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Biodiversity loss and its impact on humanity

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The most unique feature of Earth is the existence of life, and the most extraordinary feature of life is its diversity. Approximately 9 million types of plants, animals, protists and fungi inhabit the Earth. So, too, do 7 billion people. Two decades ago, at the first Earth Summit, the vast majority of the world's nations declared that human actions were dismantling the Earth's ecosystems, eliminating genes, species and biological traits at an alarming rate. This observation led to the question of how such loss of biological diversity will alter the functioning of ecosystems and their ability to provide society with the goods and services needed to prosper.

In the past 20 years remarkable progress has been made towards understanding how the loss of biodiversity affects the functioning of ecosystems and thus affects society. Soon after the 1992 Earth Summit in Rio de Janeiro, interest in understanding how biodiversity loss might affect the dynamics and functioning of ecosystems, and the supply of goods and services, grew dramatically. Major international research initiatives formed; hundreds of experiments were performed in ecosystems all over the globe; new ecological theories were developed and tested against experimental results.

Here we review two decades of research that has examined how biodiversity loss influences ecosystem functions, and the impacts that this can have on the goods and services ecosystems provide (Box 1). We begin with a brief historical introduction. We then summarize the major results from research that has provided increasingly rigorous answers to the question of how and why the Earth's biological diversity influences the functioning of ecosystems. After this, we consider the closely related issue of how biodiversity provides specific ecosystem services of value to humanity. We close by considering how the next generation of biodiversity science can reduce our uncertainties and better serve policy and management initiatives.

A brief history

During the 1980s, concern about the rate at which species were being lost from ecosystems led to research showing that organisms can influence the physical formation of habitats (ecosystem engineering[1]), fluxes of elements in biogeochemical cycles (for example, ecological stoichiometry[2]), and the productivity of ecosystems (for example, via trophic cascades and keystone species[3]). Such research suggested that loss of certain life forms could substantially alter the structure and functioning of whole ecosystems.

By the 1990s, several international initiatives were focused on the more specific question of how the diversity of life forms impacts upon ecosystems. The Scientific Committee on Problems of the Environment (SCOPE) produced an influential book reviewing the state of knowledge on biodiversity and ecosystem functioning (BEF)[4]. The United Nations Environment Program commissioned the Global Biodiversity Assessment to evaluate the state of knowledge on biodiversity, including its role in ecosystem and landscape processes[5]. Building on early studies of the effects of biodiversity on ecosystem processes, DIVERSITAS, the international programme dedicated to biodiversity science, produced a global research agenda[6].

By the mid-1990s, BEF studies had manipulated the species richness of plants in laboratory and field experiments and suggested that ecosystem functions, like biomass production and nutrient cycling, respond strongly to changes in biological diversity[7–10]. Interpretation of these studies was initially controversial, and by the late 1990s BEF researchers were involved in a debate over the validity of experimental designs, the mechanisms responsible for diversity effects, and the relevance of results to non-experimental systems[11]. This controversy helped to create a decade of research that, by 2009, generated several hundred papers reporting results of >600 experiments that manipulated more than 500 types of organisms in freshwater, marine and terrestrial ecosystems[11,12].

As the field of BEF developed, a related body of research began to form an agenda for biodiversity and ecosystem services (BES) research built on the idea that ecosystems provide essential benefits to humanity[13,14]. Although BES did not evolve separately from BEF, it took a distinctly different direction. The main focus of BES was on large-scale patterns across landscapes more relevant to economic or cultural evaluation. For many BES applications, biodiversity was considered an ecosystem service in-and-of itself[15]. When biodiversity was viewed as an underlying factor driving ecosystem services, the term was often used loosely to mean the presence/absence of entire habitats or groups of organisms (for example, impact of mangrove forests on flood protection, or of all native pollinators on pollination).

The 2005 Millennium Ecosystem Assessment[16] appraised, for the first time, the condition and trends in the world's ecosystems and the services they provide, and highlighted two distinct foci of BEF and BES research. Research on BEF had developed a large body of experiments and mathematical theory describing how genetic, species and functional diversity of organisms control basic ecological processes (functions) in ecosystems (Box 1). Studies on BES were, in contrast, mostly correlative, conducted at the landscape scale and often focused on how major habitat modifications influenced 'provisioning' and 'regulating' services of ecosystems.

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BOX 1

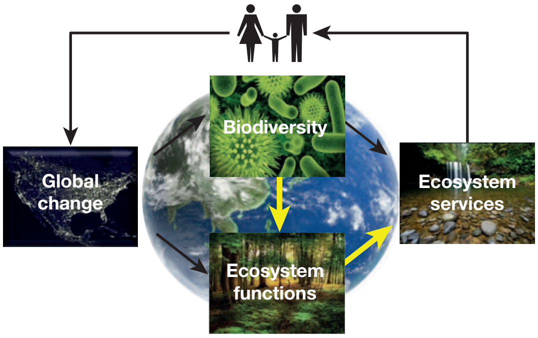
The scope of our review

In this Review we ask how biodiversity per se—that is, the variety of genes, species, or functional traits in an ecosystem—has an impact on the functioning of that ecosystem and, in turn, the services that the ecosystem provides to humanity (yellow arrows, Box 1 Fig. 1 below). This encompasses questions such as can a forest store more carbon if it has a greater variety of tree species? Can a stream clean up more pollution if it has a greater variety of microbial genotypes? Can natural enemies better control agricultural pests if they are composed of a variety of predators, parasites and pathogens?

