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Forest Diversity and Function

Temperate and Boreal Systems

With 102 Figures and 22 Tables

Springer

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Foreword

This past decade has witnessed a flurry of research activity focusing on the significance of the diversity of organisms regarding the capacity of ecosystems to capture resources and their role in regulating the stability and resilience of these systems. The results of this activity have been chronicled, debated and summarized, as noted in this volume. This discourse has been colored, of course, by the kinds of information available. Unfortunately, there are few results from explicit experiments on the diversity/functioning/stability relationships. We have had to turn to "experiments" that nature has provided, i.e. observing functioning in systems of varying diversity. However, as noted in this volume, it is difficult to draw firm conclusions from observational studies because of the complexity of natural environments in any given place and across gradients. It is just not possible to hold all habitat conditions constant, with only diversity varying, under natural conditions. This is not to say that such field observations are not of crucial importance in providing reasonable starting points for experimentation. It is just that these observations need to be augmented with experiments to clarify confounding factors, even though such experiments are difficult and costly.

During this past decade over a million hectares per year of natural forests have been converted to plantation forests, globally, as well as comparable amounts in afforestation projects on lands not previously forested. Since plantations are normally monocultures, with added fertilizers and pesticides, it becomes important to compare the full environmental and economic costs and benefits of varying species mixtures to see where savings can be made. Unfortunately, such full-cost accounting in agronomic practices is rarely done and hence society pays the price of off-site environmental impacts in the long run.

This volume is an important first step in launching the kinds of experiments and measurements that are needed to bring us much further along in our understanding of the role of diversity, at many levels, of the perennial woody systems that cover so much of the surface of the earth. The pitfalls of analysis of the information available are clearly demonstrated and yet the need for new and more comprehensive information is also made evident. In particular, a much greater investment must be made in long-term experiments that explicitly address the main questions posed in this book. This, in turn, will require that science-funding sources recognize that high-quality information on the ecosystem services provided by long-lived ecosystems, of varying complexities, which cover much of the earth's surface, will need a greater time commitment and a higher level of financial resources that are normally committed to ecological research. It has been clearly demonstrated that to unravel complex ecosystem processes in forest systems, such as those at Hubbard Brook in New Hampshire, there is no substitute for experimentation.

We have done the easy stuff, working experimentally with herbaceous communities, and have learned a great deal about the diversity/functioning/stability relationship. However, we now must move on to the next level and address those ecosystems that control a good portion of the carbon, nutrient and water balances of the earth – the forests. This volume will provide a important template for this next phase.

Stanford
September 2004 *Harold Mooney*

Preface

Evaluating the extent to which biological richness is necessary to sustain the earth's system and the functioning of individual ecosystems has emerged as one of the central research themes in ecology. Does biodiversity matter for ecosystem integrity, functioning, and the provision of goods and services?[1] This was the main question asked by the initial book summarizing this field of research (Schulze and Mooney 1993) that appeared as Volume 99 in the *Ecological Studies* Series. Since then, this field has largely been developed through the use of model systems, both mathematical and real (e.g., Hector et al. 1999; Loreau 2000; Tilman et al. 2001). For very practical reasons, the experimental/observational model systems were small in size, short-lived and even-aged, mainly herbaceous assemblages or microbial microcosms. Results obtained with these systems have stimulated the scientific debate enormously, and have been the basis and support for theory development. In essence, it was ascertained that, along with abiotic factors, biological richness is a major determinant of ecosystem functioning (Loreau et al. 2001). However, woody species were by and large excluded from this research, although forests (including plantations) cover over 30 % of the earth's land area (FAO 2001), produce 65 % of the annual carbon fixation (net primary production; Lieth 1975), and store almost 80 % of the carbon biomass of the planet (Watson et al. 2000). In addition, they are facing even larger changes in their biological diversity than herbaceous vegetation (WRI 2000), and the significance of forests for the vast majority of the world's terrestrial biodiversity has been acknowledged by the UN Convention on Biological Diversity (CBD) in its thematic work program on forest biological diversity (CBD 2001). It is thus a key ecological question whether links between diversity and functioning exist in forest ecosystems in a manner similar to those found in other ecosystems.

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[1] By "ecosystem functioning" we mean the activities, processes, and properties of ecosystems that are influenced by their biota (see also Naeem et al. 2002). By "ecosystem goods and services" we mean the benefits people obtain from ecosystems (see also Daily 1997).

