Biodiversity, Ecosystem Functioning, and Human Wellbeing

An Ecological and Economic Perspective

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CHAPTER 21

Can we predict the effects of global change on biodiversity loss and ecosystem functioning?

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21.1 Efficacy, practicability, and social will

The efficacy and practicability of an idea, and the will of individuals or society to explore it, determine whether it catalyzes change or merely enters the vast store of quiescent ideas that make up the bulk of humanity's collective wisdom. As we noted in the *Introduction*, the idea that biodiversity influences ecosystem functioning is not new. There are, for example, similarities between the *Hortus Gramineus Woburnensis* experiment of 1817 (Hector and Hooper 2002) and BIODEPTH experiments (Hector *et al.* 1999) almost two centuries apart. The *Hortus Gramineus*, however, was nearly forgotten. Perhaps it was forgotten because the idea of improving yield by manipulating vegetation gave way in the 1840s to Justus von Liebig's idea that yield was controlled by the availability of limiting mineral nutrients. In contrast, in the 1990s, individual and social concerns over the environmental consequences of worldwide changes in biodiversity raised questions about ecosystem functions in general, not just yield (Loreau *et al.* 2002). Because primary production is a convenient measure of ecosystem functioning, it has been emphasized in biodiversity and ecosystem functioning work, which creates the uncanny resemblance between modern experiments and the *Hortus Gramineus*. Although biodiversity and ecosystem functioning research shows no sign of abating some 15 years later, we might nevertheless ask whether it too will be forgotten like the *Hortus Gramineus*?

As in all science, there remain differences among researchers on the interpretation of biodiversity and ecosystem functioning research, but the efficacy of the idea that the diversity of life, not just its mass, influences both the biogeochemical and biotic properties of ecosystems, is well established. Even in 1997, although they guessed a stronger, less complex role for diversity than meta-analyses would eventually support (Chapter 2), researchers had the right sense of things with just a small number of studies to hand. The rapid rise in numbers of studies (Chapter 2), their influence on the literature (Chapter 3), incorporation of the idea into the Millennium Assessment framework (Millennium Ecosystem Assessment 2003), and the achievement of scientific consensus (Loreau *et al.* 2001, Hooper *et al.* 2005), all suggest that today the efficacy of the idea is no longer in doubt. Many questions concerning mechanisms, generality, and the relative strength of biodiversity effects compared to other factors that influence ecosystem functioning, such as temperature, precipitation, ocean depth, and physical substrate, remain, but few question that changes in biodiversity influence ecosystem functioning.

Although efficacy may be less of an issue than it was in the 1990s, practicability and societal will remain significant challenges. By *practicability* we mean the ability to test the idea empirically and translate it into real-world applications, and by *societal will* we mean the willingness of individuals and society to adopt the idea as a foundation for decision-making. In this chapter, we look across the many contributions in this volume and consider a few messages the current field of biodiversity and ecosystem functioning research give us concerning efficacy, practicability and societal will.

From a rich set of cross-cutting ideas embodied in this book we focus on just three that are shaping the trends in biodiversity and ecosystem functioning research. First, concerning efficacy, there is a struggle in the discipline to make the research more realistic. Unfortunately, what constitutes realism in ecology can sometimes be subjective, thus if biodiversity and ecosystem functioning research is to avoid another round of debate, further clarity on the issue of realism is needed. Second, concerning practicability, we revisit the Millennium Assessment's framework and restructure it based on current empirical and theoretical findings. Our hope is that this modified framework points the way to practicable, coupled, natural–social research and policy. Finally, in order to facilitate individual and societal will, we provide a graphical device that may better communicate the core idea of the importance of biodiversity to ecosystem functioning and link it more directly to sustainable development. We suggest that the preservation, management, and intelligent use of biodiversity may be our only hope for achieving environmental sustainability which, in turn, is our only hope for achieving overall sustainable development and its many goals (e.g. the United Nations' Millennium Development Goals) of social and economic equity across the globe.