Biodiversity is the variety of life, including variation among genes, species and functional traits. It is often measured as: richness is a measure of the number of unique life forms; evenness is a measure of the equitability among life forms; and heterogeneity is the dissimilarity among life forms.

Ecosystem functions are ecological processes that control the fluxes of energy, nutrients and organic matter through an environment. Examples include: primary production, which is the process by which plants use sunlight to convert inorganic matter into new biological tissue; nutrient cycling, which is the process by which biologically essential nutrients are captured, released and then recaptured; and decomposition, which is the process by which organic waste, such as dead plants and animals, is broken down and recycled.

Ecosystem services are the suite of benefits that ecosystems provide to humanity. Here we focus on two types of ecosystem services—provisioning and regulating. Provisioning services involve the production of renewable resources (for example, food, wood, fresh water). Regulating services are those that lessen environmental change (for example, climate regulation, pest/disease control).



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The 20th anniversary of the 1992 Earth Summit is an opportune time to review what has been learned from both fields, and to continue their synthesis towards a data-driven consensus. In the sections that follow, we summarize how biological variation per se acts as an independent variable to affect the functions and services of ecosystems.

20 years of research on BEF

In addition to the proliferation of experiments (>600 since 1990)[12], BEF research has developed a substantial body of mathematical theory[17–19], and expanded its scope to include global patterns in natural ecosystems[20–22]. More than half of all work has been published since the last consensus paper in 2005 (ref. 23), and since that time, several milestones have been crossed: the field has coalesced around a series of key findings and themes that have been fostered by the publication of 13 quantitative data syntheses[12,24–35]; many of the early scientific debates have subsided as data have amassed to resolve key controversies; a new consensus is emerging concerning the field's unanswered questions and how to address them. These milestones provide a unique opportunity to re-evaluate earlier conclusions and to identify emerging trends.

Six consensus statements

We conclude that the balance of evidence that has accrued over the last two decades justifies the following statements about how biodiversity loss has an impact on the functioning of ecosystems.

Consensus statement one

There is now unequivocal evidence that biodiversity loss reduces the efficiency by which ecological communities capture biologically essential resources, produce biomass, decompose and recycle biologically essential nutrients.

Meta-analyses published since 2005 have shown that, as a general rule, reductions in the number of genes, species and functional groups of organisms reduce the efficiency by which whole communities capture biologically essential resources (nutrients, water, light, prey), and convert those resources into biomass[12,24–28,30–35] (Fig. 1). Recent meta-analyses further suggest that plant litter diversity enhances decomposition and recycling of elements after organisms die[12], although the effects tend to be weaker than for other processes. Biodiversity effects seem to be remarkably consistent across different groups of organisms, among trophic levels and across the various ecosystems that have been studied[12,24,25,31]. This consistency indicates that there are general underlying principles that dictate how the organization of communities influences the functioning of ecosystems. There are exceptions to this statement for some ecosystems and processes[12,32,36], and these offer opportunities to explore the boundaries that constrain biodiversity effects.

Consensus statement two

There is mounting evidence that biodiversity increases the stability of ecosystem functions through time.

Numerous forms of 'stability' have been described, and there is no theoretical reason to believe that biodiversity should enhance all forms of stability[37]. But theory and data both support greater temporal stability of a community property like total biomass at higher levels of diversity. Five syntheses have summarized how diversity has an impact on variation of ecosystem functions through time[38–42], and these have

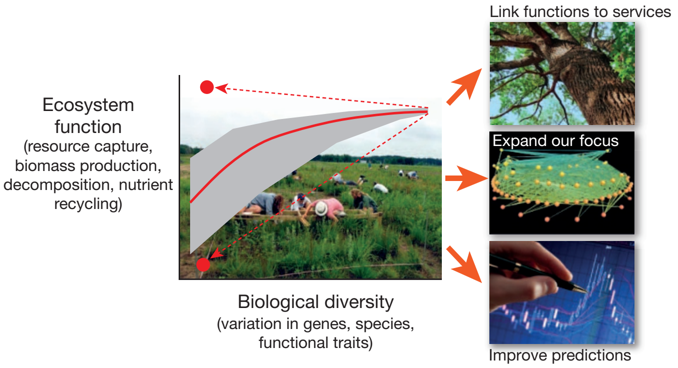


Figure 1 | The form of a typical diversity–function relationship. This conceptual diagram summarizes what we know about the shape of the biodiversity–ecosystem functioning (BEF) relationship based on summaries of several hundred experiments[12,24–35]. The red line shows the average change across all combinations of genes, species, or traits. The grey polygon represents the 95% confidence interval, whereas red dots give maximum and minimum values of the most or least productive species grown alone in monoculture (see main text about uncertainties associated with the upper bound). To improve our predictions of how diversity loss influences the goods and services of ecosystems, we must now take this experimental relationship and (1) link the ecosystem functions measured in experiments to the provisioning and regulating services of ecosystems; (2) expand the focus of research to better mimic realistic extinction scenarios and trophic structures of natural ecosystems; and (3) develop mathematical models that can scale experimental results to whole landscapes. Images from D.T., N. Martinez and Shutterstock.com; used with permission.

shown that total resource capture and biomass production are generally more stable in more diverse communities. The mechanisms by which diversity confers stability include over-yielding, statistical averaging and compensatory dynamics. Over-yielding enhances stability when mean biomass production increases with diversity more rapidly than its standard deviation. Statistical averaging occurs when random variation in the population abundances of different species reduces the variability of aggregate ecosystem variables[43]. Compensatory dynamics are driven by competitive interactions and/or differential responses to environmental fluctuations among different life forms, both of which lead to asynchrony in their environmental responses[18,44]. We have yet to quantify the relative importance of these mechanisms and the conditions under which they operate.

