BIODIVERSITY AND ECOSYSTEM FUNCTIONING: BASIC PRINCIPLES

M. Scherer-Lorenzen
Institute of Plant Sciences, Swiss Federal Institute of Technology Zurich (ETH), Switzerland

Keywords: biodiversity, conservation, ecosystem functioning, ecosystem management, ecosystem processes, experimental studies, functional traits, functional groups, niche differentiation, observational studies, resource use complementarity, sampling, species richness, stability.

Contents

Summary

Since the mid 1990s, ecologists have intensified their efforts to describe and quantify the effects that biodiversity can exert on the various processes within ecosystems. Both theoretical and experimental work has shown that within a habitat, changing diversity has profound effects on biomass production, nutrient retention, and other ecosystem characteristics such as stability. In most experiments, a positive relationship between plant diversity and productivity has been found, while the level of unconsumed resources was inversely related to diversity. The diversity of functional groups in general had more pronounced effects than the number of species, emphasizing the importance of functional traits of species. As underlying mechanisms, niche differentiation leading to complementary resource use, facilitative interactions among species, and probabilistic sampling effects have been identified. For management or conservation purposes, it is crucial to distinguish results obtained from within-habitat manipulative experiments, from those of observational studies comparing across-habitat patterns of diversity and ecosystem functioning. As the understanding of the

biodiversity-ecosystem functioning relationship progresses, conservation and management will more and more benefit from these basic insights into how communities and ecosystems function.

1. Introduction

'Does biodiversity matter for the functioning of ecosystems?' or 'Does it make any difference to the processes within an ecosystem if there are many or only a few species?' These are the central questions that arise when one is looking at the many ecosystems on earth differing very much in their biological richness, but which all have a similar basic set of energy-, matter-, and information-fluxes. For example, both tropical forests with their overwhelming richness in flora and fauna, and extremely species-poor systems such as lichen communities in Antarctica, fix carbon through photosynthesis of the plant compartment, and organic matter is decomposed by microorganisms into mineral components, which are partly taken up by the primary producers again. Although admittedly simple, this example shows that processes central for the functioning of ecosystems might be maintained by many or very few organisms, which suggests the question whether there is any relationship between biodiversity and ecosystem functioning. The answer to this question is not only of pure academic interest, but it becomes more and more relevant as the loss of biodiversity is dramatic and globally accelerating. From a human point of view, the key question may thus be formulated: 'Does biodiversity matter for the provision of ecosystem services?', which are the benefits people obtain from ecosystems.

This contribution focuses on the relationship between biological diversity and two aspects of ecosystem functioning: resource dynamics at a given point in time such as primary production or nutrient cycling, and long-term stability in the face of environmental change. The anthropocentric 'value' of biodiversity and its importance for the ecosystem services that humanity obtain are dealt with in *The Value of Biodiversity* and is in the focus of another large international initiative, the Millennium Ecosystem Assessment (MA 2003, www.millenniumassessment.org).

2. A historical perspective

It was not until the beginning of the 1990s that, alarmed by the increasing loss of biodiversity, scientists started to systematically seek answers to the basic question outlined above. Before that time, a related topic was discussed mainly from a theoretical perspective: the relation between diversity and stability of food webs. While early theory predicted more stable properties in more complex food webs of producers and consumers, later models predicted less stable population dynamics (see also section 5). Therefore, the notion that diversity may influence ecosystem processes in a 'positive' way was not apposite. In addition, research from agronomy demonstrated that mixtures of crop species were often less productive than the best monoculture. Experience from agriculture also showed that in the course of intensification of production, productivity increased through higher input of fertilizers and pesticides, while diversity within fields decreased.

