Biodiversity, Ecosystem Functioning, and Human Wellbeing

An Ecological and Economic Perspective

EDITED BY

Shahid Naeem,
Daniel E. Bunker,
Andy Hector,
Michel Loreau,
and
Charles Perrings

OXFORD
UNIVERSITY PRESS

CHAPTER 1

Introduction: the ecological and social implications of changing biodiversity. An overview of a decade of biodiversity and ecosystem functioning research

Shahid Naeem, Daniel E. Bunker, Andy Hector, Michel Loreau, and Charles Perrings

1.1 Biodiversity, ecosystem functioning, and human wellbeing: An unconventional perspective

Conventional approaches to ecology often lack the necessary integration to make a compelling case for the critical importance of biodiversity to ecosystem functioning and human wellbeing. Traditional ecology textbooks (e.g. Ricklefs and Miller 1999, Krebs 2001, Smith and Smith 2005, Begon *et al.* 2006), for example, often begin with species adaptations to local environmental conditions and then proceed through topics such as the population biology of single species, the dynamics of interacting populations (e.g. competitors, predator–prey, host–parasite, mutualisms, food webs), the relationship between stability and complexity, biogeography, and biomes, with little mention of ecosystem ecology. Ecosystem ecology is included, but treated separately. Topics such as C, N, P, and S biogeochemistry, primary and secondary production, decomposition, trophic pyramids, and energy flow make sparse reference to population or community ecology. Today, most ecology texts also include treatment of environmental issues such as pollution, the ozone hole, climate change, collapsing fisheries, disappearing forests, the adverse consequences of unbounded human population growth, emerging diseases, and conservation biology; this last topic being where the value of biodiversity dominates. These topics, however, are often tacked on as final chapters that are poorly integrated with the earlier 'pure' ecology. This approach obscures the inextricable links between biodiversity, ecosystems, and human wellbeing.

This linear march through the biological hierarchy, loosely coupled with its significance to human wellbeing, while of some pedagogical merit, does not prepare one for understanding and applying ecology in the context of the modern world. In today's world, almost everything, especially biodiversity, has been impacted by human activities (Millennium Ecosystem Assessment 2005c, Kareiva *et al.* 2007). A different, rather unconventional approach is needed for understanding ecology and environmental biology, one that asks the question that is rarely asked by ecology texts – *What is the significance of biodiversity to human wellbeing?*

Rather than the conventional perspective, which sees biodiversity as a culmination of population and community ecological processes with ecosystem processes being separate, ecologists at a conference in 1992 in Bayreuth, Germany, considered an alternative perspective, one that added biotic feedback from biodiversity to ecosystem processes (Schulze and Mooney 1993). Although this concept of biotic feedback was unconventional and controversial, it actually dates back to Darwin. In the *Origin*, Darwin (1859) hypothesizes, based on his *principle of divergence*, that as diversity evolves and fills niche space it will lead to an increase in productivity and other ecosystem processes due to the ecological 'division of labour' (Hector and Hooper 2002). There are also a few later echoes of this idea before it was fully reborn at the 1992 Bayreuth conference. Carlander (1952) found a positive relationship between the diversity of freshwater fishes and their overall secondary productivity, which he interpreted as coming about due to more complete filling of niche space. Similarly, in two papers that are underappreciated in the biodiversity and ecosystem functioning literature, Bell (1990, 1991) found that complementary differences amongst species of *Chlamydomonas* led to increased productivity and greater temporal stability of production. Nevertheless, it was only following the 1992 Bayreuth conference that investigation of the effects of biodiversity on ecosystem functioning coalesced as a focused research area.

The first generation of research on the relationship between biodiversity and ecosystem functioning consisted largely of experimental confirmations that the two were indeed linked with one another – changes in biodiversity had predictable effects on ecosystem functioning (Loreau *et al.* 2002). Both the design of the experiments and interpretation of the results, however, were surrounded by much debate (e.g. Guterman 2000, Kaiser 2000, Naeem 2000, Tilman 2000, Wardle *et al.* 2000b). Solan *et al.* (Chapter 3) review the history and impacts of biodiversity and ecosystem functioning research, providing an in depth analysis of what began as a rather unconventional approach to ecological research, but which has since grown into a major paradigm in ecology.