Consensus statement three

The impact of biodiversity on any single ecosystem process is nonlinear and saturating, such that change accelerates as biodiversity loss increases.

The form of BEF relationships in most experimental studies indicates that initial losses of biodiversity in diverse ecosystems have relatively small impacts on ecosystem functions, but increasing losses lead to accelerating rates of change[12,25,31](Fig. 1). We do not yet have quantitative estimates of the level of biodiversity at which change in ecosystem functions become significant for different processes or ecosystems, and this is an active area of research[12,31]. Although our statement is an empirical generality, some researchers question whether saturating curves are an artefact of overly simplified experiments[45]. Saturation could be imposed by the spatial homogeneity, short timescales, or limited species pools of experiments that minimize opportunities for expression of niche differences. In support of this hypothesis, select case studies suggest that as experiments run longer, saturating curves become more monotonically increasing[46]. In addition, biodiversity–ecosystem function relationships in natural ecosystems sometimes differ from saturating curves[22], and future research needs to assess when and why these differences occur.

Consensus statement four

Diverse communities are more productive because they contain key species that have a large influence on productivity, and differences in functional traits among organisms increase total resource capture.

Much of the historical controversy in BEF research involved the extent to which diversity effects are driven by single, highly productive species versus some form of 'complementarity' among species[47,48]. Research and syntheses over the past 10 years have made it clear that both the identity and the diversity of organisms jointly control the functioning of ecosystems. Quantification of the variance explained by species identity versus diversity in >200 experiments found that, on average across many ecosystems, each contributes roughly 50% to the net biodiversity effect[12]. Complementarity may represent niche partitioning or positive species interactions[48], but the extent to which these mechanisms broadly contribute to ecosystem functioning has yet to be confirmed[12,49].

Consensus statement five

Loss of diversity across trophic levels has the potential to influence ecosystem functions even more strongly than diversity loss within trophic levels.

Much work has shown that food web interactions are key mediators of ecosystem functioning, and that loss of higher consumers can cascade through a food web to influence plant biomass[50,51]. Loss of one or a few top predator species can reduce plant biomass by at least as much[52] as does the transformation of a diverse plant assemblage into a species monoculture[12]. Loss of consumers can also alter vegetation structure, fire frequency, and even disease epidemics in a range of ecosystems[51].

Consensus statement six

Functional traits of organisms have large impacts on the magnitude of ecosystem functions, which give rise to a wide range of plausible impacts of extinction on ecosystem function.

The extent to which ecological functions change after extinction depends greatly on which biological traits are extirpated[23,53]. Depending on the traits lost, scenarios of change vary from large reductions in ecological processes (for example, if the surviving life form is highly unproductive) to the opposite where the efficiency, productivity and stability of an ecosystem increase. To illustrate this latter possibility, a summary of BEF experiments showed that 65% of 1,019 experimental plots containing plant polycultures produced less biomass than that achieved by their most productive species grown alone[27]. This result has been questioned on statistical grounds[54], and because the short duration of experiments may limit the opportunity for diverse polycultures to out-perform productive species[27]. Even so, the key point is that although diversity clearly has an impact on ecosystem functions when averaged across all genes, species and traits, considerable variation surrounds this mean effect, stemming from differences in the identity of the organisms and their functional traits (Fig. 1). To predict accurately the consequences of any particular scenario of extinction, we must know which life forms have greatest extinction risk, and how the traits of those organisms influence function[55]. Quantifying functional trait diversity and linking this to both extinction risk and ecosystem processes is a rapidly expanding area of research[53,55].

Four emerging trends

In addition to the consensus statements above, data published in the past few years have revealed four emerging trends that are changing the way we view the functional consequences of biodiversity loss.

Emerging trend one

The impacts of diversity loss on ecological processes might be sufficiently large to rival the impacts of many other global drivers of environmental change.

Although biodiversity has a significant impact on most ecosystem functions, there have been questions about whether these effects are large enough to rank among the major drivers of global change. One recent study[56] compared 11 long-term experiments performed at one research site, and another[57] used a suite of meta-analyses from published data to show that the impacts of species loss on primary productivity are of comparable magnitude to the impacts of drought, ultraviolet radiation, climate warming, ozone, acidification, elevated CO_2, herbivory, fire and certain forms of nutrient pollution. Because the BEF relationship is nonlinear (see above), the exact ranking of diversity relative to other drivers will depend on the magnitude of biodiversity loss, as well as magnitudes of other environmental changes. Nevertheless, these two studies indicate that diversity loss may have as quantitatively significant an impact on ecosystem functions as other global change stressors (for example, climate change) that have already received substantial policy attention[58].

Emerging trend two

Diversity effects grow stronger with time, and may increase at larger spatial scales.

Diversity effects in small-scale, short-term experiments may underestimate the impacts of diversity loss on the functioning of more natural ecosystems[45]. At larger spatial scales and with greater temporal fluctuations, more environmental heterogeneity may increase opportunities for species to exploit more niches. Consistent with this argument, a growing body of research now shows that the net effects of biodiversity on ecosystem functions grow stronger as experiments run longer[27,46,59]. Limited data also support the notion that diversity effects grow stronger at larger spatial scales[12,60,61] and with greater resource heterogeneity[62–64]. Thus, BEF research so far may have underestimated the minimum levels of biodiversity required for ecosystem processes.

Emerging trend three

Maintaining multiple ecosystem processes at multiple places and times requires higher levels of biodiversity than does a single process at a single place and time.

