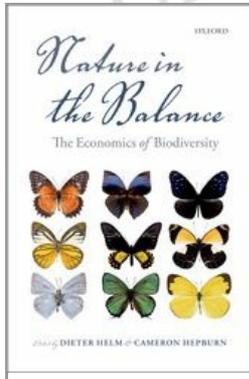


University Press Scholarship Online

Oxford Scholarship Online



Nature in the Balance: The Economics of Biodiversity

Dieter Helm and Cameron Hepburn

Print publication date: 2014

Print ISBN-13: 9780199676880

Published to Oxford Scholarship Online: January 2014

DOI: 10.1093/acprof:oso/9780199676880.001.0001

Biodiversity: Its Meanings, Roles, and Status

Georgina M. Mace

DOI:10.1093/acprof:oso/9780199676880.003.0003

[+] Abstract and Keywords

This chapter reviews biodiversity science concepts that lead to both definitions and metrics for tracking change. Beyond its general meaning, the term “biodiversity” is now common in a wide range of situations, from ecology, through conservation biology, nature conservation, environmental sciences, and environmental policy. Common approaches to measuring biodiversity are outlined and its roles, state, and trends described in way that is relevant for economics. There are many perceptions of what biodiversity includes and how to measure changes over time and space. It is argued that the starting point for economic valuation must come from accounting properly for the benefits that flow from biodiversity. Included are the general categories of intrinsic and extrinsic values, ecosystem services, heritage, adaptability, and resilience, and relevant components and metrics of biodiversity for each of these are indicated, and areas where there are significant gaps in knowledge and information identified.

Keywords: biodiversity, environmental policy, intrinsic values, extrinsic values, ecosystem services, heritage, adaptability, resilience

3.1 Introduction

A concern for nature and the conservation of the natural world trace back over centuries, but the term 'biodiversity' and some of the concepts it encapsulates are relatively new, tracing back to discussions in the US in the mid-1980s (Wilson, 1988). The word is simply a compression of the two-word term 'biological diversity', meaning essentially the variety of life (Reaka-Kudla et al., 1996). Numerous recent analyses have documented the state of, and trends in, biodiversity, and all conclude that while our knowledge is far from complete, global biodiversity is spectacular, extensive, and widely appreciated. To very many people the rich diversity of life on Earth is the defining feature of our planet. Yet, at the same time, biodiversity is in decline everywhere, largely as a result of a growing human population and the demands for land and resources that result. Concern about the loss of biodiversity also has a long history, but in its recent form traces back to the Convention on Biological Diversity signed in Rio de Janeiro in 1992, from which many concepts in turn have their origins in the Brundtland Report (1987). Pearce and Moran (1994) examined the economics of biodiversity just after the Rio conference. They spelled out clearly how failures to capture the economic values of biodiversity result in economic incentives being stacked against biodiversity conservation and in favour of activities that deplete biological resources. Since then, the same patterns have been observed repeatedly and, if anything, matters have deteriorated further. Biodiversity is not included in economic accounts, because it is a public good, its values are hard to estimate, and impacts of loss are often dispersed or remote from the causal processes. In this chapter I review the growing understanding of what biodiversity is and what it does for people (p.36) and the rest of life on Earth. I use this to draw some conclusions about how biodiversity might best be reflected in economic analysis.

3.2 What is Biodiversity?

Beyond its general meaning reflecting the variety of life on Earth, the term 'biodiversity' is now common in a wide range of situations, from ecology, through conservation biology, nature conservation, environmental sciences, and environmental policy. It is used to mean many different things, usually centred on the variety of species in a location (DeLong, 1996), but it can mean all of life on Earth or sometimes, more symbolically, it is perceived to represent wilderness, wild nature, or even natural heritage more broadly, sometimes even including human history and artefacts (Fischer and Young, 2007). In this chapter I will outline common approaches to measuring biodiversity, then describe its roles, state, and trends—and in a way that is relevant for economics. There are many other comprehensive discussions of the definitions of biodiversity dealing with the range of theories and concepts involved (Gaston, 1996; Maclaurin and Sterelny, 2008; Faith, 2013), or with approaches to its measurement (Magurran, 2003).

Biodiversity describes variation among units of life, but the units of biodiversity are themselves many and varied. They include species, genes, populations, communities, biomes, and ecosystems. In this list, genetic diversity is the most fundamental unit, but species richness is used most often. Species are on the whole objective units on which

evolutionary pressures act, and they share a common genetic history packaged up into functioning organisms that have evolved, adapted, and interbred in a shared environment. Species lists are relatively straightforward to compile, and resonate with public and specialist interest in natural history. In many ways, therefore, species are the natural units with which to measure biodiversity. Some problems arise because species concepts are variable and fluid (Hey, 2000), they may not work well for microorganisms (Fraser et al., 2009), and can lead to lists containing different numbers of species, with different distributions, depending on the species concepts used (Agapow et al., 2004; Mace and Purvis, 2008; Maclaurin and Sterelny, 2008); but in practice species are practical, biologically meaningful, and widely understood. On its own, however, the species level is inadequate for biodiversity assessment because other biological dimensions vary systematically in ways that are important for biodiversity form and function.

Genetic variation that exists within and between species and populations represents the raw material for structure, form, and function. It is changes in the genotypes (the genetic make-up of an organism) resulting from natural (p.37) selection acting on genetic variation that lead to the variation in phenotypes (the physical characteristics of an organism) observed in the natural world. Many will argue that the fundamental unit for biological diversity is therefore genetic variation which further enhances the adaptive capacity of living systems (Mace and Purvis, 2008). After discounting genetic diversity shared among species via a common evolutionary history, the entire suite of unique diversity reflected in a phylogenetic tree is the best representation of the overall diversity of those elements (species or populations) represented at the end of the branches of the tree (Vane-Wright et al., 1991). The metric, phylogenetic diversity (Faith, 1992) is a surrogate for disparity or character diversity, and for information content more generally. Character diversity seems likely to be more important for ecosystem function than simple species richness, so maximizing the character diversity conserved has obvious value and can be used for efficient conservation planning.

Populations and communities are significant units below the species level. This is where ecological and evolutionary processes mostly act. Environmental and species interactions within populations and communities comprise a rich and complex suite of dynamics which have a large influence on future abundance and distribution of populations, and hence of species. These interactions, both biotic (involving other organisms) and abiotic (involving the physical environment), drive both the functioning of ecosystems and the fate of species. Some have argued, therefore, that population declines, biomass, and community change are more responsive measures of biodiversity change than species-level metrics, have a greater relevance to ecosystem functions and services, and should take precedence over species extinction rates for monitoring biodiversity change (Hughes et al., 1997; Balmford et al., 2003).

In practice, any effort at biodiversity measurement is faced with enormous problems due to gaps and biases in the information available. Probably less than 10 per cent of all the species on Earth have been described and named, and what is known is strongly biased

towards vertebrates, terrestrial, and temperate areas. Some of the most numerous and diverse taxa, such as the invertebrates and fungi, are extremely poorly studied, and estimates of the total number of species are still very uncertain (Costello et al., 2013).

