surviving during the considered century. The greater the 'area/species index' (= percent endemics of Earth's species/percent of Earth's land surface) the higher the phytodiversity of a region (Myers 1990). Hotspots recognised by Conservation International, Washington DC, contain 44 % of all vascular plant species and cover only 1.4 % of the land surface worldwide (Myers 1990). Hotspots are mainly in tropical zones, but are also in the Mediterranean region, for example, species richness in Mediterranean areas is similar to those of the Cape fynbos (Ojeda et al. 2000). Moreover, hotspots are present on islands or parts of them (Myers et al. 2000).

Initially, the biodiversity hotspot theory determines key localities of biodiversity under acute threat at a continental or global scale. This could be one instrument used to verify conservation priorities, but it is important not to rule out other criteria (Myers 1990, 2003, Reid 1998, Jennings et al. 2008). The hotspot approach encompasses many critical points, e.g. less representation of other forms of species richness (e.g. the total number of species, the number of threatened or rare species). The classic approach is less valuable for other taxa than vascular plants (e.g. vertebrates, fungi). Moreover, there is a lack of overlap considering different taxa, endemic and rare species, and with phylogenetic diversity (Forest et al. 2007). For example, in South Africa, richness hotspots show the highest overlap with rarity hotspots for vascular plants; but overlap of different taxa is especially low when groups have very different ecological requirements (Prendergast et al. 1993, Dobson et al. 1997). Otherwise, positive correlations are shown between diversity of trees and species richness of specialist-birds (Caprio et al. 2009). For conservation, sites selected should be species-rich for one taxon as well as for others, and should include rare species (Prendergast et al. 1993). Moreover, the classical hotspot approach does not include the protection of smaller species-rich regions, although the approach could be used for nature conservation on regional scales (Venevsky & Venevskaia 2005). Biodiversity hotspots vary with scale depending on the methods used, especially maps, (Carolan 2009). Further critical points of the hotspot approach are missing consideration of changing land use patterns, no protection of ecosystem services, lack of reliable biodiversity indices and comparable measurements (Reid 1998, Possingham & Wilson 2005, Krishnankutty & Chandrasekaran 2007). These problematical aspects will be more visible, for example by

the circumstance, that South Africa's fynbos is species-rich and contain many endemic species, but is relatively poor in rare species (Latimer et al. 2005). Moreover, habitat loss also on small scales is dramatic, for example, species-rich calcareous grasslands have declined locally in Germany by up to 60 % in the last 100 years (Krauss et al. 2004).

In general, biodiversity hotspots are considered as areas of high conservation priority (Kati et al. 2004), but can also be used to designate for example 'Sites of Special Scientific Interest', for example in Wales (Blackstock et al. 1996). Furthermore, the term biodiversity hotspot has recently been used in a broader sense and in relation to a geographical area dealing independently with high species richness, levels of endemism, number of rare or threatened species, or intensity of threat, and can be used for conservation aspects at smaller scales too (Dobson et al. 1997, Myers et al. 2000). For example at a national level, large-scale national biodiversity hotspots were identified from abiotic factors, and regions were determined by species-energy relationships for vascular plants using climate (e.g. mean temperature and precipitation) and topographical and land use data (Francis & Currie 2003). At regional scales, at Great Britain for example, a grid of 10 km × 10 km was used to detect possible sites for conservation, and hotspots were defined as the top 5 % of record-containing 10-km squares; in contrast so-called coldspots are the most species-poor 5 % recorded squares (Prendergast et al. 1993).

## Endemism

Endemism, the number of species that occur only in a restricted distribution area (Gaston & Spicer 2004), is as much of an attribute to biodiversity as species richness is. Both, endemism and species richness represent the complexity and uniqueness of natural ecosystems and allow biodiversity hotspots to be identified (Myers 1990, Caldecott et al. 1996). Endemism is maintained through the development of endemics by speciation, the inability of an endemic species to enlarge its geographic distribution, and the survival of the endemic species over time due to a low extinction rate (Huston 1994). Nevertheless, positive endemics-diversity relationships are not necessarily generated by an increasing speciation rate (Chen & He 2009). The area of endemism can either be relatively large, or else restricted to a well-identified ecosystem (Lévêque & Mounolou 2004). Thus, in relation to the relative extension of the distribution area, local, regional, transregional or continental endemics, and widespread species are distinguished. For local endemism in plants, a distribution area of less than 50000 km<sup>2</sup> has been defined (Gaston & Spicer 2004). Considering evolutionary aspects, there is a differentiation between **neo-endemics**, species that have evolved more recently, and **palaeo-endemics**, species representing evolutionary relicts (Gaston & Spicer 2004). Endemics of European coastal areas are mostly neo-endemics of postglacial or more recent origin. Although the littoral character often supports a wider distribution and large population sizes, due to e.g. restricted habitat specifics, many coastal sites promote the differentiation and adaptive radiation of new taxa (May 1988). For example, cliffs that have a function both as refuge for ancient isolated palaeo-endemics and act as an isolated ecological niche, stimulate the adaptive radiation of neo-endemics (Lovrić 1997). In general, many oceanic island endemics formerly showed a larger, continental distribution (Whittaker 1998). This is probably not the case for vascular endemic plants of the Dutch, German and Danish Wadden Sea Islands, because of the islands origin, their comparable young age, and their close proximity to the mainland.

Levels of endemism often show similar patterns of variation like total species richness (Cowling & Samways 1995). The number and proportion of endemics increase with area, although species-area relationships (Chapter 7) are weaker than such considering total species richness (Major 1988, Anderson 1994, Cowling & Samways 1995, McKinney 2002, Gaston & Spicer 2004). There are many exceptions, e.g. oceanic islands such as Hawaii tend to have high levels of endemism but relatively low total species richness (Gaston & Spicer 2004). The number of endemic species varies in different floristic regions (Whittaker 1975, Richter 1998), and the level of endemism increases towards lower latitudes (Chapter 8) (Fischer 1960, Pianka 1966, Major 1988, Cowling et al. 1992, Cowling & Samways 1995). Thus, in the Mediterranean, also due to recent speciation and isolation, 10 % of the genera and 40 % of the species are found nowhere else in the world (Tallis 1991). On the other hand, only 0.001 % of the vascular plants are **cosmopolites**, each occupying about a quarter of the earth's surface (Anderson 1994). In particular, regions in the northern hemisphere with glaciations during the Pleistocene contain lower numbers of total species, as well as of endemic ones. Thus, the number of endemic species in Europe represents only about 2-6 % of global species richness (Cowling & Samways 1995).

There are different reasons for the **cause of endemism**, for example, independent evolution of local adaptations due to different environmental conditions speciation. Environmental conditions and resulting barriers determine, for example, the high value (63 %) of endemic cactus species (Hernández et al. 2001). Geographic or other possibilities of isolation facilitate independent evolution; endemism on isolated oceanic islands often reaches high levels, due to patterns of dispersal, genetic isolation, and speciation. Endemism is correlated with species traits, e.g. short-distance dispersal, there are few endemics that are wind dispersed (McDonald et al. 1995, Caldecott et al. 1996). Thus, endemism is often low in landscapes with homogeneous topographic relief, because of the absence of topographic or environmental barriers (Anderson 1994, Huston 1994). Furthermore, the longer an area has been isolated, the greater the number of endemic species that occurs there (Caldecott et al. 1996).

The proportion of endemic species on islands increases with increasing geographic distance to the mainland. About 20 % of plant species found on the Canaries are endemic (100 km distance), and about 90 % on Samoa and Hawaii (1200 km distance) (Adersen 1995, Whittaker 1998, Carine et al. 2009). Historical changes in environmental conditions can limit formerly more widespread species to restricted areas (Kruckeberg & Rabinowitz 1985, Major 1988). On the mainland high endemic richness is often related to long-term climatic stability; facilitating the survival of periods of major global climatic change, like glaciations in the Alps. Such areas often also represent evolutionary hotspots, where various evolutionary events have taken place (Gaston & Spicer 2004). Moreover, many areas of high endemism are characterised by low productivity, because of low levels of soil nutrients or water (Huston 1994). The ratio of endemic/total species number on islands is between 0.43-0.52, but can reach values up to 0.81 in biological hotspots (Prendergast et al. 1993, Venevsky & Venevskaia 2005).

## Endemic Species in Coastal Areas

In coastal areas, especially in areas directly connected to the sea like driftlines and saltmarshes, the endemic richness is lower than in inland areas. This is because of the high number of littoral species with a wide distribution like *Cakile maritima* and *Salsola kali*. Along with their coastal distribution, littoral plant species often show a continental, Asian distribution. Otherwise, approximately 20 % of all European endemics occur in coastal areas (Van der Maarel & Van der Maarel-Versluys 1997). Similar to inland areas, the number of endemic species of dry coastal ecosystems reaches higher values at lower latitudes e.g. at the Adriatic coast, and thus Mediterranean European coastal areas represent higher levels of endemism. Local endemics often occur on islands, such as the Canary Islands, New Zealand, Cuba, the British Isles, Corsica, Sardinia, Sicily, and Malta (Van der Maarel & Van der Maarel-Versluys 1997).

One example of endemic species in coastal areas of the world is the shrub *Chamaecrista chamaecristoides* var. *chamaecristoides*, which is commonly found on the sand dunes along the Gulf of Mexico (Martínez 2003). Along coastal areas of the Wadden Sea, endemism occurs mainly below the species level (Westhoff 1947), for example, in saltmarshes, *Juncus articulatus* ssp. *litoralis* and *Odontites vernus* ssp. *pumilus* (Dijkema et al. 1993). Sometimes there are different subspecies in coastal as well as inland areas, e.g. *Anthyllis vulneraria* or *Festuca rubra*, with different subspecies on dunes, saltmarshes, and cliffs. Furthermore, coastal ecotypes, often with less clear morphological characteristics but with considerable amounts of genetic variation, occur, e.g. *Tripleurospermum maritimum*, *Rumex crispus*, and *Sonchus arvensis* (Dijkema et al. 1993, Akeroyd 1997).

Endemic status of species is dynamic, and there are shifts from common to rare and the reverse. For example, *Lactuca tatarica* was considered as locally endemic on the islands of Hiddensee between the years 1902 and 1910. *Lactuca tatarica* has spread widely during the last century and is now distributed along the entire coast of Mecklenburg-Vorpommern (Krisch 1989), and currently represents a naturalised neophyte, that plays an important role in some plant communities e.g. with *Honckenya peploides* (Isermann 2004). Many taxa throughout the world began as local introductions, which then spread in varying degrees. A further example is *Spartina x townsendii*, which occurs in saltmarshes. Originally found at few localities, this species has become more widespread over time (Kruckeberg & Rabinowitz 1985).

Comparing species distributed in Lower Saxony (Garve 2007), many coastal endemics occur, especially in **saltmarshes**: *Armeria maritima* ssp. *maritima*, *Artemisia maritima*, *Blysmus rufus*, *Centaureum littorale* ssp. *littorale*, *Cochlearia anglica*, *Cochlearia officinalis*, *Elymus athericus*, *Festuca rubra* ssp. *litoralis*, *Limonium vulgare*, *Odontites litoralis*, *Oenanthe lachenalii*, *Parapholis strigosa*, *Puccinellia maritima*, *Ranunculus peltatus* ssp. *baudotii*, *Ruppia maritima*, *Sagina maritima*, *Spartina anglica*, *Taraxacum obliquum* and other *Taraxacum* species, and in the marine environment *Zostera marina* and *Zostera noltii*. Some endemics occur in **dune valleys**: *Carex extensa*, *Carex punctata*, *Carex trinervis*, *Epipactis heleborine* ssp. *neerlandica*, *Gentianella campestris* ssp. *baltica*, *Gentianella uliginosa*, *Juncus anceps*, *Juncus maritimus*, *Schoenus nigricans*. Others on **driftlines**: *Atriplex glabriuscula*, *Atriplex lacinata*, *Atriplex longipes* ssp.

*longipes*, *Atriplex portulacoides*, *Beta vulgaris* ssp. *maritima*, *Cakile maritima* ssp. *maritima*, *Glaucium flavum*, *Honckenya peploides*, *Salsola kali* ssp. *kali*.

Furthermore, some endemics occur in **dunes**: *Anthyllis vulneraria* ssp. *maritima*, *XCalammophila baltica*, *Calystegia soldanella*, *Cerastium diffusum*, *Elymus* x *obtusiusculus*, *Elymus farctus* ssp. *boreoatlanticus*, *Erodium ballii*, *Eryngium maritimum*, *Festuca rubra* ssp. *arenaria*, *Koeleria arenaria*, *Lathyrus maritimus*, *Phleum arenarium*, *Rosa spinosissima*, *Senecio jacobaea* ssp. *dunensis*, *Thalictrum minus* ssp. *saxatile*, *Tuberaria guttata*.

Due to the restriction to coastal areas, these species are often of special conservation value, and therefore protected, for example, as red-book-species.

## 5 Scales: Taxonomic, Spatial and Temporal Scale

Biodiversity encompasses a hierarchy of scales and varies like other biogeographic patterns with scale (Myers & Giller 1988, Keeley & Swift 1995, Willis & Whittaker 2002). The description of species-distribution patterns and their underlying mechanisms are of importance in ecological research (Ricklefs & Schluter 1993, Gaston 2000, Whittaker et al. 2001). More recently, spatial and temporal scales have been recognised as further factors determining the mechanisms explaining species diversity and distribution (Wiens 1989, Gross et al. 2000, Whittaker et al. 2001). Scale can affect results and even more the comparison of outcomes between similar studies (Scheiner et al. 2000). Relationships between species and environment vary at different spatio-temporal scales (Levin 1992, Holt 1993, Scheiner et al. 2000). Parameters and processes important at one scale are often less important at another (Turner 1990, Whittaker 1998, Ricklefs 2005).

There are three types of scale in accordance to biodiversity:

- **taxonomic scale**, from populations to higher taxa like families,
- **spatial scale**, from local to global patterns, and
- **temporal scale**, from short-term ecological periods (over tens of years) to long-term evolutionary periods.

Objects of biodiversity investigations, often according to the three main types of scale, are, for example, genes, populations, species, assemblages (phylogenetically related members of a community), communities (set of species occurring at a specified area usually with geographic boundary and at a specified time), and whole systems at the ecosystem or landscape level (Soulé 1991, Magurran 2006).

### Taxonomic Scale

In relation to phyto-diversity, it is, for example, possible to distinguish between:

- **systematic entities**, such as subspecies, species, genera, families etc.,
- **functional groups**, e.g. nitrogen and non-nitrogen fixing species,
- **life-forms**, for example, according to Raunkiaer (1934), it is possible to differentiate between groups such as phanerophytes, nanophanerophytes, therophytes and others, and
- **life-form groups**, which mix different aspects of the three first mentioned types, e.g. herbs and grasses, shrubs and trees.

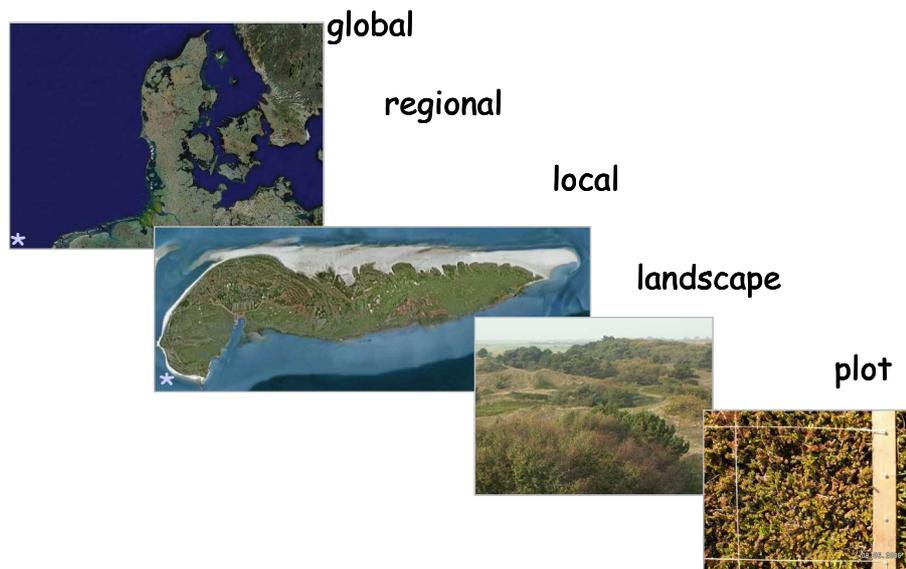
Relations between biodiversity and environmental factors are often more visible regarding, for example, functional groups or life-forms, because these entities often reflect general conditions of an ecosystem.

### Spatial Scale

Patterns and processes determining species diversity change across spatial scales (Table 2) (Crist et al. 2003, Pearson & Dawson 2003).

Although limiting criteria keep moving, three main magnitudes (global, regional, and local scale) are distinguished (Figure 2):

- **global scale**, concerning worldwide patterns of species diversity,
- **regional scale**, considering aspects across different biotopes. Regional scales range in size from tens or hundreds of metres to an entire continent (Leser & Nagel 1998), and include the landscape scale, and
- **local scale**, reaching sizes up to few hundreds of metres, and including plot scale.



**Figure 2.** The spatial scale describes a hierarchy of different levels from the global scale, to regional scales such as the Wadden Sea area, to local scales like the island of Spiekeroog, to the landscape scale considering for example different dune habitats and to the plot scale (\* Earth.Google).

In more detail, it is possible to differentiate between global, continental, interregional, regional, landscape, local, site information, and plot or micro scale (Whittaker 1977, Caldecott et al. 1996, Veech et al. 2002, Pearson & Dawson 2003, Legendre et al. 2005). This study defined large scale as global to landscape scale, and small scale as local to micro scale (Table 2). More precise, the spatial scale concept refers to the size of the sampling unit, and the geographical extent represents the geographical distance used for comparisons (Whittaker et al. 2001). The combination of various factors over different spatial and temporal scales supports understanding of biodiversity in a hierarchical model (Table 2) (Whittaker et al. 2001, Willis & Whittaker 2002).

In relation to spatial patterns in biodiversity, species richness of an area is affected by sampling effects (Chapter 6.4), and heterogeneity of the environment (Chapter 7.2). Furthermore, historical patterns (Chapter 9.1.1) such as glaciations, available resources, niche partitioning, environmental stress i.e. favourable and unfavourable sites, stability of the system, as well as disturbance (Chapter 8.3.2), and biological interactions like competition (Chapter 8.3.3) (Whittaker et al. 2001). Different environmental factors and types of ecological processes are important drivers both at different scales, and to a different extent (Field et al. 2009). For example at small scales, ecological interactions are the most important process predicting plant diversity, but at large scales, patterns such as

macroclimate or landscape topography are more important (Crawley & Harral 2001, Whittaker et al. 2001, Willis & Whittaker 2002, Dufour et al. 2006).

## **Temporal Scale**

The temporal scale represents the variation of biodiversity in time. Although, similar to spatial patterns, temporal variation has a large range; two main temporal scales were distinguished (Brown 1988):

- long-term or **evolutionary** periods (Chapter 9.1), and
- short-term or **ecological** periods (Chapter 9.2, 9.3).

In general, independent to the event when the observation has started, species richness at first increases fast and then levels off or declines (Brown 1988). In the long-term, changes in biodiversity result from the differences between rates of speciation and extinction, while in the short-term this is from establishment and disappearance, and the coexistence of different species (Yamamura 1997).

Measuring biodiversity over time belongs to monitoring concepts, collecting ecosystem information at different time to assess ecosystem changes (Yoccoz et al. 2001, Duelli & Obrist 2003). Temporal changes in diversity are usually measured as turnover in time. The turnover rate is the number of different species between two adjacent areas divided by the total number of species in two adjacent areas. Similar to other ecological aspects, few long-term biodiversity investigations exist (Willis et al. 2005).



## 6 Measuring Biodiversity

Quantifying biodiversity is important for the assessment of areas in relation to nature conservation, for the development of conservation strategies and for management measures. Therefore, it is, for example, also necessary to consider biodiversity patterns over time and in different geographical zones (Lévêque & Mounolou 2004), as well as in relation to different scales.

Many measurement methods of biodiversity exist and are described in detail, for example by Magurran (2006), consequently only some of them are mentioned here. Moreover, a universal measure, considering all aspects of biodiversity in a specified system is not available (Lévêque & Mounolou 2004), and diversity indices are often not appropriate for ecological applications (Peet 1975). Species richness and measures of heterogeneity and evenness respectively could be independent, and therefore both should be assessed (Weiher & Keddy 1999, Ma 2005, González-Megías et al. 2007). Especially, because evenness considers not only the number of species but also species abundances, indices often allow a better description of the communities (Kempton 1979). Due to different forms of calculation, the comparison of different diversity indices is sensible for conservation decisions (Pitkänen 1998, Lennon et al. 2001).

Biodiversity measures are traditionally categorised into two main concepts: **species richness** and **equitability, evenness** whereas **richness** is the number of species and **evenness** the equitability with which the individuals are distributed among them. Evenness is a measure of how similar species are in their abundance (Good 1953, Connell 1961, Lloyd & Ghelardi 1964, McIntosh 1976). Although, the term diversity very often represents the number of species of one or several ecosystem components, the term species diversity includes both, the number of species in a specified area at a given time (**species richness**) and the species equitability (**species evenness**) with which the according individuals are distributed (Hurlbert 1971, Kempton & Wedderburn 1978).

### 6.1 *Species Richness, Equitability, Abundance, Functional Diversity*

#### Species Richness

The simplest and oldest measure of diversity is the number of species (Peterson 1976). There are two main methods measuring species richness: **species richness**, in its strictest sense, is expressed as the number of species per specified number of individuals or biomass and **species-density** is measured as the number of species per specified area (Whittaker 1975, Lomolino 2001, Whittaker et al. 2001, Magurran 2006). This distinction represents an **individual-based** approach, with special indices, like Margalef's diversity index, dividing the number of species recorded by the total number of individuals in the sample; and a **sample-based** approach (Gotelli & Colwell 2001, Magurran 2006).

This study does not distinguish between both terms. The term species richness is generally used as number of species per area, and in the case of productivity-diversity pattern (Chapter 8.3.3.2) it is used as number of species per specified biomass per square metre.

## Equitability, Evenness

The distribution of species in the environment is not equally common, some species are very abundant, others rare. Highest evenness is reached if most species of an assemblage are equally abundant. It is necessary to distinguish between both diversity concepts, i.e. the number of species and evenness, because an area with few, evenly represented species can have the same diversity value as one with many, unevenly represented species (Peet 1974, Pielou 1975, Moreno et al. 2006).

Diversity indices are subdivided into **parametric measures** of diversity on the one hand. On the other hand, there are various **nonparametric measures** of diversity, which are distinguished into indices of **information statistics** as well as abundance-weighted diversity (**dominance** and **evenness**), and **divergence measures** (Magurran 2006, Ricotta 2007).

One of the most used **information indices**, despite its disadvantages e.g. depending on the plot size investigated, is the **Shannon index  $H'$**  also known as Shannon **information index** or the Shannon and Wiener index (Hurlbert 1971, Martin & Rey 2000, Southwood & Henderson 2000, Magurran 2006). The Shannon index emphasises the **species richness** component of diversity, and rigorously assumes random sampling (Pielou 1975). There are many other information-indices such as Brillouin's index (Brillouin 1962), that could be used especially in the case of non-random sampling (Pielou 1975).

The second group of diversity indices, often weighted by abundance of the commonest species, usually represents either **dominance indices** or **equitability (evenness) indices** (Lloyd & Ghelardi 1964). Typical indices of compositional diversity such as Shannon index or Simpson index based on species relative abundance. Although each index considers rare and abundant species differently, high species richness and high equitability in species relative abundances jointly imply high compositional diversity (Ricotta 2007).

One common **dominance index** is the **Simpson index ( $D$ )**, also called Simpson's index of concentration (Simpson 1949). It does not increase with area or depend on the log-series or any other distribution, but it is necessary to count individuals. Simpson index increases as diversity declines and reached the value 1.0, if all individuals belong to a single species (Rosenzweig & Abramsky 1993). In its original form Simpson index is less favourable for interpretation due to the circumstance that increasing  $D$  represents decreasing diversity. Therefore Simpson's index is often expressed as the **complement ( $1-D$ )** or **reciprocal ( $1/D$ )** form, both representing increasing values with increasing dominance of one or few species (Pielou 1975). Similar to Shannon index, Simpson's index stressed values of the most abundant species in the sample, but in contrast to the Shannon index, it is less sensitive to species richness (Kempton & Wedderburn 1978). Furthermore, Simpson's index in some cases is scale dependent (Simpson 1949), nevertheless, it is one of the most meaningful and robust measures of diversity (Magurran 2006).

**Evenness** quantifies the equality of species abundances, whereas maximum value (1.0) of evenness is reached in the case of an equal distribution of species abundances, and the more the relative abundances of species differ, the lower the evenness. The **Shannon evenness ( $J'$ )** is often used, derived from the Shannon index  $H'$  (Pielou 1975) this

represents the ratio of observed diversity ( $H'$ ) to maximum diversity. More recently, indices combining richness and abundance are of interest (Gorelick 2006).

**Divergence measures** represent diversity indices, which include inter-species differences, such as the quadratic diversity  $Q$  that incorporates both species relative abundances and pairwise distances between species (Ricotta & Szeidl 2006, Ricotta 2007).

In addition, evenness is affected by spatial scale, and increases with plot size in the case of random sampling; but decreases with plot size in the case of non-random sampling. Changes in evenness with scale are based on small-scale environmental variations (Wilson et al. 1999).

## Abundance Measures

Estimating the number of plant individuals, i.e. the abundance, can be difficult, for example, in the case of clonally growth or in dense vegetation. Thus, substitutes could be used, like the number of **modular units** per species in a plant community (Harper 1977). These units are relatively constant in size within a species, and include the shoots and tillers of a species. A more suitable measure of abundance is **phytomass**, which is especially related to resource uses (Pielou 1966, Hector et al. 1999). Vegetation studies generally use plant **cover** as abundance measure, expressed as the percentage of a specified area (Whittaker 1965). Plant cover can be estimated in different ways: directly in the field, in certain circumstances from aerial photographs and with remote sensing techniques. Although more applicable, cover scales such as that of Braun-Blanquet, has little relevance in diversity measurement, and were mainly transformed into percentage values. Furthermore, abundance could be estimated using **frequency** or **incidence**, the number of sampling units in which a species occur.

Each abundance measure affects biodiversity patterns with varying amount, so the comparison of cover and phytomass show little differences between rank/abundance plots as well as species richness patterns, but there is less congruence regarding evenness (Chiarucci et al. 1999). In distinctive vertical structured vegetation the use of phytomass, due to its volume relation, strengthens differences between species of high and low abundances in relation to growth height (Magurran 2006).

## Functional Diversity

Biodiversity includes the numbers of entities (how many genotypes, species), the evenness of their distribution, but also the differences in their **functional traits** (Hooper & Vitousek 1997, Chapin et al. 2000, Hooper et al. 2005).

**Functional diversity (FD)** refers to the range and the value of organismal traits that influence ecosystem properties, which means to those components of biodiversity that influence the run, the function of an ecosystem (Tilman 2000). It can be measured as the extent of functional differences among the species in a community and is a key to ecosystem processes (Grime 1979, Chapin et al. 2000, Tilman 2000, Loreau et al. 2001). Thus, functional diversity represents community diversity associated to its effects on ecosystem functioning (Ricotta 2007), and in addition, ecosystem functioning encompasses a variety of phenomena such as ecosystem properties, ecosystem goods, and ecosystem services.

Differences in traits of species verify the substitution of species diversity with functional diversity measures, to emphasise the extent of functional differences in a community (Ricotta 2005). There are different approaches to define and measure functional diversity, such as the variation in the functional characters of plant species, or the number of functional groups present in an assemblage (Hooper & Vitousek 1997, Tilman et al. 1997, Naeem 1998, Hector et al. 1999, Tilman & Lehman 2001, Tilman et al. 2001, Moles & Hayes 2002, Petchey & Gaston 2002a, b, Mason et al. 2003, 2005, Petchey 2004, Ricotta 2005, De Bello et al. 2009). Functional groups can be broadly defined (legumes, grasses, herbs, wintering birds, woody plants, butterflies), or more finely divided (early and late annuals, perennial grasses) (Hooper & Vitousek 1997, Lawton 2000). Analogue to species diversity, functional diversity can be split into **functional richness**, i.e. the amount of functional traits, and **functional evenness**, i.e. the evenness of abundance distribution of functional traits (Mouillot et al. 2005).

The concept of functional diversity is based on the one end at the assumption, that some species are functionally identical, such that functional groups exist. On the other end, there is the assumption that every species is functionally unique, thus species are not redundant in their functions, so that species-loss always reduce functional diversity. However, in reality, it is probably a gradual relation, some species are more similar in their function than others at rough functional scales are, and all species vary at smaller scales (Petchey & Gaston 2002b).

The positive relationship between species diversity and particularly long-term ecosystem functioning is related to the greater number of functional groups in richer assemblages (Schulze & Mooney 1993, Diaz & Cabido 1997, Tilman 1997, 1999, 2000, Hector et al. 1999, Chapin et al. 2000, Schwartz et al. 2000, Kinzig et al. 2001, Loreau et al. 2001, Hooper et al. 2002). However, the general concept between species diversity and ecosystem functioning is probably limited due to the existence of a maximum species pool for each assembly (Schmid et al. 2001). Comparing effects of abiotic factors on plant diversity, ecosystem functions were low at both extremes of species diversity (Kutiel & Danin 1987). According to scale, there is the assumption of unimodal relationships between diversity and ecosystem functioning at local scales, and positive linear ones with levelling-out at regional scales due the principle of complementarity (Loreau et al. 2001, Bond & Chase 2002, Hooper et al. 2002). Additionally, there are negative linear ones for example with increasing agricultural land use intensity (Flynn et al. 2009).

Ecosystems containing numerous species with similar functions appear to have a higher **stability** than those with only few species with similar traits (Lévêque & Mounolou 2004). Thus, the assumption is that ecosystem function depends not on the number of species itself, but on the number of functional traits of those species (Hooper & Vitousek 1997). Functional group richness enhances niche exploitation, for example, due to more efficient resource use complementarity. Complementarity probably results in a higher performance of a mixture than those of each species of an assemblage, which is often attributed to niche partitioning or facilitation (Tilman et al. 1997, Duffy et al. 2007). Thus, FD measures the extent of resource use complementarity among species and thereby is an explanation for effects of resource complementarity on ecosystem processes (Tilman et al. 1997, Hooper et al. 2002, Petchey 2004).

High degree of niche differentiation and thus low resource competition is indicated by high functional divergence. Thus, communities with high functional divergence may have increased ecosystem function, maintaining the system in a dynamic equilibrium. Consequently, an ecosystem with a higher functional diversity operates more efficiently (Hooper & Vitousek 1997, Tilman et al. 1997, Mason et al. 2005). Increasing functional diversity supports productivity (Tilman et al. 1997), improves stability according to disturbance events and other environmental changes (Kinzig et al. 2001) and enhances resilience and resistance to invasions. High native species richness is required to maximise ecosystem stability and maintain function (Tilman 1997, Schwartz et al. 2000). Lower functional diversity possibly reduces **invasion resistance** (Chapter 9.3), due to available gaps in niche space, which an invader can exploit (Petchey 2004, Mason et al. 2005, Ricotta 2005).

Increasing biodiversity tends to increase **biomass**, thus there is generally a positive relationship between biodiversity and ecosystem functioning (Kinzig et al. 2001, Jiang et al. 2008). Considering functional traits, the loss of one or few abundant and dominant species respectively, eventually results in a distinct change in ecosystem function due to the loss of representative species with essential traits and only secondly based on the loss of biomass (Sala et al. 1996). However, functional groups have stronger effects on ecosystem functioning than species richness, which was shown, for example, by increasing decomposition rates with increasing number of functional groups (Scherer-Lorenzen 2008), as well as in changes of bird and mammal communities (Flynn et al. 2009).

Biodiversity affects ecosystem functioning (Schmid et al. 2001). Three main approaches describe the relationship between decline in species richness and ecosystem functioning (Lawton 1994, Naeem 1998): 1) **Redundancy**: many species are similar in their function, thus only a minimum number of species are necessary for basic ecosystem process, and species loss of little importance. Thus at first, ecosystem function increases with increasing biodiversity more or less linearly, and levels-out once the minimum number of necessary species is reached. 2) **Rivet-popping**: it is assumed that the loss of few species has no obvious influence on ecosystem functioning, but beyond a limit, the ecosystem function declines. The relationship between biodiversity and ecosystem functioning can be described as an increasing stair-formed curve. 3) **Idiosyncrasy**: Each change in diversity results in a change of ecosystem function, but without predictable magnitude and direction of the change, because each individual species have complex and different functions. The resulting relation represents an irregularly waved line. Thus, biodiversity can at least partly act as insurance for ecosystem functioning against environmental changes (Loreau et al. 2003).

In general, the argument that the maintenance of biodiversity is essential for the sustainable provision of ecosystem services is perhaps the most powerful justification for the conservation of biodiversity (Ridder 2008). However, the redundant species hypothesis implies that there is a minimal species richness required for ecosystem functioning (Lawton 2000), but this has disastrous consequences for nature conservation, because rare species will possibly be of lower interest. On the other hand, habitat modifications that change functional diversity have large impacts on ecosystem processes, in comparison to changes in species richness. Nevertheless, it is a gradient, and both, the effects of species

richness and of functional diversity increase with the extent of the differences among species or functional groups (Tilman et al. 1997).

## 6.2 Spatial Levels of Species Diversity

According to spatial scale, different levels of species diversity were distinguished (Table 3), although diversity scales are not discrete entities and represent more or less a continuum, without a completely strong hierarchical structure and with different proportions of the diversity levels (Loreau 2000). The main **diversity levels** ( $\alpha$ ,  $\beta$  and  $\gamma$ -diversity) were gained from the increasing species diversity across transects, for example, from the beach inland, whereas species diversity based on two phenomena, the diversity of each individual stand and the relative differentiation of vegetation patterns along environmental gradients (Whittaker 1960). Hence, different diversity levels are related to two approaches.

The first one, the **inventory diversity** represents the diversity of a specified geographic unit. **Point diversity** represents the diversity of a single sample, the number of species in a single plot;  **$\alpha$  (alpha) diversity** is the diversity of a set of samples (or within-habitat diversity);  **$\gamma$  (gamma) diversity** represents the diversity of a landscape and  **$\epsilon$  (epsilon) diversity**, the diversity of one biogeographic province (Table 3).

The second approach, the **differentiation diversity**, describes the variation in the diversity between different geographic units of the same spatial scale. **Pattern diversity** describes the variation between samples within one habitat,  **$\beta$  (beta) diversity** that of between-habitat diversity,  **$\delta$  (delta) diversity** is the change in species composition and abundance between landscapes, along geographical gradients of one biogeographic province (Whittaker 1960, 1972, Cowling et al. 1992, Magurran 2006). The concrete size of the area associated with diversity levels is defined very differently in the literature (Whittaker et al. 2001).

**Table 3. Levels of inventory and differentiation diversity in relation to spatial scale (according to Whittaker 1972, Whittaker et al. 2001, Magurran 2006, enhanced).**

Scale	inventory diversity	differentiation diversity	relation in dunes, diversity
within sample	point diversity		of one plot
between samples, within habitat		pattern diversity	between plots of one dune series, e.g. yellow, grey or brown dunes
within habitat	$\alpha$ -diversity		of one dune type
between habitat, within landscape		$\beta$ -diversity	along a transect from the beach inland to the brown dunes
within landscape	$\gamma$ -diversity		of one island
between landscape		$\delta$ -diversity	between dunes in NW-Germany
within biogeographic province	$\epsilon$ -diversity		of the dunes in the Wadden Sea area

In general, each level of inventory diversity can be measured with the same methods (see above), but often the larger the scale, the less species-abundance and the more species richness or higher taxon diversity are used. However, differentiation diversity, the comparison of areas, requires different measures (Whittaker 1960, Gaston 1996, Magurran 2006).

## Main Diversity Levels

### $\alpha$ -diversity

Alpha diversity (primary diversity), is a small-scale measure and represents the species richness of a particular stand, a community, a given stratum or a group of organisms in a stand and refers to the number of species in a homogeneous entity, and represents within habitat diversity. Thus, it is sensitive to the definition of homogeneity and habitat, respectively. In general, it is expressed by the number of species (Brown 1988); in large vegetation databases it is sometimes defined as the number of plant species occurring in one relevé (Willner et al. 2004). According to vegetation science, correlations between  $\alpha$ -diversity and environment can be shown on the level of single relevés, but also on the community level (Willner et al. 2004).

### $\beta$ -diversity

Beta diversity (secondary diversity), the so-called **habitat diversity**, measures the extents of composition change between communities or the degree of community differentiation along an environmental gradient (Whittaker 1972). It corresponds to the spatial turnover in species composition between sites of a heterogeneous region (Brown 1988). Various terms of similar meanings are e.g. rate of species-composition change, species turnover, species replacement rate, as well as rate of biotic change (Pielou 1975).  $\beta$ -diversity describes the degree to which habitats have been partitioned by species, and represents a possibility to compare habitat diversity of different systems (Wilson & Shmida 1984); hence, it has direct relevance for nature conservation (Cody 1986, Thomas 1990, Harrison et al. 1992).

There are various indices measuring  $\beta$ -diversity, which could be divided into three categories:

- 1) Measures that show the **difference in  $\alpha$ -diversity** between two or more areas relative to  $\gamma$ -diversity, whereas  $\gamma$ -diversity generally is expressed as total species richness of the area. Beta diversity may be calculated simply as the inverse of the mean number of habitats occupied by each species occurring in the region (1/mean number of habitats per species) (Ward et al. 1999).
- 2) Measures that focus on the differences in species composition amongst areas of  $\alpha$ -diversity, and stressed complementarity/distinctness or similarity/dissimilarity. **Complementarity indices**, for example **Jaccard** and **Bray-Curtis coefficients** describe the difference between sites related to the occurring species. The more complementary two sites are, the higher their  $\beta$ -diversity. Usually combined are three variables: the total number of species present in two sides, the number of species present only in one side and the number of species present in the other side. According to nature conservation, complementarity indices can be used to select a group of areas, which mutually represent

the maximum of species (Pimm & Lawton 1998). **Similarity** and **dissimilarity coefficients**, respectively, are common indices such as the **Sørensen's** similarity index (Sørensen 1948) that measure the proportion of species shared between any two plots. Furthermore, the **Jaccard similarity index** (Jaccard 1902) divides the number of species in both samples by the number of species in one of both, resulting in similar results to the Sørensen index, but with a slightly less straight-forward interpretation (Vellend 2001, Burnham 2004, Lévêque & Mounolou 2004).

3) Measures that take advantage of the species-area relationships (Chapter 7) and consider **turnover** of species in relation to area (Harte et al. 1999, Lennon et al. 2001, Ricotta et al. 2002). The slope ( $z$ ) in the relation between log species and log area (Chapter 7), or the slope ( $m$ ) in the relation between the number of species and log area, can be considered as a measure of turnover if plots represent nested design (Lennon et al. 2001, Mumby 2001). For example, species turnover of vascular plants and bryophytes across distance gradients in Great Britain, using distribution maps in a 10 km  $\times$  10 km grid system, was expressed as the proportion of the total number of species in the transect to the mean number of species in each 50 km  $\times$  50 km square (Harrison et al. 1992).

Most indices of  $\beta$ -diversity are scale dependent, declining with increasing area (Lévêque & Mounolou 2004), and increasing with the number of communities in an area, reflecting environmental heterogeneity, which is obviously the predominant factor (Økland et al. 1990, Harrison et al. 1992, Willner et al. 2004). In addition, turnover varies among taxa due to niche speciation. The rate at which species are added, with increasing area is strongly related to the heterogeneity of the environment (Harner & Harper 1976). Thus, habitat diversity has been assumed as the ecological determinant of  $\beta$ -diversity (Shmida & Wilson 1985, Harrison et al. 1992). However, areas with similar habitat diversity may have very different rates of species turnover (Shmida & Wilson 1985).

Similar to the measurement of  $\beta$ -diversity,  $\delta$ -diversity can be measured and represent the change of species composition from one landscape, to another. Differences between floras are measured, for example, by means of the Sørensen coefficient (Kruger & Taylor 1979).

### **$\gamma$ -diversity**

Gamma diversity (tertiary diversity) is a measure for **landscape diversity** (Table 3) and is sometimes called ecodiversity (Barthlott et al. 1996). It is given by the number of species that live in a more or less heterogeneous region, i.e. the total number of species in all habitats, within a geographical area. Species richness of landscapes depends on two patterns, species-rich communities ( $\alpha$ -diversity) and a high turnover along environmental and geographical gradients ( $\beta$ -diversity) (Weibull & Rydin 2005). High species-turnover due to steep habitat gradients is one reason for the high species diversity of the Cape Peninsula (Simmons & Cowling 1996).

In general, environmental heterogeneity is often the strongest determinant of total species richness (Wohlgemuth 1998). There is a strong relationship between  $\alpha$ - and  $\gamma$ -diversity; on the one hand, the regional species pool is determined by the species richness of local sites, probably heterogeneous in environmental conditions, while on the other hand,  $\alpha$ -diversity is limited by the number of species of these climatic regions due to microclimate (Rickleffs 1987).

Therefore,  $\gamma$ -diversity considers species diversity of both a number of samples as well as across various habitats; hence,  $\gamma$ -diversity is a resultant of both  $\alpha$ - and  $\beta$ -diversity. Traditionally  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity are related in a multiplicative way ( $D\gamma = D\alpha * D\beta$ ) or, as explained in the following, in an additive way. When the same species occur in all habitats of a region, then  $\alpha$ - and  $\gamma$ -diversity are equal. Thus, the landscape diversity can be partitioned into  $D\gamma = D\alpha + D\beta$  (Whittaker 1960, 1972, 1977, MacArthur 1965, Wilson & Shmida 1984). In more detail,  $D\gamma = D\alpha + D\beta_s + D\beta_r$ , whereas  $D\beta_s$  is the between-site and  $D\beta_r$  the between-region  $\beta$ -diversity. In the case of vascular plants, the proportion of  $\alpha$ -diversity is between 18 and 40 % of the total diversity.  $\beta$ -diversity between sites ( $D\beta_s$ ) is often very similar for all taxa; and  $\beta$ -diversity between regions ( $D\beta_r$ ) seems to be lowest for plants with values of about 20 % (Clough et al. 2007).

Gamma diversity can be measured by most of the indices mentioned in relation to  $\beta$ -diversity, for example, with Shannon index or Simpson index, based on the proportion of area of different habitat types (Ricklefs & Lovette 1999, Krauss et al. 2004, Ewers et al. 2005). Nevertheless, most of these indices, independent of the multiplicative or additive relation, fail comparing communities of different continents, of different hierarchical levels or different ecosystems, because  $\beta$  is dependent on  $\alpha$ -diversity (Jost 2007).

### 6.3 Monitoring and Field Measurements

#### Monitoring

Monitoring is at least necessary to evaluate biodiversity changes, in relation to the aim of 2010 Biodiversity Target of the Convention on Biological Diversity, to reach a distinct reduction of the rate of biodiversity loss (Buckland et al. 2005). Monitoring biodiversity can be described as **measuring biodiversity over time** (Willis et al. 2005), and is the collection of ecosystem information at different times to estimate changes in relation to nature conservation. It is the collection and analysis of repeated measurements for the assessment of an area in relation to nature conservation, in order to evaluate changes in condition and progress and to facilitate the development of conservation strategies and management measures (Lévêque & Mounolou 2004). Furthermore, monitoring can be related to compositional, structural or functional diversity (Duelli & Obrist 2003).

In addition to pure ecological measurements, monitoring represents a feedback link between humans and the environment. Monitoring to maintain conservation of biodiversity integrates socioeconomic factors and quantitative and qualitative information, such as the type, the amount and/or the frequency of humans influence. Therefore monitoring is important to assess the efficiency of conservation measures achieving the sustainable protection of biodiversity (Bawa & Menon 1997, Niemelä 2000). Because of the severe decline in biodiversity, inventory and monitoring should have high priority in relation to policy-making and public opinion (Stork et al. 1996).

Furthermore, it is necessary to consider biodiversity patterns over time in **different geographical regions**, because conservation measures operate differently in relation to time, as well as at local and regional scales, respectively (Lévêque & Mounolou 2004). Consequently, methods beside budget vary in relation to spatial and temporal scale (Chapter 9). Monitoring programs often insufficiently consider the entities and the methods

(Yoccoz et al. 2001). Monitoring is often cost intensive, thus to some extent alternative possibilities are carried out at a local scale, for example, in developing countries (Danielsen et al. 2005). Alternative possibilities to access species richness by indicator species are, for example, also carried out in relation to maintaining biodiversity in NW Germany (Wittig et al. 2006).

## Field Measurements

Field measurements methods of phytodiversity vary, depending on the taxa, the environment, the size of the total area investigated and the intention of the investigation. At the **global scale**, for example, about 1400 standard floras and checklists are used for estimation of global vascular species richness (Barthlott & Wininger 1998). Monitoring habitat diversity at large scales is possible using satellite imageries, for example (Nagendra & Gadgil 1999). At a **regional scale**, species richness could be estimated by field observations, such as presence/absence data of species at grid systems resulting in distribution data. Different sized grid systems were used, for example 10 km x 10 km in Great Britain (Harding & Sheail 1992, Prendergast et al. 1993), or 2.8 km x 2.8 km in an area of Lower Saxony and Bremen (Cordes et al. 2006). The used grid-width often varies considerably between regions, and up- or downscaling, often necessary when comparing different regions exposes serious problems, such as overestimating the occurrence of a species in the case of more rough grids (Witte et al. 2008).

Lists of vascular plants species, for example, in 100 m altitudinal belts from sea level to the highest mountain, are used to estimate species richness for **altitudinal gradients**. Beside  $\alpha$ -diversity, this data can describe  $\beta$ -diversity, by considering compositional differentiation along the altitudinal gradient (Odland & Birks 1999). Incidentally, when comparing species richness along altitudinal gradients, it is necessary to vary the width of the altitudinal belts, because total species richness ( $\gamma$ -diversity) differs directly with the total area of each elevation zone (Lomolino 2001). Sometimes only special taxa were recorded, for example, in tropical forests only plants equal or larger than 2.5 cm in stem diameter were listed (Gentry 1988). Because of difficulties of monitoring all taxa, indicator species can be used to estimate biodiversity changes (Lindenmayer 1999, Wittig 2006). Thus, trends in the abundance and distribution of threatened species, mainly red-book-species, are often regularly monitored (Lughada et al. 2005).

Alternatives for the investigation of large areas are, for example, to record species richness of various 0.1-ha samples, each as the result of sum of ten 2 m x 50 m plots (Gentry 1988), with consideration paid to sampling design (Chapter 6.4). Furthermore, like the usage of indicator or red-book-species, only nature conservation areas were monitored, for example fauna-flora-habitat areas.

