Linking the influence and dependence of people on biodiversity across scales

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Preface

Biodiversity enhances many of nature's benefits to people, including the production of wood in forests, livestock forage in grasslands, and fish in aquatic ecosystems. And yet people are now driving the sixth major extinction event in the history of life on Earth. The dependence of people on biodiversity, and our influence on it, have mainly been studied separately and at contrasting scales of space and time, but new multiscale knowledge is beginning to link these relationships. These advances will help assess the sustainability of human use of biodiversity and improve forecasts of future supplies of nature's societal benefits.

Introduction

Human-driven biodiversity loss[1-3] could substantially diminish ecosystem services[4-6] because species losses often cause losses of ecosystem functioning and stability[7-9]. Research in this area is timely because the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) is currently assessing changes in biodiversity, ecosystems, and their contributions to people in the face of anthropogenic drivers[10]. Biodiversity is also explicitly targeted in the United Nations Sustainable Development Goals. It remains difficult, however, to predict the extent to which human-driven changes in biodiversity will alter ecosystem services, especially at the larger spatial and longer temporal scales most relevant to policy and conservation, due to mismatches in the scales of knowledge of the influences and dependence of people on biodiversity.

Here we argue that linking our understanding of the influence and dependence of people on biodiversity will require new multiscale knowledge of several relationships (Fig. 1a-c) that have thus far been separately studied at contrasting scales (Fig. 1d). We first briefly introduce studies that have independently considered how anthropogenic drivers alter biodiversity at large scales, such as those over which species become globally extinct (Fig. 1a), how changes in biodiversity alter ecosystem functioning at small scales, such as those over which species interact (Fig. 1b), and how changes in ecosystem functioning alter ecosystem services at intermediate scales, such as those over which land use decisions are made (Fig. 1c). Then, we highlight recent advances in developing multiscale knowledge at the intersections of these areas of biodiversity science. Finally, we conclude by suggesting ways to strengthen biodiversity science in support of multiscale environmental policy.

Brief overview of disparate knowledge

The unprecedented scale and impacts of human activities on land and in the oceans are dramatically altering global biodiversity[1-3] (Fig. 1a). In fact, people are driving the sixth major extinction event in the history of life on Earth[1,2]. There is now overwhelming evidence that habitat loss and fragmentation, overexploitation of biological resources, pollution, species invasions, and climate change have increased global extinctions to levels far above background rates[1-3]. Human impacts may be immediate, such as when land is cleared for agriculture[11], but often extinctions occur decades or centuries later as reduced population sizes, restricted movements, and limited suitable habitat finally take effect[12,13]. Thus, the global species extinctions that have been documented in the recent past are but the tip of an iceberg of massive ongoing biodiversity changes, which include substantial declines in the population sizes of native species, local extinctions, local gains of new species, and spatial homogenization of the world's biota[13-15].

Local species losses often decrease ecosystem functioning (Fig. 1b). In particular, local species losses decrease the efficiency with which ecological communities capture biologically essential resources and produce biomass[8,9]. These biodiversity and ecosystem functioning (BEF) relationships have been rigorously investigated over the past quarter century in hundreds of biodiversity experiments[8,9,16] and dozens of theoretical[17,18] and observational studies in a wide range of ecosystems, including grasslands[19,20], forests[21-23], drylands[24], and marine[25] systems. Effects of biodiversity on ecosystem functioning often arise because coexisting species occupy different ecological niches, such as by differing in the way they exploit their resources, resist their natural enemies, or facilitate one another[8,26,27]. Results from biodiversity experiments[28,29] also support theory predicting that increased biodiversity enhances the stability of ecosystem biomass production because it enhances temporal complementarity between species[30-32] and other forms of asynchrony in population dynamics[33].

Changes in ecosystem functioning often lead to tradeoffs in the supply of ecosystem services flowing from different land uses and ecosystems (Fig. 1c). For example, food or fuel production have often been prioritized at the expense of the regulation of climate or the aesthetic inspiration provided by nature. Ecosystem service assessments account for a fuller suite of benefits and costs, finding, for example, that it can sometimes be more valuable in economic terms to manage land to enhance climate regulation and recreation than to expand food production[34,35]. Many of these studies project how, over the next few decades, anthropogenic drivers might alter the supply of ecosystem services by altering underlying ecosystem functions at landscape spatial scales[34,35].

In each of the following sections, we review recent results that are expanding the scales of knowledge of each of these relationships (Fig. 1a-c) and beginning to link them to one another. We show that the cascading impacts of human activities on biodiversity, ecosystems, and their consequences for people will likely increase at larger spatial and longer temporal scales. Further development of multiscale knowledge linking these relationships will help assess the sustainability of human use of biodiversity and improve forecasts of future supplies of nature's benefits to people. Much of our review focuses on species richness (numbers of species), which is a well-studied, albeit incomplete, surrogate for several other dimensions of biodiversity (Box 1).

Multiscale effects of anthropogenic drivers

Effects of anthropogenic drivers on biodiversity strongly depend on spatial and temporal scales. In this section, we highlight recent empirical evidence suggesting that the greatest net species loss will likely occur at large scales. Linking the impacts and dependence of people on biodiversity will require scaling down from long-term global extinction trends to under-explored contemporary trends in local and regional biodiversity (Fig. 1d).

From global extinction to local gain and loss

Although human activities are unarguably driving many global extinctions over centuries, impacts on biodiversity at local or regional spatial scales during recent decades are less clear. On one hand, rates of global extinctions may be slower than rates of local species loss because a species is not globally extinct until it has been lost from each and every local community. For example, in tropical forests, rates of species extinctions have been estimated to be three orders of magnitude lower than rates of population extirpation[36]. On the other hand, there may be greater *net* species loss at global than at local scales, if local species losses are offset by local species gains[37], such as when there are species introductions or range shifts[38]. In other words, loss of global (γ) diversity can be explained not only by loss of local (α) diversity, but also by spatial homogenization (loss of β diversity). Regardless of whether global extinction rates are slower or faster than the mean rate of net species loss locally, averaged across all local communities worldwide, there are certainly places on Earth where a large fraction of species has been lost, and other places where the number of species has recently increased.

Patterns of changes in local biodiversity are becoming increasingly clear at many places worldwide. In areas that have been converted to croplands or pastures, there has been substantial net loss of local biodiversity[11]. Specifically, land-use changes have decreased local species richness by approximately 14% on average worldwide, with losses of up to 76% of species in the worst-affected habitats[11]. Some of these human-driven losses of local biodiversity have likely emerged over centuries or millennia, given the long history of conversion and use of land by people. In remaining habitats, there have been local species gains in some places and local species losses elsewhere during recent decades[37,39-41]. Some of these recent gains may have caused a net increase in local species richness, for example through exotic species introductions or the colonization of new species shifting their ranges in response to climate change. But some apparent gains may simply be recovery of former species richness following relaxation of disturbance[42,43]. New studies are needed that attribute recent species gains to anthropogenic drivers, community assembly (or recovery), observation error, or other causes. The primary drivers of local species loss are better understood. A recent synthesis of hundreds of experiments and observational studies[44] found that local species loss was greater in response to land-use change (24.8%) and species invasions (23.7%) than to nutrient enrichment (8.2%) or warming (3.6%). Furthermore, species loss was greater for terrestrial biomes (22.4%) than for aquatic biomes (5.9%), and greater for endotherms (33.2%) and producers (25.1%) than for ectotherms (10.5%).

It is not yet known whether local species gains in some places tend to functionally compensate for local species losses elsewhere[45]. Gains of exotic species can have large positive or negative impacts on ecosystem functioning because exotic species often have different traits than do native species[45-47] (Fig. 2a,b). Independent of these shifts in species composition and traits, ecosystem functioning will tend to respond more to local species losses than to local species gains (of natives or exotics). This is because ecosystem functioning tends to increase in a decelerating manner[8,9,21] as species richness increases (thick black line in Fig. 2a). This means that, starting from any particular level of richness, losing a given number of species will impact ecosystem functioning more than gaining the same number of species[9]. Furthermore, at least for plants, the gain of an exotic species might not compensate completely for the loss of a native species in terms of function, because exotic species can exhibit less complementarity[48] than native species, which have interacted for a longer period of time, providing a greater opportunity for selection for niche differentiation[49]. Down-scaling knowledge of the effects of anthropogenic drivers on biodiversity in a manner that can be linked to knowledge of local biodiversity and ecosystem functioning relationships will require developing a much better understanding of the kinds of species that are coming and going (see *Human-driven changes in biodiversity* below) and of the drivers of species gains.

