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Grand challenges in biodiversity-ecosystem functioning research in the era of science-policy platforms require explicit consideration of feedbacks

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Abstract [100-200 words]:

Feedbacks are an essential component of resilient socio-economic systems, yet the feedbacks between biodiversity, ecosystem services and human wellbeing are not 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, iii) more effective use of emerging technologies in biodiversity science and policy, iv) and a more inclusive and integrated global community of biodiversity observers. 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. Dynamic feedbacks are causes and consequences of biodiversity change

Increasing recognition of irreversible biodiversity change and unsustainable ecosystem exploitation has spurred unprecedented collaboration among scientists and policymakers worldwide to mitigate these ecological crises (1–4). Biodiversity is in crisis as a result of habitat loss, overharvesting and other pressures associated with humanity's accelerated use of natural resources (2,5–7). The diversity of life – from genes to social-ecological systems and beyond - plays a major role in driving ecosystem dynamics throughout the biosphere; higher biodiversity enhances ecosystem functioning (8,9) and services (or also referred to as 'nature's contributions to people', see Glossary in Box 1). Biodiversity and ecosystem services 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) (10).

The science underpinning these major initiatives has clearly demonstrated direct effects of biodiversity on ecosystem functioning and human wellbeing (B-E-H) (Figure 1), as well as dynamic feedbacks (Section II) that influence how biodiversity, functioning 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 (8,11,12), increased productivity and food quality benefitting humans through an ecosystem service such as food provision (9,13–15), and food management systems that facilitate biodiversity (16,17)(Figure 1).

The next generation of biodiversity scholarship will expand the scale and scope of this topic to more effectively understand feedbacks. This knowledge will better 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 dynamic 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 functioning, and thus is missing from our understanding of the full relationships between people and biodiversity. Next, we briefly review how current leading policy platforms consider the role of feedbacks and highlight opportunities for strengthening consideration of feedbacks (Section III). We then identify key scientific knowledge gaps (Section IV) that we suggest limit the full uptake of scientific understanding into policy platforms, and we list six grand challenges (Section V) that deserve organized and collaborative investment for rapid progress. Finally, we outline an agenda for collaborative action (Section VI) to meet these challenges to support policy-relevant science in a changing world, as our understanding of that world also changes.

II. Feedbacks drive biodiversity – ecosystem functioning – human relationships

Biodiversity and its relationship to ecosystem functioning and human systems depend on feedbacks within and between these elements (Figure 1; Box 2) (18–20). The concept of feedback is often used to describe specific dynamic interactions, but also is used to refer to interaction networks (21) 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 (22). Feedbacks 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 (23,24). Additionally, feedbacks between human and ecological systems have become an important area of interdisciplinary research and for guiding discourse (25–27). These research programs all contribute to the solution we are addressing here – which is to better understand feedbacks specifically in the B-E-H system as a whole (28), and how best to apply this understanding to broad scale policy, communication and knowledge integration programs.

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 (29,30). In contrast, *positive feedbacks* are self-reinforcing and can be destabilizing (31) (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. 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 (32,33), from shallow lakes (34) to tropical rainforests (35) to coral reefs (36). 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 (3,37,38)(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 (20,39–41). 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 (3,38,42).

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 (32), and the conversion of kelp forests to barrens in coastal oceans (43). One reasonably well understood example is that of pollinator diversity and plant diversity (44,45)(Figure 1). The abundance of pollinators is known to increase the abundance of plants 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

(46,47), causing humans to lose value in crop yields, and in turn motivating conservation and management actions.

III. Feedbacks have been under-emphasized 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 The Group on Earth Observations Biodiversity Observation Network (GEO BON). The IPBES framework (2,10) provides the broader community a system for understanding how biodiversity, inclusive of humanity and human diversity (Box 1), are related to a sustainable biosphere (48). This framework is offered with the purpose of aligning assessments of change and knowledge development in biological and social sciences with policy needs (48,49). It also channels and motivates scholarship and scientific research to fill gaps and improve methods for modeling scenarios.

