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Biodiversity dynamics in the Anthropocene: how human activities change equilibria of species richness

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We are living in a time of rapid environmental changes caused by anthropogenic pressures. Besides direct human exploitation of plant and animal populations and habitat transformation, biodiversity changes in the Anthropocene are affected by less trivial processes including rapid spreading of non-native species, emergence of novel communities and modifications of ecosystem functioning due to changing nutrient cycles and climate changes. These processes are so complex that confident predictions and effective biodiversity conservation cannot be obtained without a suitable theory of biodiversity dynamics. We argue that such dynamics have particular attractors, i.e. stable equilibria, that are determined by environmental conditions. These stable equilibria set biodiversity limits, i.e. carrying capacities for biodiversity, from local to global scales. We point out the evidence of such limits at various spatiotemporal scales and show, using the new equilibrium theory of biodiversity dynamics (ETBD), how dynamics of diversity depend on non-linear relationships between number of species, community abundance and population size-dependent processes of species extinction and origination (speciation or colonization). We show that non-linear effects of biodiversity on ecosystem functioning can lead to multiple biodiversity equilibria and tipping points. Various human activities, including species introductions, human appropriation of primary production and trophic downgrading, can change local, regional and global diversity equilibria by affecting processes that set equilibrium diversity levels. The existence of equilibrium and out-of-equilibrium states has important implications for conservation, restoration and reconciliation ecology. It highlights the need to more effectively and intentionally balance the historical focus on the preservation of natural habitats with management specifically directed towards the processes responsible for long-term maintenance of biodiversity equilibria. The Anthropocene represents a unique situation in which people make decisions concerning the dynamics of the natural world, and we argue that ecological restoration requires wisely deciding which of the alternative equilibria are worth maintaining.

Keywords: Anthropocene, biodiversity conservation, biodiversity–ecosystem functioning relationship, biological invasions, ecological restoration, equilibrium theory of biodiversity dynamics, extinction, multiple equilibria, speciation, stable states

Introduction

The contemporary pressure of human civilization on nature and planetary dynamics is higher than any time in the past, reaching the extent comparable to the effect of major geological forces (Zalasiewicz et al. 2011). It has thus become generally accepted that we live in a new geological era called the Anthropocene. Regardless of the exact dating of the beginning of the Anthropocene (Lewis and Maslin 2015) and its exact delimitation, it is clear that the current situation is unique, comprising, among many other things, unprecedented reorganization of biota on Earth, including reshuffling of the spatial distribution of individual species and changes in biodiversity. One of the most pressing issues facing ecosystems and the whole Earth system is without doubt augmented species extinctions due to factors such as direct human exploitation, habitat transformation, spreading of invasive species and pollution. Traditional nature conservation based on attempts to limit human activities as much as possible thus seemed as a straightforward solution to this global biodiversity crisis.

The situation, however, is not that simple. In contrast to early environmental concerns of the second half of the 20th century, the ascertainment that we live in the Anthropocene involves also the appreciation of the tight interlinkage between natural and human processes that have been modulating ecosystems for millennia (Ellis 2015, Cockerill et al. 2017). Nature as we know it is a result of intertwined human–natural dynamics, which have affected not only regions characterized by the long persistence of civilizations like the Middle East or Europe, but also ecosystems long thoughts of as 'true' wilderness, such as Amazonia (Clement et al. 2015, Levis et al. 2017). Additionally, the effect of human activities on biological diversity has not been necessarily only negative, at least at local-to-regional scales. In Europe at the beginning of the Neolithic, for instance, extensive agriculture helped to maintain diverse habitat mosaics that had previously been sustained by fire and large herbivores, which were extirpated at the end of the Pleistocene (Vera 2000, Bocherens 2018). Human activities are thus now increasingly recognized as not necessarily harmful to biological diversity, implying that biodiversity protection needs more refined tools than just restrictions on human influences (Brechin et al. 2002, Kueffer and Kaiser-Bunbury 2014, Gillson 2015).

Even very recent changes of ecosystems do not necessarily result in biodiversity loss. Local and regional extinctions are often balanced by unprecedented spreading of non-native species, so that throughout much of the world local or regional diversity reveals increases as often as decreases (Dornelas et al. 2014). Moreover, species are facing new contexts and many are rapidly adapting to novel habitats, which is complemented with a wave of hybridization events leading to accelerated evolution including the emergence of new species (Abbott 1992). Thomas (2017) estimated that should the negative effects of humans disappear, these rapid human-mediated evolutionary changes would double species richness on Earth compared to an Earth absent of humans. On the other hand, although the current magnitude of extinction (in terms of the proportion of extinct species) is still orders of magnitude lower than mass extinction events recognized in the fossil record, the current rate of extinction is considerably higher (Barnosky et al. 2011). All these findings suggest that understanding and predicting future biodiversity changes require not only consideration of what has happened so far, but also understanding of the general determinants of diversity dynamics.

Here we argue that developing reliable scenarios of future biodiversity changes requires a proper theoretical framework, which could then provide baselines for effective biodiversity management. Such a framework must be based on robust determinants of biodiversity dynamics, which result from complex links between species diversity, total community abundance and population size-dependent processes of species origination (speciation plus colonization) and extinction. We will show that the dynamics of biodiversity is essentially equilibrial, meaning that it tends towards particular attractors determined by properties of the environment (Box 1 for an overview of concepts of attractors, equilibria and carrying capacity). Although this does not mean that biodiversity is always, or even most of the time, in equilibrium, it has straightforward implications for preserving biological diversity. If biological diversity is fundamentally determined by the properties of diversity equilibria and the conditions for their existence, then the struggle for biodiversity preservation should focus on nurturing the conditions supporting sufficiently species-rich equilibria. Drawing on the recently proposed equilibrium theory of biodiversity dynamics (ETBD, Storch et al. 2018, Storch and Okie 2019), we will examine consequences of this – perhaps seemingly outdated – equilibrial view on biodiversity dynamics, show how biodiversity equilibria can change due to various anthropogenic effects, and provide guidance for biodiversity maintenance based on this theoretical framework.

## The existence of equilibria in diversity dynamics

Here, for simplicity, we will consider 'biodiversity' and 'diversity' as synonyms to 'species richness' – the number of species within an ecological system. Biodiversity has a quite broad meaning (Wilson 1992) and can be expressed using many measures (Magurran and McGill 2011, Jarzyna and Jetz 2016). For our purposes, however, species richness provides the most convenient measure of biodiversity. First, it is typically well correlated with other aspects of biodiversity unless these aspects are specifically designed to control for variation in species richness (Miller et al. 2017, Li et al. 2020). Second, species richness is most frequently used as a biodiversity measure. Third, there is good evidence of general behaviour of this variable (Rosenzweig 1995). Finally, there are relatively well developed theoretical tools for formalizing the dynamics of species richness (MacArthur and Wilson 1967, Rosenzweig 1975, Hubbell 2001, Storch et al. 2018).

There has been a longstanding debate as to whether biodiversity dynamics is unbounded or if there are some

Box 1. Fundamental concepts of diversity dynamics: attractors, equilibria, carrying capacity

Much of the controversy around diversity dynamics, such as whether it is bounded or unbounded and equilibrial or disequilibrial, stems from a misunderstanding of the general concepts and theoretical framing of dynamics. A general theoretical framework represents dynamics as movement in an abstract state space (or phase space) representing a set of all possible states of a system. Every state has a potential to move to another state. If such movement is not entirely random, the dynamics ends up in a subset of state space called the attractor. Attractors (red rectangle in the figure) comprising just one state in which small movements away from the state lead back to the same state are called point attractors. Alternatively, there may be more complex attractors, including strange attractors characteristic of chaotic dynamics in which the exact sequence of states is sensitive to initial conditions, and cyclic attractors leading to sustainable cycles (such as in predator–prey systems or in successional community dynamics).

