1 The Functional Significance of Forest Diversity: the Starting Point

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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