



Approaches to defining a planetary boundary for biodiversity



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ABSTRACT

The idea that there is an identifiable set of boundaries, beyond which anthropogenic change will put the Earth system outside a safe operating space for humanity, is attracting interest in the scientific community and gaining support in the environmental policy world. Rockstrom et al. (2009) identify nine such boundaries and highlight biodiversity loss as being the single boundary where current rates of extinction put the Earth system furthest outside the safe operating space. Here we review the evidence to support a boundary based on extinction rates and identify weaknesses with this metric and its bearing on humanity's needs. While changes to biodiversity are of undisputed importance, we show that both extinction rate and species richness are weak metrics for this purpose, and they do not scale well from local to regional or global levels. We develop alternative approaches to determine biodiversity loss boundaries and extend our analysis to consider large-scale responses in the Earth system that could affect its suitability for complex human societies which in turn are mediated by the biosphere. We suggest three facets of biodiversity on which a boundary could be based: the genetic library of life; functional type diversity; and biome condition and extent. For each of these we explore the science needed to indicate how it might be measured and how changes would affect human societies. In addition to these three facets, we show how biodiversity's role in supporting a safe operating space for humanity may lie primarily in its interactions with other boundaries, suggesting an immediate area of focus for scientists and policymakers.

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1. Introduction

The identification of global-scale thresholds underpins the planetary boundaries concept introduced by Rockstrom et al. (2009a, 2009b). Nine boundaries were proposed, representing specific thresholds of climate change, ocean acidification, stratospheric ozone, global nitrogen and phosphorus cycles, atmospheric aerosol loading, freshwater use, land-use change, biodiversity loss, and chemical pollution (Rockstrom et al., 2009a) that collectively delimit 'a safe operating space for humanity'. While some of the proposed boundaries were relatively simple to define because local inputs or changes make a predictable contribution to global processes with known thresholds, others (such as land-use change and biodiversity loss) are recognised as complex human system-ecosystem processes not easily associated with known global or continental thresholds (Rockstrom et al., 2009a).

Transgressing any of the nine boundaries is expected to lead to an increased risk to one or more aspects of human wellbeing, or would undermine the resilience of the Earth system as a whole. While some boundaries operate in a top-down manner driven by systemic global processes (e.g. climate change), others may be bottom-up processes driving large-scale responses so that the processes might be local or regional only, but sufficiently widespread to have significant aggregate consequences at the global-scale (e.g. N and P nutrient pollution) (Rockstrom et al., 2009a).

The planetary boundary for biodiversity has been particularly problematic. The original analysis emphasised the difficulty of describing and quantifying a boundary for biodiversity loss, noting that it is a slow process without known global-level thresholds, that there is incomplete knowledge on the role of biodiversity for ecosystem functioning across scales, and that the suggested boundary position was therefore highly uncertain (Rockstrom et al., 2009a). However there are more fundamental problems with the biodiversity boundary than just setting its position. Brook et al. (2013) questioned the existence of a global biodiversity threshold, noting the large spatial heterogeneity in the drivers and responses associated with biodiversity loss, the lack of abrupt shifts at global scale, and the absence of the large-scale interconnectivity that would be needed to propagate local ecosystem regime shifts globally. In contrast, Hughes et al. (2013) suggest that local changes could scale up to regional or global-level, especially given the interconnectedness of human systems, and Barnosky et al. (2012) note that slow drivers over human timescales can still lead to thresholds. The extent to which a biodiversity boundary might be experienced at local, regional or global scales, and indeed whether accumulations of local biodiversity change can imperil large-scale processes, is currently unresolved.

The discussion of a biodiversity boundary is also clouded by confusion over the use of the term 'biodiversity', which can simply mean species richness, but is often used for functional or ecosystem diversity, or more generally to represent the whole variety of life on Earth, sometimes with connotations of naturalness or intactness (Convention on Biological Diversity, 2010; DeLong, 1996; Fischer and Young, 2007). Biodiversity loss is generally manifested as a reduction in species numbers (ultimately to global extinction rates), but it is more often the extent and biomass of the biosphere that has a dominant influence on Earth system processes and the ecosystem services on which people depend (Díaz and Cabido, 2001; Díaz et al., 2006; Mace, 2005; Mace et al., 2012). The broad definitions of biodiversity in current usage do not allow such distinctions to be drawn, despite their importance.

Discussions of thresholds for biodiversity are further confused about whether the proposed threshold is intended to represent (i) changes in elements of biodiversity that cause a large-scale change in other processes in the Earth system, (ii) physical or biogeochemical changes in the Earth system that cause rapid, large-scale

biodiversity change, or (iii) localised ecosystem changes that may propagate and scale up to large-scale or even global biodiversity change. There is some evidence that each of these takes place (Barnosky et al., 2012; Leadley et al., 2010; Lenton and Williams, 2013), but none is quite what is defined by the planetary boundaries concept with its clear implication that the boundary position is set by the level of a driver (in this case biodiversity loss) where there is a raised risk of impact on human welfare.

Here, we review the current biodiversity boundary as determined by Rockstrom et al. (2009b). Drawing on recent research we develop a conceptual basis for a biodiversity boundary which proposes alternative approaches that could delimit the safe operating space for humanity. We use this conceptual basis to identify key research directions needed to move towards the identification of actual metrics and quantitative boundaries or thresholds.

2. A critique of the biodiversity boundary

According to the planetary boundaries concept, all boundaries are defined in terms of response and control variables (Fig. 1) (Rockstrom et al., 2009a). Response variables are measures of Earth-system responses relevant to humans. Control variables represent the metric(s) related to the specific boundary that determines the Earth system response, while the boundary is defined as a human-determined level of the control variable set at a "safe" distance from a global threshold or a potentially dangerous level. Currently the planetary boundary for biodiversity uses ecosystem functioning as the response variable and the global species extinction rate as its control variable. The boundary is set at 10 times the average background extinction rate, which is 10 extinctions per million species per year (E/MSY), roughly equivalent to Holocene rates. Species extinction rate is arguably the most fundamental measure of global biodiversity loss, but not an ideal metric in this context for a number of reasons. First, it tends to be estimated most often for vertebrate species (an unrepresentative <2% of all described species). Second, it is insensitive to important changes in species abundance, community composition and distribution of species (Balmford et al., 2003; Millennium Ecosystem Assessment, 2005; Pereira et al., 2012). Third, it is hard to estimate with high certainty until long after the extinction has occurred (Heywood et al., 1994). Finally it is not clear how global species extinction rates will influence ecosystem functioning at scales relevant to the safe operating space.

