CHAPTER 1

Biodiversity and ecosystem functioning: the emergence of a synthetic ecological framework

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1.1 Understanding the significance of biodiversity

Earth's biota is not a passive epiphenomenon of Earth's physical conditions and geochemical processes. Through the collective metabolic and growth activities of its trillions of organisms, Earth's biota[1] moves hundreds of thousands of tons of elements and compounds between the hydrosphere, atmosphere, and lithosphere every year. It is this biogeochemical activity that determines soil fertility, air and water quality, and the habitability of ecosystems, biomes, and ultimately the Earth itself (Lovelock 1979; Butcher *et al*. 1992; Schlesinger 1997). Indeed, biogeochemistry makes Earth a unique planet in the solar system (Ernst 2000).

While the functional[2] significance of Earth's biota to ecosystem or Earth-system functioning is well established, the significance of Earth's *biodiversity*[3] has remained unknown until recently. For example, we have a well-developed understanding of photosynthetic production at minute (e.g. subcellular) scales (Hall *et al*. 1993) and a well-developed understanding of primary productivity at global scales (Roy *et al*. 2001), yet we have, by comparison,

little understanding of how plant diversity in a grassy meadow, desert, or forest affects production at the ecosystem, biome, or global scale.

At a time when biodiversity is undergoing dramatic changes in distribution and abundance (Ehrlich 1988; Wilson 1988; Soulé 1991; Reaka-Kudla *et al*. 1997; Stork 1997), predicting the ecosystem or Earth-system consequences of such change is a critical issue (Ehrlich and Wilson 1991; Chapin III *et al*. 2000). At a conference in Bayreuth, Germany, organized by E.-D. Schulze and H. A. Mooney in 1991, the proceedings of which were published in 1993 (Schulze and Mooney 1993), ecologists formerly reviewed what was known about the relationship between biodiversity and Earth-system and ecosystem functioning (henceforth, 'biodiversity-functioning' research). Since then, this focus has become a major thrust in contemporary ecology, reflecting a modern synthesis in which the study of biodiversity (e.g. distribution and abundance) is merged with the study of ecosystem functioning (e.g. biogeochemical processes). H. A. Mooney (Chapter 2) traces the events that led to this 1991 symposium and the explosion of research that followed shortly after its publication.

Although the studies that have contributed to this discipline represent a broad array of individuals and their collective expertise, a considerable amount of debate has arisen concerning its findings (André *et al*. 1994; Givnish 1994; Aarssen 1997; Garnier *et al*. 1997; Grime 1997; Huston 1997; Tilman *et al*. 1997a; Wardle *et al*. 1997c, 2000b; Hector 1998; Hodgson *et al*. 1998; Lawton *et al*. 1998; Loreau 1998b;

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[1] By 'biota' we mean all biological entities in a habitat, ecosystem, or larger region, independent of its diversity.

[2] By 'functional' or 'functioning', we mean the activities, processes, or properties of ecosystems that are influenced by its biota. In no case is 'purpose' inferred in our usage of these terms.

[3] 'Biodiversity' refers to the extent of genetic, taxonomic, and ecological diversity over all spatial and temporal scales (Harper and Hawksworth 1995).

Wardle 1998, 1999; Naeem 1999; van der Heijden *et al.* 1999; Hector *et al.* 2000b; Huston *et al.* 2000; Naeem 2000; Tilman 2000) and its presentation in the press has been negative (Guterman 2000; Kaiser 2000).

A conference held in Paris, France, in December 2000, entitled *Biodiversity and ecosystem functioning: synthesis and perspectives* (henceforth, the Synthesis Conference), brought together researchers representing the full gamut of expertise and opinion on the empirical and theoretical foundations of biodiversity-functioning research. This volume is the outcome of that conference (see Preface), and this chapter provides a brief review of the topic and the content of this volume.

1.2 A brief history of biodiversity and ecosystem functioning

1.2.1 Early history

Initially, there may have been little question concerning the relationship between biodiversity and ecosystem functioning, though the perspective was predominantly one of metaphysical harmony among species and their environment (Egerton 2001). For example, Aristotle (384–322 BC) considered all entities to be made up of five elements (earth, fire, water, air and a fifth element known as the ether or the *quinta essencia*). Thus organisms, habitat, and environment were seen as one and it would likely have been an uninteresting question to ask if biodiversity and ecosystem functioning were related. This powerful construct endured nearly 2000 years until the scientific revolution of seventeenth-century Europe. While the positive aspects of the revolution are well documented, the abandonment of Aristotelian thinking fractionated the sciences, and natural history in particular underwent considerable transformation (Henry 1997). This hindered progress in biodiversity-functioning research, which requires multi-disciplinary approaches that integrate across such fields as botany, zoology, microbiology, chemistry, physics, and geology, to name just a few.

Today, ecologists and environmentalists understand that environment and habitat are the endpoints of the collective activities of abiotic and biotic processes shaped by history. The biosphere[4] is recognized as a vast, staggeringly complex, highly dynamic system made up of some 10–100 million species that share over 3.5 billion years of history and currently occupies virtually all 5.10×10^{14} m^2 of the Earth's terrestrial and aquatic surfaces. Clearly, to understand the functioning of Earth systems requires not only understanding biogeochemistry, but also the role that biodiversity plays in this complex system.

In spite of its rapid growth, however, the inclusion of biodiversity in Earth-system and ecosystem science has only recently become a growing part of ecological research (Mooney, Chapter 2). This lack of inclusion most likely stems from the fact that ecology has been historically divided primarily into two disciplines: community ecology and ecosystem ecology (Likens 1992; Grimm 1995; Loreau 2000b; Loreau *et al.* 2001). Community ecology focused on how extrinsic factors[5] such as climate, disturbance, or site fertility affect biodiversity and how intrinsic factors[6] affect biodiversity dynamics. In contrast, ecosystem ecologists have focused on the rates, dynamics, and stability of energy flow and nutrient cycling within ecosystems. Over the last decade, however, synthetic studies that consider both biodiversity and ecosystem functioning have grown to become an integral part of the ecological literature (Fig. 1.1).