Equilibria (blue rectangle in the figure) are those points in the state space where individual processes responsible for the movement in state space balance each other, so that the system tends to maintain its state unless it is perturbed by external forces. Examples include natality and mortality in the case of population dynamics, and origination and extinction in the case of diversity dynamics. Unstable equilibria do not have a tendency to return back to the equilibrium following a perturbation, in contrast to stable equilibria where the system has the tendency to return to the equilibrium state after being moved away. Stable equilibria are thus equivalent to point attractors of the system, so here the two concepts overlap.
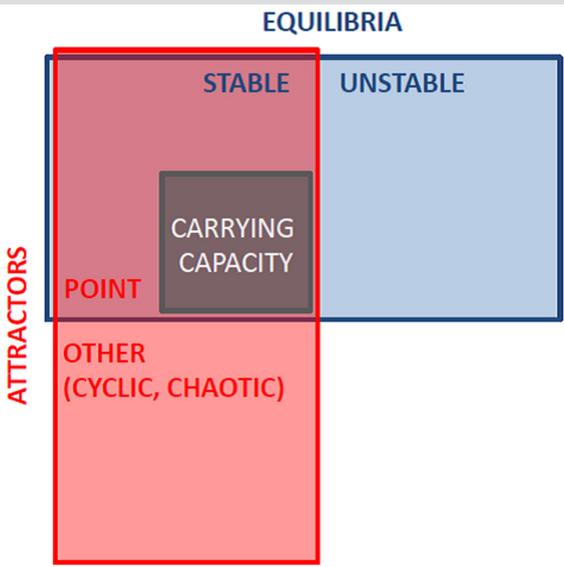
Carrying capacity is a concept that is sometimes vaguely defined, but within the classical theory of population dynamics it is a single stable equilibrium, i.e. the population size where each deviation from it leads to dynamics approaching this population size again. Carrying capacity is thus a point attractor of dynamical system. The concept can also be applied to the carrying capacity for species richness (Storch and Okie 2019). In population dynamics, it is typically assumed that there is just one such stable equilibrium and so this stable equilibrium is the carrying capacity. However, since more complex dynamics can potentially have multiple stable equilibria (Fig. 4, 5), for clarity the carrying capacity concept should only be used to refer to the special case in which there is only one stable equilibrium or as the stable equilibrium having the highest value of the variable of interest (i.e. as a subset of stable equilibria; grey square in the figure).

Importantly, all the above concepts comprise the dynamics of state variables, so that they make sense only if these variables are well defined. State space can be one-dimensional, being represented by a variable like population size or the number of species, or multidimensional, so that states are characterized by combinations of values of several variables (e.g. abundances of both predator and prey). It does not make sense to speak about the general stability of, say, a community, unless the community is characterized by a set of variables. Some variables may be in stable equilibria even though some other properties change – a good example is the theory of island biogeography, in which an island's number of species hovers around stable equilibria even though species composition changes through time. Some ecologists denied equilibrium dynamics in nature simply based on the observation that nature is permanently changing. But this continuous change does not preclude the existence of equilibria for particular state variables, including species richness.

Note also that whether a natural system is or is not in an equilibrium is a matter of scale and perspective – while a single disturbance pushes a system away from an equilibrium, repeated disturbances integrated over a long period can be accounted for as a variable with a specific rate that influences the equilibrium level. Equilibrium is a theoretical, idealized concept that depends on the exact definition of state space as well as respective processes, so it is meaningless to ask whether nature by itself is equilibrial or not.

diversity limits that determine regional or local diversity patterns (Cornell 2013, Harmon and Harrison 2015, Rabosky and Hurlbert 2015). Over the last decade, evidence has accumulated that there are ecological limits to species richness and diversification, and that equilibrial diversity dynamics represent a useful framework for interpreting diversity patterns (Rabosky and Hurlbert 2015). We have reviewed this evidence elsewhere (Storch and Okie 2019), so here we summarize only the major and most convincing lines of evidence, stressing recent findings, ordered from large to small spatial and temporal scales:

1) *Paleontological time series.* Although classical analyses of biodiversity changes during the Phanerozoic indicated a continuous increase of diversity at least since the mass extinction at the Cretaceous–Paleogene boundary (Benton and Emerson 2007), scholars have subsequently argued that these findings may reflect the 'pull of the recent' and unequal sampling of different geological periods (Alroy et al. 2008, Alroy 2010). Sophisticated analyses accounting for these biases have demonstrated that taxonomic diversity is remarkably stable during long periods (Close et al. 2020a, b), although shifts in these equilibria do occur in times of major biota rearrangements (Close et al. 2019).

2) *Consistency of biodiversity patterns regardless of variable diversification histories.* Large-scale diversity patterns are universally linked to primary productivity and climate, namely temperature and rainfall (Field et al. 2009), and these patterns do not seem to be directly linked to historical processes of diversification (Belmaker and Jetz 2015, Oliveira et al. 2016). Recent evidence shows that regions with high diversity (namely those at low latitudes and elevations) are typically not those revealing high diversification rates (Rabosky et al. 2018, Harvey et al. 2020, Igea and Tanentzap 2020, Machac 2020), and that evolutionary histories of regions hosting similar diversity levels are very different.

3) *Community patterns.* These often reveal remarkable stability of species richness regardless of species turnover (Brown et al. 2001, Gotelli et al. 2017). This finding stimulated the development of the equilibrium theory of island biogeography (MacArthur and Wilson 1967), and recent models and analyses of community assembly confirm the existence of diversity equilibria on islands (Valente et al. 2017a, 2020).

This support for the existence of biodiversity equilibria does not imply that nature is mostly in equilibrium or that these equilibria do not change – on the contrary, species richness may fluctuate relatively widely around equilibria and equilibrium diversity levels themselves are expected to change depending on both abiotic and biotic conditions (Storch and Okie 2019). There are certainly cases in which biota has been in disequilibrium for a long time. For example, boreal or mountain biomes that significantly expanded since the onset of colder global climate in the mid-Miocene seem to still be below an equilibrium state (Lagomarsino et al. 2016, Condamine et al. 2018, Ding et al. 2020), and many areas impacted by dramatic climatic changes of the Pleistocene glacial–interglacial cycles likely have not yet reached the diversity equilibria expected under the warm and stable Holocene climate (Svenning et al. 2008, Dullinger et al. 2012, Smyčka et al. 2017). However, even in such non-equilibrial cases it is crucial to have a theoretical understanding of biodiversity equilibria – after all, without such a theory there would be no chance to recognize a disequilibrium. Moreover, if the dynamics have stable equilibria, the long-term biodiversity preservation must firstly ensure that the conditions

of these equilibria are maintained. This requires explicit and realistic theory on how these stable equilibria emerge.

Biodiversity equilibria as a result of species originations and extinctions modulated by resources

Current equilibrial theories of biodiversity dynamics differ slightly in the ways and reasons for how stable diversity equilibria emerge. Within the theory of island biogeography, equilibria simply follow from the existence of a stable mainland species pool from which species are sampled (MacArthur and Wilson 1967). This scenario may be accurate also for many local non-insular communities, but it is insufficient as a general theory of biodiversity dynamics without addressing the stability of the mainland species pool itself. More general theories, such as those based on Neutral Theory (Hubbell 2001, Allen et al. 2007, Worm and Tittensor 2018), predict a stable equilibrium of species richness due to a constant total number of individuals (J) and consequent diversity dependence of the dynamics – for a given number of individuals, more species mean smaller populations which go quickly extinct due to community drift. Although valuable, there are several conceptual problems with this framework that limit its practical applicability (Storch and Okie 2019). First, it does not address differences among species in terms of their access to various resources. Second, it does not explicitly account for various, potentially complex extinction drivers. Third, and probably most importantly, these approaches assume that the total number of individuals is a constant directly determined by the environment. This is oversimplification, as the total number of individuals is set by population dynamics of all individual species and their complex interactions with the environment (Storch et al. 2018).