The simple heuristic of plotting a trajectory of ecosystem functioning against a gradient in biodiversity in a bivariate plot (Fig. 1.1), an approach begun by Vitousek and Hooper (1993), and asking what the shape of the trajectory might be, provoked much research and discussion, but such simple plots belie the underlying complexity of the problem. *Biodiversity* and *ecosystem function* are both difficult to define and quantify; thus trajectories in such a poorly defined bivariate space are difficult to interpret. Furthermore, biodiversity does not exist in nature outside of ecosystems; nor does an ecosystem exist without biodiversity – plotting one orthogonal to the other as dependent and independent variables is a strange thing to do. The bivariate plot, various biodiversity and ecosystem functioning trajectories, and their interpretation are reviewed elsewhere (e.g. Schläpfer and Schmid 1999, Naeem 2001b, Naeem *et al.* 2002), thus we will not dwell on them here. Research on the relationship between biodiversity and ecosystem functioning has moved well beyond this early framework. Today, the complexities underlying the relationships between biodiversity and ecosystem

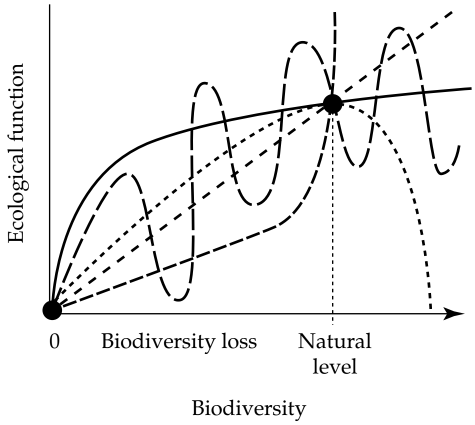

Figure 1.1 A plethora of trajectories of ecosystem function in response to changes in biodiversity. Historically, initial discussions of the relationship between biodiversity and ecosystem functioning were facilitated by the heuristic device of plotting hypothetical responses of ecosystem functions, such as primary production or nutrient cycling rates, against a gradient in biodiversity that was considered to embody taxonomic, functional, phylogenetic, and even the spatial and temporal dimensions of biological diversity. 'Natural' indicates the maximum level of diversity typical for an ecosystem, whereas positions to the right of 'natural' indicate the addition of exotic or domestic species that lead to higher levels of diversity. The solid line reflects the hypothesis that many species were redundant, which would lead to a ceiling in gains per species added. The dotted, hump-shaped line reflects a linear increase in which species contributed similarly to functioning, followed by a decline when exotic species were added. The small-dash, linear line indicates improvements in ecosystem functioning with every species added, suggesting no redundancy. The dashed, concave up curve indicates a dramatic decline in function as soon as diversity drops below natural levels due to the loss of keystone species. The long-dashed line indicates an idiosyncratic or unpredictable response of functioning to biodiversity loss. Over fifty different hypothetical trajectories have been described.

functioning consume contemporary research. The thought experiment that follows will serve to illustrate these complexities.

1.2 Sterilizing Earth: a thought experiment in three parts

As an introduction to this topic and to provide the context for this volume, let us perform the following thought experiment in three parts. First, consider a space anywhere on Earth's surface at any scale – a park, city, farm, lake, river, wetland, sea, biome, or the biosphere – and then sterilize it. Every plant, animal, and microorganism that occupies this space is destroyed, leaving nothing behind but rocks, sand, water, dead organic matter, and a variety of atmospheric gasses. Second, humans are spared but now find themselves in the barren space, their wellbeing entirely dependent on how one restores the ecosystem. Third, we erect a barrier to all living organisms and we use this barrier to control the functional, phylogenetic, and biogeographic identity of the species we allow to enter. We also allow for the direct importation of species, be they native, exotic, domestic, or genetically engineered. We also use the barrier to control the timing and order of entry, the abundance, and spatial distribution of the species that enter. In other words, we, the human occupants of the space, fully control every aspect of the biodiversity of organisms that will re-populate the sterile space. The importance of biodiversity, ecosystem functioning, and the wellbeing of the humans occupying the space would begin to be revealed as biodiversity is reestablished. If the experiment sounds a little bizarre, recall that the ill-fated Biosphere II had much the same aims.