Most BEF research has focused on one diversity–function relationship at a time. An emerging body of work suggests that the number of species needed to sustain any single process is lower than the number of species needed to sustain multiple processes simultaneously[21,65–67]. Moreover, organisms that control ecological processes at any single location, or in any particular year, often differ from those that control processes in other locations or years[67]. As such, more biodiversity is required to maintain the 'multi-functionality' of ecosystems at multiple places and times.

Emerging trend four

The ecological consequences of biodiversity loss can be predicted from evolutionary history.

BEF research has been dominated by studies that have used species richness as their primary measure of biodiversity. But species represent 'packages' for all the genetic and trait variation that influences the efficiency and metabolism of an organism, and these differences are shaped by patterns of common ancestry[68]. Recent meta-analyses suggest that phylogenetic distances among species (that is, a measure of genetic divergence) may explain more variation in biomass production than taxonomic diversity[34,35]. This suggests that evolutionary processes that generate trait variation among organisms are, in part, responsible for the ecosystem consequences of biodiversity loss.

20 years of research on BES

Over the past 20 years, researchers have developed a rigorous understanding of the services that natural and modified ecosystems provide to society[16]. We have learned that (1) optimizing ecosystems for certain provisioning services, especially food, fibre and biofuel production, has greatly simplified their structure, composition and functioning across scales; (2) simplification has enhanced certain provisioning services, but reduced others, particularly regulating services; and (3) simplification has led to major losses of biodiversity[16]. However, critical questions remain about whether biodiversity loss per se is the cause of impaired ecosystem services in simplified landscapes.

The BES field has resulted in fewer syntheses than has the BEF field, in part because many services cannot be measured directly or manipulated experimentally. We have, therefore, summarized the balance of evidence with our own literature review (Box 2). We began by collating lists of ecosystem services that have been used in recent summaries[15,24,33,69]. We did not include cultural services in our review, which would describe people's non-consumptive uses of biodiversity such as recreation, tourism, education, science and cultural identity. Whether people are motivated by an interest in particular species (for example, totemic or charismatic megafauna) or particular landscapes (for example, wilderness areas or national parks), their demand for cultural services implies a demand for the biodiversity and ecosystem functions required to support the species or communities of interest. Even so, cultural services have rarely been investigated with respect to diversity per se. Here we focused our efforts on the provisioning and regulating services of ecosystems (Box 1), as these are the services that biodiversity studies have most often measured, and that are most frequently related to ecosystem functions.

We began our review by identifying data syntheses that have used either 'vote-counting' (in which the authors tallied the number of studies showing positive, negative, or nonsignificant relationships) or formal statistical meta-analyses (in which authors analysed previously published data to measure standardized correlation coefficients, regression slopes or effect sizes) to quantify relationships between biodiversity and each ecosystem service. For any service for which a data synthesis was not found, we performed our own summary of peer-reviewed articles using search terms in Supplementary Table 1. Papers were sorted by relevance to maximize the match to search terms, after which, we reviewed the top 100 papers for each ecosystem service (leading to a review of >1,700 titles and abstracts). For papers with data, we categorized the diversity–service relationship as positive, negative, or nonsignificant according to the authors' own statistical tests.

Detailed results of our data synthesis are summarized in Supplementary Table 2, and the most salient points are given in Table 1. We believe the following statements are supported by this peer-reviewed literature.

Balance of evidence

Statement one

There is now sufficient evidence that biodiversity per se either directly influences (experimental evidence) or is strongly correlated with (observational evidence) certain provisioning and regulating services.

The green arrows in Table 1 show the ecosystem services for which there is sufficient evidence to conclude that biodiversity has an impact on the service as predicted. For provisioning services, data show that (1) intraspecific genetic diversity increases the yield of commercial crops; (2) tree species diversity enhances production of wood in plantations; (3) plant species diversity in grasslands enhances the production of fodder; and (4) increasing diversity of fish is associated with greater stability of fisheries yields. For regulating processes and services, (1) increasing plant biodiversity increases resistance to invasion by exotic plants; (2) plant pathogens, such as fungal and viral infections, are less prevalent in more diverse plant communities; (3) plant species diversity increases aboveground carbon sequestration through enhanced biomass production (but see statement 2 concerning long-term carbon storage); and (4) nutrient mineralization and soil organic matter increase with plant richness.

Most of these services are ones that can be directly linked to the ecosystem functions measured in BEF experiments. For example, experiments that test the effects of plant species richness on aboveground biomass production are also those that provide direct evidence for effects of diversity on aboveground carbon sequestration and on fodder production. For services less tightly linked to ecosystem functions (for example, services associated with specific populations rather than ecosystem-level properties), we often lack rigorous verification of the diversity–service relationship.

Statement two

For many of the ecosystem services reviewed, the evidence for effects of biodiversity is mixed, and the contribution of biodiversity per se to the service is less well defined.

The yellow arrows in Table 1 show ecosystem services for which the available evidence has revealed mixed effects of biodiversity on the service. For example, in one data synthesis, 39% of experiments in crop production systems reported that plant species diversity led to greater yield of the desired crop species, whereas 61% reported reduced yield[70]. Impacts of biodiversity on long-term carbon storage were similarly mixed, where carbon storage refers to carbon stocks that remained in the system (in plants or soils) for ≥10 years. Comparably few studies have examined storage rather than sequestration. Evidence on the effect of plant diversity on pest abundance is also mixed, with four available data syntheses showing different results. Evidence for an effect of animal diversity on the prevalence of animal disease is mixed, despite recent claims that biodiversity generally suppresses disease[71]. Important opportunities exist for new research to assess the factors that control variation in the response of these services to changes in biodiversity.

