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140

**MACROECOLOGICAL APPROACH
IN VEGETATION SCIENCE: GENERALITY
OF ECOLOGICAL RELATIONSHIPS
AT THE GLOBAL SCALE**

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers which are referred to in the text by Roman numerals:

- I. Pärtel, M.; Laanisto, L.; Zobel, M. (2007). Contrasting plant productivity-diversity relationships in temperate and tropical regions: the role of evolutionary history. *Ecology*, 88(5), 1091–1097.
- II. 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(3), 320–326
- III. Pärtel, M.; Laanisto, L.; Wilson, S.D. (2008). Soil nitrogen and carbon heterogeneity in woodlands and grasslands: contrasts between temperate and tropical regions. *Global Ecology and Biogeography*, 17(1), 18–24

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The participation of the author in preparing the listed publications is as follows:

Paper I. – participated in data gathering and analysis, and in writing as well.

Paper II. – gathered the data, designed and performed statistical analysis and wrote the paper.

Paper III – participated in data gathering and writing.

INTRODUCTION

Macroecology

“Spectacular advances have been made in ecology, biogeography, systematics, paleontology and evolutionary biology in just the last two or three decades. Much has been learned about the processes that regulate the abundance, distribution, and diversity in local habitats; the effects of history and contemporary environment on the geographic distribution of species; the phylogenetic relationships among organisms; and the fossil history of life on earth. Most of this progress is due to advances within traditional disciplines: to application of mathematical models and rigorous experimental methods in ecology, to new conceptual approaches to historical and ecological biogeography, to development of robust theoretical and molecular methods to reconstruct phylogenetic history, and to insights into the processes of diversification and extinction obtained from fossil record.” This compendious paragraph is taken from James H. Brown’s *Macroecology* (1995, pp 6) – a book which proposes a radical new agenda, called “macroecology”, designed to broaden the scope of ecology to encompass vast geographical areas and very long time spans.

Macroecology is generally considered to be part of biogeography (Lomolino et al 2006, but see Blackburn & Gaston 2002); a branch which studies broad, consistent patterns in the ecological characteristics of organisms and ecosystems. In their textbook on biogeography (Lomolino et al 2006), macroecology is defined as follows: *“A top-down and multi-scale approach to investigating the assembly and structure of biotas, which identifies general patterns and underlying mechanisms by focusing on the statistical distributions of variables across spatial and temporal scales, and among large numbers of equivalent (but not identical) ecological particles (e.g., particles can include individual organisms within a local population or entire species, replicated sample areas or patches of habitat, or species within local communities or larger biotas).”* (Lomolino et al 2006, pp 763).

In 1999, a scientific journal, *Global Ecology and Biogeography Letters*, shortened its name to *Global Ecology and Biogeography* and added a significant subtitle – *Journal of Macroecology*. Since then there has been rapid growth in the publication of scientific articles concerning macroecology (Fig 1), not only in *Global Ecology and Biogeography*, but also in other prominent biology journals, such as *Ecology*, *Journal of Ecology* etc.

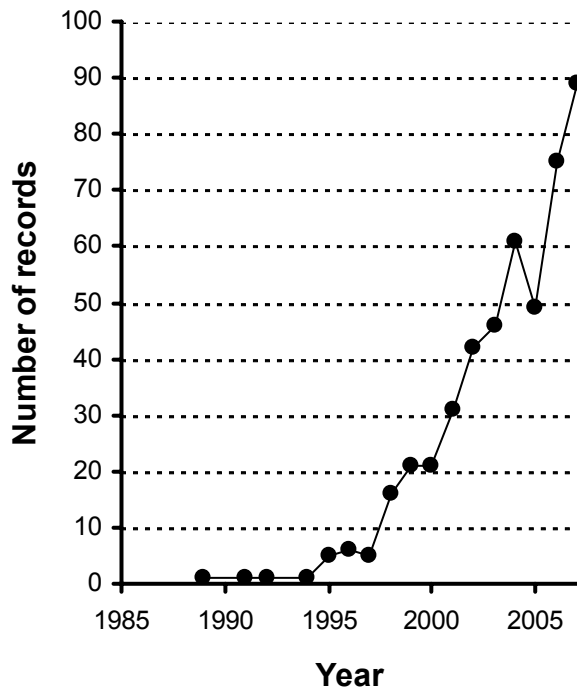


Figure 1. Number of scientific articles published since 1989 that have *macroecology* (or variants: *macroecological* etc) included in title, abstract or keywords (data from ISI Web of Knowledge, search string: macroecol*).

Although the term “macroecology” was coined by James H. Brown and Brian A. Maurer about two decades ago (Brown & Maurer 1989), similar studies have been made throughout the history of natural sciences. For example, global diversity patterns were explored by Karl Linné (Carolus Linnaeus), Georges-Louis Leclerc Comte de Buffon, Augustin Pyramus de Candolle, Alexander von Humbolt and many others. Despite biases in their view of the world and significantly less scientific knowledge available at the time, they managed to describe several global patterns in ecology, biogeography, paleontology etc. (for example, Buffon’s law, plant species distribution centers, the influence of elevation on climate).

Despite centuries of progress in biology, especially within specialized, narrow disciplines, many fundamental questions have remained unanswered and many new ones have been raised. For instance, patterns of abundance, diversity and distribution are among the oldest and best known phenomena in ecology, but it is apparent that the answers to many of these questions lie beyond and across the boundaries of the traditional disciplines (Brown 1995). In addition to disciplinary barriers, geographical limitations still play a surprisingly important

role in our scientific range, as most ecological studies and experiments are restricted to either Europe or North-America, i.e. the temperate zone (Pärtel 2006).

Over time, and especially during the last few decades, scientific information has accumulated exponentially, thereby making it possible to carry out global analyses with exact and specific, comparable data. One way of doing comprehensive ecological surveys is to perform meta-study or meta-analysis, which combines the results of several studies that address a set of related research hypotheses. The difference between meta-study and meta-analysis is that meta-analysis entails the reanalysis of an aggregate of data from similar experimental studies, whereas meta-study concerns the analysis of the original data extracted from case-studies in a novel context (Osenberg et al 1999, Pärtel 2006). Although the first meta-analysis was performed by Karl Pearson more than hundred years ago (Pearson 1904), publication of meta-results escalated not until the 1990s. Pearson's first meta-analysis was done on typhoid fever inoculation results of soldiers of British Empire, in an attempt to overcome the problem of reduced statistical power in studies with small sample sizes (O'Rourke 2006). Applying global analyzes, however, often falters, not only because of spatial patchiness of published cases, but also because the original analyses in published case-studies suffer from methodological and statistical problems (Mittelbach et al 2001) and lack of background descriptive data (Pärtel 2006).

In addition to technical and methodological advances, macroecological studies also required a change in philosophical approach. With the development of community ecology as a mature discipline in the 1960s, a mechanistic understanding of nature began to prevail. Species richness was regarded as a general feature of biological systems regulated locally by processes with deterministic outcomes (MacArthur 1965). Local determinism emerged vigorously because local population interactions seemed to achieve equilibrium within tens of generations, and were thought, therefore, to be fast enough to override regional and evolutionary processes, such as long-distance dispersal, geological history of landmass etc. (Ricklefs 1989, 2006). This mindset resulted in theoretical constructs wherein biological interactions in a community limited membership of ecologically similar species (May 1975, Morton et al 1996). Accordingly, differences in the number of species between communities reflected the different outcomes of species interactions under particular environmental conditions (Ricklefs 2006). With this kind of local dogmatism determining the approach towards science, it is rather inconceivable to gain meaningful macroecological insight, especially when studying a concept as all-embracing as biodiversity and its patterns.

Aspects of biodiversity patterns

Biodiversity – the variation of forms of life – is one of the most extensive topics in macroecology. Biodiversity pertains essentially to ecosystems, giving them both quantitative and qualitative magnitude. Biodiversity is a considerably wider concept than just species richness, which is the most common measure of diversity in ecology (Huston 1994). Diversity at the molecular level of organisms has gained increasing significance since the discovery of DNA structure in 1953, but biodiversity is also recognized in the structure of a community: is it a forest, shrubland or grassland?; what life forms dominate?, etc. Yet the number of species found in given area – species richness – is the prevalent measure of biodiversity (Gaston & Spicer 2004).

Understanding species richness patterns has been a central quest for biologists since at least the times of von Humbolt, Darwin, and Wallace (Gillman & Wright 2006). Although species richness at the large scale is primarily regulated by abiotic environmental gradients, explanations of diversity patterns have traditionally relied on small-scale, local processes occurring in ecological time (Tilman 1989, Huston 1994, Rosenzweig 1995). Mechanisms by which species avoid competition have received most attention and the availability of species has been largely disregarded (Zobel 1997). As well as the possible contribution of species dispersal, recent works in evolutionary ecology have opened new perspectives on diversity studies. The outcome of large-scale processes that control the speciation and distribution of species within regions has a significant influence on the number of species in local assemblages (Ricklefs 2006).

The importance of species dispersal has been accentuated especially in the context of island biogeography (Whittaker & Fernández-Palacios 2007), and is a central component of the theory of island biogeography (MacArthur & Wilson 1967) as well. Additionally, several population and community ecological theories have also underlined distribution as an significant aspect in shaping species richness patterns, for example, the theory of metacommunities – sets of local communities that are linked by dispersal of multiple potentially interacting species (Hanski 1999, Leibold et al 2004), unified neutral theory of biodiversity and biogeography (Hubbell 2001), which aims to account for the diversity and relative abundance of species in ecological communities, assuming that the differences among members of an ecological community of trophically similar species are neutral, or irrelevant to their success.

Evolutionary aspects, such as the phylogenetic background, have been emphasized particularly by Robert Ricklefs (Ricklefs 1987, 1989, 2006). According to the niche conservatism theory (also known as phylogenetic inertia) species have a tendency to retain ancestral ecological characteristics (Peterson et al 1999, Wiens & Graham 2005, Ricklefs 2006). Several other theories consist of a similar kernel, for example, biogeographical affinity theory

(Harrison & Grace 2007), tolerance hypothesis (Currie et al 2004), and tropical conservatism theory (Wiens & Donoghue 2004). Consequently, the dispersal, evolutionary and ecological processes should not be treated as mutually exclusive, and the patterns and origins of diversity ought to be studied in the context of some sort of unified theory.

The species pool concept

The species pool concept (Pärtel et al 1996, Zobel 1997, Pärtel 2002) unifies all three approaches necessary to study adequately species diversity patterns: ecological, evolutionary and dispersal processes. Species pool is the set of available species that are potentially capable of living in given ecological conditions (Eriksson 1993). According to the species pool concept, the species richness of local communities is determined mainly by the size of the pool of available species (the pool of species able to grow under given environmental conditions and that can migrate to a particular site) (Taylor et al 1990, Zobel 1997). Three types of species pool have been distinguished. The regional species pool is defined as the set of species capable of coexisting in a target community, and that are occurring in a certain region. The local pool is defined as the set of species occurring in the landscape around a target community that are capable of coexisting in that community. The actual species pool (or community species pool) is defined as the set of species present in a community (Pärtel et al 1996, Zobel 1997). Consequently, according to the species pool paradigm, species richness of a certain community depends, in addition to ecological processes, on evolutionary aspects and dispersal as well.

This paradigm has its roots in the species reservoir idea by Philip J. Grime (Grime 1979), along with Hodgson's (1987) observation that the present-day abundance of productive habitats is in evolutionary terms a novel situation without precedence in the evolutionary history of British flora. Rather similar ideas were proposed by Keddy (1992) and Diaz and others (1998), who called it "environmental filtering". The term "species pool hypothesis" was coined by Taylor and others in 1990, and since advancing from a hypothesis into a concept or paradigm at the end of 1990s, this approach has fostered several developments, such as the dynamic equilibrium theory (Huston 1994), quasi-neutral concept of plant community diversity (Zobel 2001), and the shifting limitation hypothesis (Foster et al 2004).

Plant species richness-productivity relationship

In addition to knowledge of species richness, it is also important to know how richness varies along environmental gradients. The relationship between species richness and net primary productivity has been one of the central topics in ecology for several decades. The first one to imply a possible importance of a relationship between diversity and productivity was G. Evelyn Hutchinson in his seminal essay *Homage to Santa Rosalia* (1959). The first actual observations were made in the 1960s (eg Whittaker 1966), but truly intensive research in this field began after J. P. Grime introduced the unimodal or “hump(ed)-back” species richness-productivity relationship for British herbaceous vegetation (Grime 1973, Al Mufti et al 1977, Grime 1979).

Unimodal curved relationships between species richness and productivity have remained the most common for plants (Waide et al 1999, Mittelbach et al 2001), although some case-studies have revealed positive, negative and U-shaped response patterns as well. The unimodal relationship became very popular and during the 1980s and 1990s it was considered almost ubiquitous, to quote, for example Begon, Harper, Townsend’s prominent textbook in ecology: *“The evidence, especially from plants, suggests that a decrease in species richness with resource enrichment is most common, or at least that a humped curve of species richness will be found if the whole productivity range is examined.”* (Begon et al 1996, pp 893).

When considering the entire productivity range, few organisms are expected to survive at the extremely low productivity due to a lack of resources. Simultaneous increase in number of individuals and species has been observed along increasing gradients of productivity (Waide et al 1999, Mittelbach et al 2001), but the main question remains: what happens to diversity at high productivity levels?