The IPBES platform relies on synthesis of scientific evidence for the causes and consequences of biodiversity change. The evidence is combined with scientific models to project and forecast future scenarios for biodiversity change and human activities (50). There is little mention of full feedback cycles between biodiversity and ecosystem functioning (e.g., Figure 1A) in the summary of models used to generate projections and scenarios for the most recent IPBES report. The few existing examples are in the integrated assessment models involving social and economic systems coupled with natural systems (50). The assessment report indicates that feedbacks are identified as an *outcome* of integrated system models, rather than an architectural feature (50). 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 (51). 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.

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. It is recognized that feedbacks need to be included more, and that knowledge gaps - both scientific and in the general understanding and application of science – are a barrier.

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) ***How do current or recent biodiversity temporal trends influence future trajectories of biodiversity change?*** 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 (33,50,52,53). When feedbacks are at play, trajectories of a system observed over a short time span are not necessarily indicative of longer-term patterns (54–56). 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 (21,57). Furthermore, we need to distinguish when positive vs negative feedbacks dominate if they require very different management actions.

2) ***How do trends in biodiversity affect 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. Because feedbacks determine how biodiversity, ecosystem functioning and human activities change *together* over time, future trajectories of diversity, ecosystem functioning 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 / ecosystem functioning feedbacks (58). One pervasive consequence of this knowledge gap is the persistent decoupling of biodiversity and functioning in assessment and monitoring programs; most of the biodiversity observations being assembled for biodiversity change assessments (e.g., BioTIME, PREDICTS, GEO BON) do not include accompanying measures of ecosystem processes. Though GEO BON is moving in this direction with essential ecosystem variables, such an advance must be made in the context of statistical approaches that can allow detection and attribution of joint changes in biodiversity, ecosystem functioning and human wellbeing.

3) ***Experimental tests for direct BEF effects have omitted feedbacks.*** The majority of experimental tests of the relationship between biodiversity and ecosystem functioning has employed an experimental design that intentionally disrupts potential feedbacks – for example, by weeding out species that colonize (59) or by replacing species that are lost (60) 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 ecosystem functioning (e.g., Figure 2, C) from playing out over time. Consequently, the hundreds of experiments frequently reviewed and synthesized as strong evidence for direct effects of diversity on ecosystem functioning (8,61) cannot be used to demonstrate consequences of the feedbacks between diversity and functioning (40,62).

4) ***Human-biodiversity feedbacks are still not well understood,*** allowing to persist a perception that people affect biodiversity but that there is no feedback from biodiversity to people (2,26,28,63,64). 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" (50). 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 communication of existing knowledge to policy makers are barriers to a fuller treatment of feedbacks in biodiversity scenarios.

V. Grand challenges in biodiversity research.

Filling these knowledge 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. Here, we outline 6 scientific challenges to prioritize 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, ecosystem functioning and humans.

The goal is to fully integrate the multiple human (behavioral, demographic, social, political, economic, institutional) components of feedbacks in the B-E-H system that includes biodiversity and human societies (26,65). Meeting this challenge requires 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 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 functioning and human well-being across scales.

We require new theory to guide experimental tests and observation programs that allow us to more deeply understand feedbacks between diversity change and ecosystem functioning, and how these are linked in coupled human-natural systems across scales of space, time and organization (66) (Figure 3). 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 ecosystem functioning. Such theory and experimental work would be explicit about temporal patterns in biodiversity and ecosystem functioning, spatial and temporal variation, and would identify links between feedbacks involving ecosystem functioning and multiple dimensions of diversity, and the role that human systems play in these biodiversity-ecosystem functioning linkages.

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 operational taxonomic units, OTU), and models of phylogenies. Not only do we still require great investment (Section VI) in organized biodiversity sampling and monitoring (62), we also lack the scientific knowledge to relate changes in observed diversity at different levels of biological organization (genes vs species; Figure 3) to changes in ecosystem functioning, and feedbacks between biodiversity and ecosystem functioning. 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 play a role in which genes and genomes persist in communities (67). 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 in the context of and as consequences of ecosystem functioning and human actions.