However, the 'biodiversity crisis' again raised interest in the question whether diversity has effects on ecosystem functioning or not. The launch of the Scientific Committee of Problems of the Environment (SCOPE) program of 1991 entitled 'Ecosystem Functioning of Biodiversity', initiated the recent rapid development in this field of research. This program helped to bridge the gap between two disciplines in ecology that had followed separate ways in studying ecosystems, namely 'population or community ecology' and 'ecosystem ecology'. The former discipline accumulated knowledge on the distribution and abundance of species as a function of abiotic (physical and chemical) and biotic (interactions among species such as competition) conditions. The latter discipline has studied the flow of energy and the fluxes and pools of elements within ecosystems, without explicitly considering the diversity of organisms involved and their functional roles. In the first product of that SCOPE program, a hypothesis-based and comprehensive framework on how biodiversity may affect ecosystem processes was expressed for the first time (see Schulze & Mooney 1993, section 3).

In the second half of the SCOPE program, an in-depth exploration of the functional role of biodiversity in various biomes was published in three books (Mooney *et al* 1996, Solbrig *et al* 1996, Orians *et al* 1996). This effort was largely based on the evaluation of observational studies comparing communities with different levels of diversity, e.g. species poor temperate forests of mid-Europe with species rich ones of East Asia. Quickly it became obvious that such correlational studies could hardly detect any causal mechanisms of biodiversity effects due to co-varying factors (see section 3.2. for more details) and that they have to be complemented by experimental approaches. Parts of that program were then included into the Global Biodiversity Assessment (GBA; Heywood & Watson 1995), an independent, peer-reviewed analysis of the biological and social aspects of biodiversity, commissioned by the United Nations Environment Programme (UNEP). This assessment was done to fulfill the need of a comprehensive review of current knowledge in the framework of the United Nations Convention on Biological Diversity (CBD).

Based on the insight gained from correlational studies and on the formulation of the early hypotheses, a first generation of experiments were conducted that sought to reject the null hypothesis of no relationship between biodiversity as an independent variable and ecosystem functioning as the dependent variable (see examples listed in the bibliography). All those experiments adopted a basic common design: establishment of a gradient in biodiversity (most often plant species richness or the number of functional groups), while keeping extrinsic conditions (e.g. climate, fertility, land use history) as constant as possible. They were conducted in microbial microcosms, in controlled environmental facilities, or in the field. A variety of ecosystem processes were monitored as response variables, with a focus on biomass production (primary productivity). For very practical reasons, these experiments used fast-growing, small sized, mainly early successional model systems such as grasslands. In essence, most studies reported a positive, but asymptotic relationship between diversity and ecosystem processes, wherein the loss of species from an ecosystem initially has only a weak effect, but which accelerates as the system impoverishes. More diverse systems consistently had higher biomass production, higher nutrient uptake and consequently lower leaching losses to the groundwater, and they were more resistant against invasion by other species (see *Biodiversity and Ecosystem Functioning: Experimental Systems*). More recently, experimental work on the biodiversity–ecosystem functioning relationship increased strongly in number and many different ecosystem types such as wetlands, marine systems or forests were tackled. In addition, more mechanistically driven experiments were initiated, focusing on nutrient dynamics, trophic interactions, population dynamics or below/above-ground interactions, for instance. Parallel to the empirical work, theoretical studies began to explore the functional significance of diversity, building upon concepts of intercropping theory from agriculture and upon models of resource competition and niche differentiation.

These experiments have spurred a tremendous controversy among ecologists about the importance of biodiversity for ecosystem functioning. The debate focused on the validity of the experimental designs, on the relevance of several distinct mechanisms responsible for the observed diversity effects (see section 3.3.), and on the relevance of the findings for interpreting biodiversity loss in natural ecosystems. In part, this controversy arose from the apparent discrepancy between the results obtained from the artificially assembled model communities and observational studies (for details see sections 3.2. and 4., and also *The Role of Above- and Below-ground Linkages in Ecosystem Functioning*.

After almost a decade of intensive research, two conferences held in 1999 and 2000 under the auspices of the International Geosphere-Biosphere Program – Global Change and Terrestrial Ecosystems (IGBP-GCTE) and the international program of biodiversity science DIVERSITAS summarized and synthesized the empirical findings and theoretical concepts. The resulting books are another two landmarks in the fast-growing area of research addressing biodiversity and ecosystem functioning (Kinzig et al. 2002; Loreau et al. 2002), providing both thorough reviews of all relevant studies and perspectives and challenges for future work. A recent article by Hooper and colleagues summarizes these issues too (Hooper et al. 2005). Recently, a synthesis book explicitly focused on the role of insects for ecosystem functioning (Weisser and Siemann 2004), whereas another one extended the biodiversity-ecosystem functioning issue to the temperate and boreal forest realm (Scherer-Lorenzen *et al* 2005).

