Agenda 2050: Challenges for biodiversity-ecosystem functioning research

Mary I. O'Connor, Akira Hori, Andrew Gonzalez, Michel Loreau, Meghan Avolio, Jarrett Byrnes, Jane Cowles, Laura Dee, Yann Hautier, Andy Hector, Forest Isbell, Kim LaPierre, Tim Newbold, Charlie Outhwaite

(please correct this list, I'm sure it's missing people!)

Possible venues:

Current Opinions in The Environment and Sustainability (these are really short <2000 words, and invited; there is a longer version (<3000 words) and we can inquire). I'd like to know if, after reading this, you think we should aim for super-concise and the shorter version, or explain in more detail and aim for something longer - Bioscience perhaps?]

Abstract [100-200 words]:

Humans have become a major component of global biodiversity; our well-being depends on sustainable biodiversity and ecosystem services, and our actions drive changes in biodiversity and ecosystem services at local and global scales. Ecological science has demonstrated how feedbacks between biodiversity and ecosystem function govern the consequences of biodiversity change. Yet, major policy platforms are still catching up to this integrated perspective, at times treating biodiversity, ecosystem functions and services separately, ignoring feedbacks between them. Seven knowledge gaps impede integration of feedbacks into policy and research platforms. These include the need for more comprehensive theory for how people interact with biodiversity - function feedbacks across scales, theory for how to relate observations of biodiversity to dynamic change in the biodiversity-ecosystem function system, and how ecosystem services depend on feedbacks at different scales of the biosphere. To meet these challenges, we outline a 5-point agenda for action based on collaboration and connection among scientists and policy-makers that emphasizes open and international access to data, projects and products. We argue that efforts to protect biodiversity require the best possible scientific understanding of biodiversity trends, ecosystem functions, and - critically - the feedbacks between them across spatial scales.

I. Global science and policy efforts require scientific understanding of biodiversity and ecosystem functioning feedbacks across scales

Minimizing irreversible biodiversity change and identifying sustainable limits to ecosystem changes are two of the greatest ecological challenges of our time (Watson and Zakri 2005, Ceballos et al. 2017, Diaz et al. 2019). Achievingsustainable levels of biodiversity change is a primary motivation of international agreements and targets aimed at biodiversity and ecosystem functions (United Nations 1992). Policies and conservation efforts guided by these agreements require robust scientific models that allow identification of solutions and visualization of possible futures to guide decisions about how people can best influence drivers of change in biodiversity and its functions and services {IPBES:uq}. These models must integrate scientific understanding of the complex nature of biodiversity and ecosystem function feedbacks at multiple spatial, temporal and biological scales.

The conceptual framework of the IPBES (Diaz:2015ja; Diaz et al. 2019) outlines some of the pathways through which nature contributes to people (Box 1). This framework is offered with the purpose of aligning assessments of change and scientific knowledge development with policy needs (Pascual et al. 2017, Díaz et al. 2018). The IPBES framework is also offered to the broader community as a system for understanding how biodiversity, inclusive of humanity and human diversity (Box 1, Glossary), are related to a sustainable biosphere (Pascual et al. 2017). While this framework does incorporate interactions between people and nature (Box 1), it does not yet fully reflect our knowledge (and limits to knowledge) of the feedbacks between biodiversity and function that underlie the human well-being and biodiversity that are central to the framework (Mace 2019).

Biodiversity, ecosystem function and human well-being are intricately related in a complex living system defined by feedbacks within and between these elements (see Glossary for definitions) (Ross et al 2017 Eco Letts), yet the characterization of these elements in the policy frameworks that guide high-level assessments does not fully incorporate feedbacks. Biodiversity science has demonstrated biodiversity - ecosystem function feedbacks (Odorico et al. 2013)(good refs?), as well as feedbacks between people, biodiversity and function (Isbell et al. 2017, Dee et al. 2017a). Most evidence supporting these feedbacks comes from theory and empirical evidence that builds on our understanding of how ecosystem processes generate and maintain biodiversity, and biodiversity in turn increases stability of ecosystem functions such as productivity (Schindler et al. 2010, Wang and Loreau 2014), provides of food and nutrition to people (Frison et al. 2011), and responds to conservation decisions (Dee et al. 2017b).

Failure to consider biodiversity (inclusive of people, Box 1) and ecosystem functions as a system of interactions and feedbacks at multiple scales likely underestimates the severity of the sustainability challenges we face and risks missing key opportunities for mitigation and solutions. Furthermore, if policy frameworks that do not fully integrate the current state of scientific knowledge guide major investments in scientific research, they may limit the scope of

efforts to understand of nature as the diverse, complex adaptive system we know it to be. We cannot afford this just when we need science urgently to guide our planning for the future.