Extinction and ecosystem functioning debts

Biodiversity changes often continue to accumulate over many decades and centuries following initial disturbances. Past and present anthropogenic impacts have already accumulated an extinction debt, i.e., a large number of species that are committed to extinction because of these impacts but whose extinctions have yet to occur[12,13,50]. For instance, habitat fragmentation has created extinction debts that unfold over decades or longer, due to reduced population sizes and movements[12,13,50]. Extinction debts have been intensively studied over the past two decades and several experiments have now been running long enough to find that habitat fragmentation gradually reduces species richness in remnant fragments by 13-75% over a decade[13]. Similarly, the pace of climate change over recent decades has likely created extinction debts by generating a mismatch between the thermal preferences of many species and the new climate they are experiencing in their current geographic distribution[51]. The ability of species to tolerate or avoid changes in climatic conditions is limited, so the current failure of some species to adjust their geographic distribution in response to climate change is expected to lead to many local, and eventually global, future extinctions[51]. Delayed species extinctions were originally viewed as a tragic deterministic inevitability[12], but have more recently been more optimistically viewed by some as an opportunity to avert an impending extinction crisis through habitat restoration, assisted migration, and other conservation actions.

Extinction debts in turn are likely to generate biodiversity-dependent debts in ecosystem functioning and ecosystem services with local and global significance[43,52,53]. For example, habitat loss is likely leading to carbon emissions not only where carbon- and species-rich forests are converted to croplands, but also in remaining forest fragments where extinction debts are emerging[43]. Long before species become globally extinct, they first become rare or absent, and thus functionally extinct, within many local communities. Consequently, ecosystem functioning and service debts will likely occur gradually, rather than emerging only after extinction debts are paid in full. Long-term fragmentation experiments find ecosystem function debts in the form of delayed changes in nutrient cycling and as changes to plant and consumer biomass in small and isolated fragments. These functioning debts amounted to 30% loss after 1 year, rising to 80% loss after a decade[13]. New research is needed to forecast the magnitudes and rates of extinction, functioning, and service debts.

Multiscale effects of biodiversity

Ecosystem functioning strongly depends on biodiversity. In this section, we highlight theoretical and empirical evidence suggesting that these relationships often become stronger at larger scales of space and time. Linking the impacts and dependence of people on biodiversity will require scaling-up from intensively-studied local biodiversity effects to under-explored effects emerging at larger scales (Fig. 1d).

Emerging biodiversity effects

Predicting how ecosystem functioning will depend on biodiversity changes at larger spatial scales first requires determining whether local biodiversity effects are widespread and will therefore accumulate across ecosystems worldwide. Effects of local species richness on ecosystem productivity have recently been found across ecosystems globally in grasslands[19] and forests[21], with strengths of local relationships similar to those commonly found in local-scale biodiversity experiments[9]. Aggregating these local effects suggests that local plant species richness significantly affects the productivity of forests worldwide[21].

Predicting the ecosystem consequences of biodiversity changes at larger spatial and temporal scales also requires consideration of positive or negative biodiversity effects that could emerge at larger scales. At any point in time within a local community, ecosystem functioning depends on changes in biodiversity because of differences between species that result in selection effects, in which the most productive species dominates the community, complementarity effects, which include several types of niche partitioning and facilitation, or both[26]. Theory predicts that effects of changes in biodiversity on ecosystem functioning and stability could be greater at larger scales than they are on average at a particular place and time due to performance-enhancing spatial[54] and temporal[32] insurance effects (Fig. 3) that can emerge at larger scales.

Additional biodiversity effects can emerge at larger spatial scales when dispersal allows species to be present and dominate at places where they are best adapted to the local environment (Fig. 3). At larger scales, natural ecosystems are heterogeneous and connected by flows of species, energy, and resources. This connectivity governs how biodiversity change affects ecosystem function at different scales[55]. Theory[54] shows that spatial insurance effects are maximized at intermediate species dispersal rates that promote species coexistence, enhance ecosystem functioning, and stabilize temporal variability in ecosystem functioning across the landscape. Habitat fragmentation disrupts connectivity, leading to species loss and the degradation of ecosystem functions across entire networks of habitat patches[13,52,56,57]. Empirical[19,58,59] and simulation[55,60] studies provide evidence consistent with the spatial insurance hypothesis. For example, one study of many grasslands worldwide found that ecosystem productivity depended more on species richness across sites than within sites[19], and another study found that different sets of species promoted ecosystem functioning at different places[58].

Additional biodiversity effects can also emerge over longer temporal scales. Higher biodiversity tends to reduce the variability of ecosystem functioning[28,61] because species or populations differ in their growth responses to environmental fluctuations[31,58] through temporal niche complementarity[32], responses to competition[30], neutral random demographic variation[62] or a combination of all three[33]. The result is that although no single species can consistently provide ecosystem functioning at all times[58], many different species[31] or populations[61] can average out the fluctuations in the environment, providing temporal insurance[32] (Fig. 3). Interestingly, temporal insurance effects tend to be stronger as spatial scale increases because differences in species composition across space (β-diversity) desynchronize fluctuations in ecosystem properties at different locations[60]. As a result, ecosystem properties and services becomes less variable and more predictable at larger spatial scales. Anthropogenic drivers, however, could reduce ecosystem stability more at large than at small spatial scales if they not only drive local species loss, but also synchronize species fluctuations by homogenizing biota and abiotic conditions[60].

It is less well-known that insurance effects of diversity not only reduce temporal variance, but also enhance the temporal mean, of ecosystem productivity[32]. Thus, just as spatial insurance effects[54] can enhance biodiversity effects at larger spatial scales in heterogeneous landscapes[19,58,59], temporal insurance effects[32] can enhance biodiversity effects over longer temporal scales in fluctuating environments[8,31,58] (Fig. 3). Conversely, if species tend to dominate communities where and when they are least productive, then negative biodiversity effects could emerge at larger spatial and temporal scales. This possibility deserves further consideration. The loss of these temporal insurance effects of biodiversity will manifest in several ways: increases in the variance of ecosystem functioning, decreases in the mean of ecosystem functioning, and losses of community resistance to perturbations. For example, in grasslands, loss of local plant diversity substantially reduced the resistance of ecosystem productivity to climate extremes[29]. New studies are needed to determine how the magnitudes of insurance effects that emerge over space and time compare to those of short-term local biodiversity effects that are evident within snapshots of time and space.

In addition to stronger biodiversity effects emerging over longer temporal scales, the strength of local biodiversity effects within years might also gradually shift as anthropogenic drivers alter species' niches and competitive hierarchies. Recent experimental results suggest that local, intra-annual biodiversity effects will be of similar or stronger magnitude under future environmental conditions in grasslands[63-66]. For example, there is some evidence that increasing grassland plant species richness may increase ecosystem productivity more under future conditions that are warmer[63] and that have elevated concentrations of atmospheric carbon dioxide[64]. Across all studies included in a meta-analysis, grassland plant species richness increased productivity as much under nutrient enrichment and drought as under ambient resource conditions, though individual studies showed a wide range of responses[65]. Much more work is needed in many more ecosystems to determine the generality of these results and understand how drivers alter the many mechanisms by which changes in biodiversity alter ecosystem functioning.

Human-driven changes in biodiversity

The ecosystem consequences of human-driven changes in biodiversity depend not only on how many species are lost or gained, but also on which kinds of species are increasing or decreasing in abundance. Some species are more vulnerable to anthropogenic drivers than others[67]; and some species are more critical for ecosystem functioning than others[68-74]. The sheer number of species precludes studying the vulnerability and functional roles of each and every one. Instead, considerable progress has been made by approaches that use functional traits and phylogenetic diversity to predict which kinds of species are most vulnerable or critical[70-75].