Interestingly, the first ecological experiment documented that was analyzed by Darwin and mentioned in *On the Origin of Species* (1872, p. 113) had a similar aim as the manipulative biodiversity experiments of the last decade: to determine which species growing in monoculture or in mixtures make the most productive grasslands on different soil types. From that experiment Darwin concluded that mixtures of several distinct plant genera produce higher yields than species grown in monocultures, which essentially was endorsed by the modern experiments.

3. A new paradigm in ecology: the 'Biodiversity-Ecosystem Function Paradigm'

The recent advances made in functional biodiversity research led to a new synthetic ecological framework, which has even been denoted as a new paradigm of ecology. While biodiversity has historically been seen as a response variable that is affected by climate, nutrient availability and disturbance, this new emerging paradigm, called 'Biodiversity-Ecosystem Function Paradigm' (Naeem 2002), sees the environment primarily as a function of diversity, underlining the active role of the biota in governing environmental conditions. It does not deny, of course, the influence of the environment on organisms. More specifically, within this framework, a specific ecosystem function is thus seen as a function of (i) biodiversity and the functional traits of the organisms involved, (ii) associated biogeochemical processes, and (iii) the abiotic environment. This is not only of pure academic interest, but it has important implications for the conservation and sustainable management of biological diversity (see section 6).

3.1. Hypotheses

At the beginning of the 1990s, three main hypotheses were formulated concerning how species richness as a surrogate for biological diversity (as the independent treatment variable) may affect ecosystem processes (as the dependent response variable); namely that diversity shows (i) no effect ('null hypothesis'), (ii) a linear relationship between diversity and ecosystem processes, or (iii) an asymptotic relationship where species at higher levels of diversity might be redundant in their function. These early hypothetical relationships have been expanded since then (see Figure 1 for examples) and they represent a variety of underlying mechanisms. However, they can be classified into three classes:

- *Species are primarily redundant*: Loss of species is compensated for by other species with a similar function. Conversely, the addition of such species adds nothing new to the system. The graphical presentation show an asymptotic relationship in which a major proportion is insensitive to changes in diversity. The basis for this view is a classification of species into functional groups where those species within one group have a similar function in the system. For the maintenance of ecosystem functioning, a minimal set of functional groups is essential, but species within a group are at least partially substitutable and thus 'redundant' (Lawton and Brown, chapter 12 in Schulze and Mooney 1993). While this might be true under stable environmental conditions, such 'redundant' species might replace species that are lost under changing conditions such as disturbance events or climate change. In consequence, the 'insurance hypothesis' predicts more stable ecosystem functioning with higher diversity under fluctuating environmental conditions (Yachi and Loreau 1999, see also section 5.), highlighting the context-dependency of the 'redundancy hypothesis'. Related to this class of hypotheses is the so-called 'rivet hypothesis' that compares the role of species with rivets holding together a machine: some rivets (species) are redundant in their function, increasing the reliability of the system. However, after the number of rivets drops below a certain threshold, the system fails.
- *Species are primarily singular*: Loss or addition of species causes detectable changes in ecosystem process rates, i.e. species make unique contributions to ecosystem functioning. The graphical presentations have a positive (or negative, depending on the process under study) slope. Cases of singular species with extreme impacts are 'keystone species' or 'ecosystem engineers', the former being species with disproportionate effects on ecosystems relative to their abundance (e.g. predators controlling dominance of other species), the latter being species that modify the resource availability for other members of the community through modification of the habitat (e.g. dam-building beavers) (Lawton 1994).
- *Species impacts are context-dependent and therefore idiosyncratic*: The impact of loss or addition of species depends on environmental conditions (e.g. community

composition, fertility, disturbance regime), so that a species makes different contributions to ecosystems depending on conditions. The graphical presentation shows a variety of different slopes over different proportions of their trajectory and shows no clear trend. The 'idiosyncratic response hypothesis', however, does not mean that there is no effect of diversity (i.e. the 'null hypothesis'), but that it is rather difficult to predict the effects due to the complexity of species' roles in ecosystems.

