Six grand challenges for biodiversity-ecosystem functioning research in the era of science-policy platforms

Mary I. O'Connor[1], Akira Mori[2], Andrew Gonzalez[3], Michel Loreau[4], Meghan Avolio[5], Jarrett E. K. Byrnes[6], William Cheung, Jane Cowles[7], Adam Clark[8], Laura E. Dee[9], Yann Hautier[10], Andrew Hector[11], Kimberley Komatsu[12], Timothy Newbold[13], Charlie Outhwaite[14], Peter Reich[15], Eric Seabloom[16], Laura Williams[17], Alexandra Wright[18], Forest Isbell[19].

1. *Department of Zoology and Biodiversity Research Centre, University of British Columbia, Vancouver, Canada*
2. *Graduate School of Environment and Information Sciences, Yokohama National University, Yokohama, Japan*
3. *Department of Biology, McGill University, Montreal, QC, Canada*
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18.
19. *Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN, USA*
20.

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Abstract [100-200 words]:

Human-driven biodiversity change alters ecosystems, with consequences for human wellbeing. Feedbacks are an essential component of resilient socio-economic systems, yet the feedbacks between biodiversity, ecosystem services and human wellbeing are not yet fully accounted for in global policy efforts that consider future scenarios for human activities and their consequences for nature. Failure to integrate feedbacks in our knowledge frameworks exacerbates uncertainty in future projections and potentially prevents us from realizing the full benefits of actions we can take to enhance sustainability. We identify six scientific research challenges that, if addressed, could allow future policy, conservation and monitoring efforts to quantitatively account for ecosystem and societal consequences of biodiversity change. Placing feedbacks prominently in our frameworks would lead to i) coordinated observation of biodiversity change, ecosystem functions and human actions, ii) joint experiment and observation programs, and iii) more effective use of emerging technologies in biodiversity science and policy. To meet these challenges, we outline a 5-point action plan for collaboration and connection among scientists and policy-makers that emphasizes diversity, inclusion, and open access. Efforts to protect biodiversity require the best possible scientific understanding of human activities, biodiversity trends, ecosystem functions, and - critically - the feedbacks among them.

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

Increasing recognition of irreversible biodiversity change and unsustainable ecosystem exploitation has spurred unprecedented collaboration among scientists and policymakers worldwide to mitigate these ecological crises (Ceballos et al., 2017; Diaz et al., 2019; Loreau, 2010a; Watson and Zakri, 2005). Biodiversity is in crisis as a result of habitat loss, overharvesting and other pressures associated with humanity's accelerated use of natural resources (Diaz et al., 2019; Maxwell et al., 2016; McCauley et al., 2015; Newbold et al., 2015). The diversity of life at all scales – from genes to social-ecological systems and beyond - plays a major role in driving ecosystem dynamics throughout the biosphere; higher biodiversity enhances numerous ecosystem functions (Cardinale et al., 2011; Isbell et al., 2017), and together these amount to ecosystem services (or also referred to as 'nature's contributions to people', see Glossary in Box 1) that are now at the center of global science-policy initiatives such as the Intergovernmental Panel on Biodiversity and Ecosystem Services (IPBES) and the Convention on Biodiversity (CBD) (Díaz et al., 2015).

The science underpinning these major initiatives has clearly demonstrated direct effects between biodiversity, ecosystem functions and human wellbeing (B-E-H) (Figure 1, Box 1), as well as dynamic feedbacks [Box 2] that influence how biodiversity, function and human systems change over time. Direct effects include the positive effect of species diversity on productivity and nutrient dynamics in plant and animal systems (Cardinale et al., 2011; Duffy et al., 2003; Tilman et al., 2012), increased productivity and food quality benefitting humans through an ecosystem service such as food provision (Bernhardt and O'Connor, in press; Cardinale et al., 2012; Frison et al., 2011; Isbell et al., 2017; Schindler et al., 2010), and food management systems that facilitate biodiversity (Bogard et al., 2018; Laura E Dee et al., 2017)(Figure 1A).