Grime originally proposed that competition becomes too intensive for species to co-exist at the higher productive end (Grime 1973). Competition has remained the most frequent explanation, and, although dozens of other possible reasons have been proposed, the majority of these theories have emphasized the effects of local scale processes in ecological timescale (reviewed in Rosenzweig & Abramsky 1993, Scheiner & Willig 2005). However, a few large-scale interpretations attributing the impact of distribution or evolutionary aspects to productivity-diversity patterns have been proposed. For example, seed addition experiments combined with local disturbances (Foster 2001, Foster et al 2004) have cemented the effects of dispersal (together with disturbance) to the species-richness productivity relationship. Variation in dispersal probability can influence the shape of productivity-diversity relationship as well (Pärtel & Zobel 2007).

From an evolutionary point of view the theories considering productivity-diversity relationship are mainly linked with phylogenetic background of

species (Ricklefs 2006, Harrison & Grace 2007), but also with differences in diversification rates of evolutionary lineages (Bruun & Ejrnaes 2006). The theory of niche conservatism (also called phylogenetic inertia) states that species are likely to maintain their niche characteristics after migrating to a different climatic zone (e.g. from the tropics to the temperate zone or vice versa) (Ricklefs 2005, 2006).

Since the size of the species pool is determined by speciation and historical migration, environmental conditions for speciation should be considered. Productive habitats have been rare in the temperate regions, and relatively few species have evolved for such conditions (Hodgson 1987, Taylor et al 1990, Aarssen 2004). Therefore, at high productivity levels, species richness is expected to be less, and unimodality of species richness-productivity relationship can be assumed. In contrast, productive habitats have been common in the tropics (Beerling 1999), and the species pool for such conditions should be relatively large, resulting in positive species richness-productivity relationships. For example, due to differences in evolutionary history, plant diversity is related positively with soil pH at higher latitudes, but negatively in the equatorial zone (Pärtel 2002). When taking into account the geological and evolutionary differences between tropical and temperate zones, one can assume that the shape of species richness-productivity relationship could vary in different locations as well, depending on the terrestrial geological history and evolutionary history of (plant) species.

One way to ascertain the causes underlying an ecological relationship is to study different functional groups. Peter J. Grubb noticed that the plant species richness-productivity relationship differs between woody and herbaceous species: in Northern Hemisphere, unimodal species richness-productivity relationship was common for herbaceous species, but woody species tended to have positive productivity-diversity relationships (Grubb 1987). This theory was later tested by William K. Cornwell and Peter J. Grubb (2003) on European plant communities and similar relationships emerged. Grubb's original explanation pointed out dissimilarities in clonality between herbaceous and woody species as the cause of different "behavior" of the species richness-productivity relationship (Grubb 1987). Indeed, clonality, which has evolved several times in several phylogenetic clades (Klimeš et al 1997), has a wide array of ecological and evolutionary consequences (Stuefer et al 2002). In a broad sense, clonal growth is considered to lead to competitive advances (Sackville-Hamilton et al 1987, van Groenendael et al 1996, Peterson & Jones 1997, Svennson et al 2005), especially at higher productivity levels, where competition is considered generally more intensive. Unlike herbaceous species, few trees are clonal (Aarssen 2007), and moreover, clonal woody and clonal herbaceous species have evolved in rather different regimes of natural selection (Peterson & Jones 1997) and several benefits of clonality in herbaceous species may not be beneficial for woody species (Jenik 1994). Furthermore, the evolutionary

history of woody and herbaceous species is essentially different. Most temperate zone trees originate from tropical lineages (Axelrod 1966, Richards 1996, Ricklefs, 2005, 2006). Due to niche conservatism, woody species may continue to possess characteristics that were ecologically needed by their ancestors (Ricklefs 2005, 2006). Hence, the shape of species richness-productivity relationship in plants may depend on the phylogenetic background of species of which community is assembled.

Consequently, both the dispersal-related and evolutionary explanations join closely together with the outcome of ecological processes in the context of species pool concept. Patterns of diversity represent the regional increase of species through immigration and diversification, their loss through extinction, and the sorting of species ecologically within the region (Ricklefs 2007). The species richness-productivity relationship needs a comprehensive approach on both macro- and microscale.

Contrasting soil heterogeneity patterns

One of the broadest divisions of vegetation is classification according to the main characteristics of dominant species, i.e. whether they are woody or herbaceous; e.g., woodlands (including forests and shrublands) and grasslands. As noted earlier, the difference between woodlands and grasslands, from an evolutionary point of view, can be rather significant, as temperate and tropical tree species are closely related, but herbaceous species are not. It would be interesting to know how woodlands and grasslands operate along climatic gradient. At large scales, the balance between woodlands and grasslands is defined by climate (Whittaker 1975, Woodward et al 2004), but at fine scales, local conditions, management and biotic interactions are also important (Wilson 1998, Pärtel & Wilson 2002, Pärtel & Helm 2007). Consequently, both woodlands and grasslands can be found in almost every region in the world.

One of the most important issues concerning the interactions between woodlands and grasslands is the ongoing and continuous repartition of land. Woody species are invading grasslands throughout the world, resulting in a major change in global vegetation (Van Auken 2000, Schroter et al 2005, Hobbs et al 2006). Disappearing grasslands leads to disappearing plant species (Pärtel et al 1999, Watkinson & Ormerod 2001, Motzkin & Foster 2002, Gauthier & Wiken 2003). Apart from several factors related to the expansion of woody species (for example, fire control, nitrogen pollution, increasing atmospheric carbon dioxide etc.), the invasion of woody plants into grasslands in temperate climatic zone is often attributed to an increase in soil resource heterogeneity (Schlesinger et al 1990, Schlesinger et al 1996, Kleb & Wilson 1997, Pärtel & Wilson 2002, Pärtel & Helm 2007).

The differences in soil heterogeneity of vegetation types has been attributed to the variance of root architecture of the dominating life form: woody species have widespread root systems especially competitive in heterogeneous soils (Campbell et al 1991, Grime 1994); herbaceous species tend to prefer more homogeneous soils, because their roots are short and therefore their exploring range is not as extensive as that of woody species (Farley & Fitter 1999). Furthermore, plants are able to change soil heterogeneity according to their soil resource distribution preferences; woody species turn soil more patchy (Garcia-Moya & McKell 1970, Kleb & Wilson 1997, James et al 2003), while herbaceous species homogenize soil (Pärtel & Wilson 2002, Lane & BassiriRad 2005).

Most studies concerning soil heterogeneity of woodlands and grasslands have been done in temperate zone, and the results from moderate climatic conditions dominate our scientific knowledge. However, ecological patterns should be tested for generality in different conditions and regions (Knapp et al 2004). For example, plant root morphology varies significantly in different biomes and regions (Jackson et al 1997, Craine et al 2005), and that variation is at least partly attributed to the geological age of soils: older soils are often phosphorus (P)-limited whereas younger soils are mostly nitrogen (N)-limited (Walker & Syers 1976, Vitousek & Farrington 1997, Lambers et al 2008). Differences in N and P availability result in differences of dynamics and importance of mycorrhiza (Fitter et al 2002, Craine et al 2005), thus the coevolutionary history of woody and herbaceous species and mycorrhiza may influence global patterns of soil heterogeneity.

Hypotheses

The purpose of this study was to examine the generalities of two ecological relationships: the relationship between plant species richness and productivity, and the relationship between vegetation type and soil heterogeneity. Both relationships were explored at the global scale, along a latitudinal gradient. The objectives of this thesis were as follows:

1. to examine the species richness-productivity relationship for plants across climatic and geographical gradients at the global scale (**Paper I**),
2. to test whether the unimodal species richness-productivity relationship is globally less common in woody species and in forests than in herbaceous species and grasslands (**Paper II**),
3. to test whether unimodal species richness-productivity relationship is more common if the dominant species in the productive sites are clonal or have a temperate evolutionary background (**Paper II**),
4. to test whether woodland and grassland soil heterogeneity varies in the same way with latitude, temperature and precipitation (**Paper III**).

MATERIAL AND METHODS

All three papers presented data collected from case-studies published in peer-reviewed journals, i.e. meta-studies. There were several common methodological aspects concerning all three studies: 1) metadata was extracted from published scientific literature by searching the most popular web databases (Blackwell-Synergy, JSTOR, ISI Web of Knowledge, ScienceDirect, Google Scholar etc.) and included inspection of citations of published articles to locate papers not included in the electronic databases; 2) geographical coordinates were extracted, mean annual temperature and annual precipitation were determined for each case-study from CLIMATE database version 2.1 (W. Cramer, personal communication; <http://www.pik-potsdam.de/~cramer/climate.html>); 3) all statistical analysis were performed using Statistica 6.1 (StatSoft 2004). In a result, all vegetated continents and all major climatic zones were represented in each meta-study.

Paper I – Generality of species richness-productivity relationship

Species richness-productivity data were extracted from scientific literature. We selected studies in which terrestrial, experimentally not manipulated plant ecosystems were studied. The measure of diversity was species richness, i.e., the number of species present in an area. Productivity was defined as the rate of energy flow to a system, but as this rate is rarely measured in nature, we used several indirect measurements that are known to correlate quite strongly with productivity. We accepted indirect measures and estimates of productivity since species richness-productivity relationship is generally independent of the productivity measure (Groner & Novoplansky 2003).

Mittelbach and others (2001) classified the shape of species richness-productivity relationship into five patterns: positive, negative, unimodal, U-shaped, or no significant relationship. We simplified that classification, and divided cases into three groups: unimodal, positive, and no relationship. The negative productivity–diversity relationship was merged with the unimodal relationship because most studies reporting a negative correlation focused on intermediate and high productivities. Because the U-shaped relationship has been reported so infrequently, and no viable biological explanation for it has been proposed, it was merged with the group with no relationship.

Multinomial logit regressions were used to test whether the shape of the productivity–diversity relationship was related to latitude, temperature and precipitation. Regressions were calculated and the best model was selected according to the Akaike Information Criterion (Akaike 1973).

Additionally, we studied how proportions of unimodal and positive relationships vary across latitudes. Latitudinal gradient was divided into 10°-wide zones from the equator to latitude of 70°, and looked for proportions of different species richness-productivity relationships within each zone. Each latitudinal zone contained at least 11 studies. Logratios for positive and unimodal relationships (both divided by cases with no relationships) were used for statistics in order to derive independent and normal distributions from the compositional data (Aitchison 1986). Polynomial regressions were used to relate logratios to latitudinal zones.

Paper II – Species richness-productivity relationship for woody species

The metadata for this paper was based directly on metadata of paper I, so the methods of choosing case-studies and classifying parameters are the same as those in paper I. Additionally, we recorded whether each case-study was done in forests or open communities. Some studies were done in forest ecosystems, but only herbaceous species were studied, therefore, some forests in our dataset are dominated by herbs.

We divided the sites or plots used in each case-study into three relative productivity classes: low, intermediate and high. Of the case-studies used in paper I, we extracted information on the dominant species at the highest productivities. When the dominant specie or species were not identified, we used species biomass, frequency or abundance as the estimate dominance. For dominant species, we determined life-form (woody or herbaceous), clonality (species that reproduce mainly with seeds, equally with seeds and vegetatively, or mainly vegetatively), and the evolutionary background of its lineage (temperate, global or tropical). Information concerning dominant species was available only for less than quarter of case-studies included in the metadata of paper I.

Data concerning the life-form and clonality were gathered from different databases, such as BiolFlor (<http://www.ufz.de/biolflor/>), the Fire Effects Information System (<http://www.fs.fed.us/database/feis/>), the PLANTS data base (<http://plants.usda.gov/>) etc. Evolutionary history was determined on the basis of the geographical distribution of species clade (mostly at the subfamily level) using descriptions from the Angiosperm Phylogeny Website (<http://www.mobot.org/MOBOT/research/Apweb>). This database is based on the latest phylogeny of plants and includes data on geographical distribution.

We used 2×2 Fisher exact tests on the paper I data set to verify whether the unimodal species richness-productivity relationship is globally less common for woody species and in forests than for herbaceous species and in grasslands. Similarly, we used a 2×3 Fisher exact test to check whether the cases with

dominant species from the species richness-productivity relationship case studies show dependence between life-form and clonality.

To analyze the dominant species, we used generalized linear models (binomial distribution, Type 1 likelihood-ratio test) linking species richness-productivity relationship type to life-form, clonality and evolutionary background, based on individual parameters and in a single model including all pairwise interactions.

Paper III – Soil heterogeneity in woodlands and grasslands

Metadata was extracted from the literature on the requisite that each case-study contained the following: 1) paired woodland–grassland stands with similar edaphic conditions and sampled in a similar way (scale, number of replicates, methods of soil analyses). We omitted studies in which small woody patches were studied in grasslands or vice versa. Similarly, early successional stands were omitted (e.g., young plantations, old-field series, recent forest clear-cuts). If multiple locations were reported within a single case study, all locations were included; replicated measures of soil nitrogen (N; total nitrogen was used when reported) or carbon (C; organic matter content was used as an alternative) in the topsoil (mostly the upper 10 cm); coefficients of variation ($CV = SD/mean$; Zar 1996), or data that allowed us to calculate the CV of N and C.

We used the CV to estimate soil heterogeneity since it is unitless and can be used with different original units of measurement (e.g., percentage, g/m^2 , etc.). The CV is also independent of the average value of soil N or C, and thus relative variability at both low and high resource conditions can be compared. In most cases, CVs were between 0 and 1. The CV rarely exceeded 1, and such cases were omitted due to extreme heterogeneity.