21.2 Efficacy and realism in biodiversity research

Since its inception, biodiversity and ecosystem functioning research has sought to encapsulate the key elements of biodiversity and ecosystem functioning in its theory and experiments, but every study has been hounded by the question of realism. The full complexity of biodiversity, whose ecological and evolutionary processes scale from microscopic to planetary, can never be entirely captured in any one experiment, nor does it have to be. Rather, researchers ask focused questions and make decisions about what is and is not necessary to test a particular idea. Even focused questions about biodiversity and ecosystem functioning, however, require fairly elaborate experiments (see Chapters 2 and 7). Research in biodiversity and ecosystem functioning has pushed the envelope of empirical ecology, establishing some of the largest (e.g. Roscher *et al.* 2005, Spehn *et al.* 2005, Tilman *et al.* 2001) and most elaborate micro- and mesocosm studies ever conducted (e.g. Naeem and Li 1998, McGrady-Steed *et al.* 1997, Downing and Liebold 2002, Fukami and Morin 2003, Fox 2004a, Bell *et al.* 2005b, Cadotte and Fukami 2005). The trend of increasing the size or the number of replicates and the complexity of experimental design reflects attempts to continuously improve experimental realism. Increasing plot size, for example, is based on the notion that, in nature, some ecological processes operate at larger scales. Likewise, the use of microbial communities whose small spatial scales can be readily accommodated using bottles and Petri dishes, allows for multiple generations. The presumption here is that multiple generations better approximate the temporal scale at which ecological processes operate in nature (Petchey *et al.* 2002, Raffaelli *et al.* 2002). Microcosms also allow for much more community and trophic complexity, again presuming that greater complexity better approximates nature (Petchey *et al.* 2002, Raffaelli *et al.* 2002). Exploration of different types of systems, such as wetlands (e.g. Engelhardt and Ritchie 2001), estuarine (e.g. Duffy *et al.* 2005) and marine ecosystems (e.g, Emmerson *et al.* 2001, Stachowicz *et al.* 2002, Bracken *et al.* 2008), and organisms other than plants, such as fungi (e.g. Tiunov and Scheu 2005, Van der Heijden *et al.* 1998), soil fauna (e.g. Mikola and Setälä 1998), and zooplankton (e.g. Norberg 2000), also reflects attempts to test the generality of findings. With every year, the cumulative range of spatial and temporal scales, community complexity, and the scope of taxonomic and ecological diversity explored by biodiversity and ecosystem functioning research has grown.

The question of realism, however, continues to dog biodiversity and ecosystem functioning research (Raffaelli 2004). Clearly one should put more stock in the findings of a more realistic experiment, but how does one evaluate realism in ecological experiments? There are two features of biodiversity and ecosystem functioning studies that determine how comparable they are, both of which are determined by a large number of decisions that researchers make when conducting their studies. First, in any biodiversity and ecosystem functioning study, researchers must decide what *biodiversity* *gradient* is appropriate for the question they wish to address. Decisions concerning the biodiversity gradient include:

1) choosing the appropriate measure of diversity,
2) determining the size of the species pool to be used in the experiment,
3) establishing the low-diversity endpoint (most often monocultures) and
4) establishing the high-diversity endpoint of the gradient (most often all species in the pool).

Biodiversity gradients in experiments range from high-diversity end points that are simply convenient (e.g. the 16 plant species out of over 800 at Cedar Creek, Minnesota, were selected in part because they were known to do well in experimental settings and seeds were commercially available; S. Naeem, *pers. comm.*) to high-diversity endpoints that contain as many species as possible in abundances commonly observed in the field (e.g. when the high-diversity endpoint is an unmanipulated plot). Low-diversity endpoints are often simply monocultures, but here too one may elect to set the low-diversity endpoint at a higher richness level (and use monocultures only to calculate null predictions, as reviewed in Chapter 7).