Recent reviews of the relationships between species richness and ecosystem functions show that as species loss increases and the system approaches a monoculture, ecosystem processes such as primary production and decomposition on average decline, but also show a strongly increasing variance in response (Cardinale et al., 2012; Hooper et al., 2012). These reviews are based on multiple experimental studies where the effects of biomass and sampling of species are controlled so that the effects can be attributed to richness alone. The best monoculture often outperforms the most diverse system because certain species are very effective at a particular process on their own, but in general, especially at intermediate levels of richness, lower species richness leads to reduced ecosystem functions (Cardinale et al., 2012). Such composite relationships however have only limited applicability to the broader issue concerning the impact of biodiversity loss on people because they are based on controlled mesocosm or field experiments, usually conducted in relatively simple ecosystems over years or – occasionally – decades. They cannot represent the additional contributions from richness or diversity to ecosystem functions over time (Reich et al., 2012) and place (Godbold et al., 2011; Spehn et al., 2005) or the fact that, although certain species may appear redundant when a particular function is considered

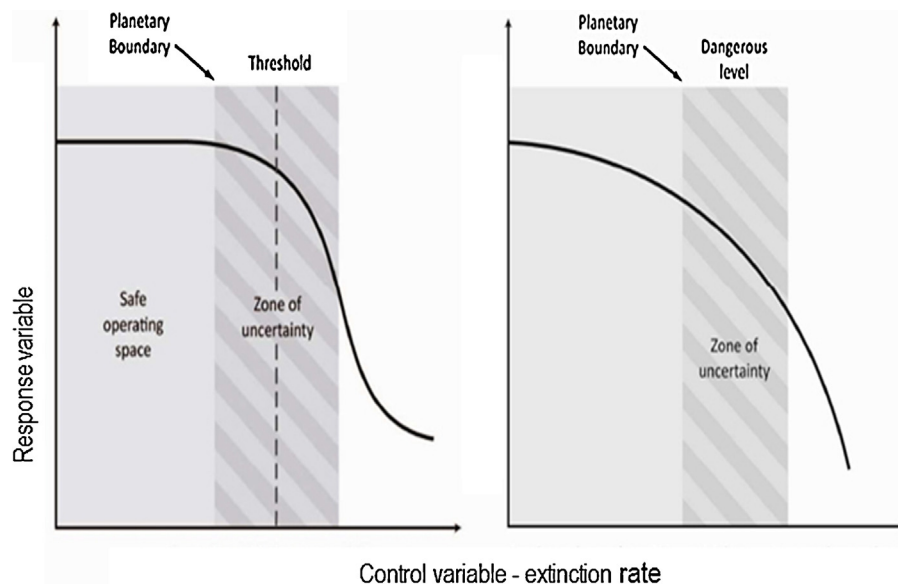


Fig. 1. Conceptual description of planetary boundaries. In the left hand panel the boundary is designed to avoid the crossing of a critical continental to global threshold in an Earth system process. In the right hand panel there is no global threshold effect as far as we know, but exceeding the boundary level will lead to significant interactions with regional and global thresholds and/or may cause a large number of undesired threshold effects at the local to regional scale, which in aggregate add up to a serious global concern for humanity. From Rockstrom et al. (2009a).

under one set of environmental conditions, many species are needed to guarantee multiple functions in a changing world (Gamfeldt et al., 2008; Hector and Bagchi, 2007; Isbell et al., 2011). Additionally, species' roles and dominance change over time, and functions are enhanced when the diversity includes species with complementary interactions (Allan et al., 2011). Furthermore, despite much evidence for loss of regional and global diversity and abundance (Butchart et al., 2010; Pereira et al., 2012), there is little evidence of declines in local species richness over time (Dornelas et al., 2014; Vellend et al., 2013), most notably in plants that are significant for ecosystem processes (de Bello et al., 2010) and which are the focus of study in many biodiversity-ecosystem function experiments. Changes to local, compared to regional and global species richness, are also not closely related for reasons to do with the local disappearance of rare species often being masked by more widespread species (Thomas, 2013).

In general, therefore, while there is a large body of work showing the links between species richness and ecosystem processes, most of these studies focus only on species richness, have been carried out at very fine scales and, because they do not consider other, more relevant, components of biodiversity, their findings are insufficient to predict a biodiversity boundary (Brook et al., 2013). While a recent

commentary states that 70% of species in any ecosystem should be retained for securing healthy and productive ecosystems (Griggs et al., 2013), there is no evidence to support this figure.

Moreover, a boundary based on species richness alone misses many more fundamental and persistent roles of broader sense biodiversity, especially related to abundance, community composition, functional traits and ecosystem-level interactions. Existing global biodiversity measures such as Mean Species Abundance (Alkemade et al., 2009), the Red List Index (Butchart et al., 2004, 2007), the Biodiversity Intactness Index (Scholes and Biggs, 2005) and others reviewed by Vackar et al. (2012) are unable to reflect the key features of biodiversity important for humanity. The most recent effort to agree even a minimum set of biodiversity indicators essential for study, reporting, and management of biodiversity change, includes 22 variables, most of which require sampling over multiple taxa or locations (GEO BON, 2013; Pereira et al., 2013).

We have identified certain problems that arise from using species extinction rates as the metric for a biodiversity boundary. In addition there are questions about how any biodiversity-related boundaries might scale up and down from local to global. Below we explore these issues and suggest three possible approaches (Table 1). In addition to the role biodiversity loss plays in

Table 1
Summary of proposals for planetary boundaries for biodiversity.

Proposed boundary	Control variable	Response variable	Relationship	Boundary
Species numbers related to ecological functions (from Rockstrom et al. 2009a,b) The genetic library of life	Extinction rate uPSV – a measure related to phylogenetic diversity	Ecosystem functioning at continental and ocean basin scales Long term innovation and resilience of ecosystem form and function	Thresholds likely at local and regional scales. Probably roughly linear but potentially with steps associated with clade and biogeographic sensitivity	Boundary position highly uncertain Could be rather arbitrary if relationship is close to linear. Likely to be more thresholds at local and regional scales
Levels of functional diversity	Measures of functional diversity relevant to key ecosystem processes	Ecosystem functions and processes linked to human wellbeing	Likely to be non-linear with discontinuities as key sets of functions are lost	Points of critical functional loss potentially linked to major ecological processes (e.g. trophic levels, production, nutrient cycles)
Biome integrity	Biome specific drivers	Biome condition and extent	Each biome will have distinct and highly non-linear form	Composite of several biomes (see Fig. 2)

supporting humanity, it also plays a key role in mediating and responding to other planetary processes; we therefore conclude with an examination of the interactions between biodiversity loss and the other planetary boundaries.

3. Alternatives to the extinction rate boundary

3.1. Genetic diversity for long-term evolutionary-ecological potential

In the long term – over centuries to millennia – human wellbeing will depend on the biota's continued ability to support desired ecosystem services and processes in the face of often rapidly-changing selective pressures. Because it is not possible to predict which functional trait combinations will be most needed, it is not possible to identify the most important species a priori with any certainty. Instead, we should aim to manage the risks, and some features of species can be used to predict how much they add to humanity's "portfolio of biodiversity insurance". For this purpose, a species' future importance depends on how much it adds to the overall diversity of unspecified functional traits, ultimately reflected in the extent of phylogenetic diversity (Faith, 1992) representing future option values of biodiversity (*sensu* Faith, 1994)

The expected variance of a neutrally-evolving phenotypic trait can be estimated from the phylogeny of the evolving species or populations. When branch lengths are expressed in terms of genetic change (Helmus et al., 2007), the unscaled version of this Phylogenetic Species Variability (PSV) measure reflects the overall diversity of unspecified traits, under the assumption of neutral evolution, and could incorporate more complicated and realistic models of trait evolution (reviewed by O'Meara, 2012). However, it can be hard to tell which of these models best approximates reality. Even with large data sets (Cooper and Purvis, 2010; Ho and Ane, 2013), rates of phenotypic evolution can be largely decoupled from rates of nucleotide substitution in gene sequences (Janečka et al., 2012) and empirical analyses indicate that phylogenetic diversity does not capture the most diverse sets of biological features, especially among more distantly related lineages (Kelly et al., 2014). An alternative approach might be to use macroecological approaches to model how rates of phenotypic change depend on features of lineages and environments. Models so far have lacked explanatory power or generality (Janečka et al., 2012), but richer data sets – capturing a larger set of traits for more populations in more species – might improve the situation. A further caveat is that, as species are lost phylogenetic diversity will not decline as rapidly as functional trait variance if the risk of extinction depends on species' values of functional traits. Such a decoupling has been shown for body size variance and other phylogenetic diversity measures in mammals (Fritz and Purvis, 2010). Lastly, phylogenetic diversity does not incorporate within-population genetic variation, on which adaptability depends. A coarse way of accommodating this could be to exclude species that are threatened with extinction (perhaps using the IUCN Red List): a meta-analysis showed that heterozygosity was on average 35% lower in a set of 170 threatened species than in close non-threatened relatives (Spielman et al., 2004).