Given the difficulty of identifying, counting, and classifying species, studies are increasingly replacing taxonomic classifications with analyses based on units that reflect structural and functional groupings. For example, estimating the abundance of trees versus crops is relatively straightforward compared with counting all the component species in an area of forest versus farmland, and can provide a practical means to measure structural diversity in a landscape and its change over time. Functional groups of organisms also allow extrapolations to ecosystem functioning—for example, examining trends in the distribution of decomposers versus consumers, or plants with relatively large versus small leaf areas, might represent high-turnover (p.38) or high-productivity areas, respectively. Other functional groupings might represent the habits of different species and potentially their vulnerability to, or impact upon, people. For example, without knowing all the species individually, a biological community can be examined to measure the biomass of predators compared to herbivores, or abundance of species that are good invaders compared to species that are strong competitors. These kinds of classifications of biodiversity based on structural and functional traits are gaining popularity because they are comparatively tractable and allow extrapolations even with limited data. Moreover, certain trait classifications allow for models and maps to be developed that are useful for assessing biological community functions (Lavorel and Garnier, 2002), modelling responses to anthropogenic pressures (Purves et al., 2013) and with Earth system models (Kattge et al., 2011), especially for the interactions between the biosphere and the climate system (De Deyn et al., 2008). They are also the norm for assessing the diversity of microorganisms where the usual concepts for species, populations, and even individuals break down. Increasingly, as the functional roles of species and ecosystems take on greater significance in arguments for conservation, traits and functions may start to eclipse the need for comprehensive identification of species, although on their own such measures may miss important diversity elements. For example, the definition of traits is often subjective or idiosyncratic, and trait diversity does not then represent phylogenetic diversity.

Finally, to avoid the difficulties of enumerating species or groups of species, some recent assessments simply consider the status of geographically defined areas such as biomes, habitats, or ecosystems. These are all different approaches to classifying distinctive areas of land or sea, distinguished by the dominant biota as well as the underlying physical environment and biogeographical history. WWF has defined over 800 'ecoregions' worldwide. It defines an ecoregion as 'a large unit of land or water containing a geographically distinct assemblage of species, natural communities, and environmental conditions'. The ecoregions are mapped and species lists are compiled for them (Olson et al., 2001), so they provide a practical unit for global analysis of the extent of pressures and environmental change affecting areas with different amounts of species-level biodiversity. Each ecoregion is unique, but they are further classified into twenty-six major habitat types, sometimes called biomes. These describe different areas of the

world that share similar environmental conditions, habitat structure, and patterns of biological complexity, and contain similar communities and species adaptations. For example, two biomes are the Tropical and sub-tropical moist broadleaf forests, and Deserts and xeric shrublands. Biomes are practical units for assessing broad patterns of biodiversity change globally (Lindenmayer et al., 2012). Further, in order to represent the unique fauna and flora of the world's continents and ocean basins, each major habitat type is further subdivided (**p.39**) into seven biogeographic realms (Afrotropical, Australasia, Indo-Malayan, Nearctic, Neotropical, Oceania, Palearctic). Analyses can then be undertaken across major biogeographical zones, across major habitat types, or both, and this approach has been effective for assessing status and trends in poorly studied groups of plants and animals that would not otherwise be represented, especially non-vertebrates.

Ecoregion- and biome-based analyses provide information on the composition and diversity in different areas, but alone these are not enough to inform about biodiversity processes. Processes are both a cause and consequence of biodiversity in a particular location. Ecosystems are structured in many ways, reflecting history, process, and function. On its own, biodiversity is an outcome of physical and biological processes that have tended over time, and in the absence of major perturbations, to increase diversity. Ecological and evolutionary processes, playing out on a biogeographical stage, generate the variety and composition to be found in any one place. In recent times the major agent of large-scale perturbations has been the growing size, distribution, and impact of people on the Earth. Recent impacts (over decades to centuries) have resulted in rates of biodiversity loss orders of magnitude higher than average rates in pre-human times, that approach rates seen in the most dramatic mass extinctions of the palaeontological past (Barnosky et al., 2011). However, different components of biodiversity are being lost at different rates; changing composition and loss of extent and biomass in major biomes are now much more marked than simple loss of diversity (Pereira et al., 2012). Modelling approaches that link patterns in the turnover of biological richness to spatial landscape units as a means to assess biological change more generally are now being developed and used, building on the growing availability of species records and tools for spatial mapping of the landscape (Ferrier et al. 2004). Such approaches provide useful trend information for both changes in biodiversity pattern and process, though the link to recognizable biodiversity units is lost.

Different disciplines favour different measures of biodiversity. Ecologists tend to think about biodiversity in terms of the forms and functions of organisms in a place, especially in a community or an ecosystem, because it is the structuring of varieties in space and time that leads to functions and dynamics that they seek to understand. Evolutionary biologists similarly think about the dynamics, but with an increasing focus on the historical or inherited variation, and therefore the genetic and phylogenetic attributes. Conservation biologists are sometimes concerned with function and process, as they should be, but often also with preservation of species or genetic diversity, seeking efficient and achievable solutions to the allocation of limited resources. For nature conservationists and wildlife managers, biodiversity often simply means the maintenance

of wild habitats and species.

(p.40) 3.3 Measuring Biodiversity

The discussion to date shows that there are very many dimensions of biodiversity (e.g. composition, function, structure). How then can all this complexity be measured, and indeed should we aim to measure it all, comprehensively or integrally? Proposals have been made to measure composition, structure, and function, independently in a nested hierarchy that incorporates each one at four levels of organization: regional landscape, community-ecosystem, population-species, and genetic (Noss, 1990). Clearly, the definition and measurement of biodiversity can then become very complicated, and can lead to requirements that greatly exceed the limited knowledge base. Even having done this, it is not clear what the result could be used for; how the different dimensions and levels should be weighted, and if it is really useful if some iconic or crucial element is lost entirely but the overall statistic shows little change. The problem of measuring biodiversity is not one that can be addressed by comprehensive suites of metrics, which quickly become too complicated, or by a single, composite metric, that attempts to capture all possible measures of interest. Despite many attempts to develop a composite measure of biodiversity, the task is doomed to failure. In almost all cases it simply confounds different metrics that represent different attributes, and the interesting and important detail is easily lost.

Because it is so impractical to think we could ever enumerate all of these measures, simple metrics, such as the number of species in a place, are most often used as indicators of biodiversity, despite their evident inadequacies. Many legal and policy instruments rely on species lists and other measurable aspects, even though these are themselves incomplete and unrepresentative. Thus, for example, the primary datasets reported by national governments tend to rely heavily on bird, butterfly, and flowering plant species recording that is largely supplied by naturalists and NGOs. Any attempt at comprehensive species monitoring faces the problem of data gaps and biases, though new coordinated databases such as the Global Biodiversity Information System (GBIF), spatial modelling approaches (Ferrier et al., 2004), the emergence of new networks such as GEOBON (Scholes et al., 2008), online efforts to integrate datasets (Jetz et al., 2012), and new sampling approaches (Baillie et al., 2008), mean that progress is now being made with available data.