Many kinds of species that are critical for ecosystem functioning are also vulnerable to anthropogenic drivers of biodiversity loss. For example, large-bodied species tend to be disproportionately vulnerable to extirpation[67,76] as well as particularly strong controllers of ecosystem functioning and services[45,77], such as pollination and dung burial[78]. Likewise, ocean acidification disproportionally threatens calcifying, reef-forming corals that provide critical habitat for vast food webs of marine species that cycle nutrients, provide primary and secondary productivity, support fisheries, and provide other values[79]. Furthermore, many top predators are both overexploited and particularly strong controllers of nutrient cycling, water quality, and other ecosystem services[9,77,80-82]. Additionally, nutrient pollution can shift plant competitive interactions, threatening e.g. native dominants[83] or rare legumes[84], the loss of either of which can substantially disrupt ecosystem functioning[83,85] (Fig. 2c). In all these cases of non-random changes in biodiversity, the systematic loss of critical biodiversity components would impact ecosystems more than would be expected based on the results of most biodiversity experiments and theory, including those reviewed above, which have considered random species loss (trajectory c in Fig. 2a).

New studies are needed to identify critical biodiversity components across spatial and temporal scales. Different plant species contribute to any particular ecosystem function during different years, at different places, and under different scenarios of anthropogenic change[58], and it remains difficult to predict which kinds of species will become increasingly dominant or rare in novel ecosystems with no historical analog in terms of biota and abiotic conditions. Conservation efforts could be short-sighted if they prioritize currently critical biodiversity components without also considering whether this same subset of biodiversity will remain critical in the future.

Nature's societal benefits depend on biodiversity

In this section, we highlight results from recent studies that are beginning to account for the dependence of ecosystem services on biodiversity. We explain how accounting for these relationships could help improve forecasts of future supplies of ecosystem services, especially at large scales. Linking the influence and dependence of people on biodiversity will require scaling ecosystem service studies up to the larger scales over which global extinctions are advancing and accounting for biodiversity effects across scales (Fig. 1d).

Decision-makers often prioritize short-term local benefits, without fully accounting for societal costs that are suffered by other people elsewhere and in the future. Ecosystem service assessments aim to correct these negative externalities by accounting for a fuller suite of benefits and costs, often by considering larger scales. For example, if one accounts not only for the immediate local economic benefits of expanding crop production across the landscape, but also for the long-term global costs of carbon emissions from land conversion, then it can be more valuable to establish parklands than to clear land for agriculture[34,35]. Similarly, if one accounts not only for the immediate local economic benefits of enhanced crop yields, but also for the long-term widespread health costs resulting from air and water pollution, then it can be valuable to reduce fertilizer use[86].

Most ecosystem service studies consider intermediate scales of space and time that match the scales at which some decisions are made (e.g., the Willamette Basin[34] or the United Kingdom[35]), but that are often smaller than those over which global extinctions are advancing and larger than those over which biodiversity effects are best-understood (Fig. 1d). Perhaps partly because of this mismatch in scales, most ecosystem services studies have not accounted for the direct dependence of ecosystem functioning on biodiversity[34,35]. This implicitly assumes that the remaining fragments of nature will continue to provide the same flows of benefits to people in the future, regardless of how their biodiversity might change over time[43]. In some cases, at scales or places where biodiversity changes little and/or ecosystem services depend much more on factors other than biodiversity, this assumption might hold. In other cases, particularly at large scales, ignoring the dependence of ecosystem services on biodiversity will lead to poor forecasts of future supplies of ecosystem services because it will fail to account for all the social costs of biodiversity loss.

Several recent studies have started to determine which ecosystem services depend on biodiversity either directly[87] or indirectly via their underlying ecosystem functions[4,5,21,43]. A recent study[5] found evidence that maintaining high biodiversity supports the production of crops in agricultural systems, wood in forests, forage in grasslands, and fisheries in aquatic ecosystems. Maintaining high biodiversity was also found to contribute to the regulation of pests by reducing invasion by weeds or pathogens, and of the climate by enhancing carbon storage[5]. However, another study noted many sources of uncertainty in several relationships between biodiversity and ecosystem services, including mismatches between the ecosystem functions measured and the final ecosystem services of interest, tradeoffs between positive and negative effects of biodiversity on service supply, and context-dependent patterns[4]. The direct contributions of biodiversity to a large number of ecosystem services, such as those related to cultural identity and aesthetic inspiration, remain under-explored. One study, however, found evidence that people appreciate high richness and evenness of plant species[87].

Recent studies have also begun to estimate the contributions of biodiversity to the monetary value of some ecosystem services[21,43,88], revealing that, if well-directed, the benefits of conserving biodiversity could be much greater than its costs. For example, it has recently been estimated that the value of biodiversity in maintaining carbon storage is on the order of US$0.3–3.1 trillion[43] and the value of tree diversity in commercial forest productivity is approximately $166–490 billion per year[21]. These values are much greater than current global conservation expenditures, which are estimated to be $21.5 billion per year[89], and even greater than the costs of meeting global biodiversity conservation targets, which are estimated to be $76.1 billion per year[90]. Estimates of the monetary value of maintaining natural habitats (i.e., habitat is present or absent) are even larger[91] than these values of maintaining biodiversity within habitats (i.e., habitat is diverse or depauperate). We emphasize, however, that biodiversity substantially contributes to many valuable societal benefits that cannot accurately be monetized, including aesthetic inspiration[87]. As the benefits of conservation are increasingly weighed against their costs, it will be critically important to account for both the indirect dependence of ecosystem services on biodiversity that is mediated by ecosystem functioning and the direct contributions of biodiversity to other ecosystem services, many of which are difficult or impossible to monetize. Both of these contributions of biodiversity to ecosystem services are currently missing from most valuation studies.

In order to further include the role of biodiversity in ecosystem service assessments, an important next step will be to identify biodiversity components that are critical for the ecosystem functions underlying ecosystem services. This is not an easy task because no species can maximize all ecosystem functions or services[27,81,92,93]. Tradeoffs limit the extent to which species that have traits associated with particular functions (e.g., high primary productivity) can also provide other functions (e.g., drought resistance). Thus, although a carefully-chosen monoculture may perform as well as a mixture of species for any single function under any particular set of environmental conditions[8], many different species contribute to many different ecosystem functions under a wider range of conditions[58,81,92,93]. Thus, multifunctional ecosystems across space and time depend not just on a few dominant species[94], but also on the contributions of many rare species[55,95] at multiple trophic levels[93]. Depending on whether the aim is to maximize a particular ecosystem service under carefully controlled environmental conditions (e.g., maize yield) or a wider bundle of services across a wider range of conditions (e.g., forage production, carbon storage, etc. across extensive landscapes), the best option might be to retain either a subset of species with particular traits or a diverse community with a wide range of traits.

Strengthening biodiversity science for policy

In addition to developing multiscale knowledge (Fig. 1d), biodiversity science will need to develop in several other new directions in order to support emerging policy priorities. The combination of increasing pressures from anthropogenic drivers of biodiversity loss along with growing demands for all kinds of ecosystem services in coming decades will present unprecedented challenges for policy and decision-makers. Well-designed research on the impacts of biodiversity changes could explore solutions to these challenges now, using combinations of theory, observations, and experiments (Fig. 4). Observations, but not experiments, are uniquely able to assess relationships at large spatial scales in natural ecosystems undergoing nonrandom changes in biodiversity. Observational studies are increasingly able to use statistical approaches to disentangle effects of changes in biodiversity and abiotic factors on ecosystems[19], bringing the conclusions of scientific studies closer to the spatial scales at which populations and species are lost, and at which societal benefits of nature are delivered to people. Experiments, but not observations, are able to create and assess future conditions that are currently unobservable. Thus, both types of empirical studies will be needed to consider the large spatial and temporal scales at which human impacts on biodiversity are expected to most significantly undermine human dependence on biodiversity. Additionally, functional trait and phylogenetic approaches[71,73,75] are uniquely able to generalize across types of species, rather than studying whether each and every species is vulnerable and critical. An important next step for this work will be to predict how vulnerable and critical species change across spatially heterogeneous, temporally fluctuating, and globally shifting environmental conditions.