If such a metric of phylogenetic diversity is viewed as a control variable on long-term evolutionary-ecological potential, how does it respond to human pressures? It declines when a species disappears from its calculation, through being declared extinct or (with the modification suggested above) being declared to be threatened; the extent of the decline then depends on the species' evolutionary distinctiveness. Smaller declines occur when local populations are extirpated. Increases occur as species' conservation statuses improve and, more passively, simply as populations survive over time.

What would constitute a threshold? Loss of species at random will reduce phylogenetic diversity only slowly, as most species lost will have close relatives that remain (Nee and May, 1997). However, both extinction and extinction risk tend to be clumped within phylogenies (Mace et al., 2003) and are often geographically correlated, increasing the likelihood that entire clades will cease to exist, and therefore potentially defining local or regional thresholds. Habitat conversion has been the dominant driver of biodiversity loss over recent decades (Hoffmann et al., 2010) and is projected to continue to be important throughout this century (Pereira et al., 2010). However, its potential to constitute a threshold may be reduced because habitat conversion is a local process, operating at different rates and affecting different sets of species in different settings; global responses might therefore be expected to be rather smooth, even if local or regional changes exhibit thresholds.

3.2. Levels of functional diversity

Functional diversity represents the value, range, distribution and relative abundance of the functional traits of the organisms present in an ecosystem or biota (Díaz and Cabido, 2001). Organisms with different functional traits can differentially affect ecosystem properties such as primary production, decomposition or detoxification and also react differently to changes in the environment (Díaz and Cabido, 2001; Diaz et al., 2007; Lavorel et al., 2011; Suding et al., 2008). As certain combinations of functional traits are lost in the face of environmental change, key functions could be at risk, especially if the traits of individual species co-vary with their risk of extinction (Solan et al., 2004), or could simply be performed less efficiently than in more diverse systems. While the genetic diversity boundary might represent all diversity and its potential future utility, the functional diversity here represents current functions that are known to be significant for humanity.

There may be a control variable of this sort that captures enough of the relationship between ecosystem structure and function to be useful at the regional to global level. It is unlikely to be as crude as a simple count of functional groups present (i.e., 'functional type richness'), since some of those functions are irreplaceable whereas others may be partly or fully redundant. It could, however, be based on a systematic assessment of relevant traits (Diaz et al., 2013; Kattge et al., 2011; Lavorel et al., 2013), potentially geared to key functions (Craine et al., 2002), after recognising and addressing the potential circularity involved in assigning functional traits to groups of species (Wright et al., 2006). A measure based on functional traits would operate effectively over short time scales and be relevant to the maintenance of adaptive variability and resilience at local-to-regional scales for key ecosystem functions (Table 1). It could be designed to be sensitive to large-scale losses in particular functional groups, such as important food and fibre species, top predators (Estes et al., 2011), plants with traits for high carbon assimilation, transfer and storage below ground (De Deyn et al., 2008), or for certain groups with significant regulatory functions, such as in Arctic peatlands or marine phytoplankton. Although there is now a wide variety of functional diversity indices applicable at the local to landscape scales (see for example Mason et al., 2013), currently there are no general metrics that could be used to assess status or trends in functional diversity at broader scales. The identification of thresholds might be challenging if there are multiple, non-linear functional relationships that are difficult to aggregate within and across ecosystems. Some pilot approaches, for instance through adapting a functional-type-based version of the Biodiversity Intactness Index (Scholes and Biggs, 2005) could be considered, and both relevant theory and observations provide a foundation for

such an approach (e.g., GEO BON) (Kattge et al., 2011; Pereira et al., 2013).

3.3. Biome integrity

Instead of asking about the consequences of progressive biodiversity loss, we now consider the large-scale biodiversity-mediated responses in Earth systems that affect the planet's suitability for complex human societies. For example, the biosphere drives global biogeochemistry, which in turn governs atmospheric composition, soil fertility and ocean productivity. The loss or degradation of entire biomes (e.g., coral reefs), or of the biodiversity components associated with large-scale ecological processes (e.g. predation, nutrient cycling) would have substantial impacts on regional and distant social and ecological systems (Barnosky et al., 2012; Leadley et al., 2010). Changes in these biospheric processes could be large enough to compromise the Earth's ability to sustain human societies as we know them, and offer a potentially simpler route to developing a boundary. For example, Running (2012) proposes the use of NPP for a global boundary, which would reflect changes to the fundamental biosphere processes of production and nutrient cycling. Here we develop a similar logic for subsets of the biosphere.

Biomes are global-scale systems, such as tundra, coral reefs or tropical grasslands and savannas, distinguished from one another by the collections of ecosystems and species assemblages found there. There are several classifications, but one widely used scheme recognises 14 terrestrial, seven freshwater and five marine biomes (Olson and Dinerstein, 2002). A biome-based approach to planetary boundaries rests on the notion that biomes embed functional diversity and some aspects of phylogenetic diversity and are therefore, at least to a degree, biophysically coherent sub-units of the whole Earth. They could connect meaningfully to other planetary boundaries. Changes in the condition and spatial extent of biomes may be appropriate for a planetary boundary because the consequences of biome-level changes on ecosystem processes, services, and human well-being are relatively well understood (Heyder et al., 2011), as are impacts on species and ecological communities within them (Alkemade et al., 2009; Kennedy et al., 2013). For example, shifts of tropical forest to savanna or pastures, if they occur at sufficiently large scales, can affect regional rainfall patterns and global-scale carbon storage (Davidson et al., 2012) and radically alter the diversity of particular functional groups and species (Gibson et al., 2011).

A general indicator of biome-level change could be identified by defining a control variable that determines the integrity and functioning of specific biomes at broad scales. For example, the marine carbonate budget controls the persistence of coral reefs, precipitation levels determine the existence of dryland-rainforest systems, nitrogen deposition controls the existence of some forests, and carbon dioxide concentrations can control the existence of grasslands with a C4 photosynthetic pathway.

Using this approach would require biophysical control variables to be identified for each biome and then for them all to be aggregated to the global-level. Box 1 describes the general approach and presents a worked example for coral reef integrity. Multiple control variables need to be identified; ideally one per biome. Given the striking differences among biomes, such as arctic tundra and coral reefs, a single control variable would not apply meaningfully to all, but one control variable could assess the security of biome function on a per-biome basis. Sub-global patterns within a biome, such as those due to biogeographical differences, could be accounted for by scaling the control variable to levels expected for each province. In certain cases, control and response variables could also be identified in long-term (i.e. palaeoecological, palaeolimnological) datasets to provide insights

Box 1. Biome integrity as a boundary

One approach is to set biodiversity boundaries that maintain the functioning of the Earth's major biomes (rainforest, savannah, coral reefs, etc.; see main text). Biomes provide a wealth of regulating ecosystem services that maintain Earth system processes, including the cycling of fresh water and carbon. We suggest that secure functioning of biomes would support Earth system function in a Holocene-like state, largely by maintaining the structure and functional diversity of ecosystems.