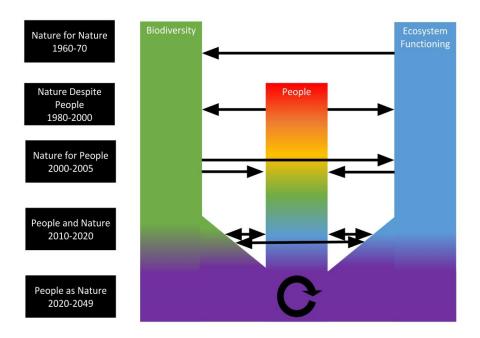
As scientists concerned with understanding nature and seeing this understanding applied in efforts to make decisions, we identify two current challenges. First, we argue that the current understanding of feedbacks between biodiversity and ecosystem functions can be more effectively integrated into existing conceptual frameworks, models and assessments. Second, the absence of emphasis on feedbacks in the current IPBES framework implies that we need a deeper and more applicable understanding of the feedbacks between biodiversity and ecosystem functioning across scales. Overcoming these challenges requires targeting these feedbacks as scientific research goals, and considering how assessments and policies can best reflect this knowledge development and subsequent gain.

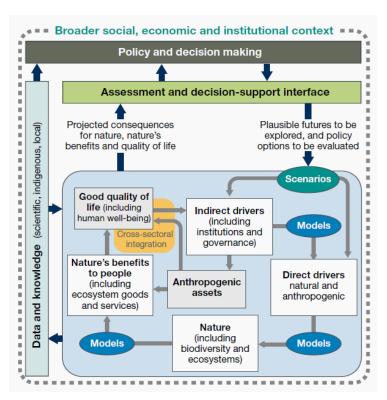
Here, we outline a research agenda to meet the second challenge. We begin by highlighting knowledge gaps in our current scientific understanding of biodiversity ecosystem function feedbacks when humans are an integral part of the dynamic system [Box 1]. Then we outline seven major scientific challenges that deserve organized and collaborative investment for rapid progress. Finally, we outline an agenda for action to meet these challenges to support policy-relevant science in a changing world, as our understanding of that world also changes.

--- Box 1--- Conceptualizations of the biodiversity - function system and its inclusion of humans have evolved over time in western science ------

The way biodiversity and ecosystem function feedbacks have been considered in the context of humanity's relationship with nature has changed over the last half-century. Though early leaders in ecology and biodiversity science noted biodiversity and ecosystem functioning feedbacks {Hector: 2002tn; Minikata ref. others?), they did not feature in the dominant paradigm of the 1950s to 1980s of conservation of nature for itself (Figure 1A). Biodiversity-functioning relationships were raised in the 1960s, with the realization that extinctions of species might reduce ecosystem functioning (the Ehrlichs' analogy of species loss as the popping of rivets in spaceship Earth; {Mace:2014bl}). In the 1990s, biodiversity and ecosystem functioning and ecosystem services became a formal field of research. This 'nature for people' framing rapidly led to the integration of ecology and environmental economics. In contemporary framings, the emphasis on biodiversity function feedbacks is mixed, with some approaches that include a link between diversity and function (e.g. ecosystem stability) while others treat biodiversity as purely responsive to global change drivers (the resilience and planetary boundary frameworks). The most recent scientific developments converge with themes in many cultures that envision biodiversity as inclusive of people and human behaviour (United Nations 2015, Diaz et al. 2019) (Figure 1B) [glossary]. The current IPBES framework maps biodiversity, function and people in ways that do not capture the important feedbacks within and among these elements of the biosphere (Figure 1B). The agenda we propose aims to frame the relationships among biodiversity – inclusive of people - and function to emphasize a strong scientific understanding of feedbacks across scales. [maybe give letters to the levels in the color figure].

Figure 1A: Progression of framings for the conservation of biodiversity over time (developed from (Mace 2014)) showing those that include the link between diversity and function (COLOUR arrows) versus the introduction and emphasis of other relationships (COLOUR arrows). Later framings complement (not replace) earlier ones, although some do not include the link between diversity and function. People and human activities were absent from earlier framings and have increasing prominence in more recent ones. Figure 1B: IPBES framework (Díaz et al. 2015).





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Glossary:

- **Biodiversity**: variety of life. We use the concept to include people in the living earth system; biodiversity is measured at many scales and in many ways, from genetic diversity to functional diversity to behavioral or cultural diversity (ref).
- **Beta diversity**: spatial or temporal variation in the composition of biodiversity
- **Ecosystems**: joint biotic/abiotic systems of life, characterized by dynamic stocks and fluxes of energy, materials and information in the form of biodiversity.
- Biodiversity-ecosystem function (BEF) relationship: refers to the relationship between diversity per se and the magnitude and stability of an ecosystem function. Biodiversity-ecosystem functioning (BEF) relationships, when broadly defined, are inclusive of the total biomass of living organisms, as well as the identities or importance of specific organisms. BEF defined more narrowly refers to the role diversity plays in an ecosystem function that is over and above the importance of total abundance, biomass or composition of the biological assemblage.
- **Ecosystem functions**: the processes of energy flow (e.g., primary production), material cycling (e.g., carbon cycling) and information processing (e.g., evolution) done by living systems. Functions are understood to reflect interaction networks involving multiple genetic and functional elements of biodiversity.
- **Ecosystem services**: the value of ecosystem functions to people (MA). Value can be assessed in a variety of ways, from economic values to cultural values, in intrinsic, instrumental or relational systems (Chan et al. 2016).
- **Natures contributions to people** = inclusive of ecosystem services as defined in MA, but also includes other ways to conceptualize nature and people (Pascual et al. 2017).