We argue that successful science-based policy requires greater consideration of the *feedbacks* within and between biodiversity, ecosystem functions and human activities and well-being (Figure 1). These frameworks have yet to comprehensively include feedback loops that drive the dynamics of biodiversity and its relationship to ecosystem function and human activities at a range of scales despite the development of such frameworks to be increasingly inclusive of philosophies beyond that traditionally underpinning western science (Ferrier et al., 2016; Isbell et al., 2017; Raymond et al., 2013; Reyers and Selig, 2020; Xiao et al., 2019). Global policy platforms and initiatives connect scientific understanding to policy guidelines using conceptual models (verbal or graphical; e.g., Figure 1B), summaries of scientific evidence (reports), and syntheses of quantitative and qualitative models that use scientific understanding of cause and effect in nature to project future states of biodiversity and humanity under likely scenarios of global change (Ferrier et al., 2016). These models rely heavily on a scientific understanding of direct and indirect causal effects of biodiversity, ecosystem function and human activities, but direct and indirect effects alone cannot capture dynamic feedbacks. Models guiding policy platforms do include some feedbacks, though most inclusion of feedbacks is across the major components (for example, Figure 1B and C) (Ferrier et al 2016).

We propose that the next generation of biodiversity science and scholarship should expand the scale and scope of this topic to more effectively understand feedbacks in the system (inclusive of humans) to build knowledge and inform policy platforms and actions taken in compliance such as monitoring biodiversity. Here, we consider the central role that feedbacks play in the generation and maintenance of biodiversity and its relationship with ecosystem services and human wellbeing (Section II). We do this because feedback is a familiar concept, yet it has been overlooked in most scientific work assessing the links between biodiversity and ecosystem function, and in understanding the full relationships between people and biodiversity. Next, we briefly review how current leading policy platforms consider the role of feedbacks in our understanding of the dynamics of biodiversity, function and people, and highlight key opportunities for strengthening consideration of feedbacks (Section III). We then identify key scientific knowledge gaps that we suggest limit the full uptake of scientific understanding into policy platforms, and then we list six grand challenges (Section IV) that deserve organized and collaborative investment for rapid progress. Finally, we outline an agenda for collaborative action (Section V) to meet these challenges to support policy-relevant science in a changing world, as our understanding of that world also changes.

II. Feedbacks

Biodiversity and its relationship to ecosystem function and human systems depend on feedbacks within and between these elements (Figure 1; Box 2). Ecologists recognize feedbacks as essential dynamical structures in ecological and evolutionary systems (Chapin et al., 2011; Davidson and Janssens, 2006; Klironomos, 2002). The concept of feedback is often used to describe specific dynamic interactions (Box 2), but also is used to refer to interaction networks (Xiao et al 2017) or dynamics of a complex system that amplify or dampen an outside signal or effect. For example, when a species' 'final descent into extinction' reflects synergistic effects of multiple stressors, the synergy may be referred to as involving a feedback (Brook et al., 2008). Feedbacks in ecosystems between biotic and abiotic processes driving the global carbon cycle have received great attention in climate science and policy because they cause human and natural systems to change in non-intuitive ways over time (Boscolo-Galazzo et al., 2018; Melillo et al., 2002). Additionally, feedbacks between human and ecological systems have become an important area of interdisciplinary research and for guiding discourse (Lafuite and Loreau, 2017; Raymond et al., 2013; Young et al., 2006). These research programs all contribute to the problem we are addressing here – which is to better understand feedbacks specifically in the B-E-H system as a whole (Blythe et al., 2017), and how best to apply this understanding to broad scale policy, communication and knowledge integration programs.

There are many examples of change in nature that we now understand to depend on feedbacks between biodiversity, ecosystem processes and human activities. These include feedbacks that lead to the conversion of grassland to desert following disturbances or biodiversity loss (Odorico et al., 2013)(Table 1), and the conversion of kelp forests to barrens in coastal oceans (Steneck et al., 2003). One reasonably well understood example is that of pollinator diversity and plant diversity (Ebeling et al., 2018; Scheper et al., 2014)(Figure 1C). The abundance of pollinators is known to increase the abundance of the plants they pollinate by facilitating plant reproduction. Higher pollinator diversity can enhance plant diversity when there are positive interactions between different plant and pollinator species. Through this positive feedback, humans benefit when the plants are of cultural or agricultural value. Human activities such as some agricultural practices and land use change have dramatically reduced pollinator abundance and diversity, causing humans to lose value in crop yields, and in turn motivating conservation and management actions (Figure 1C).