It is clear that we need to design biodiversity observation and measurement systems better (Scholes et al., 2012), but this still begs the question of what the measures should be better for. Of course, the most effective approach is to define the questions about changes in biodiversity first, and then design the monitoring, measurement, and research that specifically addresses the questions at hand (Green et al., 2005; Mace and Baillie, 2007), but even this apparently focused approach may often lead to a large suite of metrics. **(p.41)** Pereira et al. (2013), for example, suggest five classes of essential biodiversity variables needed for global monitoring of biodiversity change (genetic composition, species population abundance and distribution, species traits, community composition, ecosystem structure and ecosystem function). Each of these may have

several different metrics, reflecting different places or groups of organisms, over temporal scales ranging from one year to several decades.

This section has illustrated the complex nature of biodiversity, the many different perceptions of what it involves, and the problems that arise in determining how to measure it, especially to assess change. Solutions start to flow more quickly when addressing a narrower set of issues, or better still, asking specific questions that can then focus the measurement more narrowly. In the next session I focus on biodiversity as defined by the UN Convention on Biological Diversity (CBD), and use the CBD's goals and targets in 2010 as a basis for defining biodiversity, measuring its trends, and using this information to assess the consequences of biodiversity decline for people and their welfare.

3.4 A Widely Used Definition of Biodiversity

The Convention on Biological Diversity, established in 1992, adopted a broad, inclusive, but biologically based definition that has proven useful for many purposes:

'Biological diversity' means the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems. (CBD, Article 2)

The CBD definition has several features; it makes the point that diversity can be anywhere in land, sea, or freshwater, that the diversity can be within species (so including genetic diversity), between species, and above the species level, including ecological communities. It also includes the diversity of ecosystems. This is a slightly curious level at which to observe biodiversity because ecosystems come in a very wide variety of scales and types, ranging from a single small pond to an entire ocean, or a patch of soil to an entire savannah or prairie. Ecosystems are also recognized to include both abiotic and biotic components. Biodiversity is a part of an ecosystem, and by this definition, ecosystems are part of biodiversity. In most usages where the level of organization above the species has been used it appears as habitats or biomes, usually as defined in the WWF classification (see earlier), and the variety of these can be catalogued (p.42) and monitored over time. There are two other features of the CBD definition that cause confusion. One is that it includes reference to the 'ecological complexes' of which species are part, presumably reflecting the interactions among species and community-level processes. From an ecological and evolutionary perspective this is important; ecosystem functions and processes are mostly a consequence of interaction and dynamics, not simply of the standing stock of organisms and species. Second, the CBD definition is *only* about variability. This makes it a diversity-only definition. However, in many common usages the loss of biodiversity means the loss of area, biomass, or amount, rather than the loss of variation. Thus, to report that 10 per cent of forest area was lost could not be used to mean that 10 per cent of forest diversity was lost. Mostly this means just a loss of area, and although diversity increases with area, the relationship is allometric—even a large proportional loss of habitat, such as 50 per cent, may leave more than 90 per cent of species remaining, and for small proportional losses of habitat

there will be much smaller losses of species. To look at it another way, 50 per cent of global bird species richness can be captured in just 2.5 per cent of global land area (Orme et al., 2005), and the same pattern is evident in many other species groups.

Biodiversity is not the right term to use to reflect the changing state of nature overall, which is better reported using metrics related to population size, numbers of populations and habitat extent, instead of diversity (Balmford et al., 2003). Despite these small difficulties, the CBD definition is widely used and is sufficiently inclusive to cover most needs. Most significantly, it has led to a series of policy goals and mechanisms developed by the Parties to the CBD (Table 3.1). The CBD strategic plan for 2011 to 2020 presents a coordinated set of goals and targets, which aim to embed biodiversity conservation in wider societal value systems, reduce direct pressures on biodiversity, safeguard species and ecosystems, ensure benefits from biodiversity, and support the provision of resources. There are some significant challenges in achieving these targets that will require concerted efforts from both biodiversity scientists and natural resource economists working together. For example, targets 2, 3, and 4 require reform and redesign of policies and subsidies in order to ensure sustainable flows of resources while maintaining the system within safe limits. Targets 7 and 11 call for full accounting of biodiversity considerations in production sectors, and the secure management of genetic resources.

The Aichi targets in Table 3.1 present a clear agenda for global efforts to maintain biodiversity. But there are potential conflicts among targets that will become more apparent once the good, broad intentions are translated into practical action at and below country level. At this point it will be necessary to consider in more detail what the roles of biodiversity are, when and where it matters, and what aspects are more or less easy to forgo. (p.43)

Table 3.1. Goals and targets agreed by the 10th meeting of the Parties to the Convention on Biological Diversity

Strategic goal A: Address the underlying causes of biodiversity loss	Target 1: By 2020, people are aware of the values of biodiversity and the steps they can take to conserve and use it sustainably
	Target 2: By 2020, biodiversity values are integrated into national and local development and poverty-reduction strategies and planning processes and national accounts
	Target 3: By 2020, incentives, including subsidies, harmful to biodiversity are eliminated, phased out or reformed
	Target 4: By 2020, governments, business and stakeholders have plans for sustainable production and consumption and keep the impacts of resource use within safe ecological limits

Strategic goal B: Reduce the direct pressures on biodiversity and promote sustainable use	Target 5: By 2020, the rate of loss of all natural habitats, including forests, is at least halved and where feasible brought close to zero, and degradation and fragmentation is significantly reduced
	Target 6: By 2020 all stocks managed and harvested sustainably, so that overfishing is avoided
	Target 7: By 2020 areas under agriculture, aquaculture and forestry are managed sustainably, ensuring conservation of biodiversity
	Target 8: By 2020, pollution, including from excess nutrients, has been brought to levels that are not detrimental to ecosystem function and biodiversity
	Target 9: By 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment
Strategic goal C: To improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity	Target 10: By 2015, the multiple anthropogenic pressures on coral reefs, and other vulnerable ecosystems impacted by climate change or ocean acidification are minimized, so as to maintain their integrity and functioning
	Target 11: By 2020, at least 17 per cent of terrestrial and inland water, and 10 per cent of coastal and marine areas are conserved through systems of protected areas
	Target 12: By 2020 the extinction of known threatened species has been prevented and their conservation status, particularly of those most in decline, has been improved and sustained
Strategic goal D: Enhance the benefits to all from biodiversity and ecosystem services	Target 13: By 2020, the genetic diversity of cultivated plants and farmed and domesticated animals and of wild relatives is maintained
	Target 14: By 2020, ecosystems that provide essential services, including services, are restored and safeguarded
	Target 15: By 2020, ecosystem resilience and the contribution of biodiversity to carbon stocks has been enhanced, through conservation and restoration, including restoration of at least 15 per cent of degraded ecosystems
	Target 16: By 2015, the Nagoya Protocol on Access and Benefits Sharing is in force and operational

Strategic goal E: Enhance implementation through participatory planning, knowledge management, and capacity building

Target 17: By 2015 each Party has developed, adopted as a policy instrument, and has commenced implementing an effective, participatory and updated National Biodiversity Strategy and Action Plan (NBSAP)

Target 18: By 2020, the traditional knowledge, innovations, and practices of indigenous and local communities and their customary use, are respected

Target 19: By 2020, knowledge, the science base and technologies relating to biodiversity, its values, functioning, status and trends, and the consequences of its loss, are improved, widely shared and transferred, and applied

Target 20: By 2020, the mobilization of financial resources for effectively implementing the Strategic Plan for Biodiversity 2011–2020 from all sources should increase substantially

Note: These so-called Aichi targets were agreed by over 180 nations present in Nagoya, Japan, in October 2010, to represent the Strategic Plan for Biodiversity 2011–2020.