The CVs were arcsine-square root transformed, and the scale and number of replicates were \log_{10} -transformed in order to get normal distributions, confirmed by the Kolmogorov–Smirnov test (Zar 1996). We related CVs in grasslands to CVs in woodlands using Model II (reduced major axis) regression, since we cannot distinguish independent and dependent variables (Sokal & Rohlf 1995).

In order to study the deviance from a null model we used Model II regression residuals. Residuals of CVs were tested for relationships to latitude, annual precipitation, mean annual temperature and number of replicates. We used generalized linear models (normal distribution, identity link function) separately for residuals of N and C heterogeneity. The best model was chosen according to Akaike Information Criterion (Akaike 1973). Similar generalized linear model analyses were performed separately for CVs of woodlands and grasslands.

RESULTS

Paper I – Generality of species richness-productivity relationship

Altogether 163 case-studies qualified for inclusion in the meta-study concerning the shape of species richness-productivity relationship (I, Appendix). All climatic zones and continents (except Antarctica) were represented in the dataset (Fig 2). Of these 163 cases, 57 featured a unimodal relationship (including 20 that reported a negative relationship), 46 found a positive relationship, and 60 found no relationship (including six U-shaped relationships).

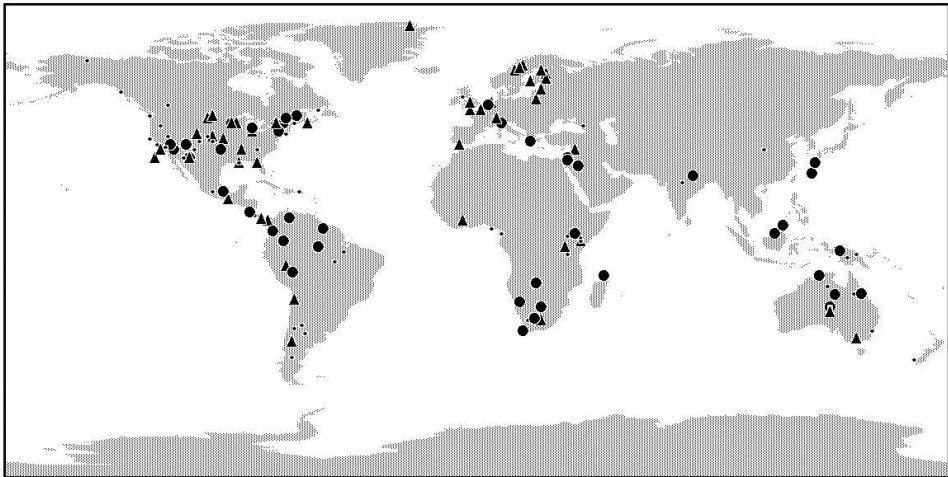


Fig. 2. Locations of plant productivity-diversity case-studies throughout the world. Symbols indicate the relationship shape (triangles = unimodal; circles = positive; points = no relationships). Some locations are slightly shifted for better visibility.

The shape of the species richness-productivity relationship was significantly different between tropical and temperate regions, as it was significantly related to mean annual temperature ($\chi^2 = 23.1$, $df = 2$, $P < 0.0001$), and latitude ($\chi^2 = 22.7$, $df = 2$, $P < 0.0001$). According to the Akaike Information Criterion, annual precipitation was not included in the best model.

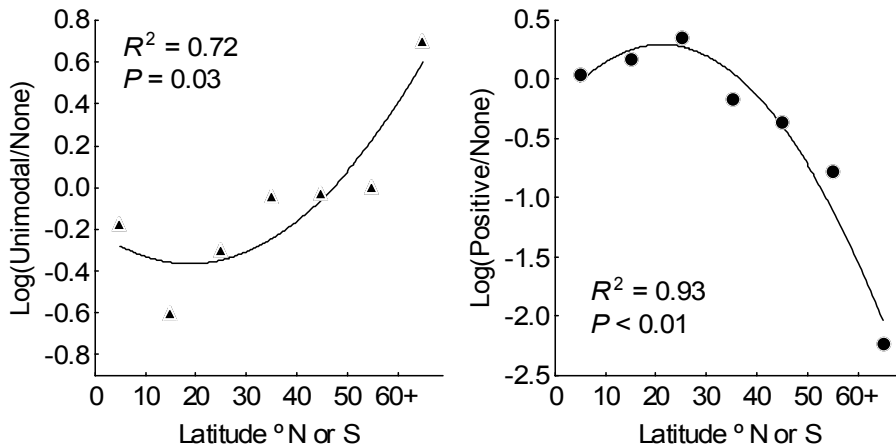


Fig. 3. Results of polynomial regression – significance of unimodal (left) and positive productivity-plant diversity relationships (right) across latitude. The logratios of proportions are used for the compositional data.

The proportions of different species richness-productivity relationships were nonlinearly related to latitude (Fig 3). From the equator to the poles, the proportion of the unimodal species richness-productivity relationship increases significantly ($R^2 = 0.72$, $P = 0.0337$), and the proportion of the positive productivity–diversity relationship decreases significantly ($R^2 = 0.93$, $P = 0.0019$).

Paper II – Species richness-productivity relationship in woody species

The analysis of the same 163 case-studies in Paper I revealed a unimodal species richness-productivity relationship to be significantly more common for herbaceous than woody species and in grasslands than forests (Table 1). Using the data set of 46 species from species richness-productivity relationship case studies (II, Appendix S2), life-form was significantly associated with clonality class, with herbaceous species being more commonly clonal than woody species (Table 2).

Table 1. 2x2 tables showing the relationship between the shape of the species richness–productivity relationship (SRPR) and a) life form (whether only woody or all species: woody + herbaceous), or b) ecosystem type (forest vs. grassland) for 163 case studies.

	SRPR		Fisher Exact test
	Unimodal	Other	
a)			
Only woody species	2	25	
All plant species	54	82	P = 0.0006
b)			
Forests	9	45	
Grasslands	47	62	P = 0.0005

Life-form, clonality and evolutionary background were all associated with unimodality of species richness-productivity relationship when analyzed separately (Table 3). In a combined model using all three parameters, however, only clonality and evolutionary background were significant, with life-form modifying the clonality effect (Table 3). When clonal species or species originating from global or temperate evolutionary lineages dominated, a unimodal species richness-productivity relationship was common. However, there was a significant interaction between clonality and woodiness. Unimodal species richness-productivity relationships were associated only with woody species that are usually or often clonal, but for herbaceous species unimodal relationships were associated with all clonality classes.

Table 2. Relationship between clonality (capability of vegetative reproduction) and growth form (woody or herbaceous) of dominant or most abundant species at the highest productivities.

	Clonality*:			Fisher Exact test
	Rare	Present	Common	
Woody species	7	12	2	
Herbaceous species	2	11	12	P = 0.0069

* Clonality values: rare – species that reproduce only or mainly with seeds; present – equally with seeds and vegetatively; common – vegetatively, or mainly vegetatively.

The complete model was significant (log-ratio $\chi^2 = 28.61$, $df = 13$, $P = 0.0074$), and after the removal of non-significant terms, the significance increased further (logratio $\chi^2 = 26.19$, $df = 7$, $P = 0.0005$). Thus clonality and evolutionary origin jointly dictate whether the SRPR is unimodal in our dataset, but woodiness is significant only in interaction with clonality.

Table 3. Unimodality of species richness-productivity relationship in relation to clonality, life form (woody/herbaceous) and evolutionary background at the highest productivities according to GLM.

	Single model				Separate models		
	Df	Log-likelihood	Chi-square	P	Log-likelihood	Chi-square	P
Intercept	1	-28.27					
Clonality	2	-24.95	6.69	0.0364	-24.95	6.69	0.0364
Life form	1	-23.91	2.09	0.1480	-25.76	5.01	0.0252
Evolutionary background	2	-19.79	8.24	0.0163	-23.43	9.68	0.0079
Clonality*Life form	2	-15.17	9.24	0.0099			
Clonality*Evolutionary background	4	-14.93	0.48	0.9753			
Life form*Evolutionary background	2	-13.96	1.94	0.3791			

Paper III – Soil heterogeneity in woodlands and grasslands

We found 72 and 81 locations with N and C data, respectively (Fig. 4; **III**, Appendix S1). Analyses revealed that the CVs of grassland and woodland resources were strongly related for both soil N and C (**III**, Fig. 2).

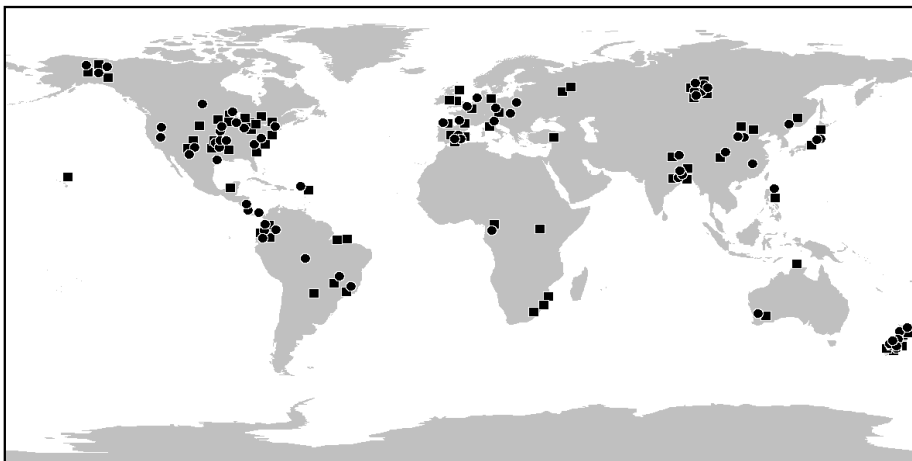


Figure 4. Locations of paired woodland-grassland sites obtained from the literature that described soil nitrogen (circles) and carbon (squares) heterogeneity. Some points are slightly shifted in order to decrease overlap.

Differences between CVs in woodland and grassland pairs (the residuals from **III** Fig. 2) were related to geographical and climatic variables. The best model included only latitude for both soil N ($\chi^2 = 12.2$, $df = 1$, $P < 0.0005$) and soil C ($\chi^2 = 6.5$, $df = 1$, $P = 0.0103$); soils were more heterogeneous in woodland in temperate regions, but in grassland in tropical regions (Fig. 5).

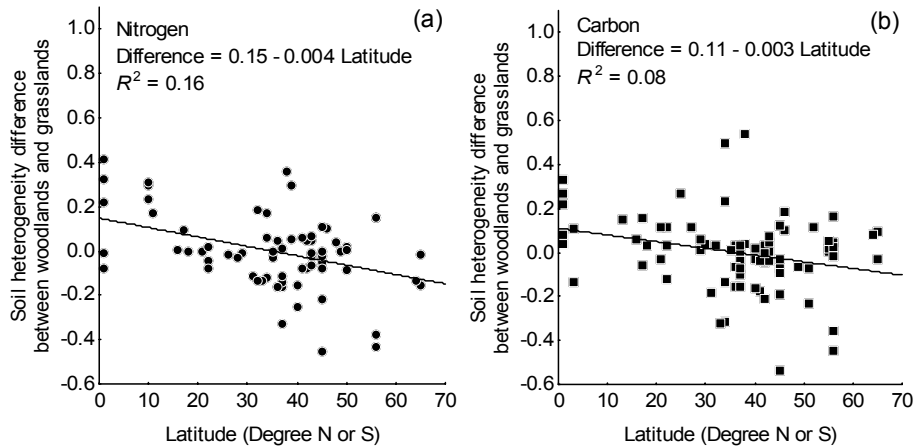


Figure 5. Relationships between differences in soil nitrogen (a) and carbon (b) heterogeneity of woodlands and grasslands, and latitude. Positive values indicates greater heterogeneity in grasslands; negative values greater heterogeneity in woodlands.

Woodland CV did not vary significantly with any geographical parameters (e.g. Fig. 6a,b for latitude). Grassland soil N heterogeneity was related to latitude (Fig. 6c, $\chi^2 = 22.1$, $df = 1$, $P < 0.0001$). The same significant relationship emerged for soil C heterogeneity, which was likewise related to latitude (Fig. 6d, $\chi^2 = 8.4$, $df = 1$, $P = 0.0038$).