Second, researchers must also make decisions concerning *species selection*, or which species should be observed or manipulated, since it is generally not possible to study every species, especially microorganisms, in ecosystems. Decisions concerning species selection include:

1) whether or not one should include exotics (naturalized, domestic, invasive, or other non-resident species);
2) what range of biotic interactions should be included among the selected species (i.e. should predators, diseases, mutualists, and other interacting species be used or just competitors for the same limiting resources); and
3) whether the subset of species should be selected at random or based on some other criteria, such as commonness, cultivability, or traits related to the likelihood of extinction.

Species selections in experiments range from investigators using whatever is convenient (e.g. whatever can be cultivated or manipulated), to selecting only biogeographically coherent sets of species (i.e. only sets of species observed to co-occur in nature), to using all species in an ecosystem.

In silico studies represent a recent, promising trend in biodiversity and ecosystem functioning experiments, but their gains in realism made possible through enormous numbers of replicates come at the cost to realism in estimating ecosystem functioning. *In silico* studies, such as those by Solan *et al.* (2004), Bunker *et al.* (2005), McIntyre *et al.* (2007), and Bracken *et al.* (2008) can generate thousands to millions of species combinations, thereby eliminating the practical constraints of field research that is often limited to hundreds of species combinations. *In silico* experiments require researchers to make the same decisions concerning species selection and the biodiversity gradient, but with fewer constraints on the size of the species pool, the number of levels of biodiversity, and the number of replicates. Ecosystem function, however, must be estimated, which is usually done by algorithms that translate individual species abundances and functional traits into likely ecosystem function, and it is here where uncertainty lies. Current *in silico* experiments ignore the multiple interactions and modes of functional complementarity between species, and hence have other limitations regarding realism. *In silico* experiments will become more realistic and accurate as we develop a greater understanding of the mechanisms of complementarity and better data on the species traits that lead to them (Chapters 5 and 20).

Considering the biodiversity gradient and species selections of multiple studies provides a basis for comparing studies. Figure 21.1 graphically illustrates how studies relate to one another. The endpoints of the biodiversity gradient axis reflect extremes in decision making by researchers. 'Fully combinatorial' refers to an experiment that uses every possible combination of species possible, irrespective of what is found in nature. 'Trait-based extinctions' refers to experiments in which combinations are constrained to those in which the presence or absence of species is determined by the particular traits of species. For example, for an *in silico* study of mammalian bush meat production, where body size determines probability of extirpation by hunting, the gradient will range from species-rich communities with both small and large

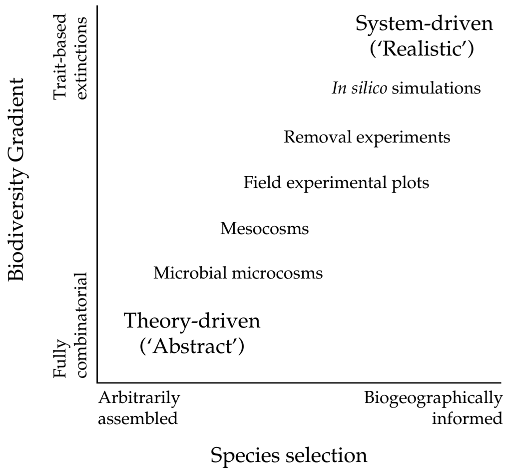

Figure 21.1 The biodiversity gradient and species selection of different kinds of studies in biodiversity and ecosystem functioning research. Each study makes decisions concerning how it establishes the gradient in biodiversity it explores as well as how it selects species. See text for discussion.

sized animals to communities composed only of small sized animals, as large mammal populations will decline first in response to hunting pressure (Cardillo *et al.* 2005).