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

Direct, one-way interactions between biodiversity and ecosystem functions, and ecosystem functions and services, are well-established for several services (e.g., 68). It is also well-recognized that many ecosystem services depend on the presence of specific species or functional groups (48,69), thus implicating biodiversity-ecosystem functioning 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 functioning feedbacks as defined more strictly to be additional to the contributions of particular species (Box 1: Glossary) (68,69). It remains unclear how ecosystem functions, or related sets of functions (sometimes called ‘multifunctionality), confer ecosystem services that are relevant for human wellbeing (70,71). 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 (72). 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

(73–77). 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 biodiversity observations and coupled measures of ecosystem functioning also present a barrier to robustly combining observations into models of change to understand change across scales. Furthermore, feedbacks are difficult to detect from most observational datasets 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), 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. Outside specialist research communities, B-E-H feedbacks 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. Greater emphasis on this representation can help minimize overlooking this important concept when identifying priorities for biodiversity observation or multifaceted conservation opportunities. 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? Additionally, many knowledge systems beyond science – such as traditional ecological knowledge systems - include knowledge of feedbacks (26,65,78), and therefore an emphasis on feedbacks may provide another scaffold to integrate biodiversity understanding across diverse forms of knowledge. 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.

VI. Agenda for action.

We have outlined five key knowledge gaps and six associated 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 programs worldwide to 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 communities worldwide must continue to engage with one another at all stages of biodiversity assessments – and at all stages of our proposed action agenda. People serving as observers, knowledge keepers and knowledge users, as ecosystem service beneficiaries and decision makers play critical roles in the actual B-E-H feedback cycles, because assessment and management are part of the cycles! Scientific and science-policy collaborations in biodiversity research should strive for cultural, geographic, political and ethnic diversity among researchers and within research projects (79). Strengthening these collaborations, especially with historically underrepresented communities, will require specific investment of time, resources and financial support. We can build on existing science-community partnerships and extending these into biodiversity observation and assessment networks (80). Doing so will result in an inclusion of a broader range of knowledge systems and perceptions of human-biodiversity interactions (79), 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 (3,81). These models must be developed and\ 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 functioning and human activity change together.*

Integrated observations should be made at different spatial scales with worldwide coverage (73), 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 (3,66,82). 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 functioning change and human activities. New statistical approaches must be developed to understand causation in the complex systems we are observing (83). 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 (84). New approaches, such as that proposed by Kühl et al (2020)(80), must emphasize community involvement and data collection supported by and integrated within a broader context of biodiversity assessment. To succeed, these require the investment and action we outline in this agenda for action.

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 functioning 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).

VII. Conclusion

Scientific progress over the last 30 years has led to recognition of the importance of feedbacks among biodiversity, functioning 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 policy 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. There is no substitute for knowledge of feedbacks. The effects of feedbacks over time cannot be approximated by static representations of direct effects (52). Without a fuller scientific understanding of feedbacks that link biodiversity change, ecosystem functioning and human wellbeing, we risk making decisions based on modeled futures that do not capture the full range of likely possibilities (21,50,53,65,85,86). We cannot afford this just when we need science urgently to guide our planning for the future. By investing in science and supporting collaborative and interdisciplinary partnerships (87) 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 1: 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.

Feedback: modification or control of a process by the results or effects of the same process.

Ecosystems: joint biotic/abiotic systems of life, characterized by dynamic stocks and fluxes of energy, materials and information and their feedbacks.

Biodiversity-ecosystem functioning (BEF) relationships: refers to the relationship between diversity *per se* and the magnitude and stability of an ecosystem functions. BEF refers to the role diversity plays in ecosystem functioning that is over and above the importance of total abundance, biomass or composition of the biological assemblage (88).

Ecosystem functions: the processes of energy flow (e.g., primary production), material cycling (e.g., carbon cycling) and information processing (e.g., evolution) carried out by living systems. Functions are understood to reflect interaction networks involving multiple genetic and functional elements of biodiversity, and include stocks and pools of biomass, elements and energy forms.

Ecosystem services: nature's contribution to people (2), including a broad and pluralistic view of contributions from economic values to cultural values, in intrinsic, instrumental or relational systems (89,90).