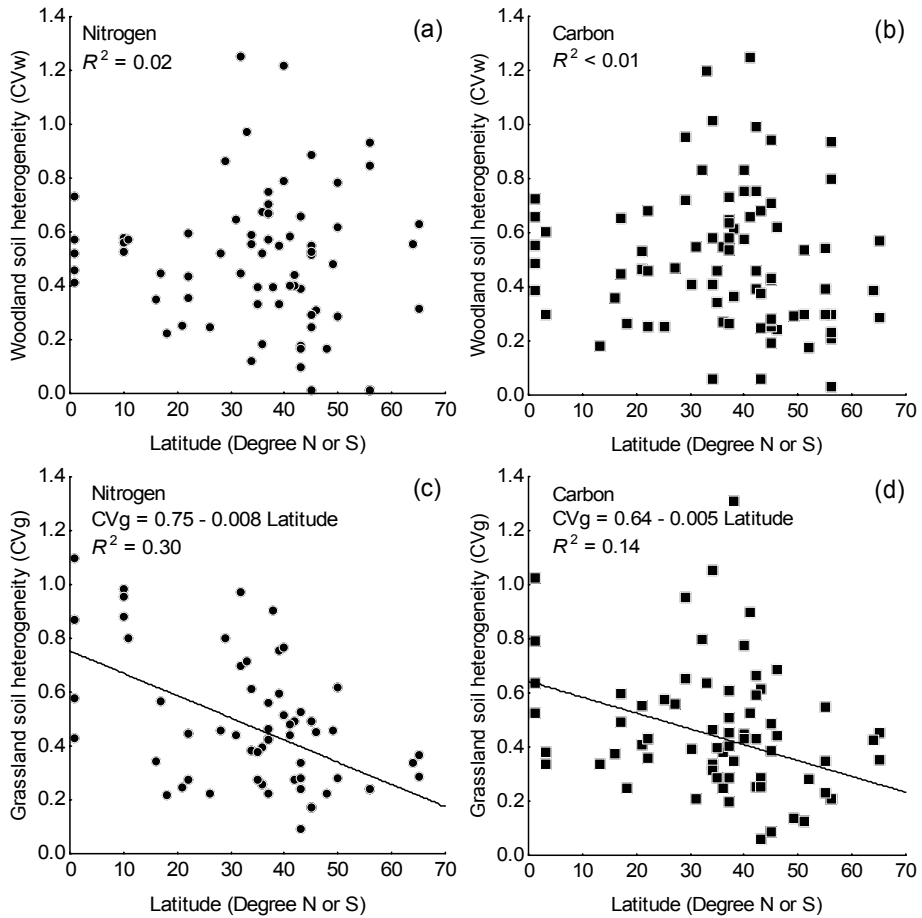


Figure 6. Relationships between soil nitrogen (a, c) and carbon (b, d) heterogeneity (arcsine-square root transformed Coefficient of Variation) in woodlands (a, b) and grasslands (c, d), and latitude. Woodland heterogeneity had no significant relationships. Grassland heterogeneity was higher at lower latitudes.

Consequently, tropical grassland soils were more heterogeneous than temperate grassland soils. The difference between soil heterogeneity in woodlands and grasslands depends on grasslands, since grassland soil heterogeneity varied with latitude whereas woodland soil heterogeneity did not.

DISCUSSION

Significant global variation was found for both ecological relationships: between plant species richness and productivity, and between soil heterogeneity and dominating life form (woody vs. herbaceous). Unimodal species richness-productivity relationship dominated in the temperate zone and positive relationship was significantly more common in the tropics. Moreover, unimodal species richness-productivity relationships were globally less prevalent for trees and in forests than for herbaceous species and grasslands, and also when community dominant species originated from tropics and were not clonal. Soil heterogeneity was higher under woody vegetation only in the temperate zone, but in the tropics grassland soils tended to be more heterogeneous than woodland soils. Since both tropical and temperate zones and woody and herbaceous species have contrasting evolutionary histories, these results can be attributed collectively to large-scale evolutionary and geographical processes. Consequently, the effects of large-scale processes on local species pools must be considered when studying local vegetation patterns.

Unimodality of species richness-productivity relationship was restricted largely to the temperate zone, whereas positive relationships dominated the tropics (Fig. 3). Latitude was the most significant attribute affecting the species richness-productivity relationship – it described approximately 80% of the variation. Our explanation for this variation is based on the dissimilar evolutionary history of species pools in different climatic zones. Evolutionary history of tropical and temperate zones show contrasting tendencies: productive habitats in tropical regions have been more prevalent throughout evolutionary history (Beerling 1999), while highly productive sites in the temperate zone are less common or are fairly young (Hodgson 1987).

Our results support a theoretical model (Stevens 2006) in which a unimodal species richness-productivity relationship was expected when low temperature or precipitation limit diversity at low productivity and high soil nutrients limit diversity at high productivity. The tropics feature high temperature and variable precipitation, though tropical soils are poor in nutrients (Thorp & Baldwin 1940, Grubb 1995, Hartemink 2002).

Grime (Al Mufti et al 1977, Grime 1979) attributed low diversity at very low productivity to evolutionary processes: very few species have managed to evolve for highly stressful conditions. The species-pool hypothesis actually began with the same idea with respect to the high end of the productivity gradient – species numbers are limited in fertile conditions due to the historical scarcity of productive habitats in the temperate zone (Hodgson 1987, Taylor et al 1990). We provide the first support for this hypothesis on the global scale, comparing species richness-diversity relationships in temperate and tropical regions, which exhibit completely different evolutionary histories.

According to Grime (1979), the role of species pools (in his terminology, species reservoir) determines local diversity primarily at intermediate productivity levels and competition remains the main force responsible for low diversity at high productivity levels. We showed that in addition to the effects of ecological processes, the differential evolutionary history of species pools may also affect local diversity at high productivity. There is increasing evidence for the important role of the evolutionary history of species pools for local biodiversity patterns; for example, the relationship between diversity and soil pH is different between tropical and temperate regions as well (Pärtel 2002).

However, our evidence for large-scale processes does not rule out ecological effects, since both evolutionary and ecological determinants of the response pattern act in unison (Huston 1999, Pärtel et al 2000, Foster et al 2004, Bruun & Ejrnæs 2006). Zobel and Liira (1997) used relative richness (the ratio of local richness to species pool size) – thus eliminating the possible effect of the size of the species pool – and still found a unimodal (albeit weaker) species richness-productivity relationship in field-layer communities in the temperate zone.

Consequently, these results indicate that the species richness-productivity relationship is not a universal ecological pattern, and significant differences in its emergence may appear between regions with different evolutionary histories (Pärtel 2002, 2006). This message is important to conservation biology because regional differences in the basic empirical relationships of diversity should be considered for predicting potential biodiversity, estimating losses, and planning conservation areas (Pärtel et al 2004). Contrary to suggestions (e.g., Wohlge-muth 1998, Hodgson et al 2005, Wassen et al 2005), it is incorrect to pay greater conservation effort to regions with low and intermediate productivity. We cannot “export” this conservation knowledge globally, since the unimodal species richness-productivity relationship is not globally dominant.

When studying the species richness-productivity relationship in woody and herbaceous species, the unimodal relationship pertained more to herbaceous species and grasslands (Table 1), which can be attributed to both ecological and evolutionary processes. Herbaceous species are significantly more clonal than woody species (Aarssen 2007) and the ability of vegetative reproduction may increase species competitiveness (Grubb 1987). Additionally, according to the ideas of niche conservatism (Ricklefs 2005, 2006) or biogeographical affinity (Harrison & Grace 2007), lineages that have migrated to other climatic conditions still demonstrate characteristics that were ecological requirements of their ancestors. Temperate woody species descend from lineages that often originate from tropical regions (Ricklefs 2006), where unimodality of species richness-productivity is rare (Fig. 3). According to the dataset (II, Appendix S2), both clonality and evolutionary background are significantly related to the pattern of species richness-productivity relationship with woodiness complicating the clonality effect (Table 3); thus there are multiple correlates of diversity patterns (Pärtel et al 2000, Foster et al 2004).

The distinctness of forests and grasslands is quite underrated in ecological generalizations (Pärtel & Wilson 2002, Cornwell & Grubb 2003). On a global-scale, support was found for the idea that unimodal species richness-productivity relationship may not be a suitable model for woody species (Grubb 1987) (Table 1). There were only two cases in which a unimodal species richness-productivity relationship was described for woody species, and neither case was truly forest, but shrubland (Table 1a). Shrubs represent the intermediate ecological form between trees and herbaceous species (Cornwell & Grubb 2003) and, for example, when growing in open communities, the ecology of shrubs is considerably more similar to that of herbs than trees (Grubb 1987). Nine forest ecosystems were found with a unimodal species richness-productivity relationship (Table 1b), but most of these cases focused only on the herbaceous species within the forest community and woody species were excluded from the analyses.

According to Grubb (1987), unimodal species richness-productivity relationships in grasslands and herbaceous species result from the dominant clonality among herbaceous species, in contrast to woody species, and in agreement with the dataset (II, Appendix S2), herbaceous dominants also demonstrated a significantly higher clonality rate than woody species on the global scale (Table 2). The significance of clonality may manifest through the higher competitive abilities of clonal species (van Groenendael et al 1996, Peterson & Jones 1997, Svennson et al 2005), especially for herbaceous species (Jenik 1994, Reynolds et al 2007). Clonality of dominant species was indeed significantly related to the unimodality of species richness-productivity relationships (Table 3). Consequently, indirect support was found for the original idea of Grime (1979) that the decline of species richness at high productivity may be due to competitive exclusion. In contrast, a meta-analysis by Goldberg and others (1999) suggested that the intensity of competition often declines significantly with productivity, instead of increasing with it. Therefore, clonality itself may be more important than general competitive ability, and the linkage between clonality and vegetation patterns needs to be explored further.

Furthermore, in addition to clonality, evolutionary history may affect species richness-productivity relationships as well. As the results from Paper I suggest, unimodal species richness-productivity relationships are largely restricted to the temperate zone (Fig. 3), where highly productive habitats have been scarce throughout evolutionary history. Temperate tree species originate mainly from tropical lineages (Axelrod 1966, Richards 1996, Ricklefs, 2005, 2006). Niche conservatism theory asserts that species tend to retain the characteristics of their ancestors and therefore dominant tree species from the temperate zone have maintained their tropical niche characteristics (Ricklefs 2006) resulting in non-unimodal species richness-productivity relationships. Analysis of the dataset shows (Table 3) that evolutionary background is related significantly to the species richness-productivity relationship, regardless of whether the dominant

species is woody or herbaceous. Consequently, niche conservatism can explain why some unimodal species richness-productivity relationships can still be found in the tropics. As a result, niche conservatism may adequately account for the shape of some species richness-productivity relationships.

Similar global variation was found in studies of soil heterogeneity in woodlands and grasslands. The previously described higher soil heterogeneity under woody vegetation (Schlesinger et al 1996, Kleb & Wilson 1997, Pärtel & Helm 2007) was restricted to temperate regions. In the tropics, grassland soils tended to be more heterogeneous than woodland soils (Fig. 5). This variability in the relationship was due to grasslands (Fig. 6), since grassland soil heterogeneity varied across latitudinal gradients (latitude described up to 30% of variation in grassland soil heterogeneity), whereas woodland soil heterogeneity did not. Although both soil N and C heterogeneity have significant geographical and climatic variation on a global scale, the relationship between soil heterogeneity and vegetation type is still significantly dependent on region, and the consequences of a global vegetation change may differ between temperate and tropical regions.

There is a diverse array of possible mechanisms underlying the given results: topographical variation, grazing, disturbance by burrowing animals, litter quality and effects of roots on soil resources (Stark 1994). Unfortunately, our dataset was too robust and descriptive to isolate any of these mechanisms, although one factor, the spatial redistribution of carbon and nutrients by root activity, is extremely important to all types of vegetation (Jobbágy & Jackson 2001). The possible contribution of roots to global patterns of soil heterogeneity was investigated. Soil may become heterogeneous if fine roots are distributed heterogeneously in space (horizontally or vertically) or in time (through root turnover).

Unfortunately no comparable data on the horizontal distribution of fine roots was available for each climatic zone. However, in addition to horizontal root distribution, vertical distribution may also influence soil patches. Rooting depth is related to the upward transport of nutrients (Jobbágy & Jackson 2001), which may create local resource-rich patches. In temperate grasslands, 95% of roots reach a depth of 89 cm, which is significantly less than in temperate woodlands (123 cm). In tropical grasslands, 95% of roots reach 123 cm, which is similar to the depth in tropical woodlands (139 cm) (Schenk & Jackson 2002). Thus, grassland rooting depth varies considerably with latitude, whilst woodland rooting depth does not. This may contribute to differences in soil heterogeneity in temperate and tropical grasslands.

High rates of root turnover would appear as high spatial variability at any given time.

Heterogeneous woodlands in temperate zone have been found to be positively correlated with root turnover on a scale of 1 m, whereas more homogeneous grassland soils are associated with lower turnover (Pärtel & Wilson

2002). In a global survey, grassland root turnover was significantly positively related to mean annual temperature, but no such relationship was found for woodland roots (Gill & Jackson 2000). Additionally, fine roots in tropical grassland had the highest turnover values of all terrestrial ecosystems. Consequently, higher root turnover in tropical grasslands may contribute to relatively higher soil heterogeneity than in temperate grasslands with longer-living roots.

The contrasting fine root behaviour of temperate (less patchy) and tropical (more patchy) grassland species may be related to their contrasting evolutionary backgrounds. Most temperate woody species originate from tropical ancestors (Ricklefs 2006). Thus, tropical and temperate woody species may be similar in their fine root behaviour due to common evolutionary history. In contrast, there is little overlap between phylogenetic lineages of tropical and temperate grassland; tropical grasslands are dominated by C4 taxa and temperate grasslands by C3 taxa (Woodward et al 2004). Thus, rooting traits in temperate and tropical grasslands may be different simply because of their dissimilar evolutionary histories.

CONCLUSIONS

Most common knowledge in ecology comes from well-studied temperate regions. Ecologists from Europe and Northern America carry out their experiments and observations mostly in suitable communities surrounding their universities and institutes. In the light of novel macroecological approach, this tendency has created some serious biases in our understanding of several ecological relationships.