Source: Convention on Biological Diversity, Aichi Biodiversity Targets.

(p.44)

(p.45) 3.5 Why Does Biodiversity Matter?

There are a wide range of answers to this question, which I will summarize here only very briefly as they are addressed elsewhere more fully (Faith, 2013).

3.5.1 Extrinsic and intrinsic values

It is useful to consider the values that biodiversity holds for people across a continuum, from use to non-use values (using the Total Economic Value typology). In addition, however, it is important to acknowledge that for some people their values lie outside of this spectrum of extrinsic values, and are intrinsic. Intrinsic value refers to the view held by many people that the natural world, and therefore biodiversity, merits conservation for reasons beyond any material benefits or measurable values. According to this view, the intrinsic value of nature cannot be compared with any other value set, and therefore proponents of this view not only find valuation unacceptable in principle, but also cannot countenance comparisons or priority-setting among different components of nature. Although some people consider that intrinsic values are captured through stated preferences and option values, this is contested.

Intrinsic value should not be confused with the various kinds of extrinsic, non-use, non-market values such as option, existence, and bequest values. These are difficult to estimate but dominate many people's concerns for the conservation and protection of biodiversity and ecosystems, and there are various techniques available for obtaining

relative measures of value, even if these are not very robust and impossible to tension against monetary values (see Chapter 6 by Atkinson et al.). Use values include biodiversity contributions to both direct and indirect values. Direct values are provided by biodiversity that contributes to products and processes such as for food, pharmaceuticals, and chemicals. Here there is a market, and market values can be established. Non-use values are provided by various functions and services underpinned by biodiversity, which include many public goods and assets for which markets do not exist. Examples include pollination, pest regulation, clean water, and recreational values. The use/non-use typology has been very influential, but for biodiversity it has been largely taken over in recent years by the emergence of the concepts of ecosystem service, and its increasing application in both science and policy (Millennium Ecosystem Assessment, 2005a).

3.5.2 Ecosystem services

Ecosystem services are the benefits people obtain from ecosystems. As defined by the Millennium Ecosystem Assessment (2005a), these include provisioning (**p.46**) services such as food, water, timber, and fibre; regulating services that control climate, floods, disease, wastes, and water quality; cultural services that provide recreational, aesthetic, and spiritual benefits; and supporting services such as soil formation, photosynthesis, and nutrient cycling. This classification has been revised recently to facilitate economic valuation. The main changes have been to remove supporting services as a category, since they are really fundamental ecosystem processes that underpin most other services, and to separate ecosystem functions and processes from 'final ecosystem services' which provide goods to people. The final ecosystem services are characterized in the ecosystem, but the goods which have measurable values are in the wider economy (Fisher et al., 2008; Bateman et al., 2011).

Biodiversity and ecosystem services are often bracketed together as if they are the same thing, and there is an interesting history about how the two concepts have co-evolved over the past twenty years (Lele et al., 2013). In the Millennium Ecosystem Assessment (2005b), biodiversity is presented at the core, as one foundation of all ecosystem services, but it is also described in many places as an ecosystem service itself, and as being an 'enabler' or regulator of ecosystem services (Díaz et al., 2006). At the same time, existence value and many of the non-use values of biodiversity are represented as being one significant type of cultural ecosystem service. The literature is further confused by frequent use of the phrase 'biodiversity and ecosystem services', linking the two together as if they are in some way distinct yet completely linked. None of these relationships is tenable on its own. Most ecosystem services rely on physical and chemical inputs as well as biological inputs, and many biological inputs to ecosystem services do not depend primarily on diversity. Some ecosystem services are enhanced with a reduction in biodiversity (Cardinale et al., 2012)—for example, food production, which is one of the successes of agricultural intensification. The conservation of diversity will therefore not necessarily maximize overall ecosystem service delivery, especially over short time scales.

Mace et al. (2012) present a typology for the different ways that biodiversity and ecosystem services are related. Here biodiversity can be (1) a regulator of underpinning ecosystem processes; (2) a final ecosystem service; or (3) a good that is subject to valuation. The first of these equates to the role of biodiversity in ecosystem processes and functions, which is itself an area of continuing active research and debate in ecology (Cardinale et al., 2012). The underpinning roles of biodiversity ecosystem functions and processes include biodiversity contributions to primary production, decomposition, nutrient cycling, as well as pollination and disease resistance. These roles are performed primarily by microorganisms in soil and water, and by invertebrates and plants. The second role concerns the extent to which diversity is itself of value to final ecosystem services—for example, in bioprospecting, or for crop and livestock varieties. The third relates to cultural values that come from wild nature and **(p.47)** ecosystems—primarily the enjoyment, inspiration, and aesthetic pleasures that people derive from nature, including striking diversity in, for example, coral reefs or the tropical rainforests, or from seeing rare and charismatic species. Interestingly, the types of species and the biodiversity metrics vary widely among these three levels. While the contribution to ecosystem processes is largely from plants and microorganisms, and trait diversity seems to be a key metric, the cultural values are largely from large-bodied, charismatic birds and mammal species. Here rarity and distinctiveness are important. At the level of goods, effectively the direct-use values, the fundamental metric is probably genetic diversity, essentially a source of evolutionary novelty. This three-way distinction is one way to view the complicated relationship between biodiversity and the benefits people derive from it. Understanding this has important implications for both conservation and ecosystem management (Mace et al., 2012) where different biodiversity components will have different values.