There is no substitute for knowledge of feedbacks. Feedbacks play out over time; consequently, compiling static representations of direct effects will not yield correct predictions about future change (Fulton et al 2019) (Box 2). Without a fuller scientific understanding of feedbacks that link biodiversity change, ecosystem services and human wellbeing, we risk making decisions based on modeled futures that do not capture the full range of likely possibilities (Carpenter et al., 2009; Ferrier et al., 2016; Lade et al., 2019; Mace, 2019; Peters et al., 2004; Xiao et al., 2019). There is growing recognition of the importance of the feedbacks that couple natural and social systems (for example, adaptive social-ecological systems); some authors now even argue that the dynamics of either natural or human systems cannot be understood without considering these feedbacks explicitly (Bennett et al., 2015; Henderson and Loreau, 2019, 2018; Lafuite and Loreau, 2017; Motesharrei et al., 2016; Raymond et al., 2013). This is especially true at the global scale, where long-term feedbacks play a prominent role, but there is evidence that these feedbacks also can be critical for projections of regional or local development or sustainability (Reyers and Selig, 2020). Our challenges now (Section V) include building on this knowledge to design the best possible policy and action frameworks.

III. Feedbacks in major science-based policy platforms

Major science-based policy platforms guide decisions about a broad range of actions that impact biodiversity change, including setting targets for sustainability (UN Sustainable Development Goals, SDGs) and biodiversity trends and investing in monitoring programs as guided by GeoBON. The conceptual framework of the IPBES (Diaz et al., 2019; Díaz et al., 2015) outlines one of the current paradigms, which include some of the pathways through which nature contributes to people (Figure 1B). This framework is offered with the purpose of aligning assessments of change and knowledge development in biological and social sciences with policy needs (Díaz et al., 2018; Pascual et al., 2017). It also channels and motivates scholarship and scientific research to fill gaps and improve methods for modeling scenarios. The IPBES framework provides the broader community a system for understanding how biodiversity, inclusive of humanity and human diversity (Box 1), are related to a sustainable biosphere (Pascual et al., 2017).

The IPBES platform, and others such as the CBD, relies on synthesis of scientific evidence for the causes and consequences of biodiversity change, and the evidence is combined with scientific models to project and forecast future scenarios for biodiversity change and human activities (Ferrier et al., 2016; IPBES, n.d.). State of the art models used in the most recent IPBES assessment report do integrate scientific understanding of some feedbacks, mostly those within the human activity components or between human activities and ecosystem functions. However, there is little mention of feedbacks between biodiversity and ecosystem functioning (e.g., Figure 1A, C) in the summary of models used to generate projections and scenarios for the most recent IPBES report. A heuristic link between biodiversity and ecosystem function is included in many models, but not a mechanistic link that includes the feedbacks between biodiversity and function mediated by density dependence (Box 2). The few existing examples are in the integrated assessment models involving social and economic systems coupled with natural systems (Ferrier et al 2016). The assessment report indicates that feedbacks are identified as an *outcome* of integrated system models, rather than an architectural feature (Ferrier et al 2016). The IPBES approach to scenarios does include qualitative modeling methods that can capture feedbacks, though these methods are largely restricted to smaller-scale social-ecological system studies. For example, subsets of interactions between fish population dynamics and fishing behavior have been represented in quantitative fisheries modelling (Wijermans et al., 2020). However, a major gap exists in the integration between different types of interactions in order to more comprehensively characterize the major feedbacks between (or within) ecosystems and fisheries. The projections and models improve over time as scientific understanding of the modeled systems, and science of modeling itself, improves (Fulton et al., 2019).