When scientific research dominates in one region, it is rational to assume that evolutionary and geological history plays a significantly lesser role in the context of extracting new knowledge from them, than from local ecological processes. The problem is that the results from temperate zone are often extrapolated all over climatic gradients, without considering regional and evolutionary differences in other climatic zones.

The results of the three global scale meta-studies discussed in this thesis show that even well-known and seemingly thoroughly explored ecological relationships vary significantly in different climatic zones, and this variation is much more pertained to large-scale and evolutionary processes than assumed by the majority of scientists exploring this field. Although the macroecological approach was launched in order to find global generalities and patterns of life, it acts as a sort of warning signal as well, proving that ecological relationships are not as ubiquitous as sometimes expected.

According to the hypothesis, the following conclusions were made:

1. The unimodal plant species richness-productivity relationship is not a global phenomenon, but is merely prevalent in the temperate zone, whereas the positive relationship is more common in the tropics.
2. Furthermore, unimodal species richness-productivity relationship was globally less common in woody species and in forests than in herbaceous species and grasslands.
3. Additionally, clonality and temperate evolutionary background of the most abundant species in community generates unimodal species richness-productivity relationships.
4. The soil in tropical grasslands is more heterogeneous than in temperate grasslands, but no such pattern was found in woodlands.

Unimodal species richness-productivity relationships have probably been widely discussed in the ecological literature because most relevant studies involve clonal species of temperate origin. This, however, cannot be generalized to other species and regions.

Tropical grasslands were more heterogeneous than temperate grasslands, but there was no such pattern found in woodlands. This pattern is consistent with global patterns in fine root distribution and turnover. Tropical grasslands are deep-rooted and characterized by high root turnover. *In situ* experiments are

needed to determine exactly which mechanisms are responsible for high soil resource heterogeneity in tropical grasslands.

The results discussed in this thesis indicate that ecological relationships should be tested for their generality across global gradients and climatic zones. Consequently, care is needed when “exporting” ecological assumptions to other regions.

REFERENCES

- Aarssen, L.W. (2004) Interpreting co-variation in species richness and productivity in terrestrial vegetation: Making sense of causations and correlations at multiple scales. *Folia Geobotanica*, 39, 385–403.
- Aarssen, L.W. (2007) Death without sex – the ‘problem of the small’ and selection for reproductive economy in flowering plants. *Evolutionary Ecology*, doi: 10.1007/s10682-007-9170-z.
- Aitchison, J. (1986) The statistical analysis of compositional data. Chapman and Hall, New York, New York, USA.
- Akaike, H. (1973) Information theory as an extension of the maximum likelihood principle. In: 2nd International Symposium on Information Theory (eds. Petrov, B.N. & Csaksi, F.) pp. 267–281. Akademiai Kiado, Budapest, Hungary.
- Al Mufti, M.M., Sydes, C.L., Furness, S.B., Grime, J.P. & Band S.R. (1977) A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *Journal of Ecology*, 65, 759–791.
- Axelrod, D.I. (1966) Origin of deciduous and evergreen habits in temperate forests. *Evolution*, 20, 1–15.
- Beerling, D.J. (1999) The role of the terrestrial biosphere in Holocene carbon cycle dynamics. *Global Ecology and Biogeography*, 9, 421–429.
- Begon, M., Harper, J.L. & Townsend C.R. (1996) Ecology: individuals, populations and communities, 3rd edn. Blackwell Scientific Publications, Boston.
- Blackburn, T.M. & Gaston, K.J. (2002) Macroecology is distinct from biogeography. *Nature*, 418, 723.
- Brown, J.H. (1995) Macroecology. The University of Chicago Press, Chicago
- Brown, J.H. & Maurer B.A. (1989) Macroecology: the division of food and space among species on continents. *Science*, 243, 1145–1150.
- Bruun, H.H. & Ejrnæs, R. (2006) Community-level birth rate: a missing link between ecology, evolution and diversity. *Oikos*, 113, 185–191.
- Campbell, B.D., Grime, J.P. & Mackey, J.M.L. (1991) A trade-off between scale and precision in resource foraging. *Oecologia*, 87, 532–538.
- Cornwell, W.K. & Grubb, P.J. (2003) Regional and local patterns in plant species richness with respect to resource availability. *Oikos*, 100, 417–428.
- Craine, J.M., Lee, W.G., Bond, W.J., Williams, R.J. & Johnson, L.C. (2005) Environmental constraints on a global relationship among leaf and root traits of grasses. *Ecology*, 86, 12–19.
- Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A.D., & Kaufman M. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7, 1121–1134.
- Diaz, S., Cabido, M. & Casanoves F. (1998) Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science*, 9, 113–122.
- Eriksson, O. (1993) The species-pool hypothesis and plant community diversity. *Oikos*, 68, 371–374.
- Farley, R.A. & Fitter, A.H. (1999) Temporal and spatial variation in soil resources in a deciduous woodland. *Journal of Ecology*, 87, 688–696.
- Fitter, A., Williamson, L., Linkohr, B. & Leyser, O. (2002) Root system architecture determines fitness in an Arabidopsis mutant in competition for immobile phosphate

- ions but not for nitrate ions. *Proceedings of the Royal Society B: Biological Sciences*, 269, 2017–2022.
- Foster, B.L. (2001) Constraints on colonization and species richness along a grassland productivity gradient: the role of propagule availability. *Ecology Letters*, 4, 530–535.
- Foster, B.L., Dickson, T.L., Murphy, C.A., Karel, I.S. & Smith, V.H. (2004) Propagule pools mediate community assembly and diversity-ecosystem regulation along a grassland productivity gradient. *Journal of Ecology*, 92, 435–449.
- Garcia-Moya, E. & McKell, C.M. (1970) Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology*, 51, 81–88.
- Gaston, K.J. & Spicer, J.I. (2004) Biodiversity: an introduction. Second Edition. Blackwell Publishing, Oxford.
- Gauthier, D.A. & Wiken, E.B. (2003) Monitoring the conservation of grassland habitats, prairie ecozone, Canada. *Environmental Monitoring and Assessment*, 88, 343–364.
- Gill, R.A. & Jackson, R.B. (2000) Global patterns of root turnover for terrestrial ecosystems. *New Phytologist*, 147, 13–31.
- Gillman, L.N. & Wright, S.D. (2006) The influence of productivity on the species richness of plants: a critical assessment. *Ecology*, 87, 1234–1243.
- Goldberg, D.E., Rajaniemi, T., Gurevitch, J. & Stewart-Oaten, A. (1999) Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology*, 80, 1118–1131.
- Grime, J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature*, 242, 344–347.
- Grime, J.P. (1979) Plant strategies and vegetation processes. John Wiley, Chichester.
- Grime, J.P. (1994) The role of plasticity in exploiting environmental heterogeneity. *In: Exploitation of environmental heterogeneity by plants: ecophysiological processes above-and belowground* (ed. by M.M. Caldwell), pp. 1–19. Academic Press, San Diego.
- Groner, E. & Novoplansky, A. (2003) Reconsidering diversity-productivity relationships: directness of productivity estimates matters. *Ecology Letters*, 6, 695–699.
- Grubb, P.J. (1987) Global trends in species-richness in terrestrial vegetation: a view from the Northern Hemisphere. *In: Organization of communities. Past and present. The 27th symposium of the British Ecological Society, Aberystwyth, 1986* (ed. by J.H.R. Gee and P.S. Giller), pp. 99–118. Blackwell Scientific Publications, Oxford.
- Grubb, P.J. (1995) Mineral nutrition and soil fertility in tropical rain forests. *In: Tropical forests: management and ecology* (ed. by A.E. Lugo and C. Lowe), pp 308–330. Springer, New York, New York.
- Hanski, I (1999) *Metapopulation Ecology*. Oxford University Press. Oxford.
- Harrison, S. & Grace, J.B. (2007) Biogeographic affinity helps explain productivity-richness relationships at regional and local scales. *The American Naturalist*, 170, S5–S15.
- Hartemink, A.E. (2002) Soil science in tropical and temperate regions – some differences and similarities. *Advances in Agronomy*, 77, 269–292.
- Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vila, M., Zamora, R. & Zobel, M. (2006) Novel

- ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, 15, 1–7.
- Hodgson, J.G. (1987) Why do so few plant species exploit productive habitats? An investigation into cytology, plant strategies and abundance within a local flora. *Functional Ecology*, 1, 243–250.
- Hodgson, J.G., Grime, J.P., Wilson, P.J., Thompson, K. & Band, S.R. (2005) The impacts of agricultural change (1963–2003) on the grassland flora of Central England: processes and prospects. *Basic and Applied Ecology*, 6, 107–118.
- Hubbell, S.P. (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton.
- Huston, M.A. (1994) Biological diversity. The coexistence of species on changing landscape. Cambridge University Press, Cambridge.
- Huston, M.A. (1999) Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos*, 86, 393–401.
- Hutchinson, G. E. (1959) Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist*, 93, 145–159.
- Jackson, R.B., Mooney, H.A. & Schulze, E.D. (1997) A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences USA*, 94, 7362–7366.
- James, S.E., Pärtel, M., Wilson, S.D. & Peltzer, D.A. (2003) Temporal heterogeneity of soil moisture in grassland and forest. *Journal of Ecology*, 91, 234–239.
- Jenik, J. (1994) Clonal growth in woody plants: a review. *Folia Geobotanica et Phytotaxonomica*, 29, 291–306.
- Jobbágy, E.G. & Jackson, R.B. (2001) The distribution of soil nutrients with depth: Global patterns and the imprint of plants. *Biogeochemistry*, 53, 51–77.
- Keddy, P.A. (1992) Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, 3, 157–164.
- Kleb, H.R. & Wilson, S.D. (1997) Vegetation effects on soil resource heterogeneity in prairie and forest. *The American Naturalist*, 150, 283–298.
- Klimeš, L., Klimešová, J., Hendriks, R. & van Groenendael, J. (1997) Clonal plant architecture: a comparative analysis of form and function. The ecology and evolution of clonal plants (ed. by H. de Kroon and J. van Groenendael) pp. 1–29. Backhuys Publishers, Leiden.
- Knapp, A.K., Smith, M.D., Collins, S.L., Zambatis, N., Peel, M., Emery, S., Wojdak, J., Horner-Devine, M.C., Biggs, H., Kruger, J. & Andelman, S.J. (2004) Generality in ecology: testing North American grassland rules in South African savannas. *Frontiers in Ecology and the Environment*, 2, 483–491.
- Lambers, H., Raven, J.A., Shaver, G.R. & Smith, S.E. (2008) Plant nutrient-acquisition strategies change with soil age. *Trends in Ecology and Evolution*, 23, 95–103.
- Lane, D.R. & BassiriRad, H. (2005) Diminishing spatial heterogeneity in soil organic matter across a prairie restoration chronosequence. *Restoration Ecology*, 13, 403–412.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 7, 601–613.

- Lomolino, M.V., Riddle, B.R., & Brown, J.H. (2006) Biogeography, 3rd Edition. Sinauer Associates. Sunderland, Massachusetts.
- MacArthur, R.H. (1965) Patterns of species diversity. *Biological Reviews*, 40, 510–533.
- MacArthur, R.H. & Wilson, E.O. (1967) The theory of island biogeography. Princeton University Press, Princeton, New Jersey.
- May, R.M. (1975) Stability and complexity in model ecosystems. Second edition. Princeton University Press, Princeton, New Jersey.
- Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. & Gough, L. (2001) What is the observed relationship between species richness and productivity? *Ecology*, 82, 2381–2396.
- Morton, R.D., Law, R., Pimm, S.L., & Drake, J.A. (1996) On models for assembling ecological communities. *Oikos*, 75, 493–499.
- Motzkin, G. & Foster, D.R. (2002) Grasslands, heathlands and shrublands in coastal New England: historical interpretations and approaches to conservation. *Journal of Biogeography*, 29, 1569–1590.
- Osenberg, C.W., Sarnelle, O. & Goldberg, D.E. (1999) Meta-analysis in ecology: concepts, statistics, and applications. *Ecology*, 80, 1103–1104.
- Pearson, K. (1904) Report on certain enteric fever inoculation statistics. *British Medical Journal*, 3, 1243–1246.
- Peterson, A.T., Sóberon, J. & Sánchez-Cordero, V. (1999) Conservatism of ecological niches in evolutionary time. *Science*, 285, 1265–1267.
- Peterson, C.J. & Jones, R.H. (1997) Clonality in woody plants: a review and comparison with clonal herbs. The ecology and evolution of clonal plants (ed. by H. de Kroon and J. Van Groenendael), pp. 263–289. Backhuys Publishers, Leiden.
- Pärtel, M. (2002) Local plant diversity patterns and evolutionary history at the regional scale. *Ecology*, 83, 2361–2366.
- Pärtel, M. (2006) Data availability for macroecology: how to get more out of regular ecological papers. *Acta Oecologica*, 30, 97–99.
- Pärtel, M. & Helm, A. (2007) Woody species invasion into temperate grasslands: the relationship with abiotic and biotic soil resource heterogeneity. *Journal of Vegetation Science*, 18, 63–70.
- Pärtel, M. & Wilson, S.D. (2002) Root dynamics and spatial pattern in prairie and forest. *Ecology*, 83, 1199–1203.
- Pärtel, M. & Zobel, M. (2007) Dispersal limitation may result in the unimodal productivity-diversity relationship: a new explanation for a general pattern. *Journal of Ecology*, 95, 90–94.
- Pärtel, M., Helm, A., Ingerpuu, N., Reier, Ü. & Tuvi, E.-L. (2004) Conservation of Northern European plant diversity: the correspondence with soil pH. *Biological Conservation*, 120, 525–531.
- Pärtel, M., Kalamees, R., Zobel, M. & Rosén, E. (1999) Alvar grasslands in Estonia: variation in species composition and community structure. *Journal of Vegetation Science*, 10, 561–570.
- Pärtel, M., Zobel, M., Liira, J. & Zobel, K. (2000) Species richness limitations in productive and oligotrophic plant communities. *Oikos*, 90, 191–193.
- Pärtel, M., Zobel, M., Zobel, K. & van der Maarel, E. (1996) The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos*, 75, 111–117.