Once we have fixed this image in our mind, we can immediately see that there is a near infinite number of ways to go about reestablishing biodiversity in a sterile space and if human wellbeing is at stake, the decisions we make take on enormous importance. Figure 1.2 illustrates this thought experiment and summarizes the key elements of biodiversity that we have to consider. First, each species we introduce possesses functional traits which reflect their tolerances and responses to (e.g. drought or salt tolerance) and impacts on (e.g. nitrogen-fixing or sulfur-reducing) environmental factors such as soil moisture, salinity, and nutrient availability (e.g. Lavorel and Garnier 2002). The species we introduce will be related to one another by their functional traits, ranging from being nearly redundant (having the full set of traits in common) or nearly singular (possessing largely unique traits) (e.g. Naeem 1998). Third, species will also possess homologous characters that reflect their shared evolutionary history or phylogeny and will be either closely or distantly related (e.g. Ackerly 2004, Edwards *et al.* 2007). Fourth, species will either consume, be consumed by, compete with, parasitize, or facilitate other species in a web of interactions that vary in strength (inset in Fig. 1.2) (e.g. McCann *et al.* 1998, Thébault and Loreau 2006). Fifth, the abundance of species, in terms of either density or mass, will vary depending on each species' growth rates, body size, metabolism and life history (e.g. Brown *et al.* 2004), resource availability (e.g. Tilman 1982), stoichiometry (Elser and Sterner 2002), interactions with other species, top down and bottom up controls within the food web (Pimm 1982, De Ruiter *et al.* 2005, McCann *et al.* 2005), and spatial factors (e.g. Tilman and Kareiva 1997, Loreau *et al.* 2003). Sixth, species are assembled by biogeographic processes (e.g. MacArthur and Wilson 1967, MacArthur 1972, Hubbell 2001, Lomolino and Heaney 2004). Seventh, the timing, order of entry, and other factors affecting assembly also influence biodiversity (e.g. Weiher and Keddy 1999, Fukami and Morin 2003, Larsen *et al.* 2005). Collectively, these many factors determine the biodiversity one finds in a community, all of them influencing flows of nutrients into and out of the inorganic pool, the use and return of water, and the flow of energy sequestered by primary producers and lost through respiration (De Angelis 1992, Loreau 1994, Loreau 1995, Grover and Loreau 1996, De Mazancourt *et al.* 1998, Hulot *et al.* 2000, Norberg *et al.* 2001).

The preceding long list of factors is meant to emphasize the overwhelming complexity of what is embodied in the structure and function of biodiversity in ecosystems and the dilemma we face if we have to construct an ecosystem from the ground up. There are three approaches we could take in

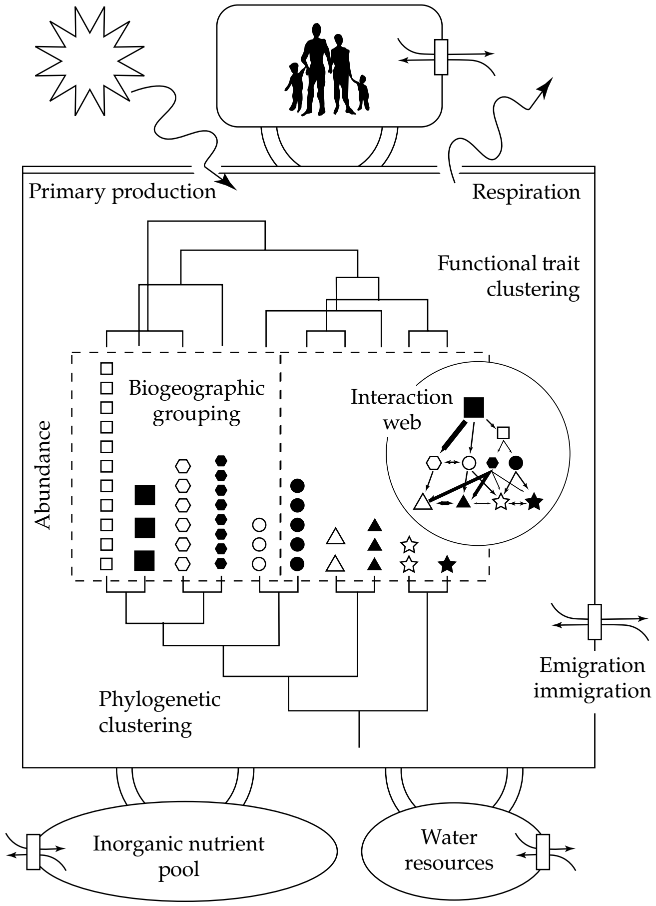

Figure 1.2 Graphic model of the relationship between biodiversity, ecosystem function, and human wellbeing. This figure reflects the thought experiment described in the text in which humans are dependent on the services derived from the functioning ecosystem within which they reside. In the central box, species are portrayed as different shapes and colors and their abundance is indicated by the number of each shape. The upper dendrogram reflects species clustering by similarity in functional traits. The lower dendrogram reflects species relations by phylogeny. The ovals below the box represent the inorganic nutrient pool and water resources. All compartments can potentially have inputs and outputs (immigration and emigration in the case of biodiversity and humans). Curved, parallel lines indicate conduits between compartments. The inset represents a web of biotic interactions (arrows linking species) of different strengths (width of arrows). The figure motivates the thought exercise of imagining how biodiversity is related to ecosystem functioning and human wellbeing by considering how such relationships are affected by the species selected to reside in the ecosystem, and the resulting mix of traits, phylogenetic relationships, biotic interactions, and other factors. The main purpose of the figure is to illustrate the complexity of what underlies otherwise simple relationships typically plotted in biodiversity and ecosystem function bivariate space (Fig. 1.1).

repopulating a sterile space, all of which reflect the rapidly evolving field of biodiversity and ecosystem functioning. We could simply restore biodiversity to what it was at the time of sterilization, under the assumption that that was the best biodiversity for the people who lived there. We could, alternatively, avoid making the assumption that resident biodiversity is the best for humanity and employ ecological principles to engineer the construction of a biota that would maximize the wellbeing of its human residents. Finally, we could explore numerous combinations of species at different relative densities and monitor ecosystem function and human wellbeing until we obtained the biodiversity that optimizes human wellbeing. We will refer to these three approaches as *restorative*, *eco-engineered*, and *explorative*, respectively.

