

Linking Biodiversity and Ecosystem Services: Current Uncertainties and the Necessary Next Steps

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Understanding when biodiversity conservation and ecosystem-service maintenance are compatible is needed within the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES). Here, we evaluate current understanding and uncertainties of the effects of biodiversity change on selected ecosystem services and suggest ways to further understand the links between biodiversity change and ecosystem services. We reviewed experiments, observations, and syntheses on the effects of species richness on six ecosystem services: forage, timber, fisheries, climate regulation, agricultural pest control, and water quality. Establishing a direct link from biodiversity to ecosystem-service provision has often been precluded by limited data (i.e., the amount, consistency, or generality of the data) and a mismatch between the variables measured and the final ecosystem service that is relevant to stakeholders. We suggest that encompassing syntheses and a network of interdisciplinary experiments under realistic conditions could fill these gaps and could inform the outcomes of alternative management and policy scenarios within IPBES.

Keywords: IPBES, management, experiment, biodiversity effects, meta-analysis

Biodiversity and ecosystem services are declining worldwide, spurring scientists and policymakers to act together to identify effective policy solutions. Recently, the recognition that these two forms of environmental change are inextricably linked inspired the creation of the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES), in 2012. IPBES is an intergovernmental body open to all countries of the United Nations. Strengthening the science–policy interface for biodiversity and ecosystem services will contribute to the conservation and sustainable use of biodiversity, to long-term human well-being, and to sustainable development (www.ipbes.net).

Identifying the impacts of biodiversity and ecosystem services on human well-being is crucial to IPBES. Understanding when the goals of biodiversity conservation and ecosystem-service maintenance are compatible or interdependent is necessary. More specifically, we need to know whether, how, and when the maintenance of biodiversity is key to sustaining the flow of services to societies. As a first step, this can be achieved through assessments of the current state of knowledge regarding the direct and indirect causal links between biodiversity and ecosystem services.

Knowledge of the effects of biodiversity change on ecosystem functioning has progressed rapidly in the past 20 years. Recent syntheses have shown that a large body of evidence

is now available, describing how biodiversity loss affects the functioning of ecosystems (Cardinale et al. 2012) and that this impact is, at least in the case of primary productivity, as large as some other global change drivers, including climate warming, elevated carbon dioxide, ocean acidification, or nutrient additions (Hooper et al. 2012, Tilman et al. 2012). Despite these impacts, current knowledge of the links between measures of biodiversity (e.g., species richness, functional diversity) and ecosystem services that directly affect human well-being is still patchy (Cardinale et al. 2012).

To contribute to the assessment and knowledge-generation roles of IPBES, we provide an assessment of current knowledge of, uncertainties about, and key scientific needs related to the relationship between biodiversity and six crucial ecosystem services. We build on a recent review, in which the direction of the effect of biodiversity on several ecosystem services was identified (Cardinale et al. 2012). We identify the uncertainties that hinder our understanding of the processes linking anthropogenic biodiversity changes to service supply. We focus on six ecosystem services of paramount importance to society: forage, timber, fishery stability, climate regulation, pest regulation, and water quality. We selected these because information on their links to biodiversity change is available, because they encompass both provisioning and regulating services, and

because they operate at different scales. We examine gaps in the current data (i.e., inadequate or missing data) and identify uncertainties in current knowledge. We then identify crucial research areas and novel approaches that would most efficiently generate the knowledge needed for policy recommendations.

Effects of richness on ecosystem services: Key uncertainties and the quality of the evidence

Biodiversity is the variability within and among species, as well as the variability at other levels of organization, such as between ecosystems and landscapes. The variability across elements within levels of organization can be measured as *richness* (the number of elements), *evenness* (the equitability of elements), and *heterogeneity* (the disparity in element form and function). In principle, the supply of ecosystem services is mediated by each measure of biodiversity and at each level of organization. The most common measure is species richness; in many studies, changes in species richness have been tied to ecosystem function. Other components of species diversity have been shown to influence function and are, therefore, likely to influence services; these include functional diversity (e.g., McGill et al. 2010), species composition, and community evenness.

Although the concept of biodiversity encompasses all of these elements, in the present article, we emphasize species richness, because it is the component of biodiversity that has most frequently been assessed in the literature on ecosystem functioning. We also emphasize the role of native species richness in providing services as a means to reveal potential synergies or trade-offs between biodiversity conservation and the maintenance of ecosystem services.