Like much of science, however, if one searches, earlier works that predate current activities are often found. For example, the importance of atmospheric greenhouse gasses in climate was recognized by Jean-Baptiste Fourier in 1827 (Houghton 1997) and the logistic model was first described by Pierre-François Verhulst in the 1830s. Similarly, Darwin himself (McNaughton 1993) and the ecological

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[4] 'Biosphere' is the global domain within which biodiversity is found. This domain is located between the Earth's lithosphere and atmosphere, occupying a layer that includes parts of the atmosphere, hydrosphere, and lithosphere.

[5] By 'extrinsic' we mean primarily abiotic processes such as disturbance and climate.

[6] By 'intrinsic' we mean biotic factors such as biotic interactions (e.g. competition, predation, mutualism) or community structure (e.g. the type, strength, and number of biotic interactions among species in a community that often describe webs or networks of material and energy flow among species).
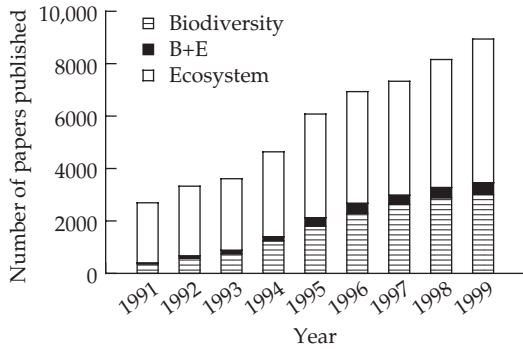
Figure 1.1 The emerging synthesis of biodiversity and ecosystem research. Results represent publications that included either 'biodiversity', 'ecosystem', or both (black fill in centre of bars). Note the dramatic increase in biodiversity research and the steady rise in papers that use both terms in their titles or abstracts. BIOSIS was the literature data base used for this figure.

experiments he cited (Hector and Hooper, 2002) predate current biodiversity-functioning research by 150 years. Perhaps the most prominent research, including that which inspired Darwin, has centred on agro-ecological efforts to improve yield through intercropping (Trenbath 1974; Vandermeer 1989; Swift and Anderson 1993). Although this research is distinct in its motivation and intent, the recent explosion of research concerning biodiversity and ecosystem functioning has venerable roots.

1.2.2 The central hypothesis of biodiversity and ecosystem functioning

The Bayreuth conference formally identified the central idea that was graphically portrayed by Vitousek and Hooper (1993) in their contribution to the symposium and has since expanded to an extensive list of hypotheses (Schläpfer and Schmid 1999). On the surface, it is a relatively simple idea with only two points in a bivariate plane that describe the central idea (Fig. 1.2). The axes defining the plane are biodiversity on the *x*-axis as the independent variable and some ecosystem process on the *y*-axis as the dependent variable. The first point of interest is the point at or near zero biodiversity. If there is no biodiversity (e.g. no plants) there is no ecosystem functioning (e.g. no production). The second point is the natural level of biodiversity where there is a highly predictable amount of
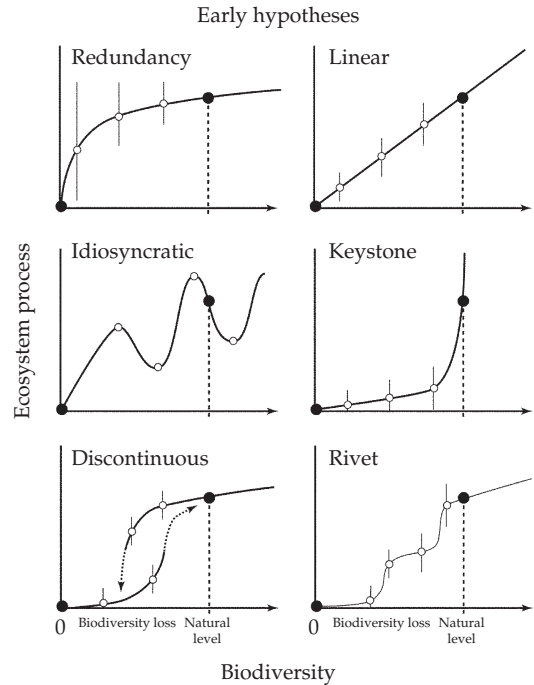

Figure 1.2 Graphical representations of early hypothetical relationships between biodiversity and ecosystem processes. These were meant primarily as heuristic devices or graphical representations of testable hypotheses representing a variety of potential mechanisms. Beyond the point at the origin (where there is no diversity and therefore no measurable processes) and the often highly predictable second point at natural levels of diversity, there was insufficient empirical and theoretical information to know under which circumstances which of the above possible relationships applied to ecosystems. Contemporary research rarely refers to these early hypotheses, although the terminology is still often in use when referring to different classes of associations.

functioning. The central question concerns what the trajectory might look like for a particular function for a given variation in biodiversity away from the second point. For example, what are the ecosystem consequences (the shape of the trajectory in the bivariate space) of local extinction (biodiversity loss, moving to the left of the second point) or invasion (biodiversity augmentation, moving to the right of the second point)?

When ecologists were asked what the shape of the trajectory might be (though the emphasis has traditionally been on biodiversity loss) a wonderful breadth of ideas emerged (Schläpfer and Schmid

1999). In fact, this bivariate space is packed with well over 50 different hypotheses concerning the ecosystem consequences of biodiversity loss. Three classes of biodiversity-functioning hypotheses can be identified.

1. *Species are primarily redundant.*[7] Hypothetical trajectories in which the major portion is insensitive or flat to variation in biodiversity imply that loss of species is compensated for by other species or the addition of such species adds nothing new to the system.

2. *Species are primarily singular.*[8] Hypothetical trajectories in which slopes are predominantly positive or negative imply that species contribute to ecosystem functioning in ways that are unique, thus their loss or addition causes detectable changes in functioning. Keystone species are often cited as examples of singular species.