To overcome these limitations, we recently proposed a more general species-based equilibrium theory of biodiversity dynamics (ETBD). ETBD also derives biodiversity equilibria from negative diversity-dependence (Fig. 1); however, this dependence simply emerges due to decreasing availability of resources for each species as species richness increases, without necessitating the assumption of constant J. Instead of assuming constant J, J is assumed to be a function of both resource availability and the actual number of species S (Fig. 2), based on the empirically and theoretically supported idea that more species can collectively better utilize resources and thus may utilize a higher proportion of available energy (Cardinale et al. 2006, Mora et al. 2014, Liang et al. 2015, O'Connor et al. 2017, Storch et al. 2018). ETBD then predicts that equilibrium species richness, as well as equilibrium J, is determined by total amount and consumption of resources, as well as the factors that drive population size-dependent species origination and extinction (which determine the equilibrium mean species abundance at which origination and extinction are balanced, i.e. the S-nullcline in Fig. 2). The total amount and consumption of resources is
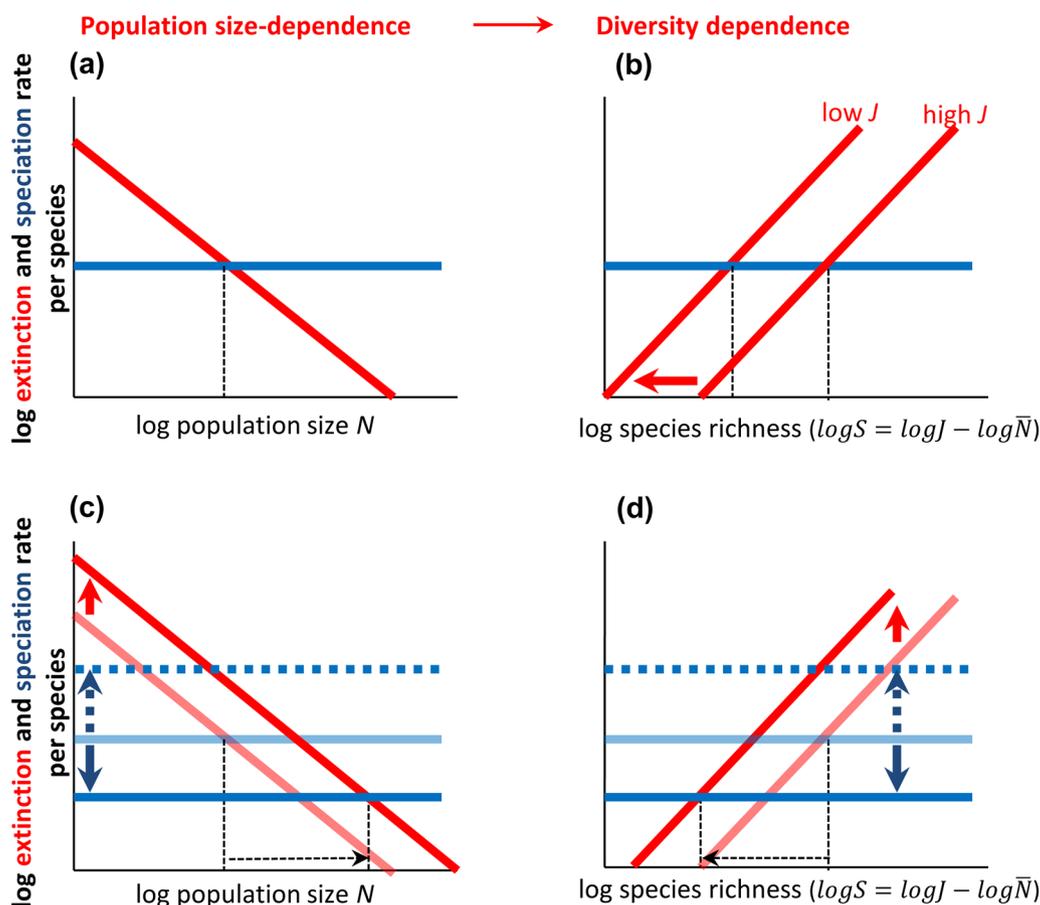
Figure 1. Overview of how biodiversity equilibria emerge and are influenced by anthropogenic changes. Here we deal with large-scale (regional) biodiversity in which biodiversity equilibrium is maintained by a balance of speciation and extinction with the contribution from colonization being negligible (Fig. 3 for the effects of colonization on local-scale dynamics). (a) Rates of speciation (blue lines) and extinction (red lines) are population size-dependent. For simplicity and with minimal loss of generality, we assume this population size-dependence can be approximated as power-laws, i.e. lines in log-log space. Additionally, we assume here that speciation rate is population size-independent (i.e. the slope of the power-law is zero), as this simplifies the figure without altering the general insights; the only condition of stable equilibrium is that the slope of the speciation function is higher than the slope of the extinction function and the lines intersect. This condition is expected to be near-universal, due to extinction rate decreasing substantially with population size, unlike speciation rate. Mean population size at equilibrium (corresponding to no net change of species richness) is determined by the intersection of the lines (vertical black line). (b) This population size-dependence translates into diversity dependence, since mean population size $\bar{N} = J / S$, where J is total community size (total number of individuals) and S is species richness. Increasing S at a given J thus implies lower $\bar{N}$ and consequently increasing average per species extinction rate. A decrease in J (e.g. due to anthropogenic removal of resources, red arrow) decreases equilibrium species richness by temporarily decreasing $\bar{N}$ and so increasing extinction rate until the new lower equilibrium is reached. (c) Equilibrium richness can also change due to an increase in the probability or level (intercept) of extinction (red arrow), e.g. due to increased populations fluctuations or direct population exploitation. Anthropogenic effects can also modify speciation rates, either towards lower (Rosenzweig 2001, blue solid arrow) or higher levels (Thomas 2017, blue dotted arrow, dotted horizontal line). Note that increased overall levels of extinction and/or decreased overall level of speciation increase the equilibrium $\bar{N}$ (dashed black arrow). (d) These changes are reflected in the shift of equilibrium species richness. Anthropogenic changes in equilibrium richness are thus predicted to be associated with changes of equilibrial mean population size when humans affect per species extinction and speciation levels, whereas no changes in equilibrial mean population size are expected if reductions in equilibrial richness are driven only by decreases in J. Note that J itself can be affected by species richness, which can lead to more complex and non-linear equilibrial dynamics (Fig. 2).

driven primarily by primary productivity, but can be taxon-dependent and linked to functional traits that determine the ability to utilize resources. Origination is the sum of speciation and colonization, the former being more important at large spatial and temporal scales while the latter is especially relevant for local communities. According to ETBD (and in line with other theories of diversity dynamics), carrying capacity for species richness is not given by any hard limits in terms of the number of available niches – it is just a stable equilibrium of biodiversity dynamics whose level is affected by the processes of species origination and extinction, modulated by environmental conditions and organismal traits.
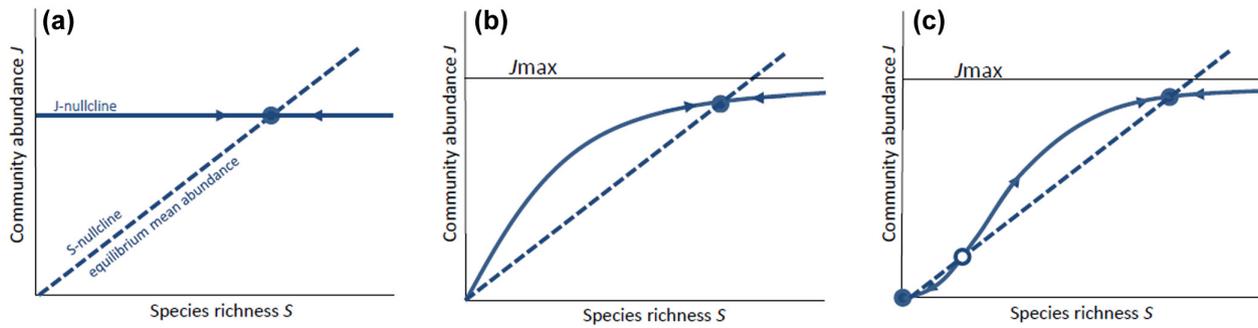
Figure 2. Graphical analysis of ETDB showing how diversity equilibria depend on the dynamics of both species richness (S) and total community abundance (J). Due to the population size-dependence of the rates of species origination and extinction, ETDB predicts that, for a given species-abundance distribution (SAD), there exists an equilibrium mean species abundance, $\hat{N}$, in which origination and extinction rates are balanced (Fig. 1). All potential diversity equilibria thus lie on an S-nullcline (dashed line) that delineates the values of S and J at which $dS/dt = 0$ and whose slope corresponds to $\hat{N}$ (i.e. $J = \hat{N}S$). However, the realized equilibrium state also depends on J being in equilibrium, so equilibrium S and J must lie on the intersection (full circle) of the diagonal S-nullcline and a J-nullcline, which relates J to S when $dJ/dt = 0$ (solid line/curve). Out-of-equilibrium communities follow near-vertical paths towards their J-nullclines and then the arrows along the J-nullcline towards stable equilibria (full circles). (a) In one extreme scenario, the J-nullcline is independent of S and so it is just a horizontal line. (b) However, a more realistic scenario is that increasing species richness increases a community's ability to utilize resources, so that the J-nullcline increases with S until it reaches its thermodynamic limit J_{max}. In the extreme that species are entirely independent of each other (strict niche complementarity), the J-nullcline increases linearly with S until it reaches its limit. However, as some species share resources and compete, the J-nullcline generally exhibits little linearity and rather likely decelerates at higher S due to increasing competition. (c) The J-nullcline may be even more complex, e.g. sigmoidal, which can lead to two equilibrium points, one stable (full circle) and the other unstable (empty circle). Such a situation can emerge when facilitation dominates over some range in S, which accelerates the J-nullcline. Here, at low S, several species need to support each other in their resource utilization in order for the J-nullcline to be high enough for communities to obtain higher rates of origination than extinction. A loss of species below the unstable equilibrium leads to inevitable extinction of further species which is not compensated by origination.