Elaboration of complete species lists, could be supported, for example, by using **model** based predictions in relation to existing floristic data and by using environmental information to find underrepresented species (Palmer et al. 2002). More recently, relationships between the number of species recorded in a set of samples and the estimation of the total possible number of species in a community were developed (Moreno et al. 2006).

**Temporal changes** in diversity are usually measured as turnover in time. The turnover rate could be expressed, for example, by the number of different species between

two adjacent areas, divided by the total number of species (Yoccoz et al. 2001, Duelli & Obrist 2003). In addition, to estimate diversity at different scales for nature conservation management, monitoring of biodiversity should consider both aspects, that of habitat-diversity and that of species diversity (Hermy & Cornelis 2000).

## 6.4 Sampling

Species richness differs with **sampling intensity**, measured as time expended per site (Lomolino 2001), moreover in relation to larger timescales it differs with the number of records (Hortal et al. 2008). Studying larger areas takes more effort, and often only 50-80 % of occurring species are recorded in floristic checklists (Stohlgren et al. 1997). The more time spent investigating larger areas, the more species that were recorded, whereas there is a levelling-out of increasing numbers of species with time sampled (Gaston 1996). Moreover, the more individuals there are, the higher the number of species that were observed (Rosenzweig 1995, Goldberg & Estabrook 1998). A general problem is the detectability of species, which can be a potential source of underestimation (Southwood & Henderson 2000, Yoccoz et al. 2001). The positive relationship between number of individuals sampled and number of species present is often used to explain the positive slope of species-area curves (Connor & McCoy 1979, Goldberg & Estabrook 1998).

Effort per site often declines with **elevation**, and reaches its highest intensity at lower, but not at the lowest, elevation (Lomolino 2001). Sampling effects, moreover, will be lower in areas with high **evenness** (Yoccoz et al. 2001), since in communities where all species are more or less similar, common sampling will rapidly provide a relatively correct estimate of the species richness. In contrast, samples in areas where few species dominate and the others are rare will tend to underestimate species richness (Yoccoz et al. 2001). In this case, sampling effects refer to the greater probability of including high productive species in an assemblage, which assume that the most productive species is also the strongest competitor (Huston 1979, Tilman et al. 1997, Duffy et al. 2007).

However, estimation of species richness depends on sampling-design, and efficient methods are necessary, especially in relation to conservation measures (Stohlgren et al. 1997). **Sampling design** (non-random or random approach) affects the estimation of species richness. For example, the United Kingdom breeding bird monitoring program was formerly based on a non-random approach. As a result, nature reserve areas, often with higher number of bird species, were more frequently investigated and species richness for the entire area was overestimated (Buckland et al. 2005). Monitoring biodiversity can be cost intensive. Thus, sampling design is often a compromise between costs and statistical requirements. For example, the comparison of different sampling design (simple random sampling, random cluster sampling, systematic cluster sampling, stratified cluster sampling) in a tropical rainforest showed that cluster sampling approaches, as well as stratified cluster sampling, are of interest regarding costs and statistical efficiency (Gimaret-Carpentier et al. 1998).

### 6.4.1 Random vs. Non-Random Sampling (Example I)

*Diekmann M, Kühne A, Isermann M (2007) Random vs. non-random sampling: effects on patterns of species abundance, species richness and vegetation-environment relationships. Folia Geobotanica 42, 179-190.*

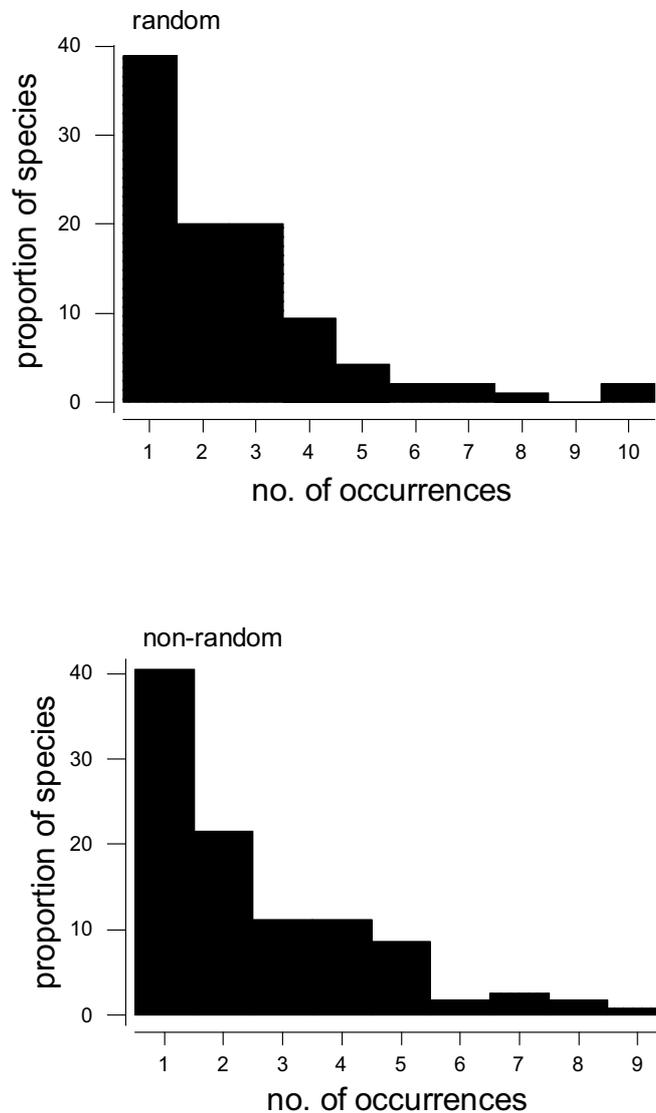
In the last 100 years, hundreds of thousands of vegetation relevés have been collected worldwide, mainly to describe the vegetation under consideration of phytosociological aspects. During the last ten years, due to computer facilities, large vegetation databases were developed and several overviews of the vegetation were established, for example, in Mecklenburg-Vorpommern (Berg et al. 2001, 2004). These relevés have been sampled for various purposes, but predominantly have not been addressed to biodiversity. Many diversity measures assume that individuals have been sampled randomly, considering the large amount of available relevés, common statistical tests are inappropriate due to the non-random sampling of the relevés (Økland et al. 1990, Lájér 2007). In contrast, random sampling is most favourable in relation to statistical analyses (Greig-Smith 1964), but has disadvantages e.g. the redundancy of dominant vegetation types.

To test whether phytosociological relevés can be used to assume patterns in community ecology, the results of a more objective sampling approach (random sampling) were compared with results of a more subjective sampling method (Kühne 2006).

When monitoring diversity, it is of interest to test if random sampling results in more common and less rare species than non-random sampling. Comparing the results of two data-sets (random, non-random), species richness in relation to their abundances, measured as number of occurrences in all investigated plots, showed that the number of species occurring only in few plots was somewhat higher in the non-random sampling approach (Figure 3). Moreover, the random sampling approach contains more species occurring in many plots.

In most plant and animal communities, there are few species of many individuals and many more species of few individuals. The largest class of species is of those that are individually rarest; this gave rise to the logarithmic series of abundance, but is often due to insufficient sampling. Alternatively, species more typically fit a log-normal series of abundances (Preston 1962), i.e. that the most numerous species were those of middling abundance (bell-shaped curve) (Whittaker 1998).

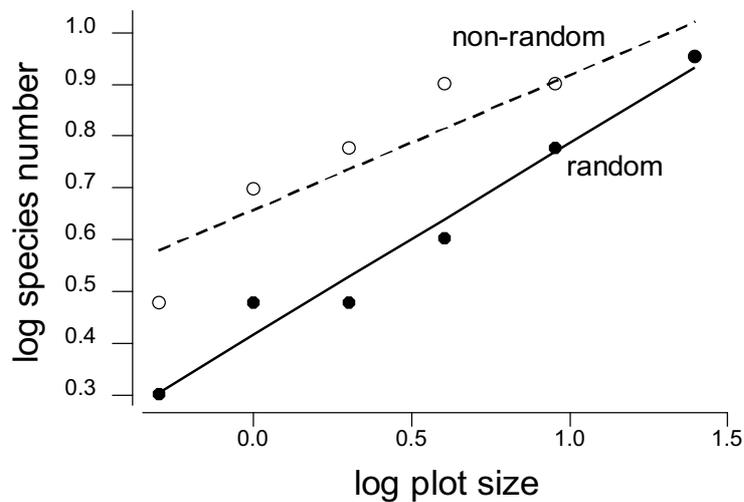
Thus, random sampling would result in more common and less rare species than non-random sampling, whereas differences, although not very pronounced, exist across all spatial scales. In the non-random approach an explicit request was to consider as much as habitats or vegetation types, so that due to landscape diversity (Chapter 7.2) number of species increase with the number of habitats, especially under consideration of species occurring in special and rare habitats, respectively.



**Figure 3. Number of species (as proportion) in relation to the number of occurrences, shown for the random approach (above) and the non-random approach (below).**

In relation to scale, it was shown that species richness at small scales was higher in the non-random approach, while the increase in species richness with area was higher in the random approach (Figure 4).

Higher species richness at small scales can be explained, for example, by the circumstance that phytosociological approaches based on character and differential species, and therefore relevés are often placed at particularly species-rich sites. Similarly, higher species richness for Iberian dung beetle was estimated with a non-random approach, whereas the used database records were proportionally greater in the richest sites, due to including rare species (Lobo 2008). Thus, non-randomly based estimates of local and regional species richness are higher than those based on random approaches are (Hobohm 2005).



**Figure 4.** Species area curves (log-log space), one of the random approach, the other of the non-random approach, both based on nested plots from 0.5 to 25 m<sup>2</sup> size.

Although sampling design is undoubtedly important, estimation of species richness is an integrated approach of both ecological patterns and sampling design, which was shown, e.g. for bird species richness, where sampling processes predicted a substantial part of species richness, but left great variation unexplained (Carnicer et al. 2008). Thus, sampling design in population and community ecology is context dependent (Kenkel et al. 1989).

## 7 Species Richness and Sampling Area

Species richness increases with increasing area, and is generally affected by three main patterns: **Area *per se* effects** (Chapter 7.1.1) whereas larger areas have more space for more individuals especially for more individuals of larger species (Figure 5); increase of species richness due to greater **landscape heterogeneity** (Chapter 7.2.1); and enhanced species richness due to larger **island size** (Chapter 7.1.2), that represents a combined pattern of the area *per se* effect and heterogeneity. Species-area relationships are traditionally based on the theory of island biogeography (Chapter 7.1).



Figure 5. Larger species such as *Corynephorus canescens* need more space than smaller ones such as the bryophyte *Campylopus introflexus*, and therefore more species can occur in larger areas.

### 7.1 Island Biogeography

Islands can be land, surrounded by water (**oceanic islands**) or surrounded by land (**habitat islands**). These can be divided into large areas (**continental islands**) like mountains surrounded by lowlands, as well as smaller areas (**habitat islands**), discrete patches of terrestrial areas surrounded by very different habitats but not by water (Walter & Straka 1970, Whittaker 1998, Lévêque & Mounolou 2004). Islands vary in many aspects, e.g. in their origins, development histories, and ages (Major 1988, Whittaker 1998); but generally they are more or less inaccessible (Brown 1988). One example of habitat islands are isolated dune patches along a rocky coast (Obeso & Aedo 1992).

Islands are not self-containing areas; and species originate by immigration from other areas or by speciation (MacArthur & Wilson 1967). In contrast, large areas such as continents are self-containing and species mostly originate by speciation within the region (Rosenzweig 1995). Islands contain mostly so-called '**source-species**', whose reproduction rates are adequate to establish a population and sufficient for maintenance (Shmida & Ellner 1984). For example, the annual *Cakile edentula* cannot usually survive landward of the yellow dunes, without yearly replenishment from driftline populations or new propagules arriving with driftline material. Therefore, *Cakile edentula* is a sink-species

landward of the yellow dunes, but a source-species on their seaward side (Keddy 1981, 1982). ‘Sink-species’, such as *Rhizinus communis* and *Helianthus annuus* in coastal driftlines, only occur temporarily on islands. The increase of species richness by sink species is called **mass-effect** (Chapter 8).

The **equilibrium theory of island biogeography** (ETIB) (MacArthur & Wilson 1967), which is not un-criticised (Sismondo 2000), first applied to oceanic islands. This represents the regulation of species diversity as a dynamic process, where immigration of species from a continental source and extinction are in a balance, so that species richness is a **dynamic equilibrium** ( $\hat{S}$ ) at a roughly constant level (Figure 6).

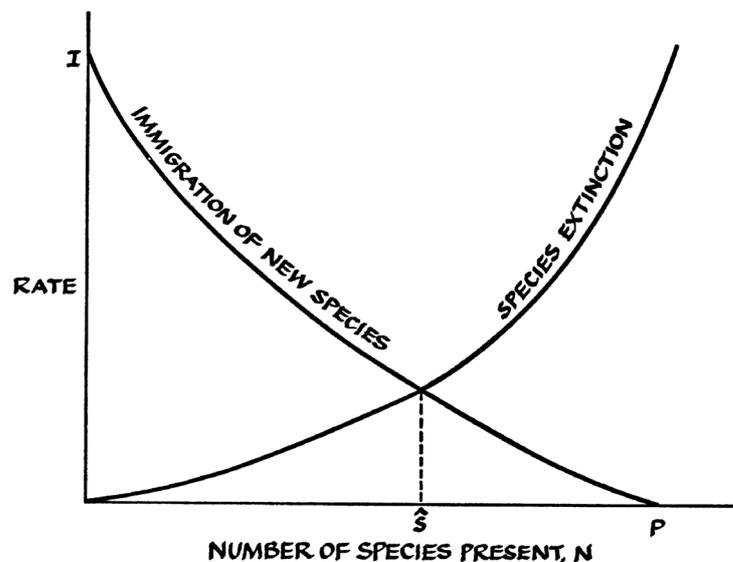


Figure 6. Equilibrium model of a single island. With immigration rate, expressing the number of new species arriving on an island per unit time ( $I$ ); and extinction rate representing the number of species on an island that become extinct per unit time.  $p$  is used to designate the number of species in the species pool, that is, the number capable of immigration to the island, whether they survive or not, and  $\hat{S}$  the equilibrium number of species (MacArthur & Wilson 1967).

The equilibrium number of species is theoretically reached at the intersection point between the immigration and extinction curve. As species richness increases, the extinction rate also increases, whereas the immigration rate decreases, as when more species become established, fewer species belong to new species (MacArthur & Wilson 1963, 1967, Simberloff 1974, Pielou 1975, Brown & Lomolino 1989, Whittaker 1998). However, a perfect balance between immigration and extinction might never be reached, thus the number of species on an island will fluctuate over time. Therefore, the theory of island biogeography is based on a dynamic equilibrium that occurs over long time scales and large spatial scales (Connor & McCoy 1979, Huston 1979). While at larger scales, speciation and extinction play a major role for species richness, immigration and loss are more significant at smaller scales (Godfray & Lawton 2001).

Extinction and immigration depend on various factors (Brown & Dinsmore 1988, Morand 2000), e.g. it is assumed, that local extinctions are inversely proportional to the population size (Simberloff 1976) and that equilibrium is determined, for example, by the size of an island (Chapter 7.1.2), and the position or and time of isolation of the island from source areas (Chapter 9.1.1).

### 7.1.1 Species-Area Effects (Example II)

Species-area relationships (SARs) express that larger areas have more species, which is one fundamental pattern supporting species diversity (Arrhenius 1921, Gleason 1922, Preston 1960, MacArthur & Wilson 1967). There are different explanations for the relationship between area and number of species. First, the **direct area effect**, which is particularly relevant to small scales, meaning within a particular and distinctive habitat, describes the limited space of an area (Whittaker 1998). The area *per se* effect expresses that larger areas have more space for more individuals, consequently allowing more species to coexist (Simberloff 1976). The area *per se* effect varies with the taxa concerned and is very small e.g. for lichens; for herbs it was only detectable in patches of less than 0.1 ha (Gibson & Greig-Smith 1986).

The relationship between size of an area and its number of species is usually described by species-area curves (Collins et al. 2002). The probable first species-area curve (Watson 1859) shows the relation between size of the area and the number of vascular plants, beginning with a bit of Great Britain's species richest county, and then enlarging to the whole island of Great Britain. Comparing sampling methods there are differences between contiguous (more or less nested) and isolated plots (Tjørve & Turner 2009). Species-area curves, in their strictest sense, start with the smallest area, followed by the larger ones in a nested sampling design. In the case of a scattered subplot design, number of species is accumulated, and the species-area relation results in a steeper slope, for example, when islands different in size are compared (Rosenzweig 1995).

There are various species-area functions (Dengler 2009, Tjørve 2009, Williams et al. 2009), whereas three main expressions are used to explain species-area relations (SAR): the exponential relation,  $S = Z \ln A + C$  (Gleason 1922), the power functional relation  $S = C \times A^Z$  (Arrhenius 1921), and the logistic relation  $S = B / C + A^{-Z}$  (Archibald 1949), where  $S$  is the number of species,  $A$  the size of the area, and  $B$ ,  $C$ , and  $Z$  are constants. Fitting of the models is scale dependent, at small sampling areas the exponential relation, at intermediate size the power model, and at large sampling areas the logistic relation generally fits best (He & Legendre 1996). Often it is indicated that species abundance distributions cause different SARs relative to scale and to vegetation type (Keeley 2003).

A standard method to plot a species-area curve is to transform both area ( $A$ ) and number of species ( $S$ ) into logarithm to the base 10 (Rosenzweig 1995), generally resulting in a straight line, and limited at both ends (Williamson et al. 2001). The equation of the log-log-relation ( $\log S = z \log A + \log c$ , where  $z$  describes the slope and  $\log c$  the intercept), is called, by Preston (1960), Arrhenius equation. Arrhenius (1921) compared different vegetation types, at small scales from 1 to 100 dm<sup>2</sup> and showed that the number of species increased with area. At small scales up to 1000 m<sup>2</sup> and on small islands (Rydin & Borgegård 1988), and especially in relation to phytodiversity, exponential species-area curves fit a straight line better in a semi-logarithmic space (log area vs. number of species) with  $S = z \log A + c$  (Gleason 1922, Rosenzweig 1995). The constant  $c$  of the Arrhenius equation is also dependant on scale (Rosenzweig 1995). Moreover, slopes are dependent on the entity investigated, for example, comparing native and non-native species, with slopes of species-areas curves generally being steeper for native species (Triantis et al. 2008). In addition, when comparing slopes of species-area curves of different size, slopes of smaller areas are usual steeper than those of larger ones (Martin 1981, Rosenzweig

1995, Fridley et al. 2005). However, in more detail, highest z-values occur at intermediate scale (1 ha to 10 km<sup>2</sup>) and lower z-values at smaller as well as larger scales. Thus, different processes determine phytodiversity at different scale. At small scales, probably ecological interactions between individuals such as competition are most relevant, at intermediate scales geology and topography effect landscape heterogeneity, and at larger scales in temperate regions a low species turnover is reflected (Crawley & Harral 2001).

Analysing species-area relations in a nested sampling design in different vegetation types of coastal dunes along the North and Baltic Sea, shows that the number of plant species (including bryophytes and lichens) increase linearly with increasing area, if presented at a log-log-graph (Figure 7).

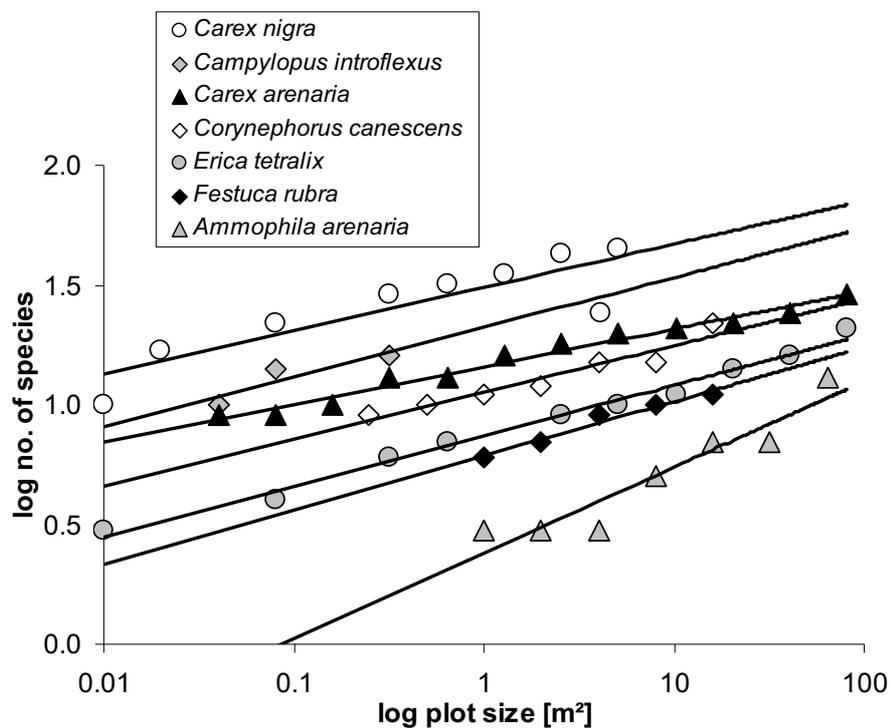


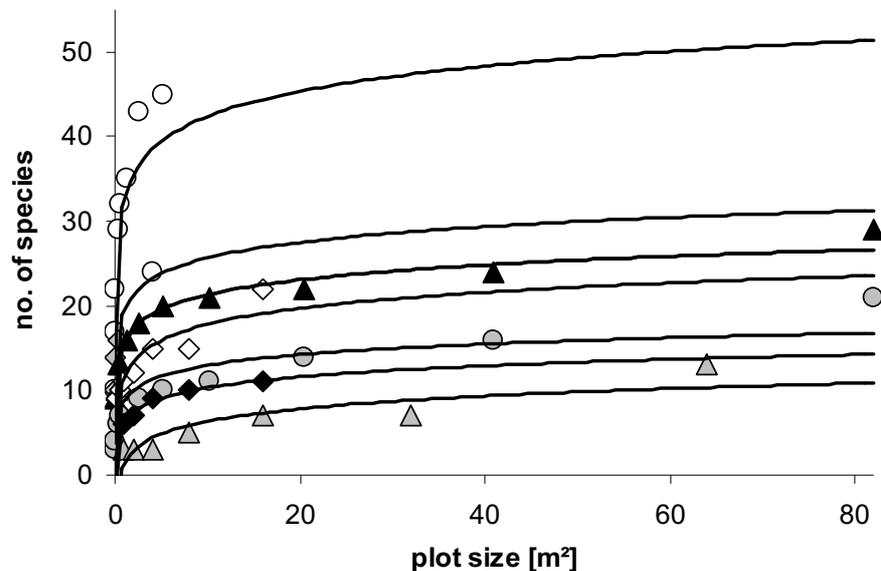
Figure 7. Species-area curves at a log-log-scale for different vegetation types in coastal dunes [unpublished data]. Curves represent the vegetation in the order shown in Table 4. (Statistics see Table 4).

Table 4. Statistical values of species-area equations ( $\log S = z \log A + \log c$ ) for different vegetation types in coastal dunes. Vegetation is named by characteristic species that represent the main aspect. ( $R^2_{adj.}$  and probability are shown).

Vegetation	log c	z	$R^2_{adj.}$	p
<i>Carex nigra</i>	1.4899	0.1807	0.72	0.002
<i>Campylopus introflexus</i>	1.3235	0.2075	0.65	0.277
<i>Carex arenaria</i>	1.1600	0.1565	0.97	< 0.001
<i>Corynephorus canescens</i>	1.0509	0.1959	0.92	< 0.001
<i>Erica tetralix</i>	0.8700	0.2109	0.99	< 0.001
<i>Festuca rubra</i>	0.7875	0.2264	0.96	0.002
<i>Ammophila arenaria</i>	0.3819	0.3576	0.88	0.001

One important prediction of species-area relations is that the slope  $z$  of the species-area curve on a log-log scale depends on the rate at which new species enter the system (Durrett & Levin 1996). It is therefore useful for the prediction and estimation of species richness in different habitats, for example, when considering conservation measures (Gitay et al. 1991). Often species abundance and spatial distribution (aggregation) are mentioned as the two most important patterns explaining species diversity (Crawley 1997), whereas for different scales it was shown that aggregation affects SAR curves less than abundances (Tjørve et al. 2008). SARs, as a description of the spatial community structure, consider only species richness and do not take into account interspecific differences in spatial patterns such as dominance, which can be described by more recent approaches as **diversity-area relations** (DAR) (Yakimov et al. 2008).

Representing the data of the coastal dunes at an arithmetic scale (Figure 8), slopes of the curves are steep at the first, but gradually become nearly flat. This hints that there is an upper limit of species richness at the local scale, but it is also valid for larger scales (Chapter 8). Hopkins (1955) showed similar results with a decreasing rise of the slope with increasing area. The curves with largest constant  $c$  increase faster, if  $z$  (the slope in a log-log-scale) is similar. In coastal dunes, the curve of wet areas with *Carex nigra* increased fastest and reached its saturation point last; in contrast, the curve of the *Ammophila arenaria* vegetation of the yellow dunes reached its saturation point earliest.



**Figure 8.** Species-area curves at an arithmetic scale for different vegetation types in coastal dunes [unpublished data]. Curves represent the vegetation in the order shown in Table 4.

Transforming the Arrhenius equation to  $S = cA^z$ , the **power function model** (MacArthur & Wilson 1963, 1967), in this case  $c$  determines the slope (not the intercept), presenting a constant related to population density and representing the biotic richness of an area. The slope of the diversity curve is represented by  $z$ , describing the rate of increase in species with area,  $z = \Delta \log S / \Delta \log A$  (Preston 1962), and is often used for comparing different studies (Martin 1981). Nevertheless, both  $c$  and the slope  $z$  are scale dependent, whereas

c increases and z decreases (Martin 1981, He & Legendre 1996). According to islands theory (Chapter 7.1), z generally relates to the isolation of islands (Whittaker 1998).

The above shows that species-area relations of coastal dunes varies with habitat type, indicating that beside area *per se* effects further patterns are important. Patterns and processes of abiotic and biotic variables often override the direct area effect (Harner & Harper 1976). Besides area *per se* effect, **habitat heterogeneity** (Chapter 8.3), the ecological concept that represents the variation of an environmental variable (Feagin 2005), is the most frequently proposed hypothesis of species-area relations (Hamilton et al. 1963, Connor & McCoy 1979). Both area and habitat heterogeneity have a pronounced effect on species richness (Kallimanis et al. 2008). In addition, the combined effect of area and heterogeneity explain up to 98 % of the variation in species richness (Harner & Harper 1976).

### 7.1.2 Species Richness and Islands Size (Example III)

*Isermann M (2004) Differences in species richness of native and non-native plants between the East and North Frisian Islands. In: Green DR (ed.) Delivering sustainable coasts. Cambridge Publications, pp. 737-738.*

Species richness of vascular plants on the East (EFI) and North Frisian Islands (NFI), including the small low islands called ‘Halligen’, was estimated using a database from the German Agency for Nature Conservation based on a floristic inventory of Germany.

The origin of the East and North Frisian Islands differs; the North Frisian Islands are formerly connected to the mainland, while the East Frisian Islands were not. Regardless of geological origin, at a semi-log scale, species richness of vascular plants of both EFI and NFI increased with increasing size of the islands (Figure 9). This result represents one of the classic biogeographical patterns, the peninsular effect, whereas large landmasses in general are species richer than small islands (MacArthur & Wilson 1967, Major 1988).

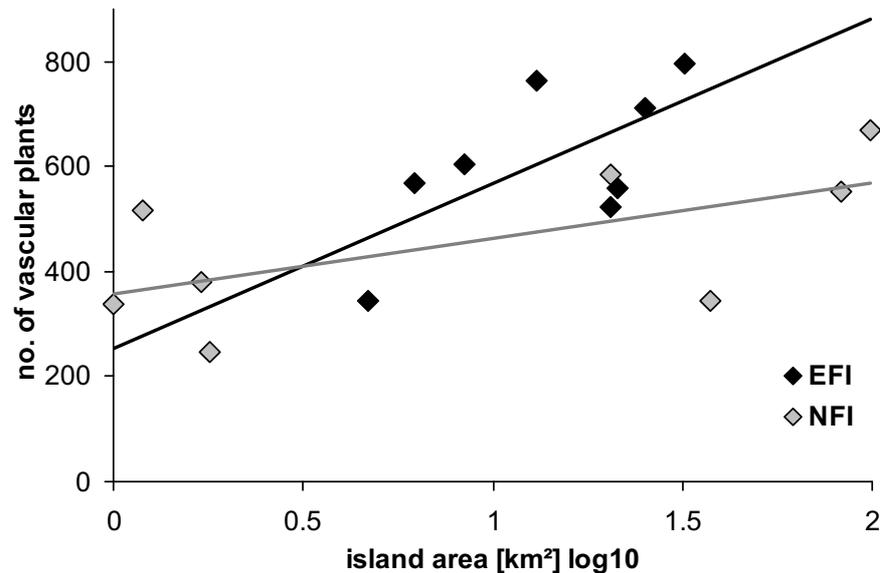
Due to the equilibrium model it is assumed, that small islands have fewer species than larger islands because small islands contain smaller populations that are more expected to become extinct (Brown & Dinsmore 1988).

Considering conservation aspects, adding up species richness of smaller islands to one large area, does not necessarily result in similar a species richness to a single large area biogeographically different (Diamond 1976, Simberloff & Abele 1976). Thus, some large refuges are essential to minimise extinction rates and to ensure maintaining species richness (Diamond 1976).

In general, species richness of islands, belonging to one archipelago, equidistant from mainland and with similar habitat diversity, increases directly with island size, as the larger the island, the lower its local extinction rate and the higher its immigration rate (Adersen 1995).

It is likely that due to the more unsaturated flora of the East Frisian Islands (Chapter 9.1), the number of vascular plant species increases at a greater rate than on the North Frisian Islands (Figure 9). Considering the lesser accessibility, islands typically have fewer species per unit area than mainland, thus the species-area relationships are stronger on islands than on the mainland (Rosenzweig 1995). The z-value in the log-log-relation of

Figure 9 is 0.11 in the case of the NFI and 0.25 in the case of the EFI. In general, the z-values of mainland and non-isolated areas, respectively, are about 0.12-0.18, and those of islands are about 0.20-0.35 (MacArthur & Wilson 1967, Rosenzweig 1995, Whittaker 1998). This confirms the general pattern that species area curves would become steeper with increasing distance to the mainland (MacArthur & Wilson 1963, 1967).



**Figure 9.** Increase of species richness of vascular plants with increasing area of East (EFI) and North Frisian Islands (NFI) at semi-log-scale. (EFI  $R^2_{adj.} = 0.34$ ,  $p = 0.075$ ; NFI  $R^2_{adj.} = 0.29$ ,  $p = 0.098$ ). Because of the different history, both groups of islands were analysed separately.

Although effects of area *per se* occur (Chapter 7.1.1), species richness is often the result of **habitat diversity** (Chapter 7.2). Variation in habitat diversity on different islands can overlay the effects of equilibrium between immigration and extinction (Huston 1994). Generally, larger islands contain more habitat types than smaller islands (e.g. Hamilton et al. 1963); nevertheless, due to landscape heterogeneity as well as in relation to lime content, regarding the West Frisian Islands, small islands can also be species rich. In addition, the number of rare species increased with the total number of species, which indicated specialisation of species in relation to unique habitat types on the West Frisian Islands (Mennema & Weeda 1983).

## 7.2 Landscape Heterogeneity

Spatial heterogeneity and temporal variability are major characteristics of ecosystems (Lévêque & Mounolou 2004) and clearly effect phytodiversity (Huston 1994). According to nature conservation aspects, it is well known that a loss in species diversity is caused by a loss in landscape structure (Tilman 1993). Spatial heterogeneity at least at two spatial scales (landscape and habitat) maintains species richness, and positive relationships are often shown (Lundholm 2009). There are various large-scaled environmental factors supporting spatial heterogeneity, e.g. climate and geological patterns (Huston 1994). Nevertheless, at large scales, species richness is caused not only by landscape

heterogeneity but also for example by the variation in available resources (Jiménez et al. 2009). The importance of factors varies with scale, e.g. habitat type at small scales, and a combination of habitat type and patchiness at larger scales are the most important factors maintaining species richness (Simmering et al. 2006). At landscape scale, different, mainly large-scale, ecological conditions create different habitats (Chapter 7.2.1) and enhance species diversity, for plants as well as for animals (Schouten et al. 2009). At the local scale, for example, niche differentiation, resource partitioning, and competition (Chapter 8.3) are of more importance (Cody 1986, Wilson et al. 1999, Stubbs & Wilson 2004).

Landscape heterogeneity represents one of the important patterns supporting species richness (Wohlgemuth 1998, Deutschewitz et al. 2003, Kühn et al. 2004), because most species occur only in a set of habitats; and extinction, origination, and co-evolution results in long-term habitat specialisation (Rosenzweig 1995). Incidentally, spatial heterogeneity was primarily assumed as the most important factor determining species richness, for example, when considering the number of lizard species in western North America, spatial heterogeneity of the vegetation was particularly crucial (Pianka 1967). In contrast the loss of habitats results in a strong decline of species richness, as shown for the loss of forest and the decline in the number of land snails (Chiba et al. 2009).

The co-evolution of species richness and habitat is based on the traditional approach that assumes a more or less fixed **niche** breadth for each species, wherein an optimal combination of species traits and ecological conditions is reached (Rosenzweig 1995). The heterogeneity approach assumed a positive relationship between area and number of potential habitats and therefore an increasing number of common, as well as rare species (May & MacArthur 1972). One explanation for the relationship between area and habitat is that in larger areas there will be more habitat types and therefore more species (Williams 1943). Furthermore, the variation in abiotic conditions, such as topography, affects the number of habitats, which in turn influence the number of species in an area (Hofer et al. 2008). However, considering regions with multi-layered vegetation, like tropical rainforest, or regarding animal species richness, habitat diversity also depends on the total number of species in an area, for example, because of the number of epiphytes (Rosenzweig 1995).

Habitat diversity allows more species with different environmental requirements to coexist (Hamilton et al. 1963, Johnson & Raven 1973, Simberloff 1974). Habitat effects are more distinct in relation to species with high degrees of habitat specialisation (Ricklefs & Lovette 1999). In larger areas, the area of each habitat type should be enlarged; therefore, more species (with similar requirements) could coexist within a single habitat type (Kohn & Walsh 1994). This probably results in larger geographical areas and a lower extinction rate, and supports species richness (Adersen 1995, Brown & Lomolino 1989, Ricklefs & Lovette 1999). According to the **concept of assembly rules** (Diamond 1976), species that overlap less in their ecological requirements, coexist more often than species with a large overlap. Therefore, species richness on islands is partly the result of competitive exclusions (Whittaker 1998).

Furthermore, there are density-dependent relationships between species richness and habitat (MacArthur-Recher pattern): One species alone spreads out into all habitats with suitable abiotic conditions, but by adding a coexisting competitor, niche breadth will be reduced (Fretwell & Lucas 1969, Rosenzweig 1995), which was shown, e.g. for

different *Banksia* species (Richardson et al. 1995). Thus, the more species, the more narrowly they specialise and the more specialised plant communities occur the more different habitats, i.e. vegetation types, will be distinguished.

Species richness at larger scales, such as landscapes, is predicted by local richness ( $\alpha$ -diversity) and differentiation diversity in relation to environmental heterogeneity. For example, the change of species composition along habitat gradients ( $\beta$ -diversity), and at larger scales the composition changes along geographical gradients ( $\delta$ -diversity) (Chapter 6.2). Dissimilar habitats are colonised by different species, therefore, regions with high local species richness, high turnover as well as with pronounced habitat and geographical gradients, obviously contribute to overall species richness and would have species-richest landscapes (Rosenzweig 1995, Vitousek & Benning 1995, Cowling et al. 1996b, Whittaker 1998).

Landscape heterogeneity moreover is linked with other gradients such as the altitudinal gradients complex (Chapter 8.1), whereas high habitat diversity along an elevation gradient in areas with greater topographic variability supports regional species richness (Kerr & Packer 1997).

Landscape heterogeneity can be expressed e.g. as the number of vegetation types, soil types or elevation zones (Harner & Harper 1976, Turner 1989); and can be measured, for example, as habitat variety index (Magurran 2006). In general, larger areas might contain more habitats due to greater topographic and environmental diversity (Gaston & Spicer 2004). Hence, the larger the area, the less the area *per se* effect (Chapter 7.1.1) and when comparing equal-sized areas, species richness is predicted more by the number of habitats. Thus, heterogeneity in many cases represents the most important factor for increasing species diversity at landscape scale (Harner & Harper 1976, Rosenzweig 1995). However, species-area relations are explained both by area *per se* effects, which are more pronounced at small scales (Chapter 7.1.1), and by habitat heterogeneity, whereas, for example, jointed effects of both patterns were shown for plant species richness in Greek nature reserves (Kallimanis et al. 2008). In general, there species richness is higher at larger areas, because larger areas contain more habitats than smaller ones, for example, because of enriched geological relief, so that landscape heterogeneity increases with area (Preston 1962, Harner & Harper 1976, Rosenzweig 1995, Whittaker 1998).

Nevertheless, very high species richness also occurs in regions with little environmental variation, e.g. in the fynbos of South Africa. However, the Cape Peninsula is characterised by a very high topographical heterogeneity, pronounced gradients in annual rainfall, very different local climatic conditions and a great diversity of especially nutrient-poor soils, so that the Cape Peninsula in the whole is characterised by a high number of habitats (Linder 1991, Cowling et al. 1996a).

## 7.2.1 Bryophytes and Landscape Heterogeneity (Example IV)

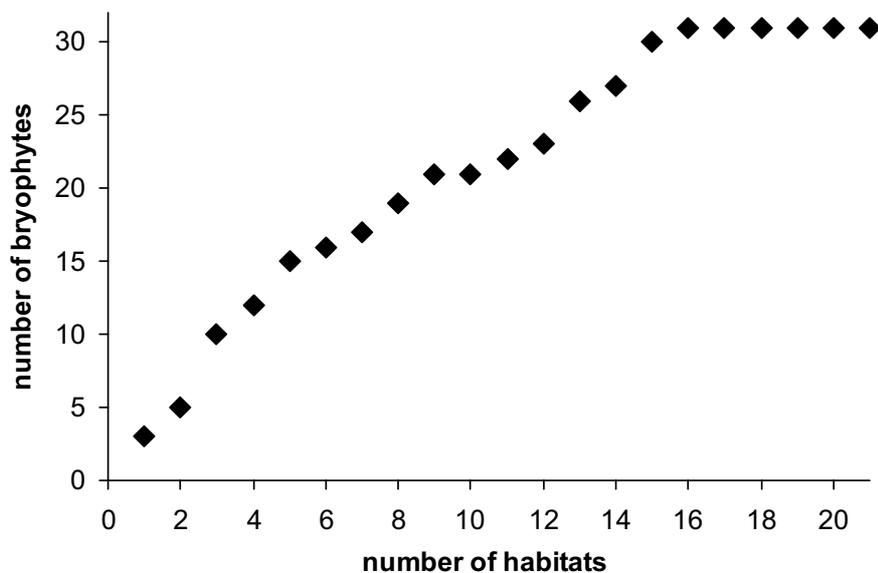
*Isermann M (2007) Diversity of bryophytes in an urban area of NW Germany. Lindbergia 32, 75-81.*

Bryophytes represent high species richness in many habitats, and constitute a relatively important component of the vegetation at a variety of habitats, such as, tropical rainforests, arctic tundra, rocks, and sandy soils. Furthermore, the preservation of bryophyte diversity

is an increasing task of nature conservation (Hylander & Jonsson 2007). Especially in urban areas, which often show reduced bryophyte richness because of climatic conditions, i.e. an increase in temperature and aridity, and especially because of environmental pollution (Koperski 1998).

Bryophyte richness was studied on the Campus of the Bremen University. The area contains many different, although often small, habitats, e.g. short grasslands, ponds, shrubberies, single trees, a small forest, gardens, and different types of walls and stones. The habitats belong to two major substrate groups: soft substrates, such as grasslands and hard substrates, like walls and stones. The environmental conditions vary with habitat type. In general, hard substrates in comparison to soft substrates were characterised by higher temperature, substrate pH, due to higher calcium content, as well as by lower water content.

Species richness of bryophytes at the Campus is comparable to other urban areas with similar size (Ziegler 1996). Bryophyte richness increased with increasing number of habitats (Figure 10); hence, the results demonstrate that habitat mosaics are important for the success of numerous species (Vitousek & Benning 1995). Also in other cities, e.g. Belgrade, occur a relation between bryophyte richness and number of habitats (Sabovljević & Grović 2009). Comparing both main substrate types at the Campus of the Bremen University, in the case of soft substrate habitats (no. 1-13), the species-habitat curve still increases, thus in the area more habitats probably occur, as well as more bryophytes. Moreover, on hard substrate habitats (no. 14-21) only few specialists are likely to occur, thus the number of bryophytes does not increase further. The results confirm that landscape diversity supports species richness and, especially when regarding hard-substrate, the number of specialists is enhanced (Krauss et al. 2004).



**Figure 10.** There is a positive relation between cumulative number of bryophytes and number of habitats ( $R^2_{adj.} = 0.99$ ,  $p < 0.001$ ). The habitats are in order of a TWINSpan classification whereas no. 1-13 are soft substrates, and no. 14-21 are hard substrates.

The study confirms that bryophyte richness increases with area, similarly to vascular plants, because of higher landscape heterogeneity expressed as number of habitats, as well as due to area *per se* effect (Weibull & Rydin 2005). Bryophyte diversity at regional or larger scales especially is related to climatic factors, while at smaller scales, species richness is mainly affected by diversity of habitats and substrate (Heegaard 2000, Hohenwallner & Zechmeister 2001, Zechmeister et al. 2003). At the Campus area, bryophyte richness is enhanced by micro-sites, similar to micro-sites like boulders or deciduous trees in otherwise coniferous forest (Sjögren 1961, Weibull & Rydin 2005).

Urban areas, especially cities, contain more native, as well as non-native, plant species than the surrounding landscapes (Klotz 1984, Kühn et al. 2004). Urban areas are usually characterised by a high degree of habitat diversity that usually supports species richness (Fojcik & Stebel 1999). Like this, the number of geological types explained a large part of the higher species richness of native plants in cities (Kühn et al. 2004). In addition, it was shown that cities are distributed non-randomly in regions with high geological diversity (Kühn et al. 2004). Urban areas often contain more habitats per area than natural ones due to human activity and the introduction of new substrates as well as by the generation of particular micro-sites (Ariño & Saiz-Jimenez 1996).

Moreover, the Campus area probably represents a **transition zone**, a large-scale ecotone, which generally contains higher values of species richness due to extended habitat diversity (Klotz 1984). Higher species richness at transition zones is caused by a greater range of environmental conditions than the adjacent, more homogeneous neighbouring areas (Shmida & Wilson 1985, Ward 1998, Whittaker 1998). The Campus is situated on the outskirts of Bremen City, close to cultivated lands as well as to habitats that are more semi-natural. It is also shown that bryophyte richness multiplies several times in neighboured surroundings of towns, where more habitats are included (Żarnowiec 1996, Fojcik & Stebel 1999, Zechmeister et al. 2002).

Considering nature conservation aspects, urban areas are partly important for bryophyte diversity (Young & Jarvis 2001), but often contain more generalists, which are able to grow under the specific conditions. Undoubtedly, urban areas are not comparable with natural or semi-natural areas, providing a diverse range of ecological niches and habitats with many specialists, and are undeniably essential for sustainable conservation of bryophyte diversity.

## 8 Species Diversity and Environment at Different Spatial Scales

**Heterogeneity** defines space as a mosaic of environmental factors, spatially delimited structures, at a given time (Lévêque & Mounolou 2004). Spatial heterogeneity occurs at different scales (Urban et al. 1987, Pausas & Austin 2001, Hofer et al. 2008). At the large scale, gradients complexes (Chapter 8.1), at landscape scale topography and climate (Chapter 8.2) may be most important (Urban et al. 1987, Riera et al. 1998, Brown 2007). At landscape scale, the number of habitats predicts landscape heterogeneity (Chapter 7.2.1). Spatial and temporal environmental heterogeneity can affect the dynamic and structure of ecosystems at many levels (Huston 1979, 1994, Tilman 1982, 1994). At medium scale it can be related, for example, to disturbances such as fire and at smaller scales to disturbances such as grazing (Chapter 8.3.2.2). At plot scale, spatial heterogeneity in vegetation is also related to the variability of environmental conditions, for example, soil pH (Chapter 8.3.1), moreover to species dispersal and competition (Chapter 8.3.3).

Species richness can be explained by various theories (Whittaker 1977, Tilman 1982, Shmida & Ellner 1984), which can be distinguished into two classes: equilibrium and non-equilibrium models. **Non-equilibrium theories** assume that external factors, such as disturbance, break off competitive interactions and therefore permit co-existence of species (Paine 1966, Connell 1978, Grime 1979, Huston 1979, Shmida & Ellner 1984). The variability of external factors, i.e. the abiotic conditions, is reflected in the degree of **habitat heterogeneity**, which is one pattern that effects at small scales species richness. Heterogeneity, expressed as variability of **environmental conditions**, affects the number of habitat types.

**Equilibrium theories** base on the competitive exclusion principle and assume that co-existing species have significant differences in their ecological niches (Grubb 1977). Thus, **co-existence** of species can be explained by habitat differentiation, whereas species use different parts of the habitats e.g. by **resource partitioning**, whereas species divide the limiting **resources** so that each species is limited by another component of the available resource (Hutchinson 1959, Levin 1974, Whittaker 1975, 1977). Coexistence in spatially structured habitats might also be supported by interspecific differences, for example, in dispersal, germination, mortality, i.e. factors that influence competitive interactions (Grubb 1977, Tilman 1982, Tilman & Pacala 1993). Therefore, habitat heterogeneity determines species richness by the number of **niches** (MacArthur & Levins 1967). In reality, both mechanisms are important in maintaining species diversity, for example, in coastal plain savannas (Walker & Peet 1983).

In accordance to equilibrium models, an ecological **niche** is a hypervolume of  $n$  dimensions (Hutchinson 1957), each representing a resource gradient (Whittaker 1998). Whereas the **fundamental niche** is the set of environmental conditions permitting a species to exist and the **realised niche**, the subset of conditions not shared with other species due to competitive exclusion (Gaston & Spicer 2004). The niche idea assumes the limitation of coexisting species by available resources (Chapter 8.3.3), the **concept of niche limitation**, because species are not completely similar in their resource requirements (Hutchinson 1959, MacArthur & Levins 1967, MacArthur 1970, Tilman 1980, 1982,

1993). The more heterogeneous the habitat, the greater, for example, the number of resource types, this results in both a greater number of species and individuals (MacArthur & Wilson 1967, Wright 1983).