Statement three

For many services, there are insufficient data to evaluate the relationship between biodiversity and the service.

There were three ecosystem services for which we found no data, about one-third had less than five published relationships, and half had fewer than ten (see Supplementary Table 2, white cells). This included some noteworthy examples, such as the effect of fish diversity on fisheries yield (as opposed to stability), and the effect of biodiversity on flood regulation. Surprisingly, each of these services has been cited in the literature as being a direct product of biodiversity[16,26]. Some of this discrepancy may be attributable to different uses of the term biodiversity (Box 1). For example, the Millennium Ecosystem Assessment reported that biodiversity enhances flood protection[16], but examples were based on destruction of entire ecosystems (forests, mangroves, or wetlands) leading to increased flood risk. We did not consider complete habitat conversion in our analyses (see Box 2 for examples).

In addition, claims about biodiversity based on ancillary evidence are not reflected in our analyses. For example, we found little direct evidence that genetic diversity enhances the temporal stability of crop yield (as opposed to total yield); yet, most farmers and crop breeders recognize that genetic diversity provides the raw material for selection of desirable traits, and can facilitate rotations that minimize crop damage caused by pests, disease and the vagaries of weather[72]. Although in some instances the ancillary evidence provides rather convincing evidence for a role of biodiversity in providing the ecosystem service, other cases are less convincing. This emphasizes the need for stronger and more explicit evidence to back up claims for biodiversity effects on ecosystem services.

Statement four

For a small number of ecosystem services, current evidence for the impact of biodiversity runs counter to expectations.

The red arrows in Table 1 illustrate cases where the balance of evidence currently runs counter to claims about how biodiversity should affect the ecosystem service. For example, it has been argued that biodiversity could enhance the purity of water by removing nutrient and other chemical pollutants, or by reducing the loads of harmful pests (for example, faecal coliform bacteria, fungal pathogens)[16]. There are examples where genetic or species diversity of algae enhances removal of nutrient pollutants from fresh water[12], or where diversity of filter-feeding organisms reduces waterborne pathogens[73]. However, there are even more examples that show no relationship between biodiversity and water quality.

Finally, there are instances where increased biodiversity may be deleterious. For example, although diverse assemblages of natural enemies (predators, parasitoids and pathogens) are frequently more effective in reducing the density of herbivorous pests[74], diverse natural enemy communities sometimes inhibit biocontrol[75], often because enemies attack each other through intra-guild predation[76]. Another example relates to human health, where more diverse pathogen populations are likely to create higher risks of infectious disease, and strains of bacteria and viruses that evolve drug resistance pose health and economic burdens to people[77]. Such examples caution against making sweeping statements that biodiversity always brings benefits to society.

Outlook and directions

If we are to manage and mitigate for the consequences of diversity loss effectively, we need to build on the foundations laid down by BEF and BES research to expand its realism, relevance and predictive ability. At the same time, we need feedback from policy and management arenas to forge new avenues of research that will make the science even more useful. Here we consider how the next generation of biodiversity science can reduce our uncertainties and better serve policy and management initiatives for the global environment.

Integrating BEF and BES research

The fields of BEF and BES have close intellectual ties, but important distinctions are evident. We see at least two avenues that could facilitate better integration. First, an important frontier involves detailing the mechanistic links between ecosystem functions and services (Box 1). The BEF field has routinely measured functions without extending those to known services, whereas the BES field has routinely described services without understanding their underlying ecological functions. A challenge to linking these two perspectives is that services are often regulated by multiple functions, which do not necessarily respond to changes in biodiversity in the same way. For example, if we want to know how biodiversity influences the ability of ecosystems to remove CO_2 from the atmosphere and store carbon over long time frames, then we need to consider the net influence of biodiversity on photosynthesis (exchange of CO_2 for O_2), carbon sequestration (accumulation of carbon in live plant

BOX 2

Linking biodiversity to ecosystem services

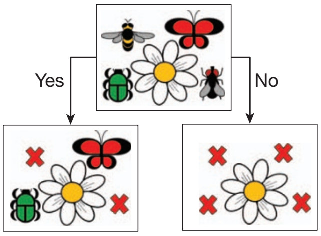
We reviewed >1,700 papers to summarize the balance of evidence linking biodiversity to the goods and services provided by ecosystems. We collated lists of provisioning and regulating services that have been the focus of recent summaries (Supplementary Table 1), and then searched the ISI Web of Knowledge to identify any previously published data syntheses that have summarized known relationships between biodiversity and each ecosystem service. When a data synthesis was not found, we completed our own summary of peer-reviewed articles and categorized the diversity–service relationship as positive, negative, or nonsignificant according to the authors' own statistical tests. Articles had to meet the following four criteria for inclusion.

Criterion 1: the study had to test explicitly for a relationship between biodiversity (defined in Box 1) and the focal ecosystem service using experimental (diversity manipulated) or observational (diversity not manipulated) data.

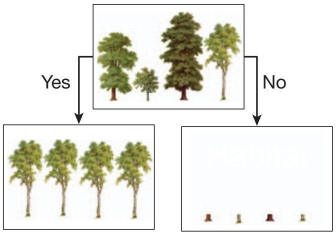
Criterion 2: the study had to quantify biodiversity and the focal service directly (that is, studies using proxies were excluded).

Criterion 3: if authors of the original study identified confounding variables, data were included only if the effects of those confounding variables were statistically controlled for before quantifying the diversity–service relationship.