Biodiversity science is also expanding to consider the dynamic interactions between people and nature in socio-ecological systems (*sensu*[96]) (Fig. 1). For example, the conceptual framework of the biodiversity-policy interface outlined by IPBES[10] includes many of the complex interactions between the natural world and human societies. This expansion has partly emerged from shifts in the framing of conservation, from protecting nature from human threats to conserving nature for its human uses, and most recently to emphasizing the interdependence of nature and people[97]. This expansion has coincided with increased recognition by the policy community that biodiversity supports human development and needs to be protected in order to fulfill fundamental human needs. For example, the 17 recently agreed Sustainable Development Goals include two goals that directly address marine and terrestrial biodiversity and natural resources, and several other goals that address biodiversity in some of their specific targets, including Goal 2 on zero hunger. Biodiversity science will also need to expand to consider a fuller range of instrumental (use and non-use) and relational values[98] of biodiversity, as well as the contributions of biodiversity to a good quality of life beyond its role in ecosystem functioning (represented by arrow from biodiversity directly to ecosystem services in Fig. 1). Expanding in these ways adds not only breadth, but also complexity, to biodiversity science and policy. One way to make such endeavors tractable will be to focus on the biodiversity and ecosystem functions that underpin critical services, perhaps by working backwards from wellbeing to services, functions, and biodiversity in the interacting elements shown in Figure 1.

There is now abundant evidence that human-driven biodiversity changes can substantially affect several ecosystem services by altering ecosystem functioning and stability at multiple scales of space and time. Environmental policy needs to account for these important effects by considering biodiversity as not only an output, but also an input, of environmental policy scenarios[99], such as future climate scenarios. In this way, well-directed biodiversity research and policy design could together secure for future generations the valuable and irreplaceable functional and other roles played by biodiversity, even under rapid global change.

References

1. Barnosky, A. D. *et al.* Has the Earth's sixth mass extinction already arrived? *Nature* **471**, 51-57 (2011).
2. Ceballos, G. *et al.* Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances* **1** (2015).
3. Pimm, S. L. *et al.* The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**, 987-+ (2014).
4. Balvanera, P. *et al.* Linking biodiversity and ecosystem services: Current uncertainties and the necessary next steps. *Bioscience* **64**, 49-57 (2014).
5. Cardinale, B. J. *et al.* Biodiversity loss and its impact on humanity. *Nature* **486**, 59-67 (2012). **Reviews and connects research on biodviersity and ecosystem functioning with research on ecosystem services.**
6. Chapin, F. S. *et al.* Consequences of changing biodiversity. *Nature* **405**, 234-242 (2000).
7. Tilman, D., Isbell, F. & Cowles, J. M. Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics* **45**, 471-493 (2014).
8. Cardinale, B. J. *et al.* The functional role of producer diversity in ecosystems. *Am. J. Bot.* **98**, 572-592 (2011).
9. O'Connor, M. I. *et al.* A general biodiversity–function relationship is mediated by trophic level. *Oikos* **126**, 18-31 (2017).
10. Díaz, S. *et al.* The IPBES Conceptual Framework — connecting nature and people. *Current Opinion in Environmental Sustainability* **14**, 1-16 (2015).
11. Newbold, T. *et al.* Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45-50 (2015). **Quantifies past changes, and projects future changes, in local species richness in response to land use changes using an unparalleled global database of biodiversity observations.**
12. Tilman, D., May, R. M., Lehman, C. L. & Nowak, M. A. Habitat destruction and the extinction debt. *Nature* **371**, 65-66 (1994).

13. Haddad, N. M. *et al.* Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* **1**, e1500052 (2015). **Synthesises the short and long term impacts of experimental habitat loss on biodiversity and ecosystem function.**

14. Butchart, S. H. M. *et al.* Global biodiversity: indicators of recent declines. *Science* **328**, 1164-1168 (2010).

15. Capinha, C., Essl, F., Seebens, H., Moser, D. & Pereira, H. M. The dispersal of alien species redefines biogeography in the Anthropocene. *Science* **348**, 1248-1251 (2015).

16. Reich, P. B. *et al.* Impacts of biodiversity loss escalate through time as redundancy fades. *Science* **336**, 589-592 (2012).

17. Tilman, D., Lehman, C. L. & Thomson, K. T. Plant diversity and ecosystem productivity: Theoretical considerations. *Proc. Natl. Acad. Sci. U. S. A.* **94**, 1857-1861 (1997).

18. Loreau, M. *From Populations to Ecosystems: Theoretical Foundations for a New Ecological Synthesis*. (Princeton University Press, Princeton, NJ, 2010).

19. Grace, J. B. *et al.* Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature* **529**, 390-393 (2016). **Shows that productivity depends on plant diversity, especially across sites, in naturally assembled grasslands worldwide.**

20. Hautier, Y. *et al.* Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature* **508**, 521-525 (2014).

21. Liang, J. *et al.* Positive biodiversity-productivity relationship predominant in global forests. *Science* **354** (2016). **Shows how tree diversity loss will lead to loss of productivity in forests worldwide and quantifies resultant economic costs.**

22. Paquette, A. & Messier, C. The effect of biodiversity on tree productivity: from temperate to boreal forests. *Glob. Ecol. Biogeogr.* **20**, 170-180 (2011).

23. Gamfeldt, L. *et al.* Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat. Commun.* **4**, 1340 (2013). **Shows that a greater number of tree species is more effective at delivering multiple ecosystem services across Sweden's forests.**

24. Maestre, F. T. *et al.* Plant species richness and ecosystem multifunctionality in global drylands. *Science* **335**, 214-218 (2012).

25. Duffy, J. E., Lefcheck, J. S., Stuart-Smith, R. D., Navarrete, S. A. & Edgar, G. J. Biodiversity enhances reef fish biomass and resistance to climate change. *Proceedings of the National Academy of Sciences* **113**, 6230-6235 (2016).

26. Loreau, M. & Hector, A. Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**, 72-76 (2001).

27. Turnbull, L. A., Isbell, F., Purves, D. W., Loreau, M. & Hector, A. Understanding the value of plant diversity for ecosystem functioning through niche theory. *Proceedings of the Royal Society B: Biological Sciences* **283**, 20160536 (2016).

28. Gross, K. *et al.* Species richness and the temporal stability of biomass production: A new analysis of recent biodiversity experiments. *The American Naturalist* **183**, 1-12 (2014).

29. Isbell, F. *et al.* Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* **526**, 574-577 (2015).

30. Lehman, C. L. & Tilman, D. Biodiversity, stability, and productivity in competitive communities. *Am. Nat.* **156**, 534 (2000).

31. Allan, E. *et al.* More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proceedings of the National Academy of Sciences* **108**, 17034-17039 (2011).

32. Yachi, S. & Loreau, M. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci. U. S. A.* **96**, 1463-1468 (1999).

33. Loreau, M. & de Mazancourt, C. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecol. Lett.* **16**, 106-115 (2013).

34. Nelson, E. *et al.* Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. *Front. Ecol. Environ.* **7**, 4-11 (2009).

35. Bateman, I. J. *et al.* Bringing ecosystem services into economic decision-making: land use in the United Kingdom. *Science (New York, N.Y.)* **341**, 45-50 (2013).

36. Hughes, J. B., Daily, G. C. & Ehrlich, P. R. Population diversity: Its extent and extinction. *Science* **278**, 689-692 (1997).

37. Sax, D. F. & Gaines, S. D. Species diversity: from global decreases to local increases. *Trends Ecol. Evol.* **18**, 561-566 (2003).

38. Hill, S. L. L. *et al.* Reconciling biodiversity indicators to guide understanding and action. *Conservation Letters* **9**, 405-412 (2016).

39. Dornelas, M. *et al.* Assemblage time series reveal biodiversity change but not systematic loss. *Science* **344**, 296-299 (2014).