Thus, in **equilibrium models** (Chapter 7.1) the number of species is so high because differences in species requirements exist (May & MacArthur 1972). In a spatially homogeneous habitat niche limitation occurs, so that only one species per limiting resource is able to exist (Tilman 1993). In an equilibrium model, the realised niche breadth decreased during succession (Mazurek & Romane 1986), and immigration and speciation would result in **saturated communities**, where all niches are filled (Cody 1968, Ricklefs 1987). Thus, for plants the idea of a saturated resource space in a spatial context is possible, where different micro-sites, with different environmental conditions were occupied by specially adapted species. Differences in rooting depth, for example, can allow species to use different water and nutrient regimes (Berendse 1982). Another example is the stratification of the canopy that represents a vertical niche axis. Nevertheless, the variation in micro-site conditions, which are most relevant for species co-existence, indicates that there is probably neither niche limitation nor saturation (Whittaker 1977, Wilson & Sykes 1988, Palmer & White 1994, Palmer & Van der Maarel 1995).

**Niche differentiation** in an equilibrium model supposes that dissimilarity in niches of coexisting plants prevent **competitive exclusion** (Crawley 1997). Heterogeneous habitats support available niches and thus coexistence of more species (MacArthur & Wilson 1967, May & MacArthur 1972, Martin 1981). Resource competition increases with species richness and supports **specialisation** (Cody 1991), for example, in salt marshes (Russell et al. 1985). The more specialised species are, the less their niches will overlap, and the more species can coexist, and in turn the species-richer the vegetation as there are no limiting resources (Gaston & Spicer 2004). In heterogeneous habitats a potentially unlimited number of species can coexist as long as interspecific competitive trade-offs occur (Tilman & Lehman 2001). Moreover, the establishment of new species is depending on occurring competitors (MacArthur & Wilson 1967). **Niche differentiation**, for example, is shown by variation in **growth forms** in the South African fynbos (Cowling et al. 1992). Because each growth form represents a particular resource strategy (Cody 1986, 1989), positive relationships between species richness and number of growth forms occur. Furthermore, niche exploitation determines **ecosystem functioning** (Chapter 6.1) which generally increases with increasing species diversity. However, as species diversity increases there is also the possibility of an increase in overlapping resource use (Schwartz et al. 2000, Loreau et al. 2001, Bond & Chase 2002).

Beside **micro-site limitation**, species richness can be limited by **seed arrival**, so that species richness, particularly at small scales, also depends on the arrival of new propagules from their close neighbourhood, and is limited by the size of the local species pool. Furthermore, species richness is related to the species composition, because dispersal of propagules depends on the life-history traits of the species (Huston 1979, Zobel et al. 2000, Dufour et al. 2006). Effects of dispersal on species richness are substantial (Lévêque & Mounolou 2004), and include, for example, the phenomenon called **mass effect**. The mass effect describes the support of species richness by continuous input of propagules from a source habitat, whereas coexistence is more or less independent of available niches (Shmida & Ellner 1984, Shmida & Wilson 1985). Existence of mass effect might be shown

e.g. by a decrease in native species with increasing distance to a source area (Hatton & Carpenter 1986). Furthermore, mass effect increases species diversity near habitat boundaries, because the effect enhances  $\alpha$ -diversity (within-site diversity) from  $\beta$ -diversity (differences between sites) (Kunin 1998). However, it is most probable that both niche-assembly and dispersal-assembly play an important role explaining coexistence of species (McKane et al. 2002, Potts et al. 2004).

## **8.1 Large Gradients Complexes: Latitude and Altitude**

At the global scale, spatial variation not only in phytodiversity, but also in biodiversity overall, is represented by the change of species richness along **latitudinal** gradients. Latitude as well as **altitude** have no direct influence on plant growth, but are related to a complex of environmental factors (Huston 1994, Gaston & Spicer 2004). The variation in species richness at large scales can be explained by different approaches, for example by latitudinal and altitudinal gradients with different underlying patterns and processes (Stevens 1989, Currie 1991, Rohde 1992, Rahbek 1995, Rosenzweig 1995, Caldecott et al. 1996, Gaston 1996, Kerr & Packer 1997, Brown & Lomolino 1989). Furthermore, large-scale gradients can be explained by **Rapoport's rule** or Rapoport's rescue hypothesis (Stevens 1989, 1992). Partly topped on the previous, species-range distributions in relation to geographical boundaries of a region (or domain) are the origin for the **mid-domain effect**.

### **Latitudinal Gradients Complex**

Species richness of most organism groups increases from higher towards lower latitudes, therefore biological diversity is greater in the tropics than in temperate regions (Huston 1994, Rosenzweig 1995, Gaston & Spicer 2004). An increase, often not linear, was shown, for example, for birds, mammals, amphibians, and reptilians (Currie 1991). The number of species in tropical regions is up to two times greater than in temperate regions, which in turn can be up to one time greater than in polar regions (Stevens 1989). Highest species richness often is not reached directly at the equator, but a little north at 20-30° N (Fischer 1960, Terborgh 1973, Gentry 1988). The gradient normally shows an asymmetrical distribution about the equator, this is due to the larger land area to the north of the equator, resulting in a more rapid increase in species richness (Gentry 1988, Rosenzweig 1995).

The latitudinal gradient is well represented for terrestrial and freshwater systems (Gaston & Spicer 2004). Exceptions are relatively rare and only in rather narrowly defined groups. Species richness increases polewards within a latitude belt before decreasing at still higher latitudes (Pielou 1975). For example, the number of bryophytes and lichens mainly determines arctic phytodiversity (Bültmann 2005), especially lichens, which tend to have their greatest abundance and diversity in dry or cold areas, where larger vascular plants are out-competed.

The latitudinal gradient in biodiversity is a complex gradient (Pianka 1967) that is related, for example, to climatic factors and consistently changes with latitude, e.g. average temperature, annual precipitation, seasonality, variability in temperature and precipitation, evapotranspiration, and solar energy (Pielou 1975, Whittaker 1977, Gentry 1982, Rohde 1992, Cowling & Samways 1995). Landscapes with the highest values of species richness,

at various scales represent high productivity at low latitudes (between 25 and 30° latitude), but with large seasonal temperature fluctuations. Greater seasonal temperature fluctuations support landscape diversity (Scheiner & Rey-Benayas 1994). The relations between climate and species diversity evident at large scales are overridden at smaller scales by effects of biological patterns and process such as competition (Greigh-Smith 1979, Woodward 1987, Wiens 1989).

The gradient is caused by various mechanisms: Tropical regions occupy larger areas on the globe than temperate or cold regions, so species-area relations *per se* effects (Chapter 7) occur (Terborgh 1973, Godfray & Lawton 2001), and due to larger area, they usually have higher rates of speciation and lower rates of extinction (Rosenzweig & Abramsky 1993). Higher levels of **energy availability** in the form of **resources**, allow more species to occur in the tropics than in high-latitude regions (Wright 1983, Currie 1991, Wright et al. 1993). Furthermore, environmental factors related to energy, like **nutrient availability**, explain more variation in species richness (Tilman & Pacala 1993, Wright et al. 1993).

Furthermore, large-scale environmental disturbances like glaciations, with an “ice-scraper effect” upon biological diversity, have been less frequent in the tropics. The resulting greater length of effective **evolutionary time** in the tropics is linked with higher rates of speciation and lower rates of extinction, and is probably the primary cause of higher species richness in the tropics (May 1990, Rohde 1992, Huston 1994, Godfrey & Lawton 2001, Gaston & Spicer 2004). The **stable climatic conditions** found in tropical regions, seasonal as well as long-term, support specialisation and the occupation of different ecological niches (Huston 1994, Dymond et al. 2003). In general, high environmental stability leads to high community stability, which in the main allows high biodiversity (Pielou 1975).

Many other mechanism and factors such as primary productivity, number of habitats, niche-width, and to some extent wilderness (Dymond et al. 2003), are linked with the latitudinal gradient, based on different mechanisms operating in the same direction (Pianka 1966, Terborgh 1971, Diamond 1976, Stevens 1989, Rohde 1992, Rosenzweig & Abramsky 1993, Huston 1994, Schreiner & Rey-Benayas 1994, Rosenzweig 1995, Dymond et al. 2003, Ricklefs 2005). However, effects of any of these mechanisms could be modified or overridden by various other factors, such as habitat heterogeneity (Chapter 8.3) (Gaston & Spicer 2004). Furthermore, the relative importance of mechanisms varies with latitude, for example, energy availability limits species richness at high latitudes, but habitat heterogeneity became more important at lower latitudes (Kerr & Packer 1997, Kerr et al. 2006). In addition, the importance of each factor varies in relation to the systematic group (Dymond et al. 2003).

Latitudinal gradients occur in many habitats, including coastal ones (Rohde 1992), although coastal areas due to their oceanic climate are quite often considered atypical for their latitude (Whittaker 1998). For example, along the north European coast, surface temperatures of the sea are at least 3 °C higher than the latitudinal average (Tallis 1991). A latitudinal gradient in coastal areas was shown for vascular plant species richness in Australian coastal dunes, whereas there was a decline in the number of species along the latitudinal gradient, ranging from about 12° S to about 42° S (Figure 11).

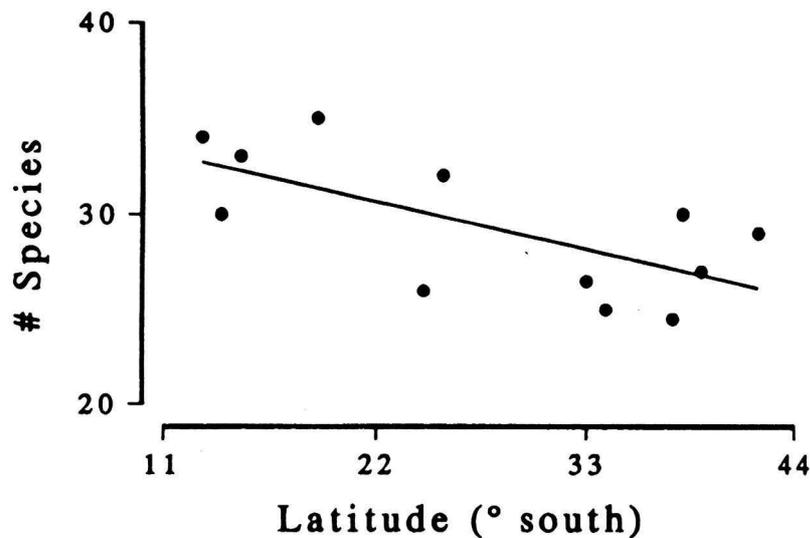


Figure 11. Plants of sandy coastal habitats in Australia show a latitudinal gradient, despite their being sampled from a single uniform biotope (Specht 1988 from Rosenzweig 1995).

Nevertheless, species richness of coastal dune ecosystems is affected less by the latitudinal gradient complex, because of the oceanic climate, which is similar to oceanic islands (Whittaker 1998). For example, in temperate regions the annual average range on islands is less than 10 °C (Whittaker 1998). Coastal dune vegetation, especially from ephemeral tidemark communities to pioneer communities in stabilised zones, shows an azonal character, independent of climatic zones (Doing 1985). Therefore, the vegetation often has a typically maritime so-called 'paracimax' (Van der Maarel 1993). Comparable vegetation zones of dunes show a similar structure worldwide, and beach and dune vegetation contain many widespread species, like *Ammophila arenaria* and *Cakile maritima* (Doing 1985). Nevertheless, a worldwide comparison of coastal dune species richness, along the latitudinal gradient complex could be of interest to evaluate a general decreasing littoral influence from driftline vegetation to inland shrub-, heath- and woodland towards a more visible latitudinal effect.

### Altitudinal Gradients Complex

Another large gradients complex similar to the latitudinal gradient is the altitudinal gradient, whereas lowland areas are in general species-richer than mountaintops (Stevens 1992). Regarding large areas, altitudinal gradients play a minor role in comparison to latitudinal gradients, because of its smaller magnitude (Gaston & Spicer 2004) and are naturally more important at the landscape scale of mountainous regions (Table 2). It is not surprising that altitudinal gradients are not relevant in coastal dunes that develop approximately at sea level and are usually only reaching a few metres high.

Species richness general decreases with increasing elevation (Gentry 1988), but there are also examples of increasing species richness with elevation (Sang 2009). Sometimes there is a linear decline in species richness with altitude, for example, the vascular plant species on mountains of the Faroe Islands (Fosaa 2004). Linear relations occur (Hamilton 1975), especially when considering only a part of the entire elevation

gradient (Kitayama 1992), for example, in the upper part of the elevation gradient herbs, shrubs, and vines decline in the number of species with increasing altitude in tropical forest (Vázquez & Givnish 1998). More often vascular plant species richness reaches highest values at **intermediate levels** of altitude, and shows a humped relationship with elevation (Whittaker 1960, Whittaker & Niering 1975, Shmida & Wilson 1985, Rahbek 1995). This was shown, for example, for plants as well as for birds in tropical forests of Costa Rica (Lieberman et al. 1996, Jankowski et al. 2009), and along a declining moisture index in Arizona (Whittaker & Niering 1975). However, the humped relationship along an elevation belt probably occurs only considering all fertile and sterile plant species, and will be linear considering only fertile ones (Kessler 2009). For animals, e.g. insects, species richness at intermediate levels of altitude is probably related to higher harvestable productivity from the plant communities at intermediate elevations (Janzen 1973).

If species richness at low altitudes is already high, or the slope primarily increases very steeply, the humped relation is often even flat, and after a plateau species richness declines with increasing elevation (Rahbek 1995, Odland & Birks 1999, Colwell & Lees 2000, Grytnes & Vetaas 2002). Altitudinal gradients are more pronounced near the sea than inland (Whittaker 1998). Furthermore, the altitudinal gradients complex appears to be less pronounced at lower latitudes; in all probability, the mean altitudinal range is smaller due to analogous patterns of the below-mentioned Rapoport's latitudinal rule (Stevens 1992).

The altitudinal gradient in species richness is similar to the latitudinal gradient but caused by different factors (Lomolino 2001, Gaston & Spicer 2004), thus decline in diversity with increasing elevation reflects, in most respects, the latitudinal gradient of species richness (Terborgh 1971, Brown 1988). **Climatic factors**, especially temperature and precipitation, are the main grounds for defining this gradient. Generally, an increase in elevation of 1000 m results in a decrease in temperature of about 6 °C, which is comparable with an increase in latitude of a linear distance of 500 to 750 km (Terborgh 1971, Huston 1994). Thus, the altitudinal gradient is also related to **energy availability**, probably reaching the highest values at low to intermediate elevations (Lomolino 2001). Moreover, surface **area** is larger at lower elevation zones, thus species richness according to sampling design can be influenced by the same processes as species-area *per se* relationships (Chapter 7). In general, lower elevation zones have a greater amount of resources, more niches and space for species with larger distribution ranges, greater environmental diversity and greater potential for the establishment of new species (Lomolino 2001).

Furthermore, higher elevations, such as mountain peaks are, for many species, much more isolated from other areas at low or intermediate elevations and are characterised by **island effects** (Chapter 7.1). Incidentally, an isolated position increases the possibility of speciation, as well as of local extinction because of the reduced connectivity of populations. Thus, higher elevations may have lower species richness, but usually have higher levels of endemism (Chapter 4.2) (Gaston & Spicer 2004).

### **Rapoport's Rule**

Rapoport's rule (Rapoport 1982) describes the general trend of increasing extent as well as increasing standard deviation of the geographic distribution range of plants and animals with increasing latitude (Stevens 1989, Rohde 1992, Brown et al. 1996, Richter 1998).

At high latitudes, for example the daily and yearly mean temperature range is much greater than in the tropics. Thus, species occurring in high latitude regions are adapted to different climatic conditions and typically have a higher environmental tolerance i.e. are more tolerant to temperature fluctuations than low-latitude species. The broader tolerances allow species to occur across wider geographical ranges than species at lower latitudes (Stevens 1989). Rapoport's rule provides an explanation for the higher species richness in the tropics (Stevens 1989), because in general, tropical species have smaller ranges than temperate taxa. The rule assumes that local species richness is strongly affected by close range margins of potentially interacting species. Therefore, low latitudinal sites have relatively more species near the margin of their range than high latitude sites (Stevens 1992). Furthermore, Rapoport's rescue hypothesis estimated that there is a protection of local populations from extinction at the range margins of a species in relation to source-sink dynamics, proportionally enhancing the ratio of species per area in the tropics (Stevens 1989, Lyons & Willig 2002).

Rapoport's rule is similar to latitude and can partially explain the decline in species richness as elevation and the altitudinal range of species increase (Brown 1988, Stevens 1992, Harcourt 2000). Species richness often peaks at intermediate altitudes and there is often no negative correlation between the number of range borders and altitude (Hausdorf 2006). In contrast to Rapoport's rule, it was shown that the latitudinal gradient is scale-sensitive (Lyons & Willig 2002).

However, as there is less temporal temperature variation at lower latitudes, the rule in the tropics is less pronounced, and regular increases in latitudinal extents are not common. Therefore, Rapoport's rule is often considered as a pattern of areas in the north respectively of higher latitude (Chown et al. 2004), but it can also be valid for tropical regions (Harcourt 2000). The best-fit models of latitudinal gradients with the real world were estimated by combining Rapoport's rule, rescue effect, and competition at both local and regional sampling scales (Taylor & Gaines 1999).

Moreover, Rapoport's rule is overridden by geometric patterns of species ranges in relation to geographical boundaries (mid-domain effect) and other phenomena discussed by Colwell & Lees (2000).

### **Mid-Domain Effect**

Biogeographic diversity patterns, such as the latitudinal gradient complex in species richness, were generally caused by climatic, ecological, evolutionary, and historical explanations. However, species richness gradients can be the result of geometric constraints on species range boundaries without any environmental or historical gradient, describing the geometry of species ranges in relation to geographical boundaries (Colwell & Lees 2000, Grytnes 2003, Colwell et al. 2004). Boundaries are geographical features that limit the geographical ranges of species by operating as dispersal barriers (Grytnes 2003).

The **mid-domain effect** (MDE) generates a pattern in geographic space. MDE is characterised by a peak of species richness towards the centre of a domain (a region), a humped-shape relation of species richness, because of an increasing overlap of species ranges, due to spatial constraints, towards the centre of a shared, bound geographic domain (Colwell & Lees 2000, Grytnes 2003, Dunn et al. 2007). The MDE is based on shared physiographical and physiological boundaries in relation to range-size distributions of species (Colwell & Lees 2000, Hawkins et al. 2005, Colwell 2008); whereas it is assumed that the geometry of land as well as oceans could, in general, limit the distribution of species (Bokma & Mönkkönen 2000, Zapata et al. 2003).

The distribution ranges of species in models are randomly arranged on a limited one- or two-dimensional area, whereas results can be different in relation to the used model (Arita 2005). Mid-domain models are null models. They explain how diversity will be distributed in space when there are no environmental gradients within the domain. That means that MDE creates patterns in species richness in the absence of environmental gradients (Colwell & Lees 2000, Grytnes & Vetaas 2002, Lyons & Willig 2002). Although, mid-domain models do not explain the underlying ecological processes resulting in those patterns of species richness (Hawkins et al. 2005), they often produce a gradient of species diversity similar to that in real assemblages and explain a large proportion of geographical variation in species richness (Colwell & Lees 2000, McCain 2004, Arita 2005).

Although concerning large scale, the degree to which mid-domain models explain the variation of species richness appears to be scale dependent. Mid-domain model's predictions of patterns of species richness seem to be most explanatory in the case of relatively large distribution ranges and large-scale of analysis (Dunn et al. 2007). Nevertheless, there are also studies where MDEs fit better in smaller latitudinal domains (Romdal et al. 2005), for example, MDEs were more pronounced within classical biogeographic regions in comparison to investigations across the entire global scale (Storch et al. 2006, Weiser et al. 2007).

MDEs occur also along altitudinal gradients in a humped-shape relation, for example, in the case of diversity patterns of small mammals, although climatic conditions such as rainfall and temperature are also correlated with the pattern of species richness (McCain 2004). There are many other examples for mid-domain effects of species richness along elevation gradients (Grytnes & Vetaas 2002, McCain 2004). In addition, mid-domain hypothesis can explain patterns of flowering species richness in sub-alpine communities (Morales et al. 2005).

## **8.2 Regional Scale**

### **8.2.1 Macroclimate (Example V)**

At regional scales, environmental heterogeneity occurs, for example, due to gradients of macroclimate. One regional macroclimate gradient occurs along the Baltic Coast that is characterised by a west-east gradient from sub-oceanic to a more continental climate (Figure 12). Thus, the coastal region of Mecklenburg-Vorpommern can be divided into

different climatic subregions (Kliewe 1951). The changing macroclimate determines the occurrence of **oceanic** and **continental** plant species.

As a result, differences in the distribution of oceanic and continental plant communities occur along the coast (Figure 12). In more oceanic and more continental areas, respectively, only few vegetation types occur predominantly. In contrast, along environmental gradients, such as this macroclimate gradient, **transitions** from one ecological zone to another occur. In contrast, in the climatic transition area, the Darß-Hiddensee-Rügen region (the so-called “Rügener Inselraum”), more vegetation types occur with similar frequency (Isermann 1998). At small scales, transitions from one ecosystem to another, ecotones are often characterised by edge effects. At small scales, ecotones occur, for example, in saltmarshes, coastal foredunes, along rivers, forming boundaries between land and water or between woodland and grassland creating so-called ‘mantel’-communities (Ward et al. 1999).

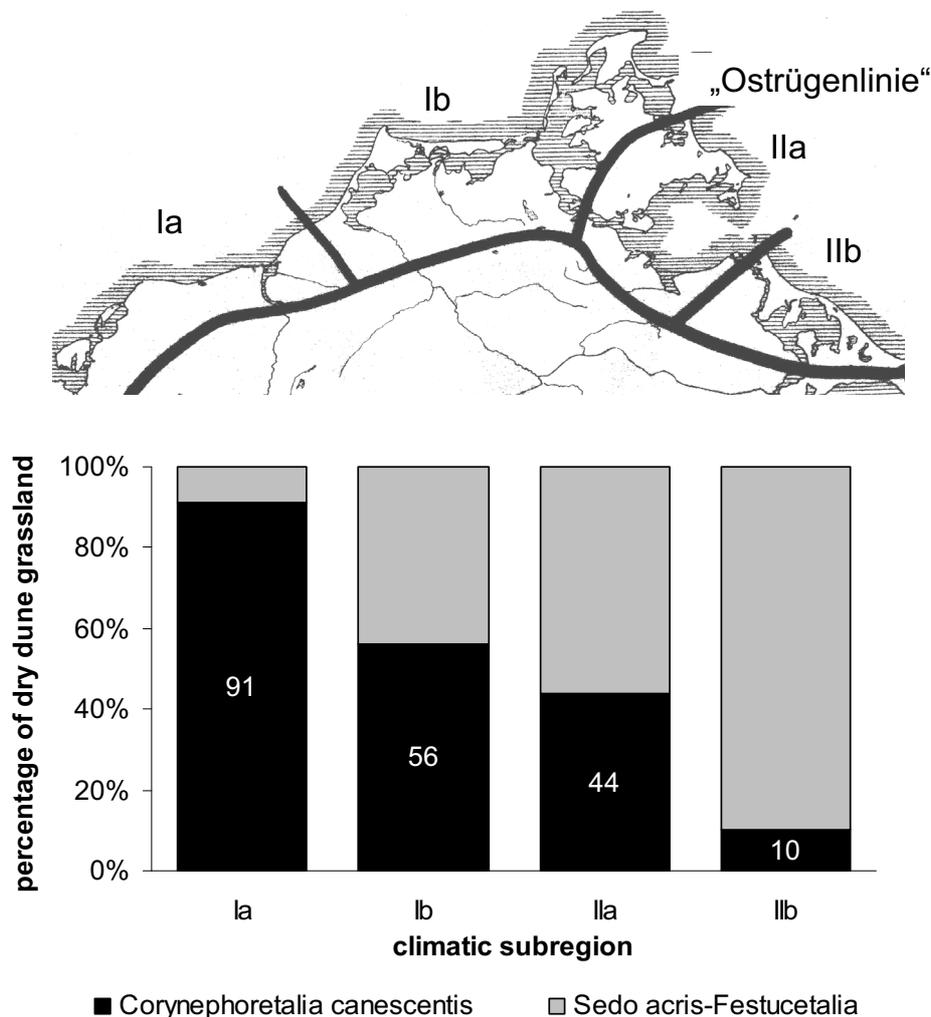
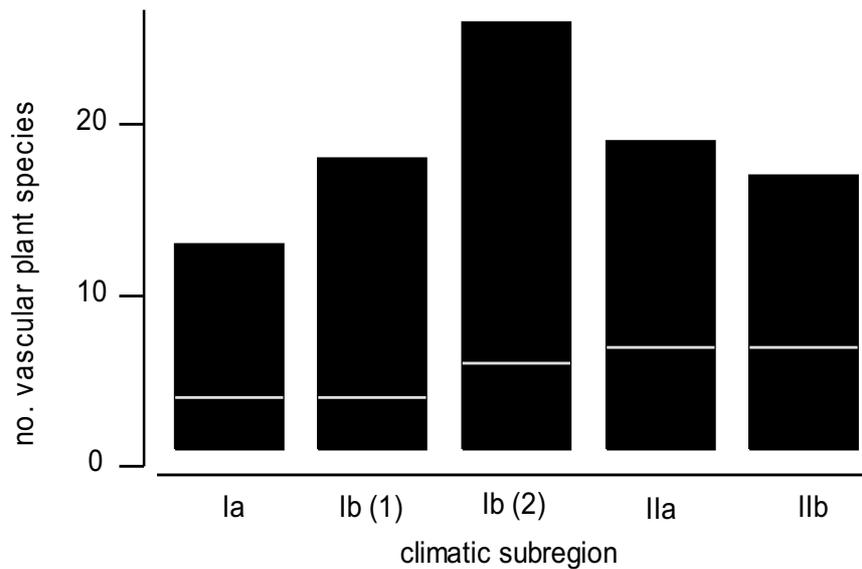


Figure 12. Distribution of dry dune grasslands of oceanic plant communities (*Corynephorretalia canescentis*) and more continental communities (*Sedo acris-Festucetalia*) along a climatic gradient along the Baltic Coast of Western-Pommerania [unpublished data]. Climatic subregions are I western coastal climatic region (Ia Westmecklenburgische Küste, Ib Nordwest-Rügener-Inselraum), II eastern coastal climatic region (IIa Nordost-Rügener-Inselraum, IIb Ostmecklenburgische Küste) (Kliewe 1951).

In general, transition zones are characterised by different environmental conditions, particularly a greater range of environmental conditions, e.g. different nutrients and climate than the adjacent, often more homogeneous neighbouring areas. Thus, a greater number of habitats occur in these zones with the potential for plant species to become established. Moreover, transitions have characteristics of the neighbouring ecosystems, in addition to their unique ones (Ward et al. 1999). Abiotic and biotic differences between the neighbouring areas enhance habitat diversity, and niche differentiation (Holt 1993). Therefore, transitions often have higher values of species richness per unit area than either of the adjoining zones (Shmida & Wilson 1985, Whittaker 1998).



**Figure 13.** Mean number of vascular plant species in dune communities of climatic subregions along the coast of Western-Pommerania. The subregion Ib is divided into two subparts, between Darß and Rügen [unpublished data]. (ANOVA  $F = 49.37$ ,  $p < 0.001$ ,  $n = 107, 403, 410, 219, 194$ ).

Consequently, on the landscape scale transitions can result in a higher degree of vegetation diversity. Moreover, species richness in dunes is on average higher in the transition zone of the Darß-Hiddensee-Rügen area (Figure 13), especially dunes in the western parts of Rügen reach higher values of species richness. Thus, regional environmental heterogeneity enhances both, diversity at communities, as well as at species level.

## 8.3 Local Scale

### 8.3.1 Soil pH (Example VI)

*Isermann M (2005) Soil pH and species diversity in coastal dunes. Plant Ecology 178, 111-120.*

Heterogeneity in environmental conditions can be expressed, for example, by abiotic factors such as climate or soil conditions. Soil conditions differ on spatial and temporal scales (Campbell & Grime 1989, Webster 2000). Coastal areas represent highly

heterogeneous areas (Ievinsh 2006) and this environmental heterogeneity refers to various patterns of environmental variability, such as scale, contrast, certainty, temporarily and spatiality (Ievinsh 2006).

In dunes, for example, the annual variation in soil pH is about one pH unit (Troelstra et al. 1990). Variability of soil contents, such as N, P or K, increases with spatial scale, due to more pronounced effects of geological processes, climate, and topography on soil structure (Beckett & Webster 1971). Besides nutrients, other soil-related factors such as pH-value are of importance in coastal dune areas (Ievinsh 2006).

Moreover, biotic factors, such as the vegetation itself, affect spatial variability in soil parameters, especially at small scales (Yang et al. 1995), as much or more than climatic processes (Goderya 1998). Soil pH is influenced by the vegetation, and interactions between plants and soils are well known (Dahiya et al. 1984). On larger scales, vegetation composition of dunes depends on soil conditions and in turn, dune vegetation has an influence on the soil, e.g. by the enrichment of organic matter. On smaller scales, spatial variability of soil conditions may cause heterogeneous plant growth (Tsegaye & Hill 1998) and probably raises species diversity.

Relationships between species diversity and variability of environmental factors, shown for soil pH, were studied at two different spatial scales in coastal dunes.

**Small-scale variability of soil pH** was measured in five dune vegetation types from the yellow dune to the brown dune on the island of Norderney. From each plant community 36 soil cores were taken from the upper soil of a square metre at 20 cm intervals on a sampling grid. Differences in soil pH were calculated between neighbouring sample points (rows and columns) for each of the five communities.

**Large-scale variability of soil pH** was studied along the Baltic coast of Mecklenburg-Vorpommern. From the upper soil, 190 samples were taken in 12 different plant communities, whereas the distance between samples was larger than 100 m. Number of species, Shannon Index ( $H'$ ), and evenness ( $E$ ) were used to express species diversity. Standard deviation (SD) and coefficient of variation (CV) were used to estimate soil pH variability.

At both scales, species richness and in most cases the Shannon index (Table 5, Table 6) were lowest in the yellow dunes and highest in the grey dunes, with exception of the wet dune valley on Norderney.

At the small scale, soil pH variability between neighbouring points, expressed as both range between minimum and maximum and as standard deviation (within each plant community), was modest in most of the plant communities with a high vegetation cover (Table 5). Soil pH variability was lowest in the community dominated by the moss *Campylopus introflexus* as well as in the *Carici-Empetretum nigri*, and highest in the *Pyrolo-Salicetum* a community of wet dune valleys.

As to the pH difference between the neighbouring points within the 20 cm-grid, soil variability again was lowest in the *Campylopus* community, and reached highest values in the *Pyrolo-Salicetum*, as well as in the *Elymo-Ammophiletum* (Table 5).

**Table 5. Vegetation, species diversity (# number of species, H' Shannon index), percentage total vegetation cover (veg. cov.), dune type, and soil pH variation across sample points of five different plant communities of dunes on Norderney (y = yellow dune, g = grey dune, b = brown dune; SD standard deviation).**

plant community	species diversity		veg. cov.	type	soil pH		Soil pH variation	
	#	H'			Min- Max	SD	Max	SD
<i>Elymo-Ammophiletum arenariae</i>	2	0.43	60	y	0.80	0.24	0.76	0.19
<i>Violo-Corynephorum canescentis</i>	10	1.22	60	g	0.79	0.19	0.64	0.15
<i>Campylopus introflexus</i> community	9	0.55	100	g	0.56	0.12	0.39	0.09
<i>Pyrolo-Salicetum repentis</i>	15	0.53	100	b	0.94	0.19	0.89	0.19
<i>Carici-Empetretum nigri</i>	9	0.94	100	b	0.69	0.16	0.62	0.15

**Species richness** increased with soil heterogeneity, shown in a positive linear trend between the number of species and the soil pH range as well as the maximum of the standard deviation. However, **species diversity** expressed as Shannon index tended to reach highest values at intermediate levels of soil pH variation. Thus, in plant communities with low soil heterogeneity only few species occur, such as in the *Campylopus introflexus* community. Nevertheless, in communities with very high soil heterogeneity only few species occur, for example, in the *Elymo-Ammophiletum arenariae*, where soil heterogeneity is probably very high due to the high level of unvegetated sandy patches. Unfortunately, this relation was only significant regarding the standard deviation of the maximum pH variation.

**At the larger scale**, variability of soil pH, expressed as total range, standard deviation or coefficient of variation, (excluding the *Honckenyetum peploidis* of the beach) was lowest in the *Deschampsia flexuosa* community and the *Carici-Empetretum* (Table 6).

**Table 6. Characteristics of the vegetation and of soil pH of 12 plant communities in Mecklenburg-Vorpommern. (n - number of samples, no - plant community number, t = dune type, # - total number of species, H' - Shannon index, range minimum-maximum, SD - standard deviation, CV - coefficient of variation).**

plant community	n	vegetation				soil pH			
		no	t	#	H'	min	max	SD	CV
<i>Honckenyetum peploidis</i>	7	1	y	6	0.45	1.0	0.38	5.5	
<i>Honckenyo-Agropyretum juncei</i>	8	2	y	6	0.73	1.7	0.62	8.7	
<i>Elymo-Ammophiletum typicum</i>	18	3	y	6	0.73	2.3	0.62	9.3	
<i>Elymo-Ammophiletum festucetosum</i>	21	4	y	12	1.11	4.3	0.91	13.9	
<i>Diantho-Festucetum polesicae</i>	23	5	g	20	1.77	3.4	0.89	16.1	
<i>Caricetum arenariae</i>	21	6	g	12	1.35	3.9	1.37	28.1	
<i>Violo-Corynephorum typicum</i>	12	7	g	12	1.07	3.6	0.96	16.5	
<i>Helichryso-Jasionetum typicum</i>	12	8	g	16	1.42	2.3	0.73	12.1	
<i>Helichryso-Jasionetum cladonietosum</i>	7	9	g	20	1.71	2.1	0.77	13.8	
<i>Violo-Corynephorum cladonietosum</i>	20	10	g	14	1.40	2.5	0.64	13.8	
<i>Deschampsia flexuosa</i> community	3	11	b	11	1.52	0.3	0.15	3.9	
<i>Carici-Empetretum nigri</i>	8	12	b	12	0.97	0.8	0.34	8.4	

The range between minimum and maximum soil pH reached highest values in the grey dunes, because of a linear decline in pH maximum and a nonlinear decline in pH minimum from the beach landwards (a). Soil pH of yellow and brown dunes was less heterogeneous than that of grey dunes. Considering the niche concept, these results show that increasing heterogeneity supports the coexistence of species and results in a higher number of species (Rosenzweig 1995).

Moreover, there was a distinct relationship between soil pH variability, expressed as standard deviation or as variation coefficient, and the zonation of vegetation (b). Soil pH reached highest heterogeneity in the grey dunes, and lower values in the yellow and brown dunes. When considering species richness, the lowest number of species occurred on the first dune ridge (b). Landwards species richness increased and reached highest values in the grey dunes, while species richness declined in the *Deschampsia flexuosa* community and the Carici-Empetretum nigri of the brown dunes.

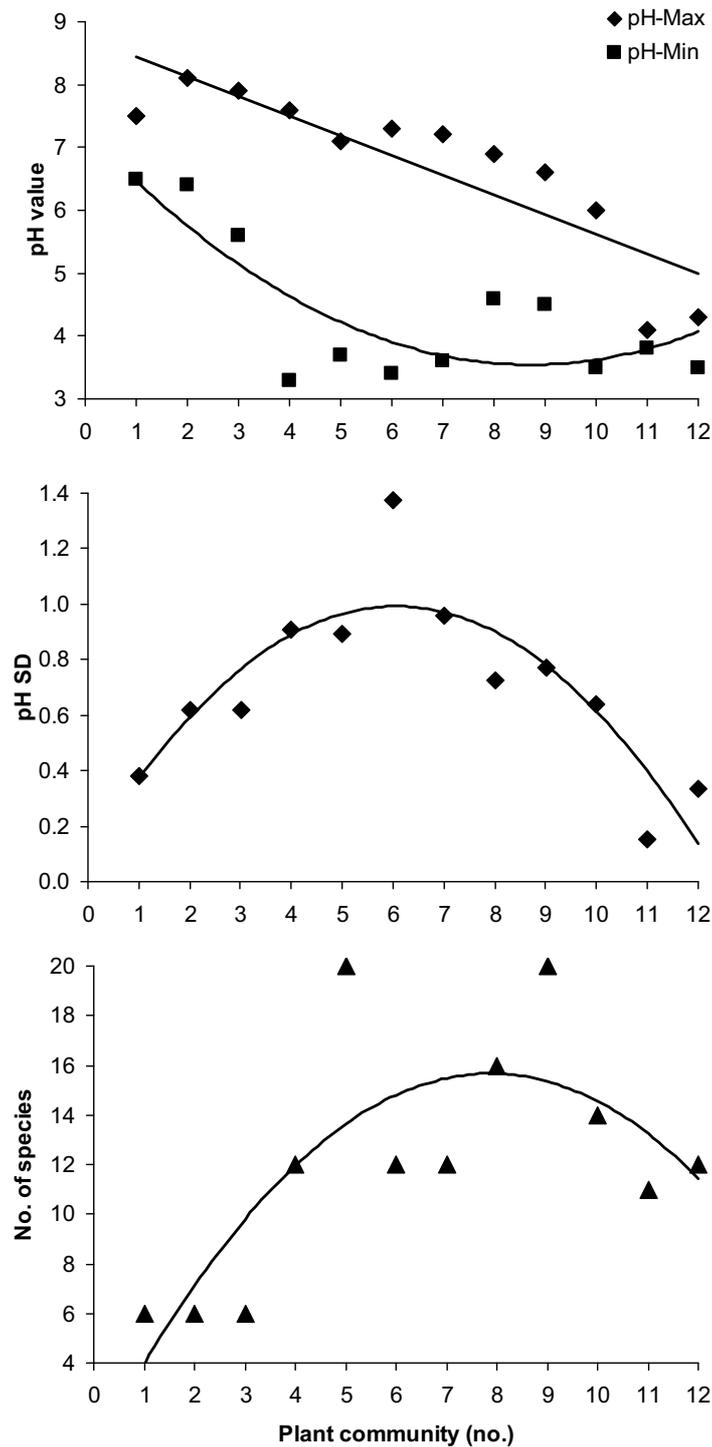


Figure 14. Relationships between parameters of the vegetation and of soil for 12 plant communities of dunes in Mecklenburg-Vorpommern. The vegetation zonation from the beach across the dunes system inland is reflected by the increasing community position (Table 6). (a) Relationship between pH (maximum and minimum) and community position,  $R^2_{adj.} (max) = 0.738$ ,  $p < 0.001$ ,  $R^2_{adj.} (min) = 0.578$ ,  $p = 0.008$ ; (b) Relationship between the standard deviation of pH within each community and community position along the dune xeroseries,  $R^2_{adj.} = 0.677$ ,  $p = 0.003$ ; (c) Relationship between species richness and community position,  $R^2_{adj.} = 0.486$ ,  $p = 0.020$ .

Furthermore, at the large scale, species diversity measured as Shannon index increased with soil pH variability (Figure 15). The greater the species diversity of vegetation, the greater the soil heterogeneity, with regard to soil pH.

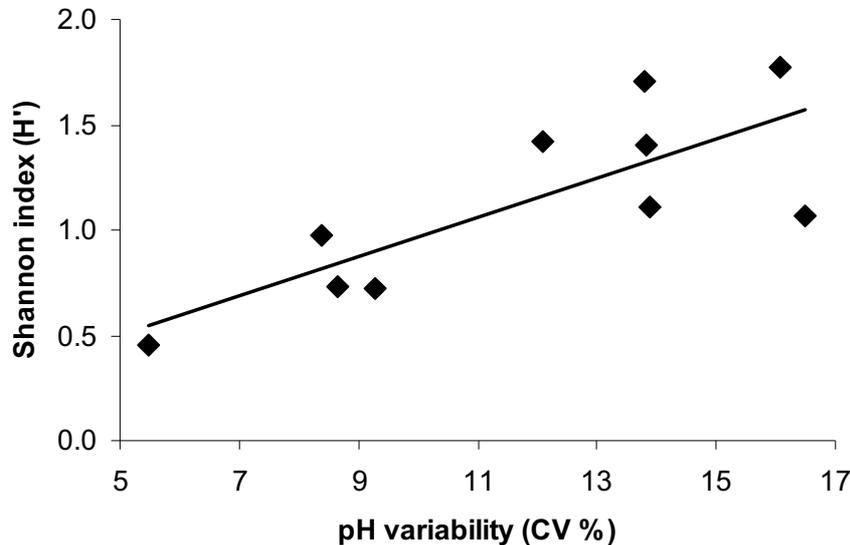


Figure 15. Relationship between the CV of soil pH and the Shannon Index, ( $H'$ ) across dune plant communities of Mecklenburg-Vorpommern; for numbers of plant communities. Grasslands with dominant *Deschampsia flexuosa* and *Carex arenaria* were not considered ( $R^2_{adj.} = 0.57$ ,  $p = 0.007$ ).

**Soil pH heterogeneity** was lower in areas with a high vegetation cover than in areas with more open vegetation, thus soil variability increases with decreasing vegetation cover. Open dune areas generate high soil pH variability because of the mosaic of vegetated and unvegetated areas, which is linked to the distribution of roots as well as organic matter in the soil (Jungerius 1990). In yellow dunes, due to missing organic matter, the sand is not water repellent, the soil is extremely permeable, and therefore rainwater penetrates the soil (Jungerius & Van der Meulen 1988, Jungerius & De Jong 1989). In contrast, grey and brown dunes, with some content of organic matter, are often strongly to extremely water repellent (Dekker & Jungerius 1990). Thus, yellow dunes with a low vegetation cover represent high soil pH variability, because minerals will be leached in open patches and will be less washed out by rain close to marram roots. The effect of individual plants on soil conditions and their spatial variability is well known (Jackson & Caldwell 1996, Tsegaye & Hill 1998) and the pH under grass-bulks is often lower than in the surrounding area (Jackson & Caldwell 1993, Schöttelndreier & Falkengren-Grerup 1999). Soil pH heterogeneity is lower in grey and brown dunes, especially in dunes with high vegetation cover, where minerals will be more fixed due to the organic matter and its water repellence. The results of the dunes confirm that soil heterogeneity is associated with the hummock-hollow-microtopography (Gibson 1988). Moreover, the large variability in soil pH in the dune slack shows that soil conditions of wet and dry dune areas differ very much and that wetland soils generally tend to be more heterogeneous than dry soils (Zeeb & Hemond 1998).

Stands dominated by one or few species (and high vegetation cover) represent the lowest soil pH variability, probably because upper soil layers are very homogeneous.

Vegetation affects soil conditions, for example, due to effects of plant roots and organic matter. Thus, increased abundance of dominant species, combined with a decrease in vegetation diversity reduces soil heterogeneity. Soil pH variability increased with increasing species diversity, and in comparison to various other studies with scale. It decreased with increasing vegetation cover, so decreasing species diversity of vegetation is likely to explain decreasing variability in soil pH. Hence, spatial variability in soil pH in dunes is likely to be caused by the vegetation structure, both at small and at large scales.

Nevertheless, heterogeneity in environmental factors contributes to the maintenance of diversity in plant communities (Ricklefs 1977, Grime 1979, Tilman 1982, Tilman & Pacala 1993, Palmer & White 1994). Soil heterogeneity increases available niches and results in increased species diversity, with vegetation reflecting changes in nutrient availability (Gough et al. 2000). The vegetation of yellow and brown dunes, both on Norderney and in Mecklenburg-Vorpommern, showed lower species richness and diversity than grey dunes. Similarly, Bogaert and Lemeur (1995) found the highest diversity in the Tortulo-Phleetum of the grey dunes and a lower diversity in the Elymo-Ammophiletum of the yellow dunes. Along the Baltic coast, species diversity tended to increase with increasing soil heterogeneity. However, at the small scale, species diversity expressed as Shannon index reached highest values at intermediate levels of soil pH variability. Similarly, at small scales, higher species richness in limestone pavement communities was associated with greater spatial heterogeneity in micro-site and soil depth variation (CV), and species richness was unimodal when related to mean soil depth (Lundholm & Larson 2003).

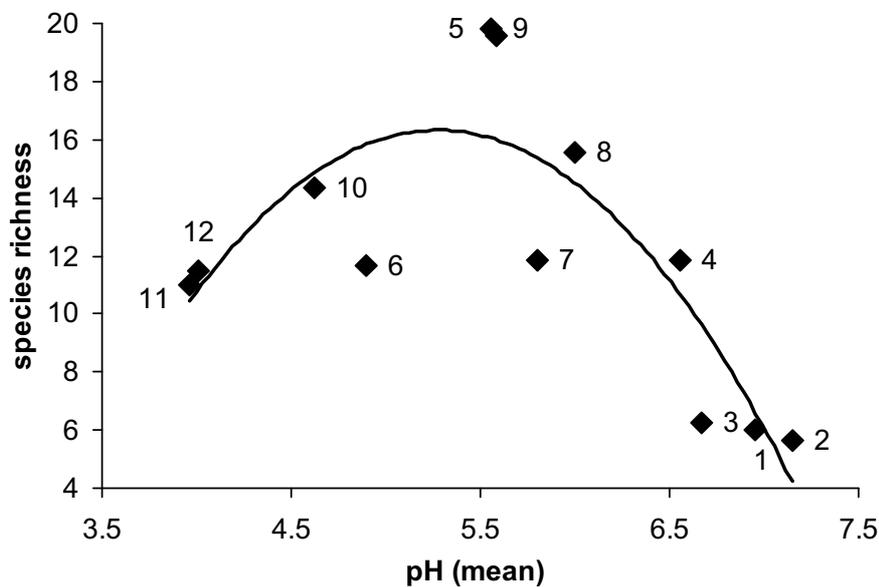
Species can differ profoundly in their ability to use soil resources (Jackson & Caldwell 1989), consequently the greater the amount of available resource-niches, the greater the species diversity. Thus, the results are in line with the often-proposed positive correlation between environmental variability and species richness (Jackson & Caldwell 1993). It is possible that increased spatial heterogeneity allows increased species richness by creating more niches for additional species (Reynolds et al. 1997). As plants vary, for example, in germination and establishment responses linked to different small patches, stands with higher environmental heterogeneity would contain more species (Grubb 1977, Zamfir 2000, Lundholm & Larson 2003). Environmental heterogeneity results in resource partitioning and coexistence of competing species (Ricklefs 1977), and therefore environmental heterogeneity explains a major part of variation in species diversity.