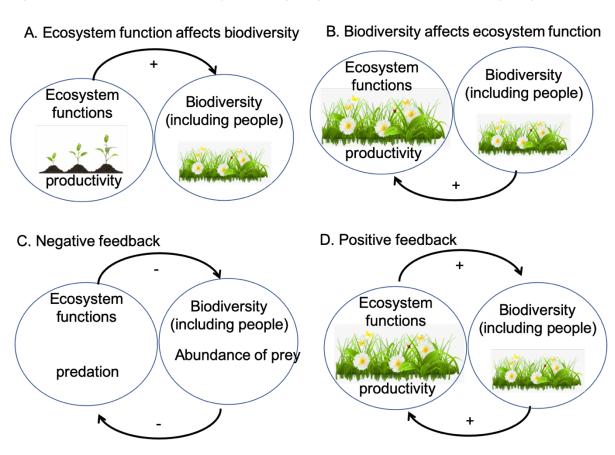
II. Planetary biodiversity and ecosystem function feedbacks

Feedbacks are sets of interactions that can determine the stability and future trajectories of living systems (Figure 2). Negative feedbacks are self-damping and stabilizing, and can buffer systems against change. Negative feedbacks between consumer diversity and prey abundance can lead to short-term increases in prey consumption that ultimately lead to declines in prey or pest abundance, and consequently predator abundance allowing prey to recover (good example). In contrast, positive feedbacks are self-reinforcing and can be destabilizing. For example, productive grasslands can shift to deserts in a process called 'desertification' when positive feedbacks between plant diversity and function (productivity, biomass, moisture retention in the system) are disrupted by diversity loss or climate change, and soils dry (ref). As the ecosystem desertifies, functions of plant production and moisture retention are lost, and biodiversity cannot recover, in a negative feedback between soil drying and plant diversity (see Sasaki et al. 2009, Ecology for the influences of wind erosion). The ultimate consequence of this positive feedback is a shift in ecosystem state to a state less desirable to humans (Odorico et al.

2013) - a landscape scale change mediated by the balance of feedbacks between plants and their environment at finer spatial scales.

Feedbacks can occur among all elements of the biosphere, and are response for rapid changes in living systems that may not be anticipated by simple one-way relationships. For example, a perception that people affect biodiversity but that there is no feedback from biodiversity to people is increasingly recognized as dangerous for human well-being in short and long-term thinking (United Nations 2015, Diaz et al. 2019). Feedbacks in socio-economic-ecological systems are affected by the fast recent and current growth of the global human population and economic activities. In turn, human growth and activities feed back to affect human population dynamics and economic activities in the long run through changes in ecosystem functioning, and thereby in the provision of ecosystem services and human wellbeing.

Figure 2. illustration of one-way effects (A, B) and two feedback loops (C, D).



III. Feedbacks are more than the sum of their parts

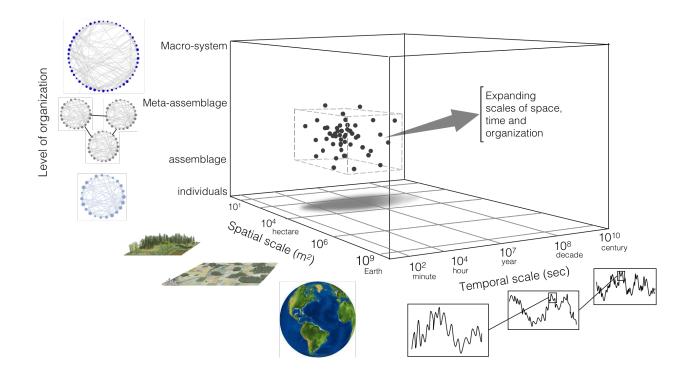
While biodiversity, ecosystem functions and human systems each change and affect the others (Figure 2), the feedbacks between these elements of complex living systems create ecological and social dynamics across scales are still not well understood. For example, we have science-based support for a general understanding of how humans affect biodiversity (Butchart et al. 2010, Dirzo et al. 2014, Newbold et al. 2015, Ceballos et al. 2017)(Ripple et al 2019 conservation biology), how humans affect ecosystem function (IPCC, other good refs), how biodiversity affects ecosystem functioning (Cardinale et al. 2011, Liang et al. 2016, Isbell et al. 2017) and how ecosystem functions affect humans (e.g., nature's contributions to people) (Balvanera et al. 2013, Isbell et al. 2014, Pascual et al. 2017) (Figure 2). These one-way effects are essential but incomplete representations of change in our biosphere.