Deepening our understanding of feedbacks is identified as a research challenge, and the IPBES methods assessment report notes that ‘Failure to consider such [feedback] dynamics can potentially render scenario analysis incomplete, inconsistent or inaccurate’. IBPES authors and ecosystem modelers also highlight the risks associated with including feedbacks based on wrong or incomplete understanding. We recognize that the current perspective and state of models is just one step in a long-term shift in perspective among biodiversity scholars and biodiversity policy makers, and we encourage the development of a perspective that emphasizes feedbacks in the framing of the future of biodiversity, ecosystem function and human wellbeing (Box 3).

IV. Key knowledge gaps

Getting feedbacks right in our models, forecasts and assessments is critical. Our survey of feedbacks in biodiversity-ecosystem functioning science and related policy frameworks reveals five knowledge gaps that may be addressed in a research agenda (Section V).

1) ***Linking observed current or recent temporal trends in biodiversity to future trajectories.*** As we have noted above, future biodiversity, and diversity's contribution to ecosystem services, may not be accurately predicted by extrapolating a historical trend in biodiversity forward in time because of feedbacks among biodiversity, ecosystem function and human activities (Ferrier et al., 2016; Fulton et al., 2019; Peters et al., 2004; Suding et al., 2004). When feedbacks are at play, trajectories of a system observed over a short time span are not necessarily indicative of longer-term patterns (Huffaker, 1958; Huisman and Weissing, 1999; Marshall et al., 2013) (Figure 3A). To predict long-term behavior of a system, the dynamics – and in particular, feedbacks such as how biodiversity can influence future biodiversity – need to be considered (Hillebrand et al., 2020; Xiao et al., 2019).

2) ***Linking observed trends in biodiversity to future trends in biodiversity, ecosystem function and human wellbeing.*** Dynamics of one part of the system (for example, diversity) depend on other parts of the system (humans, ecosystem functions), and vice versa. Achieving an empirical and even theoretical or mathematical understanding of biodiversity temporal trends (e.g., filling knowledge gap #1) does not allow us to more effectively predict what happens in full ecological systems because human activities and ecosystem functions also vary over time, affecting and being affected by biodiversity (L E Dee et al., 2017; Lafuite and Loreau, 2017; Xiao et al., 2019). One pervasive consequence of this knowledge gap is the persistent decoupling of biodiversity and function in assessment and monitoring programs; most of the biodiversity observations being assembled for biodiversity change assessments (e.g., Biotime, Predicts, GeoBON) do not have accompanying measures of ecosystem processes. As a result, and because of feedbacks determining how biodiversity, ecosystem function and human activities change *together* over time, future trajectories of diversity, function or human wellbeing 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 concurrent biodiversity estimates are difficult to project forward with confidence, given the inability to project changes in the diversity / function feedbacks (Isbell et al., 2015).

3) ***The gap between experimental evidence for direct BEF effects and the importance of feedbacks.*** The majority of experimental tests of the relationship between biodiversity

and ecosystem function has employed an experimental design that intentionally disrupts potential feedbacks – for example, by weeding out species that colonize (Tilman et al., 1996) or by replacing species that are lost (O'Connor and Bruno, 2009) over the course of the experiment to maintain diversity treatments. Though this approach does clearly isolate the effect biodiversity can have on ecosystem functions (straight arrows in Figure 1A), in doing so these procedures prevent feedbacks between diversity and function (e.g., Figure 2A, C; Table 1) from playing out over time. Consequently, the hundreds of experiments frequently reviewed and synthesized as strong evidence for effects of diversity on function (Cardinale et al., 2011; O'Connor et al., 2017) cannot be used to demonstrate consequences of the feedbacks between diversity and function that theory predicts are driving this relationship (Loreau, 2010b; Turnbull et al., 2010).