The endpoints of the species selection axis in Fig. 21.1 consist of studies in which species were selected by the researcher because they were convenient (e.g. common and cultivable) or through other arbitrary decisions to selecting combinations of species currently found co-occurring in nature or which are likely to be found in the future after extinction takes its toll. 'Theory-driven' studies are often typified by biodiversity gradients and selection well suited to testing the theory, but are perhaps not reflective of what is observed in nature. 'System-driven' studies tend to be closely modelled on the ecosystem under investigation. Obviously, all experiments have their virtues, but whether their findings refer broadly to theory or more specifically to particular ecosystems depends on the biodiversity gradient and species selection of the study. We observe that there is a tendency to consider 'realism' in studies that are more system-driven.

The biodiversity gradient and species selection properties of experiments make clear that realism in biodiversity and ecosystem functioning research is a complex issue. Our deliberations here illustrate that the value of realism is its ability to provide a reference for our findings, not to pass judgement on the efficacy of a study. The day may come when several million field plots, each fifty hectares in size, have had their diversity manipulated across every trophic level according to trait-based extinction scenarios and at densities observed in nature, and both microbial to macrobial species are manipulated, and run for a century or more. Such an experiment might be hailed as the ultimate realistic study, but it might not be the most efficient and economical way to do science, and so laboratory microcosm and *in silico* experiments would not lose their value.

21.3 Biodiversity, ecosystem functioning, and human wellbeing

The biodiversity → ecosystem functioning → ecosystem services → human wellbeing framework of the Millennium Assessment was a brilliant synthesis that united the natural and social environmental sciences by linking biodiversity, ecosystem processes, ecosystem functioning, and the services of ecosystems (see *Introduction*, Chapter 1). For the first time, it made it possible to see ecosystems as social assets whose value lies in the flow of social benefits (services) they yield. Although invaluable as a conceptual framework, however, it is too simplistic to serve as a guide for the development of practical biodiversity-based solutions to environmental problems. The biodiversity and ecosystem functioning research reviewed in this volume suggest two areas that need to be refined. First, the *biodiversity → ecosystem functioning* part of the Millennium Assessment conceptual framework needs to recognize the interdependency between the biotic and abiotic (the biological and geochemical) components of the system and its functioning. The value of ecosystems lies in their capacity to deliver services. Since the supporting services identified in the Millennium Assessment are just the processes that underpin ecosystem functioning, they are an integral part of the ecosystem as an asset – a functional unit. The supporting services accordingly need to be considered separately from regulating, provisioning, and cultural services (see Chapter 18 for a detailed treatment of ecosystem services). Second, while the conceptual framework provides a nice link between ecosystem services and human wellbeing, it does not reflect the critical importance of globalization – the closer integration of human society through trade and interactions among human populations. The interconnections between ecosystem services at different spatial and temporal scales turn out to be highly sensitive to the degree of globalization. A variant of the Millennium Assessment framework that reflects these concerns is illustrated in Fig. 21.2 and we explain these modifications below.

The ecosystem as a functional unit. The assets from which humans extract provisioning, cultural, and regulating services are functioning ecosystems. These comprise both abiotic and biotic components, and biogeochemical processes that underpin ecosystem functioning. In the absence of biological processes on Earth, geochemistry governs surface conditions as on any planet. The inclusion of biological organisms alters geochemical processes. In this modified framework, stocks are functioning ecosystems and flows are the services those systems yield. The elements within the system comprise the biotic and abiotic (atmospheric, lithospheric, and hydrospheric) pools of carbon, nutrients, and water, together with the plants, animals, and microorganisms that move carbon, nutrients, and water into and out of these biotic and abiotic pools.

If one eliminates the biota in the ecosystem, as we did in the thought exercise in the *Introduction*, the only fluxes in the pools of carbon, nutrients, and water would be those induced by geochemical processes. In a system with both biotic and abiotic elements, these fluxes are modified by biological processes. The resulting ecosystem processes are the basis for the flows of interest to human societies: the provisioning and cultural services, and their variability (the regulating services). We note that flows, in this sense, are not generally the same as fluxes in pools of carbon,