40. Elahi, R. *et al.* Recent Trends in Local-Scale Marine Biodiversity Reflect Community Structure and Human Impacts. *Curr. Biol.* **25**, 1938-1943 (2015).

41. Vellend, M. *et al.* Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proc. Natl. Acad. Sci. U. S. A.* **110**, 19456-19459 (2013).

42. Gonzalez, A. *et al.* Estimating local biodiversity change: a critique of papers claiming no net loss of local diversitY. *Ecology* **97**, 1949-1960 (2016).

43. Isbell, F., Tilman, D., Polasky, S. & Loreau, M. The biodiversity-dependent ecosystem service debt. *Ecol. Lett.* **18**, 119-134 (2015).

44. Murphy, G. E. P. & Romanuk, T. N. A meta-analysis of declines in local species richness from human disturbances. *Ecology and Evolution* **4**, 91-103 (2014).

45. Wardle, D. A., Bardgett, R. D., Callaway, R. M. & van der Putten, W. H. Terrestrial ecosystem responses to species gains and losses. *Science* **332**, 1273-1277 (2011) . **Reviews worldwide evidence of the ecosystem effects of losses and gains of particular species or functional groups.**

46. Bellingham, P. J. *et al.* Browsing by an invasive herbivore promotes development of plant and soil communities during primary succession. *J. Ecol.* **104**, 1505-1517 (2016).

47. Buckley, Y. M. & Catford, J. Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management. *J. Ecol.* **104**, 4-17 (2016).

48. Wilsey, B. J., Daneshgar, P. P. & Polley, H. W. Biodiversity, phenology and temporal niche differences between native- and novel exotic-dominated grasslands. *Perspect. Plant Ecol. Evol. Syst.* **13**, 265-276 (2011).

49. Zuppinger-Dingley, D. *et al.* Selection for niche differentiation in plant communities increases biodiversity effects. *Nature* **515**, 108-111 (2014).

50. Ewers, R. M. & Didham, R. K. Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev.* **81**, 117-142 (2006).

51. Bertrand, R. *et al.* Ecological constraints increase the climatic debt in forests. *Nat. Commun.* **7**, 12643 (2016).

52. Gonzalez, A., Mouquet, N. & Loreau, M. in *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective* (eds S. Naeem *et al.*) Ch. 10, 134-146 (Oxford University Press, 2009).

53. Gonzalez, A. & Chaneton, E. J. Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. *J. Anim. Ecol.* **71**, 594-602 (2002).

54. Loreau, M., Mouquet, N. & Gonzalez, A. Biodiversity as spatial insurance in heterogeneous landscapes. *Proc. Natl. Acad. Sci. U. S. A.* **100**, 12765-12770 (2003). **Along with reference 32, provides the theoretical basis for temporal and spatial insurance effects, which are now being tested empirically.**

55. Thompson, P. L. & Gonzalez, A. Ecosystem multifunctionality in metacommunities. *Ecology* **97**, 2867-2879 (2016).

56. Laurance, W. F. *et al.* Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conserv. Biol.* **16**, 605-618 (2002).

57. Staddon, P., Lindo, Z., Crittenden, P. D., Gilbert, F. & Gonzalez, A. Connectivity, non-random extinction and ecosystem function in experimental metacommunities. *Ecol. Lett.* **13**, 543-552 (2010).

58. Isbell, F. *et al.* High plant diversity is needed to maintain ecosystem services. *Nature* **477**, 199-202 (2011).

59. Venail, P. A. *et al.* Diversity and productivity peak at intermediate dispersal rate in evolving metacommunities. *Nature* **452**, 210-214 (2008).

60. Wang, S. & Loreau, M. Biodiversity and ecosystem stability across scales in metacommunities. *Ecol. Lett.* **19**, 510-518 (2016).

61. Schindler, D. E. *et al.* Population diversity and the portfolio effect in an exploited species. *Nature* **465**, 609-612 (2010).

62. de Mazancourt, C. *et al.* Predicting ecosystem stability from community composition and biodiversity. *Ecol. Lett.* **16**, 617-625 (2013).

63. Cowles, J. M., Wragg, P. D., Wright, A. J., Powers, J. S. & Tilman, D. Shifting grassland plant community structure drives positive interactive effects of warming and diversity on aboveground net primary productivity. *Glob. Change Biol.* **22**, 741-749 (2016).

64. Reich, P. B. *et al.* Plant diversity enhances ecosystem responses to elevated CO_2 and nitrogen deposition. *Nature* **410**, 809-812 (2001).

65. Craven, D. *et al.* Plant diversity effects on grassland productivity are robust to both nutrient enrichment and drought. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **371** (2016).

66. Hooper, D. *et al.* A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* **486**, 105-108 (2012).

67. McKinney, M. L. Extinction vulnerability and selectivity: Combining ecological and paleontological views. *Annu. Rev. Ecol. Syst.* **28**, 495-516 (1997).

68. Hobbie, S. E. Effects of plant species on nutrient cycling. *Trends Ecol. Evol.* **7**, 336-339 (1992).

69. Hooper, D. U. & Vitousek, P. M. The effects of plant composition and diversity on ecosystem processes. *Science* **277**, 1302-1305 (1997).

70. Díaz, S. & Cabido, M. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* **16**, 646-655 (2001).

71. Lavorel, S. & Garnier, E. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* **16**, 545-556 (2002).

72. Suding, K. N. *et al.* Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Glob. Change Biol.* **14**, 1125-1140 (2008).

73. Díaz, S. *et al.* Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution* **3**, 2958-2975 (2013). **Provides conceptual basis and case studies for linking functional traits and phylogenetic diversity to ecosystem services.**

74. Naeem, S., Duffy, J. E. & Zavaleta, E. The functions of biological diversity in an age of extinction. *Science* **336**, 1401-1406 (2012).

75. Cadotte, M. W., Cardinale, B. J. & Oakley, T. H. Evolutionary history and the effect of biodiversity on plant productivity. *Proc. Natl. Acad. Sci. U. S. A.* **105**, 17012-17017 (2008).

76. Payne, Jonathan L., Bush, Andrew M., Heim, Noel A., Knope, Matthew L. & McCauley, D. J. Ecological selectivity of the emerging mass extinction in the oceans. *Science* (2016).

77. Estes, J. A. *et al.* Trophic downgrading of planet Earth. *Science* **333**, 301-306 (2011).

78. Larsen, T. H., Williams, N. M. & Kremen, C. Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecol. Lett.* **8**, 538-547 (2005).

79. Anthony, K. R. N., Kline, D. I., Diaz-Pulido, G., Dove, S. & Hoegh-Guldberg, O. Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences* **105**, 17442-17446 (2008).

80. Duffy, J. E., Richardson, J. P. & Canuel, E. A. Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecol. Lett.* **6**, 637-645 (2003).

81. Lefcheck, J. S. *et al.* Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nat. Commun.* **6**, 6936 (2015).

82. Dirzo, R. *et al.* Defaunation in the Anthropocene. *Science* **345**, 401-406 (2014).

83. Isbell, F. *et al.* Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proc. Natl. Acad. Sci. U. S. A.* **110**, 11911-11916 (2013).

84. Suding, K. N. *et al.* Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proc. Natl. Acad. Sci. U. S. A.* **102**, 4387-4392 (2005).

85. Fornara, D. A. & Tilman, D. Plant functional composition influences rates of soil carbon and nitrogen accumulation. *J. Ecol.* **96**, 314-322 (2008).

86. Keeler, B. L. *et al.* The social costs of nitrogen. *Science Advances* **2** (2016).

87. Lindemann-Matthies, P., Junge, X. & Matthies, D. The influence of plant diversity on people's perception and aesthetic appreciation of grassland vegetation. *Biol. Conserv.* **143**, 195-202 (2010).