A biome is considered functionally secure if it can maintain its key structures and functions in the long term (e.g. to at least 2100, but given the Holocene focus of the boundaries concept, potentially for millennia). Clearly, an important consideration is the selection of appropriate response and control variables for each biome. The control variable (or set of variables) pertains to the functioning of the system. It should be measurable, ideally have a biotic basis and fulfil the rationale, 'if control variable X exceeds (or is below) threshold A , then the biome is intact and functioning'. The threshold might be based on levels observed in relatively pristine environments, or might be defined with respect to some key attribute (e.g. permafrost in the tundra, or stability in coral reefs). The response variable represents the security of functioning with respect to changes in the control variable. In some cases this might be the *long-term probability* of staying within the critical threshold of the control variable given the *present value* of a control variable.

An example based on coral reefs

This approach is particularly relevant for biomes that experience significant long-term impacts from slow drivers such as subsidence or climate change. Carbonate budgets in coral reefs are an example of a biome-level control variable with thresholds which, if crossed, result in the loss of that biome (Kennedy et al., 2013). The carbonate budget reflects whether the processes that construct a reef habitat, such as the calcification of living corals, outweigh those that erode the habitat, such as the boring action of sponges. If a reef's carbonate budget remains negative then the reef eventually erodes away causing a direct loss of calcifying taxa, an indirect loss of biodiversity associated with reef habitat, and a decline in ecosystem functions, such as fisheries productivity. Thus, a single metric, the carbonate budget ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$) serves as a proxy for the maintenance of biodiversity and much of the function of an entire ecosystem. Carbonate budgets are measurable in the field (Perry et al., 2013) and can be linked to both climate change and local management measures (Kennedy et al., 2013). Thus for coral reefs, the balance between growth and dissolution of the calcium carbonate skeletons of the reef-building organisms is an example of a biome-level control variable with thresholds that, if persistently crossed, result in the degradation and eventual loss of that biome. In this example, the threshold level of control variable might be, say, a carbonate budget of $1 \text{ kg m}^{-2} \text{ y}^{-1}$. However, with rising sea temperature and increased ocean acidification, a reef attaining this threshold today might fail to maintain that threshold in the long term. In this case, a higher threshold might be needed today in order to sustain ecosystem function in to the next century (e.g., $3 \text{ kg m}^{-2} \text{ y}^{-1}$). The response variable might therefore be calculated as the probability of achieving a carbonate budget of $\geq 1 \text{ kg m}^{-2} \text{ y}^{-1}$ in the year 2100.

While data currently do not exist to populate this boundary across biomes, a simulation of future carbonate budgets of Caribbean reefs under various scenarios of local management action, major changes in biodiversity (recovery of keystone species), and greenhouse gas emissions (Kennedy et al., 2013) shows that recovery of key species (from region-wide epizootics) while important, had to be complemented by low emissions scenarios (RCP2.6 from IPCC AR5) and local management of pollution and fishing. This example highlights the potential implementation of such a biome boundary, as well as the importance of boundary interactions in determining a safe operating space.

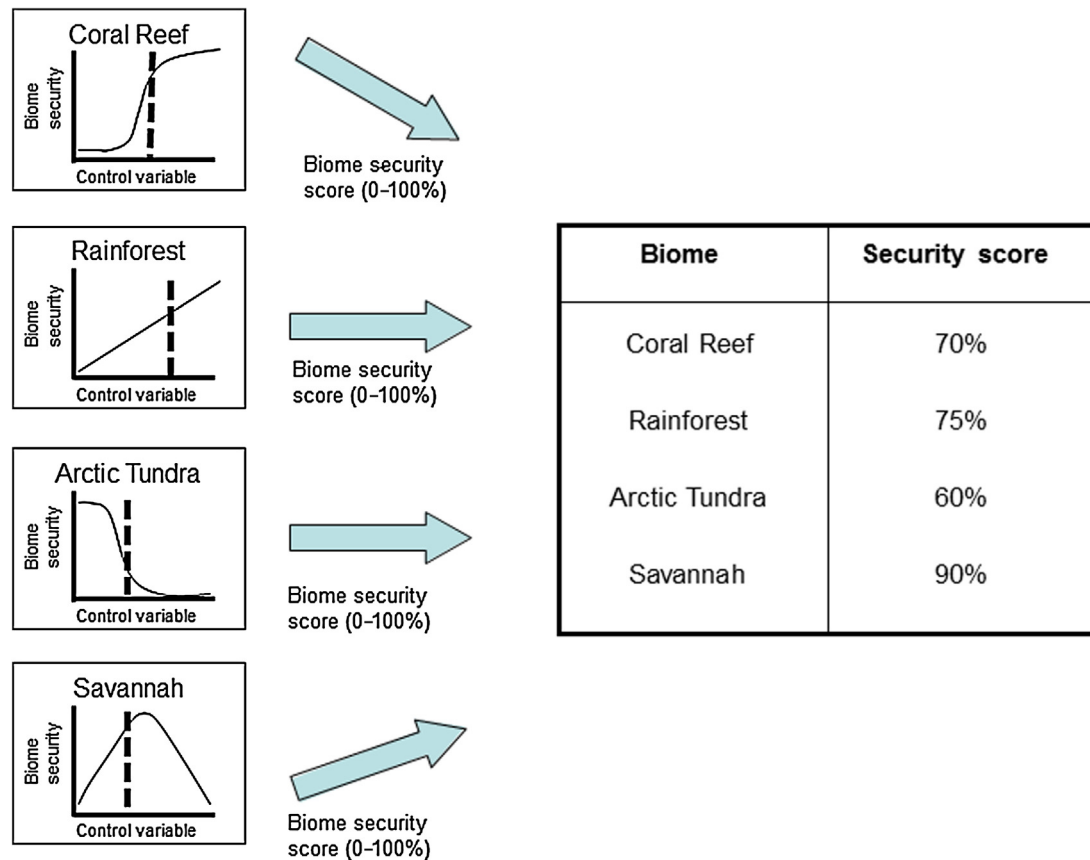


Fig. 2. Hypothetical example of how the aggregation of biome-specific metrics could contribute to a global statistic on the security of biome function. Each biome is considered independently with its own control and response variable reflecting relevant pressures and responses (see text). An overall report would highlight those biomes closest to thresholds that related to their own security of form and function. The interpretation in this example might be that there was a particular risk in Arctic tundra because of its low overall security score (60%) and that, in common with coral reefs it is close to a threshold.

into a biome's functioning over the Holocene. Biome security could then be aggregated to a global-scale to encompass the functioning of all major biomes (Fig. 2). More sophisticated means of scaling up might first disaggregate scores within each biome into categories of degradation (highly degraded, partly degraded, etc.). Global aggregation might then include the distribution of the Earth's surface that falls within a particular category overall (e.g., percentage of Earth biomes categorised as highly degraded).

The advantage of this approach is that it is a system-based approach, fully consistent with the planetary boundaries concept, with clear relevance for environmental stability in terms of maintaining a safe operating space of the Earth system. It provides a sub-global scale that is meaningful in terms of human pressures, biophysical responses and the consequences for people, and would appropriately include loss of species richness or extinction rates as a response variable, rather than as a driver as currently formulated. This deals with one potential disadvantage to this approach (that it might miss the variability component of biodiversity at species and organism levels). However the link to management interventions and decision-support at the local scale, could be relatively weak.