Ecosystem services: the value of ecosystem functions to people (91), and originally, defined as ecosystem-based goods and services for human well-being (92). Although different opinions exist such as that ecosystem services could be viewed as "rights-based approaches to biodiversity conservation and sustainable use" (49), it is important to emphasize that the value can be assessed in a variety of ways, from economic values to cultural values, in intrinsic, instrumental or relational systems (89,90,92).

Natures contributions to people: another pluralistic view for the value of ecosystems and ecosystem functions to people (89,90). Peterson et al. (90) expect the view to encourage a recognition of pluralism and the need for a richer process of articulation, translation, and discussion among many different perspectives on people's relationship with nature.

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Figure Legends

Figure 1. Feedbacks within and among biodiversity, ecosystem functioning, and human well-being. A) Feedbacks an aquatic system in which invertebrate and vertebrate diversity enhance ecosystem functions such as biomass production enhance animal biomass that may be harvested for food and livelihood by people. Harvesting may maintain some fish at high population growth rates by reducing population densities thereby maintaining biodiversity. B) similar feedbacks occur in agricultural systems. Within each element (biodiversity, ecosystem functioning and humans) feedbacks occur (dashed arrows) that can stabilize or destabilize systems (see Figure 2), and feedbacks across these elements (solid arrows) can also stabilize or destabilize the system at a larger scale. Direct one-way effects (straight arrows) are most often the focus of experiments and policy syntheses.

Figure 2. 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

Figure 3. Models, experiments and observation systems are needed that explicitly address feedbacks and scales of space, time and biological organization. **A)** Current observation or experimental programs tend to focus in one part of this space – for example, generating data within the dashed box – and we argue that we need to develop approaches for understanding feedbacks that would relate observations at multiple scales within the focal system (the box) and at other scales (the upper right-hand cloud) (modified from Gonzalez et al 2020**). B)** When possible, the knowledge we generate via observations, theory, models and experiments must involve the biodiversity, ecosystem function and human components at each level. Hypothetical data are copied from panel A, illustrating that we should strive for observations and understanding of how biodiversity, human activities and ecosystem functions change at the same levels of spatial and temporal resolution, in the context of other spatial and temporal processes (panel A).

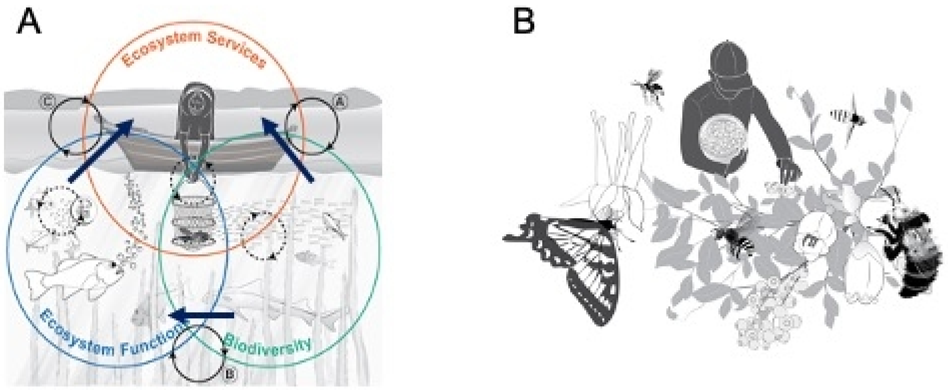

Figure 1

174x78mm (72 x 72 DPI)