88. Mace, G. M., Norris, K. & Fitter, A. H. Biodiversity and ecosystem services: a multilayered relationship. *Trends Ecol. Evol.* **27**, 19-26 (2012).
89. Waldron, A. *et al.* Targeting global conservation funding to limit immediate biodiversity declines. *Proc. Natl. Acad. Sci. U. S. A.* **110**, 12144-12148 (2013).
90. McCarthy, D. P. *et al.* Financial costs of meeting global biodiversity conservation targets: Current spending and unmet needs. *Science* **338**, 946-949 (2012).
91. Costanza, R. *et al.* Changes in the global value of ecosystem services. *Global Environmental Change* **26**, 152-158 (2014).
92. Hector, A. & Bagchi, R. Biodiversity and ecosystem multifunctionality. *Nature* **448**, 188-190 (2007).
93. Soliveres, S. *et al.* Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. *Nature* **536**, 456-459 (2016).
94. Grime, J. P. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* **86**, 902-910 (1998).
95. Soliveres, S. *et al.* Locally rare species influence grassland ecosystem multifunctionality. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371** (2016).
96. Carpenter, S. R. *et al.* Science for managing ecosystem services: Beyond the Millennium Ecosystem Assessment. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 1305-1312 (2009).
97. Mace, G. M. Whose conservation? *Science* **345**, 1558-1560 (2014).
98. Chan, K. M. A. *et al.* Opinion: Why protect nature? Rethinking values and the environment. *Proceedings of the National Academy of Sciences* **113**, 1462-1465 (2016).
99. IPBES. Summary for policymakers of the methodological assessment of scenarios and models of biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. (Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany, 2016). **Evaluates available scenarios and models to explore plausible future changes in biodiversity and their societal consequences, as a result of human drivers, and provides a road map for their use.**
100. Purvis, A. & Hector, A. Getting the measure of biodiversity. *Nature* **405**, 212-219 (2000).

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Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to F.I. (isbell@umn.edu).

FIGURE LEGENDS

Figure 1. People influence and depend on biodiversity. (a) People directly influence biodiversity by changing land use, climate, and biogeochemical cycles, as well as by introducing species. At global scales, these human activities are driving the sixth mass extinction in the history of life on Earth. (b) At local scales, species losses decrease ecosystem functioning (e.g., ecosystem productivity and resource uptake) and stability (invariability of ecosystem productivity across years). (c) At regional scales changes in ecosystem functioning can alter the supply of ecosystem services, such as the production of wood in forests, forage for livestock in grasslands, and fisheries in aquatic ecosystems. (d) There are currently mismatches between the spatial and temporal scales at which these relationships are best understood, making it challenging to link these cascading effects of human activities on biodiversity, ecosystems, and ecosystem services. Furthermore, the scales of knowledge for some of these relationships do not yet align with the scales at which policies and other decisions are often made (indicated by orange circle). Relationships are shown at the approximate scales over which they are currently best understood. Herein we emphasize the importance of extending knowledge of these relationships across scales and we highlight recent advances in developing multiscale knowledge at the intersections of these areas of biodiversity science. We also suggest ways to strengthen biodiversity science in support of multiscale environmental policy within the broader network of interactions and feedbacks between the numerous components of socio-ecological systems (including effects shown by gray arrows). Color gradient blends between ecological (blue) and social (orange) components of the integrated system.

Figure 2. Anthropogenic drivers can impact ecosystems by changing numbers of species and by favoring some species over others. Most biodiversity experiments have considered how ecosystem functioning depends on random species loss, finding an increasing, but decelerating relationship (thick black line in panel a). Nonrandom, human-driven biodiversity changes also include shifts in which species (and traits) are most vulnerable or favored, which can reinforce (b, c) or counter-balance (d) effects of changes in richness. (b) Herbivore invasion can increase plant productivity by increasing plant richness, and these positive effects can be enhanced when the favored plants contribute substantially to plant productivity[46]. (c) Nutrient enrichment can decrease plant productivity by decreasing plant richness, and these negative effects can be reinforced when the most vulnerable plants contribute substantially to plant productivity[83]. (d) Habitat fragmentation can decrease arthropod biomass by decreasing arthropod richness, but these effects can be relatively small when the most vulnerable arthropods contribute very little to arthropod biomass[53]. Trajectories labeled b-d in panel (a) correspond to panels b-d. Curved arrows in panels b-d show indirect effects. Horizontal arrows in panels b-d represent other effects of drivers on ecosystem functioning that are independent of changes in richness or traits. Gray shaded region in panel (a) shows variation across species compositions within levels of species richness. *Indicates hypothesized relationship.

Figure 3. Having many dissimilar species can enhance and stabilize ecosystem productivity at larger spatial and temporal scales in variable environments. This conceptual diagram shows the case where plant species differ in the level of soil moisture at which they are most productive (leftmost panel in row a, each distribution is a different species and is color coded by the wet [blue] or dry [red] conditions in which the species is most productive), environmental factors change as shown over time (column 2 row a) and space (column 3 row a), and species dominate communities under conditions in which they are the most productive. In this case, communities that have two dissimilar species (row c) or many species (row d) are expected to be more productive and less variable in productivity over time and space than communities with only two similar species (row b). These performance-enhancing and

stabilizing temporal and spatial insurance effects that arise over space and time can be thought of as a combination selection and complementarity effects because they emerge when species have complementary traits and dominate where and when they are most fit.

Figure 4. Multiple complementary research approaches, each with different strengths and weaknesses (green bars, top) are needed in combination to understand the ecosystem consequences of human-driven biodiversity change, and thus to inform decision making (thick purple arrow). Note that these approaches (blue boxes) enrich each other in multiple directions, and it is the result of their combination that best informs policy and decision making at the scales at which populations and species are changed, and at which nature's benefits to people are delivered (yellow boxes). It is crucial to utilize all approaches (blue boxes) simultaneously to improve our knowledge of socio-ecological systems and inform policy and decision making.

Box 1

Dimensions and scales of biodiversity

Biodiversity is a broad term that represents the variety of life on Earth. There are numerous dimensions of biodiversity reflecting genetic (e.g., genotypes), organismal (e.g., phenotypes), ecological (e.g., population, community, ecosystem), taxonomic (e.g., species, genus, family), and functional (e.g., effect and response traits) attributes at different scales of space (e.g., site, country, biome) and time. Diversity can be quantified at multiple nested scales (e.g., α, β, γ), using measures of richness (e.g., number), evenness (equity of relative abundance), dominance (concentration of abundance), or combinations of these (Shannon's diversity, Simpson's diversity, probability of interspecific encounter). While it is prohibitive to consider every dimension and scale of biodiversity, it is vital to understand the strengths and limitations of each.

Our review focuses largely on species richness because it is a common surrogate for several dimensions of biodiversity, but richness can miss some significant components of biodiversity that are relevant for ecosystem functioning. For example, phylogenetic diversity or functional traits may be better predictors of ecosystem functioning than species richness in some cases[100]. Additionally, ecosystem functioning and services depend not only on the numbers and kinds of species, but also on interactions between species, such as predator-prey, herbivore-plant, pollinator-host interactions. Further, in most biological communities, only a few species are dominant, while many are rare. Species richness does not incorporate measures of abundance that are crucial for many ecosystem functions. However, species richness may be a useful "catch all" for unknown differences or interactions between species, and may help account for the fact that species' relative abundances are not static, and instead vary across spatially heterogeneous and temporally fluctuating conditions. Additionally, species richness may usefully predict the system's capacity to respond to unknown future conditions, as there is still high uncertainty regarding which species will flourish or diminish under future novel conditions.

Studies are now moving beyond debating which components of biodiversity are the single best predictors of changes in ecosystems, instead drawing on the strengths of multiple dimensions of biodiversity and approaches to advance multiscale understanding[38].

