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PERSPECTIVES

Thresholds and tipping points are tempting but not necessarily suitable concepts to address anthropogenic biodiversity change—an intervention

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Abstract
Thresholds and tipping points are frequently used concepts to address the risks of global change pressures and their mitigation. It is tempting to also consider them to understand biodiversity change and design measures to ensure biotic integrity. Here, we argue that thresholds and tipping points do not work well in the context of biodiversity change for conceptual, ethical, and empirical reasons. Defining a *threshold for biodiversity change* (a maximum tolerable degree of turnover or loss) neglects that ecosystem multifunctionality often relies on the complete entangled web of species interactions and invokes the ethical issue of declaring some biodiversity dispensable. Alternatively defining *a threshold for pressures on biodiversity* might seem more straightforward as it addresses the causes of biodiversity change. However, most biodiversity change appears to be gradual and accumulating over time rather than reflecting a disproportionate change when transgressing a pressure threshold. Moreover, biodiversity change is not in synchrony with environmental change, but massively delayed through inertia inflicted by population dynamics and demography. In consequence, formulating environmental management targets as preventing the transgression of thresholds is less useful in the context of biodiversity change, as such thresholds neither capture how biodiversity responds to anthropogenic pressures nor how it links to ecosystem functioning. Instead, addressing biodiversity change requires reflecting the spatiotemporal complexity of altered local community dynamics and temporal turnover in composition leading to shifts in distributional ranges and species interactions.

Keywords Critical transition · Ecosystem functioning · Scale · Management target

Introduction

The transformation of biodiversity by anthropogenic pressures is one of the most dramatic aspects of global change, both globally and locally. Globally, a significant proportion of extant biodiversity is threatened or endangered (IPBES 2019) and extinction rates seem to be orders of magnitude higher than predicted from the fossil record (Barnosky et al. 2011). At the local to regional scale, we mainly observe a massive reorganization of biodiversity, with range shifts across latitudes and altitudes (Poloczanska et al. 2013; Lenoir et al. 2020) leading to novel communities and a massive temporal turnover in composition (Hillebrand et al. 2018; Blowes et al. 2019). These shifts are responses to a changing climate as well as multiple direct pressures on biodiversity from overexploitation, fragmentation, and pollution (IPBES 2019; Pörtner et al. 2021). Marine biodiversity tracks climate change especially well (Jonkers et al. 2019; Antão et al. 2020; Lenoir et al. 2020) and, at the same time, is more vulnerable to temperature change as species generally occur closer to their temperature optima (Pinsky et al. 2019).

This massive ongoing change in Earth's biosphere and the prospect of increasing climate change pressures call for action and for straightforward concepts guiding such action. One of the most widely discussed and used concepts is the threshold concept—with the core idea to prevent tipping points by remaining in safe operating spaces. All of these

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terms are elements of critical transition theory (Scheffer et al. 2001). A tipping point is reached when minor changes in the driver (e.g., environmental change) leads to large changes in the state of the system (e.g., an ecosystem) (Scheffer et al. 2001; Scheffer 2009). If such a critical transition leads to a new stable state or irreversible change, a regime shift has occurred (Scheffer and Carpenter 2003; Folke et al. 2004). In this context, a threshold is the amount of pressure or change at which the tipping of the system occurs or becomes unavoidable (Scheffer et al. 2012; Berdugo et al. 2020). Consequently, a suggested strategy for environmental management is to define safe operating spaces that prevent pressures from transgressing these thresholds (Rockström et al. 2009). While management targets can also be formulated in terms of preferred outcomes ("Living in harmony with nature"), many targets are defined to avoid transgressing critical thresholds. The interplay between thresholds and targets is especially pervasive in the climate change debate, in connection to tipping points in the climate system at planetary scales (Lenton 2011; Ritchie et al. 2021) or regionally with respect to ice-sheet stability and ocean circulation (Lohmann and Ditlevsen 2021; Rosier et al. 2021; Armstrong McKay et al. 2022).

It is therefore tempting to extend the use of critical transition theory to understand biodiversity change, where transgressing thresholds levels of pressures or of rates of biodiversity turnover lead to disproportionate consequences (Lever et al. 2014; Evans et al. 2017; Mouritsen et al. 2018; Kelly et al. 2020; Ma et al. 2021). Here, we argue that several

ethical, conceptual, and empirical issues withstand such an extension. We start by acknowledging different options for defining biodiversity thresholds and discussing their validity from a conceptual viewpoint. We continue by considering inertia in biodiversity change and how it counteracts the detectability of thresholds or associated warning signals. We mainly draw from marine examples here, as marine systems already show high rates of biodiversity transition, but our concerns apply to all types of ecosystems. These concerns become directly relevant when presumed thresholds of biodiversity change are used to develop global and regional biodiversity targets.

