Biodiversity and ecosystem services: a multilayered relationship

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The relationship between biodiversity and the rapidly expanding research and policy field of ecosystem services is confused and is damaging efforts to create coherent policy. Using the widely accepted Convention on Biological Diversity definition of biodiversity and work for the UK National Ecosystem Assessment we show that biodiversity has key roles at all levels of the ecosystem service hierarchy: as a regulator of underpinning ecosystem processes, as a final ecosystem service and as a good that is subject to valuation, whether economic or otherwise. Ecosystem science and practice has not yet absorbed the lessons of this complex relationship, which suggests an urgent need to develop the interdisciplinary science of ecosystem management bringing together ecologists, conservation biologists, resource economists and others.

Biodiversity in ecosystem assessment

Interest in ecosystem assessments (see Glossary) has been growing from both scientific and policy perspectives. The Millennium Ecosystem Assessment (MA) [1] clarified the many kinds of benefit that humans derive from ecosystems, and promoted the term 'ecosystem services' to describe them. At a global level, the MA documented that over 60% of ecosystem services were deteriorating or already overused [1]. Recent emphasis has been towards regional and national ecosystem assessments, developing methods for economic valuation and tools to support decision making. However, biodiversity is included in ecosystem assessments in very different ways. In some cases, the two terms (biodiversity and ecosystem services) are used almost synonymously, implying that they are effectively the same thing and that if ecosystem services are managed well, biodiversity will be retained and vice versa. At the other extreme, biodiversity is itself sometimes regarded as an ecosystem service, and the maintenance of wild species (especially those of conservation concern) is treated as one of the things that ecosystem management can and should deliver.

Because ecosystem assessments are intended to provide guidance for ecosystem management, the confusion over how to treat biodiversity is potentially a serious problem. Here, we review the issue and present a perspective based on recent experiences with ecosystem assessments in Europe [2,3] and the UK [4]. We ask both how biodiversity fits into the concept and practical application of ecosystem services and their values/benefits, and what the consequences are for biodiversity and ecosystem science, and for conservation.

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Glossary

Benefit: in this context, used as a general term to denote the many ways that human wellbeing is enhanced through the processes and functions of ecosystems via ecosystem services.
Biodiversity: 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. Defined here following the 1993 Convention on Biological Diversity (CBD) (http://www.cbd.int/convention/articles). (Note: the CBD formally defines 'Biological Diversity', which we assume to be equivalent to 'Biodiversity'.)
Ecological process: an interaction among organisms; ecological processes frequently regulate the dynamics of ecosystems and the structure and dynamics of biological communities.
Ecosystem: a dynamic complex of plant, animal and microorganism communities and their nonliving environment interacting as a functional unit. (Defined here following [1].)
Ecosystem assessment: a systematic evaluation of what is known about the status, trends and future trajectories of ecosystems focusing on the benefits that they deliver to people. In common with other global environmental assessments, an ecosystem assessment is a collective deliberative process by which experts review, analyse, and synthesise scientific knowledge in response to users' information needs relevant to key questions, uncertainties or decisions, and should be credible, legitimate and salient [58].
Ecosystem process: changes in the stocks and/or flows of materials in an ecosystem, resulting from interactions among organisms and with their physical-chemical environment.
Ecosystem service: an activity or function of an ecosystem that provides benefit (or occasionally disbenefit) to humans. Following [13] and the UK NEA [4], we distinguish 'final ecosystem services' that directly deliver welfare gains and/or losses to people through goods, from this general term that includes the whole pathway from ecological processes through final ecosystem services, goods and values to humans (Figure 1).
Evolutionary process: process leading to changes in gene frequencies in populations and ultimately potentially appearance of new species or infraspecific taxa.
Final ecosystem service: an ecosystem service that directly underpins or gives rise to a good.
Flow: transfer of materials in an ecosystem from stocks and between pools, forms or states.
Good: the objects from ecosystems that people value through experience, use or consumption, whether that value is expressed in economic, social or personal terms. Note that the use of this term here goes well beyond a narrow definition of goods simply as physical items bought and sold in markets, and includes objects that have no market price (e.g. outdoor recreation). (Defined here following the UK NEA [4].)
Stock: the amount of a material in a given pool, form or state in an ecosystem.
Value: the size of the wellbeing improvement delivered to humans through the provision of good(s).

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Defining the terms

What is biodiversity?