Criterion 4: the study had to compare a more diverse to less diverse ecosystem containing at least one service providing unit. Any comparison to ecosystems with no service providing unit was excluded (see Box 2 Fig. 1 and Box 2 Fig. 2 for two examples).



Box 2 Figure 1 | Pollination is an ecosystem service provided by a wide variety of organisms, and is essential to the production of many of the world's food crops. We considered studies that compare services like pollination success (for example, fruit set) in a diverse system to a less diverse system (bottom left). But we excluded studies comparing services of a diverse system to one with no service providing organisms (bottom right). Although the latter can quantify the value of service providing organisms (for example, pollinators), it says nothing about the role of biodiversity.



Box 2 Figure 2 | Forests provide a wide array of ecosystem services such as carbon sequestration, wood production and water purification. We considered studies that compare diverse to less diverse habitats (bottom left). However, we did not consider studies that compare services in diverse habitats to those where the habitat was destroyed (for example, clear cut). Although the latter may show the value of the habitat for ecosystem services, it cannot tell us the role of biodiversity.

Table 1 | Balance of evidence linking biodiversity to ecosystem services

Category of service	Measure of service provision	SPU	Diversity level	Source	Study type	*N*	Relationship	
							Predicted	Actual
Provisioning								
Crops	Crop yield	Plants	Genetic	DS	Exp	575	🟩↗	🟩↗
			Species	DS	Exp	100	🟨↗	🟨↗↘
Fisheries	Stability of fisheries yield	Fish	Species	PS	Obs	8	🟩↗	🟩↗
Wood	Wood production	Plants	Species	DS	Exp	53	🟩↗	🟩↗
Fodder	Fodder yield	Plants	Species	DS	Exp	271	🟩↗	🟩↗
Regulating								
Biocontrol	Abundance of herbivorous pests *(bottom-up effect of plant diversity)*	Plants	Species	DS*	Obs	40	🟩↘	🟩↘
		Plants	Species	DS†	Exp	100	🟩↘	🟩↘
		Plants	Species	DS‡	Exp	287	🟨↘	🟨↗↘
		Plants	Species	DS§	Exp	100	🟥↘	🟥0
	Abundance of herbivorous pests (top-down effect of natural enemy diversity)	Natural enemies	Species/trait	DS*	Obs	18	🟩↘	🟩↘
		Natural enemies	Species	DS†	Exp/Obs	266	🟩↘	🟩↘
		Natural enemies	Species	DS‡	Exp	38	🟨↘	🟨↗↘
	Resistance to plant invasion	Plants	Species	DS	Exp	120	🟩↗	🟩↗
	Disease prevalence (on plants)	Plants	Species	DS	Exp	107	🟩↘	🟩↘
	Disease prevalence (on animals)	Multiple	Species	DS	Exp/Obs	45	🟨↘	🟨↗↘
Climate	Primary production	Plants	Species	DS	Exp	7	🟥↗	🟥0
	Carbon sequestration	Plants	Species	DS	Exp	479	🟩↗	🟩↗
	Carbon storage	Plants	Species/trait	PS	Obs	33	🟨↗	🟨↗↘
Soil	Soil nutrient mineralization	Plants	Species	DS	Exp	103	🟩↗	🟩↗
	Soil organic matter	Plants	Species	DS	Exp	85	🟩↗	🟩↗
Water	Freshwater purification	Multiple	Genetic/species	PS	Exp	8	🟥↗	🟥0
Pollination	Pollination	Insects	Species	PS	Obs	7	🟨↗	🟨↗↘

For each ecosystem service we searched the ISI Web of Knowledge for published data syntheses (DS). The footnote symbols in the 'Source' column refer to different syntheses. When a synthesis was not available, we completed our own primary search (PS, see Box 2). Detailed results are given in Supplementary Table 2. Data presented here are summarized as follows: green, actual data relationships agree with predictions (whether service increases or decreases as diversity increases); yellow, Data show mixed results; red, data conflict with predictions. Exp, experimental; *N*, number of data points; Obs, observed; SPU, service providing unit (where natural enemies include predators, parasitoids and pathogens). Note that 13 ecosystem services are not included in this table due to lack of data (<5 relationships, see Supplementary Table 2).

tissue), herbivory (plant carbon eaten by animals), and decomposition (carbon returned to atmosphere as plants die and decompose). Researchers in the BEF and BES fields will need to work more closely to quantify the networks of mechanistic links between ecosystem functions and services.

Second, the fields of BEF and BES could better exploit their complementary approaches to research. Research on BEF has focused mostly on smaller spatial scales conducive to controlled experiments, which has made it difficult to scale results to real ecosystems at larger scales where services are delivered. Studies on BES have relied heavily on observational data, and often failed to separate general biotic effects on ecosystem services (for example, biomass, habitats or entire groups of organisms) from effects of biodiversity per se (that is, variation in life forms). To better merge these two programmes, BEF and BES will need to expand their scopes of research and develop theoretical approaches that can link the small-scale, mechanistic focus of BEF research to large-scale patterns that are the focus of BES. We discuss each of these in turn.

Expanding our scope

The need to explore more realistic scenarios of diversity change that reflect how human activities are altering biodiversity is now urgent. Organisms are not lost from ecosystems at random, and traits that predispose species to extinction are often those that drive ecosystem processes[55,78]. So far this issue has mostly been explored through simulations[79,80], but food web theory[81] based on using environmental stressors to cause nonrandom extinctions may provide a basis for a new generation of BEF experiments. Furthermore, invasions and range expansions driven by anthropogenic change are homogenizing Earth's biota and, in several cases, increasing local taxonomic diversity[82]. Predicting the ecosystem consequences of simultaneous gains (invasion) and losses (extinction) requires that we first understand which biological traits predispose life forms to higher probabilities of extirpation or establishment (response traits), and detail how response traits covary with traits that drive ecosystem functioning (effect traits)[55]. For example, at local scales invasive plants often have functional traits that are associated with more rapid resource acquisition and growth than those of coexisting native species[83], although global meta-analyses suggest only modest differences between native and introduced plants in their effects on ecosystem processes[84]. Statistical models[85] have been developed that allow integration of invasion and extinction into a trait framework, and these models should now be extended to predict changes in ecosystem services.