One pervasive consequence of the persistent decoupling of biodiversity and function is that most of the biodiversity observations being assembled for assessments do not have accompanying measures of ecosystem processes. As a result, future trajectories of diversity, function or human well-being are impossible to project with only observations of biodiversity. Similarly, observations of ecosystem functions such as production, carbon storage or nutrient uptake in the absence of biodiversity estimates from the same places and times are difficult to project forward with confidence, given the inability to project changes in the diversity / function feedbacks.

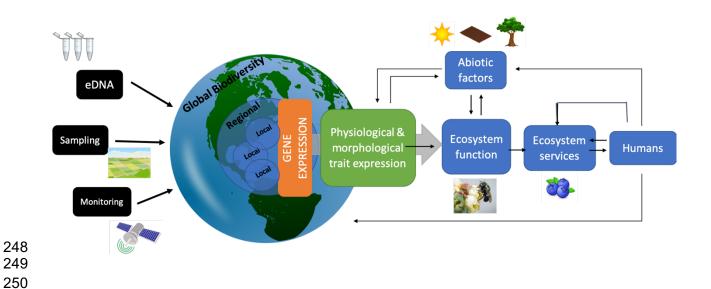
Feedbacks cause behavior in systems that can differ radically from what is predicted based on simpler models without feedback. Because feedbacks inherently introduce nonlinear relationships between elements and states of systems (Peters et al. 2004), observations of biodiversity without related observations of function in the same time and space, together with an understanding of feedbacks, cannot reliably predict future or unobserved states. In scientific, social and policy contexts, we often rely on a combination of our intuition and model projections of scenarios or context we cannot directly observe (observation may be impossible because we are in a different place or time, or because the size or scope of what we want to observe is beyond our direct abilities). Without considering feedbacks in these elements of living systems, efforts to project future states may be limited, even with large amounts of observations in hand (Peters et al. 2004). This mismatch between biodiversity data and the theory and concepts that allow projections of future states is amounting to a crisis of knowledge for sustainability scenarios.

Figure 2b. Biodiversity across dimensions of life affect the abiotic environment and ecosystem function via the metabolism, behavior and activities of individual organisms, associated with the traits they express. Feedbacks exist between the abiotic environment, ecosystem functions, people, ecosystem services and biodiversity. We observe biodiversity and functions, and we value services, but we are still learning about how to observe and monitor the feedbacks that determine the ultimate stability and change of the entire system.

A. Lifted from Gonzalez et al in review; placeholder here for a figure that illustrates the hierarchical nature of diversity – species > populations > OTUs > genotypes / phenotypes (for challenge 3) and spatial and temporal variation (for challenge 4).



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III. Grand challenges in Biodiversity Research. All existing knowledge points to unprecedented changes to the Earth system, the biosphere and human societies in the coming decades as a result of changes in biodiversity-function feedbacks. Here, we outline 7 scientific

challenges that are top priorities for major investment to enhance our knowledge frameworks to support biodiversity policies and to realize sustainability goals.

- 1. What are the feedbacks between biodiversity, and in particular its human component, and ecosystem function? A major future challenge will be to account for the indirect effects of changes in biodiversity on human societies and for the resulting feedbacks these effects have on biodiversity and ecosystems. A research agenda should aim toward an ultimate goal of fully including the multiple human (behavioral, demographic, social, political, economic, institutional) components of these feedbacks. There is growing recognition of the importance of the feedbacks that couple natural and social systems; some authors now even argue that the dynamics of either natural or human systems cannot be understood without considering these feedbacks explicitly. This is especially true at the global scale, where long-term feedbacks play a prominent role, but there is evidence that these feedbacks can be critical for projections of regional or local development or sustainability. Accounting for these feedbacks will be a particularly critical challenge for predictive models of BEF that aim to predict changes in biodiversity and ecosystems at large spatial scales. This challenge is both scientific and perhaps philosophical, fully including human systems in our understanding of the biosphere.
- 2. What are the major feedbacks between diversity and ecosystem function across scales? Many approaches to date have aimed to minimize feedbacks and isolate directional effects (e.g., effect of diversity on function) to gain clear understanding of *parts* of biodiversity-function feedbacks at a particular scale of space, time or biological organization (Figure 3A). We now require new theory and experimental tests that allow us to understand feedbacks between diversity change and ecosystem function, and how these are linked across scales of space, time and organization (Figure 3A). For example, we do not have a robust model to allow us to understand how changes in biodiversity at large scales (e.g., global or continental) interact with changes at fine spatial scales (e.g., locally operating processes such as disturbance, invasion or restoration) to influence biodiversity and function. Such theory and experimental work would be explicit about temporal patterns in biodiversity and function, would identify links between feedbacks involving ecosystem function and multiple scales of diversity (see challenge 3), and would integrate evolutionary processes of biodiversity change. It might help to resolve challenges associated with how to interpret static measures of diversity in a single place or one time to the dynamics that underlie the diversity-function feedbacks.
- **3.** How do different dimensions of biodiversity feedback on diversity, and with function? Biodiversity is hierarchical in nature (Seibold et al 2018, TREE) (Figure 3A). Much of our current and future estimates of biodiversity and its change will be based on observations of alleles, genes, traits, species (or OTUs), and even phylogenies. Yet, we lack the scientific knowledge to relate changes in observed diversity in the environment at different levels of this hierarchy to changes in ecosystem function, and feedbacks between biodiversity and function. One key element of BEF feedbacks is trait expression, which links biodiversity contained in genes and genomes to biodiversity of traits, and also plays a role in which genes and genomes persist in communities. We lack theory and empirical understanding of how the aspects of diversity that are realized through the expression of traits is related to the diversity present in genes and