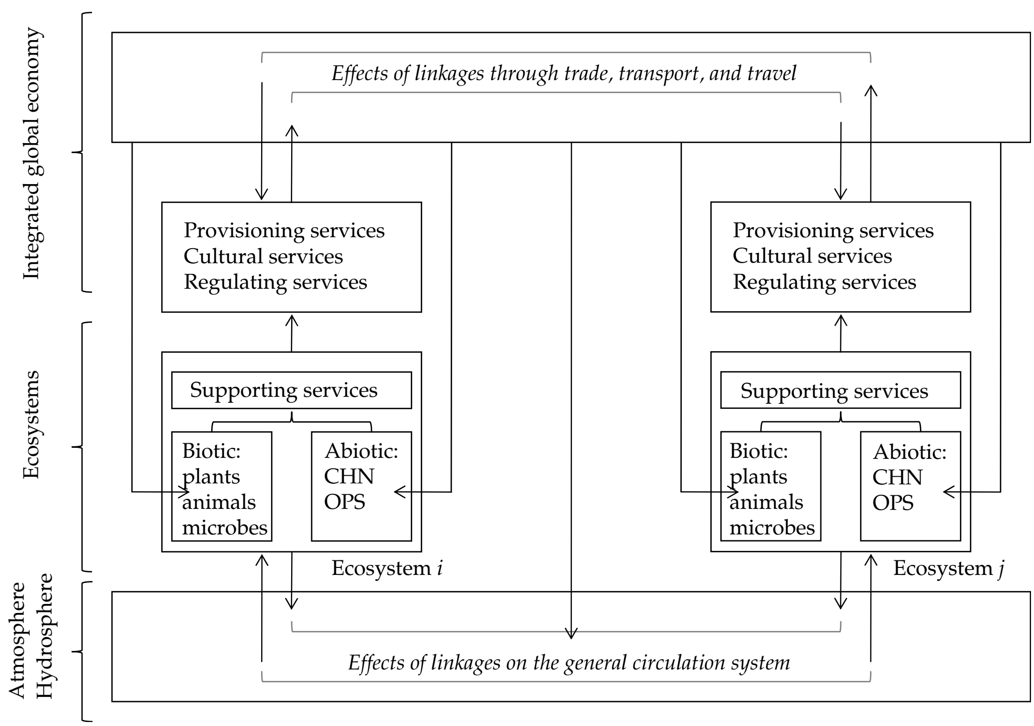

Figure 21.2 A coupled social–natural biodiversity and ecosystem functioning framework. Individual ecosystems worldwide, such as ecosystems *i* and *j* in this figure, are inextricably linked, both by market forces in the global economy and by biogeochemical fluxes through the atmosphere and hydrosphere. While more complex than the Millennium Assessment's framework, it eliminates ambiguities and facilitates integration of research, analyses, and policy development. See text for further explanation.

nutrient, or water. They are the benefit streams yielded by durable assets – functioning ecosystems in this case. It follows that the Millennium Assessment's supporting services are distinct from the other ecosystem services in that they are elements of the functioning ecosystems that yield the other ecosystem services as flows. By analogy, an automobile is a system whose components include a large number of parts organized so as to yield a flow of personal transport services. The value of a functional automobile is greater than the sum of its parts. The transport services it yields depend, *inter alia*, on the combustion processes occurring within the engine. Like the Millennium Assessment's supporting services, combustion processes help make the vehicle functional. In most managed ecosystems, the supporting services may be tailored to the production of specific services, either through direct modification of biogeochemical processes or indirectly through modifications of biodiversity, which influence biogeochemical processes. In Fig. 21.2 we therefore depict these Millennium Assessment 'services' as structuring elements of ecosystems.

Globalization and the closer integration of the biosphere. Humans impact their local biota through direct exploitation of local ecosystems, but they also impact biodiversity outside their geographic boundaries through the indirect impacts of trade, transport and travel (Chapter 17, but see also Kohn and Capen 2002, Perrings *et al.* 2002). For example, China's increasing demand for natural resources affects its own biodiversity both directly, through the exploitation of resources in China, and indirectly, through the effect of species introduced along with resources imported from other parts of the world. At the same time, imports to China affect biodiversity in the exporting countries through the indirect impact they have on, for example, rates of land conversion (and biodiversity loss) in those countries (Aide and Grau 2004), while exports from China to bioclimatically similar trading partners increase the risks that accompanying species will establish and spread in those countries (Costello *et al.* 2007). The same mechanisms operate for all trading countries.