Besides possible effects of biodiversity on ecosystem processes, biodiversity-dependent ecosystem goods and services provided by forests are important economic factors in most countries and contribute to the welfare of millions of people (WRI 2000). The search for patterns and principles of the relation between biological richness and ecosystem functioning is therefore not only of scientific importance, but should provide guidance for the sustainable use of the world's forest resources.

This volume summarizes the results of a LINKECOL workshop held in Weimar, Germany, 13–15 June 2002. The basic idea behind the workshop was to extend the ongoing debate about the relationship between biodiversity and ecosystem processes to the forest realm. The meeting assembled experts from various fields of forestry, biology, and ecology who illustrated and synthesized existing knowledge on various aspects of the functional significance of forest diversity. The linkages between species and functional group diversity among various categories of biota were explored, asking the question, whether diversity in one trophic level (in this case trees) affects diversity in other functional groups (e.g., canopy insects). The workshop examined in particular the significance of the presence of a multitude of players for ecosystem processes, such as stand productivity or biogeochemical cycles. It further explored the significance of biological richness for the robustness/sensitivity of ecosystems to extreme events, stresses, and various forms of disturbances and interventions. Finally, the importance of diversity at different scales was considered, ranging from stand management to global issues.

We thank the European Science Foundation for their support under the "Linking Community and Ecosystem Ecology" Program (LINKECOL), and the Max-Planck Society. We would also like to express our thanks to all who contributed their efforts and ideas. We believe that the discussions and personal contacts made at the workshop and the contributions to this volume will act as a starting point for exploring the field of biodiversity and ecosystem functioning in boreal and temperate forests.

Zürich, Basel, and Jena
September 2004

M. Scherer-Lorenzen
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Contents

Part A Introduction

Part B Productivity and Growth

Part C Biogeochemical Cycles

Part D Animals, Pests, and Disturbances

Part E Perspectives

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Part A Introduction

1 The Functional Significance of Forest Diversity: the Starting Point

M. SCHERER-LORENZEN, CH. KÖRNER, and E.-D. SCHULZE

1.1 Introduction

The dramatic and accelerating changes the earth's biota has undergone over the last decades have led to considerable research effort toward understanding the nature of biotic control over the processes within ecosystems. Predicting the consequences to the ecosystem of changes in species numbers, in distribution patterns of taxa, and in shifts of dominance that result in altered trophic interactions between organisms, has become a major challenge for community and ecosystem ecology. Does biodiversity matter for ecosystem integrity, functioning, and the provision of goods and services? This was the original question posed in a volume in *Ecological Studies* published in 1993 that started this field of research (Schulze and Mooney 1993). However, this question remained basically unanswered with respect to forests. It is the aim of the present book to summarize the state of knowledge with respect to forests, focusing on the temperate and boreal regions.

1.2 Applying a New Ecological Framework

The recent advances of research in the field of biodiversity and ecosystem functioning (Schulze and Mooney 1993; Kinzig et al. 2002b; Loreau et al. 2002) were accompanied by two remarkable features: first, a merging or increasing overlap of two disciplines in ecology that had followed separate ways in exploring the "nature" of ecosystems in the past, namely, population or community and ecosystem ecology (Likens 1992; Grimm 1995); second, and related to this first feature, the evolution of a new synthetic ecological framework that underlines the active role of the biota and its diversity in governing environmental conditions within ecosystems (Lawton 2000; Loreau et al. 2001; Naeem 2002) up to global processes (IPCC 2001).

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In exploring biodiversity, community ecology has seen the distribution and abundance of species as a function of abiotic (physical and chemical) conditions and biotic (interactions among species such as competition or predation) factors. Examples for forests are: (1) the apparent increase in tree species richness along latitudinal gradients from boreal to tropical regions (Ricklefs 1977) or within continents (Silvertown 1985) reflects parallel gradients in physical conditions such as temperature and moisture, differences in time periods without major climatic changes, or many other factors varying in parallel with latitude (Pianka 1966; Stevens 1989; Iwasa et al. 1993); (2) differences between highly diverse early-successional woody communities and late-successional species-poor forests in central Europe have been explained by outcompetition of light-demanding species by shade-tolerant ones (Küppers 1984). In contrast, ecosystem ecology has looked at ecosystems independently of species diversity. It was the flow of energy and the fluxes and pools of elements that were important, although data were often taken on a species level and then aggregated to the whole ecosystem (Grimm 1995). The compilation of the results from the IBP (International Biological Program) study sites in deciduous forests may serve as an example here (Khanna and Ulrich 1991; Röhrig 1991). Similarly, biogeochemistry has treated ecosystems as series of linked compartments rather than as associations of species, although this always represented an operational convenience more than a hypothesis that species traits were irrelevant (Schimel 2001). However, the similarity among species in basic functional properties such as photosynthetic pathway, and the finding that plant productivity is dependent on the energy absorbed rather than on species identities, initially led to the use of earth system models that have little diversity content, but rather use only the color of the land surface (Mooney 2001).