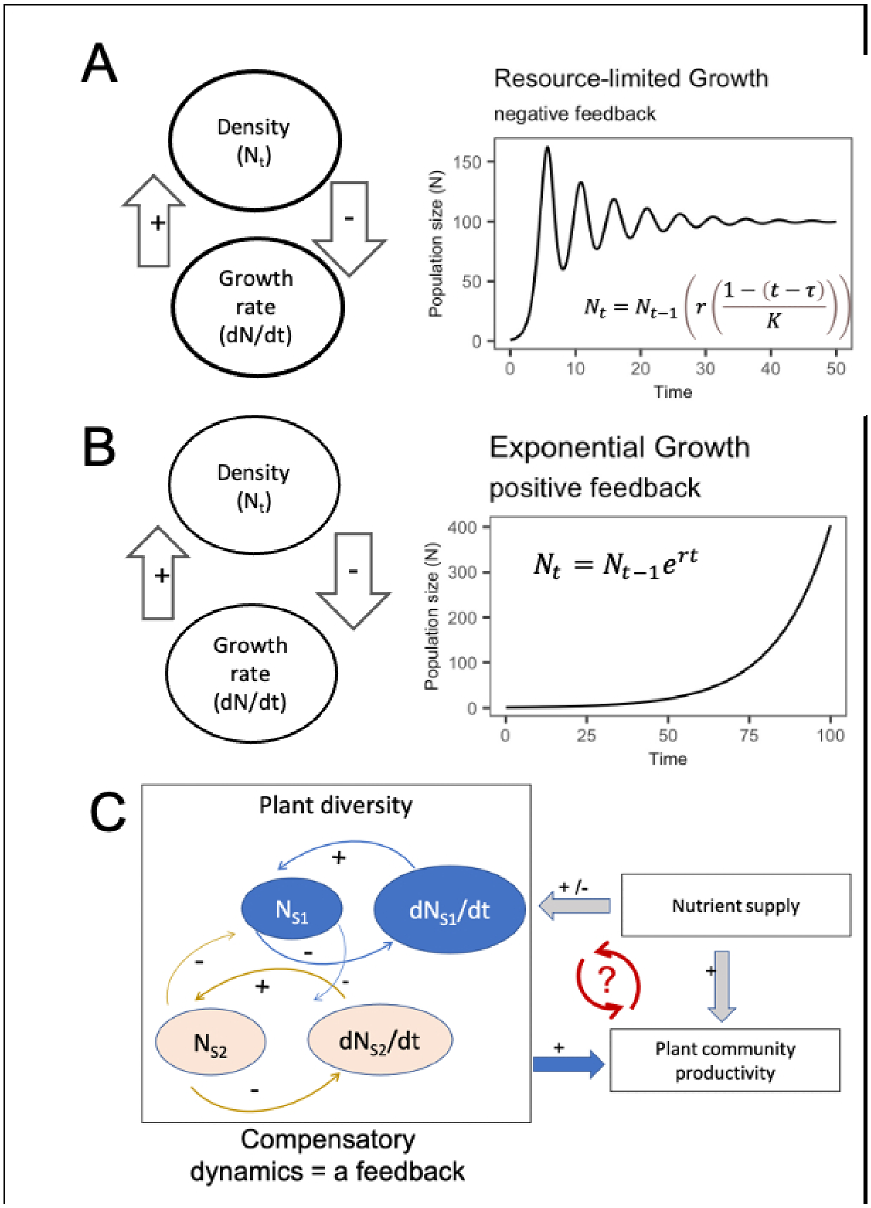
A
Density
(N$_t$)
Growth
rate
(dN/dt)
+
-
Resource-limited Growth
negative feedback
Population size (N)
Time
$N_t = N_{t-1}\left(r\left(\frac{1-(t-\tau)}{K}\right)\right)$
B
Density
(N$_t$)
Growth
rate
(dN/dt)
+
-
Exponential Growth
positive feedback
Population size (N)
Time
$N_t = N_{t-1}e^{rt}$
C
Plant diversity
N$_{S1}$
dN$_{S1}$/dt
N$_{S2}$
dN$_{S2}$/dt
+
-
Nutrient supply
+ /-
?
Plant community
productivity
Compensatory
dynamics = a feedback

Figure 2.