While genetic and functional diversity metrics and their thresholds appear not to function or scale up as global biodiversity boundaries, the possibility of a biosphere integrity boundary at biome scales appears a promising avenue for determining human wellbeing at global and sub-global scales. Furthermore there is plenty of evidence that the state of the biosphere is critical for the safe operating space conceptualised by Rockstrom et al. (2009b) through mechanistic interactions with the other eight planetary boundaries.

4. The biodiversity boundary and other planetary boundaries

The biodiversity boundary interacts with all other boundaries and could be framed explicitly as a response variable to changes in other boundaries (e.g. ocean acidification), or as a control variable for others (e.g. climate change). Fig. 3 presents a schematic of the magnitude of the effect of a given change in biodiversity state from its current position, on the position of the other planetary boundaries in relation to the state of their indicator variables. A positive feedback exists with most interactions between boundary types. As biodiversity loss moves closer to its own boundary it reduces the condition of others, moving them closer to their own boundaries with feedbacks onto biodiversity (see Fig. 3 for details). This self-amplifying perturbation will push the coupled system at an accelerating rate into a new state (thus constituting a potential tipping point) if the feedback is both positive and strong.

Fig. 3 shows that the net effects from all the interactions involving biodiversity are weakly positive. Biodiversity has no known threshold close to its current state, but does have a positive feedback on itself due to the interdependencies between species. For instance, a trophic cascade may cause loss of species at one trophic level (or functional group) to result in a further loss at other trophic levels (or functional groups). The effects of biodiversity loss have a weakly aggravating effect on the proximity of all other boundaries to their thresholds (mostly because the loss of biodiversity-based adaptive capacity brings those boundaries closer). Conversely, the effects of exceeding the ocean acidification, land use, climate change, nutrients and water boundaries have large impacts on biodiversity since they are primary drivers of

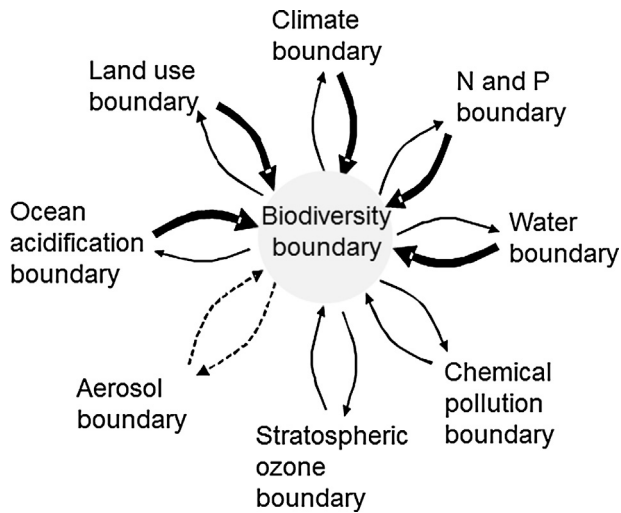


Fig. 3. The interaction between the biodiversity planetary boundary and other proposed planetary boundaries. As a given factor (i.e. boundary type, such as biodiversity or climate) moves further away from its own safe space, the arrows indicate changes in the factor (another boundary type). In all cases we suggest that positive feedbacks exist, so a change in the factor away from the safe space will also move the affected factor away from the safe space. Thicker arrows denote stronger and more closely related effects. Thinner arrows indicate weaker and less closely related effects while broken arrows indicate a negligible and/or small and variable effect.

biodiversity change. However, to the best of our knowledge, exceeding any of these boundaries does not trigger a biodiversity feedback strong enough to precipitate a threshold crossing, or an accelerating cascade in biodiversity loss, although such scenarios can be envisaged (Barnosky et al., 2012).

On the other hand, biome-level biodiversity changes can have major feedbacks to climate change, water cycles and nutrient cycles. For example, ongoing regime shifts in Arctic tundra biomes will likely result in biodiversity-mediated feedbacks to the climate system through massive releases of greenhouse gases and changes in albedo (Leadley et al., 2010; Myers-Smith et al., 2011); degradation of tropical forest biomes can alter precipitation patterns and river flow at sub-global scales (Davidson et al., 2012); and biome degradation often alters the capacity of ecosystems to retain N and P (Clow et al., 2011). While some of these biome-level biodiversity changes are driven by and therefore confounded with land use conversion to croplands (land use boundary), they are also being driven by other anthropogenic impacts on biomes, including climate change, use of fire, and logging, that are not included in the land use boundary (Anderegg et al., 2013; Davidson et al., 2012; Leadley et al., 2010).

The biodiversity boundary may be most significant through its interactions with other planetary boundaries when viewed at the biome level. There are perhaps additional significant connections between biodiversity change at biome levels and other planetary boundaries, and we recommend developing this understanding further as these interactions may suggest more urgent and important boundaries and may prove more useful for policy interventions than biodiversity alone.

5. Conclusions

The planetary boundary for biodiversity as proposed by Rockstrom et al. (2009b) was based on global species extinction rates, a metric of iconic significance in traditional biodiversity measurement, and one that acts as both a cause and consequence of global change. However, the lack of well-established, universal, scale-able or appropriate relationships and thresholds prevents

this metric from effectively defining a safe operating space for humanity. It is rather the abundance, diversity, distribution, functional composition and interactions of species in ecosystems that underlie persistent and productive life support systems and which provide the conceptual basis for the three proposed metrics on which we suggest a boundary would be better based: a measure of phylogenetic diversity representing the genetic library of life; functional-diversity; and biome condition and extent. Focusing on these aspects of biodiversity and their implications for human welfare offers promising lines of enquiry for future research with new data streams becoming available with which to develop metrics and thresholds and test them. None of the approaches yet provides an operational definition of a global boundary at present, but the first two could show threshold effects at local and regional scales while the third could represent a global-scale planetary boundary. The genetic library and the functional diversity approaches proposed here are both likely to show more and different thresholds locally, and to exhibit smoother and possibly much shallower responses at global level. The biome approach allows for sub-global boundaries that are meaningful but have weak links to the diversity component of biodiversity reflecting instead the role of biosphere process in determining a safe operating space. The boundaries set precautionary limits to human perturbations in Earth system processes, avoiding potential thresholds (and may serve as high level policy targets), but they in fact say very little about drivers of change in those Earth system processes and how to manage them. This is indeed a challenge for management and decision-makers and will require careful interpretation of the boundaries into management and practice contexts.

These three metrics offer information at different timescales (Fig. 4). The boundary based on the genetic library relates to the long-term consequences for people, where losses are effectively irreversible. Any part of the existing genetic variation may one day provide unanticipated benefits, but predicting exactly which element will be essential in future is not possible. In contrast the human benefits related to the biome extent and condition metric should be relevant for millennia, but changing global systems will lead over time to changes in stable, functioning biomes. Within the thousand-year time frames, however, the benefits to people are relatively predictable. The functional traits boundary is probably the most proximate and predictable because it is defined by traits known today to be significant.