ETBD represents a general quantitative framework for biodiversity dynamics, and it is in overall agreement with observed diversity patterns (Storch et al. 2018). Due to its assumption that J is itself affected by species richness (rather than being an independent variable, directly reflecting environment), the theory is in line with the following observations of biodiversity gradients involving variation in rates of speciation or extinction: 1) J reveals less pronounced geographic patterns than species richness, and 2) species richness typically increases disproportionately (superlinearly) with J (Currie et al. 2004). Also, since biodiversity equilibria are, according to the ETBD, driven by all the factors affecting origination and extinction rates, it predicts lower equilibrial diversity in less stable (more extinction-prone) environments (Fig. 1), which also agrees with observations (Toszogyova and Storch 2019). ETBD can thus be taken as a general framework for evaluating how various biotic and abiotic factors shape long-term species richness patterns and biodiversity dynamics in general (Box 2 comprising its application on current extinction dynamics), including the potential effects of human activities.

How can people affect biodiversity equilibria

Human activities can push biodiversity out of equilibrium, but such an effect would by definition be only temporary, even if the return time is long. More serious are those effects that change the equilibrium level itself, as they elicit long-term

consequences. There are several ways by which anthropogenic changes modulate biodiversity equilibria, which can be categorized according to parameters of ETBD that are affected by the human activities (see Fig. 4 and Table 1 for specific examples). Some of these effects are relatively straightforward and simply follow from the general principle that the equilibria are determined by the diversity-dependence of origination and extinction rates (which are linked to population size-dependence, Fig. 1) modulated by resource abundance, which affects population sizes. Other effects may be more complex due to non-trivial and multidirectional links between resource availability, resource utilization, species richness and community abundance.

Effects on diversity equilibria due to changing resource levels or extinction and speciation rates

A straightforward way that people can affect biodiversity equilibria is through affecting overall resource levels (Fig. 1). In some regions human-driven changes have increased the ecosystem productivity via nutrient pollution and other effects (Piao et al. 2020). This may lead to local diversity increases (e.g. in cities where surplus of resources may maintain relatively rich communities) or decreases, due to altered dominance structures in communities (e.g. in freshwater ecosystems). However, at the scale of biomes and the globe, humans are generally reducing the total amount of resources available to biota via habitat degradation, habitat loss and resource exploitation, as indicated by the human

Box 2. Equilibrium diversity dynamics and global extinction rates

In our framework, diversity limits (i.e. stable equilibria) are governed primarily by diversity-dependent extinction. Equilibrium framework may thus serve as a useful concept for exploring various phenomena related to species extinction that are typically hard to directly infer from data due to observation biases and other methodological artifacts (Kidwell 2001, Rabosky 2010, Louca and Pennel 2020). One example is estimating background extinction rates. These are important for evaluating the severity of human-driven extinctions compared to what is expected to occur naturally (Ceballos et al. 2015). The estimation of background extinction rates typically relies either on fossil data (Alroy 2008, Barnosky et al. 2011) or on molecular phylogenies (De Vos et al. 2015). Both these approaches have been problematic. Background extinction rates estimated from fossil evidence are only available for abundant and widespread taxa with good fossil record (Ceballos et al. 2015), thereby strongly biasing estimates towards taxa with lower extinction probability. Molecular phylogenies are available for a much broader scope of taxa, but the estimates of extinction rates rely on several a priori assumptions, which often have a weak theoretical basis (Rabosky 2010, Louca and Pennel 2020). The equilibrium theory of biodiversity dynamics provides a simple but theoretically well-backed assumption about the link between speciation and extinction processes that can be used for retrieving extinction rates from molecular phylogenies: whenever the focal species assemblage is in equilibrium, the extinction rate should be equal to the speciation rate. Even if the equilibrium changes, the longer time-averaged ('background') rate of extinction should not differ wildly from the time-averaged rate of speciation. Speciation rate can be identified from molecular phylogenies using diversification likelihood models accounting for such a balance (Morlon et al. 2010). Similarly, measures of tip diversification rates, which represent instantaneous speciation rates, can likely be used for estimating background extinction (Title and Rabosky 2019), although the robustness of this latter approach needs to be determined.

To provide an example, for mammals and birds, two groups for which complete phylogenies (Jetz et al. 2012, Hedges et al. 2015) are available, we compared the above described phylogenetic equilibrium estimates with previously used fossil-informed estimates. Using the coalescent diversification model (Morlon et al. 2010; Model 1), the background extinction estimates are 0.39 E/MSY for mammals and 0.25 E/MSY for birds, respectively. These phylogenetic equilibrium estimates are thus slightly lower than the fossil-informed estimates of 1–2 E/MSY (Pimm et al. 2006, Ceballos et al. 2015). However, since these fossil-informed estimates are considered upper estimates rather than means, estimates based on phylogenetic equilibrium are in accord with the conclusion that current extinction rates are about two orders of magnitude higher than background extinction rates (Ceballos et al. 2015). Importantly, the proposed approach also allows studying background and anthropogenic extinction rates in taxa in which fossil record is scarce.

The equilibrium framework is also useful for interpreting current rates of extinction and their consequences. Although it is clear that current extinction rates in many taxa are exceptional (Barnosky et al. 2011), it is not obvious whether this extreme pace is likely to continue in the future. Human-driven extinctions may happen due to two fundamentally different mechanisms. One possibility is that anthropogenic pressures directly increase extinction rates, e.g. via direct population exploitation (Valente et al. 2017b, Morton et al. 2021). In this case, we can expect that the extinction rates detected during the last centuries will be steady as long as pressures of the human industrial lifestyle on nature continue, and we can extrapolate the known Anthropocene extinctions from the past into the future. Under this scenario the sixth mass extinction, with a considerable proportion of existing biota disappearing in the next few hundred years, is inevitable (Ceballos et al. 2015). Alternatively, current extinctions may primarily follow from the human appropriation of energy fluxes through ecosystems (Miko and Storch 2015), habitat transformation (a major cause of extinctions) just representing an aspect of this appropriation of ecosystem production. Under this scenario, the extreme pace of extinctions observed since the onset of the Industrial Revolution reflects transient dynamics between pre-Anthropocene and Anthropocene equilibria. The high rates of extinction may thus slow down in the future as the biosphere reaches a new (lower) equilibrium, assuming habitat loss is curtailed. The proportion of these two effects may be scale- and system-specific, but their consideration is of paramount importance for predicting futures of different communities, ecosystems, biomes and the biosphere as a whole.

appropriation of net primary productivity (HANPP) nearing 25% (Haberl et al. 2007). This necessarily decreases diversity equilibrium (Fig. 1b) both globally and regionally (Haberl et al. 2004, 2005, Miko and Storch 2015). These negative effects can hardly be globally mitigated without substantial decreases in human population size and/or consumption. However, it can be restrained locally and even regionally by setting areas free from resource exploitation (creating nature reserves) or compensated by modulating the other processes responsible for equilibrium diversity levels, e.g. by lowering extinction rates through proper management. Note that when an environmental change shifts the equilibrium below the original level and insufficient time has elapsed for diversity to decrease to its new equilibrium, we

speak about *extinction debt* (Hanski and Ovaskainen 2002, Kuussaari et al. 2009) – a concept that only makes sense within a diversity equilibrium framework.