There are many definitions and even more measures of biodiversity. To many people, species are the fundamental unit of biodiversity, and the number of species (i.e. species richness) is the iconic measure. Species richness can be expressed in various ways to reflect relative abundance or the ecological or evolutionary relations among species [5,6]. However, for conservation and management, a more nuanced definition, reflecting variation at the genetic and ecosystem level, as well as one that includes spatial and compositional attributes, is necessary to represent important features such as function and resilience [7,8]. In practice and in less technical contexts, when asked what the 'word' biodiversity means to them, people will reflect on a wider range of different values, including notions of balance, interactions and wilderness [9]. One inclusive and widely used definition is that adopted by the Parties to the Convention on Biological Diversity (CBD): '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'.

This CBD definition has several features. It explicitly mentions variability as the key attribute, which we take to mean the extent of variation rather than implying some spatial or temporal component, and so the definition embraces many alternative diversity measures (e.g. reflecting relative abundance or phylogenetic diversity). It emphasises variability at three levels: within species (thus including genetic- and population-level measures), between species (all measures of species-level variation), and within ecosystems (thus including measures at landscape or regional levels, such as major vegetation types or biomes). It also includes the variability that arises from species being part of ecological complexes: that is, it recognises that ecological interactions are both causes and consequences of biodiversity. However, it excludes measures based solely on abundance or amount, both metrics that might be relevant for ecosystem services [10,11].

We recommend using the CBD definition because it is in common usage, has policy status and is inclusive. In fact, some biodiversity metrics of relevance to ecosystem services are not obviously reflected in it, for example compositional diversity and biomass. However, the definition can be interpreted broadly to make it operational for all ecosystem service assessments. Because the science indicates that different biodiversity metrics and components are relevant for different purposes, there seems little point in further debating a definition which is already broad and inclusive, and which is embedded in significant intergovernmental agreements that relate to the conservation of biodiversity and the management of ecosystem services.

What are ecosystem services?

Ecosystem services are the benefits that humans derive from ecosystems. In the MA, the services were classified into four categories: provisioning, regulating, cultural and supporting services [1]. The overlaps and interdependence of these categories, and the underpinning role of supporting services, have led to refinements. These refinements enable economic valuation which requires both the separation of the final ecosystem services that provide goods and values to humans from the underpinning ecological and environmental processes within ecosystems [12,13], and to draw out the crucial distinction between final ecosystem services and goods.

Interactions among biotic and abiotic components of ecosystems involve ecological and evolutionary processes, and ultimately lead to the stocks and flows that underpin the final ecosystem services (Figure 1). These are delivered by ecosystems, which are frequently managed for that purpose. Humans, however, use 'good(s)' that are derived from and depend on those final ecosystem services but which almost always require additional inputs. For example, primary production (an ecosystem process) is necessary for there to be a wheat crop (a final service) but the good, which may be flour, requires many other inputs (cultivation, harvesting, transport, preparation) before it can be consumed. Similarly, an ecosystem might be managed to grow trees (a final ecosystem service), which can be used for a variety of different goods such as timber, fuel wood, carbon storage or recreation. The value to humans of these goods depends on both the context and the added inputs [12,14]. Recognising final ecosystem services as the ecosystem features that lead directly to goods and values enables spatial analyses of alternative ecosystem management regimes that can be mapped along with their economic costs and benefits [14].

Ecosystems therefore represent a branching network that starts with fundamental ecological and evolutionary processes and leads through final ecosystem services to the ecosystem components and outputs from which humans directly derive goods and benefits (Figure 1). Typically, the focus for environmental and habitat management is the final ecosystem services rather than either the underpinning processes or the goods.

How does biodiversity fit into the concept of ecosystem services?

The preceding sections have demonstrated that both biodiversity and ecosystem services are complex concepts. This complexity may go some way to explaining the many ways that biodiversity has been represented in ecosystem assessments. Equating biodiversity with ecosystem services implies that managing one will automatically enhance the other [15]. Alternatively, regarding biodiversity itself as an ecosystem service reflects an intrinsic value for biodiversity, whereby organisms have value that is by definition unquantifiable and therefore nontransactable. In practice, most people intuitively assign very different values to different groups of organisms, so that when biodiversity itself is seen as a service, it is particular groups, often charismatic ones, whose conservation is sought. Nevertheless, biodiversity has existence value to many people who wish it to continue to be there, irrespective of any direct experiences or benefits they derive from it.