Another challenge is to incorporate better the real complexity of food webs into BEF and BES research[30,52]. Most research so far has focused on simplified 'model' communities. Yet, in nature, food webs are complex networks with dozens to thousands of species, have reticulate webs of indirect and nonlinear interactions, and contain mismatches in the spatial and temporal dynamics of interacting organisms. This complexity can appear to preclude predictability. But recent theory[86,87] and experiments[88,89] suggest that food-web structure, interactions and stability can be predicted by a small subset of traits such as organismal body size, the degree of dietary generalism[88] and trophic level[89]. Simple trait-based approaches hold promise for simplifying the inherent complexity of natural food webs into a few key axes that strongly control ecosystem functions and services. We need to better identify these traits and food-web structures, and need better models to explain why certain food-web properties control ecosystem functions and services.

Improving predictions

Increasing the complexity and realism of experiments, however, will not be enough to move biodiversity research towards better forecasting. We also need sets of models and statistical tools that help us move from experiments that detail local biological processes to landscape-scale patterns where management and policy take place (Fig. 2). One fruitful approach may be to use data from BEF experiments to assign parameters to local models of species interactions that predict how biodiversity has an impact on ecosystem processes based on functional traits. These local models could then be embedded into spatially explicit meta-community and ecosystem models that incorporate habitat heterogeneity, dispersal and abiotic drivers to predict relationships between biodiversity and ecosystem services at the landscape level[18]. Statistical tools like structural equation modelling might then be used to assess whether predictions of these landscape models agree with observations from natural systems, and to disentangle effects of biodiversity from other covarying environmental factors[20].

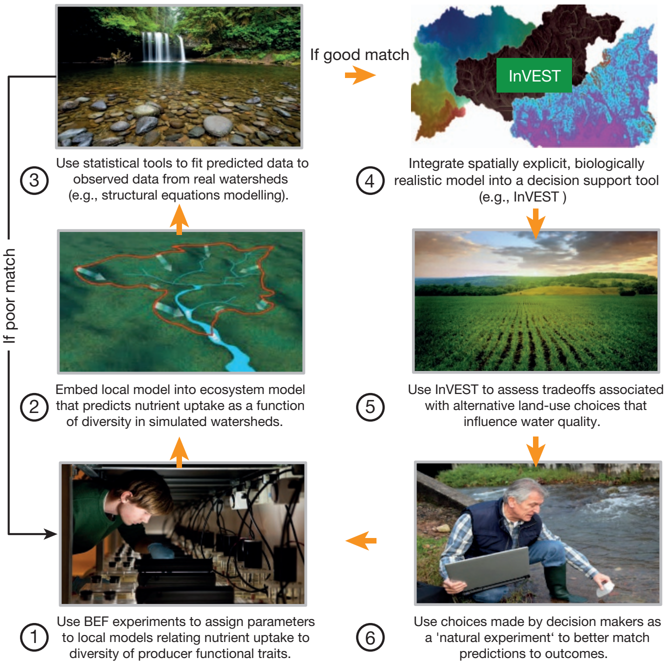


Figure 2 | Towards a better link between BEF and BES research. One of our greatest challenges now is to take what we have learned from 20 years of research and develop predictive models that are founded on empirically quantified mechanisms, and that forecast changes in ecosystem services at scales that are policy-relevant. We outline a hypothetical approach for linking biodiversity to the maintenance of water quality at landscape scales. Data from BEF experiments are used to parameterize competition or niche models that predict how biodiversity has an impact on nutrient assimilation and retention (step 1). Local models are then embedded in spatially explicit meta-community or ecosystem models that incorporate habitat heterogeneity, dispersal and abiotic drivers to predict relationships between biodiversity and water quality at landscape scales (step 2). Predictions of the landscape model are compared to observations from natural systems to assess fit, and statistical tools are used to disentangle effects of biodiversity from other environmental factors (step 3). Once a satisfactory fit is achieved, the model is integrated into a decision support tool (for example, InVEST (step 4)), which is used to simulate changes in ecosystem services at landscape scales where decision makers assess alternative land-use choices (step 5). Choices made by decision makers in real projects provide new data that allow biologists to refine their models and predictions (step 6). Images from B.J.C., G.C.D., US EPA and Shutterstock.com; used with permission.

Ideally, predictions arising from landscape-level models would be 'ground-truthed' by assessing their ability to predict the outcome of real restoration projects, or other management scenarios where policy actions are being taken to protect ecosystem services[90]. For example, given land-use pressure and climate change, freshwater supply is an ecosystem service in high demand, and water funds are becoming a common finance mechanism through which downstream water consumers pay for upstream changes in land use to achieve objectives like maintenance of water quality (nutrient, sediment and bacterial loads)[91]. Major initiatives are underway to standardize the design, implementation and monitoring of water funds, including a pilot programme supported by the World Bank, the Inter-American Development Bank, FEMSA, and The Nature Conservancy that spans 40 Latin American cities.