For each service, we assess the type of evidence (i.e., experiments, observations, or theory), the amount of evidence, the degree of agreement among different sources of evidence, and how closely the final service of interest to society relates to the variables measured by the research studies. We focus on the major uncertainties regarding the contribution of species richness to the supply of each ecosystem service.

Forage. Managed livestock grazing covers more than 25% of Earth's terrestrial surface (Asner et al. 2004). Land-use changes to increase forage production have been driven by the increasing demand for meat and dairy products but have occurred at the expense of biodiversity maintenance and contrary to an urgent need to reduce greenhouse gas emissions (Foley et al. 2011).

Evidence that species richness determines forage production is limited, because the variables that directly pertain to forage production—the final service most relevant to society in this context—have not been reported in most grassland experiments. Dozens of experiments in temperate grasslands offer considerable evidence that aboveground plant biomass production increases with plant species richness (Cardinale et al. 2011). However, in such studies, aggregate primary

productivity of the whole plant assemblage is measured, and they are not designed to consider forage production for livestock per se. Plant species marketed to feed livestock, the palatability and nutritional quality of plant biomass, and the effects of changing plant richness under actual livestock grazing have rarely been considered (but see, e.g., Isbell and Wilsey 2011).

As a result of these limitations, it remains unclear whether the increased biomass production in species-rich plant communities translates into increased production of forage used for meat or dairy products. Some evidence suggests that the quantity of palatable aboveground biomass may be greater in mixtures than in monocultures, even under intense livestock grazing (Isbell and Wilsey 2011), and that a mixed diet may be favorable for cattle performance (Rogosis et al. 2007). However, the biomass produced in diverse mixtures may be of lower quality because of a lower protein content, driven by higher nitrogen-use efficiency at high levels of diversity (van Ruijven and Berendse 2005).

Timber. Forests support approximately 80% of the world's terrestrial biodiversity and provide key services to humanity, such as timber, food, recreation, and climate and water regulation. The livelihoods of around 1.6 billion people depend directly on them, and well over \$300 billion is generated from the annual trade of forest products (FAO 2010).

Assessments of the effects of increased tree species richness on timber production are hindered by the difficulties of manipulating large, long-lived organisms (but see the TreeDivNet Web site at www.treedivnet.ugent.be). However, meta-analyses of field experiments and forest plantation trials have generally shown positive effects of tree diversity on individual commercial species' (Piotto 2008) and multiple species' productivity (Zhang et al. 2012). In most studies, total tree growth (often biomass) is reported, not the specific parts of trees that have commercial value as a service (i.e., timber). Furthermore, neither composition nor the different market values of the extant tree species are accounted for.

Observational studies can provide insight into the effects of tree diversity, provided that the effects of confounding factors (e.g., abiotic conditions) on timber production are accounted for (box 1). The few observational studies in which these links have been investigated in natural forests have mostly shown positive effects of biodiversity on productivity at the whole-stand level (Paquette and Messier 2011, Vilà et al. 2013). As diversity increases, tree biomass and berry and game production potentially increase (in a hump-shape fashion), whereas soil carbon storage increases linearly (Gamfeldt et al. 2013).

Despite the demonstrated positive effects of species richness on tree productivity, managing a forest for multiple valuable species is often perceived as not operationally or economically viable by the industry (Nichols et al. 2006). However, well-conceived, diverse, multipurpose managed forests are possible and could deliver a suite of ecosystem services (e.g., multiple plant and animal nontimber forest

Box 1. Path analysis.

Large-scale observational studies provide different and complementary insight into experimental manipulations of the links between species richness and ecosystem services. They can be performed at scales compatible with management decisions, can capture variation in service supply, and reflect real-world species composition determined by biophysical and management drivers. However, they lack control for confounding factors, such as climate and the local conditions (e.g., soil type), or stand characteristics, such as age or density, which may directly or indirectly affect the magnitude of service supply. One way to account for these multiple interactions is path analysis, in which all variables of interest and their interactions may be included. In figure 1, we show the link between functional diversity and tree productivity and how species diversity itself may be affected by a number of other factors, such as climate.