These two approaches can be categorised as an 'ecosystem services perspective' (biodiversity and ecosystem services are the same thing) and a 'conservation perspective' (biodiversity is an ecosystem service). In the latter approach, all ecosystem services are measured irrespective of the way that biodiversity contributes to them and the

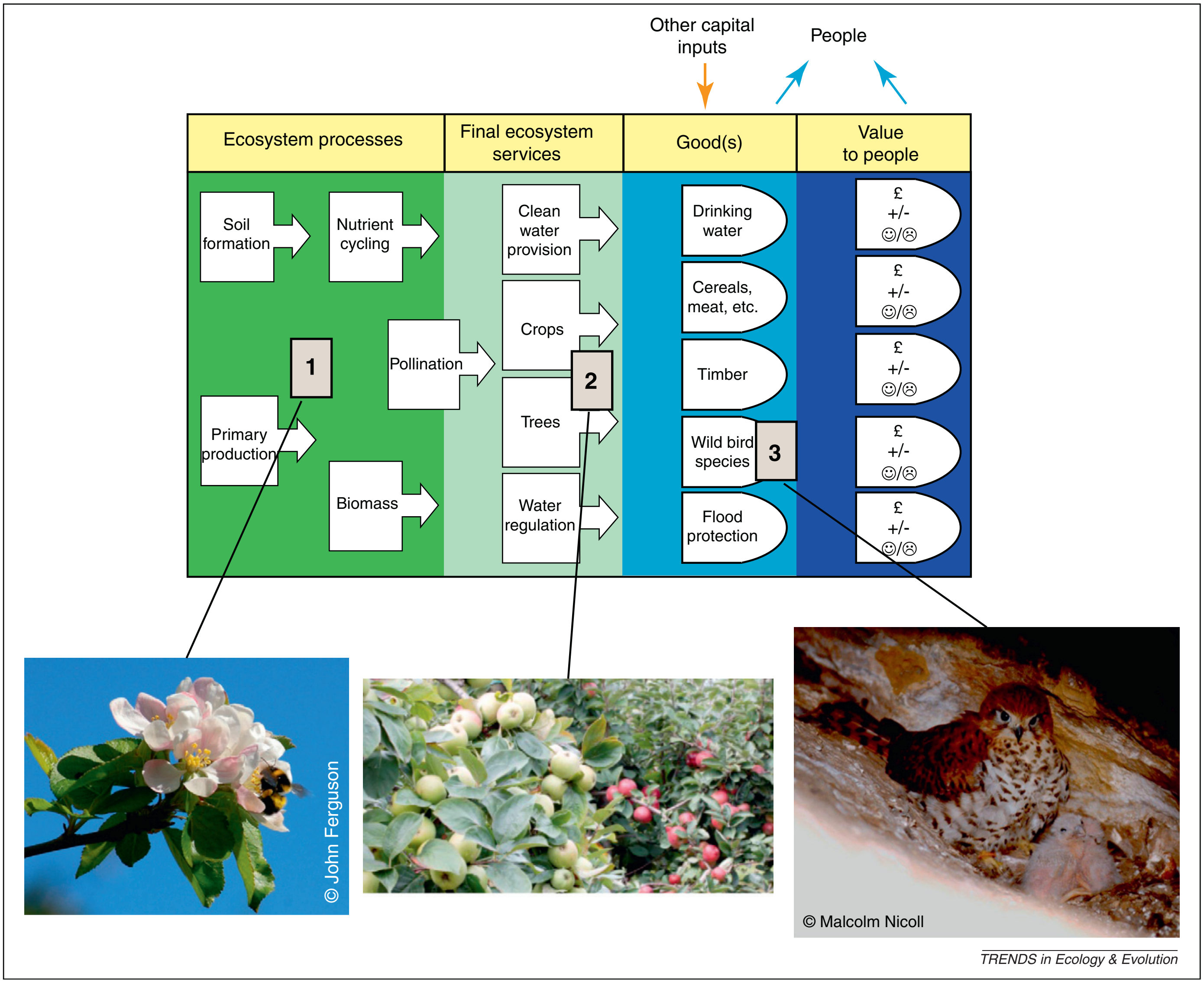

Figure 1. Schematic diagram of a selection of ecosystem processes and services that illustrates how ecosystem processes are linked to final ecosystem services and the goods and values they generate for people. The final ecosystem services are the outcomes from ecosystems that directly lead to good(s) that are valued by people. The full value is not only from the ecosystem but depends on the addition of inputs from society (other capital inputs) and the value is often context dependent. The final value of the good(s) is therefore attributable to both the ecosystem and human inputs. Values might be monetary (£), quantitative and nonmonetary (1/+) and/or qualitative (☺☹). Biodiversity might have a role as: **(1)** a regulator of ecosystem processes (e.g. a bee pollinator); **(2)** a final ecosystem service (e.g. cultivated apples), or **(3)** a good that has value of its own (e.g. Mauritius kestrel). Images reproduced, with permission, from John Ferguson (bee pollinator) and Malcolm Nicoll (kestrel). Diagram derived from [4,12].