3. *Species impacts are context-dependent and therefore idiosyncratic*[9] *or unpredictable.* Hypothetical trajectories that exhibit a variety of different slopes over different portions of their trajectory fall into this category. In such cases, the impact of loss or addition of a species depends on conditions (e.g. community composition, site fertility, disturbance regime) under which the local extinction or addition occurs.

Biodiversity-functioning research frequently uses terminology associated with these classes of hypotheses. The 'Rivet' hypothesis, accredited to Paul and Anne Ehrlich, reflects the notion that redundancy is important to a point where once so many species are lost, the system fails, much the way an engineered system fails when it looses too many rivets. The 'Redundancy' hypothesis refers to an asymptotic trajectory that asymptotes at extremely low levels of diversity. The 'Keystone' species refers to a trajectory in which functioning plummets as soon as biodiversity declines from its natural levels. The 'Idiosyncratic' hypothesis is the label ascribed to a trajectory that exhibits no clear trend. In many

cases, an idiosyncratic response is expected only when diversity is extremely low and each deletion or addition is the equivalent of adding Keystone species or groups. There is some confusion over the interpretation of this hypothesis for two reasons. First, the Idiosyncratic hypothesis applies to biodiversity loss in which a single specific pattern of loss occurs (e.g. loss of species A, then B, then C, and so on). In most experiments, however, biodiversity loss is treated as random losses of species with replicates representing different combinatorial permutations (e.g. loss of A or B or C followed by loss of A and B or B and C or C and A, and so on) and the trajectory plots the average change in functioning in response to the random biodiversity loss. The second common error is to associate the Idiosyncratic hypothesis with an inability to reject the null hypothesis or the hypothesis that the slope of the relationship is indistinguishable from zero (the absence of any evidence that biodiversity drives ecosystem functioning). Idiosyncratic does not mean that there is no effect of variation in biodiversity nor does it necessarily imply that response to variation in diversity is unpredictable. It merely implies that the slope of the relationship is not monotonic.

1.3 Articulating the hypothesis

The hypotheses outlined in Fig. 1.1 represent a heuristic framework that serves to organize our thoughts about the relationship between biodiversity and ecosystem functioning. It also provides a clear picture of what needs to be tested—reject the null hypothesis of no relationship between biodiversity as an independent variable and ecosystem functioning as a dependent variable.

New ideas are tested primarily by 'articulating the hypothesis' (Kuhn 1962) and experiments that followed the Bayreuth conference did exactly that. They created a gradient in biodiversity under homogeneous extrinsic conditions (e.g. fertility, climate, space, history) and monitored a variety of functions as response variables. Subsequent experiments, all of which are reviewed in this volume, added additional dimensions or searched for mechanisms.

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[7] 'Redundant' implies that species are at least partially substitutable.

[8] 'Singular' implies that species make unique contributions to ecosystem functioning.

[9] 'Idiosyncratic' implies that a species makes different contributions to ecosystems depending on extrinsic and intrinsic factors.

The first such experiment designed to articulate the hypothesis was conducted in the Ecotron (Naeem *et al*. 1994a, 1995), a controlled environmental facility designed for ecological research (Lawton *et al*. 1993). It established replicates of high-, intermediate-, and low-diversity, terrestrial ecosystems. Thus, each level represented increasingly depauperate versions of the highest diversity level. It also simultaneously established 164 combinations of the 16 species of plants used in the main experiment at constant densities (16 individuals per pot) following a combinatorial design (Naeem *et al*. 1996). Its initial report (Naeem *et al*. 1994a) concluded, 'Our study demonstrates for the first time under controlled environmental conditions, that loss of biodiversity, in addition to loss of genetic resources, loss of productivity, loss of ecosystem buffering against ecological perturbation, and loss of aesthetic and commercially valuable resources, may also alter or impair the services that ecosystems provide. However, different ecosystem processes respond differently to loss of biodiversity providing some support for several current hypotheses. To the extent that loss of plant biodiversity in the real world means a reduction in the ability of ecosystems to fix CO_2, we also tentatively conclude that the loss of diversity may reduce the ability of terrestrial ecosystems to absorb anthropogenic CO_2.'

The Ecotron study effectively demonstrated that the relationship between diversity and ecosystem functioning was not flat. It hypothesized that niche complementarity,[10] or a greater efficiency of light utilization in more diverse communities due to differences in growth forms among species, was the mechanism responsible for the observed positive relationship between diversity and production. It also emphasized that processes varied in response and that other factors in nature contribute to biodiversity-functioning relationships and the value of biodiversity.

Early experiments attract considerable attention in science and the Ecotron study was no exception (Moore 1996). While it successfully articulated the hypotheses, however, its design in which lower levels of diversity were nested sets of higher levels, could not address many issues that would emerge as biodiversity-functioning research evolved (Lawton *et al*. 1998; Allison 1999).

Two influential early studies by Tilman and colleagues would focus biodiversity-functioning on plant diversity and plant production and this focus would dramatically increase the visibility of biodiversity and ecosystem functioning research. They would also catalyse emerging debates over the interpretation of biodiversity-functioning studies. The first paper, by Tilman and Downing (1994), reported that nitrogen-induced reductions in plant diversity lowered ecosystem resistance and resilience. Later, Tilman *et al*. (1996) reported that controlled variation in plant diversity was positively associated with production in experimental prairie grassland plots. The larger spatial and temporal scales of these experiments and their outdoor or field nature provided greater assurance that the findings were more applicable to natural systems than the short-term, growth-chamber studies of the Ecotron. The proposed mechanism was again niche complementarity, either for nitrogen or water use, rather than light as was proposed in the Ecotron study.

From these experimental beginnings, only six years ago, an explosion of research ensued that, in each case, added important dimensions to the expanding field of biodiversity-functioning research. McGrady-Steed *et al*. (1997) manipulated diversity across a range of autotrophic and heterotrophic species using microbial microcosms. This study would also be the first to examine invasibility as an ecosystem property associated with biodiversity. Naeem and Li (1997) would similarly use microbial microcosms, this time manipulating the number of species per functional group.[11] Hopper and Vitousek (1997) would manipulate functional diversity while Tilman *et al*. (1997a) would manipulate both species and functional group richness.