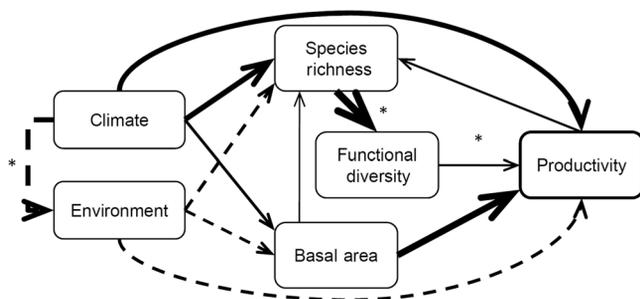


Figure 1. Links between biodiversity and tree productivity in the temperate and boreal forests of Canada. The thickness of the arrows is proportional to the path coefficient, and the style indicates direction (solid, positive; dashed, negative). The asterisks (*) highlight paths that were significantly different between the boreal (shown here) and temperate forests of Quebec, in eastern Canada. Source: Adapted from Paquette and Messier (2011).

products) beyond timber production (Paquette and Messier 2011, Gamfeldt et al. 2013).

Fisheries. Marine and freshwater ecosystems support food-provisioning services from fisheries. Fish are a major source of protein, particularly in the developing world, and support an industry worth over \$85 billion annually in landings, with indirect benefits likely to be even greater (Dyck and Sumalia 2010). These capture fisheries range from small artisanal to major industrial operations and target a wide variety of fishes and invertebrates.

The effects of fish species richness on yield variability are supported by theory and by some empirical evidence. The *portfolio effect* is a theoretical prediction that a set of populations (both within or among species), fluctuating asynchronously, will decrease variability in year-to-year aggregate yield or returns (Figge 2004). This is analogous to reducing the financial risk of market fluctuations by diversifying a portfolio of assets. A relevant test of the portfolio effect comes from sockeye salmon (*Oncorhynchus nerka*) in Alaska (Schindler et al. 2010), the most valuable fishery in the United States, with a landed value of nearly \$8 billion. Sockeye salmon are found across multiple habitats and river systems and comprise several hundred genetically and

ecologically distinct populations. Compared with expected outcomes from a single homogenous population, the diversity in habitat use and spawning times among these populations resulted in 50% less-variable annual returns of the salmon fishery over the last 50 years and an estimated 90% fewer fishery closures. However, to date, only a few observational studies have confirmed this pattern in other fisheries (Cardinale et al. 2012).

A similar pattern emerges at global scales, at which the variability in total fishery catch increases with declining catch-species richness (Worm et al. 2006). However, the specific contribution of changes in biodiversity to these patterns was not isolated from that of other variables known to influence fishery yields, such as environmental conditions or management (Fisher et al. 2010). Furthermore, species composition, more so than richness, is likely to influence yield, especially in temperate ecosystems in which relatively few species represent large proportions of the total catch (see, e.g., the Sea Around Us Project catch records at www.seaaroundus.org).

Climate regulation. Ecosystems influence climate through the exchange of greenhouse gases and by reflecting radiation and converting energy to different forms (Jackson et al. 2008). Climate regulation is a crucial ecosystem service and is increasingly valued by governments concerned with the global climate challenge. Greenhouse gas uptake and storage are now exchangeable commodities, totaling \$144 billion in the global carbon market for 2009 (Kossoy and Ambrosi 2010).

Assessments of the effects of species richness on climate change should include the final balance of how richness influences each of the components that contribute to total ecosystem carbon content. Aggregate plant biomass in a community generally increases with plant species richness (Cardinale et al. 2011), but this is not necessarily true for ecosystem-level long-term carbon storage. Plant species richness may have different effects on different carbon pools and fluxes. More-diverse tropical rainforest plantations lead to faster coarse woody debris decomposition and lower soil respiration, but changes in aboveground carbon stocks, mineral soil carbon, or litter decomposition could not be attributed to changes in richness (Potvin et al. 2011). Increasing plant species richness led to soil carbon increase

Box 2. Richness effects on long-term carbon storage.