Two approaches to defining thresholds

Abstractly, thresholds are defined on the X-axis of "drivers" and tipping behavior on the Y-axis of "response," such that transgressing a critical pressure level (threshold) leads to disproportionately large changes (tipping) of the variable of interest. In a biodiversity context, two ways of defining driver and response emerged (Fig. 1). The first considers biodiversity loss as the driver and ecosystem processes or properties as the response, asking at what threshold of biodiversity change do we observe a tipping in ecosystem functioning (Fig. 1a). The second addresses biodiversity change as the response to environmental drivers, aiming to define a threshold level of environmental pressure at which a disproportional change in biodiversity occurs (Fig. 1b). These
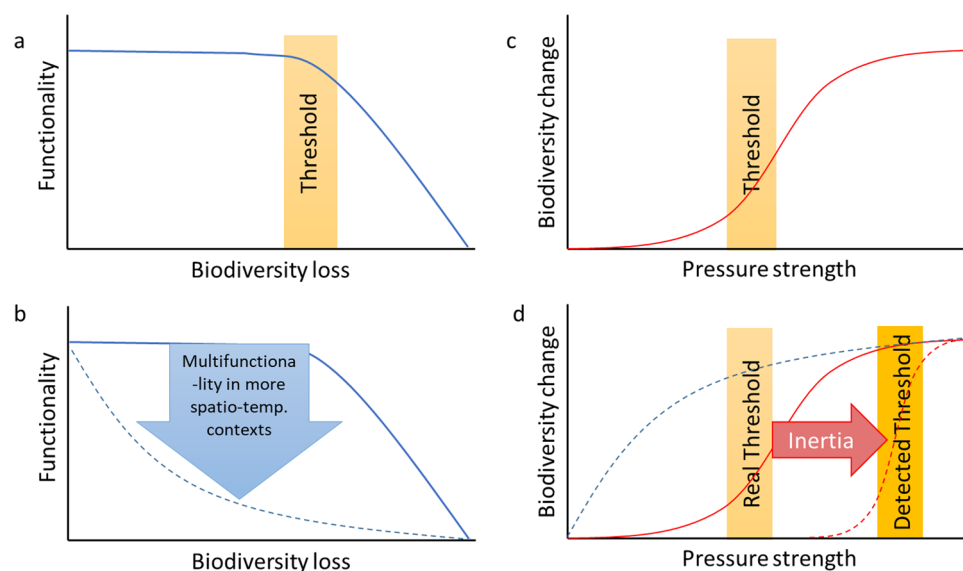
Fig. 1 Conceptual approaches to defining thresholds of biodiversity loss (**a**, **b**) or thresholds of pressures on biodiversity (**c**, **d**); **a** Functionality of an ecosystem in relation to a proportional biodiversity loss, which may not exceed a certain threshold to maintain ecosystem integrity; **b** Considering this relationship across abiotic contexts and functions leads to estimates of much earlier loss of multifunctionality

(dotted line); **c** Biodiversity change in relation to pressure strength, with a threshold pressure leading to disproportional acceleration of compositional shifts; **d** Including more gradual change in biodiversity (blue line) or delayed responses through demographic inertia (red dotted line) leads to misplaced thresholds or their absence

two views are obviously closely interlinked, as the biodiversity response in the latter case is the driver of the ecosystem change in the former. But their differentiation is useful beyond subtle semantics, as it reflects two rather distinct fields of the ecological literature on biodiversity change.

The first field focuses on the loss of species and/or intraspecific diversity and the main question is whether the functionality of an ecosystem (i.e., any emergent process such as primary production or property such as carbon storage) is impaired if a certain fraction of its biodiversity is lost. This view arose especially through the rise of the biodiversity-ecosystem functioning research over the last three decades (as reviewed by Cardinale et al. 2012; Jochum et al. 2020). In this research field, a majority of studies shows a "rivet-redundancy" type of response where significant, observable declines in functionality only appear at substantial biodiversity loss (Cardinale et al. 2011). In such cases, compensatory dynamics by the remaining species allow for maintaining functionality (Allan et al. 2011).