Many experimental studies followed, in each case adding more dimensions. Some hallmark

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[10] 'Niche complementarity' refers to the greater efficiency (in space or over time) of resource use by a community of species whose niches are complementary (i.e. non-overlapping). For example, a community of shallow-rooting and deep-rooting plant species mines mineral nutrients in a fixed volume of soil better than either group does by itself.

[11] 'Functional group' refers to a set of species that are similar, and at least partially substitutable in their contribution to a specific ecosystem process (see Hooper *et al*., Chapter 17).

contributions include Van der Heijden *et al.* (1998a,b) who examined mycorrhizal fungal diversity, and Hector *et al.* (1999) who examined within-site and across-site biodiversity-functioning relationships, and Sankaran and McNaughton (1999) who examined extrinsic factors. The explosion of research has gone on to tackle other dimensions such as different systems, like wetlands (Engelhardt and Ritchie 2001) or marine systems (Emmerson *et al.* 2001), or the role of producer–decomposer interactions (Naeem *et al.* 2000a), nutrients (Hulot *et al.* 2000), invasive species (Knops *et al.* 1999; Levine 2000b; Naeem *et al.* 2000b), and plant pathogens and insect diversity (Siemann 1998; Knops *et al.* 1999). Many other studies are reviewed in the following chapters.

1.3.1 Theoretical developments

Theory lagged slightly behind the experimental work in biodiversity-functioning research. While the earliest ideas can be traced to McNaughton (1977) and intercropping theory (Vandermeer 1989), models developed explicitly to address biodiversity-functioning really did not emerge until recently (Loreau *et al.*, Chapter 7). Tilman *et al.* (1997a) and Loreau (1998a–c) contributed early models exploring how competition for resources and niche complementarity could explain the relationship between plant species richness and plant production based on plant resource use models. Doak *et al.* (1998) made a significant contribution by arguing that statistical averaging could account for apparent stabilization of aggregate community properties (i.e. ecosystem processes) without invoking niche complementarity. Yachi and Loreau (1999) would introduce a mathematical formalization of the concept of biological insurance. Naeem (1998) would introduce the concept of ecosystem reliability. Hughes and Roughgarden (1998) would examine how interaction strengths affected biodiversity-functioning relationships. As in the experimental studies, theoretical studies began focusing on the initial issues raised by the experiments that articulated the central biodiversity-functioning hypothesis, but theory has grown to cover increasingly sophisticated topics.

1.3.2 How best to interpret the findings?

Two fundamental issues concerning the interpretation of biodiversity-functioning arose shortly after the publication of the early studies. First, given the weight of correlational studies that suggested contrary patterns of association between plant diversity and production or other ecosystem processes, it seems unlikely that patterns observed in biodiversity-functioning experiments are relevant in the face of overwhelming influences of extrinsic factors (Grime 1997; Wardle *et al.* 1997b). Second, it is difficult to separate effects due to the increasing probability that species with major impacts on whatever process is being measured are present in higher diversity experiments (the sampling effect) from effects due to niche complementarity (Aarssen 1997; Huston 1997; Wardle 2001). Additional issues such as the role of the below-ground community (Wardle *et al.* 2000b), the possibility that functional diversity is far more critical than species diversity (Hooper and Vitousek 1997, 1998), and the fact that higher diversity replicates are more similar to one another in composition than lower diversity communities were also raised (Wardle 1998; Fukami *et al.* 2001).

Although each query was met with a rebuttal by the authors of the biodiversity-functioning studies, the replies were deemed inadequate by those who disagreed with the interpretation of the findings. This is often the case in science—interpretation of results can vary dramatically among researchers. Often an experiment is deemed 'flawed' by those who disagree with the original author's interpretation, while the original authors see their rebuttals as satisfying the concerns raised and continue to perceive the original studies to be correct. Such exchange is commonplace in science although the tone of the debate in this instance was regrettable and led to negative effects when reported in the press (Mooney, Chapter 2).

1.3.3 The consequences of debate among researchers: the science/public disconnect

Given the excitement generated by the early findings, the ensuing explosion of research by a wide array of researchers, the fact that only a fraction of

the studies were under criticism, the fact that the criticisms were being incorporated into the discipline, and the importance of the issues, it may seem surprising that the emerging debate wound up being reported by the press to represent the signs of a questionable science. A couple of selected quotes from the press convey this.

A long-simmering debate among ecologists over the importance of biodiversity to the health of ecosystems has erupted into a full-blown war. Opposing camps are duelling over the quality of key experiments, and some are flinging barbs at meetings and in journals.

Kaiser (2000)

The altercation went public when, in a letter in the July issue of the *Bulletin of the Ecological Society of America*, eight ecologists bluntly charged that the report was 'biased' and 'little more than a propaganda document'; made 'indefensible statements'; and set a 'dangerous precedent' for scientific societies by presenting only one side of the debate, even though the report seemed to represent the entire 7,600-member society.

Gutterman (2000)

In reality, there is no scientific discipline that is without its debate unless it is a stagnant discipline. The more dynamic, the more rapidly a discipline is evolving, the more it is surrounded by vigorous debate. The greatest advances in science are often surrounded by the most vigorous debates (Hellman 1998).

The direction science takes follows the weight of the evidence without waiting for debate to be resolved. Public debate, however, does not operate in this fashion. In a public debate, evidence is presented by both sides and juries, judges, or oracles decide which side is right and which wrong (Franklin 2001). In a court of law, in the press, or in a public debate, each party is accorded equal privileges. Each side may identify witnesses, assemble evidence, or elect representatives to present their case. Judgment is based on the persuasiveness of the different arguments to juries, tribunals, judges, other empowered individuals, or by the public who pass judgment individually or collectively by vote.

Scientists, if they turn to the public, are often not familiar with the way it handles evidence (Mooney, Chapter 2). As the science of ecology increasingly enters the public and policy arena, it may increasingly find that scientific debate may be misunderstood much the way Creationists in the United States continue to use the debate in evolutionary biology to dismiss its findings. Synthetic approaches, however, can allow progress in scientific research while minimizing debate.