- O'Rourke, K. (2006) An historical perspective on meta-analysis: dealing quantitatively with varying study results. The James Lind Library (www.jameslindlibrary.org), http://www.jameslindlibrary.org/trial_records/20th_Century/1900_1920/pearson/pearson_commentary.html
- Reynolds, H.L., Mittelbach, G.G., Darcy-Hall, T.L., Houseman, G.R. & Gross, K.L. (2007) No effect of varying soil resource heterogeneity on plant species richness in a low fertility grassland. *Journal of Ecology*, 95, 723–733.
- Richards, P.W. (1996) *The tropical rain forest: an ecological study*, 2nd edn. Cambridge University Press, Cambridge.
- Ricklefs, R.E. (1987) Community Diversity: Relative Roles of Local and Regional Processes. *Science*, 235, 167 – 171.
- Ricklefs, R.E. (1989). Speciation and diversity: integration of local and regional processes. Pages 599–622 in D. Otte and J. A. Endler, editors. *Speciation and its consequences*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Ricklefs, R.E. (2005) Historical and ecological dimensions of global patterns in plant diversity. *Biologiske Skrifter Kongelige Danske Videnskabernes Selskab*, 55, 583–603.
- Ricklefs, R.E. (2006) Evolutionary diversification and the origin of the diversity-environment relationship. *Ecology*, 87, S3–S13.
- Ricklefs, R.E. (2007) History and diversity: explorations at the intersection of ecology and evolution. *The American Naturalist*, 170, S56–S70.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Rosenzweig, M. L., & Abramsky, Z. (1993) How are diversity and productivity related? Pages 52–65 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, Illinois, USA.
- Sackville-Hamilton, N.R., Schmid, B. & Harper, J.L. (1987) Lifehistory concepts and the population biology of clonal organisms. *Proceedings of the Royal Society B: Biological Sciences*, 232, 35–57.
- Scheiner, S.M., & Willig, M.R. (2005) Developing unified theories in ecology as exemplified with diversity gradients. *The American Naturalist*, 166, 458–469.
- Schenk, H.J. & Jackson, R.B. (2002) The global biogeography of roots. *Ecological Monographs*, 72, 311–328.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A. & Whitford, W.G. (1990) Biological feedbacks in global desertification. *Science*, 247, 1043–1048.
- Schlesinger, W.H., Raikes, J.A., Hartley, A.E. & Cross, A.F. (1996) On the spatial pattern of soil nutrients in desert ecosystems. *Ecology*, 77, 364–374.
- Schroter, D., Cramer, W., Leemans, R., Prentice, I.C., Araújo, M.B., Arnell, N.W., Bondeau, A., Bugmann, H., Carter, T.R., Gracia, C.A., de la Vega-Leinert, A., Erhard, M., Ewert, F., Glendining, M., House, J.I., Kankaanpää, S., Klein, R.J.T., Lavorel, S., Lindner, M., Metzger, M.J., Meyer, J., Mitchell, T.D., Reginster, I., Rounsevell, M., Sabate, S., Sitch, S., Smith, B., Smith, J., Smith, P., Sykes, M.T., Thonicke, K., Thuiller, W., Tuck, G., Zaehle, S. & Zierl, B. (2005) Ecosystem service supply and vulnerability to global change in Europe. *Science*, 310, 1333–1337.

- Sokal, R.R. & Rohlf, F.J. (1995) *Biometry: the principles and practice of statistics in biological research*, 3rd edn. Freeman, New York.
- Stark, J.M. (1994) Causes of soil nutrient heterogeneity at different scales. Exploitation of environmental heterogeneity by plants: ecophysiological processes above- and belowground (ed. by M.M. Caldwell), pp. 255–284. Academic Press, San Diego.
- StatSoft. (2004) STATISTICA data analysis software system. Version 6. StatSoft, Tulsa, Oklahoma, USA.
- Stevens, M.H.H. (2006) Placing local plant species richness in the context of environmental drivers of metacommunity richness. *Journal of Ecology*, 94, 58–65.
- Stuefer, J.F., Erschbamer, B., Huber, H. & Suzuki, J.I. (2002) The ecology and evolutionary biology of clonal plants: an introduction to the proceedings of Clone-2000. *Evolutionary Ecology*, 15, 223–230.
- Svennson, B.M., Rydin, H. & Carlsson, B.A. (2005) Clonal plants in the community. *Vegetation ecology* (ed. by E. van der Maarel), pp. 129–146. Blackwell Publishing, Oxford.
- Taylor, D.R., Aarssen, L.W. & Loehle, C. (1990) On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos*, 58, 239–250.
- Thorp, J. & Baldwin, M. (1940) Laterite in relation to soils of the tropics. *Annals of the Association of American Geographers*, 30, 163–194.
- Tilman, D. (1989) Ecological experimentation: strengths and conceptual problems. *Long-term studies in ecology: approaches and alternatives* (ed. by G.E. Likens), pp. 36–157. Springer-Verlag, New York.
- Van Auken, O.W. (2000) Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics*, 31, 197–215.
- Van Groenendael, J.M., Klimeš, L., Klimešová, J. & Hendriks, R.J.J. (1996) Comparative ecology of clonal plants. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 351, 1331–1339.
- Vitousek, P.M. & Farrington, H. (1997) Nutrient limitation and soil development: Experimental test of a biogeochemical theory. *Biogeochemistry*, 37, 63–75.
- Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G.G., Gough, L., Dodson, S.I., Juday, G.P. & Parmenter, R. (1999) The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*, 30, 257–300.
- Walker, T.W. & Syers, J.K. (1976) The fate of phosphorus during pedogenesis. *Geoderma*, 15, 1–19.
- Wassen, M.J., Venterink, H.O., Lapshina, E.D. & Tanneberger, F. (2005) Endangered plants persist under phosphorus limitation. *Nature*, 437, 547–550.
- Watkinson, A.R. & Ormerod, S.J. (2001) Grasslands, grazing and biodiversity: editors' introduction. *Journal of Applied Ecology*, 38, 233–237.
- Whittaker, R.H. (1966) Forest dimensions and production in the Great Smoky Mountains. *Ecology*, 47, 103–121.
- Whittaker, R.H. (1975) *Communities and ecosystems*. Macmillan, New York.
- Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island Biogeography: ecology, evolution, and conservation*, 2nd edition. Oxford University Press, Oxford.
- Wiens, J.J., & Donoghue, M. J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, 19, 639–644.

- Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology Evolution and Systematics*, 36, 519–39
- Wilson, S.D. (1998) Competition between grasses and woody plants. Population biology of grasses (ed. by G.P. Cheplick), pp. 231–254. Cambridge University Press, Cambridge.
- Wohlgemuth, T. (1998) Modelling floristic species richness on a regional scale: a case study in Switzerland. *Biodiversity and Conservation*, 7, 159–177.
- Woodward, F.I., Lomas, M.R. & Kelly, C.K. (2004) Global climate and the distribution of plant biomes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 359, 1465–1476.
- Zar, J.H. (1996) Biostatistical analysis. Prentice-Hall, London.
- Zobel, K. (2001) On the species-pool hypothesis and on the quasi-neutral concept of plant community diversity. *Folia Geobotanica*, 36, 3–8.
- Zobel, K. & Liira, J. (1997) A scale-independent approach to the richness vs biomass relationship in ground-layer plant communities. *Oikos*, 80, 325–332.
- Zobel, M. (1997) The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology & Evolution*, 12, 266–269.

SUMMARY IN ESTONIAN

Makroökoloogiline lähenemine taimkatteteadusele: ökoloogiliste seaduspärade varieerumine globaalses skaalas

Makroökoloogia, mis uurib organismide ja keskkonna vahelisi seoseid suurtes ruumiskaalades, on võrdlemisi uus teadusharu. Selle olulisimaks lähtekohaks oli James H. Browni monograafia “*Macroecology*” ilmumine 1995. aastal. Sestsati on makroökoloogiliste teadustööde hulk näidanud pidevat kasvutendentsi (Joonis 1). Tõuke makroökoloogia väljakujunemiseks andsid Teise maailmasõja järgselt loodusteadustes, eriti ökoloogias, biogeograafias, paleontoloogias ja evolutsioonilises bioloogias tehtud tähelepanuväärsed avastused. Põhjalikult kujundati ümber arusaamad sellest, millised protsessid ja kuidas mõjutavad lokaalkooslustes elavate organismide ohtrust, levikut ning mitmekesisust. Pärast aastakümneid kestnud teadmiskillukeste kogumist tekkis vajadus need ühtsesse, kõikehõlmavasse süsteemi paigutada; algandmeid tundus olevat kogunenud piisavalt selleks, et lokaalse skaala asemel saaks käsitleda globaalset skaalat. Makroökoloogia pakutigi välja kui täiesti uus lähenemine ökoloogiateadustele, mille abil oleks võimalik oluliselt laiendada ökoloogiliste protsesside uurimise haaret, seda nii ruumilises kui ka ajalises mõttes.

Globaalsed bioloogilised mustrid on makroökoloogia distsipliini vastusest hoolimata teadlasi ammustest aegadest huvitanud; ning kuigi biodiversiteedi mustreid uurisid juba näiteks Karl Linné ja Georges-Louis Leclerc Comte de Buffon, kes püüdsid seletada Noa laeval viibinud loomade levimist tagasi üle kogu maailma, siis väga paljud põhiküsimused ja nende teatud aspektid bioloogias, ja eriti ökoloogias ning biogeograafias on siiani vastuseta. Üks põhjus, miks see nii on, peitub arvatavasti teadlaste ja teadusharude liigeses spetsialiseerituses: on raske eeldada, et inimene, kes uurib aastakümneid mingit kindlat parameetrit ühes taksonoomilises üksuses, võiks hoomata niivõrd kõikehõlmavaid protsesse nagu mitmekesisus, liikide levimine, liigitelke jne, rääkimata nende äraseletamisest – ning seda kõike üleilmsel skaalal.

Viimaste aastakümnete arengud on teinud teadusliku informatsiooni märksa laialdasemalt kättesaadavaks ning lisaks on teadusliku informatsiooni hulk eksponentsiaalses tempos kasvanud. Selle tagajärjel on akumuliseerunud suurel hulgal omavahel võrreldavaid andmeid paljudest maailma paikadest, sealhulgas ka ökoloogilisi andmeid taimkatte kohta. Üks võimalus nende andmete põhjal suureskaalalisi makroökoloogilisi järeldusi teha on viia läbi metauuringuid. Kuigi esimese metaanalüüsi tegi kuulus inglise matemaatik Karl Pearson juba rohkem kui sada aastat tagasi (1904. aastal), hakati ökoloogiaalaseid metauuringuid usinamalt avaldama alles möödunud sajandi viimasel kümnendil, sest

lisaks algandmete vähesusele ei võimaldanud ka arvutustehnika tase neid enne korralikult läbi viia.

Lisaks tehnilistele eeldustele ja algmaterjali piisavale akumulatsioonile oli adekvaatsete makroökoloogiliste uuringute tegemiseks tarvis ka mõttelaadi muutumist ökoloogiateadustes. Nimelt valitses (ja paiguti valitseb siiani) taimkatteteadustes alates 1960. aastatest saati niinimetatud lokaalne determinism. Selle paradigma kohaselt valitsesid taimkattes mehhanistsitliku iseloomuga kohaliku taseme ökoloogilised protsessid (eelkõige liikidevaheline konkurents), mis kujundasid kõiki olulisemaid taimekoosluse omadusi alates biomassi produktsioonist ja lõpetades liigirikkusega. Põhjus, miks taoline evolutsiooniliselt tasakaaluline mõtteviis juurdus ning levikut, evolutsiooni ja regionaalset ajalugu oluliseks ei peetud, seisnes eelduses, et kohalikul tasandil toimuvad ökoloogilised protsessid on niivõrd kiired, et “summutavad” pikaajaliste protsesside mõju. Pealegi viidi valdav osa ökoloogilistest vaatlustest ja uuringutest läbi Euroopas ja Põhja-Ameerikas, sest ökoloogiaga tegelevad teaduslikud uurimisasutused on kogunenud just nendesse piirkondadesse. Selle tagajärjel uuriti peamiselt parasvöötme taimekooslusi, mille evolutsiooniline ja geoloogiline ajalugu oli suhteliselt sarnane, mistõttu suureskaalalisi protsesse polnudki põhjust arvestada. Tekkinud olukorras, kus põhiküsimuseks oli “miks nii palju liike koos elab?”, ei saanudki kujuneda välja vastuseid bioloogiliste süsteemide kõige suurematele ja laiahaardelisematele aspektidele, nagu näiteks biomitmekesisus, sest kolmest mitmekesisust kujundavast protsesside valdkonnast arvestati üksnes ökoloogilisi protsesse, kuid levik (mis annab juurde ruumimõõtmelise) ja evolutsiooniline/geoloogiline tagapõhi (mis annab juurde ajamõõtmelise) jäeti seletuste otsimisel kahe silma vahele.