Coastal dunes represent, along both the German North and Baltic Sea, a similar vegetation zonation of plant communities, from the beach and the foredunes, across yellow dunes with *Ammophila arenaria*, grey dunes with *Corynephorus canescens*, to brown dunes with *Empetrum nigrum* heathlands. Sand dune vegetation is closely linked with soil development and, in general, soil pH decreased landward across dune ecosystems (Averiss & Skene 2001). Yellow dunes generally have a neutral or basic soil pH; grey dunes are moderately acid, whereas brown dunes have a highly acid soil reaction. On this scale, the vegetation affects soil development, for example, by building up organic matter. Variation in soil and the supply of base cations affects plant productivity and vegetation composition (Giesler et al. 1998). Soil pH, moisture, biomass, and productivity (Chapter 8.3.3.2) are very important factors for explaining species richness (Roem & Berendse 2000, Schaffers 2002). As productivity, at least to some extent, depends on soil pH, it is assumed that there

are also relationships between species diversity and soil pH in nutrient poor stands such as dunes.

Soil pH was measured, at a regional scale, along the Baltic Coast of Mecklenburg-Vorpommern for various plant communities representing the above mentioned vegetation zonation across the dunes.

Species richness (Figure 16) and diversity, expressed as Shannon diversity  $H'$ , were highest at intermediate levels of soil pH. These intermediate levels of soil pH were found in the grey dunes. Species richness and diversity was lower in more seaward yellow dunes, as well as more landward in the brown dunes. Similar results are shown for Mediterranean dune systems, where highest species richness occurs in the transitions zone from open to stabilised dunes (Acosta et al. 2009).



**Figure 16.** Relationship between species richness and the corresponding mean soil  $\text{pH}_{\text{KCl}}$  of the plant communities ( $R^2_{\text{adj.}} = 0.615$ ,  $p = 0.006$ ). The vegetation zonation from the beach across the dune system inland is reflected by the increasing number of community position, whereas beach to typical yellow dune (1-3), various grey dune communities (4-10), and brown dunes with heath and dominant *Deschampsia flexuosa* grassland (11-12).

In other ecosystems, for example, in tundra systems, soil pH may show a linear relation with species richness (Gough et al. 2000). Others found a linear increase in local species richness across various forest communities with mean Ellenberg indicator value R and slightly with indicator value L, so the higher the **soil pH**, the greater the number of species (up to a certain upper limit) (Willner et al. 2004). Another linear increase of species richness, as well as of species diversity, with increasing soil pH was shown for grasslands and heathlands (Roem & Berendse 2000). These linear relations can be explained by different patterns, e.g. **scale-dependence**, whereas at smaller scales unimodal relations predominate, at larger scales linear relations do. On the other hand, the relationship between vascular plant species richness and soil pH varies in different regions, whereas soil pH generally increases with latitude, the relationship between vascular plant species

richness and soil pH is often positive at high latitudes, for example, in Europe, and negative at low latitudes (Pärtel 2002).

In view of the zonation of vegetation, grey dunes have the highest species diversity and the largest variability (Chapter 8.3.1) in soil pH, which is probably due to the environmental conditions along the dune xeroseries. Up to the yellow dune ridge, wind and sand movement is mostly very high. Furthermore, there occurs only a raw soil, the primary soil type of syrosem, without any organic matter. In comparison of the whole dune series, the foredunes and the yellow dunes are unfavourable habitats, because of the high sand dynamic, the higher soil and air salinity and the lower organic matter. With transition to the grey dunes, sand movement decreases and organic matter accumulates in the soil. For plants, the best soil conditions of the dune series are in the grey dunes, where the effects of the ecological factors are changed. Furthermore, in the grey dunes, the climatic conditions changed, and both soil and climate resulted in more favourable growth conditions for various plants (Carter 1988). Further landward in the brown dunes, dense heathlands with highly acid soil, due to high content of organic matter occur, allowing few species, such as *Empetrum nigrum* and *Deschampsia flexuosa*, to grow on these sites. Moreover, these species often build up dominant stands, so that the competition with smaller herbs, especially annuals, to strengthen. Similar results were shown for upper saltmarshes, where plant species diversity reached highest values in intermediate vegetation zones, and was positively correlated with phosphate availability (Theodose & Roths 1999).

Thus, along an environmental gradient, such as the coastal dune series, intermediate environmental conditions of soil, as well as of climate, favour the establishment of various plant species so that species richness, as well as diversity, reached highest values.

### 8.3.2 Disturbance

Heterogeneity is often caused by landscape diversity, for example, due to geology and soil, but also by disturbances that increase the heterogeneity of the environment as well as the amount of available ecological niches, for example, in wetlands by flooding (Ricklefs 1987). In general, disturbances eliminate species from an area and open that area for re-colonisation (Petraitis et al. 1989). At small scales, disturbances are very unpredictable, while they are more predictable over larger areas (Huston 1994). Disturbance plays a major role in preserving species diversity in many ecosystems (Huston 1979, Walker & Peet 1983, Denslow 1985), for example, mowing is considered as essential for maintaining high species diversity of grasslands (Olf & Bakker 1991, Geertsema & Sprangers 2002, Vestergaard 2008). In general, biotic and abiotic disturbances are important factors affecting community composition and structure, as well as biodiversity (Collins & Barber 1985).

Disturbance can be **defined** as any discrete event or process that removes biomass from a community (Grime 1979) and that disrupts ecosystem, community or population structure and changes resource availability or the physical environment (Hughes et al. 2007). It can be qualified by different **characteristics**: type, intensity, frequency, spatial expansion, duration, and regional context (Collins 1987, L  veque & Mounolou 2004).

Disturbances can be differentiated in **abiotic types**, such as volcanic eruption, extreme temperatures, drought, floods, fires, windstorm, erosion, and sand deposition. Furthermore, there are **biotic types**, such as tree falls, grazing, predation, burrowing

(Figure 17), digging, trampling, or agricultural activities like mowing of grasslands with removal of hay, and other anthropogenic activities (Huston 1994, Rosenzweig 1995, Shea et al. 2004). Changes in average temperature, addition or removal of nutrients and the invasion of exotic species could also be considered as disturbance, if it results in sudden removal of biomass (Huston 1994). In many cases, different disturbance types interact, such as fire and grazing (Kerby et al. 2007) and have in combination different effects than a single disturbance type.



**Figure 17. Small-scale disturbance by burrowing of a mouse.**

Disturbance effects vary with **intensity**, which is determined by the proportion of **biomass** that is removed by the specific disturbance event (Huston 1994). Sometimes the term ‘intensity’ is synonymously used for the entire **level** of disturbance (Petraitis et al. 1989), which is defined as the combination of all components of the specific disturbance (intensity, frequency, spatial expansion, duration).

Relations between disturbance and species diversity vary with **scale** and **type** of disturbance (Chaneton & Facelli 1991). For example, flooding declines diversity at patch scale but increases it in the case of grazing; and generally increases diversity at larger scales (Chaneton & Facelli 1991). Furthermore, the **size of the disturbed area** per disturbance event is of interest (Petraitis et al. 1989). Small disturbances disrupt equilibrium less because only few species and little biomass are removed (Collins & Barber 1985). Massive disturbances such as glaciations and volcanic eruptions destroy most of a habitat and may reduce species richness more or less completely (Rosenzweig 1995). Massive disturbances have major influence on species diversity (Huston 1994), which is reflected, for example, by differences in species composition of trees in Europe and America due to glaciations. Vegetation re-establishment following disturbances depends on various factors, such as soil **seed bank** and **colonisation probabilities** across eventually large distances (Cain et al. 2000). Thus, the relation of the disturbed area to the entire area similar in ecological conditions is of interest, because the undisturbed habitat has the function to be the primary source for propagules of species for re-colonisation

(Huston 1994). Due to **dispersal** limitation (Tilman 1997), large disturbances could initiate the process of natural habitat fragmentation, which is one of the major threats to biodiversity (Kerby et al. 2007), but otherwise it could be the first step in initiating speciation and ultimately increase species richness.

Disturbance events may take place as single or as regular events (Lévêque & Mounolou 2004). The rate at which disturbance of any given size occurs, the number of disturbance events per unit of time, i.e. the **frequency**, predicts to a large amount the effect on the site (Petraitis et al. 1989). Moreover, frequency can be expressed as the length of time since the last disturbance (Huston 1994). Usually the more often a patch is disturbed, the lower the species richness, but species richness is often also reduced at sites with very low disturbance rates (Rosenzweig 1995). Disturbance intensity is often inversely related to disturbance frequency. Low frequency disturbance can support the accumulation of biomass during the disturbance intervals, so that the amount of removed biomass, absolute and relative, in a single disturbance event is greater than in the case of frequent disturbances (Huston 1994). Disturbance frequency affects plant species composition and, for example, in coastal dunes of Cape Cod the seed bank was more similar to the aboveground vegetation in the case of frequent disturbance due to wash-over events, than in the case of rare disturbance (Pierce & Cowling 1991).

The point in **time** of a disturbance can also determine which species will be more sensitive to damage, or whether the landscape will be more susceptible to disturbances, such as erosion, and which species are most able to re-establish into the disturbed area (Huston 1994). Therefore, disturbances in spring for example have different effects than disturbances in autumn (Huston 1994).

The **intermediate disturbance hypothesis** (IDH) expresses that intermediate levels of disturbances maximise species diversity of a system (Grime 1973, 1979, Whittaker 1977, Connell 1978, Huston 1979). The pattern, that disturbance intensity as well as frequency at intermediate levels will maximise species richness, was shown at first by Connell (1978) for coral reefs, but the roots of the model extend back to Watt (1947), Hutchinson (1953, 1961), and Grime (1973), among others. Disturbance such as grazing, mowing, burning, trampling, pollution (Trubina 2009), as well as fragmentation and invasion of exotic species can be interpreted as **environmental stress**, which was recognised early on to propose species richness under consideration of species competition (Grime 1973, Walker & Peet 1983, Wickham et al. 1997). Moreover, occurrence of competitive interactions changes highest species richness to environments with lower environmental severity (Xiao et al. 2009).

The **gradient** of disturbance can be accessed as frequent to infrequent disturbance, soon to long after disturbance, large to small intensity, and large to smaller sized areas (Connell 1978, Huston 1979, Walker & Peet 1983, Denslow 1985, Rosenzweig 1995). There are many examples that species diversity is highest at **intermediate levels of disturbance**, with low diversity at both high and low frequency and intensity (Connell 1978). For example, tree species richness reached highest values at intermediate disturbance levels in the case of tropical rain forests (Molino & Sabatier 2001). Due to different disturbance gradients, the IDH is probably most pronounced if all three aspects **frequency**, **intensity**, and **time** since disturbance are at intermediate level (Li et al. 2004).

In addition, using diversity indices, the intermediate disturbance-diversity relation varies, for example, Shannon-Wiener diversity and Pielou's evenness fits the IDH model much more than total number of species (Li et al. 2004).

However, there are difficulties, if using, for example, the proportion of pioneer species as a measure of disturbance, because when using the proportion of one species group in relation to total species richness there will be, in all cases, humped patterns due to statistical reasons (Arim & Barbosa 2002). Due to the recognition that disturbances are common in most communities, the IDH assumes that communities are in a **non-equilibrium stage** and that high species diversity is the consequence of continuous fluctuations in the environment that prevents the ecosystem from reaching a stage of equilibrium over time (Hutchinson 1961, Connell 1978, Huston 1994, Rosenzweig 1995, Collins & Glenn 1997). The IDH pattern of highest species diversity under intermediate disturbance levels can be based on different underlying mechanisms of coexistence, but in general, disturbance changes niche opportunities available to the species in a system (Roxburgh et al. 2004, Shea et al. 2004). Changes in competition relations, spatial and temporal variability in resources and environmental conditions are some of these patterns. The IDH is probably an ecological mechanism, but it is necessary to define it as a complex of different coexistence mechanisms (Roxburgh et al. 2004).

Effects of disturbance on species diversity vary with **ecosystem** (Huston 1994). For example, in South African fynbos, as well as in North American grasslands, high frequency burned sites have the highest, and intermediate the lowest species richness at different spatial scales (Schwilk et al. 1997). A linear decrease in species richness in the case of fire, from low to intermediate levels of fire frequency, was also shown in long-term experiments (Collins et al. 1995). The IDH is also valid for animals, e.g. intermediate time levels after disturbance (sand mining) maintain rodent species richness in coastal dunes of South Africa (Ferreira & Van Aarde 2000).

Disturbance affects other ecological processes, in particular **succession** (Denslow 1980, Tilman 1983, Glitzenstein et al. 1986). The progress of ecological succession following disturbance is based on the dynamics of immigration and extinction (Collins & Glenn 1997). In general, species richness directly after a disturbance event is reduced, especially regarding large scales, for example after burning (Brooks & Matchett 2003), and starts with the arrival of propagules of a few species in the open patch. Diversity is low because time for colonization is short. As the interval between disturbances increases, diversity will also increase at first, because more time is available for the establishment of more species. In addition, it was shown, that at low disturbance levels, there is a linear increase in diversity with decreasing disturbance (Bruno et al. 2004). As frequency declines further, and in general, at lower disturbance levels, diversity will decline because competitively **dominant species** occupy resources, increase interspecific competition and eliminate other species with weaker competition (Grime 1973, 1979, Connell 1978, Petraitis et al. 1989). Disturbances thus create heterogeneous environments and can suppress dominants.

In contrast, generally increased disturbance levels i.e. too harsh, too common, very frequent, or intense disturbances, eliminate most species, and only few species that are resistant to the disruption, often colonising species, with short life cycles such as annuals, are able to establish and persist. Thus, at intermediate disturbance frequency or intensity,

diversity of plant species reaches highest values (Grubb 1977, Connell 1978, Brown 1988, Petraitis et al. 1989, Rogers 1993, Collins et al. 1995, Rosenzweig 1995, Lévêque & Mounolou 2004).

Disturbances are creating open patches for plant establishment and therefore initiate secondary **successions** at different scale and are an important pattern in relation to community structure and dynamics (Shmida & Ellner 1984), as well as in relation to dune landscape heterogeneity (Povilanskas et al. 2009). Re-establishment of vegetation can be very fast, such as in fynbos vegetation, where after fire and shrub cutting all dominants and more than 60 % of the mature fynbos species re-established after few years (Cowling & Pierce 1988). Succession dynamics depend on disturbance intensity, frequency and disturbance type in relation to life history traits of the species pool, for example, dispersal capacity (Denslow 1980, Lévêque & Mounolou 2004). Succession after disturbance generates a mosaic of patches in different successional stages, because it is a function of differential growth rates and survivorship among early and late successional species (Collins et al. 1995). Vegetation may remain in an earlier succession stage for a long time after a relatively high disturbance frequency, often with highest species diversity during earlier successional stages, due to dependence on the environmental conditions of the ecosystem. At low disturbance levels late successional stages dominate. In-between there is a mixture of various intermediate succession stages, resulting in high species diversity. Thus, a unimodal diversity-disturbance relation occurs, when early and late successional stages are separated by long-lived intermediate successional stages (Johst & Huth 2005, Pierce et al. 2007).

Species traits, such as long dispersal and the ability to survive in a dormant stage, allow early-successional species to survive in communities with low disturbance frequencies and to germinate in open patches after disturbance (Huston 1994), in line with the concept of **r-** versus **K-selection** (MacArthur & Wilson 1967, Grime 1974). Thus many plant species have a more successful seedling establishment in areas with small open patches disturbed e.g. by ants and rabbits, for example, *Corynephorus canescens*, *Spergula morisonii* and *Teesdalia nudicaulis* in dry sandy grasslands (Jentsch et al. 2002). Composition of different functional groups varies with area disturbed (Schippers & Joenje 2002); this was also shown for dunes, whereas different functional groups of plants are related to disturbances by natural sand dynamic (García-Mora et al. 1999).

Relations between diversity and disturbance depend on various factors, for example, on species composition, on landscape heterogeneity and on the level of **productivity** (Huston 1979, 1994, Cardinale & Palmer 2002, Hughes et al. 2007). In general, the higher the productivity, the more infrequent disturbance events are, due to enhanced stability of the system. Thus, disturbance is the opposite of stability. However, disturbance and productivity correlate at lower to middle productivities, but not at higher levels of productivity (Rosenzweig & Abramsky 1993).

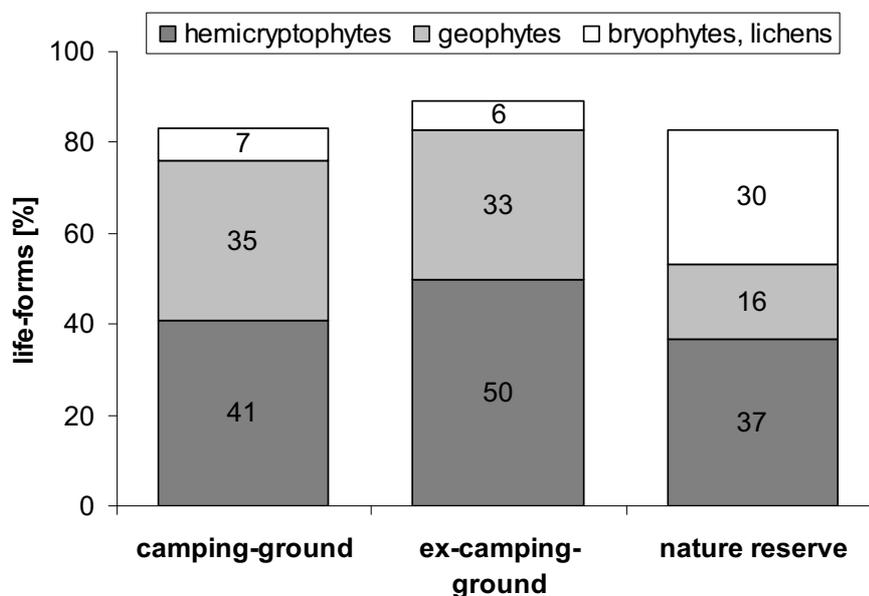
### 8.3.2.1 Human Trampling (Example VII)

Trampling by animals, as well as by humans, is one type of biotic disturbance. Intensive human trampling occurs, for example, in coastal dunes due to recreation. Dunes are especially susceptible to trampling in comparison to other terrestrial vegetation, because of the extremely low soil penetration resistance of sand (Davenport & Davenport 2006). This

results in compaction of sand, initiation of mobile sand and erosion, as well as having an effect on the vegetation (Doody 2001). Relationships between **trampling** and species richness are similar to other disturbance types, often being in line with the intermediate disturbance hypothesis. In contrast, there are examples where species richness declined at various trampling levels (McDonnell 1981). When trampling intensity or frequency is too high, species richness and species diversity show, in most cases, negative linear relationships (McDonnell 1981, Vogt Andersen 1995, Ikeda 2003). Once the vegetation cover has been severely removed, the recovery rate is very slow, because increasing vegetation removal mobilises the sand more and more, resulting in difficulties for seedling establishment (Pizzey 1975), for example, due to changes in micro-climate. Decline in the number of therophytes was also shown in other climatic regions (Kutiel et al. 2000). Moreover, trampling vulnerability for various vegetation types increases with primary productivity (Liddle 1975). Trampling effects on dune vegetation vary with dune type, mobile dunes with natural high sand dynamic are less sensitive to trampling than, for example, semi-fixed grey dunes (Lemauviel & Rozé 2003).

Trampling in coastal dunes was analysed by the comparison of an area still used as camping-ground, an area formerly used as camping-ground and an area protected as a nature reserve (Isermann & Krisch 1995). All sites are directly neighboured. Vegetation relevés along transects across the dunes were used to describe vegetation structure and species diversity in relation to the different trampling levels.

The total number of plant species reached a value of 67, and was highest at the protected area. At the camping-ground, the disturbance level (intensity and frequency) was too high, so only 29 species occurred. At the ex-camping ground area, the time after disturbance was probably too short for regeneration of semi-natural vegetation, thus the number of species was similar to the area used as camping-ground and reached 34 species.



**Figure 18.** Percentage of life-forms (hemicryptophytes, geophytes, bryophytes and lichens) in neighbouring areas of a camping-ground, a former camping-ground, and a protected area in a nature reserve (results based on Isermann & Krisch 1995).

More pronounced were the differences regarding the percentage of life-forms that vary along the trampling gradient (Figure 18). The proportion of geophytes increased with trampling intensity; due to species traits, e.g. rhizomes support resistance to trampling. Bryophytes and lichens only play a role in the undisturbed area, because they are not resistant to sand movement. Hemicryptophytes reached highest values at intermediate levels of trampling, probably because dunes are less mobile at these sites, than at the camping-ground, and are not yet so fixed, due to dense vegetation, than at the protected area. Semi-fixed dunes, which represent a transitory dynamic stage usually with highest species richness (Chapter 8.3.1), are supported by moderate levels of sand burial. Thus in fixed dunes, low disturbances maintain species richness and species diversity, while heavy ones create serious damage (Lemauiel et al. 2003).

The variation of trampling effects in relation to life-forms was also shown for Danish dunes (Vogt Andersen 1995), where in contrast to our results species richness of therophytes, hemicryptophytes, and geophytes showed indifferent effects (Vogt Andersen 1995). Effects of human trampling in coastal dune areas are especially enhanced at paths and tracks. Across a path, from inland to the beach, the area of human impact generally gets broader nearer to the beach. As the number of paths per region gets larger, driftline and dunes will be more and more effected by **fragmentation**, and regions with natural vegetation will be destroyed (Isermann 1999).

### 8.3.2.2 Grazing (Example VIII)

*Isermann M, Koehler H, Mühl M (2009) Interactive effects of rabbit grazing and environmental factors on plant species richness on dunes of Norderney. Journal of Coastal Conservation, Planning and Management DOI: 10.1007/s11852-009-0056-9.*

Grazing, representing another biotic disturbance type and can be divided in relation to the size of the **animal**, e.g. large, or small herbivores, to the type of the animal, e.g. invertebrates or vertebrates, especially mammals. Grazing varies with the status of the animal, for example, cattle or wild animals, as well as differing in relation to the combination of different grazing animals, e.g. geese, hares and cattle in salt marshes (Kuijper & Bakker 2005). Herbivory, especially by large animals, creates spatial and temporal heterogeneous environments, for example, in accordance to nutrient distribution, preferences for plants and trampling (Adler 2001, Anderson et al. 2004).

In coastal dunes, beside sand dynamic, one of the main factors for plant species diversity is herbivory and in addition to domestic livestock, wild **rabbits** have been the most important herbivores over centuries (Doody 2001). In the last century, land-use has changed and grazing by domestic stock has declined. The decline in grazing, as well as other environmental changes, such as groundwater catchments and atmospheric eutrophication, has changed dune vegetation (Van der Hagen et al. 2008). Grazing for conservation aspects often is used to reduce the increase of biomass by nutrient deposition, but in dunes it was shown that grazing only partly mitigate the negative effects (Plassmann et al. 2009). Moreover, there have been cyclic changes in population density of wild rabbits during the last 150 years, because of varying hunting intensity and diseases, such as myxomatosis and rabbit-haemorrhagic disease (Drees 2004). In the 1990s, the rabbit

population on the Frisian Islands collapsed and has subsequently stabilised at a lower level since 2003 (Drees 2007). In relation to changes in land-use and herbivory, tall and dense grasslands, as well as shrublands extended. In contrast, there has been a decline in open, species-rich vegetation (Isermann & Cordes 1992), for example, lichen-rich grasslands (Ketner-Oostra et al. 2006), which often represent priority habitat types of the European Fauna Flora Habitat Directive 92/43/EEC (Council of the European Commission 1992).

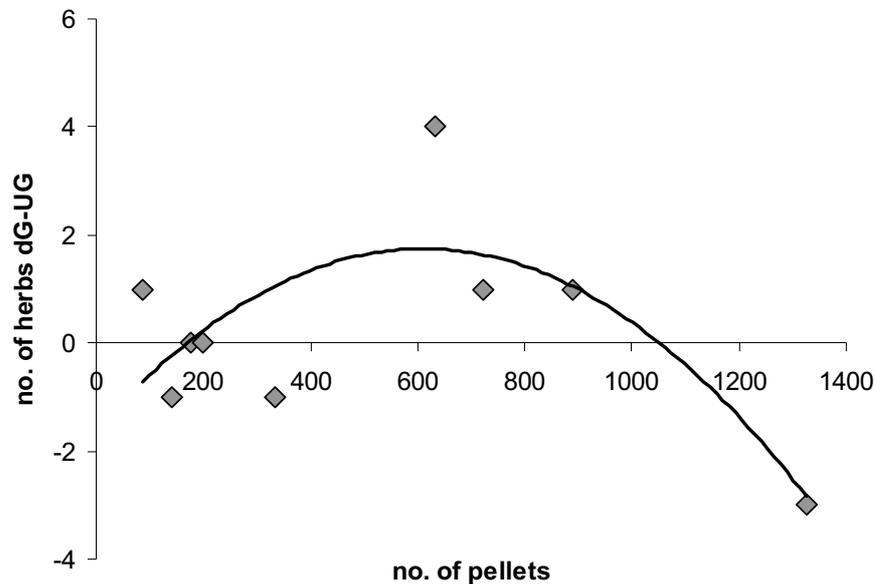
To investigate effects of rabbits on species diversity in coastal dunes, the vegetation of fenced and unfenced plots were compared. This study only included the intensity of disturbance – not the frequency. Rabbit grazing pressure was estimated indirectly by counting the faecal pellets. It was shown that grazing pressure varied in relation to the vegetation type of the dunes. Usually, grazing pressure varies in different vegetation types of salt marshes and consumption by herbivores, for example, of geese and hares, was highest at intermediate productivity levels (Kuijper & Bakker 2005). Rabbit pressure varies in relation to the vegetation type, probably due to **palability** of plants, especially to the preference of plants with the highest nutritional quality (Somers et al. 2008). Forage quality and resulting preference by large herbivores, for example, supported the seed dispersal of salt-marsh species more than the dispersal of dune species (Bakker et al. 2008). Hence, grazing influence on species-composition is also due to dispersal processes. Since rabbit's activities are mostly in the area surrounding of their burrows, rabbit pressure also differs in relation to burrow digging possibilities. To compare grazing effects in different vegetation types, differences in the number of plant species between grazed and ungrazed plots were calculated.

Species richness in general tended to be slightly higher in grazed plots. However, due to food preferences of the rabbits and adaptations against herbivores, species richness of herbs and bryophytes was higher, that of grasses was lower and species richness of shrubs and trees was clearly reduced in grazed plots.

Total species richness, as well as the number of herbs, showed a humped-back relation with increasing grazing pressure. The total number of plant species, and more clearly the number of herbs, increased at first with increasing number of pellets and showed the highest species richness at intermediate numbers of pellets (Figure 19). Thus, highest values of species richness, in this case especially of herbs and chamaephytes, were reached at intermediate grazing pressure.

As in this study, the phenomenon of the **intermediate disturbance theory** was generally found in other grazed grasslands (Tansley 1939, Zeevalking & Fresco 1977, Gibson & Brown 1991, Tallowin et al. 2005). In arid regions, highest species diversity for example is reached in areas with moderate grazing of camels in combination with small antelopes (El-Keblawy 2009). Moreover, highest species diversity under low and intermediate grazing pressure was observed not only for plants, but also for butterflies and grasshoppers (Dumont et al. 2009). The intermediate disturbance hypothesis is closely related to aspects of **heterogeneity**. To some extent, grazing and other activities of rabbits increase species diversity due to increasing habitat diversity (Collins & Barber 1985). Grazing and other activities, for example, of rabbits create open patches. The increased sand dynamics contribute to a heterogeneous, dynamic landscape (Doody 2001) with higher species diversity. Grazing often causes an increase in spatial heterogeneity, but in

other examples heterogeneity decreases, this depends on the interaction between the spatial pattern of grazing and the pre-existing spatial pattern of vegetation (Adler et al. 2001).



**Figure 19. Relationships between the number of pellets and the difference in the number of herbs between grazed and ungrazed plots. Differences was measured as grazed (G) – ungrazed (UG) plots. ( $R^2_{adj.} = 0.40$ ,  $p = 0.093$ ).**

Effects of different disturbance types vary, often various disturbance types interact and cumulative effects of different disturbance types are possible (Collins & Barber 1985, Collins 1987). Fire, grazing and soil disturbance by animals are important factors in maintaining species diversity in many different grassland systems (Burggraaf-van Nierop & Van der Meijden 1984, Belsky 1992). However, due to interactions, the IDH cannot address the various interactions among disturbances in communities with more complex disturbance regimes (Collins 1987).

Grazing affects, for example, dunes grasses and generally reduces vegetation cover, in principal species with relatively high moisture content are more grazed (Hester et al. 1994). In more detail, in more or less closed vegetation, like shrub- and heathlands, rabbit activities creates new bare patches, that can be used e.g. by light demanding annuals.

Similarly, sheep change dominance relationships between *Calluna vulgaris* heathlands and the invasion of *Deschampsia flexuosa* (Farrow 1917, Bokdam 2001). In more open vegetation, like grey dune swards, rabbit pressure appears to be too high and therophytes were out-competed or eliminated by grazing probably due to sand dynamic, high-temperatures and reduced germination. Similarly, annual species richness was highest in intermediate grazing levels in open shrubland in Israel (Naveh & Whittaker 1979). Comparable with our results, in grasslands grazing resulted in changing abundances of monocots and dicots favoured by grazing (Belsky 1992, Somodi et al. 2004). In the case of too strong grazing pressure, the total number of plant species, as well as of herbs, declined. Therefore, strong grazing pressure is a factor that reduces species richness and changes native plant communities (Chapuis et al. 2004). Moreover, input of **nitrogen** e.g. by rabbit

excrements could cause a decline in species richness (Boorman & Fuller 1982), at high grazing levels.

Relations between diversity and grazing vary in relation to **macroclimate** (Milchunas et al. 1988) and represent a unimodal relation, as in the dune example shown, in sub-humid climates, such as the Netherlands (Van Wieren & Bakker 2008).

In contrast to the humped relationship of the number of species, **floristic similarity** between ungrazed and grazed plots, measured as difference in Euclidian distance, showed an increasing linear trend with rabbit grazing pressure in dunes. However, it is not surprising that the greater the grazing pressure, the more different the grazed and ungrazed vegetation are.

In rabbit-grazed coastal dunes, species diversity measured as **evenness** tended to be lower in grazed plots; hence, species composition is more heterogeneous in the grazed plots than in the ungrazed ones. In vegetation dominated by few species such as shrub- and heathlands, the **dominance** level measured as inverse Simpson index was lower in the grazed plots. In contrast, in grasslands the dominance relations tended to be larger in grazed plots, probably because some life and growth forms with stronger competition effort, such as grasses in general, out-compete species like herbs with other traits. For example, it was shown that clonal species are more tolerant to grazing than non-clonal species (Liu et al. 2007). Thus, rabbit grazing affects, as well the dominance structure of dune vegetation, also depend on the habitat type. In addition, moderate grazing intensity also enhanced diversity of butterflies and grasshoppers at grasslands (De Vries et al. 2007).

Effects of grazing on species richness and species diversity vary not only in different habitat type but are also **scale-** and **time-dependent** (Bos et al. 2002, Olofsson et al. 2007). Rabbit grazing enhanced species richness at different plot sizes, but the mechanisms involved at different scales vary (Olofsson et al. 2008). In relation to **time**, obvious reduction in grazing results in the first years of succession, often with an increase in species richness and diversity (Van der Maarel 1971, Van Leeuwen & Van der Maarel 1971). Nevertheless, in the end, species diversity decreases without disturbance, because of the development towards dynamic equilibrium (Chapter 7.1). During succession, for example, over a time of 25 years in salt marsh exclosures, species richness decreased (Bos et al. 2002). Similarly, species richness declined during 15 years succession in mountain grasslands of Argentina (Pucheta et al. 1998).

For **conservation** of semi-fixed dunes, which represent a transitory dynamic stage, sand burial e.g., initiated by rabbit scraping, is favourable (Lemauviel et al. 2003). Moderate grazing or other disturbances like trampling in dry dune grasslands support open areas, allowing pioneer species such as annuals to develop, and reduce competition of dominant species, typical of later successional stages (Zeevalking & Fresco 1977, Doody 1989, Lemauviel et al. 2003). To prevent or reduce succession and preserve local plant species richness, moderate **cattle grazing** can be an effective substitute for rabbits (Aptroot et al. 2007). For example, total species richness in coastal dunes increased after the introduction of horses and cows (De Bonte et al. 1999). Grazing may enhance resource availability for plants, the resource availability hypothesis (Chapter 8.3.3), and is linked e.g. to the increase of gaps by trampling and scraping and to the increase in light availability by the decline of biomass (Grime 1979, Bakker et al. 2003).

Effects of **cattle** are different according to selective defoliation, which modifies the competition between plant species, both by direct removal of phytomass and by changing the light conditions. Moreover, a second mechanism is treading which creates gaps for light-demanding species and a third mechanism is the change of the nutrient cycle and probably local enrichment of nutrients (Rook & Tallowin 2003). Cattle such as donkeys, koniks and sheep were often used for the management of coastal dune grassland (Cosyns et al. 2001). Especially in relation to the spreading of *Rosa* species, *Rubus caesius*, as well as *Hippophaë rhamnoides* (Figure 20), donkeys were of interest because they feed on the fruits (Lamoot et al. 2005). Cattle, such as horses, also affect the vegetation cover and support open vegetation (De Stoppelaire et al. 2004).



**Figure 20.** *Hippophaë rhamnoides*.

Similar to temperate regions, in the Mediterranean area, protection of natural areas has often caused traditional grazing to stop. Furthermore, e.g. on the Iberian Peninsula, rabbits were abundant until the 1950s, and due to diseases similar on the Frisian Islands, there was a decline to very low levels (Catalán et al. 2008, Delibes-Mateos et al. 2008, Dellafiore et al. 2008). Resultant loss of biodiversity was related to a change from grassland and grassland-shrubland mosaic to expanded and denser shrubland. Thus, also in the Mediterranean, controlled grazing of sheep and goats maintain species diversity up to landscape diversity (Verdú et al. 2000, Catalán et al. 2008, Delibes-Mateos et al. 2008, Dellafiore et al. 2008). Moreover, moderate grazing of large herbivores also maintain species diversity in the long run (over 55 years) in short-grass steppes in the USA (Hart 2001). In North American tall-grass prairie, for example, bison grazing increases resource availability such as light. High spatial heterogeneity in light and increased species turnover in grazed grassland is associated with enhanced plant species richness. Therefore, creation of a mosaic of patches with high and low biomass and the support of a dynamic species pool are the most important mechanisms by which grazers affect species richness in high productivity grasslands (Bakker et al. 2003).

### 8.3.2.3 Shrub Expansion and Grazing (Example IX)

Isermann M, Diekmann M, Heemann S (2007) Effects of the expansion by *Hippophaë rhamnoides* on plant species richness in coastal dunes. *Applied Vegetation Science* 10, 33-42.

The Wadden Sea Islands, Spiekeroog, devoid of rabbits for many decades, and Norderney, inhabited by a dense rabbit population, were compared according to shrub expansion, species diversity and rabbit grazing effects. Plots, 16 m<sup>2</sup> in size with *Hippophaë rhamnoides* (Figure 20) and the nearest neighbouring plot without shrubs were investigated.

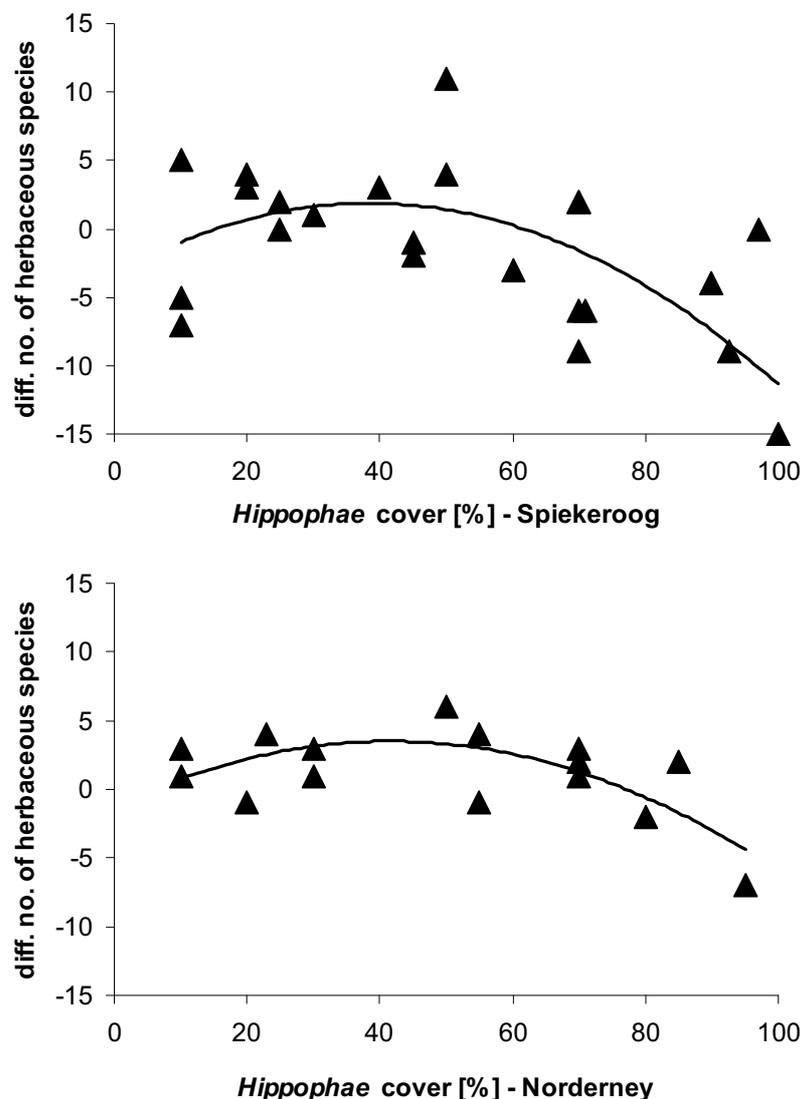


Figure 21. Relationship between the difference in the number of herbaceous species between shrubland and grassland plots and the cover of *Hippophaë rhamnoides* analysed separately for Spiekeroog (above,  $R^2_{adj.} = 0.41$ ,  $p = 0.001$ ,  $n = 24$ ) and Norderney (below,  $R^2_{adj.} = 0.38$ ,  $p = 0.022$ ,  $n = 15$ ).

Total species richness was marginally related in a humped-back relation to the cover of *Hippophaë rhamnoides* on both islands. The humped-back relationship was greatly

improved, using the difference in number of species between neighboured shrubland and grassland plots (Figure 21).

Using the differences in the number of species, species richness was highest at moderate levels of shrub expansion, while it was much reduced in very dense shrublands. Thus, a moderate level of shrub encroachment can be accompanied by an increase in species richness (Rejmánek & Rosén 1988), indicating that the extent of shrub expansion has to be taken into account. The results for shrub expansion in coastal dunes confirm that there is an interaction between disturbance and rate of competitive exclusion (Huston 1979). Similarly, competition of dominant shrubs in first dune-ridges can be reduced by other disturbances such as wash-over events, maintaining species richness (Stallins 2002).

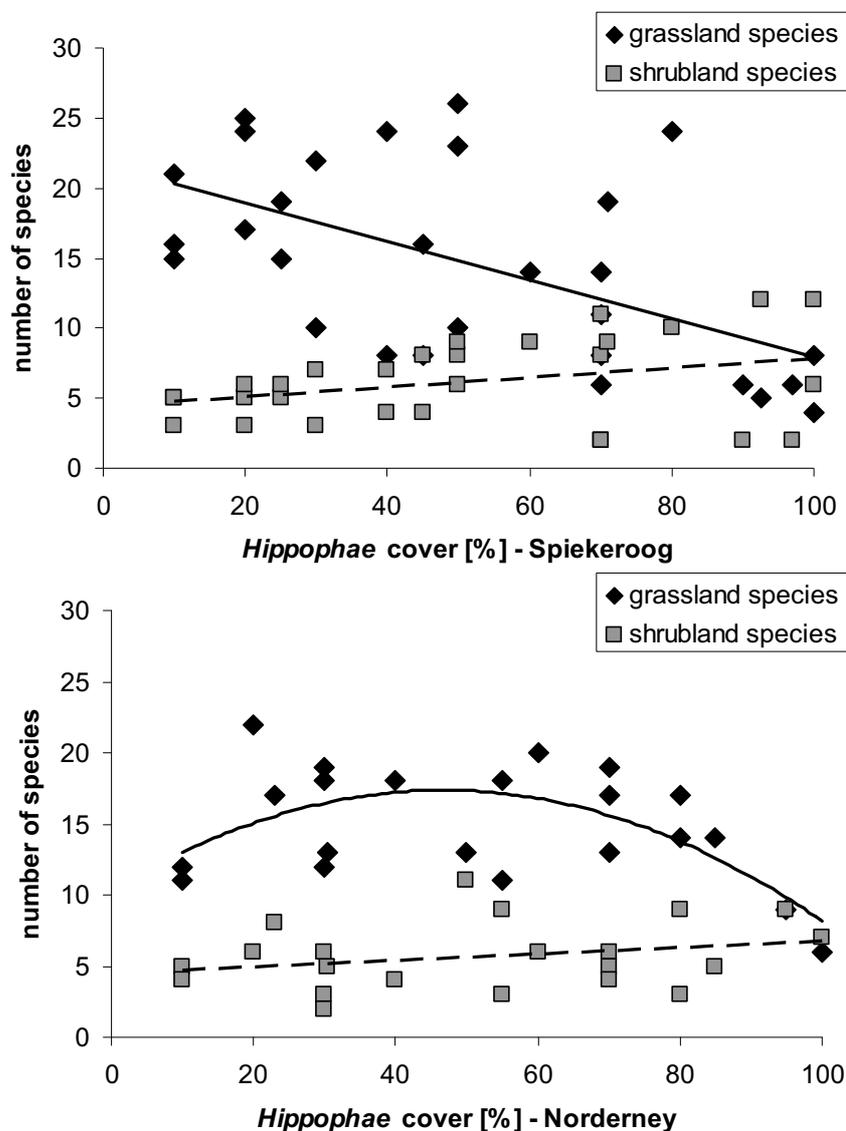


Figure 22. Effect of the abundance of *Hippophaë rhamnoides* on the number of grassland and shrubland species on Spiekeroog (above, grassland spp.  $R^2_{\text{adj.}} = 0.30$ ,  $p = 0.001$ , shrubland spp.  $R^2_{\text{adj.}} = 0.07$ ,  $p = 0.089$ ,  $n = 30$ ) and Norderney (below, grassland spp.  $R^2_{\text{adj.}} = 0.31$ ,  $p = 0.014$ , shrubland spp.  $R^2_{\text{adj.}} = 0.02$ ,  $p = 0.249$ ,  $n = 21$ ).

Disturbance effects maximising species richness depend on growth rate and hence on competitive exclusion by the dominants (Huston 1979, Walker & Peet 1983). In addition, for dunes of the East Frisian Islands, it was shown, according to richness of herbaceous species, that species richness - shrub expansion relation matches the intermediate disturbance hypothesis (see above). The decrease in the total number of species is due to the decline in grassland species typical of open dunes, especially due to shading effects. This decline is not compensated by the simultaneous, but only slight, increase in typical shrubland species (Figure 22).

However, the relation between shrub expansion and species richness is affected by grazing, e.g. by rabbits. In an ecosystem without rabbit grazing, there is a linear decline in the number of grasslands species. In contrast, with rabbit grazing there was a humped-back relationship between shrub cover and number of grassland species (Figure 22). It is probable that dune grassland species suffer a weaker rabbit grazing pressure in close proximity to moderate dense shrubs. Moreover, because of the sparse growth form of *Hippophaë rhamnoides*, grassland species are likely to remain in the gaps. Grazing changes competition between species (Belsky 1992) and species, such as typical dune grassland species, were probably favoured and not outcompeted by shading due to shrub expansion. Hence, moderate grazing e.g. by rabbits can reduce the decline in species richness caused by shrub spreading.

To conclude, moderate disturbances in coastal dunes can enhance species richness as well as species diversity. Therefore, in most dune grasslands management, such as moderate grazing or mowing, maintains high plant species richness. These disturbances keep the grasslands open, and enable the establishment of small, light-demanding species and exclude or suppress large, potentially dominant ones such as tall grasses (Rejmánek & Rosén 1988, Provoost et al. 2002, Bellingham & Coomes 2003).

### 8.3.3 Resource Availability, Competition and Productivity

**Available resources** limit local species richness (Anderson et al. 2004). The relations between the total amounts of available resources, representing the available energy in a system, and species richness are described as **species-energy theory** (Wright 1983, Currie 1991). Essential resources for plants are, for example, nutrients and space, whereas the amount of open sites reflects the limitation of **light** (Tilman 1983). One classic example is the limitation by space available for sessile organisms on rocky shores (Connell 1961).

In an equilibrium model, species richness is mostly low in **resource-poor environments**, where limitation occurs mostly due to low levels of nutrients. Only few species can exist in such unfavourable habitats (Tilman 1982, 1986, 1993). Although, unfavourable environments often contain species more flexible in their requirements, with a **wider range of ecological niches**, some habitat types probably contain fewer niches and thus fewer species (Pielou 1975). In many plant communities, species richness is higher at the local scale in relatively **nutrient-poor habitats** and lower in sites very poor or richer in nutrients (Huston 1979). The **addition of nutrients** beyond a certain level often results in a decrease in species richness (Tilman 1983).

An example of distinct changes in species-composition, due to increased inputs of air-borne nutrients, particularly N and P, during the last decades, reflects the increased dominance of grasses such *Calamagrostis epigejos*, *Carex arenaria*, as well as

*Deschampsia flexuosa* in dunes, combined with a loss of herbaceous species in calcareous grasslands (Van den Berg et al. 2005). An increase in productivity of grasslands, as well as heathlands, combined with the intensity of light competition favours fast growing grasses, which out-compete slower growing herbs (Bobbink 1991).

The relationship between species richness and resources e.g. soil fertility, is often **humped-back**, with maximum species richness, as well as species diversity, being reached on soils of **intermediate fertility** (Grime 1973, 1979, Al-Mufti et al. 1977, Tilman 1982, Pausas & Austin 2001). Species richness reached highest values on sites where dominant plant growth is limited by resources and where environmental stress is relatively low (Grime 1979, Tilman 1982). Highest species richness at intermediate resource levels can be explained by **species complementarity**, i.e. resource specialisation among coexisting species (Herbert et al. 2004). Many species can coexist due to different resource use. Complementarity could exist in **space**, e.g. differences in rooting depths, in **time**, e.g. differences in phenology and in **type**, e.g. differences in resource requirements (Hooper & Vitousek 1997, McKane et al. 2002, Dybzinski et al. 2008). The higher the level of **resource partitioning** the higher the number of species that are able to co-exist (McKane et al. 2002). The more species there are in a local assemblage, the greater the pressure on resource exploitation (Tilman & Lehman 2001, Gaston & Spicer 2004). Due to phenomenon of high levels of species richness at relatively nutrient-poor sites, the species-maximum is often moved to the left. According to species complementarity, at intermediate resource level many **generalists** will probably co-occur; whereas **specialists** should co-occur with relatively few species, and are more adapted to special resource situations, probably at the ends of the gradient (Crawley 1997, Fridley et al. 2007).