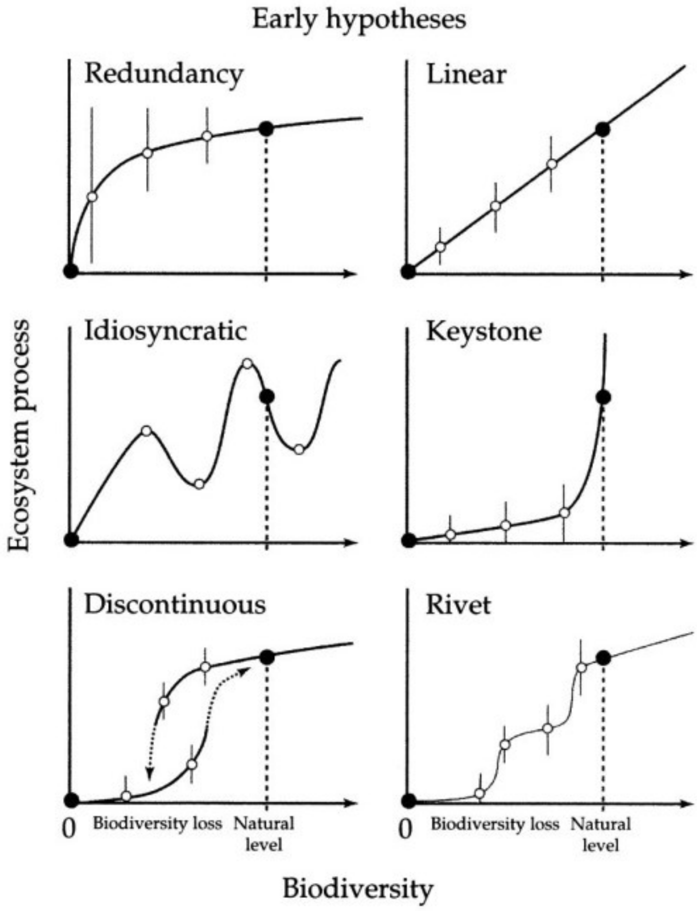

Figure 1. Graphs of early hypotheses considering the relationship between biodiversity and ecosystem functioning. Source: Naeem *et al*, in Loreau *et al* 2002.

3.2. Approaches

If one is interested in answering the question how biodiversity affects ecosystem functioning, certainly the first approach coming to one's mind would be to search for communities differing in one aspect of biodiversity, and to compare these in terms of a variety of ecosystem processes. For example, two types of forests with different number and composition of plant species would be sampled, following this comparative approach. However, unless site conditions are extremely similar, such across-habitat or across-locality comparisons may hide any potential effects that diversity exhibits within a site, because of environmental differences between the sampled sites. These environmental factors themselves determine the diversity of an ecosystem. Thus, comparative studies or sample surveys can be used to document any correlations between diversity and ecological processes, but they can never be used to establish causality or underlying mechanisms of this relationship. For example, Caspersen and Pacala (2001), using forest inventory data from the USA, plotted the number of tree species in the canopy against stand growth. They found an asymptotical increase of growth with increasing tree species (Figure 2). One conclusion from that could be that a higher diversity of trees enhances productivity due to functional differences between species leading to higher resource exploitation and, hence, higher growth. This argumentation would follow the niche complementarity hypothesis outlined in detail below (3.3.1.). However, causality could also run the opposite way: more productive stands may simply permit the coexistence of more species. Thus, cause and effect cannot be disentangled from observational and comparative studies. As a first experimental approach, so-called 'removal experiments' have been used where certain aspects of diversity (species, functional groups) are removed from intact, natural systems, thus creating a gradient in diversity levels ranging from natural to depauperate. These experiments can be very useful under certain circumstances, although the question of proper control treatments is rather difficult. In addition, other drawbacks have to be accounted for, such as large disturbance effects, changes in density, or spatial segregation of species. Díaz *et al* (2003) present a good overview on this approach.