However, this redundancy most likely is an artifact of too simplistic approaches to functionality often focusing on a single process or property whereas ecosystems are multidimensional entities, where different functions rely on the performance of different species (Gamfeldt et al. 2008; Duffy 2009). Therefore, immediate effects of biodiversity change on functioning emerge when more functional contexts are explored (Fig. 1b). Such new contexts arise if the same process is analyzed under different environmental conditions in space (heterogeneous landscapes) or time (longer observation period) or when different processes and properties are considered (Isbell et al. 2011; Lefcheck et al. 2015; Meyer et al. 2018). In this more holistic view, minor losses in biodiversity already result in observable functional changes, such that no threshold of biodiversity loss can be detected below which the ecosystem's multifunctionality remains intact (Meyer et al. 2018). Similar immediate and gradual impacts of biodiversity loss were reported in marine studies (Gamfeldt et al. 2008; Bracken and Williams 2013).

Even if functional redundancy hypothetically exists, a maximum threshold of biodiversity that can be lost does not inform target setting because it does not address what biodiversity is lost (e.g., which species, how many individuals of each species). However, the identity of the lost species is at least as important as the proportion of biodiversity lost when addressing functional consequences of biodiversity loss (Ieno et al. 2006; Bracken et al. 2008). Thus, targets based on a threshold amount or proportion of biodiversity lost are logically unconceivable as they either assume that all species are functionally equal and only a proportion of remaining species is important or that humans are actually able to steer species extinction towards "dispensable" species and protect the important ones.

The latter creates an even larger ethical dilemma of deciding which proportion of biodiversity is dispensable. In a medical triage situation, we have criteria—and methods to analyze these—that enable us to prioritize help for lives that can be potentially saved. "Ecological triage" misses both, criteria and analytical methods. The IPBES report on biodiversity values strongly makes the point that "people perceive, experience, and interact with nature in many ways," but decisions often are made on a very narrow subset of the values, often ignoring values that are bound to future generations or local valuing systems (IPBES 2022). In contrast to the situation of a medical emergency, decisions on biodiversity would have far-reaching consequences for how life on Earth deals with yet unknown environmental conditions.

The alternative is to focus on thresholds for biodiversity change by addressing the biotic responses to environmental drivers (Fig. 1c), which is the focus for the remainder of this article. Here, the quest is for identifying a level of pressure (environmental change) at which biodiversity changes at disproportional rates, e.g., a level of aridity that causes a shift between different vegetation types (Staver et al. 2011; Berdugo et al. 2020) or a level of eutrophication at which a coral-dominated system transitions to an algae-dominated one (Knowlton 1992; Mumby et al. 2007). A potential management aim is then to prevent such tipping by keeping pressures well below these thresholds.

The presence of such critical transitions seems to be undisputable, as many case studies show a rapid shift between biodiversity regimes, such as transitions between corals and macroalgae (Knowlton 1992), macrophytes, and phytoplankton (Carpenter 2005; Carr et al. 2010), or forests and savannah (Staver et al. 2011). A unifying aspect in most of these cases is their reliance on foundation species (sensu Dayton 1975) where the entire community composition is built upon the presence of a certain species or group of species. Thus, if the pressure is too large for the foundation species or group, then such a threshold transgression can lead to a massive change in biodiversity. But even in these considerably well-understood cases, a lot of uncertainty arises around the positioning of thresholds as multiple stressors can lead to the decline of foundation species (Turschwell et al. 2021).

Moreover, environmental stressors may have chronic impacts, such that the extended duration of being exposed to a small pressure, instead of the transgression of a pressure threshold, may lead to biodiversity responses of the foundation species. Taking seagrasses as an example, they respond differently to chronic nutrient enhancement than to pulses (Ruocco et al. 2018) and establish a stress memory (Nguyen et al. 2020), showing different responses depending on exposure history (Helber et al. 2021). Consequently, the placement of a threshold pressure on biodiversity might be

complex even if the compositional response is defined by a single species.

In communities that are less dependent on the presence of such foundation species (or groups), observing pressure thresholds leading to disproportional biodiversity change seems even more unlikely. Across marine, freshwater, and terrestrial ecosystems, time series analyses find a rather gradual turnover that accumulates over time than sudden compositional shifts (Dornelas et al. 2014; Hillebrand et al. 2018; Rishworth et al. 2020). Such gradual increase in compositional dissimilarity over time seems to be the main response to changing conditions as each incremental change in the driver shifts the balance between winners and losers and thus slowly transforms biodiversity. This individualistic response to environmental gradients is only violated if the pressure drives the system to an extreme end of the gradient, resulting in a complete transformation of the ecosystems such as replacing a mangrove forest by a shrimp farm.