In a long-term grassland experiment in Minnesota, researchers manipulated plant species richness from monocultures to mixtures of as many as 16 plant species typical of prairies native to the Midwestern United States. They showed that plant productivity increases with species richness and that carbon accumulated in soil over the 12 years of study at a higher rate in the plots containing more species (Fornara and Tilman 2008). We used these data to provide a rough estimate of the functional relationship between species richness and the balance of processes influencing soil carbon storage (figure 2; see the supplemental material). Our analysis suggests that the effects of losing one species from a species-rich community (e.g., containing at least 20 species) are not as dramatic on soil carbon (i.e., a depletion of about 0.05 tons of carbon per hectare) as those of losing one species from a simpler community (having, e.g., 2 species; a depletion of 2.4 tons of carbon per hectare).

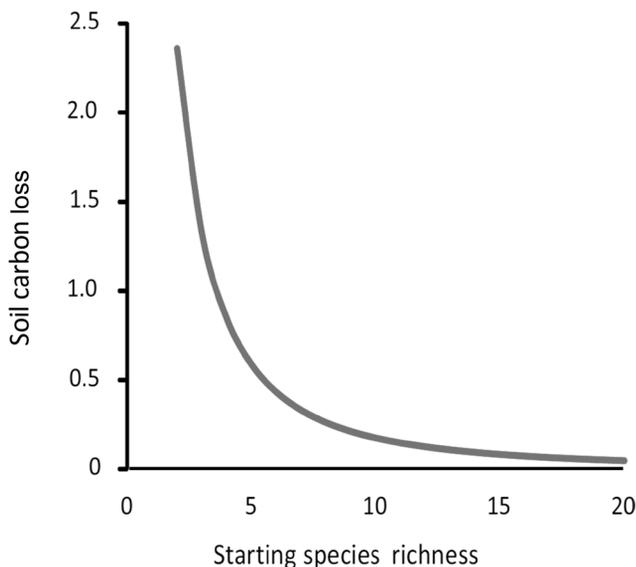


Figure 2. The effects on soil carbon of losing one species (in tons of carbon per hectare per species). The negative effects are more severe for communities with few species. The estimates are based on data from Fornara and Tilman (2006).

in one experiment (box 2; Fornara and Tilman 2008) but did not in another (Potvin et al. 2011). In deciduous forest fragments, aboveground carbon storage increased with functional diversity in unmanaged fragments but decreased with diversity in fragments managed for maple syrup and firewood extraction (Ziter et al. 2013). Simulated species-loss scenarios led to increased or decreased carbon storage, depending on the identity of the lost species (Bunker et al. 2005). Carbon storage also depends on how the rest of the food web is changing. For example, declining detritivore richness generally reduces the rate of decomposition (Cardinale et al. 2011). Plant richness effects on decomposition are variable and have been shown to be dependent on ecosystem type (Gessner et al. 2010).

Additional information gaps include the effects of species richness on the exchanges of other greenhouse gases, such as nitrous oxide and methane, which have a stronger radiative forcing than carbon dioxide. A strong influence of species

identity and inconsistent effects of richness on greenhouse gas exchanges have been found (e.g., McGill et al. 2010).

Regulation of agricultural pests. Natural control of crop damage from agricultural pests is worth an estimated \$4.5 billion annually (Losey and Vaughan 2006). The supply of these services can be influenced by on-farm biodiversity through both top-down (natural enemies—i.e., predators, parasitoids, and pathogens) and bottom-up (vegetation) processes.

The top-down effects of richness on pest regulation may be context dependent. Recent experimental work suggests that increasing enemy richness often leads to decreasing pest abundance relative to the average of individual species effects (for a review, see Finke and Snyder 2010). However, strongly negative behavioral or trophic interactions between enemy species could also generate negative effects of predator richness on prey suppression (Vance-Chalcraft et al. 2007). Furthermore, observational studies have shown both positive and negative relationships between enemy richness on pest suppression (Letourneau et al. 2009; $N = 277$, 70% positive, 30% negative). Management strategies have historically been focused on manipulations of the most effective individual enemy species within a particular system (Rosenheim et al. 1995) and not on manipulations of richness.

Bottom-up effects of richness on pest regulation have been suggested by a recent meta-analysis showing that increased crop richness promoted higher densities of natural enemies, lower densities of pests, and reduced levels of crop damage (Letourneau et al. 2011). However, the relative roles of changes in plant species richness, species composition, and the type of land cover surrounding the analyzed plots in driving these effects remain to be assessed.

Water quality. Clean water is needed for irrigation, for human consumption, and to sustain fisheries. The removal and storage of potentially harmful pollutants, such as nitrates, which degrade water quality worldwide, are key ecosystem services.