In moving forward, the conceptual basis developed here highlights the role of phylogenetic diversity, functional diversity

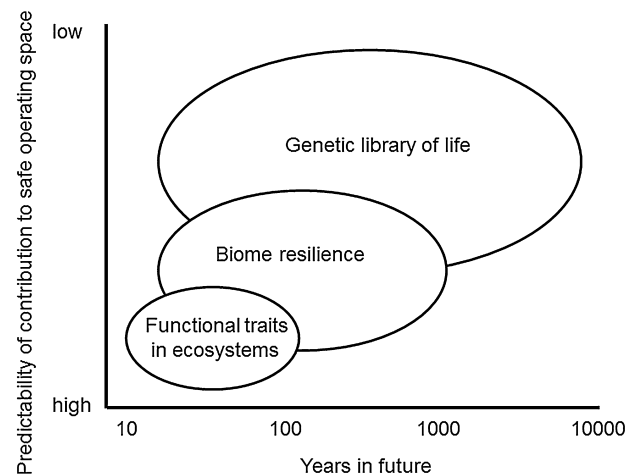


Fig. 4. Rough representation of the timescales and predictability of contribution of the three proposed biodiversity boundaries.

and biome integrity in determining a safe operating space. It further lays out avenues for metric development, data collection, and focused reviews of the evidence base for thresholds and relationships in these three aspects of biodiversity. It finally helps highlight biodiversity's key role in supporting a safe operating space for humanity through its interactions with other boundaries, suggesting an immediate area of focus for scientists and policy-makers.

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References

- Alkemade, R., Oorschot, M., Miles, L., Nellemann, C., Bakkenes, M., ten Brink, B., 2009. GLOBIO3: a framework to investigate options for reducing global terrestrial biodiversity loss. *Ecosystems* 12, 374–390.
- Allan, E., Weisser, W., Weigelt, A., Roscher, C., Fischer, M., Hillebrand, H., 2011. More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proc. Natl. Acad. Sci. U. S. A.* 108, 17034–17039.
- Anderegg, W.R.L., Kane, J.M., Anderegg, L.D.L., 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Change* 3, 30–36.
- Balmford, A., Green, R.E., Jenkins, M., 2003. Measuring the changing state of nature. *Trends Ecol. Evol.* 18, 326–330.
- Barnosky, A.D., Hadly, E.A., Bascompte, J., Berlow, E.L., Brown, J.H., Fortelius, M., Getz, W.M., Harte, J., Hastings, A., Marquet, P.A., Martinez, N.D., Mooers, A., Roopnarine, P., Vermeij, G., Williams, J.W., Gillespie, R., Kitzes, J., Marshall, C., Matzke, N., Mindell, D.P., Revilla, E., Smith, A.B., 2012. Approaching a state shift in Earth's biosphere. *Nature* 486, 52–58.
- Brook, B.W., Ellis, E.C., Perring, M.P., Mackay, A.W., Blomqvist, L., 2013. Does the terrestrial biosphere have planetary tipping points? *Trends Ecol. Evol.* 28, 396–401.
- Butchart, S.H.M., Akçakaya, H.R., Chanson, J., Baillie, J.E.M., Collen, B., Quader, S., Turner, W.R., Amin, R., Stuart, S.N., Hilton-Taylor, C., 2007. Improvements to the Red List Index. *PLoS ONE* 2, e140. <http://dx.doi.org/10.1371/journal.pone.0000140>.
- Butchart, S.H.M., Stattersfield, A.J., Bennun, L.A., Shutes, S.M., Akçakaya, H.R., Baillie, J.E.M., Stuart, S.N., Hilton-Taylor, C., Mace, G.M., 2004. Measuring global trends in the status of biodiversity: red list indices for birds. *PLoS Biol.* 2, e383.
- Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vie, J.-C., Watson, R., 2010. Global biodiversity: indicators of recent declines. *Science* 328, 1164–1168.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. *Nature* 486, 59–67.
- Clow, D.W., Rhoades, C., Briggs, J., Caldwell, M., Lewis, W.M., 2011. Responses of soil and water chemistry to mountain pine beetle induced tree mortality in Grand County, Colorado, USA. *Appl. Geochem.* 26, S174–S178.
- Convention on Biological Diversity, 2010. *Global Biodiversity Outlook 3. Convention on Biological Diversity, Montreal, Canada*.
- Cooper, N., Purvis, A., 2010. Body size evolution in mammals: complexity in tempo and mode. *Am. Nat.* 175, 727–738.
- Craine, J.M., Tilman, D., Wedin, D., Reich, P., Tjoelker, M., Knops, J., 2002. Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Funct. Ecol.* 16, 563–574.
- Davidson, E.A., de Araujo, A.C., Artaxo, P., Balch, J.K., Brown, I.F., Bustamante, M.C., Coe, M.T., DeFries, R.S., Keller, M., Longo, M., Munger, J.W., Schroeder, W., Soares-Filho, B.S., Souza, C.M., Wofsy, S.C., 2012. The Amazon basin in transition. *Nature* 481, 321–328.
- de Bello, F., Lavorel, S., Diaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R.D., Berg, M.P., Cipriotti, P., Feld, C.K., Hering, D., da Silva, P.M., Potts, S.G., Sandin, L., Sousa, J.P., Storkey, J., Wardle, D.A., Harrison, P.A., 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodivers. Conserv.* 19, 2873–2893.
- De Deyn, G.B., Cornelissen, J.H.C., Bardgett, R.D., 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecol. Lett.* 11, 516–531.
- DeLong, D.C., 1996. Defining biodiversity. *Wildl. Soc. Bull.* 24, 738–749.
- Diaz, S., Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16, 646–655.
- Diaz, S., Fargione, J., Chapin III, F.S., Tilman, D., 2006. Biodiversity loss threatens human well-being. *PLoS Biol.* 4, 1300–1305.
- Diaz, S., Lavorel, S., de Bello, F., Quetier, F., Grigulis, K., Robson, M., 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proc. Natl. Acad. Sci. U. S. A.* 104, 20684–20689.
- Diaz, S., Purvis, A., Cornelissen, J.H.C., Mace, G.M., Donoghue, M.J., Ewers, R.M., Jordano, P., Pearse, W.D., 2013. Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecol. Evol.* 3, 2958–2975.
- Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., Magurran, A.E., 2014. Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344, 296–299.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pickett, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soule, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet earth. *Science* 333, 301–306.
- Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* 61, 1–10.
- Faith, D.P., 1994. Phylogenetic pattern and the quantification of organismal biodiversity. *Philos. Trans. R. Soc. Lond. Ser. B – Biol. Sci.* 345, 45–58.
- Fischer, A., Young, J.C., 2007. Understanding mental constructs of biodiversity: implications for biodiversity management and conservation. *Biol. Conserv.* 136, 271–282.
- Fritz, S.A., Purvis, A., 2010. Phylogenetic diversity does not capture body size variation at risk in the world's mammals. *Proc. R. Soc. B – Biol. Sci.* 277, 2435–2441.
- Gamfeldt, L., Hillebrand, H., Jonsson, P.R., 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* 89, 1223–1231.
- GEO BON, 2013. Essential Biodiversity Variables (EBVs). http://www.earthobservations.org/geobon_ebv.shtml.
- Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478, 378–381.
- Godbold, J.A., Bulling, M.T., Solan, M., 2011. Habitat structure mediates biodiversity effects on ecosystem properties. *Proc. R. Soc. B – Biol. Sci.* 278, 2510–2518.
- Griggs, D., Stafford-Smith, M., Gaffney, O., Rockstrom, J., Ohman, M.C., Shyamsundar, P., Steffen, W., Glaser, G., Kanie, N., Noble, I., 2013. Policy: sustainable development goals for people and planet. *Nature* 495, 305–307.
- Hector, A., Bagchi, R., 2007. Biodiversity and ecosystem multifunctionality. *Nature* 448, 188–190.
- Helmus, M.R., Bland, T.J., Williams, C.K., Ives, A.R., 2007. Phylogenetic measures of biodiversity. *Am. Nat.* 169, E68–E83.
- Heyder, U., Schaphoff, S., Gerten, D., Lucht, W., 2011. Risk of severe climate change impact on the terrestrial biosphere. *Environ. Res. Lett.* 6, 034036.
- Heywood, V.H., Mace, G.M., May, R.M., Stuart, S.N., 1994. Uncertainties in extinction rates. *Nature* 368, 105.
- Ho, L.S.T., Ane, C., 2013. Asymptotic theory with hierarchical auto correlation: Ornstein-Uhlenbeck tree models. *Ann. Stat.* 41, 957–981.
- Hoffmann, M., Hilton-Taylor, C., Angulo, A., Báñhm, M., Brooks, T.M., Butchart, S.H.M., Carpenter, K.E., Chanson, J., Collen, B., Cox, N.A., Darwall, W.R.T., Dulvy, N.K., Harrison, L.R., Katariya, V., Pollock, C.M., Quader, S., Richman, N.I., Rodrigues, A.S.L., Tognelli, M.F., Viã, J.-C., Aguiar, J.M., Allen, D.J., Allen, G.R., Amori, G., Ananjeva, N.B., Andreone, F., Andrew, P., Ortiz, A.L.A., Baillie, J.E.M., Baldi, R., Bell, B.D., Biju, S.D., Bird, J.P., Black-Decima, P., Blanc, J.J., Bolaños, F., Bolivar, G., Burfield, W., Burton, I.J., Capper, J.A., Castro, D.R., Catullo, F., Cavanagh, G., Channing, R.D., Chao, A., Chenery, N.L., Chiozza, A.M., Clausnitzer, F., Collar, V., Collette, N.J., Collette, L.C., Fernandez, B.B., Craig, C.F.C., Crosby, M.T., Cumberlidge, M.J., Cuttelod, N., Derocher, A., Diesmos, A.E., Donaldson, A.C., Duckworth, J.S., Dutson, J.W., Dutta, G., Emslie, S.K., Farjon, R.H., Fowler, A., Freyhof, S., J. r. Garshelis, D.L., Gerlach, J., Gower, D.J., Grant, T.D., Hammerson, G.A., Harris, R.B., Heaney, L.R., Hedges, S.B., Hero, J.-M., Hughes, B., Hussain, S.A., Icochea, M., Inger, J., Ishii, R.F., Iskandar, N., Jenkins, D.T., Kaneko, R.K.B., Kottelat, Y., Kovacs, M., Kuzmin, K.M., La Marca, S.L., Lamoreux, E., Lau, J.F., Lavilla, M.W.N., Leus, E.O., Lewison, K., Lichtenstein, R.L., Livingstone, G., Lukoschek, S.R., Mallon, V., McGowan, D.P., Mclvor, P.J.K., Moehlan, A., Molur, P.D., Alonso, S., A.M. o. Musick, J.A., Nowell, K., Nussbaum, R.A., Olech, W., Orlov, N.L., Papenfuss, T.J., Parra-Olea, G., Perrin, W.F., Polidoro, B.A., Pourkazemi, M., Racey, P.A., Ragle, J.S., Ram, M., Rathbun, G., Reynolds, R.P., Rhodin, A.G.J., Richards, S.J., Rodríguez, L.O., Ron, S.R., Rondinini, C., Rylands, A.B., Sadovy de Mitcheson, Y., Sanciangco, J.C., Sanders, K.L., Santos-Barrera, G., Schipper, J., Self-Sullivan, C., Shi, Y., Shoemaker, A., Short, F.T., Sillero-Zubiri, C., Silvano, D. b.l. Smith, K.G., Smith, A.T., Snelks, J., Stattersfield, A.J., Symes, A.J., Taber, A.B., Talukdar, B.K., Temple, H.J., Timmins, R., Tobias, J.A., Tsybulina, K., Tweddle, D., Ubeda, C., Valenti, S.V., Paul van Dijk, P., Veiga, L.M., Veloso, A., Wege, D.C., Wilkinson, M., Williamson, E.A., Xie, F., Young, B.E., Akçakaya, H.R., Bennun, L., Blackburn, T.M., Boitani, L., Dublin, H.T., da Fonseca, G.A.B., Gascon, C., Lacher, T.E., Mace, G.M., Mainka, S.A., McNeely, J.A., Mittermeier, R.A., Reid, G.M., Rodriguez, J.P., Rosenberg, A.A., Samways, M.J., Smart, J., Stein, B.A., Stuart, S.N., 2010. The impact of conservation on the status of the world's vertebrates. *Science* 330, 1503–1509.
- Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L., O'Connor, M.I., 2012. A global synthesis

- reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486, U105–U129.
- Hughes, T.P., Carpenter, S., Rockstrom, J., Scheffer, M., Walker, B., 2013. Multiscale regime shifts and planetary boundaries. *Trends Ecol. Evol.* 28, 389–395.
- Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B.J., Zavaleta, E.S., Loreau, M., 2011. High plant diversity is needed to maintain ecosystem services. *Nature* 477, 199–202.
- Janecka, J., Chowdhary, B., Murphy, W., 2012. Exploring the correlations between sequence evolution rate and phenotypic divergence across the mammalian tree provides insights into adaptive evolution. *J. Biosci.* 37, 897–909.
- Katze, J., Diaz, S., Lavorel, S., Prentice, C., Leadley, P., Bonisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., van Bodegom, P.M., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., Ackerly, D.D., Anand, M., Atkin, O., Bahn, M., Baker, T.R., Baldocchi, D., Bekker, R., Blanco, C.C., Blonder, B., Bond, W.J., Bradstock, R., Bunker, D.E., Casanoves, F., Cavender-Bares, J., Chambers, J.Q., Chapin, F.S., Chave, J., Coomes, D., Cornwell, W.K., Craine, J.M., Dobrin, B.H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W.F., Fang, J., Fernandez-Mendez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.T., Fyllas, N.M., Gallagher, R.V., Green, W.A., Gutierrez, A.G., Hickler, T., Higgins, S.I., Hodgson, J.G., Jalili, A., Jansen, S., Joly, C.A., Kerkhoff, A.J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J.M.H., Kramer, K., Kuhn, I., Kurokawa, H., Laughlin, D., Lee, T.D., Leishman, M., Lens, F., Lenz, T., Lewis, S.L., Lloyd, J., Lusija, J., Louault, F., Ma, S., Mahecha, M.D., Manning, P., Massad, T., Medlyn, B.E., Messier, J., Moles, A.T., Muller, S.C., Nadrowski, K., Naeem, S., Niinemets, U., Nollert, S., Nuske, A., Ogaya, R., Oleksyn, J., Onipchenko, V.G., Onoda, Y., Ordóñez, J., Overbeck, G., Ozinga, W.A., Patino, S., Paula, S., Pausas, J.G., Penuelas, J., Phillips, O.L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negre, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J.F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S.J., Yguel, B., Zaehle, S., Zanne, A.E., Wirth, C., 2011. TRY – a global database of plant traits. *Glob. Change Biol.* 17, 2905–2935.
- Kelly, S., Grenyer, R., Scotland, R.W., 2014. Phylogenetic trees do not reliably predict feature diversity. *Divers. Distrib.* 20, 600–612.
- Kennedy, E.V., Perry, C.T., Halloran, P.R., Iglesias-Prieto, R., Schonberg, C.H.L., Wisshak, M., Form, A.U., Carricart-Ganivet, J.P., Fine, M., Eakin, C.M., Mumby, P.J., 2013. Avoiding coral reef functional collapse requires local and global action. *Curr. Biol.* 23, 912–918.
- Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.P., Garden, D., Girel, J., Pellet, G., Douzet, R., 2011. Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *J. Ecol.* 99, 135–147.
- Lavorel, S., Storkey, J., Bardgett, R.D., de Bello, F., Berg, M.P., Le Roux, X., Moretti, M., Mulder, C., Pakeman, R.J., Díaz, S., Harrington, R., 2013. A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *J. Veg. Sci.* 24, 942–948.
- Leadley, P., Pereira, H.M., Alkemade, R., Fernandez-Manjarrés, J.F., Proença, V., Scharlemann, J.P.W., Walpole, M.J., 2010. *Biodiversity Scenarios: Projections of 21st Century Change in Biodiversity and Associated Ecosystem Services*, Technical Series. Secretariat of the Convention on Biological Diversity, Montreal, pp. 1–132.
- Lenton, T.M., Williams, H.T.P., 2013. On the origin of planetary-scale tipping points. *Trends Ecol. Evol.* 28, 380–382.
- Mace, G.M., 2005. Biodiversity – an index of intactness. *Nature* 434, 32–33.
- Mace, G.M., Gittleman, J.L., Purvis, A., 2003. Preserving the tree of life. *Science* 300, 1707–1709.
- Mace, G.M., Norris, K., Fitter, A.H., 2012. Biodiversity and ecosystem services: a multilayered relationship. *Trends Ecol. Evol.* 27, 19–26.
- Mason, N.W., Bello, F., Mouillot, D., Pavoine, S., Dray, S., 2013. A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *J. Veg. Sci.* 24, 794–806.
- Millennium Ecosystem Assessment, 2005. *Ecosystems and Human Wellbeing: Biodiversity Synthesis*. World Resources Institute, Washington, DC.
- Myers-Smith, I.H., Forbes, B.C., Wilking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., Macias-Fauria, M., Sass-Klaassen, U., Levesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L.S., Weijers, S., Rozema, J., Rayback, S.A., Schmidt, N.M., Schaepman-Strub, G., Wipf, S., Rixen, C., Menard, C.B., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H.E., Hik, D.S., 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environ. Res. Lett.* 6.
- Nee, S., May, R.M., 1997. Extinction and the loss of evolutionary history. *Science* 278, 692–694.
- O'Meara, B.C., 2012. Evolutionary inferences from phylogenies: a review of methods. In: Futuyma, D.J. (Ed.), *Annual Review of Ecology, Evolution, and Systematics*, pp. 267–285.
- Olson, D.M., Dinerstein, E., 2002. The global 200: priority ecoregions for global conservation. *Ann. Mo. Bot. Gard.* 89, 199–224.
- Pereira, H.M., Ferrier, S., Walters, M., Geller, G.N., Jongman, R.H.G., Scholes, R.J., Bruford, M.W., Brummitt, N., Butchart, S.H.M., Cardoso, A.C., Coops, N.C., Dulloo, E., Faith, D.P., Freyhof, J., Gregory, R.D., Heip, C., Höft, R., Hurtt, G., Jetz, W., Karp, D.S., McGeoch, M.A., Obura, D., Onoda, Y., Petterelli, N., Reyers, B., Sayre, R., Scharlemann, J.P.W., Stuart, S.N., Turak, E., Walpole, M., Wegmann, M., 2013. *Essential biodiversity variables*. *Science* 339, 277–278.
- Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guénette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R., Walpole, M., 2010. *Scenarios for global biodiversity in the 21st century*. *Science* 330, 1496–1501.
- Pereira, H.M., Navarro, L.M., Martins, I.S., 2012. *Global biodiversity change: the bad, the good, and the unknown*. *Annu. Rev. Environ. Resour.* 37, 25–50.
- Perry, C.T., Murphy, G.N., Kench, P.S., Smithers, S.G., Edinger, E.N., Steneck, R.S., Mumby, P.J., 2013. Caribbean-wide decline in carbonate production threatens coral reef growth. *Nat. Commun.* 4.
- Reich, P.B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S.E., Flynn, D.F.B., Eisenhauer, N., 2012. Impacts of biodiversity loss escalate through time as redundancy fades. *Science* 336, 589–592.
- Rockstrom, J., Steffen, W., Noone, K., Persson, A., Chapin, F.S., Lambin, E., Lenton, T.M., Scheffer, M., Folke, C., Schellnhuber, H.J., Nykvist, B., de Wit, C.A., Hughes, T., van der Leeuw, S., Rodhe, H., Sorlin, S., Snyder, P.K., Costanza, R., Svedin, U., Falkenmark, M., Karlberg, L., Corell, R.W., Fabry, V.J., Hansen, J., Walker, B., Liverman, D., Richardson, K., Crutzen, P., Foley, J., 2009a. *Planetary boundaries: exploring the safe operating space for humanity*. *Ecol. Soc.* 14.
- Rockstrom, J., Steffen, W., Noone, K., Persson, A., Chapin, F.S., Lambin, E.F., Lenton, T.M., Scheffer, M., Folke, C., Schellnhuber, H.J., Nykvist, B., de Wit, C.A., Hughes, T., van der Leeuw, S., Rodhe, H., Sorlin, S., Snyder, P.K., Costanza, R., Svedin, U., Falkenmark, M., Karlberg, L., Corell, R.W., Fabry, V.J., Hansen, J., Walker, B., Liverman, D., Richardson, K., Crutzen, P., Foley, J.A., 2009b. *A safe operating space for humanity*. *Nature* 461, 472–475.
- Running, S.W., 2012. A measurable planetary boundary for the biosphere. *Science* 337, 1458–1459.
- Scholes, R.J., Biggs, R., 2005. A biodiversity intactness index. *Nature* 434, 45–49.
- Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L., Srivastava, D.S., 2004. Extinction and ecosystem function in the marine benthos. *Science* 306, 1177–1180.
- Spehn, E.M., Hector, A., Joshi, J., Scherer-Lorenzen, M., Schmid, B., Bazeley-White, E., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Jumpponen, A., Koricheva, J., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Palmberg, C., Pereira, J.S., Pfisterer, A.B., Prinz, A., Read, D.J., Schulze, E.D., Siamantziouras, A.S.D., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., Lawton, J.H., 2005. Ecosystem effects of biodiversity manipulations in European grasslands. *Ecol. Monogr.* 75, 37–63.
- Spielman, D., Brook, B.W., Frankham, R., 2004. Most species are not driven to extinction before genetic factors impact them. *Proc. Natl. Acad. Sci. U. S. A.* 101, 15261–15264.
- Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T., Navas, M.L., 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Glob. Change Biol.* 14, 1125–1140.
- Thomas, C.D., 2013. Local diversity stays about the same, regional diversity increases, and global diversity declines. *Proc. Natl. Acad. Sci. U. S. A.* 110, 19187–19188.
- Vackar, D., ten Brink, B., Loh, J., Baillie, J.E.M., Reyers, B., 2012. Review of multispecies indices for monitoring human impacts on biodiversity. *Ecol. Indic.* 17, 58–67.
- Vellend, M., Baeten, L., Myers-Smith, I.H., Elmendorf, S.C., Beauséjour, R., Brown, C.D., De Frenne, P., Verheyen, K., Wipf, S., 2013. *Global meta-analysis reveals no net change in local-scale plant biodiversity over time*. *Proc. Natl. Acad. Sci. U. S. A.* 110, 19456–19459.
- Wright, J.P., Naeem, S., Hector, A., Lehman, C., Reich, P.B., Schmid, B., Tilman, D., 2006. Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecol. Lett.* 9, 111–120.