Due to these difficulties, experimental approaches were initiated during the early 1990s, as described above that randomly allocate diversity treatments to plots within one site, keeping environmental conditions as constant as possible. Only by adopting this 'synthetic community approach', can within-habitat effects of diversity be detected unequivocally. In *Biodiversity and Ecosystem Functioning: Experimental Systems*, the most important aspects of these biodiversity experiments are described, focusing on grassland ecosystems. However, it is clear that for many ecosystems, one still has to rely on observational studies, simply because experimental manipulation of diversity is difficult to perform (e.g. forests, although there have been experiments established recently). Careful site characterization and large numbers of study sites are then needed to come to a reasonable 'signal-to-noise' ratio. In addition, among-site abiotic variation has to be adequately accounted for by including these 'third' variables as covariates in statistical analyses.

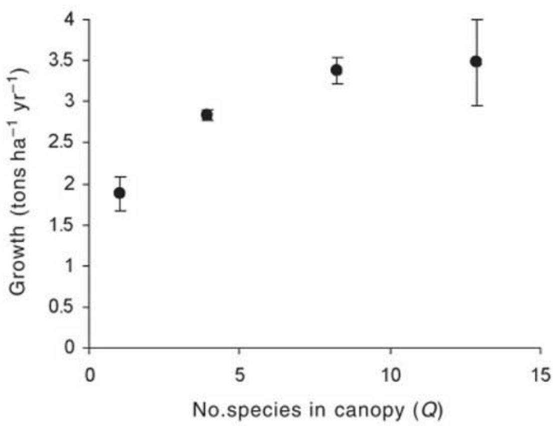

Figure 2. Relationship between tree species richness and stand growth in North American forests. Source: Caspersen and Pacala, 2001.

3.3. Mechanisms

What are the potential mechanisms to explain a causal relationship between biodiversity and ecosystem processes? For simplicity, in the following biodiversity will be restricted to one trophic level (plants as producers) and to the level of species, while ecosystem processes will be restricted to short-term resource dynamics, e.g. primary productivity. Ecological theory developed at least three potential mechanisms which can be grouped into two distinct classes.

-
-
-

Bibliography

Callaway R.M. (1995). Positive interactions among plants. *The Botanical Review* 61:306-348. [A review on positive plant to plant interactions, i.e. facilitation]

Díaz, S. and Cabido M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* 16:646-655. [This article makes the plea that the diversity of functional traits matters most for ecosystem functioning]

Díaz S., Symstad A.J., Chapin I.S., Wardle F.D.A. and Huenneke L.F. (2003). Functional diversity revealed by removal experiments. *Trends in Ecology & Evolution* 18:140-146. [This paper describes ‘removal experiments’ as a valuable tool to assess the effects of biodiversity for ecosystem functioning]

Grime, J.P. (2001). *Plant strategies and vegetation processes*. 2nd edition. 417 pp. Chichester: John Wiley and Sons. [A comprehensive overview about processes in plant communities]

Hector A., Schmid B., Beierkuhnlein C., Caldeira M.C., Diemer M., Dimitrakopoulos P.G., Finn J., Freitas H., Giller P.S., Good J., Harris R., Högberg P., Huss-Danell K., Joshi J., Jumpponen A., Körner C., Leadley P.W., Loreau M., Minns A., Mulder C.P.H., O’Donovan G., Otway S.J., Pereira J.S., Prinz A, Read D.J., Scherer-Lorenzen M., Schulze E.D., Siamantziouras A.S.D., Spehn E., Terry A.C., Troumbis A.Y., Woodward F.I., Yachi S. and Lawton J.H. (1999). Plant diversity and productivity experiments in European grasslands. *Science* 286:1123-1127. [A large-scale experiment at eight different European sites analyzing within-site and across-site biodiversity-ecosystem functioning relationships. Grassland communities of differing species richness and number of functional groups were newly established from seed]