Assessments of how richness might influence water quality include some of the ecosystem processes involved but not the final service. A synthesis of the 59 experiments in which the species richness of plants and algae in terrestrial, freshwater, and marine ecosystems was manipulated showed that, in 86% of the included studies, concentrations of nitrogen in soil

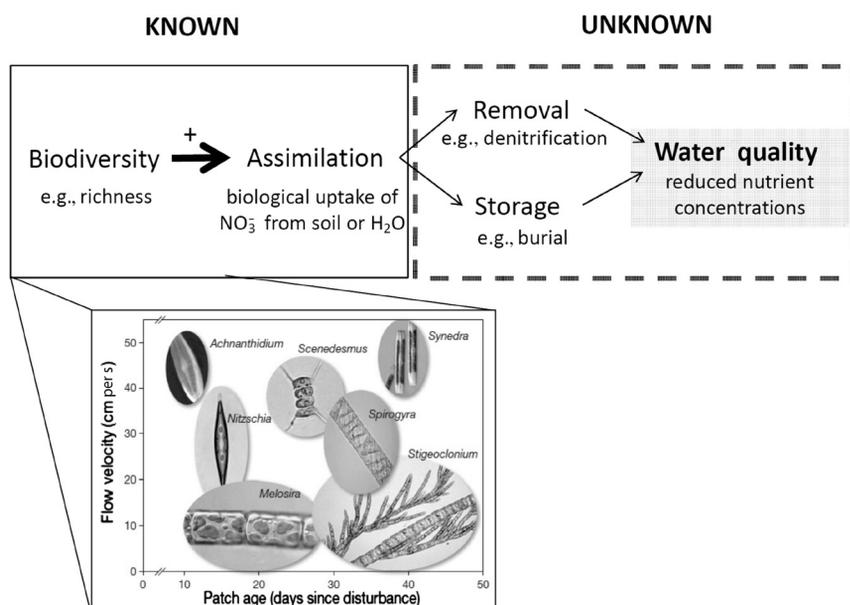


Figure 3. The known and unknown effects of richness on water quality. It is known that communities of algae with higher species richness, in which niche differentiation (i.e., the species' preferences for patches of different age and the velocity of flow vary) contributes to their coexistence, lead to higher nitrate uptake from the water than any single species could alone. It is unknown whether species richness has effects on nutrient removal and storage have not been described but need to be understood in order for the overall effects of richness on water quality to be comprehended. Abbreviations: NO_3^- , nitrate; H_2O , water; cm per s, centimeters per second.

or water decreased as the species richness of plants or algae increased (figure 3, left; Cardinale 2011). Most of these studies were performed with terrestrial plants, but it is commonly assumed (but seldom tested) that nitrogen that is not biologically immobilized by plants is ultimately leached into surface water or groundwater. On average, the least diverse assemblages showed only 48% of the uptake by the most diverse community. Diverse microbial communities, in which niche differentiation leads to more stable species coexistence, have been shown to be more efficient at assimilating biologically active resources such as nitrogen (figure 3; e.g., Cardinale 2011).

Assimilation is only the first of several crucial steps in nitrogen removal from water. The role of species richness in the pathways that lead to long-term storage (e.g., deposition, burial) or permanent removal of nitrogen (e.g., denitrification, insect emergence) from the water body still needs to be assessed (figure 3, right). Whether species richness influences other nutrient pollutants that are involved in eutrophication (e.g., phosphorus) and nonnutrient pollutants, such as metals, biocides, and nanomaterials, could also be evaluated.

Overview. For these six services, we have shown that some experimental, observational, and theoretical findings support links between richness and services, but many remaining uncertainties hinder clear conclusions (table 1).

In assessments of richness effects, the final ecosystem service that is most relevant to societies has seldom been measured. To date, we have assessed only some biodiversity effects on some of the processes that underpin ecosystem-service supply and have done so most effectively under highly controlled conditions.

Uncertainties about the effects of species richness on services also arise, because different components of biodiversity (e.g., species richness, evenness, composition, functional diversity) have simultaneous effects on services.