conservation of species is considered alongside and potentially in opposition to other benefits, such as flood regulation, carbon sequestration or agricultural productivity on the same parcel of land [16,17]. However, neither approach is wholly consistent with ecological science. Under the 'ecosystem services perspective' a functional role is implicit but in practice it is not represented other than by some simple measurement of ecosystem service flows. Also, this perspective does not reflect the values of biodiversity that are not based on its functional role in ecosystem processes. The 'conservation perspective' ignores the role of biodiversity in underpinning ecosystem processes, and usually focuses on a subset of biodiversity that includes charismatic species and those on threatened species lists. Confusion arises because biodiversity is a single word that is used for a complex set of measures and concepts, and because it does genuinely play multiple roles in ecosystem processes and services. So, how should these relations be viewed?

The multilayered relationship

Ecosystems are complexes where biotic and abiotic components interact [18]. Those interactions, including all the biodiversity components, determine the quantity, quality and reliability of ecosystem services. As the physical, chemical and biological features and components of ecosystems change, so will the processes and, consequently, the services. The complexity in these interactions is poorly understood even in simple ecosystems and, even worse, it is not yet possible to predict how these processes and interactions will change under complex and global stressors, such as climate change.

Despite our poor understanding of the physical and biological processes underpinning ecosystem services, they cannot be ignored in ecosystem management because the processes themselves – and not just the services for which ecosystems are managed – are vulnerable to change, and have their own characteristic rates and thresholds. Given that biotic–abiotic interactions largely occur at the level of ecological processes, rather than in the delivery of ecosystem services, the impacts of environmental change on ecosystem services might often be nonlinear, hard to predict and/or irreversible[19]

We propose that the confusion over the role that biodiversity plays in ecosystem services can be resolved by recognising that different relations exist at the various levels of the ecosystem service hierarchy numbered as shown in Figure 1. Biodiversity can be a regulator of fundamental ecosystem processes, a final ecosystem service itself, or a good. These distinctions are set out below and in Table 1.

(i) *Biodiversity as a regulator of ecosystem processes*: biodiversity is a factor controlling the ecosystem processes that underpin ecosystem services. For example, the dynamics of many soil nutrient cycles are determined by the composition of biological communities in the soil [20,21], resilience to pests and environmental change is also increased in more diverse biological communities [22] and, in many contexts, higher biodiversity is associated with increased ecosystem functions [23–27]. Therefore, the biological composition of ecosystems, measured as biodiversity, has a key role in ecosystem service delivery [28]. Ecosystem processes generally depend on the right combinations of certain biotic and/or abiotic components being present in an ecosystem. However, sometimes what matters is not only the presence of a particular component or its amount but also the variety or diversity of types (i.e. the biodiversity). These roles of biodiversity are closest to the ecosystems services approach outlined above but here the specific biodiversity–process interaction is recognised so that although the functional diversity of soil organisms might be important for ecosystem processes, bird species richness may not be.

(ii) *Biodiversity as a final ecosystem service*: biological diversity at the level of genes and species contributes directly to some goods and their values. For example, the potential value of wild medicines and the potential benefits from bioprospecting increase directly with the number and evolutionary distinctiveness of species. Genetic diversity of wild crop relatives is important for the improvement of crop strains, and the same will be true for biofuel crops and livestock. Therefore, both genetic diversity (or surrogates, such as wild species richness or phylogenetic diversity) and wild species diversity (implicitly including genetic and phylogenetic diversity) are final ecosystem services directly contributing to goods (Figure 1). In the case of these final ecosystem services, ecosystems could be specifically managed for the diversity of the desired biodiversity components.