Hector A. and Hooper R. (2002). Darwin and the first ecological experiment. *Science* 295:639-640. [This paper describes an experiment Darwin was referring to when he described the phenomenon that a mixture of different plant genera has a higher biomass production than monocultures]

Hooper, D.U. and Vitousek P.M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science* 277:1302-1305. [One of the early manipulative field experiments in Californian serpentine grasslands, adopting the ‘synthetic community approach’]

Hooper D.U., Chapin F.S.I., Ewel J.J., Hector A., Inchausti P., Lavorel S., Lawton J.H., Lodge D.M., Loreau M., Naeem S., Schmid B., Setälä H., Symstad A.J., Vandermeer J. and Wardle D.A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge and needs for future research. *Ecological Monographs* 75:3-35. [The most recent overview about current knowledge on the biodiversity-ecosystem functioning issue]

Kahmen A., Perner J., Audorff V., Weisser W.W. and Buchmann N. (2005). Effects of plant diversity, community composition and environmental parameters on productivity in montane European grasslands. *Oecologia* 142: 606-615 [A comprehensive study showing an unimodal pattern of plant species richness and productivity]

Kinzig A.P., Pacala S.W. and Tilman D. (eds.) (2002). *The functional consequences of biodiversity: Empirical progress and theoretical extensions.* 365 pp. Princeton, Oxford: Princeton University Press. [The results of the IGBP-GCTE meeting in 1999, reviewing and summarizing the progress made since the book by Schulze & Mooney 1993]

Lawton J.H. (1994). What do species do in ecosystems? *Oikos* 71:367-374. [This article explores the roles that species perform in ecosystems, applying concepts of 'keystone species' or 'ecosystem engineers']

Lehman C.L. and Tilman D. (2000). Biodiversity, stability, and productivity in competitive communities. *American Naturalist* 156:534-552. [An article exploring theoretically the relationship between diversity and ecosystem stability]

Loreau M., Naeem S. and Inchausti P. (2002). *Biodiversity and ecosystem functioning: Synthesis and perspectives*. 294 pp. Oxford, New York: Oxford University Press. [Results of the IGBP-GCTE and DIVERSITAS 'Synthesis Conference' in 2000, achieving a synthetic and balanced view of the knowledge and challenges in the biodiversity – ecosystem functioning research area]

MA – Millenium Ecosystem Assessment (2003). *Ecosystems and Human Well-Being: A Framework for Assessment*. 245 pp. Washington D.C., Covelo: Island Press. [This summarizes the conceptual framework of the Millennium Ecosystem Assessment, a four-year international work program designed to meet the needs of decision-makers for scientific information on the links between ecosystem change and human well-being]

McGrady-Steed J., Harris P.M. and Morin P.J. (1997). Biodiversity regulates ecosystem predictability. *Nature* 390:162-165. [One of the first biodiversity experiments done with microbial microcosms]

Mooney, H.A., Cushman J.H., Medina E., Sala O.E., and Schulze E.D. (eds.) (1996). *Functional roles of biodiversity - a global perspective.* 493 pp. Chichester, New York, Brisbane, Toronto, Singapore: John Wiley & Sons. [An in-depth examination of the role of biodiversity for ecosystem functioning in various biomes of the world]

Naeem S. (2002). Ecosystem consequences of biodiversity loss: the evolution of a paradigm. *Ecology* 83:1537-1552. [Overview of the recent biodiversity-function debate and the resulting emergence of the new 'Biodiversity-Ecosystem Function Paradigm']

Naeem S., Thompson L.J., Lawler S.P., Lawton J.H. and Woodfin R.M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature* 368:734-737. [The first experimental study analyzing the relation between diversity at the producer and consumer level, and ecosystem processes. The experiments were done in the 'Ecotron', a large and replicated climate chamber facility]

Orians G.H., Dirzo R. and Cushman J.H. (eds.) (1996). *Biodiversity and ecosystem processes in tropical forests*. 229 pp. Ecological Studies 122. Berlin, Heidelberg, New York: Springer. [An in-depth analysis on the biodiversity-functioning relationship in tropical forests]