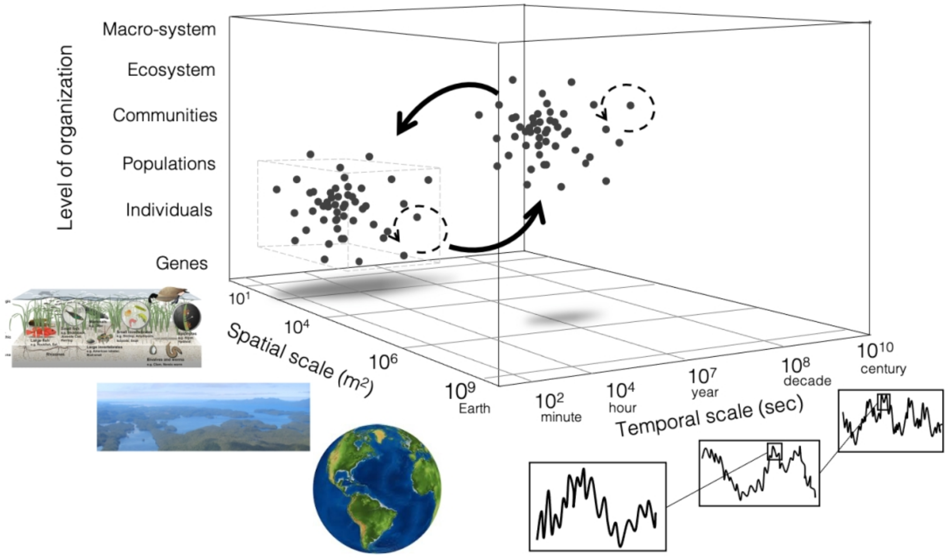
Level of organization
Macro-system
Ecosystem
Communities
Populations
Individuals
Genes
Spatial scale (m^2)
10^1
10^4
10^6
10^9
Earth
Temporal scale (sec)
10^2
minute
10^4
hour
10^7
year
10^8
decade
10^{10}
century

Figure 3A

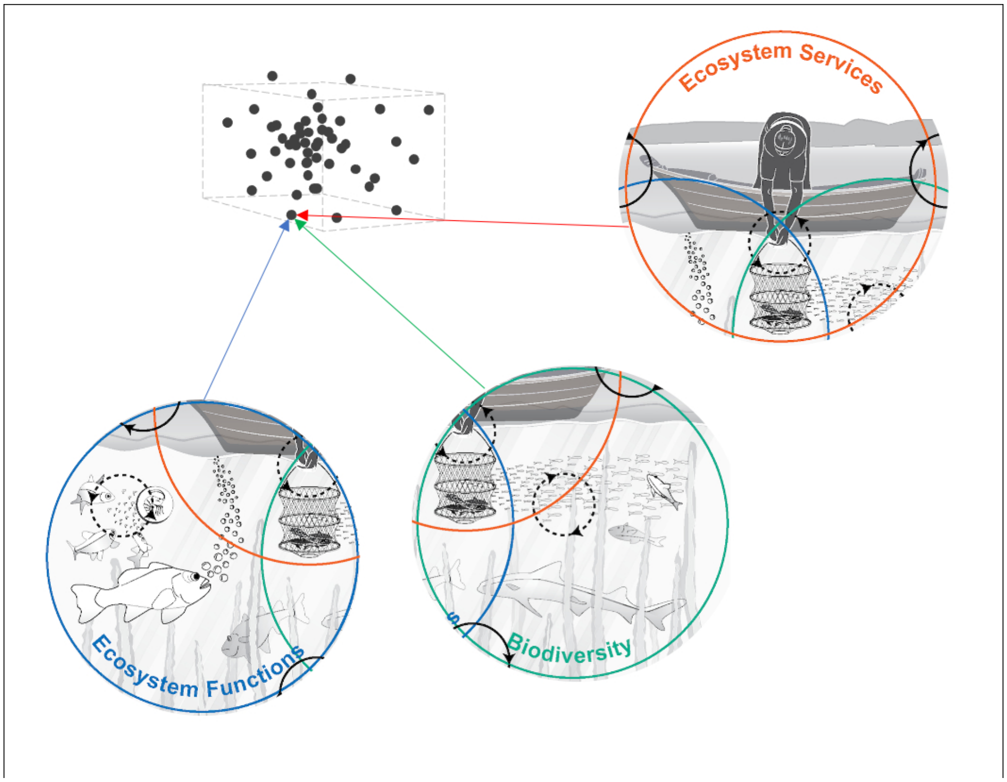

Figure 3B