As already suggested, and as is obvious from brief reflection on landscapes that have been modified for production or for some regulating services, the diversity of genes, species, and traits is not always correlated with high ecosystem service delivery. Food production has been enhanced by breeding selectively for particular strains with low diversity that can reliably produce high yields. Grasslands managed for flood control have low diversity of species; coastal dunes rely on a few species that are able to grow extensive root systems in sand in order to protect the coastal strip from erosion. However, the same is not true of biodiversity and ecosystem function relationships. Cardinale et al. (2012) undertook a systematic review of research that has examined how biodiversity loss influences ecosystem functions, and showed that almost without exception, biodiversity in terms of genes, species, or trait diversity positively increases the efficiency with which ecosystems capture and convert energy, and decompose and recycle organic material. These are the most fundamental aspects of ecosystems, and ones on which people ultimately depend for energy and nutrients. In addition, again in most cases studied for biodiversity–ecosystem function relationships, more diversity enhances stability and resilience. In contrast, a simple meta-analysis across multiple studies showed that the relationships between biodiversity and ecosystem services are often not positive, are sometimes mixed, and are often hard to predict. This is partly because some ecosystem services depend less on biological components in the

environment, and more on physical and chemical components, and partly because for some services, efficiency is improved with low diversity. These studies emphasize the important balance to be achieved between long-term resilience supported in diverse ecosystems, compared with short-term high production achieved in low-diversity systems. This is a critical area where agricultural and biodiversity scientists need to work more closely together.

(p.48)

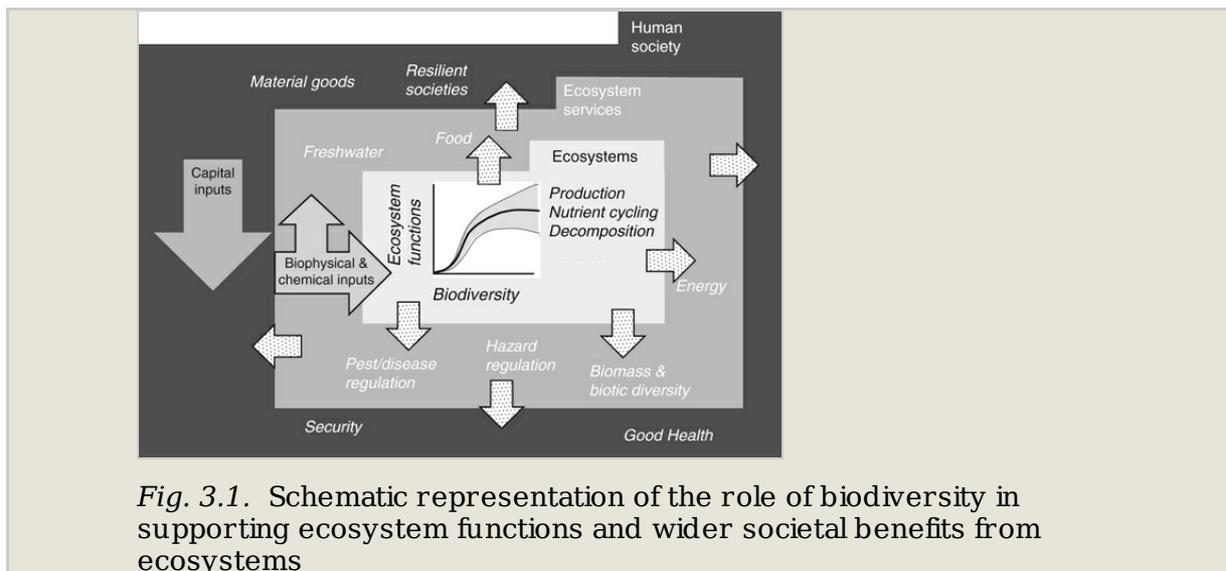


Fig. 3.1. Schematic representation of the role of biodiversity in supporting ecosystem functions and wider societal benefits from ecosystems

Figure 3.1 is a schematic representation of the way that biodiversity underpins ecosystem functions and services. It illustrates the tighter relationships between biodiversity and ecosystem functions which then underpin other services and benefits, but with increasing moderation by other factors.

Within ecosystems, fundamental processes require biotic inputs, and a positive relationship affecting biodiversity-to-ecosystem functioning is common. Ecosystem functions, such as production, nutrient cycling, and decomposition then support ecosystem services. Ecosystem services generally require other forms of biophysical inputs, as well as capital inputs for infrastructure and production systems. The biodiversity–ecosystem service relationship is therefore a little weaker than the biodiversity–ecosystem function relationship. However, resilience and security are also increased with higher levels of biodiversity. Ultimately, the core needs of human society, such as material goods, energy, security, and resilience, are underpinned in a range of ways by biodiversity, but the significance of other forms of capital inputs increases from the core areas of the diagram outwards.

There are two other key reasons to care about maintaining biodiversity, both of which contribute to ecosystem services but which also merit consideration in their own right. These are the contribution of biodiversity to heritage, adaptability, and resilience, and the significance of biodiversity in representing the complete genetic library of life. I turn now to a discussion of each of these.

(p.49) 3.5.3 Heritage, adaptability, and resilience

Current pressures from a rapidly growing human population and the intensifying demands for consumption are placing a huge strain on the world's landscapes and seascapes. At the same time, environmental change, including climate change, is resulting in species and ecosystems facing rates and intensities of change greater than at any time in their recent history. These natural systems have a range of adaptive mechanisms at their disposal. Evolution, dispersal, and adaptive radiation have allowed natural communities to develop, fill new niches, and adapt to challenges in the past. But people now dominate the Earth, natural habitats are reduced and fragmented, and dispersal may be a much more limited option than it was in the past due to the loss and fragmentation of most natural habitats. The raw material for adaptation is genetic diversity, structured in populations, distributed across species ranges in interactions with other species and different niche conditions. Without doubt, less diverse populations and communities will fare worse in the future than more diverse ones. Loss of genetic diversity at the level of individual organisms, within populations, or across species ranges, all compromise the potential for adaptation. Loss of entire species represents the loss of millions of years of adaptive evolution that can never be replaced. The genetic variability represented in life on Earth is therefore an immense genetic library that forms a source of resilience, and is our heritage and our responsibility.

It is at this point that the utilitarian needs for biodiversity come face to face with biodiversity conservation.

3.6 Conservation of Biodiversity

Concern for nature has a long history, but as currently practised became common in the twentieth and twenty-first centuries. The term conservation, as opposed to preservation, is quite recent, becoming established only in the past fifty years or so. Preservation was characteristic of colonial regimes and implied stasis, whereas conservation implies rational use (Adams, 2009). The differences between rational use and more preservationist concerns have remained in tension ever since—for example, in the debate between those who argue that conservation is most effectively based on the sustainable use of resources and those who argue for preservation, and between those who argue on behalf of conservation versus those who favour rural poverty alleviation.

The driving concern for conservation is usually expressed in terms of loss of species, but as discussed earlier, defining metrics is far from simple, and information is sparse and disorganized. Most commonly, organizations and **(p.50)** governments use measures based on information that is available, and this is often a poor sample of what exists. Until very recently, available information for conservation assessments was dominated by species lists, most often concentrating on the vertebrates, especially birds and mammals, but sometimes including butterflies, trees, or well-studied groups of flowering plants. This is very far from a comprehensive sample of all biodiversity. These groups themselves comprise much less than 10 per cent of described species, and little more than 1 per cent of the total. More recently the availability of remotely sensed information and the compilation of shared species data has led to burgeoning information on biomes,

land use, and major habitat types, that generally complement species lists (Butchart et al., 2010). These data are useful at large scales for overviews and syntheses of status and trends, but more local information appropriate to conservation planning on the ground remains patchy and incomplete, with an unhelpful bias towards better information in the least diverse areas (Collen et al., 2008).