Table 1. A preliminary assessment of the nature, management priorities and implications of biodiversity playing its three different roles in ecosystem services

Biodiversity acting as:		
A regulator of ecosystem processes	**A final ecosystem service**	**A good**
What kind of organism?		
Microorganisms: decomposition and nutrient cycling Primary producers (plants on land and in water): biomass production and carbon capture Top predators, parasites: population regulation Pollinators: stability of nonagricultural ecosystems	Wild crop and livestock relatives: ensuring genetic diversity to provide resilience of food production systems against future climate change/diseases and so on Organisms with secondary compounds: potential for commercial exploitation, for example novel pharmaceuticals Pollinators: security of many food crops	Large vertebrates, especially birds, mammals and conspicuous flowering plants: recognised for their charisma and aesthetic appeal Flagship or umbrella species: providing protection for wider communities and habitats Phylogenetically distinct species: maintaining evolutionary diversity Endangered species: maintaining taxonomic diversity
What kind of ecosystem management?		
Inputs need to be managed to achieve productivity and maintain nutrient cycles and decomposition but with the risk of reducing the ability of the system to deliver other services Importance of maintaining diversity for resilience, and resistance to predictable and unpredictable future environmental change	Management to maintain the necessary range of species groups and habitat or landscape types; has had, and will continue to have, profound implications for management practices; often potential conflicts, especially if the maximising of one service is a management goal	Directed and often very focused management for enhancing viability of individual target species or species groups
How do humans benefit?		
Healthy fertile soils, clean air, clean water, disease and pest regulation, climate regulation, and food and fibre production	Enhancing genetic variability for goods such as novel pharmaceuticals, crop strains, livestock breeds and pollinators.	Cultural services, recreation, tourism, aesthetic enjoyment, inspiration and education
How important is 'diversity' compared with biomass or composition?		
For some services and over the short term, composition and biomass might be more important attributes but little is known of the functional roles of most soil organisms and there is no reason to assume a lesser role for biodiversity here than elsewhere Biodiversity provides resilience (an 'insurance' role)	Diversity within and among relevant groups of species is essential; might be possible to preserve some elements of this diversity in gene or seed banks but these are unlikely to conserve the full range of diversity	Preserving species richness is primarily about diversity

(iii) *Biodiversity as a good*: here, biodiversity itself is the object valued by humans and this role of biodiversity therefore resembles the conservation perspective outlined above. Many components of biodiversity have cultural value, including appreciation of wildlife and scenic places and spiritual, educational, religious and recreational values. Humans value places with a diversity of species, especially the more charismatic animals and plants, and retaining a full complement of wild species is important to many. Therefore, biodiversity is a good in itself with a distinct value. Ecosystems can be managed for species of conservation importance and this is often the primary goal; however, conservation management might sometimes aim to maintain ecosystems of low biodiversity, either because a target species favours conditions that do not support a diverse community or because of ecosystem attributes unrelated to biodiversity (e.g. heather moorland in the UK). One cannot therefore assume that high biodiversity is always the goal of conservation.

Implications for biodiversity and ecosystem management

Biodiversity combines with the concept of ecosystem services at all levels: it provides the support to key processes, it directly affects the delivery of some ecosystem services and it may itself be the good that is valued. The components (e.g. genes, species or traits) and attributes (e.g. amount, variability or composition) of biodiversity that are necessary or desirable to retain any specific ecosystem service will vary according to the service or good being considered, and the processes on which it depends. There is therefore a need to understand how to manage ecosystems for particular goals, which might be to ensure the maintenance of ecosystem processes (e.g. soil fertility), of final ecosystem services (e.g. crop pollination) or of specific conservation goods (e.g. saving tigers). In practice, it will be necessary to optimise management so as to achieve many of these simultaneously, recognising that diversity *per se* has a key role in the delivery of some services (e.g. pollination or biochemicals) and a minor one in others (e.g. flood prevention or carbon storage). Within the MA classification, biodiversity probably contributes more to regulating and cultural services, and to longer term resilience of ecosystem processes, and less to provisioning services, at least over the short term [29]. There is stronger evidence for biodiversity effects on ecosystem stability than on ecosystem service stocks and flows [30]. Some diversity effects might be attributable simply to composition: that is, the presence of certain key species or the correlation between species diversity and functional trait diversity [24]. The extent to which species diversity is important compared to say, biomass or structural and trait diversity, is an area of active research [29,31]. Also important is the insurance role of biodiversity: more diversity buffers systems against change [24,32] and, therefore, offers reliability for ecosystem processes and services in an uncertain future [33].