In experimental assessments of richness effects on service supply, the conditions under which ecosystems are managed have not been considered. Under realistic conditions, many other factors potentially interact with biodiversity change to affect service supply. More realistic scenarios that reflect nonrandom declines in biodiversity may reveal effects on ecosystem functioning of different magnitudes or directions

Table 1. Sources of uncertainty for the links between species richness and ecosystem services for the six services analyzed in the text.

Source of uncertainty	Ecosystem services
Mismatch between functions measured and final ecosystem service	Forage, timber, water quality, climate
Mismatch between the study conditions and actual management conditions and service delivery to society	Forage, timber
Studies insufficiently comprehensive to assess the different processes underpinning ecosystem-service supply	Climate, water quality
Simultaneous effects of different components of biodiversity (richness, composition, functional diversity)	Timber, climate, pest regulation
Confounding environmental factors other than richness that contribute to effects on service supply	Timber, fisheries
Trade-offs between positive and negative effects of richness on the various functions underpinning service supply	Climate, pest regulation
Context-dependent patterns	Climate, pest regulation

(e.g., Zavaleta and Hulvey 2004). Research is needed on the effects of extinction sequences on different components of biodiversity and on how they affect ecosystem-service provision. The type of management, habitat connectivity, the surrounding content, and the identity of introduced species can directly or indirectly alter species richness or the processes underpinning the ultimate service.

Finally, given that a single service may result from multiple functions, positive and negative effects of richness may combine to determine the net effects of biodiversity on ecosystem services.

The necessary next steps

It is necessary to reduce the uncertainties described above in order to provide IPBES with a robust synthesis of the relationship between biodiversity and ecosystem services. In particular, improving our ability to predict the consequences of realistic biodiversity loss on the supply of a portfolio of both provisioning and regulating services is needed in order to assess the outcomes of alternative management scenarios derived from different policies.

Our understanding of how biodiversity loss directly and simultaneously affects sets of ecosystem services is still limited. This is surprising, given that, over the last decade, our ability to predict the outcomes of land-use change on biodiversity has increased greatly (Pereira et al. 2010), as has

our ability to predict the outcomes of land-use changes on several ecosystem services (Kareiva et al. 2011).

An open question is how biodiversity loss mediates the synergies and trade-offs among different ecosystem services within the portfolio. Very little is known about how biodiversity change alters the biogeochemical processes underpinning the interactions among ecosystem services. A new generation of comprehensive studies that provide robust findings on the effects of realistic biodiversity declines on ecosystem-service supply under actual management conditions is needed. Information on which services depend most on the maintenance of biodiversity, the relative contribution of biodiversity to these services, and how changes in biodiversity may result in or intensify trade-offs among services can then be obtained.

To illustrate how such a set of studies can be designed, we focus on how biodiversity regulates the capacity of soils to sustain long-term crop yields, by which we mean that yields in the future are at least equivalent to those obtained today. Sustaining long-term food yields is of paramount importance to the world’s future food security (Foley et al. 2011). However, the impacts of changes in plant, invertebrate, and microbial biodiversity on the soil properties and functions underpinning long-term crop yields are not well understood.

Soils contribute to long-term yields through interactions with environmental conditions (e.g., climate, geology, slope, soil age), management, and biodiversity (figure 4; Palm et al. 2007). Changes in above- and belowground biodiversity lead to changes in the soil’s chemical, biological, physical, and hydrologic functions. Such functions underpin both short-term yields and long-term yields; they are also important for the delivery of other services from soils, such as flood regulation and carbon storage (Palm et al. 2007).

Trade-offs between short-term and long-term yields are often at stake: Maximizing short-term yields may result in soil degradation (Foley et al. 2011). Soil degradation will not only negatively affect long-term soil yields but can also have negative impacts on the soil’s carbon storage and on the soil’s contribution to the regulation of water quality or that of flood regulation.

We use long-term crop yields as an example to illustrate the type of approach that can most efficiently inform the role of biodiversity maintenance in the provision of this service. Similar approaches can be applied to other services.