In addition, **spatial heterogeneity** (Chapter 8.3) in resource availability increases species richness, thus the species-maximum reaches higher values the greater the spatial heterogeneity of the habitat (Tilman 1993, Gaston & Spicer 2004). In a spatially homogeneous habitat only one species per limiting resource can occur, in turn in spatially heterogeneous habitats many species can coexist (Tilman 1993). Heterogeneous landscapes (Chapter 7.2) can result in resource patchiness, therefore species, due to their requirements, cannot grow everywhere. In contrast, homogeneous landscapes allow species to grow at any place, unless biotic competition is in place (Weitz & Rothman 2003). Moreover, the relationship between resources and species richness varies with scale, from a **unimodal relationship at small scales** to a **linear increasing relationship at large scale** e.g. continents (Schulze & Mooney 1993, Loreau et al. 2001). Regarding conservation aspects, reduction of soil nutrients appears to promote and sustain species-rich vegetation, whereas the level of nutrients limiting growth of more dominant species is often more or less unclear (Loreau et al. 2001).

In general, at **high levels of available resources**, only few, but **dominant** species occur due to their success at **competing for limiting resources** (Al-Mufti et al. 1977, Gaston & Spicer 2004). Low species richness, e.g. on nutrient rich sites, is often the result of competitive exclusion by few species and declining light availability (Herbert et al. 2004).

**Competition** is defined as the interaction between individuals, with reduced fitness of one of both (Begon et al. 2006). It represents, at local scales, one of the most pronounced factors predicting species diversity (Ricklefs 2005). Competition can be divided into two types. **Intraspecific competition** is competition between individuals of

the same species. **Interspecific competition** is the competition between individuals belonging to different species, over the use of limited resources (Lévêque & Mounolou 2004, Begon et al. 2006).

Success in competition may be measured as **productivity** or its substitutes, such as biomass or plant cover, more generally, it is measured with different fitness patterns. The principle of **competitive exclusion** (Lotka 1925, Volterra 1926) assumes that two species with similar ecological requirements cannot coexist over long periods in a stable environment. Thus, strong competitors may cause a decline in the growth, survival or fertility of other species of the assemblage that are less competitive (Lévêque & Mounolou 2004).

Strong competitors, often **dominants**, build up large amounts of phytomass and may therefore affect the **environmental conditions** of the ecosystem more than other species (Whittaker 1965). In general, increased nutrient supply supports the growth of dominant species (Herbert et al. 2004). Dominance of a species is enhanced due to the use of the most available soil **nitrogen** resources, which was shown, for example, in tundra vegetation in Alaska (McKane et al. 2002). The dominance of species results in the competitive exclusion of other species in a low species diversity. Furthermore, competition is a driver of successional replacement (Chapter 9.2) of species (Herbert et al. 2004).

High species richness depends on the coexistence of species, thus there must be mechanisms that reduce competition. Competition declines, for example, with disturbance (Chapter 8.3.2) creating micro-sites, increasing, for example, the number of **seedlings**, resulting in enhanced species diversity (Huston 1979, Zobel et al. 2000, Snyder & Chesson 2004). An increase in **resource partitioning** or niche differentiation (Chapter 8.3.3) declines competition too.

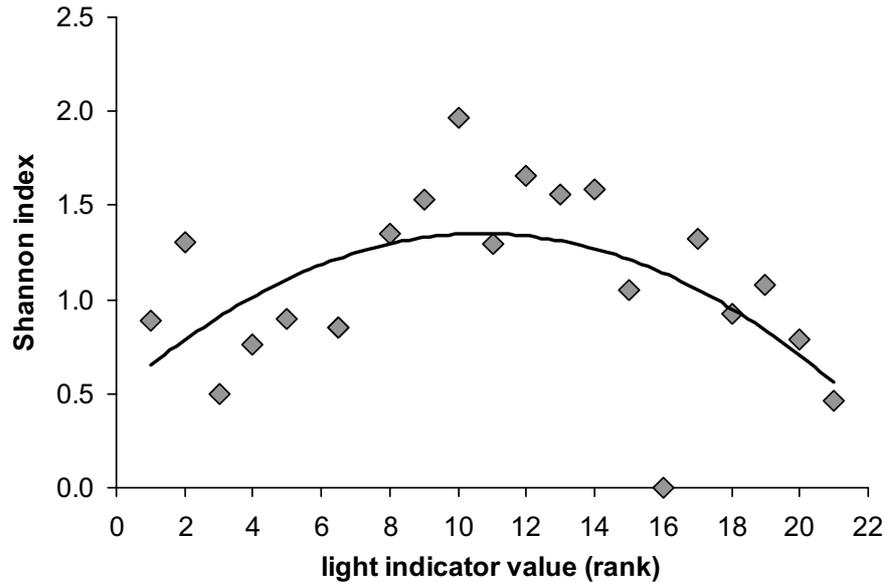
### 8.3.3.1 Light Effects (Examples X, XI, XII, XIII)

#### Bryophyte Richness and Light Conditions (Example X)

*Isermann M (2007) Diversity of bryophytes in an urban area of NW Germany. Lindbergia 32, 75-81.*

At the Campus of the University of Bremen, environmental conditions expressed as indicator values (Düll 1991) were used to estimate the relative importance of environmental gradients for bryophytes diversity. The bryophyte communities on the Campus reflected an environmental gradient from acid to neutral-slightly basic substrate pH. Along this gradient, temperature increased and water content decreased.

Bryophyte diversity expressed as Shannon index was, considering habitats of soft- and hard substrate of the University Campus, highest at intermediate levels of **light availability** (Figure 23). Furthermore, regarding only the soft-substrates, highest species richness was also reached at intermediate levels of **water content**. In addition, species diversity was not significantly related to other indicator values.



**Figure 23. Relationship between bryophyte richness, measured as Shannon index, and light availability (ranked weighted indicator values), that was highest at intermediate levels of light availability for all plots ( $R^2_{adj.} = 0.22$ ,  $p = 0.044$ ). Environmental conditions measured as indicator values were ranked. Significant better value of unimodal relation was tested with stepwise backward regression.**

Species diversity often reached highest values at intermediate levels of environmental gradients (Chapter 8.3.3). At intermediate levels of light availability, most bryophytes are able to grow if competition with vascular plants, e.g. due to non-favourableness of the habitat, is reduced. The vertical gradient of light availability and its horizontal variation, reflecting a shifting gap mosaic, plays a key role in relation to coexistence of plants (Kohyama 1997). The combination of radiation and moisture is probably optimal for bryophytes at intermediate light availability, so highest bryophyte resource efficiency exists (Bergamini et al. 2001). This unimodal relation is probably more pronounced in urban areas, while in rural areas more generalist occurs. The results indicate that many common bryophytes preferred both intermediate light intensities, as well as substrate moisture levels (Futamura & Wheelwright 2000). Moreover, light availability is probably more important in the case of bryophytes in comparison to vascular plants, of which the growth along productivity gradients may also be affected, for example, by nitrogen (Van der Wal et al. 2005). But generally, bryophyte species have different growth conditions in relation to light availability, and biomass can reach high values under different light conditions (Van der Wal et al. 2005), which is related to the habitat diversity pattern (Chapter 8.3). Therefore, this example is in line with common patterns that highest species diversity will be found at intermediate levels of environmental gradients, particularly at small scales.

### Shrub Expansion and Decline of Light Availability (Examples XI, XII, XIII)

Isermann M, Friedrichs L, Grave C, Wagner A (2005) Species richness in Sea-Buckthorn scrub. In: Herrier J-L, Mees J, Salman A, Van Nieuwenhuysse H, Dobbelaere I (eds.) *Dunes and Estuaries. Nature restoration practices in European coastal habitats*. Koksijde, Belgium, pp. 597-600.

Isermann M (2007) Effects of *Rosa rugosa* invasion in different coastal dune vegetation types. In: Tokarska-Guzik B, Brock J-H, Brundu G, Child L, Daehler CC, Pyšek P (eds.) *Plant Invasions: Human perception, ecological impacts and management*. Backhuys Publishers, Leiden, The Netherlands, pp. 289-306.

Isermann M (2008b) Expansion of *Rosa rugosa* and *Hippophaë rhamnoides* in coastal grey dunes: effects at different spatial scales. *Flora* 203, 273-280.

In many coastal dune areas of northwestern Europe, scrub, such as *Hippophaë rhamnoides* and *Rosa rugosa*, is currently spreading and shrubs are increasing in abundance, due to changing landuse during the last two centuries. Initially shrubs were mainly planted for sand stabilisation, coastal protection and as ornamental plants. Changing landuse includes patterns such as stabilisation of dunes by planting marram (*Ammophila arenaria*) and a reduction in grazing by cattle and rabbits (Fuller & Boorman 1977). In dune areas many regionally rare plants are found (Dunwiddie 1997), hence the expansion of densely growing shrub species might be a serious threat.

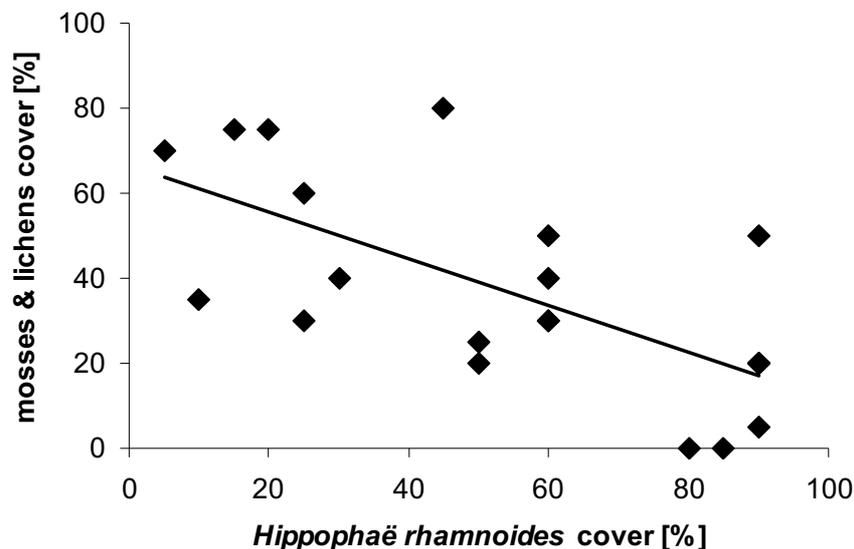


Figure 24. Decline in the cover of mosses and lichens with shrub cover of *Hippophaë rhamnoides* in coastal dunes on the islands Schiermonnikoog, NL ( $R^2_{adj.} = 0.421$ ,  $p = 0.001$ ).

To investigate effects of shrub expansion on other species, at small scale, the expansion of *Hippophaë rhamnoides*, growing in yellow and grey dunes of the Dutch island Schiermonnikoog was related to species richness.

The total species richness declined linearly with increasing shrub cover ( $R^2_{\text{adj.}} = 0.226$ ,  $p = 0.017$ ). Although the overall number of mosses and lichens was very low, their cover reached high values of up to 75 %. With increasing shrub expansion, the cover of mosses and lichens declined (Figure 24) strongly to values less than 20 %.

Light competition increased with shrub cover and biomass, respectively, and thus excludes other, probably more light demanding species, resulting in the linear decline of mosses and lichens. Effects of shading by scrub vary also at temporal scales, during successional series pioneer scrub is characterised by lesser shading effects than scrub of older successional stages (Diaz Barradas & Garcia Novo 1987).

**Shading effects** vary with the shrub species. Therefore different shrub species, *Hippophaë rhamnoides* and *Rosa rugosa*, occurring in dunes were compared. The relative light availability, measured beneath (at the bottom layer) and outside the scrub, was used to estimate shading effects of shrub expansion.

In general, relative light availability declined with increasing shrub cover, but at low levels of shrub cover there was no obvious shading-out. At about 20 % cover, light availability decreased strongly. Incidentally, there were no differences in relative light availability in the *Rosa*-scrub established in different dune vegetation types.

The shading by *R. rugosa* was more pronounced than that of *H. rhamnoides* (Figure 25). In the dense scrub, relative light availability declined in *Hippophaë* scrub to values about 20 %, but in *Rosa* scrub to values lower than 10 %.

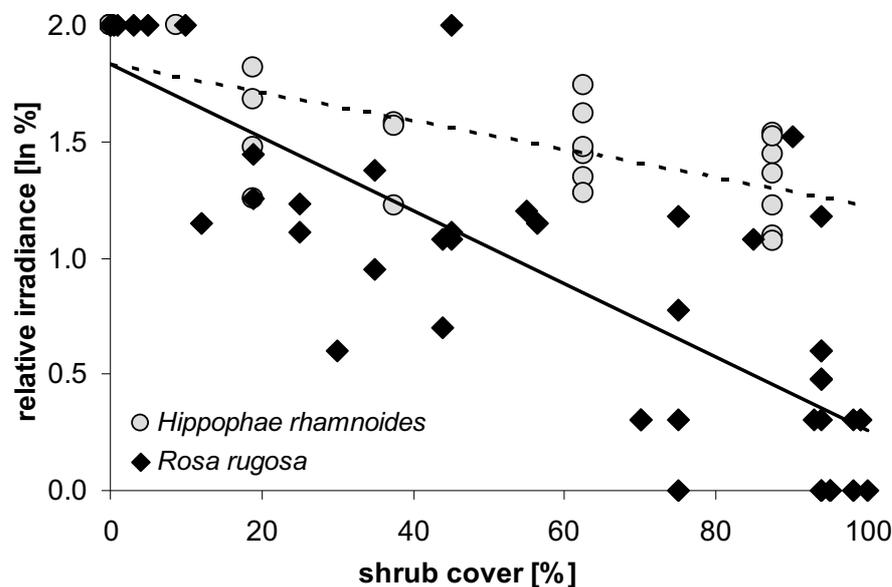


Figure 25. Decline in relative light availability (ln %) with increasing cover of *Rosa rugosa* and *Hippophaë rhamnoides* (*R. rugosa*  $R^2_{\text{adj.}} = 0.69$ ,  $p < 0.001$ ,  $n = 58$ , *H. rhamnoides*  $R^2_{\text{adj.}} = 0.46$ ,  $p < 0.001$ ,  $n = 24$ , ). Data of *H. rhamnoides* based on Isermann et al. (2005).

Analogous to *R. rugosa* and *H. rhamnoides*, a general decline in light availability in relation to shrub expansion in grasslands was shown e.g. for *Myrica pensylvanica*-scrub (Shumway 2000). When comparing grass- and shrubland, light availability is usually lower beneath scrub. A comparable negative exponential function was found in the case of

Californian scrub, where light availability declines strongly with horizontal distance inside the shrub (Alpert & Mooney 1996).

Depending on **foliage and growth form**, the shading-out effect of scrub varies. Leaves of *Hippophaë rhamnoides* are smaller than are those of *Rosa rugosa* (Figure 26) and *H. rhamnoides* appears to have a sparser growth form. Broad-leaved shrubs like *R. rugosa* shade more than small-leaved ones such as *H. rhamnoides*, therefore the effect, e.g. in relation to light competition, of broad-leaved, especially evergreen shrubs like *Rhododendron ponticum* (Erfmeier & Bruelheide 2004), can be even greater.



Figure 26. *Hippophaë rhamnoides* with small leaves (left side) and *Rosa rugosa* with broad leaves (right side).

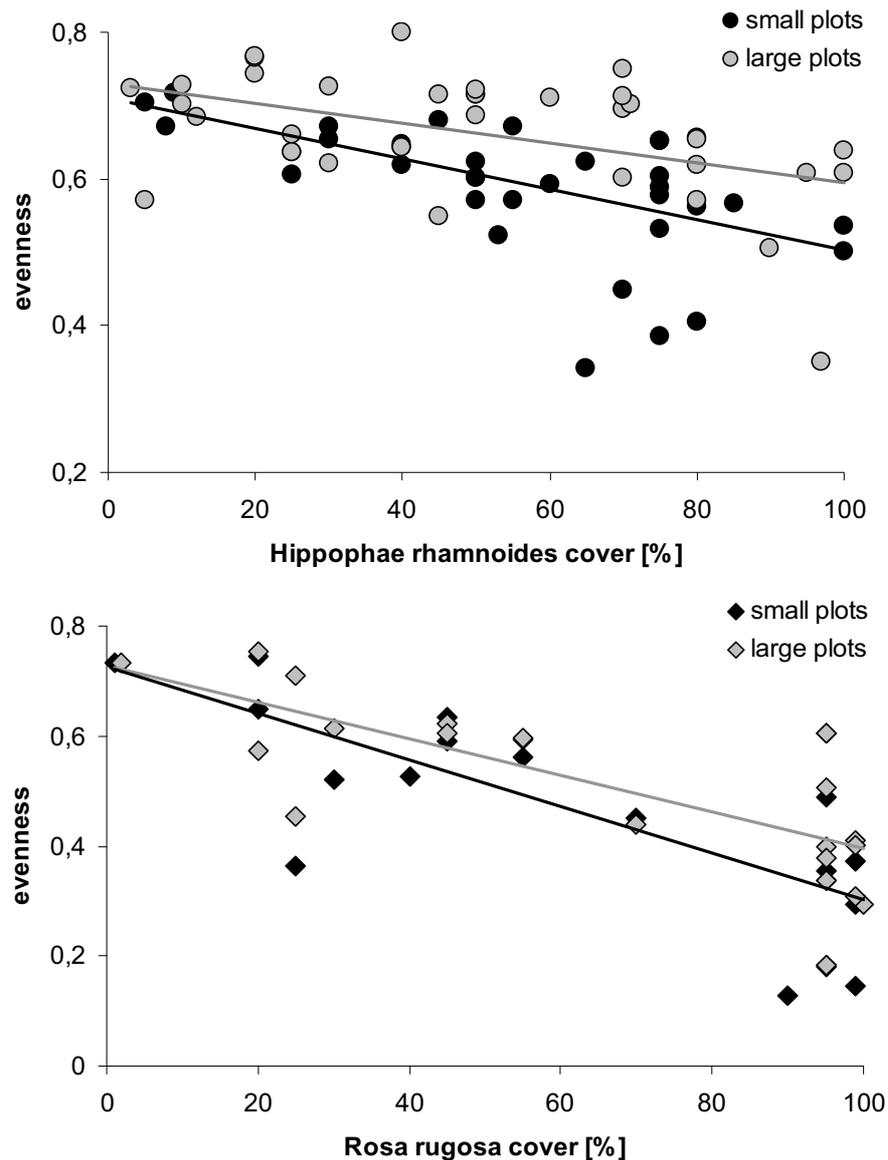
Different shading effects of broad- and small-leaved species also occur between *Potentilla fruticosa* and *Juniperus communis* in Sweden (Rejmánek & Rosén 1988, 1992). Decline in relative light availability caused by shrub expansion is followed by a decline in species richness because of shading effects. In relation to leaf- and growth form, shading effects vary, for example increasing *Potentilla fruticosa* causes a greater loss of species richness than increasing *Juniperus communis* (Rejmánek & Rosén 1988, 1992). In a similar study of Sea-Buckthorn scrub in Irish dunes, the total number of species decreased more strongly by 50 % (Binggeli et al. 1992).

The effect of shrub expansion varies with foliage and growth form of the shrub species and differs with scale investigated. To show this phenomenon, on the islands of Spiekeroog, scale-dependent effects of shrub expansion on species diversity were studied in grey dunes. Species composition at two spatial scales, 1 and 16 m<sup>2</sup>, in scrub of *Hippophaë rhamnoides* and of *Rosa rugosa* were compared.

In general, shrubland of *Rosa rugosa* was clearly species-poorer than *Hippophaë rhamnoides* scrub. Furthermore, *H. rhamnoides* scrub showed higher values of species diversity, expressed as Shannon index and evenness, than the *R. rugosa* scrub. Total number of species decreased with increasing cover of *R. rugosa* and, restricted to the large scale, with increasing cover of *H. rhamnoides*. The number of herbaceous and of typical grassland species decreased with increasing shrub cover. Both negative relationships were

more pronounced at the larger scale. In contrast, the number of shrub species increased with increasing cover of *H. rhamnoides*, but not for *R. rugosa*.

Moreover, species diversity measured as Shannon index and evenness (Figure 27) declined with increasing shrub cover at both spatial scales and the relations were improved in comparison to values of species richness. This probably started with the establishment of single shrubs, a mosaic of grassland and shrubland develop at small scales, and increased landscape heterogeneity. Thus, due to the enhanced patchiness of vegetation types, species richness at first declined less than evenness.



**Figure 27.** Relationship between evenness and scrub cover of *Hippophaë rhamnoides* (above) and of *Rosa rugosa* (below) in small plots (filled symbols) and large plots (unfilled symbols). (*H. rhamnoides* small plots  $b = -0.002$ ,  $R^2_{adj.} = 0.29$ ,  $p = 0.001$ ; large plots  $b = -0.001$ ,  $R^2_{adj.} = 0.19$ ,  $p = 0.006$ ; *R. rugosa* small plots  $b = -0.004$ ,  $R^2_{adj.} = 0.51$ ,  $p < 0.001$ ; large plots  $b = -0.003$ ,  $R^2_{adj.} = 0.45$ ,  $p < 0.001$ ).

In cases of linear relations, the decline in species diversity was more pronounced in *R. rugosa* scrub than in *H. rhamnoides* scrub. Interestingly in the case of *H. rhamnoides* at

the large scale, a humped-back relation was more improved than a linear one. This can be explained, at the one hand, by remaining gaps due to a less dense growth form, but also by the supported establishment of further shrubs and other typical shrubland species, probably due to enhanced fleshy fruit dispersal by birds.

Furthermore, when comparing the linear relation of the decline in evenness for both shrubs, the decline was more pronounced at the small scale than at the larger one. Often responses to changed environmental conditions happen faster and more distinct at smaller scales, which were, for example, shown for shrub expansion in calcareous grassland on Öland, Sweden (Rejmánek & Rosén 1988, Huber 1994, 1999). Similarly, species richness in a short-grass steppe in Colorado declined more rapidly with expansion of dominant grasses at small scales, probably due to stronger biotic interactions, such as competition (Singh et al. 1996).

Due to the denser leaf and growth form of *R. rugosa*, shading effects were stronger, thus *R. rugosa* out-competes many light-demanding species. Furthermore, *Rosa rugosa* already showed, at the small scale, a stronger linear decline in species diversity than *H. rhamnoides*, because *R. rugosa*, already at low dominance levels, has stronger shading effects. In contrast, due to the less dense growth form small gaps also remain in dense *H. rhamnoides* scrub. Thus, *H. rhamnoides* is a less strong competitor in comparison to *R. rugosa*.

### 8.3.3.2 Productivity (Examples XIV, XV)

Productivity can be **defined** as the rate of energy flow in an ecosystem, probably expressed as joules per unit time per unit area (Lonsdale 1988). In many cases, it is **measured** indirectly for example estimated from precipitation, or using other substitutes like biomass, litter-fall, vegetation cover, growth height, or multiplication of cover by growth height (Lonsdale 1988). Biomass and productivity often correlate well (Preston 1962). **Substitution** of productivity, e.g. by vegetation cover also appears possible (Ji et al. 2009), and positive linear relations between above-ground biomass and growth form, respectively, and vegetation cover, were shown, for example, in early successional stages of inland sand dunes (Röttgermann et al. 2000).

Productivity as an **environmental character** merges with different patterns and processes related to species diversity (Al-Mufti et al. 1977, Grime 1979, Grace 1999): dominance, competitive exclusion, environmental stress, disturbance, niche differentiation, resource availability (Rosenzweig & Abramsky 1993) and energy input (Wright 1983, Currie 1991, Wright et al. 1993). The general relations are very similar e.g. to those mentioned for resources availability (Chapter 8.3.3).

Species composition and species richness varies along productivity gradients (Rosenzweig 1995). Species-poor ecosystems such as deserts or tundra belong to ecosystems of **low productivity** in comparison to species-rich tropical forests. Otherwise, for example, agricultural systems with very high productivity also have a low number of species, combined with low environmental heterogeneity (Schippers & Joenje 2002). Furthermore, according to dune communities, highly productive, dense shrublands of the non-native invasive *Rosa rugosa* have low species richness (Isermann 2008). Hence, high productivity is not necessarily correlated with high biodiversity (Lévêque & Mounolou 2004) and generally, beyond a certain productivity level biodiversity declines (Shmida &

Wilson 1985, Rosenzweig 1995). Usually, species richness correlates with productivity (Waide et al. 1999), reaching highest values at **intermediate levels** of biomass production and is lower both in sites of low or high productivity (Grime 1973, Al-Mufti et al. 1977, Klinkhamer & De Jong 1985, Tilman et al. 1997, Grace 1999, Hector et al. 1999). Similar to relations considering resource availability, at **small scales**, plant species richness is more often a **unimodal function** of productivity (Al-Mufti 1977, Vermeer & Berendse 1983, Klinkhamer & De Jong 1985, Rosenzweig & Abramsky 1993, Waide et al. 1999). At **larger scales**, e.g. regional to global scale, it often represents a **linear increase** with productivity (Lonsdale 1988, Currie 1991, Scheiner & Rey-Benayas 1994, Waide et al. 1999, Gross et al. 2000, Harrison et al. 2006). At different small scales, the productivity species diversity relations were similar and the larger the plot size the higher the species richness, thus the humped relationship is not an artefact of plot size (Oksanen 1996), but is characteristic of small scales (Tilman 1982, Shmida & Wilson 1985). Furthermore, unimodal relations are probably more common for herbs and grasses than trees; and for grasslands than forests (Laanisto et al. 2008). Moreover, relationships between productivity and species richness vary with habitat type (Grytnes & Birks 2003), and in relation to temporal climatic variation (Laughlin & Moore 2009).

The humped-back theory of plant species richness is related to the **C-S-R model** (Grime 1973, 1979), suggesting that species richness is maximal at intermediate levels of productivity, i.e. at intermediate levels of a competition/dominance-environmental stress-ruderality/disturbance gradients complex (Wilson et al. 1996). Thus, low species richness occurs in both **high-stress / low-productivity** sites, because only few species are able to tolerate the harsh physical environment; and in **low-stress / high-productivity** sites due to competitive exclusion by dominant species (Wilson et al. 1996). In general, low productive vegetation is limited by the available nutrients, i.e. limitation by nitrogen, phosphate, and potassium (Van Duren et al. 1997), whereas different nutrients or combinations of nutrients may limit different productivity levels. The unimodal relation is mostly explained by resource availability and competition (Chapter 8.3.3). An increase in nutrient availability beyond a certain level enhances productivity, particularly of few dominant species, but reduces species diversity by shading-out (Grime 1979, Huston 1979, Tilman 1982, Goldberg & Miller 1990, Grace 1999, Gough et al. 2000, Fridley 2002). Increasing biomass causing competition to shift from belowground to aboveground resources, thus, from low to high productivity levels there is a shift from nutrient to light limitation (Olf et al. 1993, Wilson & Tilman 1995, Grace 1999). This shows that not extra productivity *per se*, but extra productivity caused by additive resources, especially nutrients, causes a decline in diversity (Whittaker 1998).

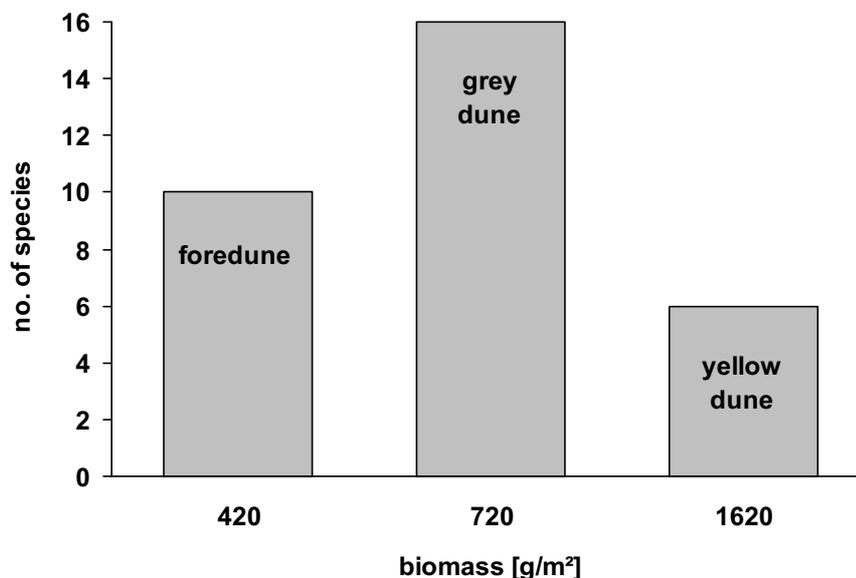
Moreover, the **overyielding-effect**, which is often a positive effect, of plant species diversity on productivity was shown (Harper 1977, Tilman et al. 1997, Hector et al. 1999). The overyielding-effect is probably caused by complementary resource use efficiency and facilitative interactions among species (Huston 1979, Tilman et al. 1997, 2001, Hector et al. 1999, Fridley 2002, Loreau 2000, Kinzig et al. 2001, Tilman & Lehman 2001, Hooper et al. 2002, 2005, Dybzinski et al. 2008). However, the positive effect of diversity on productivity is overridden because factors such as resource availability affect both diversity and productivity (Tilman 1999, Loreau 2000, Fridley 2002). Moreover, it was

shown, that species composition and fertility had a more pronounced effect on productivity than species diversity (Loreau 2000, Fridley 2002).

### Aboveground Phytomass and Species diversity (Example XIV)

The relationship between productivity and species richness was analysed across dunes on the Dutch Island Schiermonnikoog during a student course. Aboveground fresh weighted phytomass was measured in foredunes, yellow and grey dunes. The number and percent cover abundance of plant species was estimated.

In coastal dunes, species richness reached highest values at intermediate levels of productivity (Figure 28), estimated as fresh aboveground biomass, in semi-fixed grey dunes. Highest species richness is reached at intermediate levels of disturbance and of fertility (Chapter 8.3.2.2), resulting in a humped-back relation between biomass and species richness (Al-Mufti et al. 1977, Grime 1979). Increasing habitat heterogeneity (Chapter 8.3.1) increases species richness as well as productivity (Rosenzweig 1995), as shown by the high level of aboveground biomass in grey dunes (Figure 28).



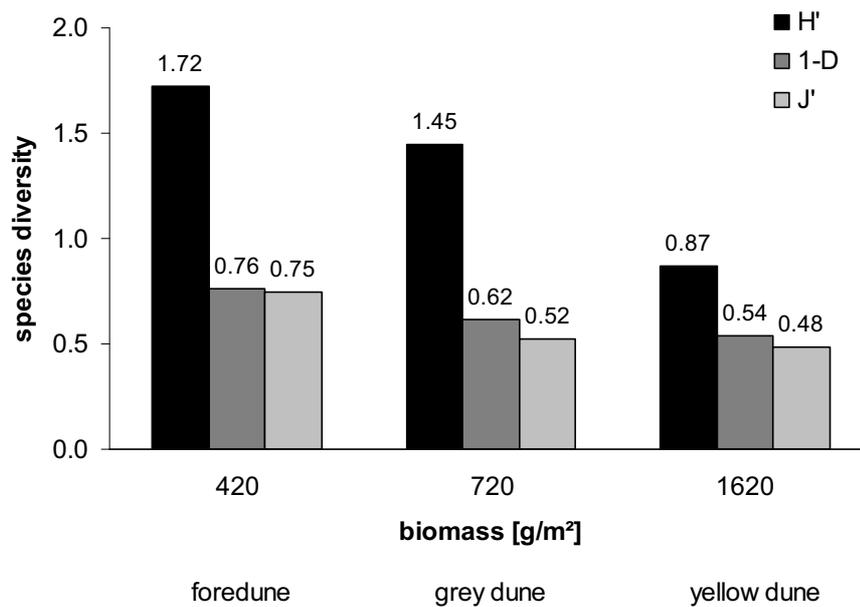
**Figure 28.** Relation between species richness and biomass [g/m<sup>2</sup>] measured as above ground, fresh weighted phytomass along a dune transect [unpublished data].

Comparing the entire dune series, foredunes are a harsh environment, due to varying and sometimes high salt content, sand movement, sand accumulation, low content of organic matter as well as low nutrient level, thus only few species, such as *Elymus farctus*, with low aboveground phytomass occur. Yellow dunes represent a habitat with less environmental stress, where species such as *Ammophila arenaria* grow best and build up large amounts of phytomass. The high level of phytomass and the vegetation homogeneity of the *Elymo-Ammophiletum arenariae*, probably indicate that this community, assuming continuous sand dynamic, represents a first ‘climax’ of the dunes series (Stankevičiūtė 2001). Succession to grey dune grasslands, is combined with less sand dynamic, a less harsh environment and soil development, whereas young grey dunes represent one of the most heterogeneous habitats of the dune series considering resource conditions (Chapter 8.3.1). Thus, highest species richness was reached in grey dunes, due to efficient resource

and niche partitioning. The productivity level of grey dunes in comparison to the whole dunes series is low and it was shown, that at low productivity levels in coastal dunes, biomass is positively correlated with soil water, nitrogen and organic matter, while at higher resource levels negative correlations were shown (Klinkhamer & De Jong 1985). Also in dunes of other regions, species richness aboveground biomass relations are in line with resource availability, with highest species richness values reached at intermediate resource levels, e.g. of total soil nitrogen (Lichter 1998). Moreover, in Dutch grasslands, biomass is humped-back related to resource availability, expressed as N/K ratio (Roem & Berendse 2000). Similar to our results, relations with highest species richness at intermediate productivity levels occur in different grassland and fen communities in the Netherlands (Vermeer & Berendse 1983).

Moreover, of interest is that the results confirm that species richness reached highest values at intermediate productivity levels of about 500 g/m<sup>2</sup> (Grime 1979). The productivity - species diversity relationship varies with vegetation type as well as in relation to climate (Rosenzweig 1995, Wilson et al. 1996, Jennings et al. 2005). Productivity and functional groups, such as annuals, are also related. For example, from mobile to stabilised coastal dunes in Israel, species diversity of annuals shows a unimodal relation with aboveground phytomass. The intermediate productivity levels support niche differentiation and habitat heterogeneity resulting in diverse annual species communities. Moreover, phytomass increased with resource availability, i.e. with soil moisture and organic matter, up to a certain level. At low productivity levels, only few species are adapted to higher environmental stress, such as sand movement in the mobile dunes. At high productivity levels, only few species best use the available resources, because of the higher competition under these conditions (Kutiel & Danin 1987). Similar interrelations, between competitive displacement, nutrient level, summer drought and moderately high frequency of disturbance by fire and grazing, were shown in other Mediterranean regions (Bond 1983, Keeley & Swift 1995).

In contrast to the number of species, species diversity (measured as Shannon index, complement Simpson's index, and Shannon evenness), decreased with increasing biomass in coastal dunes (Figure 29). In the sample group, with higher productivity levels, biomass was more unevenly distributed over the species and a few species tended to dominate the vegetation.



**Figure 29. Decreasing species diversity with increasing aboveground fresh phytomass. Indices acting in the same direction, if indices decline diversity declines and species distribution is less even. Regression statistics: H' Shannon index  $R^2_{adj.} = 0.99$ ,  $p = 0.046$ ; 1-D complement Simpson's index  $R^2_{adj.} = 0.63$ ,  $p = 0.282$ , J' Shannon evenness  $R^2_{adj.} = 0.24$ ,  $p = 0.425$ ) [unpublished data].**

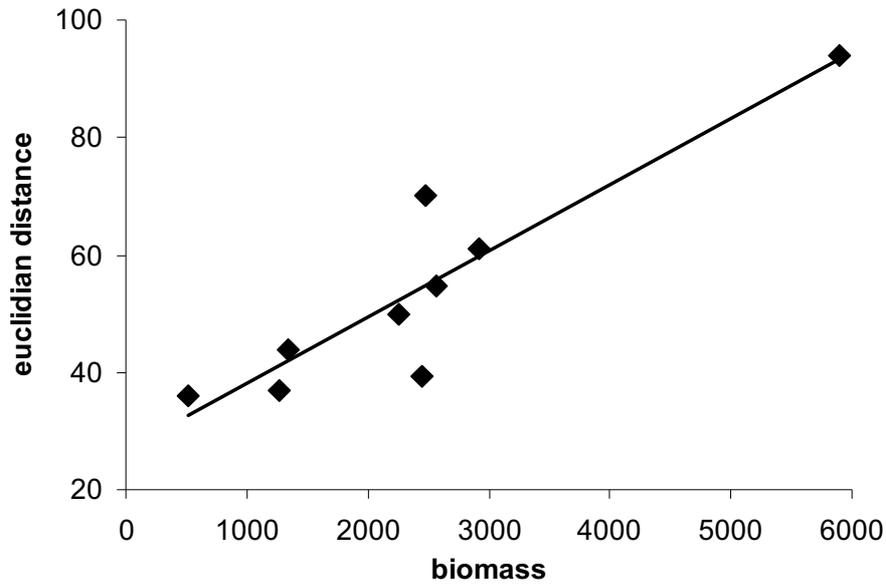
Analogous results were shown for higher saltmarshes in New England, whereas highest species richness was reached in intermediate vegetation transitions, and where the Shannon index was lowest in vegetation with highest biomass, and in turn, Shannon index was highest in vegetation with lowest biomass (Theodose & Roths 1999).

### Productivity Level and Grazing Effects (Example XV)

*Isermann M, Koehler H, Mühl M (2009) Interactive effects of rabbit grazing and environmental factors on plant species richness on dunes of Norderney. Journal of Coastal Conservation, Planning and Management. DOI: 10.1007/s11852-009-0056-9.*

**Differences in species-composition** between rabbit-grazed and ungrazed plots, expressed as Euclidian distance, increased with **biomass**, measured as substitute vegetation cover by height in coastal dunes (Figure 29). A similar increasing change in species composition with increasing productivity was shown by Milchunas & Lauenroth (1993).

The increase in floristic dissimilarity between grazed and ungrazed dune plots with increasing biomass probably reflects the enhanced palability of the plants in the dune-saltmarsh transition that represents the highest level along the measured productivity gradient.



**Figure 30.** Increasing floristic dissimilarity, measured as Euclidian distance, between grazed and ungrazed plots in coastal dune areas with increasing biomass, expressed as vegetation cover x vegetation height ( $R^2_{adj.} = 0.80$ ,  $p = 0.001$ ).

In contrast, considering the larger productivity gradient in saltmarshes, highest grazing pressure by hares, rabbits, and geese was reached at intermediate levels of primary productivity (Van de Koppel et al. 1996). Increasing changes in species composition might also indicate that rabbits reduce the dominance of a few species; as well as evenness of vegetation itself, may influence the rabbit's choice of grazing sites (Klinkhamer & de Jong 1985).

## 9 Species Diversity in Time

Species richness of the world's plant cover is caused by the available species-pools in different regions and the long-term processes of **evolutionary and distributional change**. Part of the plant species richness, visible today on a global scale, is the origin of plant species (Tallis 1991). First vascular plants developed about 410 million years ago, during the Silurian Period; a steady and striking increase in plant species richness followed (Rosenzweig 1995). However, for periods of millions of years diversity is trendless, because about 90 % of all species that have existed have become extinct (Gaston & Spicer 2004). Regarding evolutionary periods, patterns and processes of speciation and extinction are the most explaining aspects (Magurran & May 1999).

Incidentally, species richness of one taxon is often connected with species richness of other systematic groups, living on the other group, the so-called **host-age pattern** (Southwood 1961). For example, during the process of tree establishment in Great Britain, a period of increasing tree species richness that spanned approximately 13000 years, insect species richness increased.

An ecosystem is not a fixed structure; it changes its individual characteristics during ecological time. **Temporal dynamics of vegetation** are various and can be divided according to type, duration, and direction of change into four main forms (Dierschke 1994):

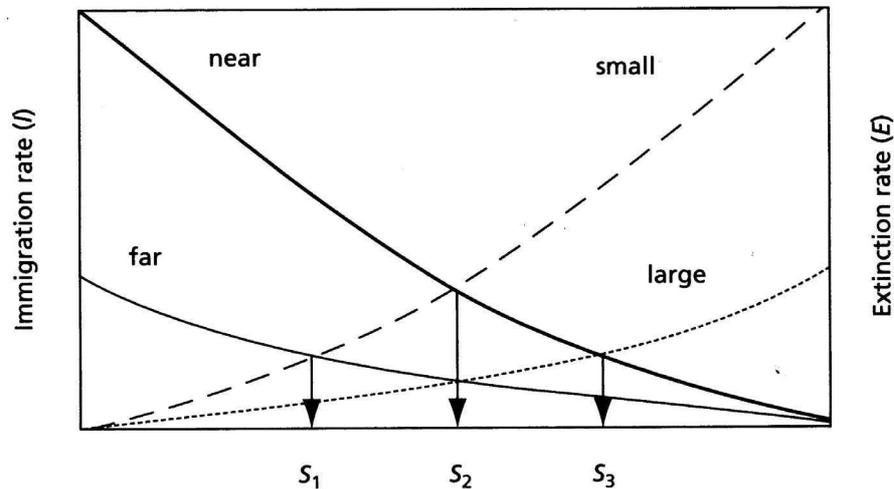
- **periodicity**, seasonal variation, phenological rhythmic, brief, regular, and yearly recurring changes within a plant community due to rhythmic climatic seasons. For example, there is a greater vascular plant species richness at the community level early in the growing season, probably because of a greater variety of available germination micro-sites, and thus of greater heterogeneity of the habitat. During the winter less species in relation to their life-forms are visible, hence species richness as well as diversity oscillates during the year (Grubb 1977).
- **fluctuation**, a little more long-termed, without a directional change, swinging around a situation, mostly within one or two plant communities, based e.g. on changing weather conditions, or depending on the groundwater table (Van der Laan 1979),
- **succession**, short- to long-term, directional change sometime cyclic, often across different plant communities, and
- **historical development**, very long-termed developments across many plant communities, often based on global climatic changes.

### 9.1 Historical Development

Species richness increased as the possibility of plant species reaching and becoming established in an area increased. Therefore, species richness, of oceanic islands of equal size, declines with distance from the mainland (Figure 31), because as distance increases the rate of immigration of new species declines. Distance and immigration effects were

shown, for example, by the number of ferns on islands near and far from the mainland, such as the Channel Islands and the Azores (Whittaker 1998).

When considering the size of an area and the distance to the mainland, which both affect species richness due to different immigration (I) and extinction rates (E), the model of the dynamic equilibrium of species richness is modified (Figure 31).



**Figure 31.** Dynamic equilibrium models of species richness on islands varying in distance from the principal source area and varying in size. An increase in distance (near to far) declines the immigration rate, while an increase in island area (small to large) lowers the extinction rate (MacArthur & Wilson 1967).

Isolation explains a significant amount of the variation in the number of species, especially on island habitats. The relationships concerning isolation due to distance to the mainland (Figure 31), can also be explained in relation to the **time of isolation**. Islands isolated from the mainland for a long period (similar to a large distance) have lower species richness than islands isolated for a short time (similar to near distance).

Isolation is not just a question of distance, but also depends on the nature of the area, for example, heterogeneity or available resources (Whittaker 1998). Therefore, it is possible that the degree of isolation will result in different species composition, but with the same number of species (Kadmon & Pulliam 1993).

### 9.1.1 Time of Isolation of the German Frisian Islands (Example XVI)

*Isermann M (2004) Differences in species richness of native and non-native plants between the East and North Frisian Islands. In: Green DR (ed.) Delivering sustainable coasts. Cambridge Publications, pp. 737-738.*

East and North Frisian Islands have more or less no differences in the distance to the mainland, but in the time of isolation. The origin of both archipelagos differ, the East Frisian Islands (EFI) have existed, since their origin approximately 1000 AC, as separate islands, whereas the North Frisian Islands (NFI) were separated from the mainland during the 14<sup>th</sup> century (Kramer 1989). The North Frisian Islands are **land-bridge islands**, those formerly connected to the mainland, which gained at least some of their biota by overland

dispersal prior to becoming islands. The East Frisian Islands are true **oceanic islands**. Due to their different origin, the North Frisian Islands have a ‘Geest’ core at least in the deeper ground, while the East Frisian Islands consists of sandy grounds. Because of their different origin, the East Frisian Islands, as true islands, are comparable with islands that are more isolated. In contrast, the North Frisian Islands, as land-bridge, islands, act similarly to islands that were formerly less isolated. Due to the different origin of both island groups, immigration rate in former times was much lower on the East Frisian Islands than on the North Frisian Islands. Land-bridge islands like the NFI often contain more species than they would have at equilibrium. Isolated islands generally have fewer species than islands in close proximity to a source of colonists because their remoteness results in a difficult accessibility and colonisation (Brown & Dinsmore 1988).

Species are divided, by humans, in relation to the way of establishment into natives and non-natives. Generally, the proportion of non-native species is higher on islands than on the mainland (D’Antonio & Dudley 1995). Although, native and non-native species occur with similar ratios of 80 to 20 % on both East and North Frisian Islands, the formerly lower immigration rate could be shown as differences in the floristic composition according to the immigration time.

Non-natives are divided in relation to the time of establishment into **archaeophytes** and **neophytes** (Figure 32), having reached the area, in this case Germany, before or after 1500 AD, respectively.

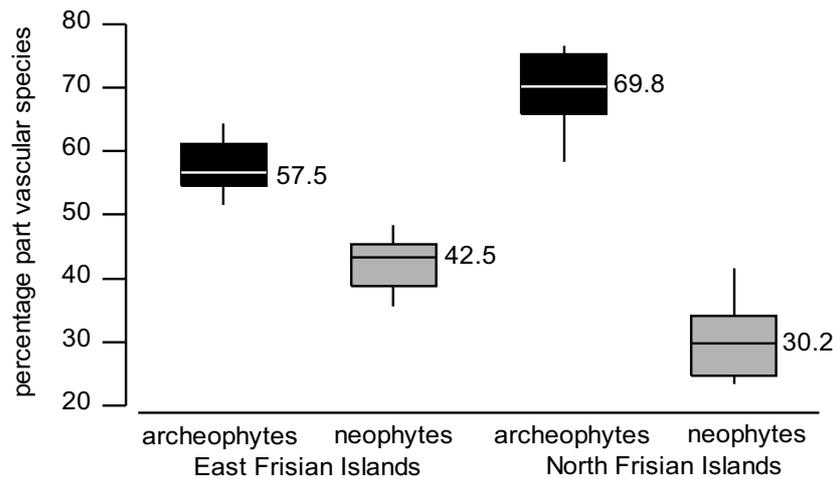


**Figure 32.** *Anchusa officinalis* (left), as example for archaeophytes and *Oenothera oakesiana* (right) as example for neophytes on the Frisian Islands.