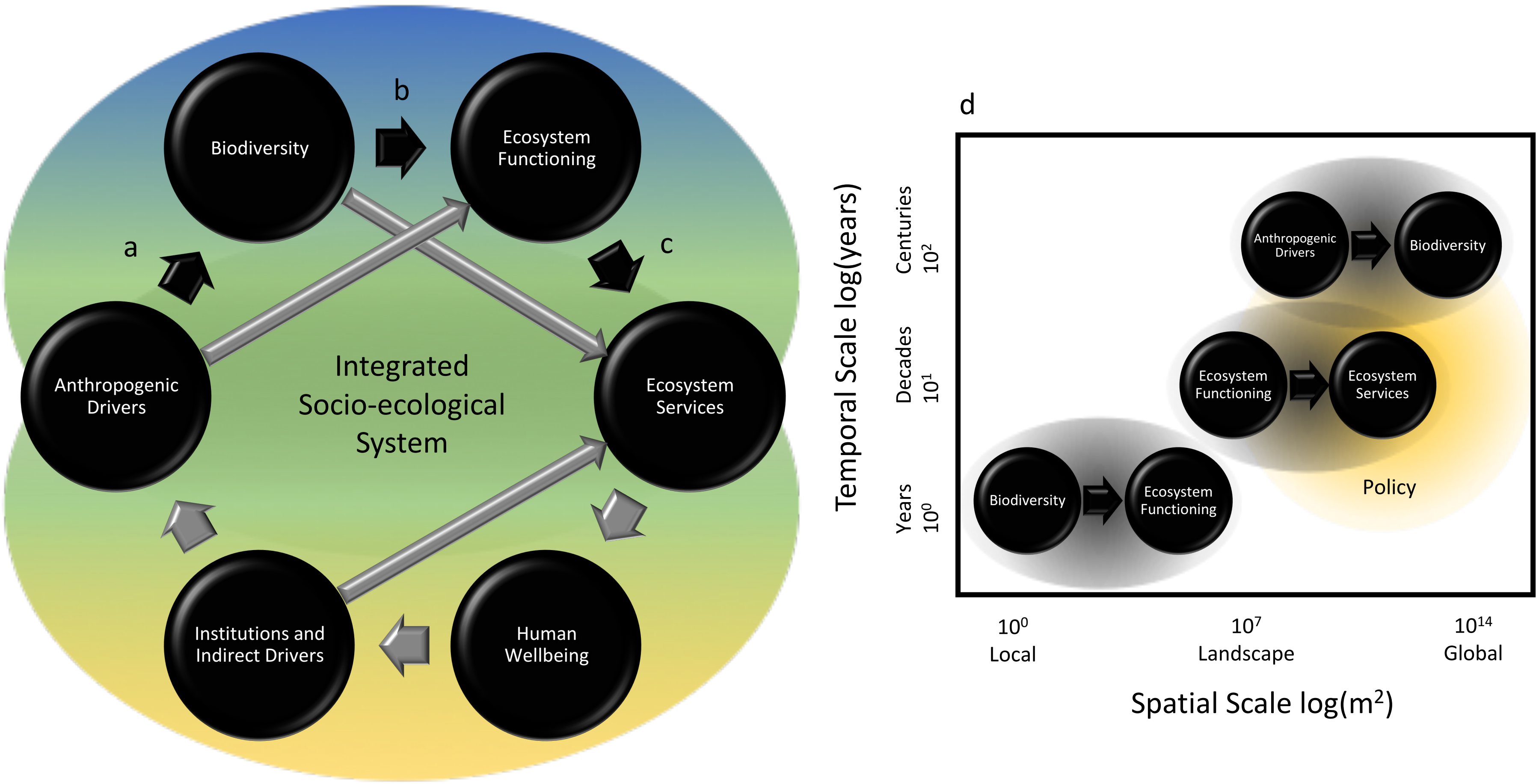
b
Biodiversity
Ecosystem Functioning
a
c
Anthropogenic Drivers
Integrated Socio-ecological System
Ecosystem Services
Institutions and Indirect Drivers
Human Wellbeing
d
Temporal Scale log(years)
Centuries 10^2
Decades 10^1
Years 10^0
Anthropogenic Drivers
Biodiversity
Ecosystem Functioning
Ecosystem Services
Policy
Biodiversity
Ecosystem Functioning
10^0 Local
10^7 Landscape
10^{14} Global
Spatial Scale log(m^2)

Figure 1

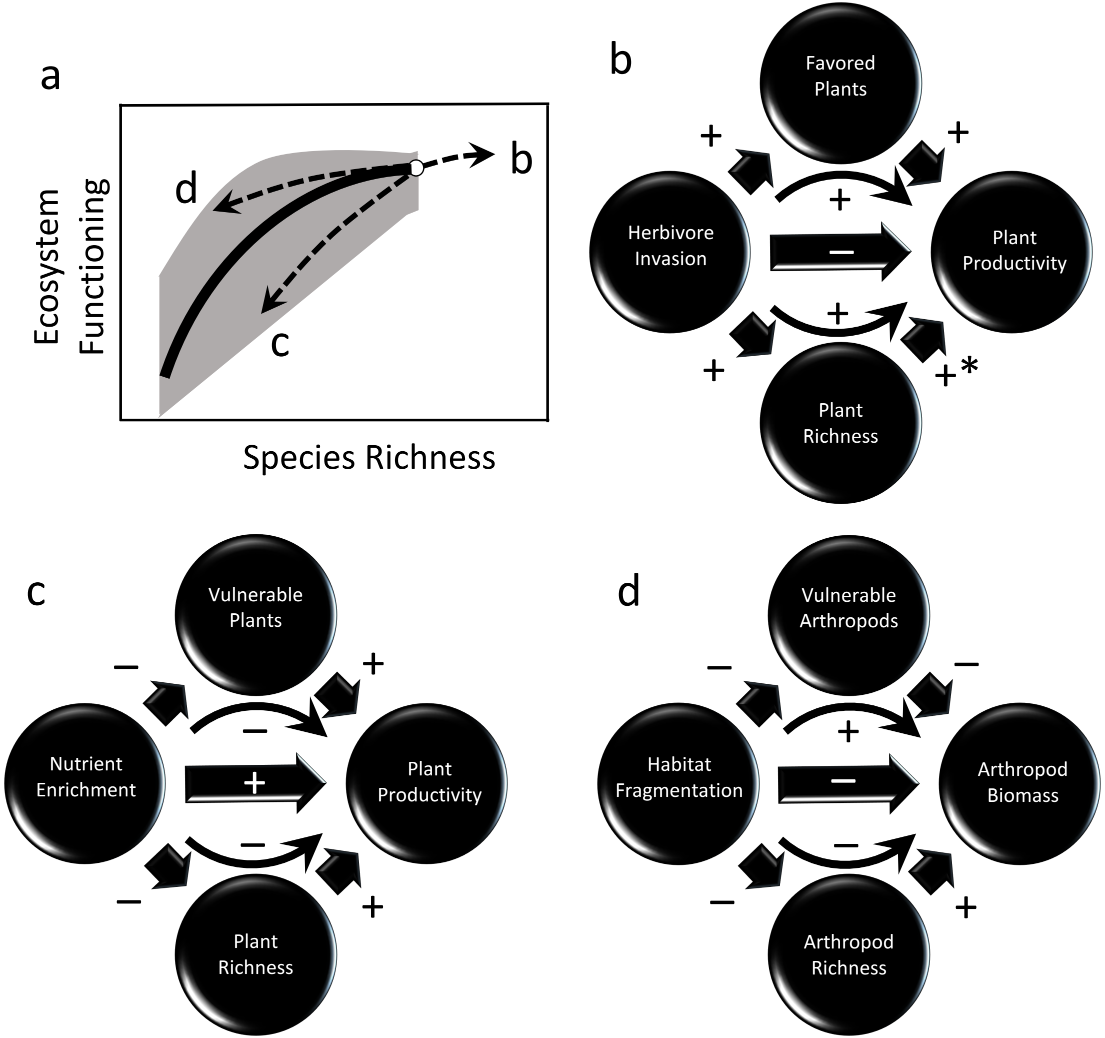
a
Ecosystem Functioning
Species Richness
b
d
c
b
Favored Plants
Herbivore Invasion
Plant Productivity
Plant Richness
+
+
+
−
+
+
+
+*
c
Vulnerable Plants
Nutrient Enrichment
Plant Productivity
Plant Richness
−
+
−
+
−
−
+
d
Vulnerable Arthropods
Habitat Fragmentation
Arthropod Biomass
Arthropod Richness
−
−
+
−
−
−
+