This thought experiment demonstrates that every species contributes to ecosystem functioning and human wellbeing in complex ways, though obviously at different levels (from negligible to enormous) and with different impacts on humans (from beneficial to harmful). We know that each species we admit into the space will change its ecosystem functions (e.g. primary productivity, nutrient cycling, decomposition), its biotic functions (e.g. its susceptibility to invasion, the likelihood that an emerging disease might spread, or the dynamic stability of its populations), and the wellbeing of its human occupants (e.g. the prevalence of poverty, hunger, and economic prosperity). (Note that we distinguish between ecosystem and biotic functions, the former referring to biogeochemical functions and the latter referring to the influences of species on one another. Some researchers, however, use *ecosystem function* to refer to both biogeochemical and biotic functions.) Obviously some species additions will have little effect while others will have dramatic impacts. Further, because all species interact with one another directly or indirectly, with strengths of interaction that vary in sign and magnitude (inset in Fig. 1.2), the impact of each species will be within the context of the community present.

Of the three approaches to restore our sterilized space, restorative, eco-engineered, and explorative, the most neutral approach, or one that requires the least commitment to any particular ecological framework, is the explorative approach that conducts hundreds (if not thousands or millions) of experiments in which each experiment randomly creates a different community, sometimes rich in biodiversity, other times poor or intermediate. With each species selection, one imports a set of traits, modifies the functional and phylogenetic clustering of the community, modifies the community web, and, depending on the density and mass of individuals initially imported, alters the relative abundance of species. In short, every biotic function is modified in some way. Immediately upon introduction, every entering species will also affect the flow of nutrients, energy, and water through the system in some way, again in ways ranging from small to large.

If during an explorative biodiversity and ecosystem functioning approach to repopulating a sterile habitat we simultaneously plot some metric of the diversity of the species we include (e.g. functional diversity, see Chapter 4) against some metric of ecosystem functioning (e.g. net primary production) or against some metric of a biotic function (e.g. resistance to the spread of an emerging disease) or against some measure of human wellbeing, what would that plot look like? Would the values for biodiversity, ecosystem function, biotic function, or human wellbeing show any correlations? Would the maximum for human wellbeing coincide with maximum biodiversity? Biodiversity and ecosystem functioning research attempts to shed light on these and many other questions.

Note that the end product of such an exercise, repeatedly plotting ecosystem function measured for different communities differing in biodiversity, is a plot like Fig. 1.1. The exercise, however, illustrates how difficult it is to obtain such plots, how complex the underlying processes are, and how difficult interpretation of such plots might be.

1.3 The evolution of biodiversity and ecosystem functioning research

Our thought experiment makes transparent how any attempt to experimentally explore the relationship between biodiversity and ecosystem functioning requires the researcher to make several decisions that ultimately determine what can and cannot be inferred from the results. What should be manipulated, for example? Should species richness, functional diversity, genetic diversity, relative abundance, or some combination of these or other factors be manipulated? Should species be selected based on biogeography (e.g. only species known to coexist in nature), or could one use any species that is likely to survive in the experiment (e.g. a series of exotic species or domestic species)? How extensive should the biodiversity gradient of the experiment be? Should the lowest level of diversity in the experimental biodiversity gradient be a sterile plot, a single species, or a complete food web with only one species per trophic level? Should the highest level of biodiversity gradient be all species that co-occur in nature, a subset, or more than what is typically found in nature, and should several trophic levels be used with as many species per trophic level as possible?