Table 1 is a preliminary overview of the different consequences of biodiversity operating at the various levels of the service hierarchy. A comprehensive assessment is beyond our scope, and is probably not possible given knowledge gaps in this area [34], but Table 1 demonstrates that not only are different services and goods involved but also different species and different conservation rationales. A major challenge for the ecosystem service framework is to incorporate this complexity into its decision-making processes.

What are the consequences for biodiversity science and conservation?

Biodiversity and ecosystem science

Biodiversity and ecosystem science already implicitly recognises the various roles of biodiversity in the ecosystem services hierarchy (Figure 1). Conservation biologists have used a range of approaches to develop the evidence base to support species conservation, which is aimed at protecting biodiversity as a 'good' that has a direct (conservation) value. Community ecologists have focused on the role of biodiversity in ecosystem processes (e.g. primary productivity) and ecosystem services (e.g. pollination or disease regulation). Given all this activity, is biodiversity science well placed to address the challenges posed by an ecosystems approach?

In broad terms, the answer is 'no'. Although the basic theory and knowledge are well founded, there is still work to be done to link community and ecosystem ecology [34] and, so far, little attention has been paid to examining the multiple ecosystem services, goods, values and benefits that are (or should be) demanded of most ecosystems. Almost any decision about the way an ecosystem is managed will involve trade-offs among services. Although some of these trade-offs are relatively well characterised, such as the way that past land-use change has increased the output of provisioning services while reducing many regulating and cultural services [35], most are rather poorly understood. Studying components of an ecosystem, such as a species of conservation concern, a pollination network or primary production, provides only a partial picture of the system.

Biodiversity is most often incorporated in ecosystem studies as a simple trophic structure to characterise the stocks and flows of biomass, energy and nutrients [36]. There is accumulating evidence that the traits of individuals and the way these vary in space and time have consequences that are propagated through ecosystems, affecting the dynamics of populations, communities and processes (e.g. nutrient cycling) [37,38]. In response to these developments, there have been recent calls for a more unified approach to biodiversity science that recognises the interactions between different levels of biological organisation within ecosystems [34].

These perspectives open up a rich array of questions on biodiversity–ecosystem function. At present, the biodiversity–ecosystem function literature largely focuses on variability at the species level [24,39] but the roles that biodiversity has in ecosystems might not be most sensitive to variability at this level. Several key questions need to be answered:

- How sensitive are ecosystem services to the type and degree of variability at different levels of biological organisation?

- What processes generate or erode this variability?
- How does this variability affect the resilience of ecosystem services to environmental change?
- What are the consequences of a focus on the stocks of ecosystem services (sometimes referred to as natural capital), as well as the flows most commonly considered in spatial assessments [14,40,41]?

These questions are inherently multidisciplinary and the answers are likely to be context dependent (i.e. ecosystem and service specific).

It is perhaps unsurprising that the biodiversity community has focused on ecosystem processes and services in which biodiversity has the dominant role and where flows of services (e.g. primary productivity, pollination, and pest and disease regulation) are more relevant than stocks [14,40,42–45]. It is perhaps also unsurprising that the biodiversity community has been less involved in other key areas, such as major biogeochemical cycles, the water cycle and biosphere–atmosphere interactions. Furthermore, humans are an important component of the system: they modify ecosystem processes and services to affect the values and benefits that they receive [46]. Despite this being recognised [47,48], there are still relatively few examples of treating humans as an integral part of the system in biodiversity or ecosystem science, even rather remarkably in studies of urban ecosystems[49]. Lastly, most ecological theory is focused within rather than across levels of biological organisation: behavioural and/or physiological ecology (individuals), and population and community ecology. Interestingly, the feedbacks between levels of organisation that are reshaping the way that communities and ecosystems are viewed, are at the interface of ecology and evolution [37,38]. It is here that predictive ecology is at its strongest because theory is based on fundamental evolutionary principles. This provides a powerful basis for developing and testing new theory that explores how the properties of populations, communities and ecosystems might emerge from the eco-evolutionary dynamics of individual organisms. These are the challenges that biodiversity science needs to address.