1.4 The Synthesis Conference: a critical phase in biodiversity-functioning research

The debate helped to crystallize several issues that served as guideposts for future directions in biodiversity-functioning research and motivated the Synthesis Conference. The first set of chapters (Chapters 3–6) highlight the core issues in the debate over the appropriate interpretation of biodiversity and ecosystem functioning research focusing primarily on the Cedar Creek and BIO-DEPTH grassland experiments. With these issues in mind, the remaining chapters explore how biodiversity and ecosystem functioning touches upon ecological stability, trophic levels and structure, and other dimensions in ecology.

In the first section, Tilman *et al.* (Chapter 3), using the Cedar Creek studies, and Hector *et al.* (Chapter 4), using the BIODEPTH studies, extensively analyse data from these experimental grassland systems to explore the relative contributions of different mechanisms to the biodiversity-functioning relationships. They interpret their evidence as a strong support to their original conclusions about the importance of niche complementarity and plant diversity in governing the positive plant biodiversity-production relations observed in these studies, but their more modern synthetic approach treats these effects as the result of multiple causes that include sampling, facilitation, and perhaps other causes. Schmid *et al.* (Chapter 6) detail the astonishing complexity involved in analysing such data, focusing on the dominant parametric statistical approaches employed in these studies. In contrast, Huston and McBride (Chapter 5), while allowing for the importance of diversity to ecosystems in general, nevertheless criticize the biodiversity-functioning programme. They argue that a variety of statistical problems limit the interpretation of current biodiversity-functioning studies and provide alternative interpretations of current findings.

While these first chapters underscore the complexities one encounters in biodiversity-functioning research, the remaining sections consider the broader scope of biodiversity's potential role in a variety of ecological processes. The second section revisits the stability-diversity debate beginning with Loreau *et al.*'s Chapter 7 that contrasts and compares traditional research in ecological stability with the emerging biodiversity-stability research. This new stability research, unlike its predecessor, explicitly addresses the links between species variability and the variability of aggregate ecosystem properties and shows how population responses to environmental fluctuations and evolutionary modifications provide new insights into this venerable issue. Hughes *et al.* (Chapter 8) derive the core theoretical foundations behind recent theoretical approaches that attempt to understand the relationship between biodiversity and variance in ecosystem properties. De Ruiter *et al.* (Chapter 9), focusing on the enormously complex belowground systems, emphasize that biodiversity may play important roles in a variety of unexpected ways, in system stability. Finally, Levine *et al.* (Chapter 10) examine how biodiversity contributes to invasibility, an aspect of stability first addressed by Elton (1958). Levine *et al.* contrast how biodiversity and the covarying extrinsic determinants of biodiversity determine ecosystem invasibility. These chapters clear up the misleading sense of *déjà vu* that some may have felt in the face of what appeared to be a re-emergence of the old stability-diversity debate.

The next section explores systems other than grassland plant communities, with an emphasis on the trophic dimension of biodiversity-functioning research. The role of trophic groups, trophic structure, food chains and food webs remains among one the largest issues in ecology, yet the role of the trophic dimension in biodiversity-functioning research has only recently begun to catch up with the progress made in plant studies. Petchey *et al.* (Chapter 11) explore the utility of microcosm research and review key microcosm experimental studies in this context, pointing to their value as proving grounds for otherwise empirically intractable theory that often calls for high levels of replication and many generations. Emmerson *et al.* (Chapter 12) shed what light they can on the role

of biodiversity in marine ecosystems given the paucity of marine biodiversity-functioning studies, emphasizing the importance of trophic groups and heterotrophic processes in these systems. Raffaelli *et al.* (Chapter 13) address the fact that linkages among species created by common energy and nutrient pathways mean that changes in one species invariably, either directly or indirectly, have impacts on others. These linkages generate patterns in distribution and abundance, feedback in population cycles, and determine the fate of energy and nutrient flow in ecosystems.

Nowhere else is the importance of these trophic linkages more clear than in below-ground or the decomposer subsystems where >90% of the energy that flows through an ecosystem ultimately passes. In fact, including de Ruiter *et al.* (Chapter 9), four chapters in this volume examine this subsystem. Wardle and van der Putten (Chapter 14) document the lack of evidence for biodiversity-functioning relationships in decomposer systems. A key issue raised in this chapter concerns the sensitivity of ecosystems to extrinsic factors, suggesting that extrinsic factors, not intrinsic factors (i.e. biodiversity), regulate functioning. Mikola *et al.* (Chapter 15) argue, based on many experimental and observational studies, that biodiversity is hardly likely to provide the kinds of relationships one has observed in contemporary biodiversity-functioning studies of grassland plots and microcosm experiments when it comes to below-ground communities. Thus, they second the cautionary message delivered by Wardle and van der Putten. Finally, van der Heijden and Cornelissen (Chapter 16) focus on the often-neglected symbiotic microorganisms that are common (up to 80%) associates of terrestrial plants emphasizing that diversity of these organisms may play important roles in governing above-ground production and carbon cycling.

The trophic dimension of ecosystems, however, is only one of several ecological dimensions that biodiversity-functioning research touches upon. The challenge of addressing the taxonomic–functional diversity dimension in biodiversity-functioning research is addressed by Hooper *et al.* (Chapter 17). In their chapter, they demonstrate that the distinction between taxonomic and functional diversity is critical not only to resolving debates, but to making

progress in effective experimental design and policy development. The spatial and temporal dimensions are addressed by Bengtsson *et al*. (Chapter 18) who remind us that the power of any ecological science is its ability to provide scale-invariant principles, but current biodiversity and ecosystem functioning research is, to be blunt, pathetically limited in scale. Finally, the human dimension is addressed by Vandermeer *et al*. (Chapter 19), who provide several insights into what managed ecosystems are in comparison to unmanaged systems, how the biodiversity-functioning debate has long been a part of management issues, and provide a number of valuable ways to begin the badly needed dialog between managers and researchers.