To be useful in the context of management decisions and target setting, we also must be able to predict pressure thresholds before they are exceeded. Most thresholds however seem to be detected retrospectively from temporal or spatial observation. Combining simulations and a meta-analysis of meta-analyses, Hillebrand and Kunze (2020) tested whether experimental studies that encompass future conditions allow identifying pressure thresholds for ecosystem functions beforehand. Few instances of transgression were observed, which might either reflect that thresholds in fact are rare or that environmental noise prevents the prediction of threshold pressure level even at the comparably simple level of univariate ecosystem process rates or properties. Thus, predicting thresholds for a multivariate biodiversity response seems even less likely, even though it is more important. Retrospective action on biodiversity change is hardly possible and a detected threshold in one system's community configuration is unlikely to be transferable to different locations or times. Moreover, most of the pressure gradients considered in a threshold context are unidimensional, although we know that biodiversity responses to cumulative impacts of multiple stressors can be very divergent (Vinebrooke et al. 2004). All these caveats even set aside the most fundamental concern that even if a tipping of biodiversity composition was observed, it potentially did not happen at that threshold because of the inertia in biodiversity change.

Inertia and the absence of warning signals

Biodiversity change is the consequence of numeric and demographic responses leading to shifts in species' abundance, ranges, and phenology as well as interaction with other species. Therefore, "winners" of an environmental change do not emerge immediately, and "losers" do not disappear abruptly. Species might persist for a long period of time even if they are under pressure ("losers"), a phenomenon well known as extinction debt (Tilman et al. 1994). Conversely, immigration credit describes the delayed arrival of "winners," especially if habitats are isolated or organisms are less able to disperse or move (Jackson and Sax 2010). Marine ecosystems and communities are thought to track climate change especially well (Lenoir et al. 2020) because they are highly connected, such that extinction debt may be more relevant than immigration credit. Consequently, marine systems show more rapid increases in local species richness than terrestrial ones (Blowes et al. 2019).

This inertia in biodiversity change has major consequences for the threshold debate as it implies that species composition changes asynchronously to environmental change (Fig. 1d). Thus, the pressure at which a disproportional shift in biodiversity is observed might not be the pressure at which it was generated. The fragmentation literature is an illustrating example as the pressure (habitat destruction) is negative for most of the species such that many "losers" exist. Still the changes in composition often only occur generations later (Vellend et al. 2006; Jackson and Sax 2010), such that it is difficult, if not impossible, to define the amount of fragmentation that committed the system to the observed biodiversity change.

In scenarios where the pressure generates both winners and losers, such as warming, it is even more complex to quantify threshold levels of pressure as the observed biodiversity response will be characterized by net imbalances between colonization and extinction (Kuczynski and Hillebrand, unpublished manuscript). Consequently, synthesis work on shifting distributional ranges often finds a faster change in the leading edge than the trailing edge (Poloczanska et al. 2013), which can be seen as a spatial reflection of a temporal extinction debt. Our analyses of modern, ecological time series potentially even underestimate the extent of delay as can be derived from paleoecological responses to abiotic changes. Strack et al. (2022) analyzed how communities of pelagic Foraminifera responded to increasing temperature after the last glacial maximum using time series data across the North Atlantic. They find consistent gradual changes in composition (without any tipping behavior), which, importantly, continued for several thousands of years after the temperature had reached its pre-industrial equilibrium.

The disconnection of the rate and extent of biodiversity change from the rate and extent of environmental change makes observing thresholds in a biodiversity context difficult. If we do not know the magnitude of the delay in biodiversity response beforehand, it seems unproductive to try to define environmental targets based on thresholds that commit natural systems to large compositional change, as this is prone to overestimate the extent of a safe operating space.

Global and regional biodiversity targets

Despite the lack of empirical support and the unresolved ethical issues, thresholds of biodiversity change have been formulated in the context of planetary boundaries, initially as a safe operating space for biodiversity (Rockström et al. 2009), later as biosphere integrity including functional and genetic diversity (Steffen et al. 2015). Avoidance of global thresholds is a logical target emerging from these planetary boundaries, such as aiming to reduce global extinction rates to rates of speciation (Rounsevell et al. 2020). However, such global targets incur a scaling issue as global extinction is only the final step of accumulated local and regional extinctions. For a given habitat or region, it is the local or regional extinction that matters, as the species' role in ecosystem functioning depends on its local presence, which is not alleviated by rescuing the species somewhere else.