Recent assessments have also emphasized the distinction to be drawn between biodiversity loss (generally species extinction, but some loss of genetic variation as local populations lose range extent and abundance) and biodiversity alteration (changes in abundance and community structure, range shifts) (Pereira et al., 2012).

Conservationists are concerned about biodiversity alteration because a range shift can be a local extinction, and community-level changes can have consequences for ecosystem stability and function. Biodiversity alteration is reversible (at least to a degree), while biodiversity loss (with current conservation interventions at least) is not; in principle habitats can be restored and local species populations recovered, while species extinction is for ever. To date, biodiversity alteration has been far more significant than biodiversity loss, especially at the species level, but future projections lead to the conclusion that rates of loss must increase (Pereira et al., 2010).

Conservationists often talk about the importance of conserving not only species and ecosystems, but also the evolutionary processes that formed them. This objective to retain the potential for species to respond to natural selection through evolution is likely to become more significant in future as environments and their pressures change at ever increasing rates and intensities. Conservation is therefore not simply aiming to retain all current species as if they were books in a library, but is seeking to maintain the elements from genetics, environment, and natural selection that will allow future species to persist and diversify, or analogously for new books to be written. Thus, conservation planning requires networks of interacting populations preserved in a coherent set of sites where habitat protection and species conservation are a primary goal of management.

Conservation plans directed at species or at habitats, and habitat conservation are most effectively pursued through protected areas. The World Commission on Protected Areas (WCPA) defines 'protected area' as:

(p.51) a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values. (Dudley, 2008, pp. 8–9)

Protected areas need to be well managed to be effectively conserved, and protected area systems need to be distributed across the full range of ecosystems—terrestrial, freshwater, and marine—to be fully representative. However, protected areas can become isolated and, once surrounded by other forms of land use (a forest surrounded by agriculture, for example), they will lose species. Greater isolation leads to increasing rates of degradation (Boakes et al., 2010), and reserves are increasingly becoming isolated in a matrix of intensively managed land (DeFries et al., 2005). These kinds of

concern have been matched by developments in the field of 'landscape ecology' and a growing literature on the possibility of creating connections between ecosystem fragments, along which species might move easily, developing further the ecology of linked or 'meta' populations. There is increasing interest in the idea that conservation should be pursued through sets of protected areas managed as part of ecological networks in landscape-scale conservation.

Though there is no single agreement on what it means to conserve a species—other than to keep it from becoming extinct—recent work has proposed six attributes of a successfully conserved species. The species should be: (1) demographically and ecologically self-sustaining; (2) genetically robust; (3) have healthy populations; (4) have populations distributed over the full ecological gradient of the historical range; (5) have more than one population in each of these ecological settings; and (6) be resilient to environmental change (Redford et al., 2011). This list might be regarded as the successful endpoint of species conservation, and is clearly far more than simply ensuring the survival of those species outside threatened species lists, such as those maintained by the IUCN and recorded in Red Lists.

A recent trend in conservation is to move from policies that are geared to the avoidance of undesirable outcomes (e.g. species extinction) towards plans with positive goals reflected in systematic conservation planning (Margules and Pressey, 2000), and to integrate these into wider goals for management of natural resources on land and in the sea. Thus, the CBD targets for 2020 (Table 3.1), for example, include species and habitat conservation (Targets 11 and 12) within a broader framework for the overall maintenance of biodiversity for the benefit of people and all of life on Earth.

3.7 Conclusions

Biodiversity is not a simple concept. It embraces not only a wide range of biological attributes and functions, but it also means different things to **(p.52)** different people, and its value is almost always going to be context-dependent. If economics is the science that analyses the production, distribution, and consumption of goods and services upon which wealth and welfare depends, then it will be necessary to disaggregate the components of biodiversity that influence and are influenced by people's wealth and welfare.

If biodiversity is going to be successfully conserved for the benefit of people and of all life on Earth, then its value must be fully incorporated into decision-making. Having no value, or holding arbitrary values, cannot support decision-making that will break the loop whereby economic forces continue to drive the extinction and loss of biodiversity, even though it is clear that it has value and is valued. The starting point for economic valuation must come from accounting properly for the benefits that flow from biodiversity. I listed these earlier in the general categories of intrinsic and extrinsic values, ecosystem services, heritage, adaptability, and resilience. These are overlapping categories, but different kinds of classifications are appropriate to different contexts. For example, for land-use planning and for achieving the successful integration of biodiversity conservation into the production sectors, then an approach based around the valuation of ecosystem

services is useful (Bateman et al., 2011) as long as longer-term considerations are not neglected. This is appropriate for near-term decision-making, but longer-term considerations for adaptability and resilience depend more on adequate stocks of different biodiversity components, including genetic, community, and ecosystem features. Natural capital accounting and inclusive wealth measures may then be relevant (Dasgupta, 2010) though there remain many uncertainties about thresholds and limits in these systems (Scheffer and Carpenter, 2003; Barnosky et al., 2012). Conservation, recreation, and cultural values tend to be dominated by a subset of species and habitats; rational and efficient conservation planning at national and international level should be able to incorporate both pattern and process if well designed (Pressey et al., 2007).

Identifying the important endpoints from biodiversity for well-being, resilience and adaptability will simplify and focus the identification of the relevant metrics, provide means for more accurate valuation, and should, in time, support the conservation of biodiversity in all its important forms and functions.

References

Bibliography references:

Adams, W. M. (2009), *Against Extinction*, London, Earthscan.

Agapow, P.-M., Bininda-Emonds, O. R. P., Crandall, K. A., Gittleman, J. L., Mace, G. M., Marshall, J. C., and Purvis, A. (2004), 'The Impact of Species Concept on Biodiversity Studies', *Quarterly Review of Biology*, **79**, 161–79.

Baillie, J. E. M., Collen, B., Amin, R., Akcakaya, H. R., Butchart, S. H. M., Brummitt, N., Meagher, T. R., Ram, M., Hilton-Taylor, C., and Mace, G. M. (2008), 'Toward Monitoring Global Biodiversity', *Conservation Letters*, **1**, 18–26.

Balmford, A., Green, R. E., and Jenkins, M. (2003), 'Measuring the Changing State of Nature', *Trends in Ecology and Evolution*, **18**, 326–30.

Barnosky, A. D., Hadly, E. A., Bascompte, J., Berlow, E. L., Brown, J. H., Fortelius, M., Getz, W. M., Harte, J., Hastings, A., Marquet, P. A., Martinez, N. D., Mooers, A., Roopnarine, P., Vermeij, G., Williams, J. W., Gillespie, R., Kitzes, J., Marshall, C., Matzke, N., Mindell, D. P., Revilla, E., and Smith, A. B. (2012), 'Approaching a State Shift in Earth's Biosphere', *Nature*, **486**, 52–8.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., and Ferrer, E. A. (2011), 'Has the Earth's Sixth Mass Extinction Already Arrived?', *Nature*, **471**, 51–7.