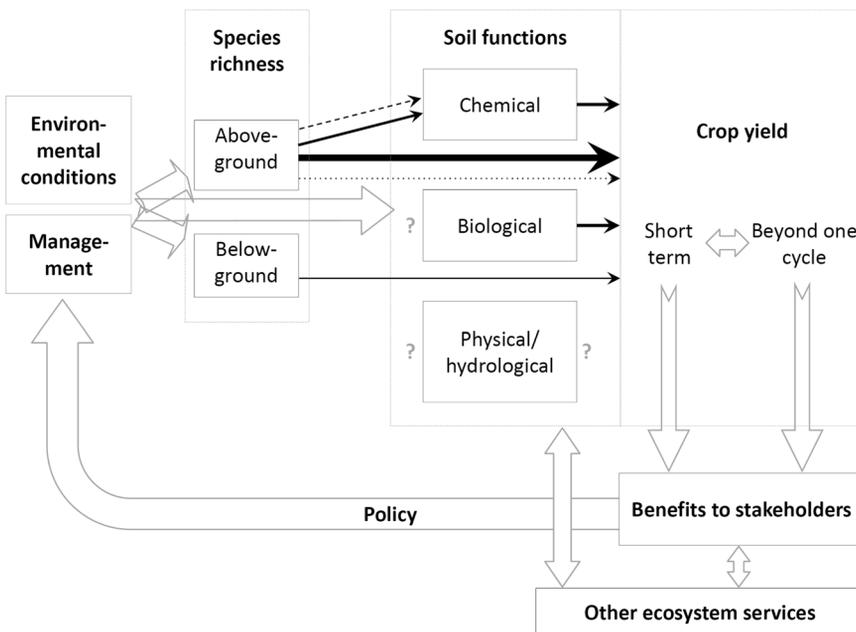


Figure 4. Current understanding of the effects of biodiversity through soil functions on long-term crop yields under management conditions. The potential interconnections that are still to be assessed are indicated by large hollow arrows. Consistent and well-supported effects of species richness assessed through meta-analyses are depicted as filled arrows (solid, positive; dashed, negative; dotted, nonsignificant) of different widths (thinner, supported by one meta-analysis; thicker, supported by five meta-analyses). Further details are provided in the supplemental material.

Integrating current understanding of the links between biodiversity and final ecosystem services through syntheses and models. The assessment of current knowledge of the links between biodiversity and long-term crop yields must include links among above- and belowground biodiversity; biological, physical, and chemical soil properties and functions; short- and long-term yields; environmental conditions (e.g., climate, geology); and stakeholder needs for the final service (see figure 4 for more details).

Although a large body of experimental and observational evidence is available on some of the above interconnections, comprehensive meta-analyses are also useful. Such syntheses can identify knowledge gaps and can distinguish those biodiversity effects on services that are most strongly context dependent from those that occur more generally.

Meta-analyses in combination with modeling approaches can identify the interconnections that are most sensitive to changes in biodiversity or that contribute the most to changes in long-term yields. They reveal the relative importance of different drivers in sustaining long-term yields, such as environmental conditions; the characteristics of management; and the species richness, composition, and functional diversity of the different groups of organisms (e.g., plants, soil microbes).

The cascading effects of reduced soil or plant biodiversity on soil functions, long-term yields, and other ecosystem services can be modeled from the synthesis obtained from the functioning of each of the interconnections. Trade-offs arising from the positive and negative effects of biodiversity on the various soil functions underpinning long-term yields can be identified.

Prioritizing the effects of biodiversity on the simultaneous provision of multiple services and the trade-offs among them. The past focus on linking biodiversity to a single ecosystem service (see the examples above) may contribute to an underestimation of biodiversity effects on service provision. The pool of species driving any single function often differs from function to function (Isbell et al. 2011). Therefore, biodiversity's influence on multiple ecosystem services could be even stronger than its influence on any single service alone, given that a single service is often a composite of several ecosystem functions.

Societies are seldom interested in a single service. Rather, we depend on ecosystems to provide multiple services. For example, we manage agroecosystems for high yields, for infiltration and runoff, for the regulation of agricultural pests and diseases, and for the maintenance of soil productive potential.

Given that a single service is the result of multiple ecosystem functions, understanding the effect of biodiversity change on the synergies and trade-offs among services will rely on those key functions that underpin the functional relationships among the services (Bennett et al. 2009). The ultimate effects of biodiversity on the configuration of a portfolio of final services will be given by the combination of the biodiversity effects on those key functions.

Changes in the magnitude of each of the services with changes in biodiversity condition are also possible. Biologically diversified farming systems, for instance, enhance the regulation of weeds, diseases, and arthropod pests and increase pollination services relative to less-diverse agroecosystems. However, the resulting magnitude of yield, pest and disease regulation, or pollination levels may not be enough to meet the needs of farmers (Kremen and Miles 2012).