alleles, and why patterns of trait expression vary in space and time. Until we meet this challenge, the rapidly accumulating data on biodiversity cannot be used to estimate future states of the biosphere.

- **4. What is the role of spatial and temporal variation in BEF feedbacks?** Biodiversity is dynamic in time, and changes over space, reflecting both biotic and abiotic processes including the direct and indirect behaviors of people. As human activities continue to change the physical and temporal structure of landscapes, our limited understanding of how biodiversity and function feedbacks depend spatial and temporal environmental variability remains a major challenge to developing models and forecasts for patterns of diversity and function for future scenarios. We need new theory for how spatial variation in biodiversity (beta-diversity) affects ecosystem functioning. Even when we can improve our understanding of causes of change in beta diversity (Glossary), we additionally need to understand what causes spatial and temporal variation in population dynamics this synchrony or asynchrony among populations in an ecosystem is a key component of the feedback between biodiversity and stability of ecosystem function. We also still lack theory to explain how landscape change, homogenization of diversity, and changing patterns of asynchrony would affect feedbacks between diversity and function.
- 5. How do ecosystem services depend on ecosystem functions and biodiversity-function feedbacks? One-way interactions between biodiversity and ecosystem functions, and ecosystem functions and services, are well-established. It is also well-recognized that many ecosystem services depend on the presence of specific species or functional groups (Balvanera et al. 2013, Pascual et al. 2017), thus implicating biodiversity-ecosystem function feedbacks as broadly defined (glossary). However, the strengths of interactions between biodiversity and services remains less established for many services, especially with respect to the role of biodiversity-ecosystem function feedbacks as defined more strictly to be additional to the contributions of particular species (Glossary) (Balvanera et al. 2013). It remains unclear how ecosystem functions, or related sets of functions (sometimes called 'multifunctionality), confer ecosystem services that are relevant for human wellbeing (Gamfeldt et al. 2013, Renard et al. 2015). For example, although some services likely map directly to commonly studied functions e.g. carbon sequestration - for others, the link is less straightforward - e.g. existence value of conservation land or of particular species (Graves et al. 2017). Furthermore, the dependence of services upon feedbacks between biodiversity and ecosystem functions is not well characterized.
 - **6.** How can we identify critical thresholds for stability, resilience, sustainability? We currently face high uncertainty about how biodiversity and ecosystem functioning feedbacks will respond increasing dominance of humans (Steffen et al. 2004, Nature). The challenge is to understand the capacity of ecosystems and biodiversity feedbacks to remain in the states needed to ensure vital levels of ecosystem services supplies. Consideration of feedbacks suggests the possibility of nonlinear change and critical thresholds that could cause rapid and possibly irreversible shifts in ecosystem states, as invoked in the 'planetary boundaries' paradigm (). However, existing theory for biodiversity-ecosystem function feedbacks does not allow us yet to apply this global concept of tipping points at local and regional scales. It is likely that critical thresholds and state shifts occur differently between spatial scales and it is therefore

highly uncertain how local changes and potential shifts to an undesired state could be related from local to large scales.

7. How can we ensure emerging technologies produce information that can be used to deepen our understanding of biodiversity-function feedbacks? Technological tools for observing biodiversity allow high throughput and remote sensing of dimensions of biodiversity (Bush et al 2017 NEE). In addition to the challenges of building a knowledge framework for relating dimensions of biodiversity to ecosystem functions, we face the additional challenges of understanding how to interpret these observations. With the tidal waves of new information about diversity comes new forms of uncertainty in how well a data point actually represents what it attempted to observe. For eDNA, it is unclear how much of the diversity in the environment is sampled, and over what time period. If diversity is sampled (to an unknown extent) over a spatial - temporal window, how can we use that information to understand function? Without knowing how close observations are to the current state of nature, it is difficult to relate these observations to models of feedbacks. (current limitations are that we don't know the area sampled, or how long the DNA donor was present for, how observed DNA concentrations relate to abundance, etc.)

IV. Agenda for action. We have outlined 7 gaps in scientific knowledge that limit our current capacity to assess changes to the biosphere. Resolving these knowledge gaps will require investment in scientific research by research teams worldwide, who employ diverse and multidisciplinary approaches in the field, lab, and in silico. Here, we outline five 'action items' for implementing the research agenda to maximize benefits to the science-policy community.