Figure 2

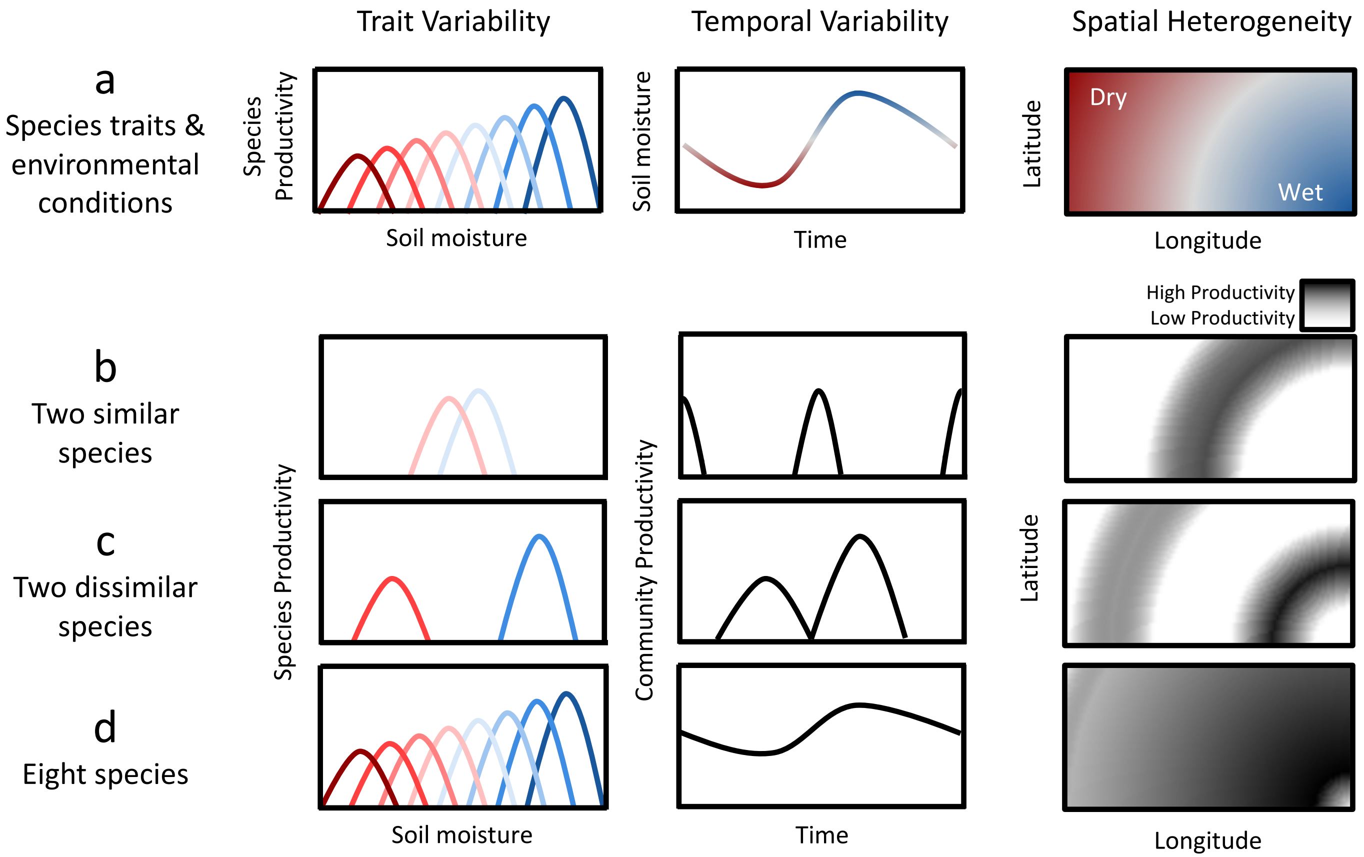
Trait Variability
Temporal Variability
Spatial Heterogeneity
a
Species traits & environmental conditions
Species Productivity
Soil moisture
Soil moisture
Time
Latitude
Dry
Wet
Longitude
High Productivity
Low Productivity
b
Two similar species
c
Two dissimilar species
d
Eight species
Species Productivity
Community Productivity
Latitude
Soil moisture
Time
Longitude

Figure 3

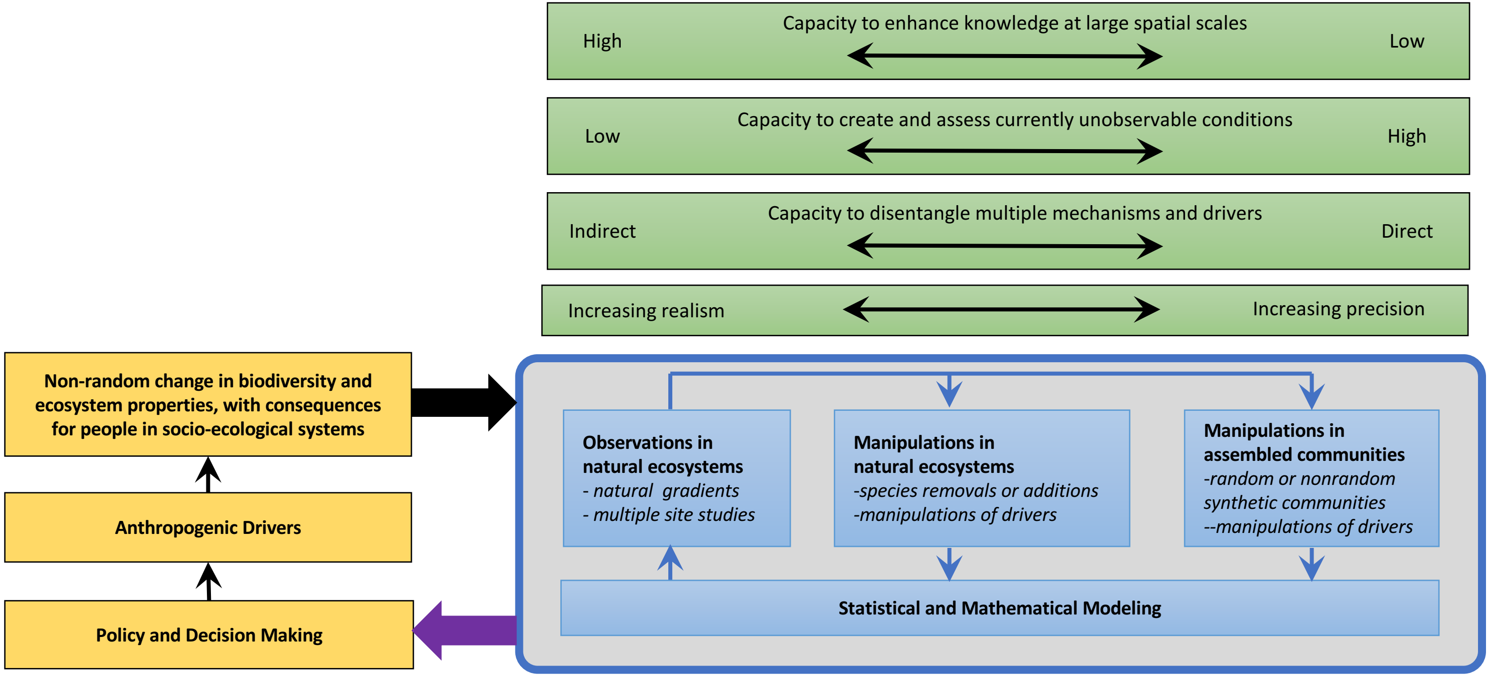
Capacity to enhance knowledge at large spatial scales
High
Low
Capacity to create and assess currently unobservable conditions
Low
High
Capacity to disentangle multiple mechanisms and drivers
Indirect
Direct
Increasing realism
Increasing precision
Non-random change in biodiversity and ecosystem properties, with consequences for people in socio-ecological systems
Anthropogenic Drivers
Policy and Decision Making
Observations in natural ecosystems
- natural gradients
- multiple site studies
Manipulations in natural ecosystems
-species removals or additions
-manipulations of drivers
Manipulations in assembled communities
-random or nonrandom synthetic communities
--manipulations of drivers
Statistical and Mathematical Modeling

Figure 4