Bateman, I. J., Mace, G. M., Fezzi, C., Atkinson, G., and Turner, K. (2011), 'Economic Analysis for Ecosystem Service Assessments', *Environmental & Resource Economics*, **48**, 177–218.

Boakes, E., Mace, G. M., McGowan, P. J. K., and Fuller, R. A. (2010), 'Extreme Contagion in Global Habitat Clearance', *Proceedings of the Royal Society of London: Biological Sciences*, **277**, 1081–5.

Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., Galloway, J. N., Genovesi, P., Gregory, R. D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M. A., McRae, L., Minasyan, A., Morcillo, M. H., Oldfield, T. E. E., Pauly, D., Quader, S., Revenga, C., Sauer, J. R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S. N., Symes, A., Tierney, M., Tyrrell, T. D., Vie, J.-C., and Watson, R. (2010), 'Global Biodiversity: Indicators of Recent Declines', *Science*, **328**, 1164–8.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., and Naeem, S. (2012), 'Biodiversity Loss and its Impact on Humanity', *Nature*, **486**, 59–67.

Collen, B., Ram, M., Zamin, T., and McRae, L. (2008), 'The Tropical Biodiversity Data Gap: Addressing Disparity in Global Monitoring', *Tropical Conservation Science*, **1**, 75–88.

Costello, M. J., May, R. M., and Stork, N. E. (2013), 'Can We Name Earth's Species Before They Go Extinct?', *Science*, **339**, 413–16.

Dasgupta, P. (2010), 'Nature's Role in Sustaining Economic Development', *Philosophical Transactions of the Royal Society: Biological Sciences*, **365**, 5–11.

De Deyn, G. B., Cornelissen, J. H. C., and Bardgett, R. D. (2008), 'Plant Functional Traits and Soil Carbon Sequestration in Contrasting Biomes', *Ecology Letters*, **11**, 516–31.

DeFries, R., Hansen, A., Newton, A. C., and Hansen, M. C. (2005), 'Increasing Isolation of Protected Areas in Tropical Forests over the Past Twenty Years', *Ecological Applications*, **15**(1), 19–26.

DeLong, D. C. (1996), 'Defining Biodiversity', *Wildlife Society Bulletin*, **24**, 738–49.

Development; W.C.o.E.a. (1987), *Our Common Future*, Oxford, Oxford University Press.

Díaz, S., Fargione J., Chapin F. S. III, and Tilman, D. (2006), 'Biodiversity Loss Threatens Human Well-being', *Public Library of Science Biology*, **4**, 1300–5.

Dudley, N. (ed.) (2008), 'Guidelines for Applying Protected Areas Management Categories', Gland, Switzerland, IUCN.

Faith, D. P. (1992), 'Conservation Evaluation and Phylogenetic Diversity', *Biological Conservation*, **61**, 1–10.

Faith, D. P. (2013), 'Biodiversity', in E. N. Zalta (ed.), *The Stanford Encyclopedia of Philosophy*, Stanford University, Stanford, California.

Ferrier, S., Powell, G. V. N., Richardson, K. S., Manion, G., Overton, J. M., Allnutt, T. F., Cameron, S. E., Mantle, K., Burgess, N. D., Faith, D. P., Lamoreux, J. F., Kier, G., Hijmans, R. J., Funk, V. A., Cassis, G. A., Fisher, B. L., Flemons, P., Lees, D., Lovett, J. C., and van Rompaey, R. (2004), 'Mapping More of Terrestrial Biodiversity for Global Conservation Assessment', *Bioscience*, **54**, 1101–9.

Fischer, A., and Young, J. C. (2007), 'Understanding Mental Constructs of Biodiversity: Implications for Biodiversity Management and Conservation', *Biological Conservation*, **136**, 271–82.

Fisher, B., Turner, K., Zylstra, M., Brouwer, R., de Groot, R., Farber, S., Ferraro, P., Green, R., Hadley, D., Harlow, J., Jefferiss, P., Kirkby, C., Morling, P., Mowatt, S., Naidoo, R., Paavola, J., Strassburg B., Yu, D., and Balmford, A. (2008), 'Ecosystem Services and Economic Theory: Integration for Policy-relevant Research', *Ecological Applications*, **18**, 2050–67.

Fraser, C., Alm, E. J., Polz, M. F., Spratt, B. G., and Hanage, W. P. (2009), 'The Bacterial Species Challenge: Making Sense of Genetic and Ecological Diversity', *Science*, **323**, 741–6.

Gaston, K. J. (ed.) (1996), *Biodiversity: A Biology of Numbers and Difference*, Oxford, Blackwell Science.

Green, R. E., Balmford, A., Crane, P. R., Mace, G. M., Reynolds, J. D., and Turner, R. K. (2005), 'A Framework for Improved Monitoring of Biodiversity: Responses to the World Summit on Sustainable Development', *Conservation Biology*, **19**, 56–65.

Hey, J. (2000), *Genes, Categories and Species: The Evolutionary and Cognitive Causes of the Species Problem*, Oxford, Oxford University Press.

Hughes, J. B., Daily, G. C., and Ehrlich, P. R. (1997), 'Population Diversity: Its Extent and Extinction', *Science*, **278**, 689–92.

Jetz, W., McPherson, J. M., and Guralnick, R. P. (2012), 'Integrating Biodiversity Distribution Knowledge: Towards a Global Map of Life', *Trends in Ecology & Evolution*, **27**, 151–9.

Kattge, J., Diaz, S., Lavorel, S., Prentice, C., Leadley, P., Bonisch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., van Bodegom, P. M., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., Atkin, O., Bahn, M., Baker, T. R., Baldocchi, D., Bekker, R., Blanco, C. C., Blonder, B., Bond, W. J., Bradstock, R., Bunker, D. E., Casanoves, F., Cavender-Bares, J., Chambers, J. Q., Chapin, F. S., Chave, J., Coomes, D., Cornwell, W. K., Craine, J. M., Dobrin, B. H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W. F., Fang, J., Fernandez-Mendez, F.,

Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G. T., Fyllas, N. M., Gallagher, R. V., Green, W. A., Gutierrez, A. G., Hickler, T., Higgins, S. I., Hodgson, J. G., Jalili, A., Jansen, S., Joly, C. A., Kerkhoff, A. J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J. M. H., Kramer, K., Kuhn, I., Kurokawa, H., Laughlin, D., Lee, T. D., Leishman, M., Lens, F., Lenz, T., Lewis, S. L., Lloyd, J., Llusia, J., Louault, F., Ma, S., Mahecha, M. D., Manning, P., Massad, T., Medlyn, B. E., Messier, J., Moles, A. T., Muller, S. C., Nadrowski, K., Naeem, S., Niinemets, U., Nollert, S., Nuske, A., Ogaya, R., Oleksyn, J., Onipchenko, V. G., Onoda, Y., Ordonez, J., Overbeck, G., Ozinga, W. A., Patino, S., Paula, S., Pausas, J. G., Penuelas, J., Phillips, O. L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negre, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J. F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S. J., Yguel, B., Zaehle, S., Zanne, A. E., and Wirth, C. (2011), 'TRY: A Global Database of Plant Traits', *Global Change Biology*, **17**, 2905–35.