4) ***Integration of human-biodiversity feedbacks at all levels*** of models in projections and assessments of change in biodiversity, ecosystem functioning and human wellbeing (Reyers and Selig, 2020). Failure to recognize feedbacks has been highlighted as a problem: a perception that people affect biodiversity but that there is no feedback from biodiversity to people is increasingly considered as dangerous for human well-being in short and long-term thinking (Blythe et al., 2017; Diaz et al., 2019; Raymond et al., 2013; United Nations, 2015). This need has been articulated not only by the IPBES community, and also by ecologists and other concerned scientists, as well as indigenous peoples and social scientists (Motesharrei et al., 2016; Reyers and Selig, 2020; Turnhout et al., 2013). The current IPBES framework acknowledges this gap: in the assessment of methods, one of the high-level messages (Key Finding 3.3) is that scenarios and models 'need to be better linked in order to improve understanding and explanation of important relationships and feedbacks between components of coupled social-ecological systems" (Ferrier et al., 2016). The high-level treatment of feedbacks in the IPBES and its methods assessment suggests that recognition of the importance of feedbacks is not the only issue, but perhaps scientific understanding of these feedbacks and how to model them at ecologically relevant scales, as well as or communication of existing knowledge to policy makers are barriers to a fuller treatment of feedbacks in biodiversity scenarios.

5) ***The gap between scientific knowledge and what is emphasized in policy frameworks.*** Outside specialist research communities, B-E-H feedbacks (such as plant-soil feedbacks or diversity-desertification, Table 1) and their consequences are not well represented in conceptual diagrams and models used by policy experts and decision makers to understand biodiversity change and its likely consequences over time (Figure 1B). Greater emphasis on this representation can help minimize overlooking this important concept when identifying priorities for biodiversity observation or multifaceted conservation opportunities.

IV. Grand challenges in biodiversity research.

The knowledge gaps we have identified are empirical as well as theoretical. Filling these gaps with science-based understanding requires targeting feedbacks as scientific research goals, and considering how assessments and policies can best reflect this knowledge development and subsequent gain. This will require scientific and scholarly efforts, as well as actions (Section VI) that include additional experiments, including new experimental designs, or coupled experiments, monitoring and theory. Here, we outline 6 scientific challenges that are top priorities for major investment to expand the biodiversity-ecosystem functioning paradigm and enhance our knowledge frameworks to support biodiversity policies and to realize sustainability goals.

Challenge 1: Identify the feedbacks between biodiversity, humans and ecosystem function.

A research agenda should aim toward an ultimate goal of fully integrating the multiple human (behavioral, demographic, social, political, economic, institutional) components of feedbacks in the system that includes biodiversity and human societies (Carpenter et al., 2009; Raymond et al., 2013). Meeting this challenge requires scientific work and transdisciplinary scholarship to identify the most important feedbacks, as well as to develop approaches to model these feedbacks. The models and concepts must be tested and explored with theory and experiments, including new and innovative approaches that address feedbacks across scales (Challenge 2). Additionally, new ways of representing feedbacks in non-scientific communications and representations of biodiversity change will aid in bridging the science-policy, cross-disciplinary gaps. Including human systems in our understanding of the biosphere is not only a scientific but also philosophical challenge.

Challenge 2: Identify major feedbacks that link biodiversity-ecosystem function and human well-being systems across scales.

We now require new theory to guide experimental tests and observation programs that allow us to more deeply understand feedbacks between diversity change and ecosystem function, and how these are linked across scales of space, time and organization to influence how systems change over time (Gonzalez et al., 2020) (Figure 4). For example, we do not have a robust model defining 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 (Figure 3). Such theory and experimental work would be explicit about temporal patterns in biodiversity and function, spatial and temporal variation, and would identify links between feedbacks involving ecosystem function and multiple scales of diversity (see Challenge 3). 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.

Challenge 3: Develop an operational understanding of how different dimensions of biodiversity are involved in feedbacks over time.

Until we meet this challenge, the rapidly accumulating data on biodiversity cannot be used to estimate future states of the biosphere. 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 models of phylogenies. Not only do we still require great investment in organized biodiversity sampling and monitoring (Loreau, 2010b), we also lack the scientific knowledge to relate changes in observed diversity at different levels of biological organization (genes vs species; Figure 4) 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 as such BEF feedbacks also plays a role in which genes and genomes persist in communities (Zuppinger-Dingley et al., 2014). We require new theory, models 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.