Most decisions in biodiversity and ecosystem functioning experiments concern two things; the rationale for species selection and the extent of the biodiversity gradient to be used in re-populating the replicates. One of the first biodiversity and ecosystem functioning experiments (Naeem *et al.* 1994, Naeem *et al.* 1995), for example, was a complex, multi-trophic terrestrial mesocosm built in a system of growth chambers known as the Ecotron (Lawton *et al.* 1993, Lawton 1996). Researchers selected species known to co-occur in the field, and were likely to survive in the growth chambers; they paid little attention to whether the species were exotic or not. The researchers also decided to use a biodiversity gradient of just three levels of species richness, but to retain multiple trophic levels throughout. Experiments that followed took similar approaches – they began with a pool of species that were known to co-occur in nature, were not overly concerned with whether they were exotic or not, and established replicate systems (microcosms, artificial ponds, flower pots, and grassland plots) cleansed of the species they wanted to manipulate. The experimenters then repopulated their cleansed replicates with species. Each experiment, however, took slightly different approaches. For example, the experiments of Cedar Creek, Minnesota, focused exclusively on plants (Tilman *et al.* 1996, Reich *et al.* 2001) as did the European BIODEPTH experiments (Hector *et al.* 1999), though one BIODEPTH site manipulated insect abundance (Mulder *et al.* 1999). Hooper manipulated only plants in Californian serpentine grasslands, but focused on functional groups rather than species (Hooper and Vitousek 1997). In fact, most grassland experiments did a combination of both functional group and species manipulations (Tilman *et al.* 1997b, Naeem *et al.* 1999, Wardle *et al.* 2000a, Reich *et al.* 2004).

Early theory and experiments were confirmatory; they primarily sought to examine the possibility that diversity could indeed affect ecosystem functioning. As biodiversity and ecosystem functioning research shifted out of its early confirmatory phase, however, it increased the scope of organisms and systems it investigated and became more exploratory in scope. Hundreds of experiments explored freshwater, stream, wetland, microbial, coral reefs, marine ecosystems, and grassland ecosystems, many of which are discussed directly in this volume or indirectly as parts of meta-analyses. Although each experiment is unique, common to all of them was the need to decide rationally which species to select for inclusion or exclusion and what would constitute the gradient in biodiversity.

The expansion in extent, scope, and complexity of biodiversity and ecosystem functioning experiments led the field to become more predictive rather than confirmatory and exploratory, with an increased emphasis, first, on developing theory with which to interpret these experimental results (Hector *et al*. Chapter 7, Loreau and Hector 2001, Fox and Harpole 2008), and later on applying these findings to real-world problems associated with biodiversity loss. Key features of this new research include greater precision in its metrics as well as increasing integration of the many processes and factors known to impact biodiversity. Greater precision in metrics, for example, involved the evolution of better, more appropriate and applicable measures of biodiversity. In this regard, functional diversity has emerged as the frontrunner for the most relevant component of biodiversity with respect to ecosystem functioning (Díaz and Cabido 2001, Naeem 2002a, Petchey and Gaston 2002a). How one defines, quantifies, and uses functional diversity to interpret how changes in biodiversity can impact ecosystem functioning has become a dominant part of biodiversity and ecosystem functioning research (see Petchey *et al*., Chapter 4).

Biodiversity and ecosystem functioning research has also expanded to include important elements of ecological systems previously understudied. Among them, trophic complexity has become a major theme in contemporary biodiversity and ecosystem functioning research. Rather than working within a single trophic level like many early plant-only experiments, trophic complexity has become an important part of biodiversity and ecosystem functioning experiments and theory (see Cardinale *et al*., Chapter 8). Additionally, rather than black-boxing the microbial world or using them for microcosm tests of theory, biodiversity and ecosystem functioning is expanding to uncover the role of microbes in more complex and natural systems (see Bell *et al*., Chapter 9).

Research on the relationship between biodiversity and stability has also gone beyond the initial attempt to simply confirm if there was or was not a relationship between the two to recognizing multiple relationships (mostly positive, some neutral, and a few negative) and multiple mechanisms (see Griffin *et al*., Chapter 6). Theory has also gone well beyond resource-based or Lotka–Volterra type models to explore multitrophic systems, metacommunities, and other theoretical advances (see e.g. Gonzalez *et al*., Chapter 10).

With advances in experiments, observational studies, precision in metrics, tools, and theory, knowledge on biodiversity and ecosystem functioning is now sufficiently developed that the first projections of the ecosystem consequences of biodiversity loss have begun. Developing means for biodiversity and ecosystem functioning projections was the goal of the National Science Foundation research coordinating network known as Biotic Mechanisms of Ecosystem Regulation in the Global Environment (BioMERGE) (Naeem and Wright 2003, Naeem *et al.* 2007). This is an ambitious and important trend in biodiversity and ecosystem functioning research. It is ambitious because it incorporates many factors that impact biodiversity (see the long list we provided above) into simulations to project future states of ecosystem functioning. It is important because these projections are meant to be realistic and large-scale and useful to researchers, managers, and policymakers alike. Currently, studies that have used this approach are limited, but show promise. Duffy *et al.* (Chapter 5) review this emerging field in biodiversity and ecosystem functioning research.