Pimm S.L. (1991). *The balance of nature?* 434 pp. Chicago: The University of Chicago Press. [This book addresses the often debated question of stability in ecological communities. Theories and concepts are related to the conservation of species and communities]

Scherer-Lorenzen M., Körner C., and Schulze E.-D. (eds.) (2005). *Forest Diversity and Function: Temperate and Boreal Systems*. 400 pp. Ecological Studies 176. Berlin, Heidelberg, New York: Springer. [A review of the state of knowledge about the relationship between biodiversity and ecosystem functioning in forests]

Schulze E.-D. and Mooney H.A. (eds.) (1993). *Biodiversity and ecosystem function*. 525 pp. Ecological Studies 99. Berlin, Heidelberg, New York: Springer. [The first milestone summarizing the knowledge on the relationship between biodiversity and ecosystem functioning, mainly based on results from comparative studies. It served as a kick-off for experimentally driven modern research on the issue]

Solbrig O.T., Medina E. and Silva J.F. (eds.) (1996). *Biodiversity and savanna ecosystem processes: a global perspective*. 233 pp. Ecological Studies 121. Berlin, Heidelberg, New York: Springer. [An in-depth analysis on the biodiversity-functioning relationship in savanna ecosystems]

Tilman D. (1996). Biodiversity: population versus ecosystem stability. *Ecology* 77(2): 350-363. [This paper provides data on temporal variability of biomass after drought, supporting the view that aggregated ecosystem or community properties may be stabilized by species diversity, while variability of individual populations may be increased]

Tilman D., Wedin D., and Knops J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379:718-720. [One of the first, well replicated biodiversity experiments adopting the 'synthetic community approach' at Cedar Creek Natural History Area in Minnesota, US]

Walker B., Kinzig A., and Langridge J. (1999). Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2:95-113. [An article which underlines the importance of dominant species for ecosystem functioning]

Weisser W.W. and Siemann E. (eds.) (2004). *Insects and ecosystem function*. 413 pp. Ecological Studies 173. Berlin, Heidelberg, New York: Springer. [This books examines the role of (herbivore) insects on ecosystem functioning]

Yachi, S., and M. Loreau (1999). Biodiversity and Ecosystem Productivity in a Fluctuating Environment: the Insurance Hypothesis. *Proceedings of the National Academy of Sciences of the U.S.A.* 96:57-64. [This article postulates that biodiversity provides an insurance for ecosystems against environmental changes]

Biographical Sketch

Dr. Michael Scherer-Lorenzen was born in September 1968 in Rottweil (Germany). He is married and has one son. He finished his studies in Biology at the University of Bayreuth (Germany) in 1995 with a master thesis on impacts of land use changes on biodiversity in Chile. During his PhD (University of Bayreuth) he investigated the effects of plant species loss on ecosystem functioning. This work was done within the European BIODEPTH project. After that, he held positions as Research Assistant at the German Advisory Council on Global Change (WBGU) and as Executive Director of the Institute of Biodiversity Network (IBN) in Germany. He did a post-doc at the Max-Planck-Institute for Biogeochemistry in Jena, Germany, and is now Senior Scientist at the Institute of Plant Sciences at the Swiss Federal Institute of Technology Zurich (ETH). In 2000, he won the International Horst-Wiehe Award for the Promotion of Ecological Sciences of the Ecological Society of Germany, Austria, Switzerland and Liechtenstein. One year later, he was finalist, with the BIODEPTH project, of the Descartes Prize of the European Union.

His research interests are related to the central question: "Does biodiversity matter for ecosystem functioning, and the provision of goods and services?" Within this huge field, he focuses on the relationship between biodiversity (focusing on plants) and ecosystem processes, with special emphasis on productivity, soil nitrogen dynamics, nitrogen allocation within and among plants, decomposition, mineralization and other soil processes. He is especially interested to elucidate the mechanisms behind diversity effects on these processes, such as resource use complementarity and facilitation.

He is working in mid-European grassland systems, and in afforestation in temperate and tropical regions, using experimental approaches to manipulate plant diversity. In addition, he is now expanding this work into natural alpine grasslands differing in biodiversity due to land use changes.