Closer integration of world markets has another important impact on local biota. By increasing the number and accessibility of substitutes for particular ecosystem services, it reduces the cost of running down the associated assets – the ecosystems themselves. One manifestation of this is the 'roving bandit' phenomenon in the exploitation of open ocean fisheries, which has led to the sequential depletion of one fish stock after another (Berkes 2005, Worm *et al.* 2006). Another manifestation is the substitution between, for example, food sources. So reductions in West African fish supplies due to overharvesting have increased demand for bush meat as an alternative source of protein (Brashares *et al.* 2004). The role of the integrated economy in affecting local ecosystems is captured in the trade-mediated feedbacks between those systems in Fig. 21.2.

As the chapters in Part 3 all indicate, and especially Chapters 17–19, a more synthetic framework is needed if we are to move forward on finding biodiversity-based solutions to environmental problems. Brock *et al.* (Chapter 19) note: 'economists now understand that the gap between private and social optima depends on a complex set of feedbacks between the ecological and economic components of the coupled system'. Understanding the pathways and feedbacks that link biogeochemical (i.e. ecological) and social (i.e. economic) systems is critical to the development of practicable solutions to environmental problems that involve biodiversity change of one kind or another.

21.4 Implications for sustainable development

What is the main message of biodiversity and ecosystem functioning research? Can it be effectively and clearly communicated to the public and policymakers? Is it likely to resonate with their perceptions of the environmental dimensions of a sustainable development strategy?

The main message from this volume, but particularly from Part 3, is that biodiversity conservation is an essential element in any strategy for sustainable development. In 1987, *Our Common Future*, also known as the Brundtland Report (World Commission on Environment and Development 1987), laid down a convincing argument that the benefits to humanity of the last century's economic development were tremendous, but that they were experienced largely by rich developed nations and came at the cost of severe depletion of the world's natural capital.

The goal of sustainable development currently enjoys an enormous subscription among policy-makers (e.g. World Commission on Environment and Development 1987, Reid 1989, Annan 2000, National Research Council 2000, Kates *et al.* 2001, Folke *et al.* 2002, Raven 2002, Sachs 2004). The largest international summits in human history, the UN Conference on Environment and Development, also known as the Earth Summit, held in Rio de Janeiro in 1992, and the 2002 World Summit on Sustainable Development in Johannesburg, were centred on the ideas of sustainable development. The UN Convention on Biological Diversity and the Millennium Assessment are also founded on the idea that biodiversity conservation is essential for achieving sustainable development. This has stimulated an intense effort to understand the scientific implications of the concept (Clark 1987, Kates 2001).

Communicating a complex message simply. The Brundtland Commission's call to abandon development by unsustainable spending of natural capital was essentially a call for biodiversity conservation in some measure to secure ecosystem services. It has been interpreted as a call to protect the value of natural capital, where natural capital comprises both the biotic and the abiotic components of the natural environment. In the wake of the Millennium Assessment we can think of the world's ecosystems as being amongst the most important elements of this. It thus includes biodiversity – the mix of plants, animals, microorganisms – and the ecosystem processes it supports. Most ecosystems have been shaped or at least impacted by human actions, but all still rely on a set of processes that are independent of human action. Man may have structured the system to promote or reduce particular processes, but the processes – along with the organisms and abiotic components they interact with – are properties of the natural world.