1.4 Biodiversity and humanity: strains in a productive partnership

The minute humanity began to manipulate nature beyond what is common for ecosystem engineers like beavers or termites (Jones *et al.* 1994), or what might be expected from niche construction (Laland and Sterelny 2006), humans began a path that would lead to extraordinary success, but at an extraordinary price. Success can be seen in terms of humans becoming the dominant geomorphic (Wilkinson 2005), biogeochemical (Vitousek *et al.* 1997), and consumer species (Imhoff *et al.* 2004). In the last two centuries, aided by access to fossil fuel and fossil water, humanity has appropriated an ever-increasing proportion of terrestrial surfaces (Foley *et al.* 2005, Worm *et al.* 2005), net primary productivity (Haberl *et al.* 2007), fresh water (Vörösmarty *et al.* 2000, Oki and Kanae 2006), and marine resources (Worm *et al.* 2006). In so doing, levels of output and consumption have grown everywhere – albeit at very uneven rates. Success has meant a process of economic development that has built up stocks of 'produced' and 'human' capital (infrastructure, buildings, equipment, and financial assets on the one side, technology, skills, education, and learning on the other), whilst running down stocks of 'natural' capital (Dasgupta 2001). Running down natural capital does not only mean the depletion of non-renewable resources like oil, minerals, fossil water, it also means the loss of biodiversity (Sala *et al.* 2000, Millennium Ecosystem Assessment 2005b) and ecosystem services (Millennium Ecosystem Assessment 2005a, Kareiva *et al.* 2007). In some cases, this has left people little better off than they were before. Many of the two billion people in poverty, or the one billion in hunger, are dependent on common-pool environmental resources for their livelihoods. In other cases, the costs associated with the loss of natural capital are simply not taken into account by those whose actions have caused it. Indeed, there is a widespread view that our systematic neglect of the human costs of the erosion of natural capital stocks has to change (World Commission on Environment and Development 1987, United Nations Environmental Program 2007, Holdren 2008). For change to be well-informed, we need to better understand the consequences of eroding the natural capital base.

The replacement of naturally occurring animals and plants with domesticated species began in terrestrial systems over ten thousand years ago and is now increasing in aquatic and marine systems as well (Duarte *et al.* 2007). When human populations were small, such substitutions of naturally diverse systems with smaller numbers of more manageable, higher-yielding species, was not likely to have major impacts on ecosystem functioning at large scales. As the scale of human activity has increased, however, so has its ecological impact.

The initial conditions of the thought experiment, that of complete human domination of ecosystems, are admittedly extreme, but they represent an important endpoint in a continuum that structures the conceptual framework of biodiversity and ecosystem functioning research. At one end, all of humanity's needs are met by managing ecosystems using only the species necessary to maximize human wellbeing. At the other end of the continuum is a state in which every need of humanity is met by nature – a state that probably last existed six million years ago when our primate ancestors started down the evolutionary pathway that would lead to the origination of the human species.

Where in the gradient, from complete human domination of ecosystems to being no different from other species in their impacts, is human wellbeing optimized? The right balance remains unknown, but it is clear that humanity is shifting to the end where all of humanity's needs are met by heavily managed ecosystems. In the case of agro-ecosystems, Jackson *et al*. (Chapter 13) note such systems now comprise 65 per cent of terrestrial ecosystems, with 10 per cent in high-input agriculture, 15 per cent in low-input agriculture, and 40 per cent in mixed use. By 2050 an additional 10^9 hectares of wildlands are likely to be converted to managed lands to feed our growing population.

Managed ecosystems reflect a production-simplification tradeoff in which the production of utilitarian biomass (i.e. edible plants and animals, biofuel, lumber) is increased at the expense of native biodiversity that may appear at first glance to have less utility, though its full utility has yet to be understood or inventoried. The transformation of complex landscapes that typically housed hundreds of species of plants and vertebrates, thousands of species of invertebrates, and untold numbers of species of microorganisms, to managed systems always lowers local (e.g. species per square meter) taxonomic richness to a tenth or hundredth of its original value. More importantly, biodiversity loss associated with simplification often brings with it concomitant reductions in trait diversity and reductions in the number, type, strengths, and arrangement of biotic interactions among species in the community web. Simplification refers more specifically to such reductions in functional diversity and complexity than it does to taxonomic loss.

Initially, biodiversity and ecosystem functioning research focused on the single function of production which would prove to be neither a persuasive argument for conserving biodiversity nor an accurate reflection of the true costs of ecological simplification. Biodiversity and ecosystem functioning studies generally found a positive, asymptotic relationship between biodiversity and production, suggesting that biodiversity loss meant loss in production and implying that human wellbeing would decline in the face of such declining production. The demonstrated relationships, however, typically described strong gains in production with just a few species and vanishingly small gains in production with each species added (Schmid, Chapter 2). Furthermore, monocultures or combinations of just two or three species could often out-produce communities that were much more species-rich. In terms of production, it seemed one could get by with far fewer species in an ecosystem than was typically found in nature.