Challenge 4: Understanding how changing ecosystem services over time depend on ecosystem functions and biodiversity-function feedbacks.

One-way interactions between biodiversity and ecosystem functions, and ecosystem functions and services, are well-established for several services (e.g., Ricketts et al., 2016). 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 (Box 1: 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 (Box 1: Glossary) (Balvanera et al., 2013; Ricketts et al., 2016). 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.

Challenge 5: Develop theory and workflows that explicitly relate information from emerging technologies to knowledge that can be used to deepen our understanding of feedbacks.

Observation of nature is at the core of the research approaches that will allow us to meet these challenges. Technological tools for observing biodiversity allow high throughput and remote sensing of dimensions of biodiversity and ecosystem functioning at the finest levels of biological organization (viruses, genes and microbes) as well as some measures of ecosystem functions (Bush et al., 2017; Cavender-Bares et al., 2017; Pettorelli et al., 2014; Schweiger et al., 2018). As vast amounts of observational data become available, we face the challenges of understanding how to interpret these observations in the context of dynamic feedbacks. Uncertainty in these observations remains a major obstacle to robust inference of change over time. Uncertainty in biodiversity observations and coupled measures of ecosystem function also present a barrier to robustly combining observations into models of change to understand change across scales. Furthermore, feedbacks are difficult to observe with limited time or resources because they require coordinated observations of several facets of a system (e.g., biodiversity, an ecosystem function such as biomass production, human use of the biomass, plus any human – biodiversity interactions) (e.g., Grace et al., 2016), and in nearly all cases, these coupled measurements are not made. New technologies open new perspectives on dimensions of biodiversity and how it is dynamically related to ecosystem functioning, yet these perspectives cannot be robustly integrated into models of change over time without accompanying theory and empirical evidence for relationships between observations and biological processes.

Challenge 6. How can an understanding of feedbacks best inform decisions about biodiversity conservation policy?

As we deepen our scientific understanding of feedbacks that drive biodiversity change and its consequences, we still face the challenge of relating this complex information to accessible policy information and social messaging. How can knowledge of feedbacks best inform decision guidance? And, does considering this question guide our research to questions that yield the most actionable new information? Many knowledge systems include knowledge of feedbacks (Carpenter et al., 2009; Raymond et al., 2013; Turnhout et al., 2013), and therefore an emphasis on feedbacks may provide another scaffold to integrate biodiversity understanding across diverse philosophies. Additionally, feedbacks can guide decisions about how to invest observation effort, about prioritization of conservation actions to vulnerable or stable systems, and in optimal workflows to convert knowledge into action to protect future biodiversity.

V. Agenda for action.

We have outlined six challenges in B-E-H scientific knowledge that limit our current capacity to assess changes to the biosphere. Resolving these knowledge gaps will require investment in scientific research worldwide, who employ diverse, interdisciplinary and even transdisciplinary 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.

1. *Collaborate and connect*

   Scientists, policy makers and the public must continue to engage with one another from the beginning, as observers, knowledge users, as ecosystem service beneficiaries and decision makers about scientific activities at the local scale. Scientific and science-policy collaborations in biodiversity research should strive for cultural, geographic, political and ethnic diversity among researchers and within research projects (Mori, 2020). Doing so will result in an inclusion of a broader range of knowledge systems and perceptions of human-biodiversity interactions, benefitting an understanding of feedbacks that is both globally and locally relevant worldwide.

2. *Develop multi-scale models of the biosphere.*

   Models that integrate B-E-H function feedbacks may be used to hind-cast what has happened over recent centuries, and forecast future patterns under various human development scenarios (Loreau, 2010a; Motesharrei et al., 2016). These models must be developed an improved in conjunction with the increased effort in biodiversity observatories, advancing statistical procedures for robustly detecting and attributing change, and within the context of the kinds of decisions that will need to be made. Such an effort is large-scale, complex and likely involves partnerships across institutions, public and private sector, and across nations and cultures.