Applying the new emerging framework, a specific ecosystem function is seen as a function of (1) biodiversity and the functional traits of the organisms involved, (2) associated biogeochemical processes, and (3) the abiotic environment. Thus, the active role of the biota and its diversity in governing environmental conditions is underlined. It is important to note, however, that even Tansley in his first definition of an ecosystem mentioned the influences of the organisms on the physical system, although not from a diversity perspective (Tansley 1935). The insight that biodiversity and the feedback of the biosphere on global processes cannot be neglected, and have a profound impact, has also been recognized by the modeling community: all but the most aggregated climate and ecosystem models incorporate the role of different functional types of plants defined by morphological and physiological traits (Schimel 2001; Schulze and Schimel 2001) – for instance being "broadleaf tree", "needleleaf tree", "C_3 grass", "C_4 grass", or "shrub" (Cox et al. 2000).

This volume explores the significance of tree diversity in temperate and boreal forests within this ecological framework, i.e., by exploring the relationship between forest biodiversity and ecosystem functioning.

1.3 The Road from Weidenberg to Weimar

More than 10 years of intensive research on biodiversity and ecosystem functioning has resulted in an exponentially growing number of publications, accentuated and synthesized by several important conferences and meetings. Although ecologists have been interested in effects of species and their numbers on ecological processes for a long time, the launch of the Scientific Committee of Problems of the Environment (SCOPE) program of 1991 entitled "Ecosystem Functioning of Biodiversity" definitively marked the start of the recent development of this scientific field. The start-up meeting held in Weidenberg/Bayreuth, Germany, in that year reviewed the state of knowledge (Schulze and Mooney 1993), which mostly consisted of a compilation of related studies from community and ecosystem ecology. It also marked the start of a hypothesis-based formulation of a comprehensive and articulated conceptual framework, graphically represented by a small number of hypothetical relationships between biodiversity and ecosystem processes, namely, that diversity shows (1) no effect on ecosystem function ("null hypothesis"), (2) a linear relationship, or (3) an asymptotic relationship wherein species loss initially has only a weak effect, but which accelerates as more species are lost (Vitousek and Hooper 1993). In the following period, an in-depth examination of the functional role of biodiversity in various ecosystems of the world was performed within the SCOPE program, later to be expanded as part of the Global Biodiversity Assessment (GBA; Heywood and Watson 1995; Mooney et al. 1996). It became clear that correlation studies looking at the impact of biodiversity on ecosystem processes could hardly detect any causal mechanisms of biodiversity effects and that covarying factors such as soil acidity or nitrogen could mask potential biodiversity-functioning relations. These ideas were originally formulated in a workshop at Mitwitz, Germany, in 1988, in which various experimental approaches of ecosystem studies were discussed (Mooney et al. 1991), ranging from natural catastrophes to designed layouts. Based on this knowledge and on results from earlier experiments on species interactions in multi-species communities, e.g., with algae (Tilman 1977) or with grasslands differing in species richness and composition (Tilman 1987), several experiments were initiated, manipulating biodiversity while keeping abiotic factors as constant as possible (e.g., Naeem et al. 1994; Tilman et al. 1996; Hector et al. 1999; for an overview see Schmid et al. 2002). Interestingly, the very first ecological experiment documented until now, which had also been analyzed by Darwin and mentioned in *On the Origin of Species* (Darwin 1872 p. 113), had a similar aim: to establish, on the basis of experiments, which species – both alone and in mixtures – make the most productive grasslands on different soil types (Hector and Hooper 2002). It is mainly these recent experiments that have spurred the tremendous debate and controversy among ecologists about the importance of biodiversity for ecosystem functioning, focusing on the validity of such experimental approaches, and on the relevance of several mechanisms responsible for the observed relations between diversity and function. In short, in the experiments that assemble communities differing in biodiversity by random draws of species from a fixed pool, it is difficult to separate effects due to the increasing probability that certain species with major impacts on ecosystem processes are present in higher diversity levels (the sampling effect) from effects due to niche complementarity (Aarssen 1997; Huston 1997; Wardle 1999; Scherer-Lorenzen, Chap. 17, this Vol.). Basis for the sampling-effect model is the notion that the functional characteristics of the dominant plants rather than their number largely control ecosystem processes (Grime 1997). Additionally, given the strong influence of extrinsic factors on both biodiversity and ecosystem processes, it has been questioned how relevant the patterns observed in biodiversity-functioning experiments are for interpreting species loss in natural communities (Grime 1997; Wardle et al. 1997; a review of this controversy is found in Kinzig et al. 2002a; Mooney 2002; Naeem et al. 2002). In 1999, a meeting held under the auspices of the International Geosphere-Biosphere Program–Global Change and Terrestrial Ecosystems (IGBP-GCTE focus 4) in Santa Barbara, California, USA, summarized the empirical findings and theoretical concepts that were published during the first 8 years since the first conference in Weidenberg. The resulting book documents the progress made in this field – in both conducting and interpreting experimental results and in developing sound ecological theory (Kinzig et al. 2002b). Another milestone in this series of important conferences was the "Synthesis Conference" held in Paris, France, in 2000, again organized under IGBP-GCTE and DIVERSITAS, which achieved a synthetic and balanced view of the knowledge and challenges in the fast growing area of research addressing biodiversity and ecosystem functioning (Loreau et al. 2001, 2002).