Initiatives like these represent opportunities to assess and refine our ability to predict biodiversity–ecosystem service relationships on realistic scales in situations where stake holders are expecting positive returns. For example, BEF and BES researchers have amassed substantial experimental evidence showing that species diversity of plants and algae increase uptake of nutrient pollutants from soil and water[12,24,25,33,63]. We have statistical models that quantify the functional form of these effects[12,31], and extensive data on the functional traits that influence such processes in different habitats[53,63,92]. One approach could involve developing spatially explicit predictions of how biodiversity influences water quality in a modelled watershed where local nutrient assimilation and retention are a function of the number and types of functional traits that locally co-occur (that is, traits of plants in a riparian zone, or of algae in a stream reach). One could then integrate this spatially explicit, biologically realistic model into a decision support tool (for example, InVEST (Integrated Valuation of Ecosystem Services and Tradeoffs))[93] to simulate changes in ecosystem services at landscape scales where decision makers can assess trade-offs associated with alternative land-use choices (Fig. 2). Choices made by decision makers in real projects could, in turn, serve as 'natural experiments' that provide biologists with an opportunity to test their predictions against outcomes.

Valuing biodiversity

Economists have developed a wide array of tools to estimate the value of natural and managed ecosystems and the market and non-marketed services that they provide[94]. Although there are good estimates of society's willingness to pay for a number of non-marketed ecosystem services, we still know little about the marginal value of biodiversity (that is, value associated with changes in the variation of genes, species and functional traits) in the production of those services. The economic value of biodiversity loss derives from the value of the affected services. Estimating this value requires calibration of ecosystem service 'production' functions that link biodiversity, ecosystem processes and ecosystem services. The derivative of such functions with respect to biodiversity defines the marginal physical product of biodiversity (for example, carbon sequestration or water purification), and when multiplied by the value of the service, yields the marginal value of biodiversity change.

Researchers in the BEF and BES fields need to work more closely to estimate the marginal value of biodiversity for ecosystem services. In doing so, at least three challenges require attention. First, ecosystems deliver multiple services, and many involve trade-offs in that increasing the supply of one reduces the supply of another. For example, carbon sequestration through afforestation or forest protection may enhance timber production but reduce water supplies[95]. The value of biodiversity change to society depends on the net marginal effect of the change on all ecosystem services[96]. Future work needs to quantify the marginal benefits of biodiversity (in terms of services gained) relative to marginal costs (in terms of services lost).

Furthermore, many trade-offs among services occur at very different spatial and temporal scales. The gains from simplifying ecosystems are often local and short term, whereas the costs are transmitted to people in other locations, or to future generations. For society to make informed choices about land uses that have mixed effects, the science linking biodiversity to ecosystem functioning and services must be extended to explore trade-offs between services at multiple temporal and spatial scales so that information can be incorporated into models of optimal land use.

Finally, there is increasing interest in developing incentives to encourage land holders to take full account of the ecosystem services that are affected by their actions. The concept of 'payments for ecosystem services' has emerged as one tool for bringing market value to ecosystems. Our Review has emphasized that many ecosystem services ultimately depend on the variety of life forms that comprise an ecosystem and that control the ecological processes that underlie all services. Therefore, successful plans to use payments for ecosystem services will need to be founded on a solid understanding of the linkages among biodiversity, ecosystem functioning and the production of ecosystem services[97]. This will require that such plans explicitly manage for biodiversity change.

Responding to the call of policy initiatives

The significance of biodiversity for human wellbeing was recognized 20 years ago with the formation of the Convention on Biological Diversity—an intergovernmental agreement among 193 countries to support the conservation of biological diversity, the sustainable use of its components, and the fair and equitable sharing of benefits. Despite this agreement, evidence gathered in 2010 indicated that biodiversity loss at the global scale was continuing, often at increasing rates[98]. This observation stimulated a set of new targets for 2020 (the Aichi targets) and, in parallel, governments have been negotiating the establishment of a new assessment body, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). The IPBES will be charged with conducting regional, global and thematic assessments of biodiversity and ecosystem services, and will depend on the international scientific community to assess trends and evaluate risks associated with alternative patterns of development and changes in land use[99].

Significant gaps in both the science and policy need attention if the Aichi targets are to be met, and if future ecosystems are to provide the range of services required to support more people sustainably[99]. We have reported the scientific consensus that has emerged over 20 years of biodiversity research, to help orient the next generation of research on the links between biodiversity and the benefits ecosystems provide to humanity. One of the greatest challenges now is to use what we have learned to develop predictive models that are founded on empirically quantified ecological mechanisms; that forecast changes in ecosystem services at scales that are policy-relevant; and that link to social, economic and political systems. Without an understanding of the fundamental ecological processes that link biodiversity, ecosystem functions and services, attempts to forecast the societal consequences of diversity loss, and to meet policy objectives, are likely to fail[100]. But with that fundamental understanding in hand, we may yet bring the modern era of biodiversity loss to a safe end for humanity.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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CORRIGENDUM

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Corrigendum: Biodiversity loss and its impact on humanity

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In Table 1 and Supplementary Table 2 of this Review, under the 'Category of service' called 'Regulating', the first two 'Measures of service provision' related to 'Biocontrol' should read 'Abundance of herbivorous pests' instead of 'Control of herbivorous pests'. With this word change, a downward arrow for either the predicted or actual diversity–service relationship would indicate that the abundance of herbivorous pests declines (and biocontrol increases) with increasing plant diversity. This does not alter any of our conclusions, because all diversity–service relationships were correctly described in the text of the manuscript itself. These errors have been corrected online in the HTML and PDF versions of the original Review, and in the original Supplementary Information.