3. *Observe biodiversity, ecosystem function and human activity change together.*

   Integrated observations should be made at different spatial scales with worldwide coverage (Bush et al., 2017), 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 (Loreau, 2010a; Martin et al., 2012). To meet the research challenges we outline above, observation programs based on international collaborations and local investment must jointly and simultaneously observe biodiversity change, ecosystem function change and human activities. New statistical approaches must be developed to understand causation in the complex systems we are observing. Further, biodiversity change observatories need to be comprehensive in their inclusion of areas and biomes on our planet, breaking the historical pattern of emphasis on developed countries and the socially dominant communities within them.

4. *Experimentally and iteratively test the models.*

   To understand feedbacks, observational programs should be guided by theory that includes feedbacks, and coupled with experimental programs to understand feedbacks. As with observatories, the experimental and modelling programs must be run by collaborations of scientists, modelers and end users from a broad range of biomes, countries and cultural backgrounds, specifically including indigenous and local peoples from the global north and south.

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. The leadership team must facilitate diversity and comprehensive inclusion of nature and people in the research programs, can promote the research agenda to potential users and supporters, can lead public engagement activities, and can ensure fully open science practices and data archiving so the findings are available to everyone in the world.

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 are not spatially coordinated, and ii) the clear need for more balanced engagement from global community (through research and citizen science).

VI. 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 recognition, 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. 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 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.

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. This does not mean that complex models involving feedbacks are always the most appropriate tool – complexity can be a barrier to understanding and communication in some circumstances. Still the community of biodiversity change scholars must allow ourselves the option to use models that are based on our best understanding of nature, and we know that this understanding includes feedbacks. By investing in science and supporting collaborative and interdisciplinary partnerships (G-Science Academies Statement, 2020) 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.

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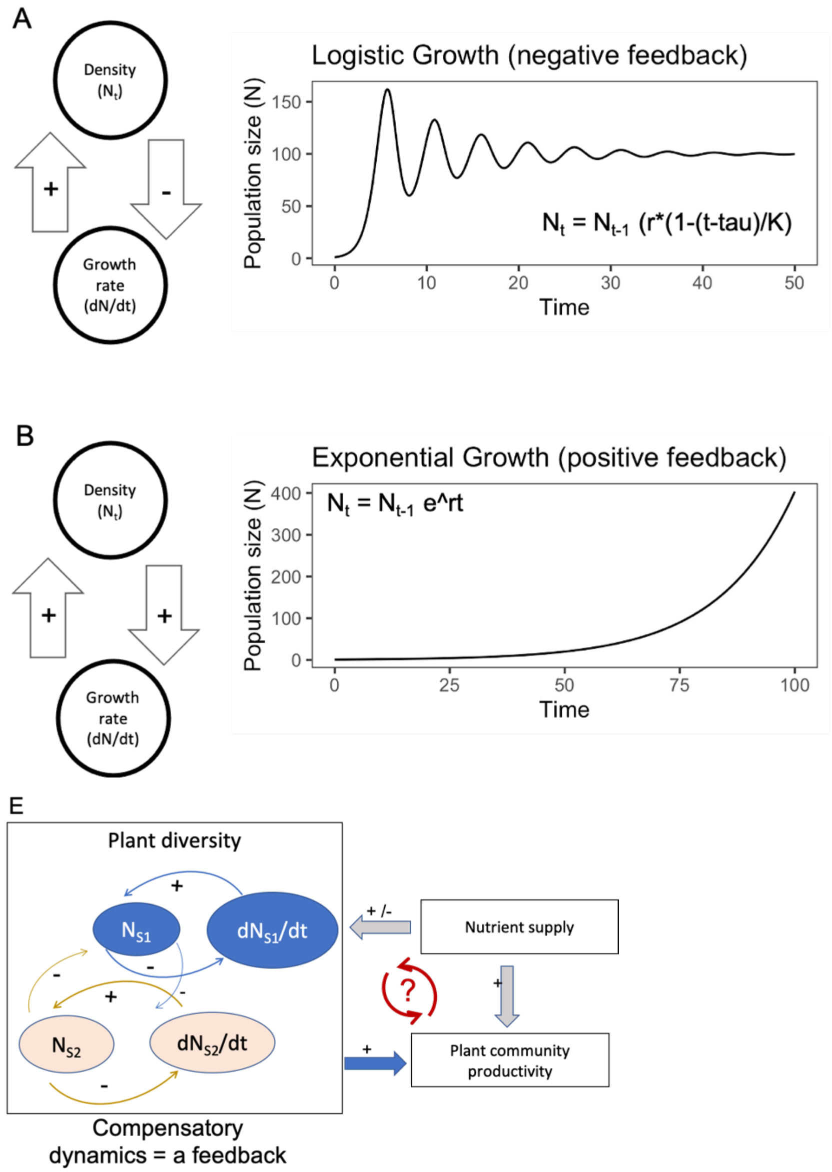
Box 2: Feedbacks. A simple definition of feedback is when one part of a system affects another part of that system that in turn affects the first part; in other words, a system output affects the input of the same system. This definition is consistent with systems biology, recognizing feedback as a control mechanism in complex systems. *Negative feedbacks* (Figure 2A) are self-dampening and stabilizing, and can buffer systems against change (Jia et al., 2020; Zhao et al., 2019). In contrast, *positive feedbacks* are self-reinforcing and can be destabilizing (Ware et al., 2018) (Figure 2B). To model feedbacks, specific tools (equations) are required that relate the *behavior* over time of a system to the *state* of that same system in some way. Models that include feedbacks may allow model terms to change over time in relation to the state of the system, which itself reflects those parameter values (Figure 2). It is this self-dependent relationship that distinguishes models with dynamic feedbacks from models that include direct and indirect effects but do not relate these in feedbacks (Figure 2).