Thus, the long-time connection to the mainland resulted in a higher species richness of archaeophytes on the North Frisian Islands than on the East Frisian Islands (Figure 33). The flora of the EFI is probably unsaturated, because there has not been sufficient time for colonisation, and especially not for speciation, to result in the species rich flora particular of archaeophytes. The positive relationship between time of colonisation and unsaturated floras in general is known for the native-species in the whole (Brown 1988), but must be restricted in the case of EFI and NFI to archaeophytes. In addition, the theory that

ecological communities can be saturated with species, that an upper limit of species richness exists, is generally not accepted (Cornell 1993).

The long-time connection to the mainland probably resulted in a more **floristically saturated situation** on the North Frisian Islands, with available ecological niches being much more occupied than on the East Frisian Islands. Therefore, the proportion of archaeophytes to neophytes differs between the East and North Frisian Islands (Figure 33). On the East Frisian Islands, the number of neophytes is around 10 % higher than on the North Frisian Islands. In addition, on the East Frisian Islands the proportion of archaeophytes is only slightly higher than that of the neophytes, while on the North Frisian Islands the number of archaeophytes is twice as high as the one of neophytes (Figure 33). In general, islands are more prone to **biological invasions** (Chapter 9.3) because of fewer buffering mechanisms against changes. Generally, the high degree of specialisation of island species results in unsaturated communities, lower competitive ability, and in ‘open niche space’ on islands. In contrast, mainland communities are more resistant against biological invasions, because they are normally in equilibrium stage due to interactions of competitors, determined by resource availability (D’Antonio & Dudley 1995).



**Figure 33. Proportion of archaeophytes and neophytes on the East and North Frisian Islands (T-tests all  $p < 0.001$ , SD EFI 4.16, NFI 6.21).**

The different proportions of archaeophytes and neophytes are likely to be caused by the different origin and historical development of both island groups. The North Frisian Islands represent former mainland with Pleistocene bedrock, a long colonisation time and a long agricultural tradition, thus more species had already had the possibility to settle the area in former times. In contrast, the East Frisian Islands represent sand plates that were settled by plants, as well as by humans at later periods.

## 9.2 Succession

According to the direction of the succession, different main types are distinguished (Dierschke 1994):

- **progressive succession** (primary as well as secondary succession), continuous development in one direction,
- **regressive succession**, backward development from an older succession stage, e.g. because of suddenly occurring disturbances like a single slope erosion, and
- **cyclic succession**, alternation between progressive and regressive succession in relation to regular occurring events, like yearly high tides.

Concerning the starting-point of the succession in relation to the origin of the area, two types are distinguished:

- **primary succession**, starts at a site where no earlier vegetation development occurred e.g. development on new islands in Swedish lakes (Rydin & Borgegård 1988), or sand dune formation (Olson 1958, Tilman 1988), and
- **secondary succession**, starts on sites probably with remaining organic matter as well as propagules in the soil (Tilman 1988).

Plant species reoccupy a habitat after new origin (**primary succession**) and after disturbance (**secondary succession**), and over the course of succession diversity relations change (Westman 1981).

Concerning the duration time, two main types are differentiated:

- **current succession**, succession happening at present or during few decades, and
- **secular succession**, vegetation development during long periods, often illustrated by pollen analysis. For example, the scrub establishment in Dutch coastal dunes on the mainland during a period of 3000 yr, where the succession started with *Hippophaë rhamnoides*, followed by *Juniperus communis* and succeeded by *Salix*, mainly *Salix repens*. This succession most probably reflects changing conditions related to leaching of calcium carbonate, originally abundant in the sand (Zagwijn 1971).

The main changes during succession are an increase in **species diversity** up to a certain level, beyond this species diversity levels-out or declines, an increase in resource use efficiency, an accumulation of biomass and an increase in stability (Margalef 1963, 1968).

Changes in plant species composition during succession are the result of a dynamic equilibrium between colonisation, persistence and extinction of species, whereas diversity expresses the balance between colonisation and extinction. It is assumed that succession represents the development towards an (dynamic) equilibrium between organisms and environment (Margalef 1958, Odum 1969). During succession, life history traits and strategies of plant species vary, whereas the frequency, extent and nature of disturbances are important selective factors on life history traits (Denslow 1980). Early successional stages are characterised by species with a short life-span (**r-selection**), while older successional stages contain more species with a long life-span (**K-selection**), such as

phanerophytes (Odum 1969). Therefore, the changes in relative values of woody species during succession are inversely related to the amount of herbs (Nicholson & Monk 1974).

During succession, the average in plant size and biomass increases simultaneously with primary production (Margalef 1958, 1968, Odum 1969). These processes are coupled with a light-resource mechanism, called '**resource ratio hypothesis**' (Tilman 1988). Increasing species diversity during succession depends on the number of potential ecological niches, also resulting from increased biomass and stratification of the vegetation (Margalef 1963).

Relations between species richness and biomass change during succession, but there are different examples from enhanced to lowered effects of diversity on biomass during succession (Schwartz et al. 2000, Schmid et al. 2001, Hooper et al. 2005, Weis et al. 2007). During succession organic matter as well as soil resources like nitrogen increase, this results in an increase in plant biomass, thus at early successional stages, the relationship between productivity and diversity is often positively linear (Bischoff et al. 2005). Successional younger sites are often characterised by higher productivity, the relationship between total biomass and primary production declines during succession, because equilibrium is not reached and new species that establish faster than others are lost (Margalef 1968, Rosenzweig 1995).

Moreover, the larger **size** of individuals of later successional stages leads to decreased penetration of light to the soil surface (Tilman 1988), as a result for example in young forest stages plant species richness is enhanced than in older stages (Widenfalk & Weslien 2009). The proportion of species to individuals especially decline towards later successional stage, but in general, there are fewer individuals (as well as species) per area as succession replaces, at later successional stages, herbaceous species with woody species (Preston 1960, Tilman 1988).

In general, during succession **spatial heterogeneity** develops from poorly to well organised, entropy from high to low, niche specialisation from broad to narrow and stability, the resistance to external perturbations, from low to high (Odum 1969). Hence, species diversity increases from simple plant communities of early succession to the richer communities of later succession stages (Whittaker 1975).

Similarly to resource partitioning, a **temporal niche theory** occurs (so-called **storage effect**), which assumes that temporal similarities to spatial partitioning will reduce competitive exclusion and facilitate species coexistence (Norden et al. 2007).

Species diversity is maintained by successional dynamics especially in relation to **disturbance**. Disturbance (Chapter 8.3.2) enhances patchiness of the environment at different scales and is one of the fundamental mechanisms of species-coexistence (Weis et al. 2007). After disturbance, species richness generally increases during secondary succession, especially during the first years of succession (Lloyd & Ghelardi 1964, Bazzaz 1975, Denslow 1980, Burrows 1990). The increase in the number of species becomes less pronounced during **primary succession**, than during **secondary succession** because of the missing seedbank as well as undeveloped soil at the starting-point of primary succession (Whittaker 1975).

Preston (1960) assumed that the increase in species richness during succession is similar to the species-area curve, and represented a straight line in a log-log space. Biodiversity patterns of temporal development depend on spatial scale. Species richness

during succession increases both at plot and landscape scale. At landscape scale, increase is faster than at plot scale, because there is more space and there are more ecological niches than at plot scale (Zobel et al. 1993, Bossuyt et al. 2005).

Comparing early and late successional relationships during a succession, species richness often levels off or decreases towards the mature stage of succession (Margalef 1963, Nicholson & Monk 1974, Whittaker 1975, Denslow 1980, Rydin & Borgegård 1988). This was shown for long-term succession over 200 years e.g. in the development towards old *Quercus* stands, as well as in abundant fields succession (Nicholson & Monk 1974, Bazzaz 1975, Houssard et al. 1980). A decrease in accumulation rate was also shown for different dune slacks (Bossuyt et al. 2005). Levelling off or decrease in species richness is caused, for example, by less fluctuations and increasing stability, probably due to the continuous addition of species to the community, which may result in a higher degree of evenness (Bazzaz 1975). Moreover, the levelling-off represents the possibility of a limited number of species per community, i.e. community saturation at the small scale. Thus **highest species richness** often occurs in early and **intermediate succession stages** (Margalef 1958, 1963, 1968, Whittaker 1975); and it appears that a semi-logarithmic curve best describes the relationship between years after succession and species richness (Rosenzweig 1995).

An increase in the variety of species together with missing dominance by any one species increases species richness, as well as evenness, and often represents a general probability during succession (Lloyd & Ghelardi 1964, Odum 1969). However, diversity does not increase monotonically. Often diversity increases to a certain level and then decreases toward later stages of succession (Pielou 1966, Margalef 1968, Westman 1981). Highest species diversity during the first quarter of the entire succession period was shown, for example, after fire in boreal forests (Shafi & Yarranton 1973). In other cases such as Mediterranean forest, after fire the number of woody species was highest at intermediate succession stages, with a more heterogeneous vertical vegetation structure (Álvarez et al. 2009). In cases of development towards a strong dominance by one or few species, low species richness, as well as low diversity, occurs in later successional stages (Bazzaz 1975). Therefore, diversity indices show different trends than the number of species in the same succession series (Odum 1969). Moreover, diversity indices tend to stabilise during succession in the order: richness, information content and equitability, and in proportion to the time of establishment of the analysed plant group (Nicholson & Monk 1974).

Biodiversity patterns show contrasting effects on the temporal stability of communities and populations (Tilman 1999, Lehman & Tilman 2000, Hooper et al. 2005). Stability increases with diversity at the community-level (Lehman & Tilman 2000, Van Ruijven & Berendse 2007), probably because communities with more interacting species show less temporal variability than species-poor ones (MacArthur 1955, Elton 1958). Species richness at small scales increased within short periods, probably due to regeneration gaps, microsites, that favour species establishment and coexistence (Van der Maarel & Sykes 1993). Nevertheless, the stability at the population level could show positive, negative and neutral relationships between population stability and diversity (Van Ruijven & Berendse 2007).

## 9.2.1 Coastal Dune Succession (Example XVII)

Isermann M (submitted) Coastal dune succession and plant diversity on a German Wadden Sea Island. *Journal of Coastal Research*.

Succession of coastal dune vegetation on the island of Spiekeroog was investigated **directly** using permanent plots, as well as **indirectly**, because these plots represent a **chronosequence** across the dunes (Figure 34).

According to the historic land-use, as well as natural landscape dynamic, there might be difficulties concluding from a chronosequence to successional patterns and processes. Thus, for example, there is no absolute certainty if this entire xerosere represents a primary succession series, or if larger disturbances happened, followed by secondary succession. At the small scale for some plots, a secondary succession is known, because the disturbance happened during the time of investigation.

The investigated dry dune ridges on Spiekeroog are different in age. The origin of these dune ridges is known roughly: foredunes are due to sand dynamic up to 20 years old, the main yellow dune ridges are 45 to 70 years old, the grey dunes 70-170 and the brown dunes are up to 270 years old (Gerlach et al. 1994). The investigated chronosequence represents different successional stages (Figure 34); starting in the young grey dunes (younger yellow dunes are not included because of the high sand dynamic) and represents: young grey dunes with herbaceous rich short grasslands (plot no. 1, 2), old grey dunes with lichen rich *Corynephorus canescens* swards (plot no. 3-6), grasslands with dominance of *Carex arenaria* (plot no. 7) and with dominance of *Deschampsia flexuosa* (plot no. 8), brown dunes with heathlands (plot no. 9-11).

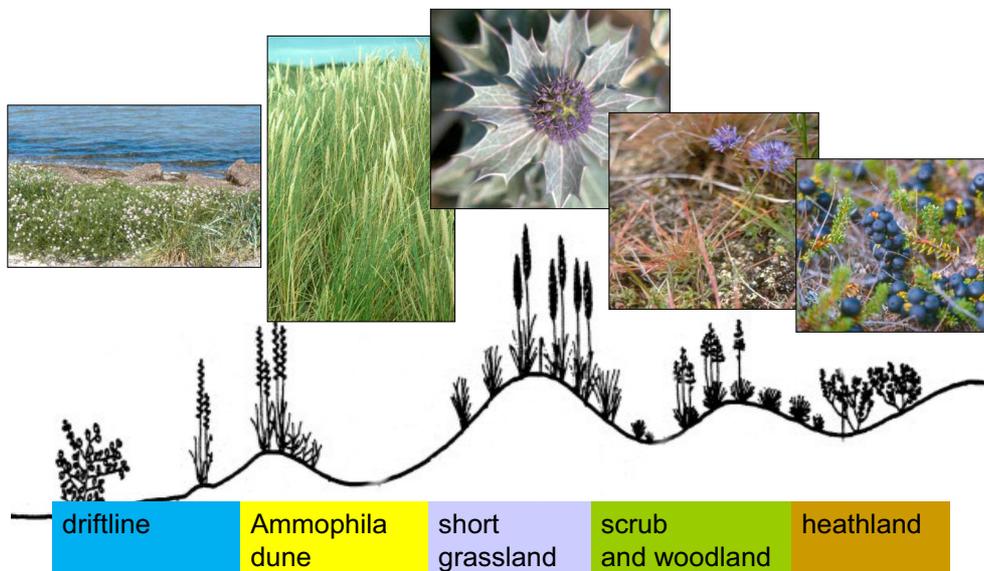


Figure 34. Chronosequence of dune vegetation; starting with ephemeral driftlines with *Cakile maritima*; embryo dunes and yellow dunes with *Ammophila arenaria*, grey dunes with *Eryngium maritimum*, *Corynephorus canescens* and *Jasione montana*; green dunes with shrubland and develop to brown dune heathlands with *Empetrum nigrum*.

Plant **species richness** varied along the xeroseries (Figure 35). Total number of plant species decreased significantly from the young grey to the old brown dunes (Figure 35a). The number of **trees and shrubs** was higher in the young grey dunes as well as in the brown dune heathlands. The number of herbaceous plant species reached higher numbers in the young grey dunes. The number of **bryophytes** and especially of lichens tended to show a humped-back relationship, similar to their cover abundance, with a higher number of species in the old grey dunes (Figure 35b).

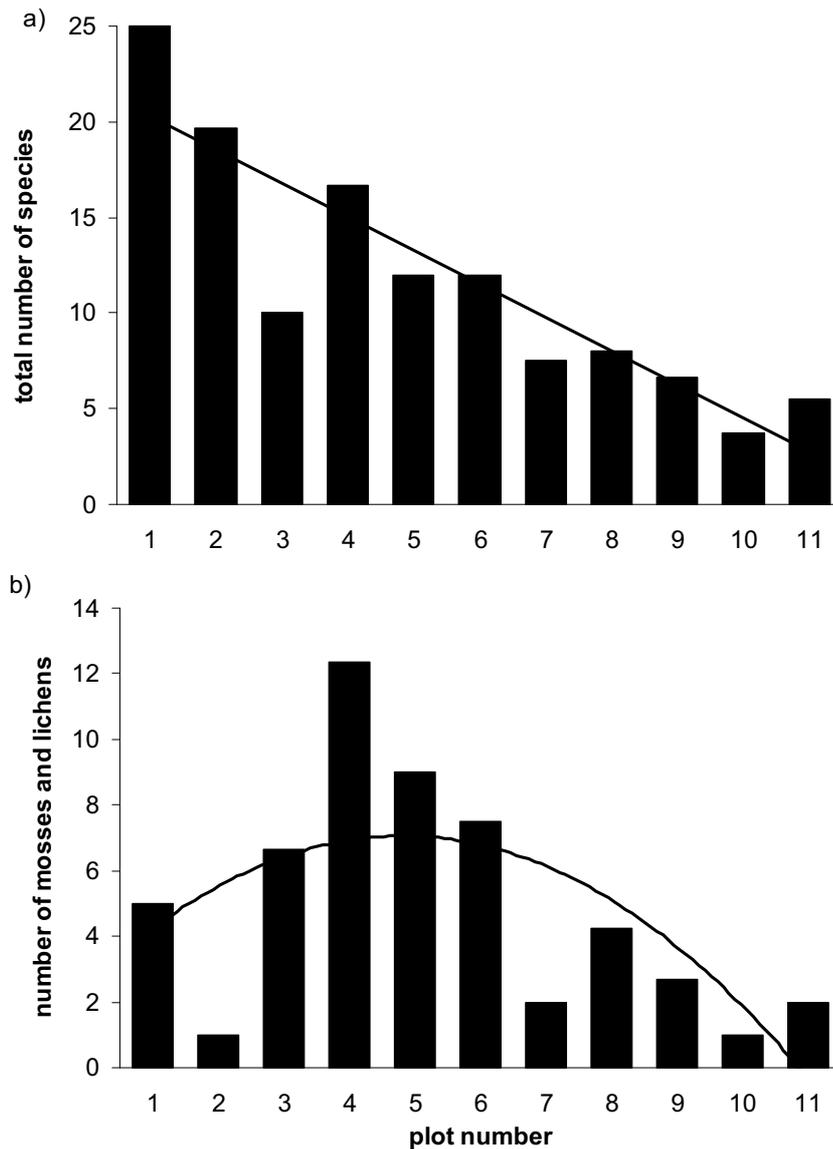


Figure 35. a) Total plant species richness along the chronosequence ( $R^2_{adj.} = 0.77$ ,  $p < 0.001$ ), and b) number of bryophytes and lichens ( $R^2_{adj.} = 0.26$ ,  $p = 0.123$  for lichens only  $R^2_{adj.} = 0.31$ ,  $p = 0.091$ ).

Like the total species richness, **species diversity** expressed as Shannon diversity decreased along the chronosequence. Moreover, Simpson **dominance** index was highest in the old brown dunes, thus the *Empetrum* heathlands were clearly characterised by a dominance structure. Succession in coastal dunes generally leads from species-poor pioneer vegetation, across species-rich intermediate stages and in the following to a steadily

decreasing species richness combined with an increase in dominance by dwarf shrubs and low trees (Aptroot et al. 2007). Thus along the xerosere, **life form groups** changed, from short grasses and herbs on young grey dunes, to bryophytes and lichens on old grey dunes, to dwarf shrubs on brown dunes. These results are in line with the change of **life history strategies** from r-selection to K-selection and partly confirm the increasing **size** of species during succession.

**Species richness** is highest in the **intermediate successional stages**, represented by the young grey dunes, because of their **spatial heterogeneity**. During the transition from yellow to grey dunes, high patchiness of open and unvegetated areas occur (Yarranton & Morrison 1974, Franks 2003, Cutler et al. 2008). Habitat heterogeneity of these areas is related, for example, to topography and substrate (Paal 1998). Highest total plant species richness on the young grey dunes is most probably caused by intermediate **resource availability** (Chapter 8.3.3). Spatial heterogeneity and resource availability enhance the number of available potential ecological niches.

In coastal dunes an inverse relationship between the species richness and homogeneity along the succession series occurs. At the Baltic Coast, regarding to longer dune xeroseries from yellow dunes to forest, homogeneity reached highest values at the first and at the last successional stage. Moreover, species richness and homogeneity showed an inverse relationship (Stankevičiūtė 2001). Highest species richness was reached in both regions in the transition zones, at Spiekeroog as well as in the Baltic, in the transition from yellow to grey dunes and in the Baltic region due to the longer xeroseries and furthermore in the transition from heathlands to forest.

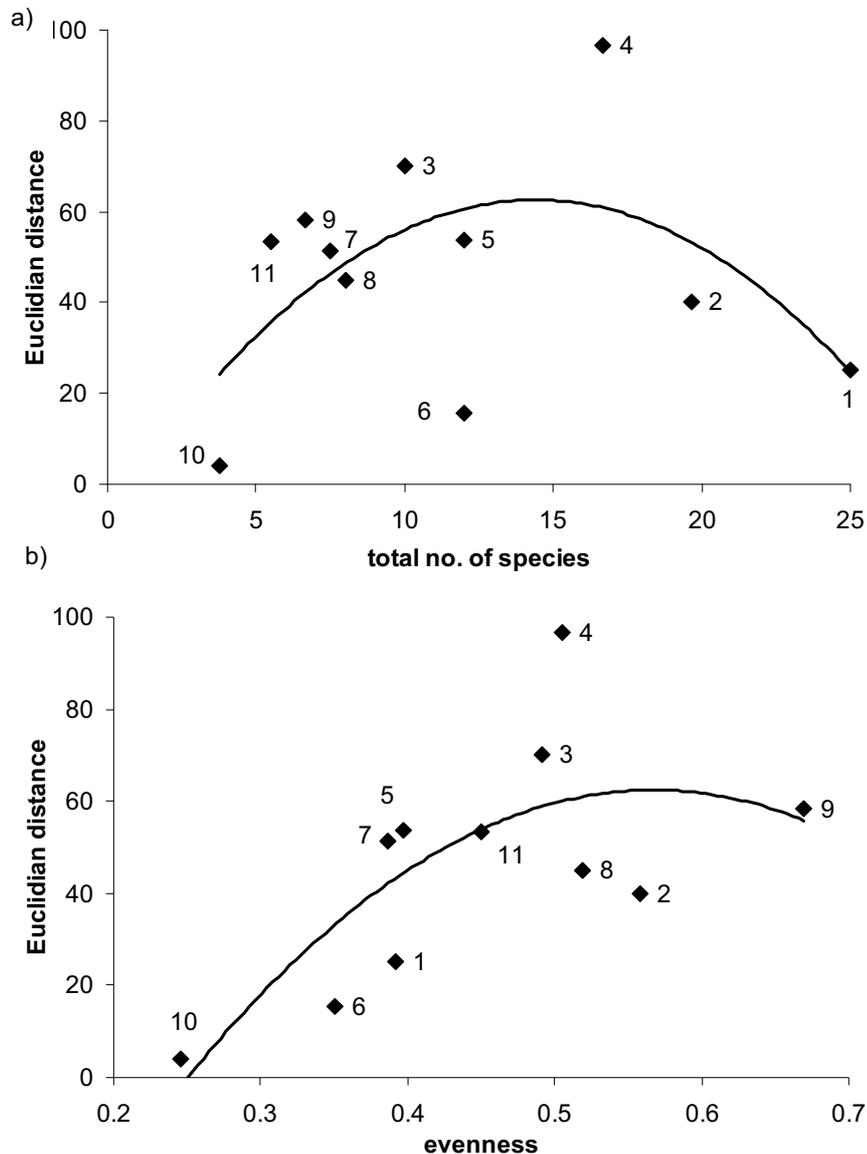
According to the relative habitat heterogeneity, species with different life forms, as well as competition strategies, coexist. The number of potential niches resulting from increased biomass and stratification probably reached highest values in intermediate successional stages, resulting in a high number of species richness and species diversity. In this study, there was only a linear decline in total species richness because the studied chronosequence did not include the yellow dunes, which contain less species than the grey dunes.

Plant species turnover, measured as Euclidean distance between the first and the last year of observation, showed a slight trend to a humped-back relationship with the total number of plant species (Figure 36a). Hence, low succession rates were in species-poor communities, as well as in species-rich ones. Moreover, there was a significant slight humped-back relationship between succession rate and evenness (Figure 36b). The succession rate at first increased with increasing evenness and level off at higher values of evenness.

**Species-poor** communities, dominated by only a few species, like the **brown dune heathlands**, probably have low turnover rates because it represents a metastable stage. This is in line, that vegetation changes are generally **lower in older successional** stages than in earlier ones, because the rate of successional change in the later-stages generally declines over time (Foster & Tilman 2000).

**Species-rich** communities like the young grey dune vegetation are, due to their high **diversity**, more or less **stable**. Succession rate of the first plots of the series, for example, is lower due to environmental stress, such as remaining sand dynamic. Similar

results were shown for semi-fixed dunes with moderate rabbit grazing, trampling and sand-burial, in comparison to areas such as blowouts with high values of environmental stress (Franks & Peterson 2003, Lemauviel et al. 2003). Moreover, succession is slowed down by **herbivores**, which initiate, for example, the re-development from old to younger successional stages, especially from shrublands to herbaceous rich grassland (Aptroot et al. 2007).



**Figure 36.** a) Relationships between overall succession rates measured as total Euclidian distance between the first and the last year of observation and species richness shown as average of total number of species of each plot ( $R^2_{adj.} = 0.10$ ,  $p = 0.266$ ) b) Relationship with the average evenness ( $R^2_{adj.} = 0.41$ ,  $p = 0.048$ ).

Communities with a balanced distribution of species, with **high values of evenness**, showed lowest succession rates. Because stability in ecosystems has to be considered as a dynamic process, diverse communities are more stable since communities with higher species richness showed less temporal variation during succession.

### 9.3 *Biological Invasions*

The process of biological invasions is generally divided into different stages, relating to a series of abiotic and biotic barriers (Richardson et al. 2000). Richardson et al. (2000) describes the invasion process as follows. **Introduction**, propagules or individuals arrive, through human influence, at a site away from their native geographical range, thus crossing a major geographical barrier. Many introduced species, so-called **casuals**, will reproduce but will be unsuccessful at maintaining their populations over longer periods. **Naturalisation**, species establish self-perpetuating populations and have therefore, crossed environmental, reproductive and dispersal barriers. Generally, species are defined as naturalised after establishing at one site for at least 10 years (Richardson & Pyšek 2006). **Invasive** species are naturalised species, which establish new populations at considerable distances from parent plants. They also occur in semi-natural environments, where they can compete with the native species of their new range. Invasive species are often associated with negative effects on ecosystems of the invaded area. Furthermore, about 10 % of the invasive species represent **transformers**, changing the semi-/natural ecosystems in an enhanced manner, often over substantial areas.

Not all introduced species develop during the invasion process to transformers. According to the **tens rule** (Williamson & Brown 1986), 10 % of introduced species run off to be casuals, 10 % of the casuals become naturalised, and 10 % of naturalised species become invasive species (Richardson & Pyšek 2006).

**Temporal aspects** affect biological invasions. Generally, there is a so-called **time lag** between the first introduction of a species and the start of widespread distribution (Richardson 2001). The duration of the lag phase depends on species life history traits, and can reach up to about 170 years (Richardson 2001). The probability of invasion increases with the time since the introduction, the so-called **residence time** (Richardson & Pyšek 2006). The longer the residence time, the longer the species occurs in the region, the greater the propagule bank is, and therefore the greater the probability of dispersal and establishment (Rejmánek et al. 2005). This can be shown by the wider distribution of archaeophytes ranges in Europe, than those of neophytes (Pyšek & Jarošík 2005). That the logarithmic number of establishments, increases linearly with residence time is of further interest (Pyšek et al. 2004b).

Moreover, **ecological effects** are enhanced with residence time (Collier et al. 2002). Consequences of the expansion of non-native invasive plants represent an increasing environmental problem worldwide (Richardson et al. 2000). Biological invasions of non-native species are one of the strongest processes, along with habitat loss, over-exploitation and extinction, which can lead to a decline in native species diversity (Purvis et al. 2000). The number of non-native species has rapidly increased during recent decades due to increasing movement of goods and people (Lockwood et al. 2008). The effects of invasive species are scale-dependent (Sax & Gaines 2003). Biological invasions potentially result in an increase in species richness, as the invading species are added to the existing species pool (Huston 1994). However, in many cases they result in a decline in community diversity, as well as landscape diversity, but in general increase regional diversity, whereas nothing is told about changes in genetic diversity of native species (Rosenzweig 2001, Collins et al. 2002).

Pattern and processes that influence biological invasions can effect composition, structure and diversity of natural communities, thus biological invasions belong to fundamental ecological processes (Stachowicz & Tilman 2005). Therefore, most of the explaining patterns and processes are demonstrated in previous chapters. The **diversity-resistance hypotheses** assumed that **species diversity** maintains **stability** and enhances resistance to invasion (MacArthur 1955, Elton 1958, Kennedy et al. 2002). Diverse communities inhabit more space and generate more biomass. Higher levels of species richness strengthen resource competition (Chapter 8.3.3), enhance resource use efficiency and increase niche exploitation. Species diversity therefore reduces available resources and available niches for new colonists in general, as well as for invasive plants. Moreover, environmental patterns, such as nutrient status or disturbance regime (Chapter 8.3.2), determine invasion success (Elton 1958, Drake et al. 1989, Huston 1994, Tilman 1999, Richardson et al. 2000, Tilman et al. 2001, Kennedy et al. 2002, Fargione & Tilman 2005, Stachowicz & Tilman 2005). Incidentally, biological invasions themselves can be considered as disturbance or as an agent, which alters a disturbance regime (Lockwood et al. 2008). Various experimental studies confirm the decrease of invasion success with increasing species diversity (Kennedy et al. 2002, Fargione et al. 2003). In general, effects of biological invasions depend on two basic pattern-complexes: on the **invasibility** of the community and on the qualities of the successful invader, the **invasiveness** of the species (Rejmánek & Richardson 1996).

### 9.3.1 Native Species Richness and Biological Invasion (Example XVIII)

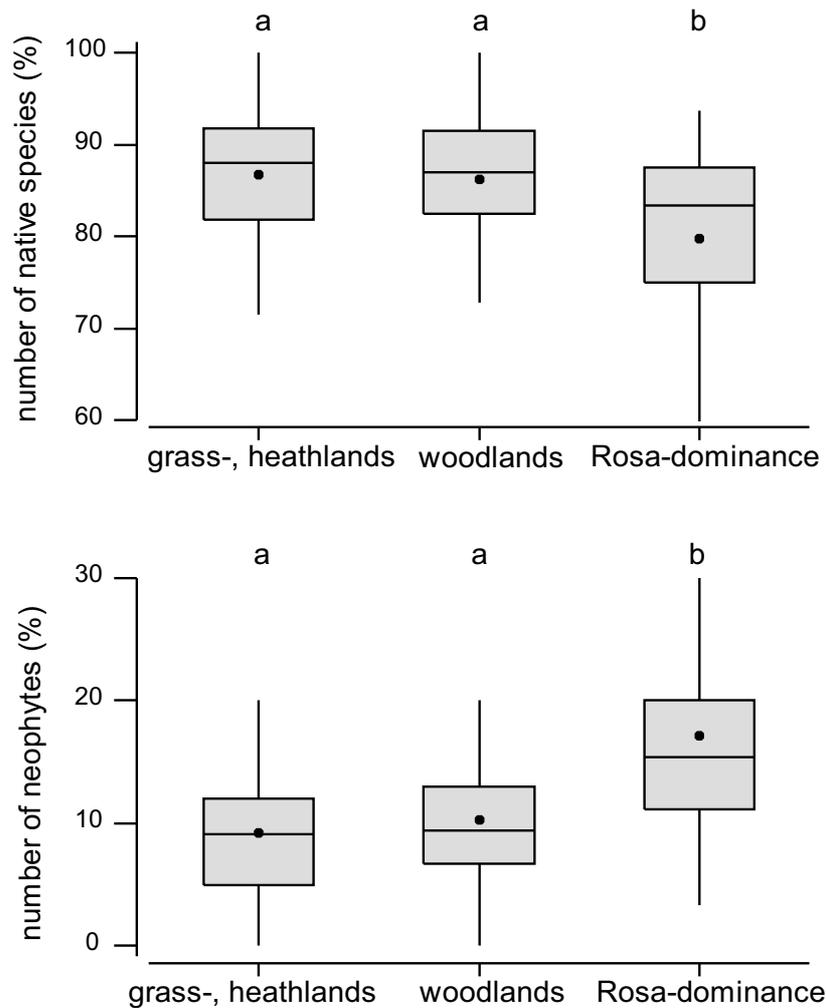
*Isermann M (2008a) Classification and habitat characteristics of plant communities invaded by the non-native Rosa rugosa Thunb. in NW Europe. Phytocoenologia 38, 133-150.*

The shrub *Rosa rugosa* (Figure 38) is an invasive neophyte in Europe (Bruun 2005) that, especially in coastal areas, represents a conservation problem to semi-natural vegetation (Kollmann et al. 2007). It spreads vegetatively by tillers and builds up large clones. Long-distance dispersal of fruits and seeds probably takes place due to dispersal in seawater and by animals, particularly birds (Bruun 2005).

NW European vegetation invaded by *Rosa rugosa* was analysed using 383 relevés collected from literature and from databases. By TWINSpan classification, two main groups were distinguished wood- and shrublands as well as grass- and heathlands, in which *R. rugosa* builds up dominant stands. In comparison to its native range, *R. rugosa* established in various plant communities and at a wide range of ecological conditions. Thus, it seems that the shrub in its new range has a broader environmental niche.

As shown in other studies (Chapter 8.3.3.1), due to stronger shading effects, expansion of *R. rugosa* changes species composition and decreases species richness, especially the number of herbs, as well as bryophytes and lichens.

Beside general changes of environmental conditions of the invaded system, there is a change of the proportion of native and non-native species related to the invasion by *Rosa rugosa*. Dominated stands, that means due to a TWINSPAN classification more than 80 % *R. rugosa* cover, have a lower percentage number of native species (Figure 37a) and a higher percentage number of neophytes (Figure 37b) than the corresponding stands without dominant *R. rugosa*.



**Figure 37.** Species richness of three by TWINSPAN analysis main vegetation types: grass- and heathlands, woodlands and *Rosa rugosa* dominated stands. Proportion of native species (above) and proportion of neophytes (below). (*Rosa rugosa* is excluded. Boxplots are median connected, limited by quartiles; mean is shown as a dot. Kruskal-Wallis test all with  $p < 0.01$  followed by Mann-Whitney tests,  $n =$  grass- and heathlands 117, woodlands 77, *Rosa*-dominance 189).

This confirms, that *R. rugosa* itself, acts as a disturbance. The biological invasion facilitates other non-native species in a self-preventing system of positive feedback circles. Thus, positive interactions amongst biological invaders improve the establishment of other non-native species (Parker et al. 1999, Lockwood et al. 2008).

Spreading of non-native species often declines native species richness and affects ecosystem processes (Simberloff 2005). Shrublands formed by neophytes generally

support the growth of other neophytes probably by increased availability of nutrients. For example, soil nitrogen content in *Crataegus monogyna* scrub (Hodgkin 1984) as well as in *Rosa rugosa* dominated shrubland was higher than in open dune grasslands. In general, shrubs, as well as bulk grasses, in relatively dry climates operate as ‘**islands of fertility**’ e.g. because of increasing organic matter and nitrogen mineralisation in the nearby roots surroundings (Jackson & Caldwell 1993, Anderson et al. 2004). Nitrogen content and nutrient content in general, are enhanced in invaded sites, probably due to a higher primary productivity of non-native invasive plants compared to native vegetation (Vanderhoeven et al. 2005). Therefore, the primary productivity of *R. rugosa* dominated shrubland in its new range is eventually so high, that it out-competed most of the native species, which is in line with the relations between productivity and species richness (Grime 1979). Furthermore, a higher invasibility of warmer sites is often assumed, as *Rosa rugosa* probably prefers lighter and warmer conditions, which could be another reason why neophytes are supported in *Rosa* shrubland.



**Figure 38.** *Rosa rugosa*

Environmental conditions of the invaded system are changed by *Rosa rugosa* (Figure 38). Effects of *Rosa rugosa* are proportional to increasing abundance and probably to increasing biomass. Such biological invaders, fundamentally changing environmental conditions, ecosystem, or community properties, are called ecosystem engineers (Jones et al. 1994) or transformers (Pyšek et al. 2004a). These types of biological invasions are a major threat to natural ecosystems (D’Antonio & Vitousek 1992).

## **10 Short Conclusion**

Variables determining species richness vary with scale; the larger the scale, the greater the role that they play, and the more complex are the processes involved in determining species richness. A more or less hierarchical structure of patterns and processes predict species richness. At the global scale large gradient complexes, at the landscape scale the number of habitats, and at the plot scale the variability of soil factors, affect species diversity. Moreover, biotic patterns and related processes influence species diversity, often by changing environmental conditions, e.g. disturbance by grazing or competition by shrub encroachment. The spatial hierarchical structure is connected with the temporal scale and complexity of species area relations is enhanced by temporal dynamics. Thus for nature conservation aspects as well as for studying general biodiversity patterns and processes there is a necessity to consider different spatial and temporal scales.

## 11 References

- Acosta A, Carranza ML, Izzi CF (2009) Are there habitats that contribute best to plant species diversity in coastal dunes? *Biodiversity and Conservation* 18, 1087-1098.
- Adersen H (1995) Research on islands: classic, recent, and prospective approaches. In: Vitousek PM, Loope LL, Adersen H (eds.) *Islands. Biological diversity and ecosystem function. Ecological Studies* 115, 7-21.
- Adler PB, Raff DA, Lauenroth WK (2001) The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128, 465-479.
- Akeroyd JR (1997) Intraspecific variation in European coastal plant species. In: Van der Maarel E (ed.) *Ecosystems of the world. Vol. 2C. Dry coastal ecosystems. General aspects. Elsevier, Amsterdam.* pp. 145-162.
- Allem AC (2000) The terms genetic resource, biological resource, and biodiversity examined. *The Environmentalist* 20, 335-341.
- Al-Mufti MM, Sydes CL, Furness SB, Grime JP, Band SR (1977) A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *Journal of Ecology* 65, 759-791.
- Alpert P, Mooney HA (1996) Resource heterogeneity generated by shrubs and topography on coastal sand dunes. *Vegetatio* 122, 83-93.
- Álvarez R, Muñoz A, Pesqueira XM, García-Duro J, Reyes O, Casal M (2009) Spatial and temporal patterns in structure and diversity of Mediterranean forest of *Quercus pyrenaica* in relation to fire. *Forest Ecology and Management* 257, 1596-1602.
- Anderson S (1994) Area and endemism. *Quarterly Review of Biology* 69, 451-471.
- Anderson TM, McNaughton SJ, Ritchie ME (2004) Scale-dependent relationships between the spatial distribution of a limiting resource and plant species diversity in an African grassland ecosystem. *Oecologia* 139, 277-287.
- Aptroot A, Van Dobben HF, Slim PA, Olf H (2007) The role of cattle in maintaining plant diversity in wet dune valleys. *Biodiversity and Conservation* 16, 1541-1550.
- Archibald EEA (1949) The specific character of plant communities. II. A quantitative approach. *Journal of Ecology* 37, 274-288.
- Arim M, Barbosa O (2002) Humped pattern of diversity: fact or artifact? *Science* 297, 1763-1764.
- Ariño X, Saiz-Jimenez C (1996) Biological diversity and cultural heritage. *Aerobiologia* 12, 279-282.
- Arita HT (2005) Range size in mid-domain models of species diversity. *Journal of Theoretical Biology* 232, 119-126.
- Arita HT, Rodríguez-Tapia G (2009) Contribution of restricted and widespread species to diversity: the effect of range cohesion. *Ecography* 32, 210-214.
- Arrhenius O (1921) Species and area. *Journal of Ecology* 9, 95-99.
- Averiss RJ, Skene KR (2001) Changes in nutrient heterogeneity along sand dune and slack chronosequences at Tentsmuir Point, Eastern Scotland. *Botanical Journal of Scotland* 53, 45-56.

- Bakker C, Blair JM, Knapp AK (2003) Does resource availability, resource heterogeneity or species turnover mediate changes in plant species richness in grazed grasslands? *Oecologia* 137, 385-391.
- Bakker JP, Gálvez Bravo L, Mouissie AM (2008) Dispersal by cattle of salt-marsh and dune species into salt-marsh and dune communities. *Plant Ecology* 197, 43-54.
- Barthlott W, Lauer W, Placke A (1996) Global distribution of species diversity in vascular plants: towards a world map of phytodiversity. *Erdkunde* 50, 317-327.
- Barthlott W, Winiger M (eds.) (1998) Biodiversity. A challenge for development research and policy. Springer, Berlin.
- Bawa KS, Menon S (1997) Biodiversity monitoring: the missing ingredients. *Trends in Ecology & Evolution* 12, 42.
- Bazzaz FA (1975) Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology* 56, 485-488.
- Beckett PHT, Webster R (1971) Soil variability: a review. *Soils and Fertilizers* 34, 1-15.
- Begon M, Townsend CR, Harper JL (2006) Ecology: from individuals to ecosystems. Blackwell, Malden.
- Bellingham PJ, Coomes DA (2003) Grazing and community structure as determinants of invasion success by Scotch broom in a New Zealand montane shrubland. *Diversity and Distributions* 9, 19-28.
- Belsky AJ (1992) Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science* 3, 187-200.
- Berendse F (1982) Competition between plant populations with different rooting depths. *Oecologia* 53, 50-55.
- Berg C, Dengler J, Abdank A (eds.) (2001) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung. Tabellenband. Landesamt für Umwelt, Naturschutz und Geologie Mecklenburg-Vorpommern. Weissdorn-Verlag, Jena.
- Berg C, Dengler J, Abdank A, Isermann M (eds.) (2004) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung. Textband. Landesamt für Umwelt, Naturschutz und Geologie Mecklenburg-Vorpommern. Weissdorn-Verlag, Jena.
- Bergamini A, Pauli D, Peintinger M, Schmid B (2001) Relationships between productivity, number of shoots and number of species in bryophytes and vascular plants. *Journal of Ecology* 89, 920-929.
- Binggeli P, Eakin M, Macfadyen A, Power J, McConnell J (1992) Impact of the alien sea buckthorn (*Hippophaë rhamnoides* L.) on sand dune ecosystems in Ireland. In: Carter RWG, Curtis TGF, Sheehy-Skeffington MJ (eds.) Coastal dunes. Geomorphology, ecology and management for conservation. Balkema, Rotterdam, Brookfield. pp. 325-337.
- Bischoff A, Auge H, Mahn E-G (2005) Seasonal changes in the relationship between plant species richness and community biomass in early succession. *Basic and Applied Ecology* 6, 385-394.
- Blackstock TH, Stevens DP, Howe EA (1996) Biological components of sites of special scientific interest in Wales. *Biodiversity and Conservation* 5, 897-920.
- Bobbink R (1991) Effects of nutrient enrichment in Dutch chalk grassland. *Journal of Applied Ecology* 28, 28-41.

- Bogaert G, Lemeur R (1995) The use of diversity indices in the detection of succession and ecological disturbances in Belgian dune vegetation (at Koksijde). *Mededelingen Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen; Universiteit Gent (Belgium)* 60, 61-68.
- Bokdam J (2001) Effects of browsing and grazing on cyclic succession in nutrient-limited ecosystems. *Journal of Vegetation Science* 12, 875-886.
- Bokma F, Mönkkönen M (2000) The mid-domain effect and the longitudinal dimension of continents. *Trends in Ecology & Evolution* 15, 288-289.
- Bond EM, Chase JM (2002) Biodiversity and ecosystem functioning at local and regional spatial scales. *Ecology Letters* 5, 467-470.
- Bond W (1983) On alpha diversity and the richness of the Cape flora: a study in southern Cape fynbos. In: Kruger FJ, Mitchell DT, Jarvis JUM (eds.) *Mediterranean-type ecosystems. The role of nutrients*. Springer, Berlin. pp. 337-356.
- Boorman LA, Fuller RM (1982) Effects of added nutrients on dune swards grazed by rabbits. *Journal of Ecology* 70, 345-355.
- Bos D, Bakker JP, De Vries Y, Van Lieshout S (2002) Long-term vegetation changes in experimentally grazed and ungrazed back-barrier marshes in the Wadden Sea. *Applied Vegetation Science* 5, 45-54.
- Bossuyt B, Honnay O, Hermy M (2005) Evidence for community assembly constraints during succession in dune slack plant communities. *Plant Ecology* 178, 201-209.
- Brillouin L (1962) *Science and information theory*. Academic Press, New York.
- Brooks ML, Matchett JR (2003) Plant community patterns in unburned and burned blackbrush (*Coleogyne ramosissima* Torr.) shrublands in the Mojave Desert. *Western North American Naturalist* 63, 283-298.
- Brown BL (2007) Habitat heterogeneity and disturbance influence patterns of community temporal variability in a small temperate stream. *Hydrobiologia* 586, 93-106.
- Brown JH (1988) Species diversity. In: Myers AA, Giller PS (eds.) (1988) *Analytical biogeography. An integrated approach to the study of animal and plant distributions*. Chapman & Hall, London. pp. 57-89.
- Brown JH, Lomolino MV (1989) Independent discovery of the equilibrium theory of island biogeography. *Ecology* 70, 1954-1957.
- Brown JH, Stevens GC, Kaufman DM (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* 27, 597-623.
- Brown M, Dinsmore JJ (1988) Habitat islands and the equilibrium theory of island biogeography: testing some predictions. *Oecologia* 75, 426-429.
- Bruno JF, Kennedy CW, Rand TA, Grant MB (2004) Landscape-scale patterns of biological invasions in shoreline plant communities. *Oikos* 107, 531-540.
- Bruun HH (2005) *Rosa rugosa* Thunb. ex. Murray. *Biological Flora of the British Isles*. *Journal of Ecology* 93, 441-470.
- Buckland ST, Magurran AE, Green RE, Fewster RM (2005) Monitoring change in biodiversity through composite indices. *Philosophical Transactions of the Royal Society B* 360, 243-254.
- Bültmann H (2005) Syntaxonomy of arctic terricolous lichen vegetation, with a survey and an example from Southeast-Greenland. *Phytocoenologia* 35, 909-949.