Large-scale field network to quantify biodiversity effects on final ecosystem services under realistic management conditions. A new generation of long-term, interdisciplinary, adaptive, and participatory studies can be used to fully assess the effects of soil and plant biodiversity on long-term yields, ecosystem services, and people. One approach is the creation of a network of sites under contrasting social and ecological conditions that can be monitored for correlated responses of ecosystem services to biodiversity change. The use of a common experimental design across sites was pioneered by the BIODEPTH experiment (Hector et al. 1999) and was recently called on to address today's environmental issues (Fraser et al. 2013). Treatments can include management regimes that are the most desirable or most likely to emerge from predicted changes in policies. They can simulate realistic changes in plant and soil biodiversity and soil properties in response to alternative management options. Additional treatments can be introduced as new insight is gained, to enable stakeholders to make decisions that optimize the trade-offs among the services that are most crucial to their context.

The variables to be monitored should include the different components of biodiversity (for the key types of organisms—e.g., plants, soil organisms), both long-term and short-term crop yields, soil contributions to sustaining and reducing variability in long-term yields, benefits to different stakeholders from short- and long-term yields, and any values (e.g., economic, cultural) attributed to such benefits. Codesign with stakeholders will enable the variables that are the most relevant to both the researchers (e.g., ecologists, agronomists, economists, anthropologists) and the stakeholders to be monitored.

Trade-offs between long-term yields and other ecosystem services (e.g., flood regulation, climate regulation), as well as their implications for stakeholders, need to be assessed. Doing so can identify the management practices that optimize multiple objectives—biodiversity conservation, the delivery of a portfolio of services, and the preferences of key stakeholders.

A network of experimental sites can be used to account for the marginal contribution of biodiversity to the key ecosystem services. Stakeholders directly involved in the monitoring can then assess how the biodiversity levels and service magnitudes relate to the satisfaction of their needs and can be asked to indicate the value of the benefits or losses in each of the services.

The good news is that progress along these lines is under way. Meta-analyses of a large number of sites ($N > 600$) under actual management conditions distributed across the globe are being used to analyze the contributions of wild

insect abundance on fruit crop production (Garibaldi et al. 2013), the final ecosystem service derived from pollination. Derived models have shown effects of farm management and characteristics of the surrounding landscape on such abundance (Kennedy et al. 2013). New networks of sites for assessing pollinators and pollination under actual management conditions and with stakeholder involvement are being established across the globe (www.step-project.net, www.icp-bees.org). Therefore, the integration of current understanding through syntheses and models can happen in the short term, while field networks under realistic management conditions are established and expanded. Explorations of the effects of biodiversity on multiple services can be enhanced as a larger suite of ecosystem services is measured at each site.

Conclusions

Advancing our current understanding of the effects of biodiversity change on ecosystem services will require assessments of how ecosystem functions cascade into service supply, delivery, and value. We need to move beyond ideal experimental conditions to realistic management scenarios in which services are actually delivered to particular stakeholders.

Syntheses are needed in order to understand the relative contribution of biodiversity to the supply of ecosystem services under actual management conditions. Such syntheses, drawing from current literature, would provide information on the universality or site dependence of biodiversity effects within a range of management contexts. Insight into which services depend on the maintenance of biodiversity and into how much and what kind of biodiversity is required to maintain the full set of services demanded by different stakeholders in a given context could be gained.

A new approach can fill these gaps, taking the best from a range of disciplines and approaches. A network of long-term, interdisciplinary, adaptive, and participatory experiments could cover a range of landscapes and seascapes, as well as a range of socioeconomic conditions. The results from across sites and across bundles of ecosystem services would provide information on the outcomes of alternative management conditions for a range of stakeholders and would allow an exploration of the contribution of biodiversity change to such outcomes.

Our analysis suggests that a new generation of research, conducted within the guiding context of IPBES, can inform on the causal chain of links between biodiversity change and ecosystem services. This knowledge is essential if we are to develop a multiscale decision and policy framework designed to effectively manage for biodiversity and ecosystem services over the coming century.

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Supplemental material

The supplemental material is available online at www.bioscience.oxfordjournals.org.

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