Collaborate and connect scientists and non-scientists from the beginning, as
observers, knowledge users, and decision makers about scientific activities at the local
scale.

2. **Develop multi-scale PBEFF models** to estimate what has happened over recent centuries, and forecast future patterns under various human development scenarios.

3. **Observe biodiversity, ecosystem function and human activity change together** at different spatial scales with worldwide coverage, going beyond the *ad hoc* approaches to sampling of biodiversity throughout the world that has produced a set of observations of diversity that is highly biased to developed countries and terrestrial habitats.

4. **Experimentally and interactively test the model.** Observatories must be intimately linked with experimental programs that provide information for the models to help with understanding and projection.

5. **Identify and support a leadership team**. A leadership team must assemble, must be able to draw on existing scientific knowledge and work with the research community to develop research programs.

Along the way, the research community will need to confront additional logistical challenges that currently limit rapid scientific advances. These include i) the current lack of open science and the fact that data for biodiversity and ecosystem function knowledge from many places is not curated or made available in a central database (like GenBank), ii) limited technology integration such that observations from different methods not spatially coordinated, and ii) the clear need for more balanced engagement from global community (through research and citizen science).

Conclusion

Scientific progress over the last 30 years has led to recognition of the importance of feedbacks among biodiversity, function and people across scales. Despite this understanding, and major progress with models, experiments and observations, major challenges remain to integrate this knowledge with new capabilities to meet the challenges of the coming decades. As major policy-guiding scientific assessments grow in importance, it is essential to keep striving for the scientific advances, and in particular theoretical advances, that will foster integration of state-of-the-art scientific understanding with international and local policy objectives.

Meeting these knowledge challenges will lead to a deeper and truer understanding of our biosphere. As our technological capacity to observe our world and influence accelerates, we must harness these abilities to also understand the complex feedbacks and interactions that govern the dynamics of biodiversity and ecosystem functioning. By investing in science and supporting collaborative and interdisciplinary partnerships we can realize the fullest potential of a collective knowledge system to project possible futures and act on our understanding of those projects in the best possible way for our planet.