- Burggraaf-van Nierop YD, Van der Meijden E (1984) The influence of rabbit scrapes on dune vegetation. *Biological Conservation* 30, 133-146.
- Burnham RJ (2004) Alpha and beta diversity of Lianas in Yasuní, Ecuador. *Forest Ecology and Management* 190, 43-55.
- Burrows CJ (1990) Processes of vegetation change. Unwin Hyman, London.
- Cain ML, Milligan BG, Strand AE (2000) Long-distance seed dispersal in plant populations. *American Journal of Botany* 87, 1217-1227.
- Caldecott JO, Jenkins MD, Johnson TH, Groombridge B (1996) Priorities for conserving global species richness and endemism. *Biodiversity and Conservation* 5, 699-727.
- Caprio E, Ellena I, Rolando A (2009) Assessing habitat/landscape predictors of bird diversity in managed deciduous forests: a seasonal and guild-based approach. *Biodiversity and Conservation* 18, 1287-1303.
- Campbell BD, Grime JP (1989) A comparative study of plant responsiveness to the duration of episodes of mineral nutrient enrichment. *New Phytologist* 112, 261-267.
- Cardinale BJ, Palmer MA (2002) Disturbance moderates biodiversity-ecosystem function relationships: experimental evidence from caddisflies in stream mesocosms. *Ecology* 83, 1915-1927.
- Carine MA, Humphries CJ, Guma IR, Reyes-Betancort JA, Santos Guerra A (2009) Areas and algorithms: evaluating numerical approaches for the delimitation of areas of endemism in the Canary Islands archipelago. *Journal of Biogeography* 36, 593-611.
- Carnicer J, Brotons L, Sol D, De Cáceres M (2008) Random sampling, abundance-extinction dynamics and niche-filtering immigration constraints explain the generation of species richness gradients. *Global Ecology and Biogeography* 17, 352-362.
- Carolan MS (2009) This is not a biodiversity hotspot: the power of maps and other Images in the Environmental Sciences. *Society and Natural Resources* 22, 278-286.
- Carter RWG (1988) Coastal environments. An introduction to physical, ecological and cultural systems of coastlines. Academic Press, London.
- Catalán I, Rodríguez-Hidalgo P, Tortosa FS (2008) Is habitat management an effective tool for wild rabbit (*Oryctolagus cuniculus*) population reinforcement? *European Journal of Wildlife Research* 54, 449-453.
- Chaneton EJ, Facelli JM (1991) Disturbance effects on plant community diversity: spatial scales and dominance hierarchies. *Vegetatio* 93, 143-155.
- Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OS, Hobbie SE, Mack MC, Diaz S (2000) Consequences of changing biodiversity. *Nature* 405, 234-242.
- Chapuis J-L, Frenot Y, Lebouvier M (2004) Recovery of native plant communities after eradication of rabbits from the subantarctic Kerguelen Islands, an influence of climate change. *Biological Conservation* 117, 167-179.
- Chen X-Y, He F (2009) Speciation and endemism under the model of island biogeography. *Ecology* 90, 39-45.
- Chiarucci A, Wilson JB, Anderson BJ, De Dominicis V (1999) Cover versus biomass as an estimate of species abundance: does it make a difference to the conclusions? *Journal of Vegetation Science* 10, 35-42.

- Chiba S, Okochi I, Ohbayashi T, Miura D, Mori H, Kimura K, Wada S (2009) Effects of habitat history and extinction selectivity on species-richness patterns of an island land snail fauna. *Journal of Biogeography*, doi: 10.1111/j.1365-2699.2009.02115.x
- Chown SL, Sinclair BJ, Leinaas HP, Gaston KJ (2004) Hemispheric asymmetries in biodiversity - a serious matter for ecology. *PLoS Biology* 2, 1701-1706.
- Cincotta RP, Wisniewski J, Engelman R (2000) Human population in the biodiversity hotspots. *Nature* 404, 990-992.
- Clough Y, Holzschuh A, Gabriel D, Purtauf T, Kleijn D, Kruess A, Steffan-Dewenter I, Tschardt T (2007) Alpha and beta diversity of arthropods and plants in organically and conventionally managed wheat fields. *Journal of Applied Ecology* 44, 804-812.
- Cody ML (1968) On the methods of resource division in grassland bird communities. *American Naturalist* 102, 107-147.
- Cody ML (1986) Structural niches in plant communities. In: Diamond J, Case TJ (eds.) *Community ecology*. Harper and Row Publishers, New York. pp. 381-405.
- Cody ML (1989) Growth-form diversity and community structure in desert plants. *Journal of Arid Environments* 17, 199-209.
- Cody ML (1991) Niche theory and plant growth form. *Vegetatio* 97, 39-55.
- Collier MH, Vankat JL, Jughes MR (2002) Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. *American Midland Naturalist* 147, 60-71.
- Collins MD, Vázquez DP, Sanders NJ (2002) Species-area curves, homogenization and the loss of global diversity. *Evolutionary Ecology Research* 4, 457-464.
- Collins SL (1987) Interaction of disturbances in tallgrass prairie: a field experiment. *Ecology* 68, 1243-1250.
- Collins SL, Barber SC (1985) Effects of disturbance on diversity in mixed-grass prairie. *Vegetatio* 64, 87-94.
- Collins SL, Glenn SM (1997) Intermediate disturbance and its relationship to within- and between-patch dynamics. *New Zealand Journal of Ecology* 21, 103-110.
- Collins SL, Glenn SM, Gibson DJ (1995) Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. *Ecology* 76, 486-492.
- Colwell RK (2008) RangeModel: tools for exploring and assessing geometric constraints on species richness (the mid-domain effect) along transects. *Ecography* 31, 4-7.
- Colwell RK, Lees DC (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution* 15, 70-76.
- Colwell RK, Rahbek C, Gotelli NJ (2004) The mid-domain effect and species richness patterns: what have we learned so far? *American Naturalist* 163, E1-E23.
- Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42, 710-723.
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199, 1302-1310.
- Connor EF, McCoy ED (1979) The statistics and biology of the species-area relationship. *American Naturalist* 113, 791-833.
- Cordes H, Feder J, Hellberg F, Metzinger D, Wittig B (eds.) (2006) *Verbreitungsatlas der Farn- und Blütenpflanzen im Elbe-Weser-Gebiet*. Verlag Hauschild, Bremen.

- Cornell HV (1993) Unsaturated patterns in species assemblages: the role of regional processes in setting local species richness. In: Ricklefs RE, Schluter D (eds.) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, IL. pp. 243-252.
- Cosyns E, Degezelle T, Demeulenaere E, Hoffmann M (2001) Feeding ecology of Konik horses and donkeys in Belgian coastal dunes and its implications for nature management. *Belgian Journal of Zoology* 131, Suppl. 2, 111-118.
- Council of the European Commission (1992) Council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Communities. Series L*. 206, 7-49.
- Cowling RM, Holmes PM, Rebelo AM (1992) Plant diversity and endemism, in *The Ecology of fynbos. Nutrients, Fire and Diversity*. In: Cowling RM, (ed.) *The ecology of fynbos. Nutrients, fire and diversity*. Oxford University Press, Cape Town. pp. 62-112.
- Cowling RM, MacDonald IAW, Simmons MT (1996a) The Cape Peninsula, South Africa: physiographical, biological and historical background to an extraordinary hot-spot of biodiversity. *Biodiversity and Conservation* 5, 527-550.
- Cowling RM, Pierce SM (1988) Secondary succession in coastal dune fynbos: variation due to site and disturbance. *Vegetatio* 76, 131-139.
- Cowling RM, Rundel PW, Lamont BB, Arroyo MK, Arianoutsou M (1996b) Plant diversity in mediterranean-climate regions. *Trends in Ecology & Evolution* 11, 362-366.
- Cowling RM, Samways MJ (1995) Predicting global patterns of endemic plant species richness. *Biodiversity Letters* 2, 127-131.
- Crawley MJ (1997) *Plant ecology*. Blackwell, Oxford.
- Crawley MJ, Harral (2001) Scale dependence in plant biodiversity. *Science* 291, 864-868.
- Crist TO, Veech JA, Gering JC, Summerville KS (2003) Partitioning species diversity across landscapes and regions: a hierarchical analysis of  $\alpha$ ,  $\beta$  and  $\gamma$ -diversity. *American Naturalist* 162, 734-743.
- Currie DJ (1991) Energy and large-scale patterns of animal- and plant-species richness. *American Naturalist* 137, 27-49.
- Cutler NA, Belyea LR, Dugmore AJ (2008) The spatiotemporal dynamics of a primary succession. *Journal of Ecology* 96, 231-246.
- Dahiya IS, Richter J, Malik RS (1984) Soil spatial variability: a review. *International Journal of Tropical Agriculture* 2, 1-102.
- Danielsen F, Burgess ND, Balmford A (2005) Monitoring matters: examining the potential of locally-based approaches. *Biodiversity and Conservation* 14, 2507-2542.
- D'Antonio CM, Dudley TL (1995) Biological invasions as agents of change on islands versus mainlands. In: Vitousek PM, Loope LL, Adersen H (eds.) *Islands. Biological diversity and ecosystem function. Ecological Studies* 115. Springer, Berlin. pp. 103-121.
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23, 63-87.
- Davenport J, Davenport JL (2006) The impact of tourism and personal leisure transport on coastal environments: a review. *Estuarine, Coastal and Shelf Science* 67, 280-292.

- De Bello F, Thuiller W, Lepš J, Choler P, Clément J-C, Macek P, Sebastia M-T, Lavorel S (2009) Partitioning of functional diversity reveals the scale and extent of trait convergence and divergence. *Journal of Vegetation Science* 20, 475-486.
- De Bonte AJ, Boosten A, Van der Hagen HGJM, Sýkora KV (1999) Vegetation development influenced by grazing in the coastal dunes near The Hague, The Netherlands. *Journal of Coastal Conservation* 5, 59-68.
- De Stoppelaire GH, Gillespie TW, Brock JC, Tobin GA (2004) Use of remote sensing techniques to determine the effects of grazing on vegetation cover and dune elevation at Assateague Island National Seashore: impact of horses. *Environmental Management* 34, 642-649.
- De Vries MFW, Parkinson AE, Dulphy JP, Sayer M, Diana E (2007) Effects of livestock breed and grazing intensity on biodiversity and production in grazing systems. 4. Effects on animal diversity. *Grass and Forage Science* 62, 185-197.
- Dekker LW, Jungerius PD (1990) Water repellency in the dunes with special reference to The Netherlands. *Catena, Suppl.* 18, 173-183.
- Delibes-Mateos M, Ferreras P, Villafuerte R (2008) Rabbit populations and game management: the situation after 15 years of rabbit haemorrhagic disease in central-southern Spain. *Biodiversity and Conservation* 17, 559-574.
- Dellafiore CM, Gallego Fernández JB, Muñoz Vallés S (2008) Habitat use for warren building by European rabbits (*Oryctolagus cuniculus*) in relation to landscape structure in a sand dune system. *Acta Oecologia* 33, 372-379.
- Dengler J (2009) Which function describes the species-area relationship best? A review and empirical evaluation. *Journal of Biogeography* 36, 728-244.
- Denslow JS (1980) Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46, 18-21.
- Denslow JS (1985) Disturbance mediated coexistence of species. In: Pickett STA, White PS (eds.) *The ecology of natural disturbance and patch dynamics*. Academic Press, New York. pp. 261-284.
- Deutschewitz K, Lausch A, Kühn I, Klotz S (2003) Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. *Global Ecology & Biogeography* 12, 299-311.
- Diamond JM (1976) Island biogeography and conservation: strategy and limitations. *Science* 193, 1027-1029.
- Díaz S, Cabido M (1997) Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science* 8, 463-474.
- Diaz Barradas MC, Garcia Novo F (1987) The vertical structure of Mediterranean scrub in Doñana National Park (SW Spain). *Folia Geobotanica et Phytotaxonomica* 22, 415-433.
- Dierschke H (1994) *Pflanzensoziologie*. UTB Ulmer, Stuttgart.
- Dijkema KS, Doing H, Van der Maarel E (1993) Dry coastal ecosystems of the Danish, German and Dutch Wadden Islands. In: Van der Maarel E (ed.) *Ecosystems of the world. Dry coastal ecosystems*. Vol. 2 A. Polar regions and Europe. pp. 245-269.
- Dobson AP, Rodriguez JP, Roberts WM, Wilcove DS (1997) Geographic distribution of endangered species in the United States. *Science* 275, 550-553.

- Doing H (1985) Coastal fore-dune zonation and succession in various parts of the world. *Vegetatio* 61, 65-75.
- Doody JP (1989) Conservation and development of the coastal dunes in Great Britain. In: Van der Meulen F, Jungerius PD, Visser JH (eds.) *Perspectives in coastal dune management*. SPB Academic Publishing, Den Haag. pp. 53-67.
- Doody JP (2001) *Coastal conservation and management: an ecological perspective*. Conservation Biology Series 13. Kluwer Academic Publishers, Boston, USA.
- Drake JA, Mooney HA, Di Castri F, Groves RH, Kruger FJ, Rejmánek M, Williamson M (1989) *Biological invasions: a global perspective*. *Scope* 37. Wiley, Chichester.
- Drees M (2004) Epidemieën onder wilde konijnen en de gevolgen. *Vakblad natuur bos landschap* 1, 9-11.
- Drees M (2007) Komt het nog goed met het konijn? *Vakblad natuur bos landschap* 4, 7-10.
- Duelli P, Obrist MK (2003) Biodiversity indicators: the choice of values and measures. *Agriculture, Ecosystems and Environment* 98, 87-98.
- Duffy JE, Bradley JC, France KE, McIntyre PB, Thébault E, Loreau M (2007) The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10, 522-538.
- Dufour A, Gadallah F, Wagner HH, Guisan A, Buttler A (2006) Plant species richness and environmental heterogeneity in a mountain landscape: effects of variability and spatial configuration. *Ecography* 29, 573-584.
- Düll R (1991) Zeigerwerte von Laub- und Lebermoosen. In: Ellenberg H, Weber HE, Düll RPG, Wirth V, Werner W, Paulissen D (eds.) *Zeigerwerte von Pflanzen in Mitteleuropa*. *Scripta Geobotanica* 18. Erich Goltze, Göttingen. pp. 175-214.
- Dumont B, Farruggia A, Garel J-P, Bachelard P, Boitier E, Frain M (2009) How does grazing intensity influence the diversity of plants and insects in a species-rich upland grassland on basalt soils? *Grass and Forage Science* 64, 92-105.
- Dunn RR, McCain CM, Sanders NJ (2007) When does diversity fit null model predictions? Scale and range size mediate the mid-domain effect. *Global Ecology and Biogeography* 16, 305-312.
- Dunwiddie PW (1997) Long-term effects of sheep grazing on coastal sandplain vegetation. *Natural Areas Journal* 17, 261-264.
- Durrett R, Levin S (1996) Spatial models for species-area curves. *Journal of Theoretical Biology* 179, 119-127.
- Dybzinski R, Fargione JE, Zak DR, Fornara D, Tilman D (2008) Soil fertility increases with plant species diversity in a long-term biodiversity experiment. *Oecologia* 158, 85-93.
- Dymond C, Carver S, Phillips O (2003) Investigating the environmental cause of global wilderness and species richness distributions. *USDA Forest Service Proceedings* 27, 231-237.
- El-Keblawy A, Ksiksi T, El Alqamy H (2009) Camel grazing affects species diversity and community structure in the deserts of the UAE. *Journal of Arid Environments* 73, 347-354.
- Elton CS (1958) *The ecology of invasions by animals and plants*. Chapman & Hall, London.

- Erfmeier A, Bruelheide H (2004) Comparison of native and invasive *Rhododendron ponticum* populations: growth, reproduction and morphology under field conditions. *Flora* 199, 120-133.
- Ewers RM, Didham RK, Wratten SD, Tylianakis JM (2005) Remotely sensed landscape heterogeneity as a rapid tool for assessing local biodiversity value in a highly modified New Zealand landscape. *Biodiversity and Conservation* 14, 1469-1485.
- Fargione JE, Brown CS, Tilman D (2003) Community assembly and invasion: an experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences of the United States of America* 22, 8916-8920.
- Fargione JE, Tilman D (2005) Diversity decreases invasion via both sampling and complementarity effects. *Ecology Letters* 8, 604-611.
- Farrow EP (1917) On the ecology of the vegetation of Breckland. III. General effects of rabbits on the vegetation. *Journal of Ecology* 5, 1-18.
- Feagin RA (2005) Heterogeneity versus homogeneity: a conceptual and mathematical theory in terms of scale-invariant and scale-covariant distributions. *Ecological Complexity* 2, 339-356.
- Ferreira SM, Van Aarde RJ (2000) Maintaining diversity through intermediate disturbances: evidence from rodents colonizing rehabilitating coastal dunes. *African Journal of Ecology* 38, 286-294.
- Field R, Hawkins BA, Cornell HV, Currie DJ, Diniz-Filho AF, Guégan J-F, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Turner JRG (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography* 36, 132-147.
- Fischer AG (1960) Latitudinal variations in organic diversity. *Evolution* 14, 64-81.
- Flynn DFB, Gogol-Prokurat M, Nogeire T, Molinari N, Trautman Richers B, Lin BB, Simpson N, Mayfield MM, DeClerck F (2009) Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* 12, 22-33.
- Fojcik B, Stebel A (1999) Preliminary studies on the bryoflora of Katowice town (Silesian Upland, Southern Poland). *Fragmenta Floristica et Geobotanica* 44, 129-140.
- Forest F, Grenyer R, Rouget M, Davies TJ, Cowling RM, Faith DP, Balmford A, Manning JC, Procheş S, Van der Bank M, Reeves G, Hedderson TAJ, Savolainen V (2007) Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* 445, 757-760.
- Fosaa AM (2004) Biodiversity patterns of vascular plant species in mountain vegetation in the Faroe Islands. *Diversity and Distributions* 10, 217-223.
- Foster BL, Tilman D (2000) Dynamic and static views of succession: testing the descriptive power of the chronosequence approach. *Plant Ecology* 146, 1-10.
- Frahm J-P (2001) *Biologie der Moose*. Spektrum Verlag, Berlin.
- Frahm J-P (2008) Diversity, dispersal and biogeography of bryophytes (mosses). *Biodiversity and Conservation* 17, 277-284.
- Francis AP, Currie DJ (2003) A globally consistent richness-climate relationship for angiosperms. *American Naturalist* 161, 523-536.
- Franks SJ (2003) Facilitation in multiple life-history stages: evidence for nucleated succession in coastal dunes. *Plant Ecology* 168, 1-11.

- Franks SJ, Peterson CJ (2003) Burial disturbance leads to facilitation among coastal dune plants. *Plant Ecology* 168, 13-21.
- Fretwell SD, Lucas HL (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19, 16-36.
- Fridley JD (2002) Resource availability dominates and alters the relationship between species diversity and ecosystem productivity in experimental plant communities. *Oecologia* 132, 271-277.
- Fridley JD, Peet RK, Wentworth TR, White PS (2005) Connecting fine- and broad-scale species-area relationships of Southeastern U.S. flora. *Ecology* 86, 1172-1177.
- Fridley JD, Vandermast DB, Kuppinger DM, Manthey M, Peet RK (2007) Co-occurrence based assessment of habitat generalists and specialists: a new approach for the measurement of niche width. *Journal of Ecology* 95, 707-722.
- Fuller RM, Boorman LA (1977) The spread and development of *Rhododendron ponticum* L. on dunes at Winterton, Norfolk, in comparison with invasion by *Hippophaë rhamnoides* L. at Saltfleetby, Lincolnshire. *Biological Conservation* 12, 83-94.
- Futamura C W, Wheelwright NT (2000) The mosses of Kent Island, New Brunswick. *Northeastern Naturalist* 7, 277-288.
- García-Mora MR, Gallego-Fernández JB, García-Novo F (1999) Plant functional types in coastal foredunes in relation to environmental stress and disturbance. *Journal of Vegetation Science* 10, 27-34.
- Garve E (2007) Verbreitungsatlas der Farn- und Blütenpflanzen in Niedersachsen und Bremen. *Naturschutz und Landschaftspflege Niedersachsen* 43, 1-507.
- Gaston KJ (1996) Species-range-size distributions: patterns, mechanisms and implications. *Trends in Ecology & Evolution* 11, 197-201.
- Gaston KJ (2000) Global patterns in biodiversity. *Nature* 405, 220-227.
- Gaston KJ, Spicer JI (2004) *Biodiversity: an introduction*. Blackwell, Malden, Massachusetts.
- Geertsema W, Sprangers JTCM (2002) Plant distribution patterns related to species characteristics and spatial and temporal habitat heterogeneity in a network of ditch banks. *Plant Ecology* 162, 91-108.
- Gentry AH (1982) Patterns of neotropical plant species diversity. *Evolutionary Biology* 15, 1-84.
- Gentry AH (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75, 1-34.
- Gerlach A, Albers EA, Broedlin W (1994) Development of the nitrogen cycle in the soils of a coastal dune succession. *Acta Botanica Neerlandica* 43, 189-203.
- Gibson CWD, Brown VK (1991) The effects of grazing on local colonisation and extinction during early succession. *Journal of Vegetation Science* 2, 291-300.
- Gibson DJ (1988) The maintenance of plant and soil heterogeneity in dune grassland. *Journal of Ecology* 76, 497-508.
- Gibson DJ, Greig-Smith P (1986) Community pattern analysis: a method for quantifying community mosaic structure. *Vegetatio* 66, 41-47.
- Giesler R, Högberg M, Högberg P (1998) Soil chemistry and plants in Fennoscandian boreal forest as exemplified by a local gradient. *Ecology* 79, 119-137.

- Gimaret-Carpentier C, Pélissier R, Pascal J-P, Houllier F (1998) Sampling strategies for the assessment of tree species diversity. *Journal of Vegetation Science* 9, 161-172.
- Gitay H, Roxburgh SH, Wilson JB (1991) Species-area relations in a New Zealand tussock grassland, with implications for nature reserve design and for community structure. *Journal of Vegetation Science* 2, 113-118.
- Gleason HA (1922) On the relation between species and area. *Ecology* 3, 158-162.
- Glitzenstein JS, Harcombe PA, Steng DR (1986) Disturbance, succession, and maintenance of species diversity in an East Texas forest. *Ecological Monographs* 56, 243-258.
- Goderya FS (1998) Field scale variations in soil properties for spatially variable control: a review. *Soil and Sediment Contamination* 7, 243-264.
- Godfray HCJ, Lawton JH (2001) Scale and species numbers. *Trends in Ecology & Evolution* 16, 400-404.
- Goldberg DE, Estabrook GF (1998) Separating the effects of number of individuals sampled and competition on species diversity: an experimental and analytic approach. *Journal of Ecology* 86, 983-988.
- Goldberg DE, Miller TE (1990) Effects of different resource additions on species diversity in an annual plant community. *Ecology* 71, 213-225.
- González-Megías A, Gómez JM, Sánchez-Pinero F (2007) Diversity-habitat heterogeneity relationship at different spatial and temporal scales. *Ecography* 30, 31-41.
- Good IJ (1953) The population frequencies of species and the estimation of population parameters. *Biometrika* 40, 237-264.
- Gorelick R (2006) Combining richness and abundance into a single diversity index using matrix analogues of Shannon's and Simpson's indices. *Ecography* 29, 525-530.
- Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4, 379-391.
- Gough L, Shaver GR, Carroll J, Royer DL, Laundre JA (2000) Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH. *Journal of Ecology* 88, 54-66.
- Grace JB (1999) The factors controlling species density in herbaceous plant communities: an assessment. *Perspectives in Plant Ecology, Evolution and Systematics* 2, 1-28.
- Greig-Smith P (1964) *Quantitative plant ecology*. Butterworth, London.
- Greig-Smith P (1979) *Pattern in vegetation*. *Journal of Ecology* 67, 755-779.
- Grime JP (1973) Control of species density in herbaceous vegetation. *Journal of Environmental Management* 1, 151-167.
- Grime JP (1974) Vegetation classification by reference to strategies. *Nature* 250, 26-31.
- Grime JP (1979) *Plant strategies and vegetation processes*. Wiley, Chichester.
- Gross KL, Willig MR, Gough L, Inouye R, Cox SB (2000) Patterns of species density and productivity at different spatial scales in herbaceous plant communities. *Oikos* 89, 417-427.
- Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52, 107-145.
- Grytnes JA (2003) Ecological interpretations of the mid-domain effect. *Ecology Letters* 6, 883-888.

- Grytnes JA, Birks HJB (2003) The influence of scale and species pool on the relationship between vascular plant species richness and cover in an alpine area in Norway. *Plant Ecology* 169, 273-284.
- Grytnes JA, Vetaas OR (2002) Species richness and altitude: a comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *American Naturalist* 159, 294-304.
- Hamilton AC (1975) A quantitative analysis of altitudinal zonation in Uganda forests. *Vegetatio* 30, 99-106.
- Hamilton TH, Rubinoff I, Barth RH (1963) Species abundance: natural regulation of insular variation. *Science* 142, 1575-1577.
- Harcourt AH (2000) Latitude and latitudinal extent: a global analysis of the Rapoport effect in a tropical mammalian taxon: primates. *Journal of Biogeography* 27, 1169-1182.
- Harding PT, Sheail J (1992) The Biological Records Centre a pioneer in data gathering and retrieval. In: Harding PT (ed.) *Biological recording of changes in British wildlife* HMSO, London. pp. 5-19.
- Harner RF, Harper KT (1976) The role of area, heterogeneity, and favorability in plant species diversity of Pinyon-Juniper ecosystems. *Ecology* 57, 1254-1263.
- Harper JL (1977) *Population biology of plants*. Academic Press, London.
- Harrison S, Davies KF, Safford HD, Viers JH (2006) Beta diversity and the scale-dependence of the productivity-diversity relationship: a test in the Californian serpentine flora. *Journal of Ecology* 94, 110-117.
- Harrison S, Ross SJ, Lawton JH (1992) Beta diversity on geographic gradients in Britain. *Journal of Animal Ecology* 61, 151-158.
- Hart RH (2001) Plant biodiversity on shortgrass steppe after 55 years of zero, light, moderate, or heavy cattle grazing. *Plant Ecology* 155, 111-118.
- Harte J, McCarthy S, Taylor K, Kinzig A, Fischer ML (1999) Estimating species-area relationships from plot to landscape scale using species spatial-turnover data. *Oikos* 86, 45-54.
- Hatton TJ, Carpenter AT (1986) An empirical test of the mass effect determinant of species richness. *Vegetatio* 68, 33-36.
- Hausdorf B (2006) Latitudinal and altitudinal diversity patterns and Rapoport effects in north-west European land snails and their causes. *Biological Journal of the Linnean Society* 87, 309-323.
- Hawkins BA, Diniz-Filho JAF, Weis AE (2005) The mid-domain effect and diversity gradients: is there anything to learn? *American Naturalist* 166, E140-E143.
- He F, Legendre P (1996) On species-area relations. *American Naturalist* 148, 719-737.
- Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, Höglberg P, Huss-Danell K, Joshi J, Jumpponen A, Körner C, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Pereira JS, Prinz A, Read DJ, Scherer-Lorenzen M, Schulze E-D, Siamantziouras A-S D, Spehn EM, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH (1999) Plant diversity and productivity experiments in European grasslands. *Science* 286, 1123-1127.

- Heegard E (2000) Patch dynamics and/or species-environmental relationship in conservation bryology. *Lindbergia* 25, 85-88.
- Herbert DA, Rastetter EB, Gough L, Shaver GR (2004) Species diversity across nutrient gradients: an analysis of resource competition in model ecosystems. *Ecosystems* 7, 296-310.
- Hermý M, Cornelis J (2000) Towards a monitoring method and a number of multifaceted and hierarchical biodiversity indicators for urban and suburban parks. *Landscape and Urban Planning* 49, 149-162.
- Hernández HM, Gómez-Hinostrosa C, Bárcenas RT (2001) Diversity, spatial arrangement, and endemism of Cactaceae in the Huizache area, a hot-spot in the Chihuahuan Desert. *Biodiversity and Conservation* 10, 1097-1112.
- Hester MW, Wilsey BJ, Mendelsohn IA (1994) Grazing of *Panicum amarum* in a Louisiana barrier island dune plant community: management implications for dune restoration projects. *Ocean and Coastal Management* 23, 213-224.
- Hobohm C (2005) Die Erforschung der Artenvielfalt in Pflanzengesellschaften - eine Zwischenbilanz. *Tuexenia* 25, 7-28.
- Hodgkin SE (1984) Scrub encroachment and its effects on soil fertility on Newborough Warren, Anglesey, Wales. *Biological Conservation* 29, 99-119.
- Hofer G, Wagner HH, Herzog F, Edwards PJ (2008) Effects of topographic variability on the scaling of plant species richness in gradient dominated landscapes. *Ecography* 31, 131-139.
- Hohenwallner D, Zechmeister HG (2001) Factors influencing bryophyte species richness and populations in urban environments: a case study. *Nova Hedwigia* 73, 87-96.
- Holt RD (1993) Ecology at the mesoscale: the influence of regional processes on local communities. In: Ricklefs RE, Schluter D (eds.) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, IL. pp. 77-88.
- Hooper DU, Chapin III FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75, 3-35.
- Hooper DU, Solan M, Symstad A, Díaz S, Gessner MO, Buchmann N, Degrange V, Grime P, Hulot F, Mermillod-Blondin F, Roy J, Spehn E, Van Peer L (2002) Species diversity, functional diversity, and ecosystem functioning. In: Loreau M, Naeem S, Inchausti P (eds.) *Biodiversity and Ecosystem functioning. Synthesis and perspectives*. Oxford University Press. pp. 195-281.
- Hooper DU, Vitousek PM (1997) The effects of plant composition and diversity on ecosystem processes. *Science* 277, 1302-1305.
- Hopkins B (1955) The species-area relations of plant communities. *Journal of Ecology* 43, 409-426.
- Hortal J, Jiménez-Valverde A, Gómez JF, Lobo JM, Baselga A (2008) Historical bias in biodiversity inventories affects the observed environmental niche of the species. *Oikos* 117, 847-858.
- Houssard C, Escarré J, Romane F (1980) Development of species diversity in some Mediterranean plant communities. *Vegetatio* 43, 59-72.

- Huber R (1994) Changes in plant species richness in a calcareous grassland following changes in environmental conditions. *Folia Geobotanica* 29, 469-482.
- Huber R (1999) Patterns of species richness in a limestone grassland under different treatments in relation to spatial scale. *Applied Vegetation Science* 2, 257-266.
- Hughes AR, Byrnes JE, Kimbro DL, Stachowicz JJ (2007) Reciprocal relationships and potential feedbacks between biodiversity and disturbance. *Ecology Letters* 10, 849-864.
- Hurlbert SH (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52, 577-586.
- Huston M (1979) A general hypothesis of species diversity. *American Naturalist* 113, 81-101.
- Huston MA (1994) *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, New York.
- Hutchinson GE (1953) The concept of pattern in ecology. *Proceedings of the Academy of Natural Sciences of Philadelphia* 105, 1-12.
- Hutchinson GE (1957) Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology* 22, 415-427.
- Hutchinson GE (1959) Homage to Santa Rosalia; or, why are there so many kinds of animals. *American Naturalist* 93, 145-159.
- Hutchinson GE (1961) The paradox of the plankton. *American Naturalist* 95, 137-145.
- Hylander K, Jonsson GG (2007) The conservation ecology of cryptogams. *Biological Conservation* 135, 311-314.
- Ievinsh G (2006) Biological basis of biological diversity: physiological adaptations of plants to heterogeneous habitats along a sea coast. *Acta Universitatis Latviensis* 710, 53-79.
- Ikeda H (2003) Testing the intermediate disturbance hypothesis on species diversity in herbaceous plant communities along a human trampling gradient using a 4-year experiment in an old-field. *Ecological Research* 18, 185-197.
- Isermann M (1998) Synchorologische Aspekte des Elymo-Ammophiletum festucetosum entlang der Küste Vorpommerns. *Natur und Naturschutz in Mecklenburg-Vorpommern* 99, 106-112.
- Isermann M (1999) Zur Gefährdung von Pflanzenarten und deren Habitate in Küstendünen Mecklenburg-Vorpommerns. *Abhandlungen des Naturwissenschaftlichen Vereins Bremen* 44, 511-521.
- Isermann M (2004) *Cakiletea maritimae*. In: Berg C, Dengler J, Abdank A, Isermann M (eds.) *Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung*. Textband. Weissdorn-Verlag, Jena. pp. 246-256.
- Isermann M (2008) Effects of *Rosa rugosa* invasion in different coastal dune vegetation types. In: Tokarska-Guzik B, Brock J-H, Brundu G, Child L, Daehler CC, Pyšek P (eds.) *Plant Invasions: human perception, ecological impacts and management*. Backhuys Publishers, Leiden. pp. 289-306.
- Isermann M, Cordes H (1992) Changes in dune vegetation on Spiekeroog (East Friesian Islands) over a 30 year period. In: Carter RWG, Curtis TGF, Sheehy-Skeffington MJ (eds.) *Coastal dunes*. Balkema, Rotterdam, Brookfield. pp. 201-209.
- Isermann M, Friedrichs L, Grave C, Wagner A (2005) Species richness in Sea-Buckthorn scrub. In: Herrier J-L, Mees J, Salman AHPM, Van Nieuwenhuysse H, Dobbelaere I

- (eds.) Dunes and Estuaries. Nature restoration practices in European coastal habitats. Koksijde, Belgium. pp. 597-600.
- Isermann M, Krisch H (1995) Dunes in contradiction with different interests. An example: the camping ground Prerow (Darß/Baltic Sea). In: Salman AHPM, Berends H, Bonazountas M (eds.) Coastal management and habitat conservation. Marathon, Greece. pp. 439-449.
- Izsák J, Papp L (2000) A link between ecological diversity indices and measures of biodiversity. *Ecological Modelling* 130, 151-156.
- Jaccard P (1902) Gesetze der Pflanzenverbreitung in der alpinen Region. Auf Grund statistisch-floristischer Untersuchungen. *Flora* 90, 349-377.
- Jackson RB, Caldwell MM (1989) The timing and degree of root proliferation in fertile-soil microsites for three cold-desert perennials. *Oecologia* 81, 149-153.
- Jackson RB, Caldwell MM (1993) Geostatistical patterns of soil heterogeneity around individual perennial plants. *Journal of Ecology* 81, 683-692.
- Jackson RB, Caldwell MM (1996) Integrating resource heterogeneity and plant plasticity: modelling nitrate and phosphate uptake in a patchy soil environment. *Journal of Ecology* 84, 891-903.
- Jankowski JE, Ciecka AL, Meyer NY, Rabenold KN (2009) Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes. *Journal of Animal Ecology* 78, 315-327.
- Janzen DH (1973) Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* 54, 687-708.
- Jennings MD, Hoekstra J, Higgins J, Boucher T (2008) A comparative measure of biodiversity based on species composition. *Biodiversity and Conservation* 17, 833-840.
- Jennings MD, Williams JW, Stromberg MR (2005) Diversity and productivity of plant communities across the Inland Northwest, USA. *Oecologia* 143, 607-618.
- Jentsch A, Friedrich S, Beyschlag W, Nezadal W (2002) Significance of ant and rabbit disturbances for seedling establishment in dry acidic grasslands dominated by *Corynephorus canescens*. *Phytocoenologia* 32, 553-580.
- Ji S, Geng Y, Li D, Wang G (2009) Plant coverage is more important than species richness in enhancing aboveground biomass in a premature grassland, northern China. *Agriculture, Ecosystems and Environment* 129, 491-496.
- Jiang L, Pu Z, Nemergut DR (2008) On the importance of the negative selection effect for the relationship between biodiversity and ecosystem functioning. *Oikos* 117, 488-493.
- Jiménez I, Distler T, Jørgensen PM (2009) Estimated plant richness pattern across northwest South America provides similar support for the species-energy and spatial heterogeneity hypotheses. *Ecography* 32, 433-448.
- Johnson MP, Raven PH (1973) Species number and endemism: the Galápagos Archipelago revisited. *Science* 179, 893-895.
- Johst K, Huth A (2005) Testing the intermediate disturbance hypothesis: when will there be two peaks of diversity? *Diversity and Distributions* 11, 111-120.
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69, 373-386.
- Jost L (2007) Partitioning diversity into independent alpha and beta components. *Ecology* 88, 2427-2439.

- Jungerius PD (1990) The characteristics of dune soils. *Catena* (Suppl.) 18, 155-162.
- Jungerius PD, De Jong JH (1989) Variability of water repellence in the dunes along the Dutch coast. *Catena* 16, 491-497.
- Jungerius PD, Van der Meulen F (1988) Erosion processes in a dune landscape along the Dutch coast. *Catena* 15, 217-228.
- Kadmon R, Pulliam HR (1993) Island biogeography: effect of geographical isolation on species composition. *Ecology* 74, 977-981.
- Kallimanis AS, Mazaris AD, Tzanopoulos J, Halley JM, Pantis JD, Sgardelis SP (2008) How does habitat diversity affect the species-area relationship? *Global Ecology and Biogeography* 17, 532-538.
- Kati V, Devillers P, Dufrière M, Legakis A, Vokou D, Lebrun P (2004) Hotspots, complementarity or representativeness? Designing optimal small-scale reserves for biodiversity conservation. *Biological Conservation* 120, 471-480.
- Keddy PA (1981) Experimental demography of the sand-dune annual, *Cakile edentula*, growing along an environmental gradient in Nova Scotia. *Journal of Ecology* 69, 615-630.
- Keddy PA (1982) Population ecology on an environmental gradient: *Cakile edentula* on a sand dune. *Oecologia* 52, 348-355.
- Keeley JE (2003) Relating species abundance distributions to species-area curves in two Mediterranean-type shrublands. *Diversity and Distributions* 9, 253-259.
- Keeley JE, Swift CC (1995) Biodiversity and ecosystem functioning in Mediterranean-climate California. In: Davis GW, Richardson DM (eds.) *Mediterranean-type ecosystems: the function of biodiversity*. Ecological studies 109. Springer, Berlin. pp. 121-183.
- Kempton RA (1979) The structure of species abundance and measurement of diversity. *Biometrics* 35, 307-321.
- Kempton RA, Wedderburn RWM (1978) A comparison of three measures of species diversity. *Biometrics* 34, 25-37.
- Kenkel NC, Juhász-Nagy P, Podani J (1989) On sampling procedures in population and community ecology. *Vegetatio* 83, 195-207.
- Kennedy TA, Naeem S, Howe KM, Knops JMH, Tilman D, Reich P (2002) Biodiversity as a barrier to ecological invasion. *Nature* 417, 636-638.
- Kerby JD, Fuhlendorf SD, Engle SM (2007) Landscape heterogeneity and fire behavior: scale-dependent feedback between fire and grazing processes. *Landscape Ecology* 22, 507-516.
- Kerr JT, Packer L (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature* 385, 252-254.
- Kerr JT, Perring M, Currie DJ (2006) The missing Madagascan mid-domain effect. *Ecology Letters* 9, 149-159.
- Kessler M (2009) The impact of population processes on patterns of species richness: lessons from elevation gradients. *Basic and Applied Ecology* 10, 295-299.
- Ketner-Oostra R, Van der Peijl MJ, Sýkora KV (2006) Restoration of lichen diversity in grass-dominated vegetation of coastal dunes after wildfire. *Journal of Vegetation Science* 17, 147-156.

- Kinzig AP, Pacala SW, Tilman D (eds.) (2001) The functional consequences of biodiversity. Empirical progress and theoretical extensions. Monographs in Population Biology 33. Princeton University Press, Princeton.
- Kitayama K (1992) An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio* 102, 149-171.
- Kliewe H (1951) Die Klimaregionen Mecklenburgs. Dissertation EMAU Greifswald.
- Klinkhamer PGL, De Jong TJ (1985) Shoot biomass and species richness in relation to some environmental factors in a coastal dune area in The Netherlands. *Vegetatio* 63, 129-132.
- Klotz S (1984) Die Gesellschaftsdiversität (Ökotoptdiversität) in urbanen Ökosystemen, dargestellt am Beispiel von Halle/Neustadt. *Ekológia* 3, 171-178.
- Kohn DD, Walsh DM (1994) Plant species richness - the effect of island size and habitat diversity. *Journal of Ecology* 82, 367-377.
- Kohyama T (1997) The role of architecture in enhancing plant species diversity. In: Abe T, Levin SA, Higashi M (eds.) *Biodiversity. An ecological perspective*. Springer. New York. pp. 21-33.
- Kollmann J, Frederiksen L, Vestergaard P, Bruun HH (2007) Limiting factors for seedling emergence and establishment of the invasive non-native *Rosa rugosa* in a coastal dune system. *Biological Invasions* 9, 31-42.
- Koperski M (1998) Die Moose der Stadt Delmenhorst und ihrer Umgebung. *Abhandlungen des Naturwissenschaftlichen Verein zu Bremen* 44, 185-204.
- Koperski M, Sauer M, Braun W, Gradstein SR (2000) Referenzliste der Moose Deutschlands. *Schriftenreihe für Vegetationskunde* 34, 1-519.
- Kramer J (1989) Kein Deich, kein Land, kein Leben. *Geschichte des Küstenschutzes an der Nordsee*. Rautenberg, Leer.
- Krauss J, Klein A-M, Steffan-Dewenter I, Tschardt T (2004) Effects of habitat area, isolation, and landscape diversity on plant species richness of calcareous grasslands. *Biodiversity and Conservation* 13, 1427-1439.
- Krisch H (1989) Analyse der Verbreitung von *Agropyron x obtusiusculum* Lange und *Lactuca tatarica* (L.) C. A. Meyer an der Ostseeküste der Deutschen Demokratischen Republik. *Flora* 183, 73-86.
- Krishnankutty N, Chandrasekaran S (2007) Biodiversity hotspots: defining the indefinable? *Current Science* 92, 1344-1345.
- Kruckeberg AR, Rabinowitz D (1985) Biological aspects of endemism in higher plants. *Annual Review of Ecology and Systematics* 16, 447-479.
- Kruger FJ, Taylor HC (1979) Plant species diversity in Cape fynbos: gamma and delta diversity. *Vegetatio* 41, 85-93.
- Kühn I, Brandl R, Klotz S (2004) The flora of German cities is naturally species rich. *Evolutionary Ecology Research* 6, 749-764.
- Kühne A (2006) Untersuchungen zur Abschätzung der Phytodiversität auf Landschaftsebene. Unpubl. Diploma Thesis, Bremen.
- Kuijper DPJ, Bakker JP (2005) Top-down control of small herbivores on salt-marsh vegetation along a productivity gradient. *Ecology* 86, 914-923.
- Kunin WE (1998) Extrapolating species abundance across spatial scales. *Science* 281, 1513-1515.

- Kutiel P, Danin A (1987) Annual-species diversity and aboveground phytomass in relation to some soil properties in the sand dunes of the northern Sharon Plains, Israel. *Vegetatio* 70, 45-49.
- Kutiel P, Eden E, Zhevelev Y (2000) Effect of experimental trampling and off-road motorcycle traffic on soil and vegetation of stabilized coastal dunes, Israel. *Environmental Conservation* 27, 14-23.
- Laanisto L, Urbas P, Pärtel M (2008) Why does the unimodal species richness-productivity relationship not apply to woody species: a lack of clonality or a legacy of tropical evolutionary history? *Global Ecology and Biogeography* 17, 320-326.
- Lájer K (2007) Statistical tests as inappropriate tools for data analysis performed on non-random samples of plant communities. *Folia Geobotanica* 42, 115-122.
- Lamoot I, Callebaut J, Demeulenaere E, Vandenberghe Ch, Hoffmann M (2005) Foraging behaviour of donkeys grazing in a coastal dune area in temperate climate conditions. *Applied Animal Behaviour Science* 92, 93-112.
- Latimer AM, Silander JA, Cowling RM (2005) Neutral ecological theory reveals isolation and rapid speciation in a biodiversity hot spot. *Science* 309, 1722-1725.
- Laughlin DC, Moore MM (2009) Climate-induced temporal variation in the productivity-diversity relationship. *Oikos* 118, 897-902.
- Lawton JH (1994) What do species do in ecosystems? *Oikos* 71, 367-274.
- Lawton JH (2000) Biodiversity and ecosystem processes: theory, achievements and future directions. In: Kato M (ed.) *The biology of biodiversity*. Springer, Berlin. pp. 119-131.
- Legendre P, Borcard D, Peres-Neto PR (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs* 75, 435-450.
- Lehman CL, Tilman D (2000) Biodiversity, stability, and productivity in competitive communities. *American Naturalist* 156, 534-552.
- Lemauviel S, Gallet S, Rozé F (2003) Sustainable management of fixed dunes: example of a pilot site in Brittany (France). *Comptes Rendus Biologies* 326, 183-191.
- Lemauviel S, Rozé F (2003) Response of three plant communities to trampling in a sand dune system in Brittany (France). *Environmental Management* 31, 227-235.
- Lennon JJ, Koleff P, Greenwood JJD, Gaston KJ (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* 70, 966-979.
- Leser H, Nagel P (1998) Landscape diversity – a holistic approach. In: Barthlott W, Winiger M (eds.) *Biodiversity. A challenge for development research and policy*. Springer, Berlin. pp. 129-143.
- Lévêque C, Mounolou J-C (2004) *Biodiversity*. Wiley, Chichester.
- Levin SA (1974) Dispersion and population interactions. *American Naturalist* 108, 207-228.
- Levin SA (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* 73, 1943-1967.
- Li J, Loneragan WA, Duggin JA, Grant CD (2004) Issues affecting the measurement of disturbance response patterns in herbaceous vegetation. A test of the intermediate disturbance hypothesis. *Plant Ecology* 172, 11-26.
- Lichter J (1998) Primary succession and forest development on coastal Lake Michigan sand dunes. *Ecological Monographs* 68, 487-510.

- Liddle MJ (1975) A theoretical relationship between the primary productivity of vegetation and its ability to tolerate trampling. *Biological Conservation* 8, 251-255.
- Lieberman D, Lieberman M, Peralta R, Hartshorn GS (1996) Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology* 84, 137-152.
- Lindenmayer DB (1999) Future directions for biodiversity conservation in managed forests: indicator species, impact studies and monitoring programs. *Forest Ecology and Management* 115, 277-287.
- Linder HP (1991) Environmental correlates of patterns of species richness in the southwestern Cape Province of South Africa. *Journal of Biogeography* 18, 509-518.
- Liu H-D, Yu F-H, He W-M, Chu Y, Dong M (2007) Are clonal plants more tolerant to grazing than co-occurring non-clonal plants in inland dunes? *Ecological Research* 22, 502-506.
- Lloyd M, Ghelardi RJ (1964) A table for calculating the "equitability" component of species diversity. *Journal Animal Ecology* 33, 217-225.
- Lobo JM (2008) Database records as a surrogate for sampling effort provide higher species richness estimations. *Biodiversity and Conservation* 17, 873-881.
- Lockwood JL, Hoopes MF, Marchetti MP (2008) *Invasion Ecology*. Blackwell, Oxford.
- Lomolino MV (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography* 10, 3-13.
- Lonsdale WM (1988) Predicting the amount of litterfall in forests of the world. *Annals of Botany* 61, 319-324.
- Loreau M (2000) Are communities saturated? On the relationship between  $\alpha$ ,  $\beta$  and  $\gamma$  diversity. *Ecology Letters* 3, 73-76.
- Loreau M, Mouquet N, Gonzalez A (2003) Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences of the United States of America* 100, 12765-12770.
- Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294, 804-808.
- Lotka AJ (1925) *Elements of physical biology*. Williams & Wilkins, Baltimore.
- Lovrić AŽ (1997) Origin and evolution of dry coastal ecosystems. Van der Maarel E (ed.) *Ecosystems of the world. Vol. 2C. Dry coastal ecosystems. General aspects*. Elsevier, Amsterdam. pp. 127-144.
- Lughadha EN, Baillie J, Barthlott W, Brummitt NA, Cheek MR, Farjon A, Govaerts R, Hardwick KA, Hilton-Taylor C, Meagher TR, Moat J, Mutke J, Paton AJ, Pleasants LJ, Savolainen V, Schatz GE, Smith P, Turner I, Wyse-Jackson P, Crane PR (2005) Measuring the fate of plant diversity: towards a foundation for future monitoring and opportunities for urgent action. *Philosophical Transactions of the Royal Society B* 360, 359-372.
- Lundholm JT (2009) Plant species diversity and environmental heterogeneity: spatial scale and competing hypotheses. *Journal of Vegetation Science* 20, 377-391.
- Lundholm JT, Larson DW (2003) Relationships between spatial environmental heterogeneity and plant species diversity on a limestone pavement. *Ecography* 26, 715-722.