Biodiversity conservation

As outlined above, when viewed in the context of ecosystem services, the traditional species-based approach to conservation largely concerns biodiversity as a good which has a range of cultural values (e.g. aesthetic, recreational and existence values) (Figure 1; Table 1). Interestingly, the cultural values involved are rarely explicit in setting priorities, understanding the causes of population decline or designing remedial conservation action. There is an implicit assumption in much conservation debate that species have ‘intrinsic’ value and that there is no need to provide an explicit justification for their conservation. This apparent intrinsic value is usually applied only to charismatic taxa and lacks a clear conceptual basis [50,51]. In practice, all conservation judgements are value judgements and the values involved are human values, not properties of the organisms involved. Nevertheless, the fact that traditional species-based conservation can be embodied within an ecosystem services framework, shows that an ecosystems approach is not an alternative paradigm to current conservation but simply that current conservation is part of a bigger picture [52].

Conservation efforts have only recently begun to recognise the role of biodiversity in ecosystem services but usually only where the service delivers a good that has an easily determined economic value as, for example, in conserving the wild relatives of crop plants or the diversity of domesticated crop varieties and animal breeds that are important for food production. The first steps are being taken to apply conservation policies in relation to the role biodiversity has in ecosystem processes, such as land management practices designed to conserve insect pollinators [53]. Current conservation activities are, therefore, biased towards biodiversity as a good. A simple explanation for this is that humans are less able to recognise the role of biodiversity in their values the more indirect this role becomes. A similar bias is evident in the status and trend information available for biodiversity groups in the UK. The recent UK National Ecosystem Assessment (NEA) [4] showed that the quality of this information was highest for groups considered important for cultural values. However, the NEA also showed that there is little information on the distribution and population trends of the microorganisms, fungi, lower plants and micro-invertebrates that have key roles in the basic processes (e.g. nutrient cycling, decomposition, etc.) that are important in all ecosystems or, indeed, on the particular roles of species within these groups.

Do these biases matter? If biodiversity as a good acts as an adequate surrogate for wider biodiversity and its functional role, then they are relatively unimportant. Although the use of such indicator groups is often advocated by conservationists, the evidence base justifying this use is weak [54]. This suggests that a new strategy for conservation is required that develops conservation and management objectives around defined needs and explicit values [55], which might be anywhere on a spectrum from strictly utilitarian (e.g. to maximise carbon sequestration) to completely cultural values (e.g. to conserve a rare endemic species) [56]. These objectives are based around societal values and, although ecological science can contribute to maintaining them once they are accepted, the process of acceptance is a political and social endeavour about which there has been little experience. The conservation community needs to have a much wider role in understanding the roles of biodiversity in ecosystems and the range of values humans derive from these roles.

There is no reason why viewing biodiversity conservation in this way should threaten existing conservation priorities and activities. In fact, a broader perspective may provide additional arguments for the conservation of biodiversity beyond those on which the conservation community has traditionally relied. For example, the loss of tropical forests will not only reduce biodiversity and carbon storage but can also result in atmospheric pollution and associated reductions in human health as a direct consequence [57]. Although it would be naive to think that these additional arguments will apply in all cases, the key message to the conservation community is that viewing biodiversity in the context of ecosystem services is an opportunity rather than a threat.

Concluding remarks

'Biodiversity' is a term that has suffered from a plethora of definitions. Given that it is a complex phenomenon, we recommend accepting and using the broad inclusive definition from the CBD, which makes it straightforward to recognise the complexity of biodiversity and then to consider the ways that it is involved in ecosystem services.

Biodiversity has multiple roles in the delivery of ecosystem services, as a regulator of ecosystem processes, as a service in itself and as a good. Effective ecosystem management now, but even more in the future as pressures intensify, will require identifying and analysing all roles both for the optimisation of ecosystem service delivery and for the conservation of species, habitats and landscapes.

New approaches underpinned by ecological science will be needed for assessments to reflect the many roles that biodiversity has in ecological processes, in final ecosystem services and in the goods that humans obtain from the natural world. Conservation and ecosystem management plans have largely developed independently and tend to operate in parallel. Bringing these together will be essential as it becomes clear that most areas must be used for multiple services. A focus on the underpinning processes will be necessary to understand where there are trade-offs and synergies and how these vary with environmental change. There are important gaps in how biodiversity science is approached that need to be addressed before these potential gains can be realised. In particular, conservation biologists and ecosystem managers need to work together to ensure that multiple goals are identified and addressed; ecologists need to address ecosystem-level functions, not just the biotic components in isolation; ecologists, natural resource managers and economists need to build a stronger science for stocks and flows, and to link this work to natural capital studies; and a stronger socio-ecological science is needed to reflect the fact that ecosystems are coupled human–environment systems.

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