As one browses through the three important books that reviewed and summarized the knowledge about biodiversity-ecosystem-functioning research until now (Schulze and Mooney 1993; Kinzig et al. 2002b; Loreau et al. 2002), with the exception of the paper by Iwasa and colleagues (Iwasa et al. 1993) who modeled tree species diversity along latitudinal gradients (with a "traditional" community ecology perspective), no single contribution explicitly focuses on forest ecosystems. If forests are mentioned at all, it is only in relation to varying decomposer or litter diversities and their implications for soil processes such as decomposition (Mikola et al. 2002; Wardle and van der Putten 2002). Has the new field of research bypassed the forests? On the other hand, much work has been carried out in the forest sector on the ecological and socio-economic consequences of mixing (mostly commercially important) tree species, as compiled by Cannell et al. (1992), Kelty et al. (1992) and Olsthoorn et al. (1999). Further, the establishment of diverse forests is a legislative aim in European forest operations. But why have these findings been left almost unanalyzed within the biodiversity-ecosystem functioning framework (Scherer-Lorenzen et al., Chap. 17, this Vol., but see Bengtsson et al. 2000)? Among other reasons, it is this question that inspired the idea to organize a workshop in Weimar, Germany, in 2002 on the "Functional Significance of Tree Diversity in Temperate and Boreal Forests," experts from various fields of forest ecology invited to attend. This book summarizes the results of this workshop that was held under the auspices of the "Linking Community and Ecosystem Ecology" Program (LINKECOL) of the European Science Foundation.

1.4 Aims and Topics

The aim of our workshop was to check whether the statement made by von Cotta more than 175 years ago (1828) can be supported by re-analyzing the large amount of literature on mixed forests stands accumulated since then, and by compiling new data on this topic. In his "Instructions for silviculture" von Cotta noted: "Since not all tree species utilize resources in the same manner, growth is more lively in mixed stands and neither insects nor storms can do as much damage; also, a wider range of timber will be available everywhere to satisfy different demands …" (translation by H. Pretzsch). Productivity, resource use, pests, and disturbances: all these topics raised in this single sentence by von Cotta have been re-examined in the present volume. We only excluded socio-economic aspects – satisfaction of different demands – from our compilation, referring here to the work, for instance, of Olsthoorn et al. (1999).

To equally cover all forest biomes in one workshop and the volume at hand would clearly go beyond the scope of a concise review of existing knowledge and a focused discussion of diversity–function relationships. We therefore concentrate here on temperate and boreal forests, hoping that other forest types might be in the center of future discussions. Equally, a focus on a certain set of ecosystem traits and processes and functions is needed, and we selected three major groups that we think cover the most important aspects of ecosystem functioning: productivity and growth (Part B); biogeochemical cycles (Part C); and animals, pests, and disturbances (Part D).

The contribution by Körner (Chap. 2) introduces the concept of functional trait diversity, compiling a large amount of data on several traits of temperate tree species. The variation in those functional traits among species is enormous, and thus species richness and composition of forest communities could potentially have significant effects on ecosystem processes.