Alongside natural capital, it is conventional to identify at least two other forms of capital: produced or manmade capital and human capital (Fig. 21.3). Manmade capital, by contrast, involves assets that are produced, and that do not replicate nature – factories, roads, bridges, power plants, financial institutions and assets, etc. Human capital is the store of knowledge, culture, and social structure of people. Humans benefit from natural capital directly (e.g. natural resource extraction, such as lumber or fish harvesting) or indirectly (e.g. processing lumber in sawmills or transforming landscapes into agricultural systems). Fossil resources, such as petroleum, natural gas, and aquifers of fossil water, can supplement natural resource inputs, but renewal of these resources is so slow (tens of thousands to tens of millions of years) that they are best considered as non-renewable. Essentially, humanity controls the levers that open or close the flow of energy, nutrients, and water to either manmade or natural capital.

Sustainable development requires that the value of all three sets of assets is not declining over time. It allows for substitution between the different forms of capital, but respects the fact that there are not manmade substitutes for all forms of natural capital. It also respects the fact that ecosystems, like human technology and preferences, evolve over time. Hence sustainable development involves a strategy that builds the aggregate wealth of countries whilst allowing for their evolution. Biodiversity is critical in this for three main reasons.

First, a mix of species enhances the functioning of ecosystems and hence the value of those systems, regardless of the state of nature. That is, in any given state of nature, any positive diversity–functioning relationship that does not rely on sampling effects (i.e. that enhances the efficiency of resource exploitation through niche partitioning) implies complementarity between species. So too does any obligate or symbiotic relationship between species. The complementarity between species in this sense, like the complementarity between factors of production in economic systems, enhances the productivity and hence value of ecosystems.

Second, the redundancy of some species in functional groups provides insurance against changes in conditions that compromise the ability of other species in the same groups. In this sense, biodiversity is like a portfolio of assets. The value of the portfolio depends on both the range of conditions that is expected to occur, and the covariance in the performance of all assets in the portfolio over that range of conditions.

Third, and related to this last point, the evolutionary potential of the system is an increasing