Lost production due to simplification in natural systems (which was counter to the production-simplification tradeoff in managed systems where production appears to improve under simplification) was only one part of the picture; stability could also be affected by biodiversity loss. Proof that stability and diversity were positively related, however, was much more difficult to demonstrate (McCann 2000, Cottingham *et al.* 2001). Biodiversity was seen as a means of enhancing system reliability (Naeem and Li 1997, Naeem 1998, Naeem 2003) and a means of improving and stabilizing long-term gains in ecosystem function (e.g. Doak *et al.* 1998, Tilman *et al.* 1998, Yachi and Loreau 1999).

An important point that many researchers have made, but which is seldom demonstrated, was that production was not the only function that was affected by biodiversity loss. There is increasing evidence that the maintenance of multiple ecosystem processes requires many more species than does the maintenance of a single process (Eviner and Chapin 2003, Hector and Bagchi 2007, Gamfeldt *et al.* 2008). An important example of a multiple function is the role of biomass production as both a provisioning ecosystem service (i.e. timber and non-timber forest products) as well as regulatory service in terms of carbon storage (Díaz *et al.*, Chapter 11).

While understanding the true costs of the production-simplification tradeoff in terms of changes in the magnitude, reliability, and stability of multiple biogeochemical functions is a major thrust in biodiversity and ecosystem functioning research, of equal importance are the impacts of simplification on biotic functions. Jackson *et al.* (Chapter 13) note that biocontrol and pollination (see Klein *et al.*, Chapter 14), both biotic functions, have received attention in the biodiversity and ecosystem functioning literature and are frequently cited as examples of ecosystem services relevant to agro-ecosystems (Balvanera *et al.* 2005, Tscharntke *et al.* 2005, Philpott and Armbrecht 2006, Kremen *et al.* 2007, Priess *et al.* 2007). Two other examples of biotic functions include the influences of biodiversity over invasive species (see Engelhardt *et al.*, Chapter 16) and diseases (see Ostfeld *et al.*, Chapter 15).

The question of restoration, especially restoration targets, takes on new meaning in light of the production-simplification tradeoff and the relationship between biodiversity and ecosystem functioning. Most habitats designated for restoration have lost biodiversity either due to simplification (e.g. for agriculture) or degradation by pollution or unsustainable extraction, such as clear cutting lumber or over harvesting fish. Restoring simplified or degraded habitats to some version of their former self requires thinking about restoring not only lost diversity, but lost functioning and services as well (Wright *et al.*, Chapter 12).

1.5 The emergence of a unified natural–social biodiversity and ecosystem functioning framework

Biodiversity and ecosystem functioning research can and should supply managers, conservation biologists, policy makers, and other interested parties, with the information they need to make the best decisions they can regarding their effects on biodiversity. Although it has so far done poorly at informing management and policy (Solan *et al.*, Chapter 3), it is founded on a central construct that clearly indicates that it can do so. This construct is written simply as,

Biodiversity → **E**cosystem **F**unctioning →
Ecosystem **S**ervices → **H**uman **W**ellbeing,

where each arrow represents a causal relationship and *ecosystem services* are ecosystem functions that benefit humans. This framework, in fact, became the central framework for the Millennium Assessment (2003).

Typically, biodiversity and ecosystem functioning researchers assumed that if they demonstrated that biodiversity was important to the magnitude and stability of any ecosystem function, then it would automatically follow that biodiversity is important to the magnitude and stability of ecosystem services and, by extension, to the magnitude and stability of human wellbeing. That is, they took for granted that if the left-hand side of the construct was demonstrated, then the right-hand part of the construct, the link between ecosystem services and human wellbeing, would follow. And if it did not follow automatically, then it was up to economists to separately pursue the right-hand side of the construct.

In principle, the logic of working on individual parts of the construct was sound and in keeping with the tradition of ecologists and economists working separately. In practice, however, the result was that the natural science of biodiversity and ecosystem functioning, though published in high-profile scientific journals, failed to carry through to management and policy (Solan *et al.*, Chapter 3). The apparent simplification–biodiversity tradeoff, which was the hallmark of human development, was pitted against scientific cautions about hidden costs. The value of land, water, farms, lumber, fisheries, and other natural resources are, however, far greater than the potential gains suggested by biodiversity and ecosystem functioning research. Vanishingly small gains in production in abstract experimental systems or arguments about improved stability were not translated into ecosystem services (i.e. the right-hand side of the construct). Indeed, in spite of the adoption of the biodiversity → ecosystem functioning → ecosystem services → human wellbeing framework by the Millennium Assessment and over a decade of biodiversity and ecosystem functioning research, only a handful of case studies were available to support the Assessment's conclusions that greater biodiversity provides more ecosystem services. A case study approach was similarly used by Balmford *et al.* (2002). Early attempts to estimate the economic value of the ecosystem services supported by biodiversity received considerable attention (e.g. Costanza *et al.* 1997, Costanza and Folke 1997, Pimentel *et al.* 1997), but because they rested on questionable methodology were dismissed by most economists. Nevertheless, they did serve to emphasize that non-marketed ecosystem services were more important than previously believed. At the same time, there is little evidence from over a decade and a half of research – comprising hundreds of biodiversity and ecosystem functioning and economic analyses and the adoption of the principles by the Millennium Assessment – that biodiversity conservation as a route to improve human wellbeing has become a strong part of the private or public consciousness.