Part B covers a primary aspect of ecosystem functioning, namely, productivity and growth at the stand level, which integrate various processes in space and time, ranging from photosynthesis to mortality. Pretzsch (Chap. 3) first reviews theoretical considerations about consequences of mixing species for productivity. These hypotheses are then tested in long-term experiments that compare biomass production of species grown in monocultures and two-species mixtures. Following Pretzsch, who shows that generalizations about mixture effects are difficult to make even under standardized experimental conditions, the chapter by Vilá et al. (Chap. 4) explicitly focuses on factors that may confound diversity–productivity relationships resulting from observational studies. Exemplarily, they analyze a large data-set from the forest inventory of Catalonia, Spain, that supports a positive association between tree-species richness and stemwood production of trees (excluding the shrub layer). One aspect often ignored in studying biodiversity effects is the contribution of variation at the genetic level. Although the database for genetic diversity of tree species is relatively scarce, this aspect of biodiversity nevertheless has profound implications for an individual's ability to respond to stress, for its reproductive success, and for growth, as shown by Müller-Starck and colleagues for European tree species (Chap. 5).

Part C on biogeochemical cycles starts with a case study of a long-term mixture experiment at Gisburn, UK, where various aspects of nutrient cycling were studied in single-species stands and two-species mixtures (Jones et al., Chap. 6). How tree species diversity may or may not affect water use of plants is examined by Baldocchi (Chap. 7), theory and experimental data being reviewed across the scales of leaves, tree, and canopy. A crucial step in the cycling of nutrients within an ecosystem is decomposition of leaf litter. Because the chemical composition and structure of litter differs among tree species, diversity could also influence decomposition rates, as is discussed by Hättenschwiler (Chap. 8). The next two chapters explore potential effects of tree diversity for the carbon balance of forests, focusing on pools and fluxes within the soil compartment. While Gleixner et al. (Chap. 9) look at the processes and mechanisms responsible for the formation and the dynamics of soil organic matter at the molecular level, Mund and Schulze (Chap. 10) analyze the influence of silvicultural systems and their interactions with biodiversity for the soil carbon balance.

Part D on animals, pests, and disturbances deals with two widely accepted views, namely, that tree diversity should be positively correlated with the diversity of other trophic levels, and that it should lead to higher stability against biotic or abiotic disturbances. Scheu (Chap. 11) examines the plant diversity–animal diversity relationship by concentrating on the below-ground food web. He not only describes how tree diversity may determine the food web structure, but also how the below-ground community feeds back on the plant community. The link between plant diversity effects on higher trophic levels and a forest's response to disturbances is presented by Jactel et al. (Chap. 12) who performed a meta-analysis of tree diversity effects on insect pest infestations, testing the biodiversity–stability hypothesis. They explore the relevance of several responsible factors for such a relationship at both the stand and landscape levels, and conclude with implications for pest management. Pautasso and colleagues (Chap. 13) present a thorough review on the susceptibility of forest stands to fungal pathogens, which represents another important factor, besides pest insects, of economic risk in managed forests. They discuss how forest diversity may or may not influence this susceptibility, and how adopting the reverse view, i.e., how pathogens influence tree diversity, helps to understand the complex plant–pathogen dynamics. One of the most often cited examples for a positive diversity–stability relationship in forests is the presumed higher resistance of diverse tree communities to strong winds. However, as shown by Dhôte (Chap. 14), a closer look reveals a magnitude of interactions between factors contributing to the physical stability of a tree, including, besides wind itself, effects of location, developmental stage, and canopy characteristics. Finally, Wirth (Chap. 15) closes this section by relating the diversity of functional traits of boreal trees to the fire regime observed. He discusses implications for the biogeography of boreal forests and explores the significance of fire plant functional types for carbon cycling, linking the sections on disturbance and biogeochemistry.

What have we learned from analyzing the relationship between forest biodiversity and ecosystem functioning from different angles and what are the perspectives for future research? This is the subject of Part E. Scherer-Lorenzen et al. (Chap. 16) describe some experimental approaches for studying diversity–function relationships in forests that can overcome the big dilemma of observational studies, namely, that because of covarying factors it is nearly impossible to assign causality (see also Vilá et al., Chap. 4). Finally, in Chapter 17 we discuss the applicability of the main hypothesized mechanism for a positive relationship between plant diversity and ecosystem processes derived from grassland studies, namely, resource use complementarity, to forest ecosystems. The final synthesis reveals both the foresight of von Cotta (1828), and the progress made since then. But as in other prospering fields of science, a variety of questions about the significance of forest biodiversity remains to be answered.

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