Besides the shifts of biodiversity equilibria due to changing resource levels, equilibrium diversity may also shift due to human effects on long-term origination or extinction rates. For instance, hunting or increased environmental variation due to changing disturbance regimes can increase extinction rates (Pimm et al. 2006, Wan et al. 2019), lowering equilibrium diversity levels (Fig. 1c). Long-term changes in speciation rates are also possible, e.g. due to increased temperatures (Allen et al. 2006) or changes to gene flow, genetic drift and selection forces resulting from the emergence of barriers, altered dispersal, biotic homogenization and hybridization events, and shrinking species geographic ranges. These changes are hard to predict – although it has been argued that in the long run reductions in habitat area will cause substantial reductions in the Earth's overall speciation rate (Rosenzweig 2001), some of the mentioned changes may actually increase speciation rates (Thomas 2015, Bull and Maron 2016).

Shifting diversity equilibria via increased spreading of non-native species

With respect to the processes happening in the Anthropocene at local-to-regional spatial scales and decadal timescales, much more relevant than speciation are changes in colonization rates. Although some species have experienced declining migration rates due to habitat fragmentation and consequent selection against dispersal (Tucker et al. 2018, Berti and Svenning 2020), the spreading of non-native organisms is higher than any time before and still accelerating (Seebens et al. 2017). Unprecedented increases in colonization rates thus represent a prominent feature of the Anthropocene biosphere. Although it is tempting to interpret this as evidence against the existence of biodiversity limits or equilibria, a more appropriate interpretation is that elevated colonization rates actually pushed up local and regional diversity equilibrium way above current species richness.

Let us develop this idea more formally (Fig. 3). While local diversity equilibria are set by the balance of extinction and colonization (red and blue lines in the left part of Fig. 3), at regional or global scales colonization plays a negligible role and extinction and speciation (red and green lines) set the balance of equilibrium. A diversity-dependence of the total community-level rate of each process arises in several ways. It occurs 'passively' if a per-species rate is independent of population size, in which case the total extinction or speciation rate would increase linearly with the number of species. A 'passive' diversity-dependence is also expected for total colonization rate, since all-else-being equal, total colonization rate decreases with local species richness due to the depletion of potential colonizers from the species pool (MacArthur and Wilson 1967). According to the ETBD, diversity-dependence can additionally result from a dependency of a per-species rate on population size (Storch et al. 2018), as is almost certainly the case for extinction (Ovaskainen and Meerson

2010). For simplicity, and without compromising generality, we can express these dependencies as power-laws, i.e. straight lines in log-log space. Per-species speciation rate v may be invariant or positively related to population size N (green lines), so that $v \sim N^q$, where $q \geq 0$. Since mean abundance $\bar{N} = J / S$, assuming constant J (corresponding to a stable amount of resources), $v \sim S^{-q}$ (Fig. 1). Total speciation rate $v_{tot} = Sv$, so that $v_{tot} \sim S^1 S^{-q} = S^{1-q}$, meaning that it decreases with species richness if $q > 1$ and increases with species richness with a slope less than 1 if $0 \leq q < 1$. Either way, the slope of the total speciation line is shallower than the extinction line (a condition necessary for the existence of a global stable diversity equilibrium), since per-species extinction rate, x, almost certainly decreases with population size, $x \sim N^z$ where $z < 0$. Consequently $x_{tot} \sim S^{1-z}$, which means that the slope of the total extinction line is higher than one.

Now consider pre-Anthropocene local equilibrium species richness (Fig. 3a), which is given by the balance of extinction and colonization. Colonization rate is determined by the effective size of the species pool, which represents a fraction (depicted by blue arrow) of global equilibrium richness. During the Anthropocene (Fig. 3b), the increased movement of organisms across the planet has increased the fraction of global biodiversity available to colonize local communities (shorter blue arrow), increasing the effective species pool size and consequently colonization rate and local equilibrium richness. New combinations of species in local communities may, at least temporally, increase speciation rates (e.g. due to hybridization or novel adaptations), thus elevating global diversity (Thomas 2017) (Fig. 3c). This may further elevate local equilibrium diversity due to further enriching species pools (Fig. 3d).

The problem is that this elevated local diversity equilibrium driven by elevated colonization rates is necessarily only temporary, since the pool of non-native species is limited and so progressively depleted as non-natives become increasingly widespread. When human-driven colonization and/or speciation drop, high local extinction rates resulting from the elevated local diversity prevail over the lowered origination rate. Consequent waves of local extinctions are thus expected until communities reach the lowered equilibrium. These local extinctions can translate to global extinctions when they affect species confined to restricted areas. If previous spreading of non-native species decreased beta-diversity by increasing biotic homogenization, then the decrease of local (alpha) diversity back to equilibrium levels necessarily decreases also regional or global (gamma) diversity.