- Lyons SK, Willig MR (2002) Species richness, latitude, and scale-sensitivity. *Ecology* 83, 47-58.
- Ma M (2005) Species richness vs evenness: independent relationship and different responses to edaphic factors. *Oikos* 111, 192-198.
- MacArthur RH (1955) Fluctuations of animal populations and a measure of community stability. *Ecology* 36, 533-536.
- MacArthur RH (1965) Patterns of species diversity. *Biological Reviews* 40, 510-533.
- MacArthur RH (1970) Species packing and competitive equilibrium for many species. *Theoretical Population Biology* 1, 1-11.
- MacArthur RH, Levins R (1967) The limiting similarity, convergence and divergence of coexisting species. *American Naturalist* 101, 377-385.
- MacArthur RH, Wilson EO (1963) An equilibrium theory of insular zoogeography. *Evolution* 17, 373-387.
- MacArthur RH, Wilson EO (1967) *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey.
- Magurran AE (2006) *Measuring biological diversity*. Blackwell, Oxford.
- Magurran AE, May RM (1999) *Evolution of biological diversity*. Oxford University Press, Oxford.
- Major J (1988) Endemism: a botanical perspective. In: Myers AA, Giller PS (eds.) *Analytical biogeography: an integrated approach to the study of animal and plant distributions*. Chapman & Hall, London. pp. 117-146.
- Margalef DF (1958) Information theory in ecology. *General Systems* 3, 36-71.
- Margalef R (1963) On certain unifying principles in ecology. *American Naturalist* 97, 357-374.
- Margalef R (1968) *Perspectives in ecological theory*. Chicago University Press, Chicago, London.
- Martín MA, Rey J-M (2000) On the role of Shannon's entropy as a measure of heterogeneity. *Geoderma* 98, 1-3.
- Martin TE (1981) Species-area slopes and coefficients: a caution on their interpretation. *American Naturalist* 118, 823-837.
- Martínez ML (2003) Facilitation of seedling establishment by an endemic shrub in tropical coastal dunes. *Plant Ecology* 168, 333-345.
- Mason NWH, MacGillivray K, Steel JB, Wilson JB (2003) An index of functional diversity. *Journal of Vegetation Science* 14, 571-578.
- Mason NWH, Mouillot D, Lee WG, Wilson B (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111, 112-118.
- May RM (1988) How many species are there on earth? *Science* 241, 1441-1449.
- May RM (1990) How many species? *Philosophical Transactions of the Royal Society B* 330, 293-304.
- May RM, MacArthur RH (1972) Niche overlap as a function of environmental variability. *Proceedings of the National Academy of Sciences* 69, 1109-1113.
- Mazurek H, Romane F (1986) Dynamics of young *Pinus pinaster* vegetation in a Mediterranean area: diversity and niche-strategy. *Vegetatio* 66, 27-40.

- McCain CM (2004) The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *Journal of Biogeography* 31, 19-31.
- McDonald DJ, Juritz JM, Cowling RM, Knottenbelt WJ (1995) Modelling the biological aspects of local endemism in South African Fynbos. *Plant Systematics and Evolution* 195, 137-147.
- McDonnell MJ (1981) Trampling effects on coastal dune vegetation in the Parker River National Wildlife Refuge, Massachusetts, USA. *Biological Conservation* 21, 289-301.
- McIntosh RP (1976) An index of diversity and the relation of certain concepts to diversity. *Ecology* 48, 392-404.
- McKane RB, Johnson LC, Shaver GR, Nadelhoffer KJ, Rastetter EB, Fry B, Giblin AE, Kielland K, Kwiatkowski BL, Laundre JA, Murray G (2002) Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature* 415, 68-71.
- McKinney ML (2002) Why larger nations have disproportionate threat rates: area increases endemism and human population size. *Biodiversity and Conservation* 11, 1317-1325.
- Mennema J, Weeda E (1983) Vascular plants. In: Dijkema KS, Wolf WJ (eds.) *Flora and vegetation of the Wadden Sea islands and coastal areas*. Report 9 Wadden Sea Working Group. Balkema, Rotterdam. pp. 38-50.
- Milchunas DG, Lauenroth WK (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63, 327-366.
- Milchunas DG, Sala OE, Lauenroth WK (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* 132, 87-106.
- Moles R, Hayes K (2002) Evaluating biodiversity through functional groups: a comparison of functional groups and biodiversity measures. *Proceedings of the Royal Irish Academy B* 102, 113-117.
- Molino J-F, Sabatier D (2001) Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science* 294, 1702-1704.
- Mooney HA, Cushman JH, Medina E, Sala OE, Schulze E.-D (eds.) (1996) *Functional roles of biodiversity. A global perspective*. Wiley, Chichester.
- Morales MA, Dodge GJ, Inouye DW (2005) A phenological mid-domain effect in flowering diversity. *Oecologia* 142, 83-89.
- Morand S (2000) Geographic distance and the role of island area and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups: a complementary note to Ricklefs & Lovette. *Journal of Animal Ecology* 69, 1117-1119.
- Moreno C, Zuria I, García-Zenteno M, Sánchez-Rojas G, Castellanos I, Martínez-Morales M, Rojas-Martínez A (2006) Trends in the measurement of alpha diversity in the last two decades. *Interciencia* 31, 67-71.
- Mouillot D, Masin WHN, Dumay O, Wilson JB (2005) Functional regularity: a neglected aspect of functional diversity. *Oecologia* 142, 353-359.
- Mumby PJ (2001) Beta and habitat diversity in marine systems: a new approach to measurement, scaling and interpretation. *Oecologia* 128, 274-280.
- Mutke J, Barthlott W (2005) Patterns of vascular plant diversity at continental to global scales. *Biologische Skrifter* 55, 521-531.

- Myers AA, Giller PS (1988) Analytical biogeography. An integrated approach to the study of animal and plant distributions. Chapman & Hall, London.
- Myers N (1990) The biodiversity challenge: Expanded hot-spot analysis. *The Environmentalist* 10, 243-256.
- Myers N (2003) Biodiversity hotspots revisited. *BioScience* 53, 916-917.
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403, 853-858.
- Naeem S (1998) Species redundancy and ecosystem reliability. *Conservation Biology* 12, 39-45.
- Nagendra H, Gadgil M (1999) Satellite imagery as a tool for monitoring species diversity: an assessment. *Journal of Applied Ecology* 36, 388-397.
- Naveh Z, Whittaker RH (1979) Structural and floristic diversity of shrublands and woodlands in northern Israel and other Mediterranean areas. *Vegetatio* 41, 171-190.
- Nicholson SA, Monk CD (1974) Plant species diversity in old-field succession on the Georgia Piedmont. *Ecology* 55, 1075-1085.
- Niemelä J (2000) Biodiversity monitoring for decision-making. *Annales Zoologici Fennici* 37, 307-317.
- Norden N, Chave J, Caubère A, Châtelet P, Ferroni N, Forget P-M, Thébaud C (2007) Is temporal variation of seedling communities determined by environment or by seed arrival? A test in a neotropical forest. *Journal of Ecology* 95, 507-516.
- Obeso JR, Aedo C (1992) Plant-species richness and extinction on isolated dunes along the rocky coast of northwestern Spain. *Journal of Vegetation Science* 3, 129-132.
- Odland A, Birks HJB (1999) The altitudinal gradient of vascular plant species richness in Aurland, western Norway. *Ecography* 22, 548-566.
- Odum EP (1969) The strategy of ecosystem development. *Science* 164, 262-270.
- Ojeda F, Marañón T, Arroyo J (2000) Plant diversity patterns in the Aljibe Mountains (S. Spain): a comprehensive account. *Biodiversity and Conservation* 9, 1323-1343.
- Økland RH, Eilertsen O, Økland T (1990) On the relationship between plot size and beta diversity in boreal coniferous forests. *Vegetatio* 87, 187-192.
- Oksanen J (1996) Is the humped relationship between species richness and biomass an artefact due to plot size? *Journal of Ecology* 84, 293-295.
- Oloff H, Bakker JP (1991) Long-term dynamics of standing crop and species composition after the cessation of fertilizer application to mown grassland. *Journal of Applied Ecology* 28, 1040-1052.
- Oloff H, Huisman J, van Tooren BF (1993) Species dynamics and nutrient accumulation during early primary succession in coastal sand dunes. *Journal of Ecology* 81, 693-706.
- Olofsson J, De Mazancourt C, Crawley MJ (2007) Contrasting effects of rabbit exclusion on nutrient availability and primary production in grasslands at different time scales. *Oecologia* 150, 582-589.
- Olofsson J, De Mazancourt C, Crawley MJ (2008) Spatial heterogeneity and plant species richness at different spatial scales under rabbit grazing. *Oecologia* 156, 825-834.
- Olson JS (1958) Rates of succession and soil changes on southern Lake Michigan sand dunes. *Botanical Gazette* 119, 125-170.
- Paal J (1998) Rare and threatened plant communities of Estonia. *Biodiversity and Conservation* 7, 1027-1049.

- Paine RT (1966) Food web complexity and species diversity. *American Naturalist* 100, 65-75.
- Palmer MW, Earls PG, Hoagland BW, White PS, Wohlgemuth T (2002) Quantitative tools for perfecting species lists. *Environmetrics* 13, 121-137.
- Palmer MW, Van der Maarel E (1995) Variance in species richness, species association, and niche limitation. *Oikos* 73, 203-213.
- Palmer MW, White PS (1994) Scale dependence and the species-area relationship. *American Naturalist* 144, 717-740.
- Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1, 3-19.
- Pärtel M (2002) Local plant diversity patterns and evolutionary history at the regional scale. *Ecology* 83, 2361-2366.
- Pausas JG, Austin MP (2001) Patterns of plant species richness in relation to different environments: an appraisal. *Journal of Vegetation Science* 12, 153-166.
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12, 361-371.
- Peet RK (1974) The measurement of species diversity. *Annual Review of Ecology and Systematics* 5, 285-307.
- Peet RK (1975) Relative diversity indices. *Ecology* 56, 496-498.
- Petchey OL (2004) On the statistical significance of functional diversity effects. *Functional Ecology* 18, 297-303.
- Petchey OL, Gaston KJ (2002a) Extinction and the loss of functional diversity. *Proceedings of the Royal Society of London B* 269, 1721-1727.
- Petchey OL, Gaston KJ (2002b) Functional diversity (FD), species richness and community composition. *Ecology Letters* 5, 402-411.
- Peterson CH (1976) Measurement of community pattern by indices of local segregation and species diversity. *Journal of Ecology* 64, 157-169.
- Petraitis PS, Latham RE, Niesenbaum RA (1989) The maintenance of species diversity by disturbance. *The Quarterly Review of Biology* 64, 393-418.
- Pianka ER (1966) Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* 100, 33-46.
- Pianka ER (1967) On lizard species diversity: North American flatland deserts. *Ecology* 48, 333-351.
- Pielou EC (1966) Species-diversity and pattern-diversity in the study of ecological succession. *Journal of Theoretical Biology* 10, 370-83.
- Pielou EC (1975) *Ecological diversity*. Wiley, New York.
- Pierce S, Luzzaro A, Caccianiga M, Ceriani RM, Cerabolini B (2007) Disturbance is a principal  $\alpha$ -scale filter determining niche differentiation, coexistence and biodiversity in an alpine community. *Journal of Ecology* 95, 698-706.
- Pierce SM, Cowling RM (1991) Disturbance regimes as determinants of seed banks in coastal dune vegetation of the southeastern Cape. *Journal of Vegetation Science* 2, 403-412.

- Pimm SL, Lawton JH (1998) Planning for biodiversity. *Science* 279, 2068-2069.
- Pitkänen S (1998) The use of diversity indices to assess the diversity of vegetation in managed boreal forests. *Forest Ecology and Management* 112, 121-137.
- Pizzey JM (1975) Assessment of dune stabilization at Camber, Sussex, using air photographs. *Biological Conservation* 7, 275-288.
- Plassmann K, Edwards-Jones G, Jones MLM (2009) The effects of low levels of nitrogen deposition and grazing on dune grassland. *Science of the Total Environment* 407, 1391-1404.
- Possingham HP, Wilson KA (2005) Turning up the heat on hotspots. *Nature* 436, 919-920.
- Potts MD, Davies SJ, Bossert WH, Tan S, Nur Supardi MN (2004) Habitat heterogeneity and niche structure of trees in two tropical rain forests. *Oecologia* 139, 446-453.
- Povilanskas R, Baghdasarian H, Arakelyan S, Satkūnas J, Taminskas J (2009) Secular morphodynamic trends of the holocene dune ridge on the Curonian Spit (Lithuania/Russia). *Journal of Coastal Research* 25, 209-215.
- Prendergast JR, Quinn RM, Lawton JH, Eversham BC, Gibbons DW (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365, 335-337.
- Preston FW (1960) Time and space and the variation of species. *Ecology* 41, 611-627.
- Preston FW (1962) The canonical distribution of commonness and rarity: part I. *Ecology* 43, 185-215; part II. *Ecology* 43, 410-432.
- Provoost S, Ampe C, Bonte D, Cosyns E, Hoffmann M (2002) Ecology, management and monitoring of dune grassland in Flanders, Belgium. In: EUROCOAST (ed.) Littoral 2002. The Changing Coast. EUROCOAST, EUCC, Porto, Portugal, pp. 11-19.
- Pucheta E., Cabido M, Díaz S, Funes G, (1998) Floristic composition, biomass, and aboveground net plant production in grazed and protected sites in a mountain grassland of central Argentina. *Acta Oecologica* 19, 97-105.
- Purvis A, Gittleman JL, Cowlshaw G, Mace GM (2000) Predicting extinction risk in declining species. *Proceedings of the Royal Society of London B* 267, 1947-1952.
- Pyšek P, Jarošík V (2005) Residence time determines the distribution of alien plants. In: Inderjit S (ed.) *Invasive plants: ecological and agricultural aspects*. Birkhäuser Verlag, Basel. pp. 345-354.
- Pyšek P, Richardson DM, Rejmánek M, Webster GL, Williamson M, Kirschner J (2004a) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* 53, 131-143.
- Pyšek P, Richardson DM, Williamson M (2004b) Predicting and explaining plant invasions through analysis of source area floras: some critical considerations. *Diversity and Distributions* 10, 179-187.
- Rahbek C (1995) The elevational gradient of species richness: a uniform pattern? *Ecography* 18, 200-205.
- Rapoport EH (1982) *Areography: geographical strategies of species*. Pergamon Press, Oxford.
- Raunkiaer C (1934) *The life forms of plants and statistical plant geography*. Clarendon Press, Oxford.
- Reid WV (1998) Biodiversity hotspots. *Trends in Ecology & Evolution* 13, 275-280.
- Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? *Ecology* 77, 1655-1661.

- Rejmánek M, Richardson DM, Higgins SI, Pitcairn MJ, Grotkopp E (2005) Ecology of invasive plants: state of the art. In: Mooney HA, Mack RM, McNeely JA, Neville L, Schei P, Waage J (eds.) *Invasive alien species: searching for solutions*. Island Press, Washington DC. pp. 104-161.
- Rejmánek M, Rosén E (1988) The effect of colonizing shrubs (*Juniperus communis* and *Potentilla fruticosa*) on species richness in the grasslands of Stora Alvaret, Öland (Sweden). *Acta Phytogeographica Suecica* 76, 67-72.
- Rejmánek M, Rosén E (1992) Influence of colonizing shrubs on species-area relationships in alvar plant communities. *Journal of Vegetation Science* 3, 625-630.
- Reynolds HL, Hungate BA, Chapin III FS, D'Antonio CM (1997) Soil heterogeneity and plant competition in an annual grassland. *Ecology* 78, 2076-2090.
- Richardson DM (2001) Plant invasions. In: Levin S (ed.) *Encyclopedia of Biodiversity*. Volume 4, Academic Press, San Diego. pp. 677-688.
- Richardson DM, Cowling RM, Lamont BB, Van Hensbergen HJ (1995) Coexistence of *Banksia* species in southwestern Australia: the role of regional and local processes. *Journal of Vegetation Science* 6, 329-342.
- Richardson DM, Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography* 30, 409-431.
- Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6, 93-107.
- Richter M (1998) Zonal features of phytodiversity under natural conditions and under human impact - a comparative survey. In: Barthlott W, Winiger M (eds.) *Biodiversity. A challenge for development research and policy*. Springer, Berlin. pp. 83-109.
- Ricklefs RE (1977) Environmental heterogeneity and plant species diversity: a hypothesis. *American Naturalist* 111, 376-381.
- Ricklefs RE (1987) Community diversity: relative roles of local and regional processes. *Science* 235, 167-171.
- Ricklefs RE (2005) Historical and ecological dimensions of global patterns in plant diversity. *Biologiske Skrifter* 55, 583-603.
- Ricklefs RE, Lovette IR (1999) The roles of island area per se and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology* 68, 1142-1160.
- Ricklefs RE, Schluter D (1993) (eds.) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, IL.
- Ricotta C (2005) A note on functional diversity measures. *Basic and Applied Ecology* 6, 479-486.
- Ricotta C (2007) A semantic taxonomy for diversity measures. *Acta Biotheoretica* 55, 23-33.
- Ricotta C, Carranza MB, Avena G (2002) Computing  $\beta$ -diversity from species-area curves. *Basic and Applied Ecology* 3, 15-18.
- Ricotta C, Szeidl L (2006) Towards a unifying approach to diversity measures: bridging the gap between the Shannon entropy and Rao's quadratic index. *Theoretical Population Biology* 70, 237-243.

- Ridder B (2008) Questioning the ecosystem services argument for biodiversity conservation. *Biodiversity and Conservation* 17, 781–790.
- Riera JL, Magnuson JJ, Vande Castle JR, MacKenzie MD (1998) Analysis of large-scale spatial heterogeneity in vegetation indices among North American Landscapes. *Ecosystems* 1, 268–282.
- Roem WJ, Berendse F (2000) Soil acidity and nutrient supply ratio as possible factors determining changes in plant species diversity in grassland and heathland communities. *Biological Conservation* 92, 151–161.
- Rogers CS (1993) Hurricanes and coral reefs: the intermediate disturbance hypothesis revisited. *Coral Reefs* 12, 127–137.
- Rohde K (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65, 514–527.
- Romdal TS, Colwell RK, Rahbek C (2005) The influence of band sum area, domain extent, and range sizes on the latitudinal mid-domain effect. *Ecology* 86, 235–244.
- Rook AJ, Tallwin JRB (2003) Grazing and pasture management for biodiversity benefit. *Animal Research* 52, 181–189.
- Rosenzweig ML (1995) *Species diversity in space and time*. Cambridge University Press, New York.
- Rosenzweig ML (2001) The four questions: what does the introduction of exotic species do to diversity? *Evolutionary Ecology Research* 3, 361–367.
- Rosenzweig ML, Abramsky Z (1993) How are diversity and productivity related? In: Ricklefs RE, Schluter D (eds.) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, IL. pp. 52–65.
- Röttgermann M, Steinlein T, Beyschlag W, Dietz H (2000) Linear relationships between aboveground biomass and plant cover in low open herbaceous vegetation. *Journal of Vegetation Science* 11, 145–148.
- Roxburgh SH, Shea K, Wilson JB (2004) The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology* 85, 359–371.
- Russell PJ, Flowers TJ, Hutchings MJ (1985) Comparison of niche breadths and overlaps of halophytes on salt marshes of differing diversity. *Vegetatio* 61, 171–178.
- Rydin H, Borgegård S-O (1988) Plant species richness on islands over a century of primary succession: Lake Hjälmaren. *Ecology* 69, 916–927.
- Sabovljević M, Grdović S (2009) Bryophyte diversity within urban areas: a case study of the city of Belgrade (Serbia). *International Journal of Botany* 5, 85–92.
- Sala OE, Lauenroth WK, McNaughton SJ, Rusch G, Zhang X (1996) Biodiversity and ecosystem functioning in grasslands. In: Mooney HA, Cushman JH, Medina E, Sala OE, Schulze ED (1996) *Functional roles of biodiversity: a global perspective*. John Wiley, Chichester, pp. 129–149.
- Sang W (2009) Plant diversity patterns and their relationships with soil and climatic factors along an altitudinal gradient in the middle Tianshan Mountain area, Xinjiang, China. *Ecological Research* 24, 303–314.
- Sax DF, Gaines SD (2003) Species diversity: from global decreases to local increases. *Trends in Ecology & Evolution* 18, 561–566.
- Schaffers AP (2002) Soil, biomass, and management of semi-natural vegetation. Part II. Factors controlling species diversity. *Plant Ecology* 158, 247–268.

- Scheiner SM, Cox SB, Willig M, Mittelbach GG, Osenberg C, Kaspari M (2000) Species richness, species-area curves and Simpson's paradox. *Evolutionary Ecology Research* 2, 791-802.
- Scheiner SM, Rey-Benayas JM (1994) Global patterns of plant diversity. *Evolutionary Ecology* 8, 331-347.
- Scherer-Lorenzen M (2008) Functional diversity affects decomposition processes in experimental grasslands. *Functional Ecology* 22, 547-555.
- Schippers P, Joenje W (2002) Modelling the effect of fertiliser, mowing, disturbance and width on the biodiversity of plant communities of field boundaries. *Agriculture, Ecosystems and Environment* 93, 351-365.
- Schmid B, Joshi J, Schlöpfer F (2001) Empirical evidence for biodiversity-ecosystem functioning relationships. In: Kinzig AP, Pacala SW, Tilman D (eds.) *The functional consequences of biodiversity*. pp. 120-150.
- Schöttelndreier M, Falkengren-Grerup U (1999) Plant induced alteration in the rhizosphere and the utilisation of soil heterogeneity. *Plant and Soil* 209, 297-309.
- Schouten MA, Verweij PA, Barendregt A, Kleukers RMJC, Kalkman VJ, De Ruiter PC (2009) Determinants of species richness patterns in the Netherlands across multiple taxonomic groups. *Biodiversity and Conservation* 18, 203-217.
- Schulze E-D, Mooney HA (eds.) (1993) *Biodiversity and ecosystem function*. *Ecological Studies* 99, Springer, Berlin.
- Schwartz MW, Brigham CA, Hoeksema JD, Lyons KG, Mills MH, Van Mantgem PJ (2000) Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* 122, 297-305.
- Schwilk DW, Keeley JE, Bond WJ (1997) The intermediate disturbance hypothesis does not explain fire and diversity pattern in fynbos. *Plant Ecology* 132, 77-84.
- Shafi MI, Yarranton GA (1973) Diversity, floristic richness, and species evenness during a secondary (post-fire) succession. *Ecology* 54, 897-902.
- Shea K, Roxburgh SH, Rauschert ESJ (2004) Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters* 7, 491-508.
- Shmida A, Ellner S (1984) Coexistence of plant species with similar niches. *Vegetatio* 58, 29-55.
- Shmida A, Wilson MW (1985) Biological determinants of species diversity. *Journal of Biogeography* 12, 1-20.
- Shumway SW (2000) Facilitative effects of a sand dune shrub on species growing beneath the shrub canopy. *Oecologia* 124, 138-148.
- Simberloff DS (1974) Equilibrium theory of island biogeography and ecology. *Annual Review of Ecology and Systematics* 5, 161-182.
- Simberloff DS (1976) Species turnover and equilibrium island biogeography. *Science* 194, 572-578.
- Simberloff DS (2005) Non-native species do threaten the natural environment! *Journal of Agricultural and Environmental Ethics* 18, 595-607.
- Simberloff DS, Abele LG (1976) Island biogeography theory and conservation practice *Science* 191, 285-286.

- Simmering D, Waldhardt R, Otte A (2006) Quantifying determinants contributing to plant species richness in mosaic landscapes: a single- and multi-patch perspective. *Landscape Ecology* 21, 1233-1251.
- Simmons MT, Cowling RM (1996) Why is the Cape Peninsula so rich in plant species? An analysis of the independent diversity components. *Biodiversity and Conservation* 5, 551-573.
- Simpson EH (1949) Measurement of diversity. *Nature* 163, 688.
- Singh JS, Bourgeron P, Lauenroth WK (1996) Plant species richness and species-area relations in a shortgrass steppe in Colorado. *Journal of Vegetation Science* 7, 645-650.
- Sipman HJM, Aptroot A (2001) Where are the missing lichens? *Mycological Research* 105, 1433-1439.
- Sismondo S (2000) Island biogeography and the multiple domains of models. *Biology and Philosophy* 15, 239-258.
- Sjögren E (1961) Epiphytische Moosvegetation in Laubwäldern der Insel Öland, Schweden. *Acta Phytogeographica Suecica* 44, 1-149.
- Snyder RE, Chesson P (2004) How the spatial scales of dispersal, competition, and environmental heterogeneity interact to affect coexistence. *American Naturalist* 164, 633-650.
- Solbrig OT (1994) Biodiversität. Wissenschaftliche Fragen und Vorschläge für die internationale Forschung. MAB. Bonn.
- Solbrig OT (2000) The theory and practice of the science of biodiversity: a personal assessment. In: Kato M (ed.) *The biology of biodiversity*. Springer, Berlin. pp. 107-117.
- Somers N, D'Haese B, Bossuyt B, Lens L, Hoffmann M (2008) Food quality affects diet preference of rabbits: experimental evidence. *Belgian Journal of Zoology* 138, 170-176.
- Somodi I, Virágh K, Aszalós R (2004) The effect of the abandonment of grazing on the mosaic of vegetation patches in a temperate grassland area in Hungary. *Ecological Complexity* 1, 177-189.
- Sørensen TA (1948) A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. *Biologiske Skrifter* 5, 1-34.
- Soulé ME (1991) Conservation: tactics for a constant crisis. *Science* 253, 744-750.
- Southwood TRE (1961) The number of species of insect associated with various trees. *Journal of Animal Ecology* 30, 1-8.
- Southwood TRE, Henderson PA (2000) *Ecological methods*. Blackwell, Malden, Massachusetts.
- Stachowicz JJ, Tilman D (2005) Species invasions and the relationships between species diversity, community saturation, and ecosystem functioning. In: Sax DF, Stachowicz JJ, Gaines SD (eds.) *Species invasions. Insights into ecology, evolution and biogeography*. Sinauer Associates, Sunderland Massachusetts. pp. 45-64.
- Stallins JA (2002) Dune plant species diversity and function in two barrier island biogeomorphic systems. *Plant Ecology* 165, 183-196.
- Stankevičiūtė J (2001) Correlation between species number and homogeneity in plant communities of the Lithuanian seacoast. *Biologija* 2, 105-107.

- Stevens GC (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist* 133, 240-256.
- Stevens GC (1992) The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *American Naturalist* 140, 893-911.
- Stohlgren TJ, Chong GW, Kalkhan MA, Schell LD (1997) Rapid assessment of plant diversity patterns: a methodology for landscapes. *Environmental Monitoring and Assessment* 48, 25-43.
- Storch D, Davies RG, Zajíček S, Orme CDL, Olson V, Thomas GH, Ding T-S, Rasmussen PC, Ridgely RS, Bennett PM, Blackburn TM, Owens IPF, Gaston KJ (2006) Energy, range dynamics and global species richness patterns: reconciling mid-domain effects and environmental determinants of avian diversity. *Ecology Letters* 9, 1308-1320.
- Stork NE, Samways MJ, Eeley HAC (1996) Inventorying and monitoring biodiversity. *Trends in Ecology & Evolution* 11, 39-40.
- Stubbs WJ, Wilson JB (2004) Evidence for limiting similarity in a sand dune community. *Journal of Ecology* 92, 557-567.
- Tallis JH (1991) *Plant community history. Long-term changes in plant distribution and diversity.* Chapman & Hall, London.
- Tallowin JRB, Rook AJ, Rutter SM (2005) Impact of grazing management on biodiversity of grasslands. *Animal Science* 81, 193-198.
- Tansley AG (1939) *The British Islands and their vegetation.* Cambridge University Press, London.
- Taylor PH, Gaines SD (1999) Can Rapoport's rule be rescued? Modeling causes of the latitudinal gradient in species richness. *Ecology* 80, 2474-2482.
- Terborgh J (1971) Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the Avifauna of the Cordillera Vilcabamba, Peru. *Ecology* 52, 23-40.
- Terborgh J (1973) On the notion of favorableness in plant ecology. *American Naturalist* 107, 481-501.
- Theodose TA, Roths JB (1999) Variation in nutrient availability and plant species diversity across forb and graminoid zones of a Northern New England high salt marsh. *Plant Ecology* 143, 219-228.
- Thomas CD (1990) Fewer species. *Nature* 347, 237.
- Tilman D (1980) Resources: a graphical-mechanistic approach to competition and predation. *American Naturalist* 116, 362-393.
- Tilman D (1982) Resource competition and community structure. *Monographs in Population Biology* 17, 1-296.
- Tilman D (1983) Some thoughts on resource competition and diversity in plant communities. In: Kruger FJ, Mitchell DT, Jarvis JUM (eds.) *Mediterranean type ecosystems.* Springer, Berlin. pp. 322-336.
- Tilman D (1986) Resources, competition and the dynamics of plant communities. In: Crawley MT (ed.) *Plant ecology.* Blackwell, Oxford.
- Tilman D (1988) Dynamics and structure of plant communities. *Monographs in Population Biology* 26, 1-360.

- Tilman D (1993) Community diversity and succession: the roles of competition, dispersal, and habitat modification. In: Schulze E-D, Mooney HA (eds.) *Biodiversity and ecosystem function*. Ecological Studies 99, Springer, Berlin. pp. 328-344.
- Tilman D (1994) Competition and biodiversity in spatially structured habitats. *Ecology* 75, 2-16.
- Tilman D (1997) Community invasibility, recruitment limitation and grassland biodiversity. *Ecology* 78, 81-92.
- Tilman D (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80, 1455-1474.
- Tilman D (2000) Causes, consequences and ethics of biodiversity. *Nature* 405, 208-211.
- Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of functional diversity and composition on ecosystem processes. *Science* 277, 1300-1302.
- Tilman D, Lehman C (2001) Biodiversity, composition, and ecosystem processes: theory and concepts. In: Kinzig AP, Pacala SW, Tilman D (eds.) *The functional consequences of biodiversity*. Empirical progress and theoretical extensions. *Monographs in Population Biology* 33, 9-41.
- Tilman D, Pacala S (1993) The maintenance of species richness in plant communities. In: Ricklefs RE, Schluter D (eds.) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago. pp. 13-25.
- Tilman D, Reich PB, Knops J, Wedin D, Mielke T, Lehman C (2001) Diversity and productivity in a long-term grassland experiment. *Science* 294, 843-845.
- Tjørve E (2009) Shapes and functions of species-area curves (II): a review of new models and parameterizations. *Journal of Biogeography* 36, 1435-1445.
- Tjørve E, Turner WR (2009) The importance of samples and isolates for species-area relationships. *Ecography* 32, 391-400.
- Tjørve E, Kunin WE, Polce C, Calf Tjørve KM (2008) Species-area relationship: separating the effects of species abundance and spatial distribution. *Journal of Ecology* 96, 1141-1151.
- Tregenza T, Butlin RK (1999) Genetic diversity: do marker genes tell us the whole story? In: Magurran AE, May RM (eds.) *Evolution of biological diversity*. Oxford University Press, Oxford, pp. 37-55.
- Triantis KA, Mylonas M, Whittaker RJ (2008) Evolutionary species-area curves as revealed by single-island endemics: insights for the inter-provincial species-area relationship. *Ecography* 31, 401-407.
- Troelstra SR, Lotz LAP, Wagenaar R, Sluimer L (1990) Temporal and spatial variability in soil nutrient status of a former beach plain. *Plant and Soil* 127, 1-12.
- Trubina MR (2009) Species richness and resilience of forest communities: combined effects of short-term disturbance and long-term pollution. *Plant Ecology* 201, 339-350.
- Tsegaye T, Hill RL (1998) Intensive tillage effects on spatial variability of soil test, plant growth, and nutrient uptake measurements. *Soil Science* 163, 155-165.
- Turner MG (1989) Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20, 171-197.
- Turner MG (1990) Spatial and temporal analysis of landscape patterns. *Landscape Ecology* 4, 21-30.

- Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM, Webb DA (eds.) (1980) *Flora Europea*, Vol 5. Alismataceae to Orchidaceae (Monocotyledones). Cambridge University Press, Cambridge.
- Urban DL, O'Neill RV, Shugart HH (1987) Landscape ecology: a hierarchical perspective can help scientists understand spatial patterns. *BioScience* 37, 119-127.
- Van de Koppel J, Huisman J, Van der Wal R, Olf R (1996) Patterns of herbivory along a productivity gradient: an empirical and theoretical investigation. *Ecology* 77, 736-745.
- Van den Berg LJJ, Tomassen HBM, Roelofs JGM, Bobbink R (2005) Effects of nitrogen enrichment on coastal dune grassland: a mesocosm study. *Environmental Pollution* 138, 77-85.
- Van der Hagen HGJM, Geelen LHWT, De Vries CN (2008) Dune slack restoration in Dutch mainland coastal dunes. *Journal for Nature Conservation* 16, 1-11.
- Van der Laan D (1979) Spatial and temporal variation in the vegetation of dune slacks in relation to the ground water regime. *Vegetatio* 39, 43-51.
- Van der Maarel E (1971) Plant species diversity in relation to management. In: Duffey E, Watt AS (eds.) *The scientific management of animal and plant communities for conservation*. Blackwell, Oxford. pp. 45-63.
- Van der Maarel E (1988) Vegetation dynamics: patterns in time and space. *Vegetatio* 77, 7-19.
- Van der Maarel E (ed.) (1993) *Ecosystems of the world*. Vol. 2A. Dry coastal ecosystems. Polar regions and Europe. Elsevier, Amsterdam.
- Van der Maarel E, Sykes MT (1993) Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. *Journal of Vegetation Science* 4, 179-188.
- Van der Maarel E, Van der Maarel-Versluys M (1997) Biogeographic features of dry coastal ecosystems. In: Van der Maarel E (ed.) *Ecosystems of the world*. Vol. 2C. Dry coastal ecosystems. General aspects. Elsevier, Amsterdam. pp. 163-190.
- Van der Wal R, Pearce ISK, Booker RW (2005) Mosses and the struggle for light in a nitrogen-polluted world. *Oecologia* 142, 159-168.
- Van Duren IC, Boeye D, Grootjans AP (1997) Nutrient limitations in an extant and drained poor fen: Implications for restoration. *Plant Ecology* 133, 91-100.
- Van Leeuwen CG, Van der Maarel E (1971) Pattern and process in coastal dune vegetations. *Acta Botanica Neerlandica* 20, 191-198.
- Van Ruijven J, Berendse F (2007) Contrasting effects of diversity on the temporal stability of plant populations. *Oikos* 116, 1323-1330.
- Van Vuuren DP, Sala OE, Pereira HM (2006) The future of vascular plant diversity under four global scenarios. *Ecology and Society* 11, 25-42.
- Van Wieren SE, Bakker JP (2008) The impact of browsing and grazing herbivores on biodiversity. In: Gordon IJ, Prins HHT (eds.) *The ecology of browsing and grazing*. Ecological Studies 195. Springer, Berlin. pp. 263-292.
- Vanderhoeven S, Dassonville N, Meerts P (2005) Increased topsoil mineral nutrient concentrations under exotic invasive plants in Belgium. *Plant and Soil* 275, 169-179.
- Vázquez GJA, Givnish TJ (1998) Altitudinal gradients in the tropical forest composition, structure, and diversity in the Sierra de Manantlán. *Journal of Ecology* 86, 999-1020.

- Veech JA, Summerville AM, Crist TO, Gering JC (2002) The additive partitioning of species diversity: recent revival of an old idea. *Oikos* 99, 3-9.
- Vellend M (2001) Do commonly used indices of  $\beta$ -diversity measure species turnover? *Journal of Vegetation Science* 12, 545-552.
- Venevsky S, Venevskaia I (2005) Hierarchical systematic conservation planning at the national level: identifying national biodiversity hotspots using abiotic factors in Russia. *Biological Conservation* 124, 235-251.
- Verdú JR, Crespo MB, Galante E (2000) Conservation strategy of a nature reserve in Mediterranean ecosystems: the effects of protection from grazing on biodiversity. *Biodiversity and Conservation* 9, 1707-1721.
- Vermeer JG, Berendse F (1983) The relationship between nutrient availability, shoot biomass and species richness in grassland and wetland communities. *Vegetatio* 53, 121-126.
- Vestergaard P (2008) Response to mowing of coastal brackish meadow plant communities along an elevational gradient. *Nordic Journal of Botany* 14, 569-587.
- Vitousek PM, Benning TL (1995) Ecosystem and landscape diversity: islands as model systems. In: Vitousek PM, Loope LL, Adersen H (eds.) *Islands. Biological diversity and ecosystem function. Ecological Studies* 115. Springer, Berlin, pp. 74-84.
- Vogt Andersen U (1995) Resistance of Danish coastal vegetation types to human trampling. *Biological Conservation* 71, 223-230.
- Volterra V (1926) Variations and fluctuations in the number of individuals of animal species living together. In: Chapman RN (ed.) *Animal Ecology*. McGraw-Hill, New York. pp. 409-448.
- Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L, Dodson SI, Juday GP, Parameter R (1999) The relationship between productivity and species richness. *Annual Review of Ecology and Systematics* 30, 257-300.
- Walker J, Peet RK (1983) Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. *Vegetatio* 55, 163-179.
- Walter H, Straka H (1970) *Arealkunde. Floristisch-historische Geobotanik*. Ulmer, Stuttgart.
- Ward JV (1998) Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation* 83, 269-278.
- Ward JV, Tockner K, Schiemer F (1999) Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regulated Rivers: Research and Management* 15, 125-139.
- Watt AS (1947) Pattern and process in the plant community. *Journal of Ecology* 35, 1-22.
- Webster R (2000) Is soil variation random? *Geoderma* 97, 149-163.
- Weibull H, Rydin H (2005) Bryophyte species richness on boulders: relationship to area, habitat diversity and canopy tree species. *Biological Conservation* 122, 71-79.
- Weiherr E, Keddy PA (1999) Relative abundance and evenness patterns along diversity and biomass gradients. *Oikos* 87, 355-361.
- Weis JJ, Cardinale BJ, Forshay KJ, Ives AR (2007) Effects of species diversity on community biomass production change over the course of succession. *Ecology* 88, 929-939.
- Weiser MD, Enquist BJ, Boyle B, Killeen TJ, Jørgensen PM, Fonseca G, Jennings MD, Kerkhoff AJ, Lacher Jr TE, Montegudo A, Núñez Vargas MP, Phillips OL, Swenson

- NG, Vásquez Martínez R (2007) Latitudinal patterns of range size and species richness of New World woody plants. *Global Ecology and Biogeography* 16, 679-688.
- Weitz JS, Rothman DH (2003) Scale-dependence of resource-biodiversity relationships. *Journal of Theoretical Biology* 225, 205-214.
- Westhoff V (1947) The vegetation of dunes and salt-marshes on the Dutch islands of Terschelling, Vlieland and Texel. Summary of the Thesis, Utrecht.
- Westman WE (1981) Diversity relations and succession in Californian coastal sage scrub. *Ecology* 62, 170-184.
- Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30, 279-338.
- Whittaker RH (1965) Dominance and diversity in land plant communities. *Science* 147, 250-260.
- Whittaker RH (1972) Evolution and measurement of species diversity. *Taxon* 21, 213-251.
- Whittaker RH (1975) *Communities and ecosystems*. Macmillan, New York.
- Whittaker RH (1977) Evolution of species diversity in land communities. *Evolutionary Biology* 10, 1-67.
- Whittaker RH, Niering WA (1975) Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient. *Ecology* 56, 771-790.
- Whittaker RJ (1998) *Island Biogeography. Ecology, evolution and conservation*. Oxford University Press, Oxford.
- Whittaker RJ, Willis KJ, Field R (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* 28, 453-470.
- Widenfalk O, Weslien J (2009) Plant species richness in managed boreal forests. Effects of stand succession and thinning. *Forest Ecology and Management* 257, 1386-1394.
- Wickham JD, Wu J, Bradford DF (1997) A conceptual framework for selecting and analyzing stressor data to study species richness at large spatial scales. *Environmental Management* 21, 247-257.
- Wiens JA (1989) Spatial scaling in ecology. *Functional Ecology* 3, 385-397.
- Williams CB (1943) Area and number of species. *Nature* 152, 264-267.
- Williams MR, Lamont BB, Henstridge JD (2009) Species-area functions revisited. *Journal of Biogeography*, doi: 10.1111/j.1365-2699.2009.02110.x
- Williamson M, Brown KC (1986) The analysis and modelling of British invasions. *Philosophical Transactions of the Royal Society London B* 314, 505-522.
- Williamson M, Gaston KJ, Lonsdale WM (2001) The species-area relationship does not have an asymptote! *Journal of Biogeography* 28, 827-830.
- Willis KJ, Gillson L, Brncic TM, Figueroa-Rangel BL (2005) Providing baselines for biodiversity measurement. *Trends in Ecology & Evolution* 20, 107-108.
- Willis KJ, Whittaker RJ (2002) Species diversity - scale matters. *Science* 295, 1245-1248.
- Willner W, Moser D, Grabherr G (2004) Alpha and beta diversity in Central European beech forests. *Fitosociologica* 41, 15-20.
- Wilson EO (1992) *The diversity of life*. Harvard University Press, Cambridge, MA.
- Wilson EO (1997) Introduction In: Abe T, Levin SA, Higashi M (eds.) *Biodiversity. An ecological perspective*. Springer, New York, pp. 1-5.

- Wilson EO, Peter FM (eds.) (1988) *Biodiversity*. National Academic Press, Washington DC.
- Wilson JB, Allen RB, Hewitt AE (1996) A test of the humped-back theory of species richness in New Zealand native forest. *New Zealand Journal of Ecology* 20, 173-177.
- Wilson JB, Steel JB, King W McG, Gitay H (1999) The effect of spatial scale on evenness. *Journal of Vegetation Science* 10, 463-468.
- Wilson JB, Sykes MT (1988) Some tests for niche limitation by examination of species diversity in the Dunedin area, New Zealand. *New Zealand Journal of Botany* 26, 237-244.
- Wilson MV, Shmida A (1984) Measuring beta diversity with presence-absence data. *Journal of Ecology* 72, 1055-1064.
- Wilson SD, Tilman D (1995) Competitive responses of eight old-field plant species in four environments. *Ecology* 76, 1169-1180.
- Wisskirchen R, Haeupler H (1998) Standardliste der Farn- und Blütenpflanzen Deutschlands. In: Haeupler, H. (ed.), *Die Farn- und Blütenpflanzen Deutschlands*. Ulmer, Stuttgart.
- Witte J-PM, He F, Groen CLG (2008) Grid origin affects scaling of species across spatial scales. *Global Ecology and Biogeography* 17, 448-456.
- Wittig B, Richter gen. Kemmermann A, Zacharias D (2006) An indicator species approach for success-orientated subsidies of ecological services in grasslands - an investigation in Northwestern Germany. *Biological Conservation* 133, 186-197.
- Wohlgemuth T (1998) Modelling floristic species richness on a regional scale: a case study in Switzerland. *Biodiversity and Conservation* 7, 159-177.
- Woodward FI (1987) *Climate and plant distribution*. Cambridge University Press, Cambridge.
- Wright DH (1983) Species-energy theory: an extension of species-area theory. *Oikos* 41, 496-506.
- Wright DH, Currie DJ, Maurer BA (1993) Energy supply and patterns of species richness on local and regional scales. In: Ricklefs RE, Schluter D (eds.) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, IL. pp. 66-74.
- Xiao S, Michalet R, Wang G, Chen S-Y (2009) The interplay between species' positive and negative interactions shapes the community biomass-species richness relationships. *Oikos*, doi: 10.1111/j.1600-0706.209.17588.x
- Yakimov BN, Bossuyt B, Iudin DI, Gelashviliy DB (2008) Multifractal diversity-area relationship at small scales in dune slack plant communities. *Oikos* 117, 33-39.
- Yamamura N (1997) Diversity and evolution of symbiotic interactions. In: Abe T, Levin SA, Higashi M (eds.) *Biodiversity. An ecological perspective*. Springer, New York. pp. 75-82.
- Yang J, Hammer RD & Blanchar RW (1995) Microscale pH spatial distribution in the Ap horizon of Mexico silt loam. *Soil Science* 160, 371-375.
- Yarranton GA, Morrison RG (1974) Spatial dynamics of primary succession: nucleation. *Journal of Ecology* 62, 417-428.
- Yoccoz NG, Nichols JD, Boulinier T (2001) Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution* 16, 446-453.

- Young CH, Jarvis PJ (2001) Assessing the structural heterogeneity of urban areas: an example from the Black Country (UK). *Urban Ecosystems* 5, 49-69.
- Zagwijn WH (1971) Vegetational history of the coastal dunes in the Western Netherlands. *Acta Botanica Neerlandica* 20, 174-182.
- Zamfir M (2000) Effects of bryophytes and lichens on seedling emergence of alvar plants: Evidence from greenhouse experiments. *Oikos* 88, 603-611.
- Zapata FA, Gaston KJ, Chown SL (2003) Mid-domain models of species richness gradients: assumptions, methods and evidence. *Journal of Animal Ecology* 72, 677-690.
- Żarnowiec J (1996) The bryoflora of urban areas - a floristic ecological case study of Oświęcim town (S Poland). *Fragmenta Floristica et Geobotanica* 41, 355-377.
- Zechmeister HG, Tribsch A, Moser D, Peterseil J, Wrבka T (2003) Biodiversity 'hot spots' for bryophytes in landscapes dominated by agriculture in Austria. *Agriculture, Ecosystems and Environment* 94, 159-167.
- Zechmeister HG, Tribsch A, Moser D, Wrבka T (2002) Distribution of endangered bryophytes in Austrian agricultural landscapes. *Biological Conservation* 103, 173-182.
- Zeeb PJ, Hemond HF (1998) Hydrologic response of a wetland to changing moisture conditions: modeling effects of soil heterogeneity. *Climatic Change* 40, 211-227.
- Zeevalking HJ, Fresco LFM (1977) Rabbit grazing and species diversity in a dune area. *Vegetatio* 35, 193-196.
- Ziegler R (1996) Spontane Moosvorkommen im Botanischen Garten der Johann Wolfgang Goethe-Universität Frankfurt am Main. *Geobotanische Kolloquien* 12, 46-50.
- Zobel K, Zobel M, Peet RK (1993) Change in pattern diversity during secondary succession in Estonian forests. *Journal of Vegetation Science* 4, 489-498.
- Zobel M, Otsus M, Liira J, Moora M, Möls T (2000) Is small-scale species richness limited by seed availability or microsite availability? *Ecology* 81, 3274-3282.