Regionalizing the biodiversity target formulations such as "no net loss of biodiversity" will not be more useful. Superficially, it seems valid to assume that as long as extinction is less than species gains, a potential critical threshold for biodiversity change is avoided. However, the extinction side of the equation is hampered by the above-described inertia, such that "winners" and "losers" show shifted temporal dynamics poising towards transient increases in diversity rather than losses. Additionally, the local gain of species depends on the availability of further species in the regional species pool (Hodapp et al. 2018), i.e., temporal compositional shifts are inseparably connected to changes in spatial biodiversity (Eriksson and Hillebrand 2019). Additionally, there are implementation issues as well, for example when offsets for biodiversity loss unintentionally risk further biodiversity declines (Maron 2017).

The alternative is to formulate targets that address a certain amount of biodiversity change. Doing so at local to regional scales reflects the scale at which local assemblages and regional species pools respond to such pressures (Suding and Hobbs 2009) but would require a case-by-case analysis of thresholds for all relevant pressures. As this will rarely be possible, data synthesis efforts were used to estimate at which level biodiversity disproportionately responds to pressures such as hypoxia (Vaquer-Sunyer and Duarte 2008), aridity (Berdugo et al. 2020), fragmentation (Andren 1999), or nitrogen fertilization (Bai et al. 2010). However, these studies often stress the high variability of the threshold estimates such that it seems highly uncertain to derive a target for one system by extrapolating local results from other regions without a proof that this generalization is possible.

Norberg et al. (2022) conceptually addressed the question whether basing a management decision on the assumed presence of a threshold does good or harm when the existence or position of this threshold is uncertain. Their simple model shows that the answer depends on (i) how "wrong" the threshold estimate is and (ii) how negative the effects of sub-thresholds pressures are on the management target. As long as we do not know the answer to either of these items, we must be aware that we should not set targets for pressures in the intellectual darkness of having limited knowledge on the magnitude and timing of the response of the entangled biodiversity web to these pressures. Precautionary principles would require setting targets at very low levels of pressure to prevent any threshold transgression, but this strategy often fails when negotiating the use and protection of natural resources and ecosystems. Taking deep sea mining as an example, a true precautionary principle would require stopping all mining pursuits for decades, as this is the time estimated for filling gaps in our current knowledge (Amon et al. 2022).

In summary, the threshold and tipping point narratives have little validity in the context of biodiversity change and the formulation of targets to mitigate this change. There is little empirical evidence for biodiversity showing a tipping response to environmental drivers and our ability to predict such threshold pressure levels seems highly limited. Likewise, assuming a tolerable amount of biodiversity change is conceptually flawed and ethically disputable. Thus, formulating targets as if such thresholds existed seems dangerous as they further suggest a "manageability" that in fact is not feasible. We further fear that suggesting actions based on a threshold that does not hold up to scrutiny in discussions of conflicting use and conservation undermines the biodiversity position in such target negotiations.

There is no easy alternative to propose, but that does not invalidate our argumentation. On the contrary, it might be even more important as the current lack of convincing alternatives increases the temptation to accept biodiversity targets based on an uncertain tipping point narrative. However, we can propose a number of important steps that might inform the formulation of future operational biodiversity targets. First, we need to understand the scale sensitivity and inertia in biodiversity responses better that lead to the intertwined temporal changes in composition and spatial changes in species distribution. Second, we must upscale our current knowledge on critical transitions from simple, species-poor systems to communities with a multitude of species interactions (Kéfi et al. 2022). Biodiversity itself might be the reason why ecological systems are able to absorb environmental change without tipping into different states. Third, we need to accept that our ability to manage biodiversity is limited in the first place. Targets are often formulated as if biodiversity responses to further anthropogenic transformation were deterministic,

but even in the case of simple pulse disturbances, a recent meta-analysis showed that functional recovery was the norm when the pressure ended, but not to compositional recovery (Hillebrand and Kunze 2020). All three aspects together indicate that further actions potentially affecting biodiversity need to be discussed under the premise that their impact on biodiversity cannot be easily predicted or made undone.

Declarations

Conflict of Interest The authors declare no competing interests.

Ethics approval No animal testing was performed during this study.

Sampling and field studies The study does not contain sampling material or data from field studies.

Data availability The study does not contain data.

Author contributions HH conceived the paper. The authors contributed to the text. All authors read and approved the final manuscript.

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