In these scenarios, we did not account for the almost inevitable decrease of the total amount of resources in the Anthropocene (Fig. 1b) nor possible long-term decreases in speciation rates due to habitat loss (Rosenzweig 2001), both of which would lower the equilibria in the long term. Additionally, human civilization pressures are not confined to solely affecting biodiversity equilibria; some changes may just shove biodiversity out of equilibrium. The wave of biological invasions may be interpreted equally well this way, i.e. as a singular event pushing local diversity high above equilibrial
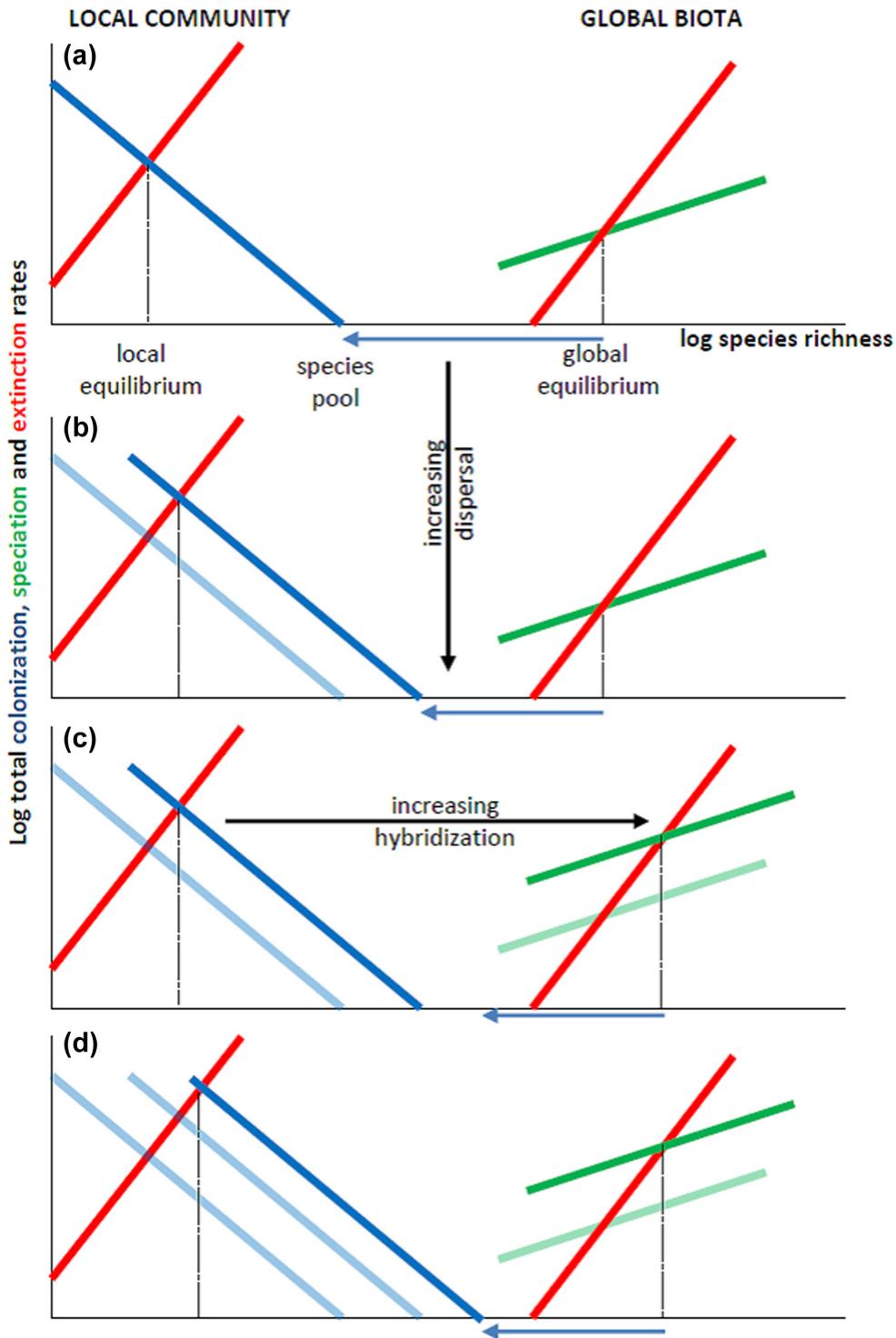
Figure 3. Effects of spreading of non-native species on local (left) and global (right) diversity equilibria (see the text for explanations). Here we assume that the diversity-dependent rates of speciation, colonization and extinction can be expressed as power-laws (lines in log-log space) and that the slopes of these lines (reflecting the strength of diversity dependency) are fixed, but that humans can affect their overall levels (intercepts). Note that in contrast to Fig. 1 where per-species rates are depicted, the lines here refer to total rates across all species. (a) Pre-Anthropocene situation, in which local equilibrium species richness is given by the balance of extinction (red) and colonization (blue), and colonization rate is determined by the effective size of the species pool, which represents a fraction (depicted by blue arrow) of global equilibrium richness, which is itself a result of extinction and speciation (green). (b) During the Anthropocene, increased movement of organisms across the planet have increased the fraction of global biodiversity available for local communities (shorter blue arrow), which increases colonization rate and thus local equilibrium richness. (c) Higher local species richness leads to new species combinations, increasing speciation rates (e.g. due to hybridization, or novel adaptations) and thus elevating global diversity. (d) This further elevates local equilibrium diversity due to further enriching species pools. These effects, however, may be only temporary, due to the gradual depletion of the pool of non-native colonizers.
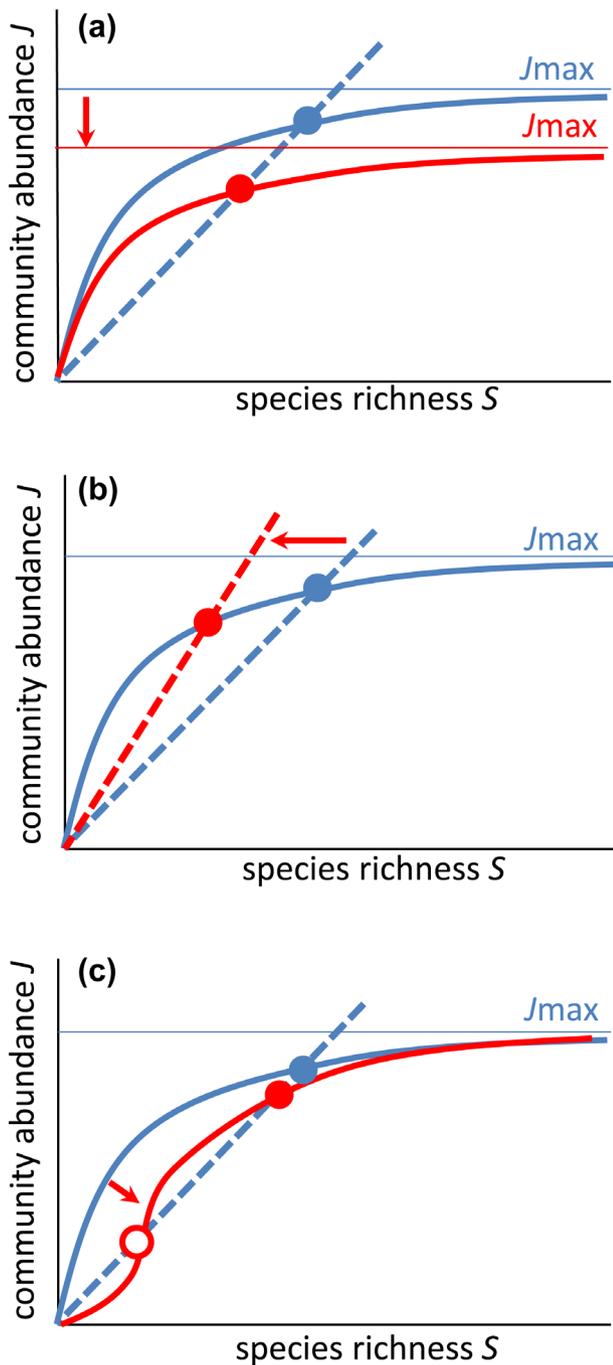
Figure 4. Humans may modify equilibrium diversity by several conceptually distinct ways (red arrows). Dashed curves indicate S-nullclines, bold solid lines are J-nullclines, filled circles are stable equilibria, blue refers to the pre-Anthropocene condition and red to the anthropogenic modifications. (a) Reduction of resource supply by appropriation of primary productivity or habitat degradation leads to lowering maximum community abundance J_{max} (which is given by total potential energy flow through the community E divided by mean metabolic rate B; $J_{max} = E / \bar{B}$). Due to non-linear J-nullclines, this leads to non-linear effects on the shifts of diversity equilibria. (b) Alternatively, humans may affect extinction or origination rates (Fig. 1c–d), increasing the mean population abundance

level, inducing extinction debt. The difference of interpretation lies in the temporal scale and relative permanency of given effects (Box 1).

Non-linear effects of HANPP on diversity equilibria due to complex relationships between S and J

All the effects mentioned above are expected under a very general theoretical framework which can be formalized using simple assumptions on community-wide rates, as depicted in Fig. 1 and 3. However, less-obvious, but important predictions follow when we take a more elaborated ETBD that explicitly deals with interspecific ecological differences and interlinkages between resource availability, species richness, actual resource utilization and total community abundance (Storch et al. 2018). One of these predictions is a disproportionate decrease in equilibrium species richness with decreasing resource supply, such as due to HANPP (Fig. 4a). The reason is that due to the positive relationship between diversity and resource utilization, lowering species richness is expected to decrease the ability of a community to utilize resources, which consequently lowers total community abundance J (Cardinale et al. 2006, Duffy et al. 2017, O'Connor et al. 2017) and augments per-species extinction rates. This then leads to substantially lower diversity equilibria compared to the scenario in which richness has no effect on resource utilization.

This effect can be estimated quantitatively. Consider that according to ETBD the balance of extinction and speciation sets large-scale equilibrium mean species abundance $\hat{N}$ in which these processes are balanced (Fig. 1) and thus, in equilibrium, $S = J / \hat{N}$. Maximum resource supply E (habitat area multiplied by resource supply rate per unit area, measured in units of energy per unit time) and the positive effects of diversity on the utilization of resources both positively influence J (see the J-nullclines in Fig. 2), such that $J = g(S)E/B$, where B is average individual metabolic rate and $g(S)$ is the function quantifying the average effect of S on the proportion of E consumed by the community. $g(S)E$ is thus the total consumption of resources. Generally, $g(S)$ is empirically and theoretically equivalent to the function quantifying the effects of species richness on biomass production and standing biomass W (Cardinale et al. 2006), since $W = JM = g(S)E\frac{M}{B}$ (M being mean body mass) (Brown et al. 2004). The intersection

required to maintain equilibrium (increasing the S-nullcline slope). (c) Also, humans may modify the way species utilize their resources, modifying the J-nullcline (e.g. by extirpation of keystone species). This can lead to an emergence of new, unstable equilibria (open circle). Such effects may also reduce community resilience by narrowing the distance between unstable and stable equilibria. Before human impacts, communities typically hovered around their equilibria, while human impacts have simultaneously lowered both their current diversity and their equilibrium points, such that communities are temporally above their new diversity equilibria (resulting in extinction debt).