1.5 Concluding comments

We have tried, in a limited space, to provide a brief synopsis of the biodiversity-functioning research programme, its central ideas, its terminology, and the issues it contends with to facilitate the reading of this volume for the uninitiated. We have also indicated, though it might be surprising to some, that the ecological consequences of changing patterns in biodiversity, either through extinction or addition, was poorly known until recently, but that over a brief span of time (<10 years) some insights have been derived from empirical and theoretical studies. Not surprisingly, early studies that articulated the hypotheses introduced more questions than they addressed and the ensuing debate that surrounded interpretations of the rapidly accumulating findings generated a sense that it was possible that biodiversity really did not matter.

Few, however, if any would claim that there is no role for biodiversity in ecosystem processes or ecosystem functioning and that the ecosystem services humans derive from them are affected by the nature of the biota that govern these processes. There is still a debate over the relative or specific role of extrinsic factors, genetic, taxonomic, or functional diversity in ecosystem processes, but the scientific community should not ignore the issue because it is complex, confusing, or unclear. Rather, this should be seen as a challenge to be met. Although the relative contribution of multiple causes to ecological effects, such as the relative importance of soil fertility and plant species richness to production, are important and unresolved, the scientific exchange and debates should stimulate scientists towards resolving the issue, not deter further investigation. A fortunate outcome of the debate is that it has stimulated the quest for a better understanding of mechanisms.

One thing this volume makes clear is that ecological truth lies at the confluence of observation, theory, and experiment. It is through discourse among empiricists and theorists that findings and theory are sorted and matched and where there is a lack of correspondence, new challenges identified. This volume represents a critical step in this direction.

The debate on the role of biodiversity in ecosystem functioning

H. A. Mooney

2.1 The issue

During the past decade there has been an impressive development of research inquiry into the issue of the role of biodiversity in the functioning of ecosystems. Large numbers of research scientists have been attracted to this area, rooms in research meetings have been filled with people presenting and listening to the results of new inquiries into this topic. The literature is burgeoning with new findings and insights. However, recently there has been an unusual discord within this research area that is having some unfortunate consequences in both the larger realm of science and policy but also at the fundamental level of a negative feedback to further inquiry. Young scientists are expressing some fear of stepping into an area where the community is divided and where chances of approval of proposed work might be thwarted by partisan review. This is certainly unfortunate. Of course, vigorous debate and falsification of hypotheses are the basic stuff of scientific inquiry, but it would seem that the present situation has escalated beyond the norms for science and that we are in danger of losing credibility for ecosystem ecology as a discipline because of a small technical battle over an ephemeral issue. Headlines by science journalists such as 'Have ecologists oversold biodiversity?' (Guterman 2000) and 'Rift over biodiversity divides ecologists' (Kaiser 2000) give the impression that ecologists have circled the wagons and are shooting inward as one noted ecologist has observed. The language of doubt used in the debate has escalated from science words such 'hidden treatments' and 'sampling effects' to *ad hominen* attacks such as 'selective citation of literature' and 'stating opinions as facts'. How did we get to this state of affairs, and more importantly how do we get out of it?

2.1.1 One road to here

Before looking to the future I look backward to how we got into this issue in the first place. There of course is a long history of interest by ecologists in the role of biodiversity in ecological processes. The recent interest in the ecosystem functioning aspect of biodiversity specifically can be traced to the results of a meeting that was held in Mitwitz, Germany in 1991 and published in 1994 (Schulze and Mooney 1994). What sparked my own personal interest in this area and what stimulated the organization of that meeting along with Detlef Schulze was the development of the international research programme of global change (International Geosphere Biosphere Programme). I noted elsewhere (Mooney 1990, 1991, 1999) that the development of Earth system science was progressing in such a way that the role, in any meaningful way, of the biota in regulating the Earth's biogeochemical and energy cycles was being ignored. The physical scientists who were leading the development of global models could not accommodate biotic complexity and were quite satisfied with a simple biosphere that was essentially a green slime over the terrestrial parts of the biosphere and with the water cycle represented,

in part, by a bucket rather than by vegetation. The early Earth system models had no biotic texture of any sort and it looked unlikely that those putting together earth system science would incorporate such complexity.

In the past decade, the ecological community did move from their plot-size based science to the incorporation of the larger scales needed for Earth system models. However, even the best of these models incorporates little consideration of diversity, although they do consider ecosystem-averaged biological processes such as canopy roughness, rooting depth, stomatal behaviour, allocation, and even phenology. The scientific triumph of the past decade has certainly been the linking of earth surface biological processes with atmospheric phenomena. Still, however, the actual biotic richness of the Earth surface has been poorly included in these models.

2.1.2 Mitwitz—laying the foundation

The Scientific Committee on the Problems of the Environment (SCOPE) initiated a research programme on the ecosystem functioning on biodiversity to help close the gap between knowledge on biological diversity and research on the functioning of ecosystems. The starting point of this research effort was the Mitwitz meeting noted above. Two things happened at the meeting. One, a series of contributed papers provided the state of the knowledge at that time on this issue and, two, on the basis of these contributions the goals of the remaining SCOPE programme were set. The stated goals of the programme were:

1. Does biodiversity 'count' in system processes (e.g. nutrient retention, decomposition, production etc.), including atmospheric feedbacks, over short- and long-term time spans, and in face of global change (climate change, land-use, and invasions)?
2. How is system stability and resistance affected by species diversity, and how will global change affect these relationships?

It is important to note the breadth of the first statement. First it is couched in terms of atmospheric feedbacks and global changes reflecting its origins from the Earth system science perspective. Secondly, the term utilized is biodiversity and not species

diversity and in fact diversity was defined at this meeting in terms of populations, species, functional groups, systems and landscapes, keeping with the approach defined in the Convention on Biological Diversity noted below.