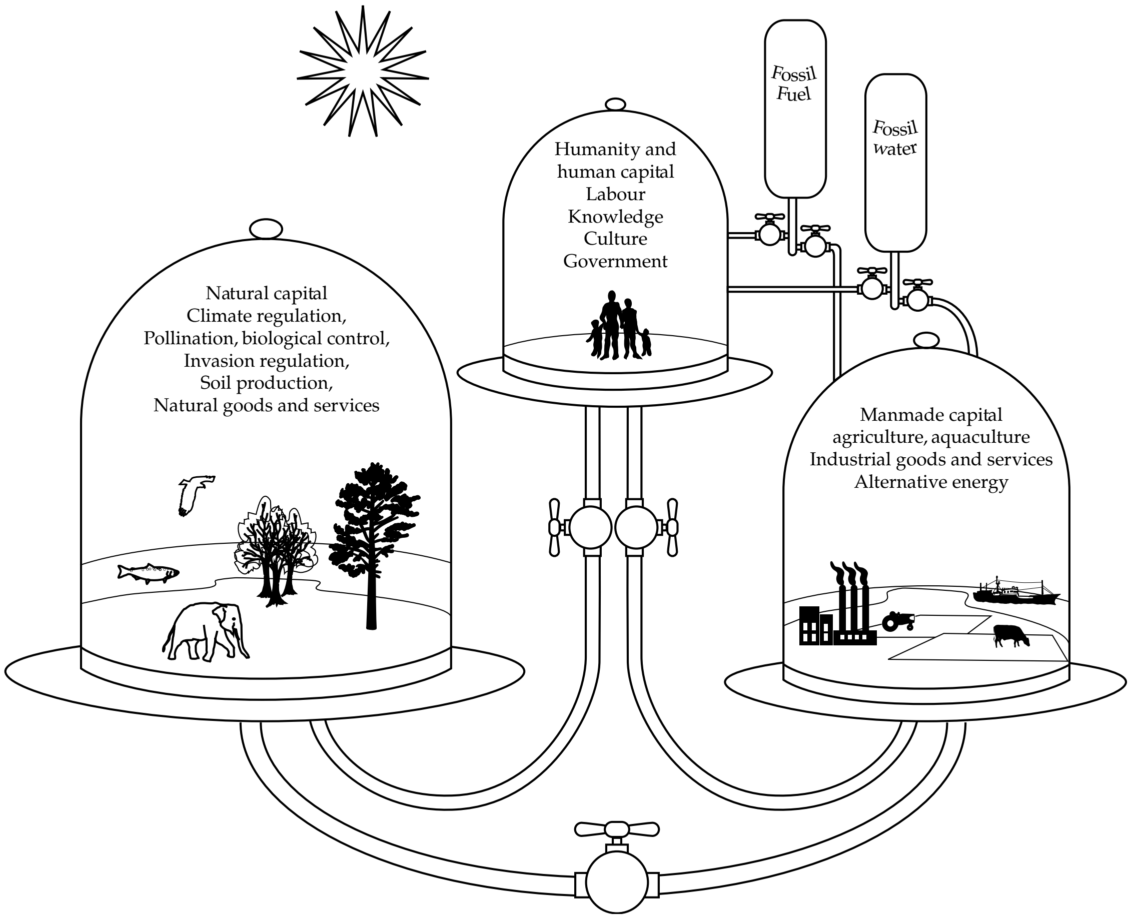

Figure 21.3 Human domination of the biosphere: a graphical device for communicating the importance of biodiversity and ecosystem services in environmental sustainability and sustainable development. This figure illustrates humanity and human capital supported by inputs from natural and manmade capital as well as current inputs from fossil fuel and water supplies. The series of pipes and valves illustrate how humanity's wellbeing and fate are controlled by the ways in which we balance the flows of nutrients, energy, and water among the different compartments. For example, if we allocate greater flows to manmade capital, natural capital shrinks, as do the services we derive from natural capital. See text for further explanation.

functioning of the gene combinations that enable species to exploit novel conditions. In economic terms, gene combinations have an option value – more particularly a quasi option value (the potential value of the yet to be uncovered information they offer).

Note that this does not mean that more biodiversity is always more valuable than less biodiversity. Indeed, simplification of ecosystems to enhance the productivity of one or more services has been the cornerstone of development in the past. The elimination of pests, predators, and pathogens has substantially enhanced human wellbeing in many cases. The problem identified in Chapters 17 and 18 is that neglect of the external effects of decisions to convert habitat to 'productive' uses, or to eliminating pests, competitors, predators, and pathogens to enhance productivity, may have undesirable and potentially unexpected consequences, for instance on other ecosystem services whose costs and benefits are externalized. Only by understanding the relationship between biodiversity, ecosystem functioning, and the production of ecosystem services is it possible to identify the degree to which biodiversity in any given system should be conserved.

21.5 Concluding comments

Hooper *et al*. (2005) listed five areas in need of expansion or resolution in biodiversity and ecosystem functioning research. Although published in 2005, the first outline of the consensus was produced in 2000, but even with this earlier date it remains remarkable that all five areas have been explored. These five areas were: (1) the relationship between taxonomic and functional diversity, (2) the importance of multiple trophic levels, (3) effects on temporal stability, (4) the relative influence of extrinsic factors versus biodiversity effects, and (5) the exploration of a wider array of ecosystems. Much, much more needs to be done, but expansion into these areas has strengthened the central message that biodiversity influences ecosystem functioning.

Current challenges to the field are multifold. Researchers must strive to: (1) incorporate greater realism into experimental approaches, (2) unify natural and social science methodology to address the full scope of the effects of diversity on human wellbeing, and (3) convey our findings to the non-scientific community, where environmental decisions are made and policy developed. These issues will dominate the field for the next phase of research into the effects of biodiversity on human wellbeing. The loss of biodiversity beyond levels that contribute to human wellbeing will decelerate only once the interactions between biodiversity, ecosystem functioning, ecosystem services, and human wellbeing are properly understood, since it is only then that the consequences of excessive rates of biodiversity loss will become apparent.