Acknowledgments

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References

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- Balvanera, P., I. Siddique, L. Dee, A. Paquette, F. Isbell, A. Gonzalez, J. Byrnes, M. I.
 O'Connor, B. A. Hungate, and J. N. Griffin. 2013. Linking Biodiversity and Ecosystem
 Services: Current Uncertainties and the Necessary Next Steps. Bioscience 64:49–57.
- 415 Butchart, S. H. M., M. Walpole, B. Collen, A. van Strien, J. P. W. Scharlemann, R. E. A. Almond, 416 J. E. M. Baillie, B. Bomhard, C. Brown, J. Bruno, K. E. Carpenter, G. M. Carr, J. Chanson, 417 A. M. Chenery, J. Csirke, N. C. Davidson, F. Dentener, M. Foster, A. Galli, J. N. Galloway, 418 P. Genovesi, R. D. Gregory, M. Hockings, V. Kapos, J.-F. Lamarque, F. Leverington, J. Loh, 419 M. A. McGeoch, L. McRae, A. Minasyan, M. Hernández Morcillo, T. E. E. Oldfield, D. Pauly, 420 S. Quader, C. Revenga, J. R. Sauer, B. Skolnik, D. Spear, D. Stanwell-Smith, S. N. Stuart, 421 A. Symes, M. Tierney, T. D. Tyrrell, J.-C. Vié, and R. Watson. 2010. Global biodiversity: 422 indicators of recent declines. Science 328:1164-1168.
 - Cardinale, B. J., K. L. Matulich, D. U. Hooper, J. E. Byrnes, E. Duffy, L. Gamfeldt, P. Balvanera, M. I. O'Connor, and A. Gonzalez. 2011. The functional role of producer diversity in ecosystems. American Journal of Botany 98:572–592.
 - Ceballos, G., P. R. Ehrlich, and R. Dirzo. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proceedings of the National Academy of Sciences 114:E6089–E6096.
 - Chan, K. M. A., P. Balvanera, K. Benessaiah, M. Chapman, S. Díaz, E. Gómez-Baggethun, R. Gould, N. Hannahs, K. Jax, S. Klain, G. W. Luck, B. Martin-Lopez, B. Muraca, B. Norton, K. Ott, U. Pascual, T. Satterfield, M. Tadaki, J. Taggart, and N. Turner. 2016. Opinion: Why protect nature? Rethinking values and the environment. Proceedings of the National Academy of Sciences 113:1462–1465.
 - Dee, L. E., M. De Lara, C. Costello, and S. D. Gaines. 2017a. To what extent can ecosystem services motivate protecting biodiversity? Ecology Letters 20:935–946.
 - Dee, L. E., M. De Lara, C. Costello, and S. D. Gaines. 2017b. To what extent can ecosystem services motivate protecting biodiversity? Ecology Letters 20:935–946.
 - Diaz, S., J. Settele, E. Brondizio, H. T. Ngo, M. Gueze, J. Agard, A. Arneth, P. Balvanera, K. Brauman, S. Butchart, K. Chan, L. Garibaldi, K. Ichii, J. Liu, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff, S. Polasky, A. Purvis, J. Razzaque, R. Roy Chowdhury, Y.-J. Shin, I. Visseren-Hamakers, K. Willis, and C. Zayas. 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Pages 1–39.
 - Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. Science 345:401–406.
- Díaz, S., S. Demissew, J. Carabias, C. Joly, M. Lonsdale, N. Ash, A. Larigauderie, J. R. 446 447 Adhikari, S. Arico, A. Báldi, A. Bartuska, I. A. Baste, A. Bilgin, E. Brondizio, K. M. Chan, V. 448 E. Figueroa, A. Duraiappah, M. Fischer, R. Hill, T. Koetz, P. Leadley, P. Lyver, G. M. Mace, 449 B. Martin-Lopez, M. Okumura, D. Pacheco, U. Pascual, E. S. Pérez, B. Reyers, E. Roth, O. 450 Saito, R. J. Scholes, N. Sharma, H. Tallis, R. Thaman, R. Watson, T. Yahara, Z. A. Hamid, 451 C. Akosim, Y. Al-Hafedh, R. Allahverdiyev, E. Amankwah, S. T. Asah, Z. Asfaw, G. Bartus, 452 L. A. Brooks, J. Caillaux, G. Dalle, D. Darnaedi, A. Driver, G. Erpul, P. Escobar-Eyzaguirre, P. Failler. A. M. M. Fouda, B. Fu, H. Gundimeda, S. Hashimoto, F. Homer, S. Lavorel, G. 453 454 Lichtenstein, W. A. Mala, W. Mandivenyi, P. Matczak, C. Mbizvo, M. Mehrdadi, J. P. 455 Metzger, J. B. Mikissa, H. Moller, H. A. Mooney, P. Mumby, H. Nagendra, C. Nesshover, A. 456 A. Oteng-Yeboah, G. Pataki, M. Roué, J. Rubis, M. Schultz, P. Smith, R. Sumaila, K. 457 Takeuchi, S. Thomas, M. Verma, Y. Yeo-Chang, and D. Zlatanova. 2015. ScienceDirect 458 The IPBES Conceptual Framework — connecting nature and people. Current Opinion in 459 Environmental Sustainability 14:1-16.
- Díaz, S., U. Pascual, M. Stenseke, B. Martin-Lopez, R. T. Watson, Z. Molnár, R. Hill, K. M. A. Chan, I. A. Baste, K. A. Brauman, S. Polasky, A. Church, M. Lonsdale, A. Larigauderie, P.

462 W. Leadley, A. P. E. van Oudenhoven, F. van der Plaat, M. Schröter, S. Lavorel, Y. 463 Aumeeruddy-Thomas, E. Bukvareva, K. Davies, S. Demissew, G. Erpul, P. Failler, C. A. 464 Guerra, C. L. Hewitt, H. Keune, S. Lindley, and Y. Shirayama. 2018. Assessing nature's 465 contributions to people. Science 359:270–272.