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Table 1. Examples of published evidence of human impact on equilibrium species richness classified according to the parameters of the equilibrium process ('ETBD parameter') that have been changed due to human activities. Five parameters can be affected by human impact: (1) *resource supply* is the total amount of available resources. Human-induced decrease in resource levels (via e.g. harvest, grazing or deforestation) consequently reduces community abundance leading to lower number of viable populations and higher extinction risk. (2) *Resource utilization* comprises the effectiveness of resource utilization by given community, linked with species traits and habitat heterogeneity, so that it affects community abundance. Human activities often disproportionally affect certain trophic levels and/or functional groups, as well as species competitive ability. The resulting effect could be thus stronger than would correspond to the decrease of the amount of available resources. (3) *Extinction* comprises the direct effect of humans on species extinction levels by wildlife exploitation such as hunting, fishing, but also via less trivial links, e.g. through habitat fragmentation disrupting the gene flow among populations and reducing the capacity for species adaptation. (4) *Colonization* may be modified via habitat fragmentation via recent unprecedented human-induced increase in species movement across the globe, so that more species are available in the regional species pools. (5) *Speciation* may be affected, e.g. by reproductive isolation via habitat fragmentation or, conversely, through the decrease of reproductive isolation caused by spreading of non-native species resulting in the emergence of new species via hybridization. 'Human impact' characterizes the specific proximate human influence assessed by each study, 'Taxon' describes the target functional group and 'Temporal' represents the temporal scale of the study. In the 'Description' we additionally specify whether temporal or spatial trends were examined.

ETBD parameter	Human impact	Description	Taxon	Spatial scale	Temporal	Reference
Resource supply	Land-use change	Land-use changes decrease species resource supply, the decrease is uneven in different functional groups (spatial trend)	Animals	Global	2000–2015	Newbold et al. 2020
Resource supply	Land-use change	Land-use changes decrease species community diversity, richness and abundances in Mediterranean biomes (spatial trend)	Animals	Global (biome-specific)	2000–2017	García-Vega and Newbold 2020
Resource supply	Land-use intensity	Extensively used vineyards and abandoned grasslands have higher bird density and species richness/diversity than mainly intensively used landscapes (spatial trend)	Birds	Regional	2002	Verhulst et al. 2004
Resource supply	Land-use change	Agricultural land-use decreases the total number of bird pairs (spatial trend)	Birds	Regional	2000	Heikkinen et al. 2004
Resource supply	Land-use change	Agricultural land-use decreases biomass, abundances and the number of species in forests and grasslands (temporal trend)	Arthropods	Regional	2008–2017	Seibold et al. 2019
Resource supply	Land-use change	Defaunation and habitat fragmentation increase a dominance of one species (understory palm) resulting in a decrease in species richness and abundance of trees (via reduced light availability; temporal trend)	Trees	Regional	1975–2013	Martínez-Ramos et al. 2016
Resource supply/ Resource utilization	Land-use change	Past abrupt land changes in vegetation decrease community species richness and abundances (a lower decrease in abundances than richness indicates a decrease in resource utilization; spatial trend)	Plants, animals, fungi	Global	1982–2015	Jung et al. 2019
Resource supply/ Resource utilization	Land-use change	Land-use changes decrease community species richness and abundances (rarefied species richness loss is lower than observed indicating a decrease in resource utilization; spatial trend)	Animals	Global	2000–2014	Newbold et al. 2015
Resource supply/ Resource utilization	Land-use change	Tropical land-use change (forest conversion to plantations) disproportionately reduces biomass and species richness (spatial trend)	Animals	Regional	2012	Barnes et al. 2017
Resource utilization	Land-use change	Land-use changes via urbanization deprive bird communities of specialist species (temporal trend)	Birds	Regional	2001–2005	Devictor et al. 2007
Resource utilization	Disturbances	Species richness (but not community abundance) is highest under moderate disturbance (via military training) characterized by the greatest site heterogeneity (spatial trend)	Ants	Regional	2003	Graham et al. 2009

(Continued)

Table 1. Continued

ETBD parameter	Human impact	Description	Taxon	Spatial scale	Temporal	Reference
Resource utilization	Disturbances	Human-induced disturbances decrease species richness and diversity through the decreasing number of specialist species (spatial trend)	Butterflies	Regional	1980	Kitahara and Fujii 1994
Extinction	Exploitation	Exploitation via hunting for the wildlife trade decreases species abundances and increases extinction risk (spatial trend; meta-analysis)	Mammals, birds, reptiles	Global	Present	Morton et al. 2021
Extinction	Exploitation	Exploitation via hunting increases extinction rate in large mammals in West Africa (spatial trend)	Mammals	Regional	1995–1999	Brashares et al. 2001
Extinction	Habitat loss, exploitation, invasive species	Human-induced increase in extinction rate in Caribbean bats pushed their diversity away from an equilibrium (temporal trend)	Bats	Regional	45 My–present	Valente et al. 2017b
Colonization	Invasive species	Human-induced colonization of non-native species increases species richness and homogenization (temporal trend)	Freshwater fish	Global	Last 200 years	Su et al. 2021
Colonization	Invasive species	Human-induced invasion of common species increases species richness and homogenization (temporal trend)	Birds	Continental	1968–2003	La Sorte and Boecklen 2005
Colonization	Invasive species	Human-induced invasion of exotic and native species increases local and total species richness in a human-disturbed landscape (temporal trend)	Plants	Regional	1960, 2009	McCune and Vellend 2013
Colonization	Invasive species	Human-induced colonization increases species richness equilibrium (temporal trend)	Anole lizards	Islands	1850–present	Helmus et al. 2014
Speciation	Hybridization	Human-induced hybridization (via invasive species) reduces pre-zygotic barriers (e.g. isolation), but not post-zygotic barriers (establishment and ability to reproduce) (temporal trend; review)	Plants	Regional	Present	Vallejo-Marin and Hiscock 2016
Speciation	Hybridization	Human-induced hybridization between the introduced and native species formed the self-fertile species (*Senecio eboracensis*) (spatial trend)	Plants	Regional	1993–1995	Lowe and Abbott 2004
Speciation	Fragmentation	Human-induced forest fragmentation caused the emergence of genetically divergent populations at the species level (*Megaloprepus caerulatus*) (spatial trend)	Insect	Regional	2009–2012	Feindt et al. 2014
Speciation	Fragmentation	Human-induced fragmentation (via barriers) caused the emergence of genetically distinct populations and a possible speciation event in *Culex pipiens* in London (spatial trend)	Insect	Local	Present	Byrne and Nichols 1999

of the functions $J = S\hat{N}$, and $J = g(S)E/B$ then determines equilibrium S and J (Fig. 4).

Now consider the baseline assumption that $g(S) \sim S^b$, with $b < 1$. This is supported by extensive meta-analyses of experiments and observational studies that suggest a power function works well to quantify diversity effects over 1–2 orders of magnitude variation in S (Cardinale et al. 2006, Liang et al. 2016, Duffy et al. 2017, O'Connor et al. 2017) and is consistent with ecological theory (Liang et al. 2015). We are aware that experimental studies are typically undertaken at very local scales so that the relevance for large-scale predictions is problematic, but there are arguments that these functional relationships can be reliably up-scaled (Thompson et al. 2018, 2021, Gonzalez et al. 2020, Qiu and Cardinale 2020, Barry et al. 2021). Solving for S as a function of E, we obtain $S \sim E^{1/(1-b)}$, which suggests that equilibrium S scales supralinearly (disproportionately) with E with an exponent determined by the biodiversity–resource utilization relationship. Defining HANPP as the proportion of total net primary production (NPP) removed by humans, and assuming NPP $= E$ for consumers, HANPP is expected to reduce equilibrium species richness of consumers by the fraction $(1 - \text{HANPP})^{1/(1-b)}$.

Although there may certainly be idiosyncratic variation in b, $b \approx 1/4$ characterizes the mean relationship for communities in both experiments and observational studies across a variety of environments and trophic groups (Cardinale et al. 2006, O'Connor et al. 2017) and has been found independent of a study's maximum S (O'Connor et al. 2017). Therefore, a reasonable baseline assumption is that $b \approx 1/4$ applies to regional and global scales. An estimated global HANPP of 12% in 1905, 25% in 2005 and 27–44% in 2050 depending on land use scenarios (Krausmann et al. 2013) is thus expected to reduce, on average, the regional and global consumer species richness carrying capacity (i.e. diversity equilibrium) compared to pre-Anthropocene levels by 17% in 1905, 32% in 2005 and 34–54% in 2050. Since HANPP varies widely across biomes and regions (Newbold et al. 2015, Zhou et al. 2018), e.g. reaching levels of up to 63% in Southern Asia (Haberl et al. 2007), these effects are expected to be substantially augmented in certain regions and biomes. So far, animal regional and global diversity has not seemed to decrease as much (Dirzo et al. 2014, McGill 2015), which may indicate that biota is currently above their long-term species richness equilibrium, and more extinctions are anticipated under the status quo without interventions affecting extinction, origination and the biodiversity–resource utilization relationship.