Ecological feedbacks are at the heart of the interdependence of biodiversity and ecosystem function. Among the processes that maintain biodiversity, feedbacks determine stability and future trajectories of population, community and ecosystem dynamics (Odorico et al., 2013; Suding et al., 2004), from shallow lakes (Scheffer et al., 1993) to tropical rainforests (Bagchi et al., 2011) to coral reefs (Tanner et al., 2009). One of the most pervasive feedbacks in ecological systems is density dependence of population dynamics. Density dependence is a feedback in which population density at one time influences population growth at a future time, which in turn influences future population density (Figure 2). Stronger density dependence *within* species than *among* species is one of the primary explanations for the persistence of biodiversity in nature and for the positive relationship between biodiversity and ecosystem services (Carroll et al., 2011; Loreau, 2010; Turnbull et al., 2013)(Figure 2C). Negative (dampening) density-dependent feedbacks of predation, disease and pathogens on species performance cause diverse systems to maintain diversity and ecosystem functions over time more than less diverse systems (Klironomos, 2002; Maron et al., 2011; Schnitzer et al., 2011; Turnbull et al., 2010; van Ruijven et al., 2020). Density-dependent processes are at the heart of compensatory dynamics in which a decline in density of a competitive dominant allows competitors to increase in abundance and maintain ecosystem functions in a negative feedback (Loreau, 2010; Smith and Knapp, 2003; Turnbull et al., 2013).

Figure 2.1. Feedbacks in population dynamics (A-B) and community dynamics (C): A) negative and B) positive feedback between population growth (dN/dt) and population density (N_t). C) Density dependent feedbacks among plant populations and species can lead to a positive relationship between diversity and ecosystem functioning.



A
Density
(N_t)
+
-
Growth
rate
(dN/dt)
Logistic Growth (negative feedback)
Population size (N)
150
100
50
0
N_t = N_t-1 (r*(1-(t-tau)/K)
0
10
20
30
40
50
Time
B
Density
(N_t)
+
+
Growth
rate
(dN/dt)
Exponential Growth (positive feedback)
Population size (N)
400
300
200
100
0
N_t = N_t-1 e^rt
0
25
50
75
100
Time
E
Plant diversity
N_S1
dN_S1/dt
N_S2
dN_S2/dt
+
-
-
+
-
-
+ /-
Nutrient supply
?
+
+
Plant community productivity
Compensatory dynamics = a feedback

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