Biodiversiteet on paljuskaalaline ja mitmetimõistetav omadus, mis on iseloomulik kõikidele ökosüsteemidele. Biodiversiteedi enimlevinuim mõõtühik, liigirikkus, ja selle kujunemise põhjused on huvitanud paljusid biolooge juba sadu aastaid. Kuid nagu eelmises lõigus räägitud, seletuste otsimisel on teadlased keskendunud eelkõige ökoloogiliste ja kohalikul skaalal toimuvate protsesside uurimisele ning levimine ja evolutsioon on paljuski kõrvale jäetud. Ometigi on kauglevi olulisust rõhutatud juba Robert H. MacArthuri ja Edward O. Wilsoni kuulsas saarte biogeograafia teoorias (1967); evolutsiooniliste tegurite olulisust on propageerinud peamiselt Robert E. Ricklefs, kes on osutanud eelkõige liikide fülogeneetilise tausta ja kasvukoha regionaalse ajaloo olulisusele liigirikkuse muustrite kujundamisel.

1990. aastatel kujunes paljuski Martin Zobel ja Meelis Pärteli eestvõttel välja liigifondi kontseptsioon, mille kohaselt kujundab mingi antud koosluse liigirikkust eelkõige sealne liigifond, see tähendab, nende liikide hulk, mis on potentsiaalselt võimelised antud koosluses elama ja sinna ka levima – niisiis arvestab see kontseptsioon lisaks ökoloogiliste teguritele ka leviku ja evolutsioonilise/geoloogilise ajaloo tegureid. Liigifondi paradigma küsib pigem: “miks nii vähe liike koos elab?”, vastandudes seega otseselt lokaal-

deterministlikule mõtteviisile. Liigifondi paradigma on seega sobilik filosoofiline lähendus uurimaks liigirikkuse mustreid makroökoloogilisest vaatenurgast.

Üks kõige läbiuuritumaid, ent ometigi selge vastuseta jäänud küsimusi (taime)ökoloogias puudutab liigirikkuse ja koosluse produktiivsuse vahelist seost. Esimesed sellealased tööd tehti 1960. aastatel, kuid õige hoo said liigirikkuse ja produktiivsuse seose uuringud sisse pärast seda, kui J. Philip Grime uuris antud seost Inglismaa rohumaade taimkatte puhul ning avaldas saadud tulemuste põhjal kuulsa “küüruga kõvera” ehk joonise, kus liigirikkuse ja produktiivsuse vahel on unimodaalne ehk ühetipuline seos (keskmise produktiivsuse juures on kõige suurem liigirikkus). Väga väikese produktiivsuse korral puuduvad ressursid paljude isendite ja seega ka liikide kooseksisteerimiseks ning on üheselt selge, miks produktiivsuse skaala alguses liigirikkus väike on. Oluline oleks teada just seda, miks suure produktiivsuse korral liigirikkus uuesti langema kipub. Grime ise põhjendas liigirikkuse langust kõrge produktiivsuse juures konkurentsiga: mida kõrgem produktiivsus, seda intensiivsem konkurents ning seda enam liike välja tõrjutakse. Konkurents ja sellega suuremal või vähemal määral seotud lokaalsed ning ökoloogilised põhjendused ongi jäänud valdavateks seletusteks liigirikkuse langusele kõrgete produktiivsuste juures.

Kuigi mitmed uurimistööd said ka teisi tulemusi, kus liigirikkus ja produktiivsus olid seotud kas positiivselt või negatiivselt või siis puudus seos nende kahe vahel sootuks, on unimodaalne produktiivsuse ja liigirikkuse vaheline seos jäänud taimkatteuringutes valdavaks tulemuseks. Mitmed teadlased märkasid, et ühetipuline kõver saadi tulemuseks peamiselt siis, kui uuriti rohuringet ning tehti seda parasvöötmes. Paljud troopikas või puurindes läbiviidud uuringud andsid tulemuseks pigem positiivseid seoseid liigirikkuse ja produktiivsuse vahel. Paraku tehti valdav enamus vaatlustest just parasvöötme rohurindes, mistõttu mitteunimodaalse seose leidnud tööd jäid teaduslikus mõttes perifeerseteks ning neid käsitleti kui erandeid, mis kinnitavad reeglit.

Liigifondi kontseptsiooni kohaselt mõjutavad liigirikkust lisaks lokaalsetele ja ökoloogilistele protsessidele ka levimine ning regionaalne ja evolutsiooniline ajalugu. Seemnete juurdelisamise katsed on näidanud, et liikide kooseksisteerimisel pole looduslikes ja pool-looduslikes kooslustes veel ülempiirini jõutud, kuid seda eelkõige madala ja keskmise produktiivsuse juures. Oma osa liigirikkuse ja produktiivsuse seosele võib anda varieerumine erinevate taimede levikutõenäosustes.

Evolutsiooni vaatenurgast on liigirikkuse ja produktiivsuse seose kujundamisel rõhutatud eelkõige liikide fülogeneetilise tausta olulisust. Samuti on osutatud regionaalse ajaloo eripäradele: produktiivsed kasvukohad ei ole parasvöötmele omased ning jääaegade mõju on viljakate alade levikut selles vöötmes veelgi piiranud. Seetõttu pole parasvöötmes toimunud liigitekkeprotsessid soosinud selliste taimeliikide arengut, mis kasvaksid kõige meelsamini just kõrge produktiivsusega kooslustes. Samas on troopikas miljoneid aastaid laiunud äärmiselt produktiivsed piirkonnad ning olulisi häiringuid pole

nendel aladel olnud. Liigifondi paradigma kohaselt on parasvöötme liigifondis lihtsalt vähe kõrget produktiivsust eelistavaid liike ning seetõttu võibki eeldada, et seos liigirikkuse ja produktiivsuse vahel parasvöötmes on unimodaalne; samas võiks troopikas eeldada positiivset seost.

Paraku ei kipu ühetipulised seosed liigirikkuse ja produktiivsuse suhtes parasvöötme puurindes eriti ilmnema. Seda märkas ka Peter Grubb, kes seostas antud nähtust kлонаalsusega. Nimelt esineb puittaimedel märgatavalt harvem vegetatiivse paljunemise võimet kui rohttaimedel ning Grubbi väitel mõjutab just see puit- ja rohttaimede liigirikkuse ja produktiivsuse seose kuju. Kлонаalsust peetakse konkurentsieeliseks, eriti produktiivsetes kooslustes, kuna uutel liikidel on palju raskem kooslusesse tungida olukorras, kus koosluses domineerivad vegetatiivse paljunemisevõimega liigid. Lisaks sellele, et puittaimede hulgas on kлонаalsus oluliselt vähem levinud kui rohttaimede hulgas, on ka nende rühmade kлонаalsus erineva iseloomuga: puittaimede kлонаalsus pole suunatud niivõrd oma otseste konkurentidega ressursside pärast võitlemisele ning levimisele, nagu see on rohttaimedel, kuivõrd pigem mitmesugustest häiringutest (tuule-, tule- ja herbivooride kahjustused) taastumisele. Veelgi enam, parasvöötme puit- ning rohttaimede fülogeneetiline ajalugu on väga erinev. Nimelt pärineb enamik parasvöötme puittaimede eellasi troopikast, samas kui rohttaimed on evolutsioneerunud kohapeal. Robert E. Ricklefsi nišikonservatismi (ehk fülogeneetilise inertsuse) teooria kohaselt säilitavad liigid oma eellaste tunnused ning sellest lähtudes võivad parasvöötme puittaimed "käituda" nii, et produktiivsuse ja liigirikkuse seos tuleb unimodaalse asemel pigem positiivne, sest just selline seos on troopikakooslustes rohkem levinud.

Bioloogiline mitmekesisus ei seisne siiski üksnes liigirikkuses, vaid avaldub ka teisiti. Kui eelnevatest lõikudest selgus, et puit- ja rohttaimede vahel on märgatavaid erinevusi, mille ökoloogiategadused tihtipeale kahe silma vahele on jätnud, siis oleks huvitav teada ka, kas näiteks troopika ja parasvöötme metsade ja rohumaade ökosüsteemide olulisemates protsessides avaldub kardinaalseid erinevusi. Looduskaitse on kõikjal maailmas hädas sellega, et rohumaad kipuvad metsastuma, ning rohumaade kadumisega kipuvad kaduma ka taimeliigid. Puittaimede invasiooni rohumaadele on küll seostatud nii põlengute vähenemise ning kadumise, lämmastikureostuse kui ka süsinikdioksiidi taseme tõusmisega õhus, kuid tihti arvatakse, et antud nähtuse taga on mulla toitainete heterogeensuse erinevused rohu- ja metsamaadel.

Puittaimed eelistavad heterogeenset mulda, sest nende juured on pikad ja ulatuvad suure tõenäosusega nende laikudeni, mis sisaldavad ohtralt toitaineid. Seevastu rohttaimede juured on lühikesed ning seetõttu eelistavad rohttaimed pigem toitainete homogeenset jaotumist mullas. Lisaks eelistamisele on nii puit- kui ka rohttaimed võimelised mulla toitainete sisaldust vastavalt oma soovidele mõjutama; nii muutuvad võssakasvanud niidualade mullad heterogeensemaks ning rohttaimede domineerimine koosluses omakorda ühtlustab toitainete

ruumilist jaotust – kuid seda kõike parasvöötme tingimustes. Paraku ei ole teada, kas samasugused seaduspärasused kehtivad ka näiteks troopilises vööndis, kus mullad on märksa vanemad kui parasvöötmes, kuid puuliigid pärinevad samadest troopikas elanud eellastest, kellest parasvöötme puuliigidki.

Eelnenut kokku võttes saab öelda, et makroökoloogiline lähenemine taimkatteteadusele võib anda väga sisukaid tulemusi eelkõige ökoloogiliste seaduspärasuste üldkehtivuse kohta. Nii ruumi- kui ka ajateljel suureskaalalised protsessid on erinevate piirkondade ja eluslooduse rühmade arengut mõjutanud väga erineval viisil ning sellest tingituna tuleb enne ökoloogiliste seaduspärasuste üldkehtivaks kuulutamist põhjalikult uurida, kas antud seost leidub kõikides maailma paikades ja ka teiste taksonoomiliste või funktsionaalsete rühmade puhul. Käesolevas töös on uuritud taimede liigirikkuse ja produktiivsuse seose kuju varieeruvust globaalsel tasandil ning testitud suureskaalaliste ja evolutsiooniliste protsesside mõju antud seose kujule; samuti on uuritud mulla toitainete heterogeensuse varieeruvust erinevates keskkonnatingimustes erinevate kooslusetüüpide puhul.

Käesoleva töö eesmärkideks oli uurida, kas:

1. taimede liigirikkuse ja produktiivsuse seose kuju varieerub kliima-gradiendil,
2. liigirikkuse ja produktiivsuse unimodaalne seos taimedel on globaalses skaalas puittaimedel ja metsades vähem levinud kui rohhtaimedel ja rohumaadel,
3. koosluse liigirikkuse ja produktiivsuse seose kuju sõltub koosluses domineerivate liikide vegetatiivse paljunemise võimest ning füloge-neetilisest taustast,
4. metsade ja rohumaade mulla toitainete heterogeensus varieerub sarnaselt ka erinevates kliimaatilistes tingimustes.

Ülalloetletud eesmärkide saavutamiseks viisime läbi kolm metauuringut, mis seisnesid eelretsenseeritavas teaduskirjanduses juba avaldatud samasisuliste uuringute (teadusartiklite) tulemuste kokkukogumises ja saadud andmemaatrik-site analüüsimises. Igast sobilikust artiklist filtreeriti välja meid huvitanud andmed: liigirikkuse ja produktiivsuse seose kuju, koosluse dominantliik, mulla heterogeensuse väärtused, samuti uuritud ala(de) geograafiline asukoht, mille alusel sai vastavast andmebaasist määrata tolle punkti aasta keskmise õhutemperatuuri ja sademetehulga.

Enamik uuritavatest parameetritest jaotati diskreetseteks või binaarseteks: liigirikkuse ja produktiivsuse seose kuju oli unimodaalne/positiivne/muu või unimodaalne/muu; dominantliigi kasvuvorm jagunes puittaim/rohhtaim; dominantliigi klonaalsus jagunes harva või üldse mitte klonaalne/mõnikord klonaalne/enamasti klonaalne; dominantliigi evolutsiooniline taust: pärineb troopikast/pärineb parasvööttest/globalse levikuga. Üksnes mulla heterogeensuse mõõtmeks olnud variatsioonikoefitsient ($CV = \text{standardhälve} / \text{keskmine}$) oli pidev tunnus.

Saadud metauuringute tulemused näitasid ilmekalt, et liigirikkuse ja produktiivsuse vaheline seos ning mulla toitainete heterogeensuse ja koosluse struktuuri vaheline seos erinevad laiuskraaditi oluliselt ning parasvöötmes tehtud vaatluste ja eksperimentide tulemusi ei saa käsitleda kõikjal kehtivatena.