For some reason, this mandate for the study of the role of biodiversity in ecosystem functioning, in its broad dimensions, has not been pursued to any great extent. Rather, in what Jean-Pierre LaDanff calls 'the species vortex', virtually all efforts have been devoted to the study of species biological diversity, and even here, until recently studies have been centred on species richness. This focus is important even though it ignores the assessment of more immediate and massive changes in biodiversity that are occurring as a result of land use and even atmospheric change, nitrogen deposition in particular (Wedin and Tilman 1996; Egerton-Warburton and Allen 2000).

The tools that were to be utilized in the SCOPE programme were those readily at hand, that is, analyses of data mostly gathered for other purposes. Specifically noted were experiments or manipulations involving altering biodiversity by using additions, subtractions, fragmentation, and disturbance. At the same time, it was hoped that the programme would stimulate explicit experiments and long-term observations. The call for explicit experiments was certainly followed with extraordinary results that are reported in detail in this volume.

2.1.3 The Global Biodiversity Assessment—community 'buy-in'

As the SCOPE process was underway, a call for an assessment of the status of biodiversity was initiated (Global Biodiversity Assessment or GBA) and the SCOPE programme effort was expanded somewhat from its original study plan (it became more comprehensive in terms of the biome types it would consider). Further, and importantly, it provided an opportunity to get comprehensive input from the global scientific community on these issues. On publication (UNEP 1995) the GBA contained two chapters on ecosystem functioning and included 38 international authors on one and 66 lead authors on another with dozens of additional contributors. There were over 100 international

reviewers on these two chapters. The final SCOPE synthesis volume (Mooney *et al*. 1996) on the project had 59 authors representing many different nations.

Curiously, even though the GBA process was inclusive and consensus driven it was flawed in one way, according to certain constituencies, that is policy makers. They had not asked for the document and thus questioned its legitimacy, at least in the Convention on Biological Diversity process. In essence, the GBA represented the scientists' view of what they thought the important problems were based on literature review. It did not, evidently, take into account issues that were directly being encountered by policy makers. I will return to this issue below.

2.1.4 Further review and the roles of SCOPE and GCTE

After the conclusion of the SCOPE initial programme and GBA, SCOPE decided to take on a next phase of the effort. They reviewed the state of our knowledge on below-ground biological diversity and its relationship to ecosystem functioning, an area that did not receive sufficient attention in the GBA. Already, the new SCOPE focus on below-ground biological diversity has resulted in tremendous amount of new and exciting work (see e.g. Freckman *et al*. (1997) and special issue of BioScience, February, 1999).

Similarly, in another integrated international effort, the Global Change and Terrestrial Ecosystems (GCTE) programme of the International Geosphere Biosphere Programme initiated a programme for new experimentation in this area. The present volume is a product of that programme. Both the SCOPE assessment process and the GCTE research effort are co-ordinated through DIVERSITAS, another international programme that is concerned with biodiversity science as a whole.

2.1.5 Nature's services

An important parallel development with the SCOPE programme was an effort to try to quantify services provided by natural systems (Daily *et al*.

1997). Whereas the SCOPE programme looked at ecosystem functional traits independent of value to humans, the Nature's Services approach was societally oriented. Since there is a great amount of new research that is needed to fully understand diversity/functioning relationships, it follows that there is an equally daunting challenge ahead of us in quantifying ecosystem services. There are many non-ecological scholars, particularly economists, very interested in this approach, as is the policy community, for obvious reasons. Already, innovative approaches are being taken to establish market-places for ecosystem services (Daily and Ellison, 2002). Further, many see this issue as a way to connect the general public to some understanding of ecological principles. A recent article entitled 'Crossing the moat: using ecosystem services to communicate ecological ideas beyond the ivory tower' (Kranz 2000) conveys the idea that scientists must think in different ways to accomplish these goals.

I would now like to shift focus here for a while in order to build back to the opening issue of how we as a community can provide information to society that is helpful while maintaining the strength of the scientific process. There has been a dramatic shift in the past couple of decades in the interaction between science and policy in environmental sciences. There probably are a number of reasons for this, but one for sure is that environmental problems are becoming more acute and widespread. Mitigation or remedy of these problems may call for strong action that will not be accepted unless there is widespread scientific support for that action. In some cases new science is being done in real time with policy formulation, as was the case with the Montreal Protocol on stratospheric ozone beginning with its adoption in 1987. Policy is being made under uncertainty regarding the basis of the phenomenon under question. In such cases, policy decisions are flexible and allow for revisiting decisions as new information becomes available. As this information was being gathered, a mechanism for evaluating it in an impartial way by the scientific community was put in place—the so-called 'science assessment'. The Montreal Protocol was a dramatic success of interaction between scientists and policy makers. The relative simplicity of the issue

(a single class of compounds causing a single chain of reactions) and a relatively easy technical fix (in retrospect) to the problem certainly led to this success.

The Intergovernmental Panel on Climate Change (IPCC) has proven to be an excellent mechanism for providing quality and consensus advice to governments about the options regarding controlling or mitigating climate change beginning with the first report in 1990. There are a number of lessons learnt from this assessment that are of value for the policy/science interface. For one, the IPCC serves an international convention, the Framework Convention on Climate Change, which is science based. The IPCC, funded by governments, yet is operated independently. The very best scientists provide input into the process of assessments. These assessments utilize published information only, and go through a very rigorous peer review process that involves literally thousands of scientists and a consensus is reached on the reliability of the information that is available. The process is transparent and inclusive.

The structure of the IPCC is in part the reason for its success. Another reason may be the strategy utilized for assessing much of the data. A scenario of doubling CO_2 has been the standard under which most of the models, both climate and biology have been evaluated. Thus, the complex interactions that were put in play when modelling the future were all tested against a single metric. More recent assessments have more complicated scenario building.