Lavorel, S., and Garnier, E. (2002), 'Predicting Changes in Community Composition and Ecosystem Functioning from Plant Traits: Revisiting the Holy Grail', *Functional Ecology*, **16**, 545–56.

Lele, S., Springate-Baginski, O., Lakerveld, R., Deb, D., and Dash, P. (2013), 'Ecosystem Services: Origins, Contributions, Pitfalls, and Alternatives', *Conservation & Society*, **11** (in press).

Lindenmayer, D. B., Laurance, W. F., and Franklin, J. F. (2012), 'Global Decline in Large Old Trees', *Science*, **338**, 1305–6.

Mace, G. M., and Baillie, J. E. M. (2007), 'The 2010 Biodiversity Indicators: Challenges for Science and Policy', 1st European Congress of Conservation Biology, 1406–13.

Mace, G. M., and Purvis, A. (2008), 'Evolutionary Biology and Practical Conservation: Bridging a Widening Gap', *Molecular Ecology*, **17**, 9–19.

Mace, G. M., Norris, K., and Fitter, A. H. (2012), 'Biodiversity and Ecosystem Services: A Multilayered Relationship', *Trends in Ecology & Evolution*, **27**, 19–26.

Maclaurin, J., and Sterelny, K. (2008), *What is Biodiversity?*, Chicago and London, University of Chicago Press.

Magurran, A. E. (2003), *Measuring Biological Diversity*, New York, Wiley-Blackwell.

Margules, C. R., and Pressey, R. L. (2000), 'Systematic Conservation Planning', *Nature*, **405**, 243–53.

Millennium Ecosystem Assessment (2005a), 'Ecosystems and Human Well-being: Synthesis', Washington DC, World Resources Institute.

Millennium Ecosystem Assessment (2005b), 'Ecosystems and Human Wellbeing:

Biodiversity Synthesis', Washington DC, World Resources Institute.

Noss, R. F. (1990), 'Indicators for Monitoring Biodiversity: A Hierarchical Approach', *Conservation Biology*, **4**, 355–64.

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., and Kassem, K. R. (2001), 'Terrestrial Ecoregions of the World: A New Map of Life on Earth', *Bioscience*, **51**, 933–8.

Orme, C. D. L., Davies R. G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V. A., Webster, A. J., Ding, T.-S., Rasmussen, P. C., Ridgely, R. S., Stattersfield, A. J., Bennett, P. M., Blackburn, T. M., Gaston, K. J., and Owens, I. P. F. (2005), 'Global Hotspots of Species Richness are not Congruent with Endemism or Threat', *Nature*, **436**, 1016–9.

Pearce, D., and Moran, D. (1994), *The Economic Value of Biodiversity*, London, Routledge.

Pereira, H. M., Ferrier, S., Walters, M., Geller, G. N., Jongman, R. H. G., Scholes, R. J., Bruford, M. W., Brummitt, N., Butchart, S. H. M., Cardoso, A. C., Coops, N. C., Dulloo, E., Faith, D. P., Freyhof, J., Gregory, R. D., Heip, C., Höft, R., Hurtt, G., Jetz, W., Karp, D. S., McGeoch, M. A., Obura, D., Onoda, Y., Pettorelli, N., Reyers, B., Sayre, R., Scharlemann, J. P. W., Stuart, S. N., Turak, E., Walpole, M., and Wegmann, M. (2013), 'Essential Biodiversity Variables', *Science*, **339**, 277–8.

Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P. W., Fernandez-Manjarrés, J. F., Araújo, M. B., Balvanera, P., Biggs, R., Cheung, W. W. L., Chini, L., Cooper, H. D., Gilman, E. L., Guénette, S., Hurtt, G. C., Huntington, H. P., Mace, G. M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R. J., Sumaila, U. R., and Walpole, M. (2010), 'Scenarios for Global Biodiversity in the 21st Century', *Science*, **330**, 1496.

Pereira, H. M., Navarro, L. M., and Martins, I. S. (2012), 'Global Biodiversity Change: The Bad, the Good, and the Unknown', in A. Gadgil and D. M. Liverman (eds), *Annual Review of Environment and Resources*, **37**, 25–50.

Pressey, R. L., Cabeza, M., Watts, M. E., Cowling, R. M., and Wilson, K. A. (2007), 'Conservation Planning in a Changing World', *Trends in Ecology & Evolution*, **22**, 583–92.

Purves, D., Scharlemann, J. P. W., Harfoot, M., Newbold, T., Tittensor, D. P., Hutton, J., and Emmott, S. (2013), 'Ecosystems: Time to Model All Life on Earth', *Nature*, **493**, 295–7.

Reaka-Kudla, M. L., Wilson, D. E., Wilson, E. O., and Peter, F. M. (eds) (1996), *Biodiversity II: Understanding and Protecting Our Biological Resources*, National Academy of Sciences.

Redford, K. H., Amato, G., Baillie, J., Beldomenico, P., Bennett, E. L., Clum, N., Cook, R., Fonseca, G., Hedges, S., Launay, F., Lieberman, S., Mace, G. M., Murayama, A., Putnam, A., Robinson, J. G., Rosenbaum, H., Sanderson, E. W., Stuart, S. N., Thomas, P., and Thorbjarnarson, J. (2011), 'What Does it Mean to Successfully Conserve a (Vertebrate) Species?', *Bioscience*, **61**(1), 39–48.

Scheffer, M., and Carpenter, S. R. (2003), 'Catastrophic Regime Shifts in Ecosystems: Linking Theory to Observation', *Trends in Ecology & Evolution*, **18**, 648–56.

Scholes, R. J., Mace, G. M., Turner, W., Geller, G. N., Jürgens, N., Larigauderie, A., Muchoney, D., Walther, B. A., and Mooney, H. A. (2008), 'Toward a Global Biodiversity Observing System', *Science*, **321**, 1044–5.

Scholes, R. J., Walters, M., Turak, E., Saarenmaa, H., Heip, C. H. R., Tuama, É. Ó., Faith, D. P., Mooney, H. A., Ferrier, S., Jongman, R. H. G., Harrison, I. J., Yahara, T., Pereira, H. M., Larigauderie, A., and Geller, G. (2012), 'Building a Global Observing System for Biodiversity', *Current Opinion in Environmental Sustainability*, **4**, 139–46.

Vane-Wright, R. I., Humphries, C. J., and Williams, P. H. (1991), 'What to Protect: Systematics and the Agony of Choice', *Biological Conservation*, **55**, 235–54.

Wilson, E. (ed.) (1988), *Biodiversity*, Washington DC, National Academy Press.



Access brought to you by: University College London