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- Frison, A. E., J. Cherfas, and T. Hodgkin. 2011. Agricultural biodiversity is essential for a sustainable improvement in food and nutrition security. Sustainability 3:238–253.
- Gamfeldt, L., T. Snäll, R. Bagchi, M. Jonsson, L. Gustafsson, P. Kiellander, M. C. Ruiz-Jaen, M. Fröberg, J. Stendahl, C. D. Philipson, G. Mikusiński, E. Andersson, B. Westerlund, H. Andrén, F. Moberg, J. Moen, and J. Bengtsson. 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nature Communications 4:59-8.
- Graves, R. A., S. M. Pearson, and M. G. Turner, 2017. Species richness alone does not predict cultural ecosystem service value. Proceedings of the National Academy of Sciences 114:3774-3779.
- Isbell, F., A. Gonzalez, M. Loreau, J. Cowles, S. Díaz, A. Hector, G. M. Mace, D. A. Wardle, M. I. O'Connor, J. E. Duffy, L. A. Turnbull, P. L. Thompson, and A. Larigauderie. 2017. Linking the influence and dependence of people on biodiversity across scales. Nature 546:65–72.
- Isbell, F., D. Tilman, S. Polasky, and M. Loreau. 2014. The biodiversity-dependent ecosystem service debt. Ecology Letters 18:119-134.
- Liang, J., T. W. Crowther, N. Picard, S. Wiser, M. Zhou, G. Alberti, E. D. Schulze, A. D. McGuire, F. Bozzato, H. Pretzsch, S. de-Miguel, A. Paquette, B. Herault, M. Scherer-Lorenzen, C. B. Barrett, H. B. Glick, G. M. Hengeveld, G. J. Nabuurs, S. Pfautsch, H. Viana, A. C. Vibrans, C. Ammer, P. Schall, D. Verbyla, N. Tchebakova, M. Fischer, J. V. Watson, H. Y. H. Chen, X. Lei, M. J. Schelhaas, H. Lu, D. Gianelle, E. I. Parfenova, C. Salas, E. Lee, B. Lee, H. S. Kim, H. Bruelheide, D. A. Coomes, D. Piotto, T. Sunderland, B. Schmid, S. Gourlet-Fleury, B. Sonke, R. Tavani, J. Zhu, S. Brandl, J. Vayreda, F. Kitahara, E. B. Searle, V. J. Neldner, M. R. Ngugi, C. Baraloto, L. Frizzera, R. Ba azy, J. Oleksyn, T. Zawi a-Nied wiecki, O. Bouriaud, F. Bussotti, L. Finer, B. Jaroszewicz, T. Jucker, F. Valladares, A. M. Jagodzinski, P. L. Peri, C. Gonmadje, W. Marthy, T. OBrien, E. H. Martin, A. R. Marshall, F. Rovero, R. Bitariho, P. A. Niklaus, P. Alvarez-Loayza, N. Chamuya, R. Valencia, F. Mortier, V. Wortel, N. L. Engone-Obiang, L. V. Ferreira, D. E. Odeke, R. M. Vasquez, S. L. Lewis, and P. B. Reich. 2016. Positive biodiversity-productivity relationship predominant in global forests. Science 354:aaf8957-aaf8957.
- Mace, G. M. 2014. Ecology. Whose conservation? Science 345:1558–1560.
- Mace, G. M. 2019. The ecology of natural capital accounting, Oxford Review of Economic Policy 35:54-67.
- Newbold, T., L. N. Hudson, S. L. L. Hill, S. Contu, I. Lysenko, R. A. Senior, L. Börger, D. J. Bennett, A. Choimes, B. Collen, J. Day, A. De Palma, S. Díaz, S. Echeverria-Londoño, M. J. Edgar, A. Feldman, M. Garon, M. L. K. Harrison, T. Alhusseini, D. J. Ingram, Y. Itescu, J. Kattge, V. Kemp, L. Kirkpatrick, M. Kleyer, D. L. P. Correia, C. D. Martin, S. Meiri, M. Novosolov, Y. Pan, H. R. P. Phillips, D. W. Purves, A. Robinson, J. Simpson, S. L. Tuck, E. Weiher, H. J. White, R. M. Ewers, G. M. Mace, J. P. W. Scharlemann, and A. Purvis. 2015. Global effects of land use on local terrestrial biodiversity. Nature 520:45–50.
- Odorico, P. D., A. Bhattachan, K. F. Davis, S. Ravi, and C. W. Runyan. 2013. Global desertification: Drivers and feedbacks. Advances in Water Resources 51:326-344.
- 506 Pascual, U., P. Balvanera, S. Díaz, G. Pataki, E. Roth, M. Stenseke, R. T. Watson, E. B. Dessane, M. Islar, E. Kelemen, V. Maris, M. Quaas, S. M. Subramanian, H. Wittmer, A. 507 508 Adlan, S. Ahn, Y. S. Al-Hafedh, E. Amankwah, S. T. Asah, P. Berry, A. Bilgin, S. J. Breslow, 509 C. Bullock, D. Cáceres, H. Daly-Hassen, E. Figueroa, C. D. Golden, E. Gómez-Baggethun, D. González-Jiménez, J. Houdet, H. Keune, R. Kumar, K. Ma, P. H. May, A. Mead, P.
- 510 511 O'Farrell, R. Pandit, W. Pengue, R. Pichis-Madruga, F. Popa, S. Preston, D. Pacheco-
- 512 Balanza, H. Saarikoski, B. B. Strassburg, M. van den Belt, M. Verma, F. Wickson, and N.

- Yagi. 2017. ScienceDirect Valuing nature's contributions to people: the IPBES approach. Current Opinion in Environmental Sustainability 26-27:1–10.
- Peters, D. P. C., R. A. Pielke, B. T. Bestelmeyer, C. D. Allen, S. Munson-McGee, and K. M. Havstad. 2004. Cross-scale interactions, nonlinearities, and forecasting catastrophic events. Proceedings of the National Academy of Sciences 101:15130–15135.
- Renard, D., J. M. Rhemtulla, and E. M. Bennett. 2015. Historical dynamics in ecosystem service bundles. Proceedings of the National Academy of Sciences 112:13411–13416.
- Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S.
 Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465:609–612.
- 523 United Nations. 1992. Convention on biological diversity. Pages 1–30.
- United Nations. 2015. Transforming our world: the 2030 agenda for sustainable development. Pages 1–41.
- Wang, S., and M. Loreau. 2014. Ecosystem stability in space: α, β and γ variability. Ecology Letters 17:891–901.
- Watson, R. T., and A. H. Zakri. 2005. Ecosystems and Human Well-Being. Pages 1–155.