2.1.6 The Millennium Assessment—ecosystem services at the foundation

We are now about to embark on a new assessment that will be directed at the status of the world's ecosystems (Ayensu et al. 1999) and how it is changing. This important assessment will differ from those described above in that it is designed to serve the needs of a number of conventions including the Convention on Desertification, The Ramsar Convention (wetlands) as well as the Convention on Biological Diversity. It will both examine status and trends of ecosystems in local regions as well

as globally. Importantly, it will be designed specifically to look at the capacity of natural and managed systems to provide the goods and services upon which society depends now, and into the future. Thus, the programme will call upon the kind of information that ecologists can provide on how ecosystems operate and how human activities are disrupting the natural processes that deliver goods and services (http://www.millenniumassessment. org/en/index.htm). Of course, many disciplines, such as forestry, agriculture, and animal husbandry have worked toward delivering certain goods from natural and managed systems such as food and fibre. Hydrologists and atmospheric scientists have intensively studied the delivery of clean air and water and the control of floods and storm surges. There has not been an equal effort on managing biogeochemical cycles, except perhaps for sewage, although we are certainly heading that way in view of the massive disruption of the global nitrogen cycle and the off-site consequences of these disruptions, such as the 'dead zones' in the Gulf of Mexico (Ferber 2001). Such studies will have to be broader in geographical extent than is normally the case. The Millennium Assessment will utilize heavily the kind of information being provided by those working on the role of biodiversity in ecosystem functioning. It is important that this research area continues its strong advancement.

2.2 How did we get to this state of affairs?

Returning to the main theme of this essay, it would appear that the current disharmony among those working on the ecosystem functioning and biodiversity issue is due to the relative newness of the research area, and the development of a greater demand, and even urgency for good science in our educational and policy process. This has put a strain on our traditional science/society interaction, where the scientists provide information to technical journals and leave the translation to society to other constituencies in unspecified time frames. In the particular case at issue, some have contended that the movement from new science to policy implications has been too fast and has not been done in a

consensus manner. There is certainly merit in this argument and the issue here is how to move on in a more positive manner and in a way that gives confidence to those outside our field that we are not too busy trying to wound ourselves to give advice that is needed.

2.2.1 How to move on

At the same time that we are being asked to bring the best of science to the attention of the society at large, there are evolving mechanisms where we can do so and do so in a manner that is consensus driven. Some of these have been discussed above. Of course, there will always be dissent on any scientific issue and this dissent is taken into account in the normal process of doing science—that is by testing new hypotheses. The issue is though that policy makers often ask, 'what does your community think on this matter?'. What we need to do and have done in the IPCC-type process, is to give our best analysis of what the prevailing data shows and with what degree of certainty. In the ecosystem functioning and biodiversity issue, at present our state of knowledge is well encompassed in the 'uncertainty principle' that is the basis of much of the discussions on biodiversity. The uncertainty principle is under attack, however, and politicians want more guidance than this statement of ignorance. The GCTE programme, under whose auspices we are meeting here is a great mechanism for bringing scientists together to work toward reducing uncertainty, as well as reducing confusion among those who depend on the advice that we give. The Millennium Assessment will provide another mechanism for developing confidence in what the literature tells us at a given time, since the merits of each study will be debated among a large international group and confidences in what it says will be explicitly noted. We should work to use these evolving mechanisms and not try to end run the community process through the popular press that in the long run does not serve us well. The popular press is of course generally dedicated to providing both sides on any issue, which is certainly an admirable feature. However, it can be misleading to the public as seen in the climate change debate. In spite of the unusually comprehensive and

scrupulously adhered to open process of assessment of data, the press gives equal weight to the voice of 98% of the community and the 2% dissenters. However, in the end the voice of the assessment process has the greater credibility in influencing policy.

2.2.2 Back to the science

The past few years has seen very rapid progress in the study of species and functional-type richness in relation to ecosystem functioning. In particular, there have been some very major experiments on the issue that have led to new insights. These experiments are beginning to give us a crucial time dimension on diversity/function. Attention is now being directed to experiments with greater ecosystem richness, utilizing trophic level complexity. Landscape diversity is being considered. New models are being developed that are able to build understanding beyond our immediate present experimental capabilities. Many of these new directions are included in this volume.

We need to move back to the more difficult study of natural ecosystems. Such studies could bolster modelling and experimental study approaches. In doing so we need to pay more attention to the ecosystem functioning part of the equation since only a few parameters have been included in most studies to date. Shaver *et al*. (2000) have recently reviewed how 'changes in species composition and abundance affect ecosystem processes (net primary production, carbon and nutrient cycling, energy fluxes) through changes in tissue chemistry, demography (both parts and individuals), turnover rates, and vegetation structure (physiognomy, leaf area index)'. The interactions of the many dimensions of community and ecosystem structure and functioning, as related to diversity, need a much fuller exploration.

Further, we need those who study, in quantitative terms, the interactions among natural and managed ecosystems in terms of pollination and pest control services. The study of agroforestry, and integrated pest management has certainly given us insights into these processes. We need to integrate them more formally into the study of ecosystem functioning of biodiversity. Field studies are difficult because of

confounding variables. However, we are developing an experimental ecosystem science and approaches for manipulating natural systems should be utilized—such as the species removal experiments underway by the GCTE programme (http://www.gcte.org/).

It is my prediction that because of the richness of ideas in this area that the functioning of ecologists will continue to be stimulated to produce exciting results of importance to a wide range of information users. Let us use the available mechanisms to work toward not only getting this new information but also in providing the results to users in a way that is helpful. We have the means to do this.

2.3 Summary remarks

The research area on the role of biodiversity and ecosystem functioning is an exciting, important and rapidly developing field. Those involved in this area will certainly continue to make great research progress, however, for maximum impact of their findings they should do so in a manner that is constructive and builds on the efforts of all involved. The recent paper by Loreau *et al.* (2001) serves as an excellent model of how this research community can come together to bring light, rather than heat only, to this important field.

There are many new frontiers that need to be addressed in order to have the findings of this field have a larger utility. In particular, attention should shift away a bit from the small-scale single functional group (e.g. herbs) species richness/ecosystem functioning focus, which has dominated this research area, to examining processes involving different trophic levels, as well as phenomena at the landscape level. Also, and this is true for other areas of ecological study, we need to explore the time dimensions of responses of ecosystems to environmental and biotic changes brought on by land use and other global changes in a diversity context.