While each link in the biodiversity → ecosystem functioning → ecosystem services → human wellbeing framework is important in its own right, these links do need to be developed in unison, as neither the natural science underlying the influence of biodiversity on ecosystem functioning nor the social science underlying the link between ecosystem services and human wellbeing can carry the day on their own. Economists' perspectives on the importance of biodiversity have contributed significantly to understanding the social implications of biodiversity loss (Barbier *et al.* 1994, Perrings 1995, Perrings *et al.* 1995, Swanson 1995, Folke *et al.* 1996, Chichilisky and Heal 1998, Hollowell 2001); thus the foundation for a unified framework exists.

The economic literature on biodiversity and ecosystem services is rapidly growing (Heal 2005, Carson 2008). There are three major thrusts to this literature, which are reflected in the chapters included in this volume. One thrust addresses the reasons why markets fail to allocate biological resources efficiently, and identifies corrective measures. Perrings *et al*. (Chapter 17) identify the externality and public good problems that lie at the heart of biodiversity loss, and survey the range of corrective mechanisms discussed in the literature. These include the development of markets for services such as ecotourism or bioprospecting. But they also include a number of instruments designed to encourage resource users to take the biodiversity consequences of their actions into account, such as taxes, access charges, user fees, payment for ecosystem services, direct compensation payment, and transferable development rights.

A second thrust addresses the valuation of ecosystem services and, through this, of the biodiversity and ecosystem functioning that underpins the production of services. Barbier *et al*. (Chapter 18) review the economics of ecosystem service valuation, and illustrate the way in which the demand for basic ecosystem components may be derived from the demand for ecosystem services. They show how the approach can be used to value the biological resources that support not only provisioning services (e.g. the production of foods, fuels and fibres) and cultural services (e.g. the non-consumptive enjoyment of landscapes for recreational, educational, scientific, spiritual, or cultural reasons), but also regulating services. In the last case, the economic theory of portfolio choice provides a natural way to investigate the implications of biodiversity for risk management.

A third thrust addresses the incorporation of ecosystem components into economic decision models. Brock *et al*. (Chapter 19) review the ways in which economists model decision problems in coupled ecological–economic systems that are subject to varying levels of anthropogenic impact. They also discuss the consequences of the different objectives that motivate people, ranging from the preservation of naturalness to the management of food production systems.

Central to this unification, as both Perrings *et al*. (Chapter 17) and Brock *et al*. (Chapter 19) note, is an understanding of (a) the mechanisms that connect biodiversity and ecosystem functioning to the production of valued ecosystem services, and (b) the set of incentives that lead individuals to behave in ways that are more or less closely aligned with the social interest. All too frequently, decisions made by private resource users neglect costs that are displaced onto others.

There is a complex array of social and natural feedbacks that the simple biodiversity → ecosystem functioning → ecosystem services → human wellbeing construct does not capture. Incorporating these feedbacks will be necessary if effective economic instruments based on biodiversity and ecosystem services are to be designed to ensure that private decisions are compatible with the social interest. The chapters on economics make it clear that the emerging natural–social unified approach can occur if ecologists and economists work together.

Summary

In this introduction, we have reviewed the basic ideas that have structured the revolution in the natural and social sciences that inextricably links biodiversity with human wellbeing. Our emphasis is on the scientific basis for biodiversity's influence over ecosystem functioning and its concomitant effects on human wellbeing. Although the contemporary field of biodiversity and ecosystem functioning emerged only in 1992 (the year of the Earth Summit in Rio and the establishment of the United Nations Convention on Biological Diversity and the United Nations Framework Convention on Climate Change), the field of biodiversity and ecosystem functioning has evolved rapidly through three stages. It first survived the contentious confirmatory years of the late 1990s, moved through an exploratory phase at the beginning of this century, and is now in the throes of building a new, joint, natural–social model for humanity. The authors of these chapters are those who have spearheaded this change and are driving its leading edge. What follows are descriptions of those achievements, advances, and future directions. The reader will find what unfolds to be as scientifically fascinating as it is relevant to solving our most pressing environmental problems.