Liigirikkuse ja produktiivsuse seose kuju metauuring, mille tarbeks leiti kokku 163 sobilikku kirjandusallikat (Joonis 2), tuvastas, et kui parasvöötmes on ühetipuline seos tõepoolest kõige levinum, siis mida väiksem laiuskraad, seda valdavamaks muutub positiivne seos (Joonis 3); seega liigirikkuse ja produktiivsuse seose kuju tõepoolest sõltub olulisel määral sellest, kus paigas seda parasjagu uurida. Ühest küljest saab seda varieeruvust seletada erinevustega eri paikade regionaalses ajaloos, mis omakorda on mõjutanud antud piirkonna evolutsioonilist ajalugu. Väga produktiivsed kasvukohad pole parasvöötmes ajaloo vältel väga levinud olnud ning olemasolevadki on väga noored ja tihti otseselt inimtegevuse tagajärjel välja kujunenud. Seevastu troopikas on kõrge produktiivsusega kasvukohad laiaulatuslikult levinud juba väga pikka aega. Taolisest kontrastsest ajaloost tingituna on parasvöötme ja troopika taimede liigifondid evolutsiooni käigus kujunenud erinevateks: parasvöötme liigifondis leiduvad liigid eelistavad pigem väikese ja keskmise produktiivsusega kasvukohti, samas kui troopikaliigid kasvavad meelsamini väga produktiivsetes tingimustes.

Vaadeldes liigirikkuse ja produktiivsuse seose kuju varieeruvust metsade ja rohumaade vahel, selgus, et ühetipulist seost nende kahe tunnuse vahel leidub rohurindes ning rohumaadel oluliselt rohkem kui puurindes ja metsades (Tabel 1). Koosluste dominantliikide kasvuvormi, evolutsioonilist tausta ning vegetatiivse paljunemise võimet arvesse võttes selgus, et ka need parameetrid mõjutavad olulisel määral liigirikkuse ja produktiivsuse seose kuju (Tabel 3). Kui koosluses domineerisid troopilise taustaga liigid (ehk need, kelle esivanemad on evolutsioneerunud troopikas), puittaimed või mitte- ja väheklonaalsed liigid, siis leidis seal unimodaalset seost liigirikkuse ja produktiivsuse vahel oluliselt harvemini kui parasvöötmelise või globaalse evolutsioonilise taustaga klonaalsete rohttaimede domineerimise korral.

Kõik eelmises lõigus mainitud tunnused kokku moodustavad ühtse laiaulatusliku konteksti, kus on esindatud nii evolutsioonilised kui ka ökoloogilised aspektid, samuti levimine. Pika aja jooksul troopikapiirkondadest parasvöötmesse levinud puittaimed evivad nišikonservatismist lähtudes oma eellaste omadusi (millest üks võib olla sugulise paljunemise eelistamine vegetatiivsele reproduktsioonile), mis realiseeruvad ökoloogilistes protsessides ja ajaskaalas, kujundades vastavalt sellele muuhulgas ka koosluste liigirikkust. Seega on mitmekesisuse mustritel kompleksed põhjused ning liigirikkuse ja produktiivsuse vahelise seose kuju ei määra mitte üksnes ökoloogilised parameetrid.

Sarnaselt liigirikkuse ja produktiivsuse seose varieeruvusele laiuskraadi gradiendil erineb ka troopika ja parasvöötme mulla toitainete heterogeensus metsa- ja rohumaadel. Kui metsade mulla heterogeensus laiuskraadist ei sõltu,

siis rohumaade oma küll (Joonis 6). Väikestel laiuskraadidel on rohumaade mulla heterogeensus suurem kui metsaaladel, ent suurtel laiuskraadidel on sama seos pigem vastupidine. Seega senini suhteliselt üldkehtivaks peetud seos, et metsaalade muld on heterogeenne ning rohumaade oma homogeenne, kehtib peamiselt parasvöötmes. Täpseid põhjuseid, miks see nii on, ei ole kerge välja tuua, sest mullaparameetreid ja taimede maa-alust elu on tänu suurtele töömahtudele ja keerukatele meetodikatele väga vähe uuritud. Üheks põhjuseks võivad olla peenjuurte horisontaalse hargnemise mustrid, mis on teadaolevalt mulla heterogeensusu olulised mõjutajad näiteks Põhja-Ameerika preeriaaladel, kuid paraku puuduvad vastavasisulised andmed teiste regioonide ja kooslusetüüpide kohta. Teisalt võib mulla heterogeensusu erinemist puurinde ja rohurinde all siduda juurte sügavusulatusega: kui troopika ja parasvöötme puude juured ulatuvad keskmiselt enam-vähem sama sügavale, siis rohttaimede puhul jäävad juured parasvöötmealadel märksa madalamale kui troopikas. Võimalikke aspekte antud seose kujundamisel on veel, ent paraku napib põhjalikumate analüüside tegemiseks andmeid ning antud töö käigus saadud tulemused peaksidki muuhulgas juhtima tähelepanu sellele puudujäägile teaduskirjanduses.

Kokkuvõttes selgus käesoleva töö tulemusena, et taimede liigirikkuse ja produktiivsuse vahelise seose kuju varieerub olulisel määral kliimagradiendi pidi. Parasvöötmes on enamlevinud unimodaalne seos, samas kui troopikas kipub liigirikkus produktiivsusega pigem positiivselt korreleeruma. Lisaks konkurentsile ja teistele ökoloogilistele protsessidele mõjutavad antud seose kuju olulisel määral ka koosluses domineerivate liikide evolutsiooniline taust ja vegetatiivse paljunemise võime, samuti see, kas tegemist on metsa või rohu- maaga. Puit- ning rohttaimede erinevused ilmnisid ka mulla toitainete heterogeensusu metauuringus, kus selgus, et metsade mulla heterogeensus kliimagradiendist ei sõltunud, kuid rohumaade mullad osutusid parasvöötmes metsade muldadest homogeensemateks; seevastu troopikas oli antud seos vastupidine.

Meie tulemustest lähtudes võib öelda, et meie teadmised ja arusaamad sellest, kuidas loodus toimib, pärinevad eelkõige hästi läbiuuritud aladelt, kuid näiteks parasvöötmes saadud tulemusi ei maksa vaikumisi üldkehtivateks pidada, samamoodi nagu troopikas kehtivad seosed ei pruugi kehtida parasvöötmes. Just makroökoloogilised uuringud saavad siinkohal kummutada väga paljud eksiarvamused.

Seetõttu on tarvis ökoloogiliste seoste seletamisel rohkem arvestada suure- skaalaliste protsesside mõju. Piirkonna geoloogiline ajalugu, liikide evolutsiooniline taust ning kauglevi kujundavad olulisel määral mingi kindla koosluse või piirkonna liigifondi ning läbi selle omakorda seal toimuvaid ökoloogilisi protsesse. Ökoloogiliste protsesside olulisust kahtluse alla seadmata tuleks koosluste uurimisel osutada varasemast suuremat tähelepanu ka evolutsioonilisele ja regionaalsele ajaloole ning liikide levikule.

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PUBLICATIONS

Pärtel, M.; Laanisto, L.; Zobel, M. (2007).
Contrasting plant productivity-diversity relationships in temperate
and tropical regions: the role of evolutionary history.
Ecology, 88(5), 1091–1097.

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(3), 320–326

Pärtel, M.; Laanisto, L.; Wilson, S.D. (2008). Soil nitrogen and carbon heterogeneity in woodlands and grasslands: contrasts between temperate and tropical regions. *Global Ecology and Biogeography*, 17(1), 18–24

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- Pärtel, M.; Laanisto, L.; Zobel, M. (2007). Contrasting plant productivity-diversity relationships in temperate and tropical regions: the role of evolutionary history. *Ecology*, 88(5), 1091–1097.
- 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(3), 320–326
- Pärtel, M.; Laanisto, L.; Wilson, S.D. (2008). Soil nitrogen and carbon heterogeneity in woodlands and grasslands: contrasts between temperate and tropical regions. *Global Ecology and Biogeography*, 17(1), 18–24

Conference thesis

- 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? Biodiversity Information and Climate Change Impacts on Life, April 5–6, 2008, Aarhus University Campus, Denmark.
- Laanisto, L.; Pärtel, M.; Wilson, S.D. (2007). Links between soil heterogeneity and global vegetation change. In: New Zealand: New home; new habitat! New ideas? Book of Abstracts: 49th Annual Conference of the IAVS – New Zealand: New home; new habitat! New ideas?; Palmerston North, New Zealand; 12–16 February 2007. (Toim.) Rosemary A. van Essen., 2007, 51.
- Laanisto, L.; Pärtel, M. (2006). Clonality may cause the unimodal plant-productivity-diversity relationship. In: 8th clonal plant workshop: 8th clonal plant workshop – generality, specificity and diversity of clonal growth; Pärnu, Estonia; June 27–30, 2006. (Toim.) Sammuli, M.; Kull, T.; Kull, K.; Tali, K., 2006, 46.
- Laanisto, L.; Pärtel, M.; Zobel, M. (2006). Contrasting plant productivity-diversity relationship in temperate and tropical regions: the role of evolutionary history. In: Macroecological Tools for Global Change Research: International Conference on Macroecological Tools for Global Change Research; Potsdam, Germany; 21–23 August 2006. , 2006, 88.
- Pärtel, M.; Laanisto, L.; Zobel, M. (2005). Plant community assembly and the unimodal productivity-diversity relationship. In: XVII International Botanical Congress. Abstracts: XVII International Botanical Congress; Vienna, Austria; 17–23 July 2005. (Toim.) Anon. Vienna: IBC, 2005, 58.
- Pärtel, M.; Laanisto, L. (2005). The effect of herbaceous and woody vegetation on soil nutrient heterogeneity: a global assessment. In: X European Ecological Congress. Abstracts Book: X European Ecological Congress; Kusadasý, Turkey; 08–13 November 2005. (Toim.) Erdem, Ü.; Nurlu, R.M.. META Press, 2005, 109.
- Laanisto, L.; Pärtel, M.; Zobel, M. (2005). The generality of the Grime's : unimodal productivity-diversity relationship. In: X European Ecological Congress. Abstracts Book: X European Ecological Congress; Kusadasý, Turkey; 08–13 November 2005. (Toim.) Erdem, Ü.; Nurlu, R.M.. META Press, 2005, 468.

Popular science articles

Laanisto, L (2002) Miks taimeteadus, miks siin ja praegu. Eesti Loodus 5/2002

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Publikatsioonide loetelu:

Artiklid, mis on kajastatud ISI Web of Science andmebaasis

- Pärtel, M.; Laanisto, L.; Zobel, M. (2007). Contrasting plant productivity-diversity relationships in temperate and tropical regions: the role of evolutionary history. *Ecology*, 88(5), 1091–1097.
- 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(3), 320–326
- Pärtel, M.; Laanisto, L.; Wilson, S.D. (2008). Soil nitrogen and carbon heterogeneity in woodlands and grasslands: contrasts between temperate and tropical regions. *Global Ecology and Biogeography*, 17(1), 18–24

Konverentside ettekanded

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? Biodiversity Information and Climate Change Impacts on Life, April 5–6, 2008, Aarhus University Campus, Denmark.
- Laanisto, L.; Pärtel, M.; Wilson, S.D. (2007). Links between soil heterogeneity and global vegetation change. In: New Zeland: New home; new habitat! New ideas? Book of Abstracts: 49th Annual Conference of the IAVS – New Zeland: New home; new habitat! New ideas?; Palmerston North, New Zealand; 12–16 February 2007. (Toim.) Rosemary A. van Essen., 2007, 51.
- Laanisto, L.; Pärtel, M. (2006). Clonality may cause the unimodal plant-productivity-diversity relationship. In: 8th clonal plant workshop: 8th clonal plant workshop – generality, specificity and diversity of clonal growth; Pärnu, Estonia; June 27–30, 2006. (Toim.) Sammul, M.; Kull, T.; Kull, K.; Tali, K., 2006, 46.
- Laanisto, L.; Pärtel, M.; Zobel, M. (2006). Contrasting plant productivity-diversity relationship in temperate and tropical regions: the role of evolutionary history. In: Macorecological Tools for Global Change Research: International Conference on Macroecological Tools for Global Change Research; Potsdam, Germany; 21–23 August 2006. , 2006, 88.
- Pärtel, M.; Laanisto, L.; Zobel, M. (2005). Plant community assembly and the unimodal productivity-diversity relationship. In: XVII International Botanical Congress. Abstracts: XVII International Botanical Congress; Vienna, Austria; 17–23 July 2005. (Toim.) Anon. Vienna: IBC, 2005, 58.
- Pärtel, M.; Laanisto, L. (2005). The effect of herbaceous and woody vegetation on soil nutrient heterogeneity: a global assessment. In: X European Ecological Congress. Abstracts Book: X European Ecological Congress; Kusadasý, Turkey; 08–13 November 2005. (Toim.) Erdem, Ü.; Nurlu, R.M.. META Press, 2005, 109.
- Laanisto, L.; Pärtel, M.; Zobel, M. (2005). The generality of the Grime's : unimodal productivity-diversity relationship. In: X European Ecological Congress. Abstracts Book: X European Ecological Congress; Kusadasý, Turkey; 08–13 November 2005. (Toim.) Erdem, Ü.; Nurlu, R.M.. META Press, 2005, 468.

Populaarteaduslikud artiklid

Laanisto, L. (2002) Miks taimeteadus, miks siin ja praegu. Eesti Loodus 5/2002

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