The existence of multiple diversity equilibria

Ultimately, non-linear effects of diversity on resource utilization and ecosystem functioning may even lead to multiple equilibria (Fig. 5), just as non-linearities in metapopulation, community and ecosystem dynamics can lead to multiple equilibria and various threshold effects (Hanski et al. 1995,

Carpenter 2001, Scheffer et al. 2001, Goyal et al. 2018, Burger et al. 2019). Human effects on resource availability and rates of extinction, speciation and colonization can then influence not only equilibrium levels of species richness, but also the number of equilibria and resilience to perturbations, as measured by the width of basins of attraction of equilibria (the distance between a stable equilibrium and its neighboring unstable equilibria) (Scheffer et al. 2012). Decreases in extinction and increases in origination rates can remove lower stable equilibria and enlarge the basin of attraction for the upper equilibrium (Fig. 5b), while increases in extinction and decreases in origination rates can decrease the upper stable equilibrium richness, shrink its basin of attraction and even remove upper stable equilibria, drastically altering the carrying capacity of species richness (Fig. 5c).

Another level of complexity may emerge from the varying and disproportionate effects of individual species. Dominant species may monopolize resources so that only a tiny fraction of resources remain for other species (Cortés-Avizanda et al. 2012, Law and Parr 2020), elevating extinction rates (which positively affect the slope of dashed lines in Fig. 4 and 5), thereby decreasing equilibrium species richness. Conversely, keystone species may reduce extinction rates by suppressing dominant species and ensuring more equal utilization of resources (e.g. large herbivores suppress dominant plants and create patchy mosaics of diverse resources; Bond 1994). The presence of some keystone species and ecosystem engineers may also ensure enhanced utilization of resources, increasing J and thereby elevating equilibrium species richness (Fig. 5a). Examples include the top–down effects of predators on primary producers via regulation of key consumers (Ripple et al. 2016), such as sea otters reducing populations of sea urchins and thus ensuring maintenance of kelp forests as a primary habitat for many organisms (Rasher et al. 2020), or ecosystem engineers increasing resource availability for other species by direct physical modification of the environment (Hastings et al. 2007), such as equids providing water in drylands species by digging wells (Lundgren et al. 2021). As keystone species are often predators, the rampant human-caused trophic downgrading of Earth's biota (Estes et al. 2011) may have considerable influence on species richness carrying capacity via effects on extinction rates and community abundance. The effects of keystone species on extinction and local coexistence are well-treated in the classical community ecology theory (Tokeshi 1999, Chesson 2000), but here we stress that they can be usefully interpreted within our framework to provide additional insight on diversity regulation from local to global scales.

Predators both control and depend on populations of their prey, leading to a trophic interdependence that adds an important level of complexity to the framework of equilibrium diversity dynamics. Resources are not anymore independent of the dynamics themselves, species become resources for other trophic levels and the effects of predators can propagate through the trophic chains via predation cascades (Ripple et al. 2016). Formalizing and modeling these relationships may thus be quite complicated and an
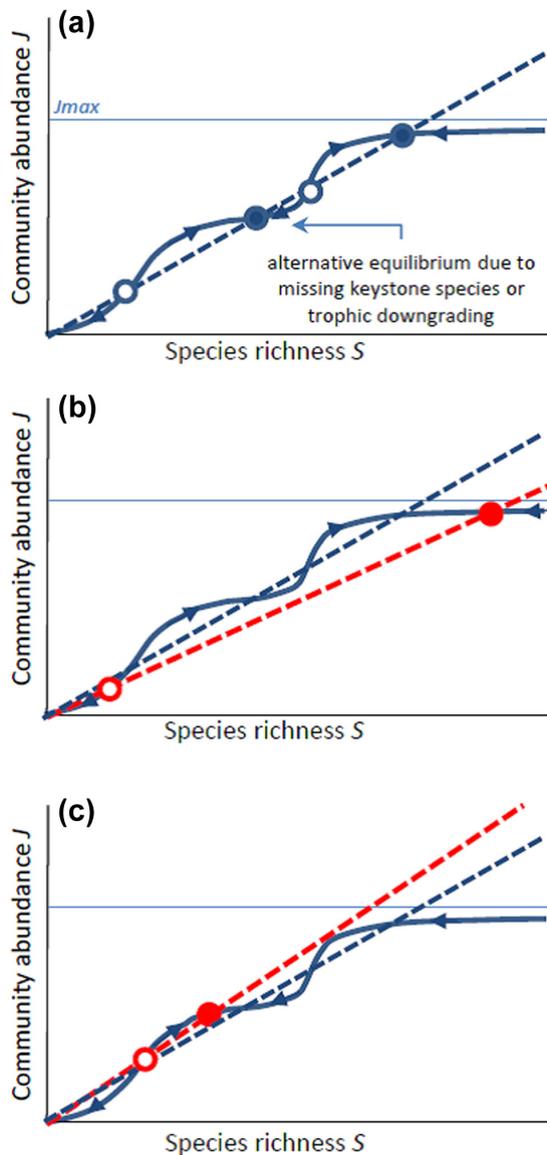
Figure 5. Schematic of the equilibrium theory of biodiversity dynamics applied to a hypothetical ecosystem or biome showing how human effects on extinction, origination and diversity's role in ecosystem functioning can create tipping points and affect the number and position of equilibria. Here we assume the *J*-nullcline (bold blue curves) is complex and reflects aggregate effect of species richness on the ability to utilize ecosystem resources and convert those resources into community abundance *J*. Dashed lines are *S*-nullclines determined by population size-dependencies of extinction and origination rates. (a) The hypothetical ecosystem/biome has two stable equilibria due to keystone species or trophic levels enhancing resource use or ecosystem functioning; declines in keystone species and trophic levels remove the second accelerating phase and thus the higher richness equilibrium. (b) Higher origination rates or reduced extinction rates (red dashed line) remove the intermediate stable richness equilibrium and increase the richness of the other stable equilibrium. (c) Lower origination rates or higher extinction rates (red dashed line) remove the higher stable richness equilibrium and reduce the richness of the intermediate richness stable equilibrium, as well as its basin of attraction (distance to the nearest unstable equilibrium), and thus the resilience of the system.

appropriate approach could comprise complex food web models (Brose and Dunne 2009, Melián et al. 2009). Still, complex multitrophic dynamics do not exclude the existence of stable diversity equilibria, as there are fundamental limits to the flow of energy and materials through an ecosystem, the metabolic rates of organisms and minimum viable population sizes. Indeed, surprisingly stable and predictable ratios of biomass of prey versus predators (combined across all species within each trophic level), as well as scaling patterns of biomass and biomass production (Hatton et al. 2015), suggest the existence of fundamental interlinkages between the diversity equilibria of different trophic levels.

These considerations help illustrate and clarify the profound implications of keystone species and ecosystem engineers for the management of protected areas, ecological restoration and rewilding (Svenning et al. 2016). They highlight that attempts at preservation and restoration are sustainable only if they are aimed towards the long-term maintenance of stable biodiversity equilibria; otherwise their effect is only temporary and ecosystem management becomes an especially wicked problem.

Ecological restoration and the balance of nature

The current paradigm for biodiversity preservation has shifted from the protection of the last remnants of relatively untouched pieces of nature to the active (re)creation of functioning ecosystems (Perino et al. 2019). It makes perfect sense in the light of equilibrium biodiversity dynamics – the last remaining habitats may harbor disequilibrium communities due to insufficient colonization rates, just as many of their metapopulations are in disequilibrium (Zartman and Shaw 2006) and predetermined to eventually disappear. If this is the case, nature preservation *sensu stricto* is not a viable option in the Anthropocene. However, active re-creation of functioning and sustainable ecosystems is challenging, as it must be based on a sound knowledge of the processes that maintain biodiversity equilibrium under the conditions relevant to the system. Such knowledge is typically based on the processes that maintained a given ecosystem type in the past (Svenning 2002, Malhi et al. 2016). The issue is that the processes that participated in maintaining past stable diversity equilibrium may have been lost and the system may have been in disequilibrium for a long time. A classic example is the loss of megafauna at the end of the Pleistocene, which had maintained species-rich open shrub-steppe or temperate savannas (Johnson 2009). The role of this megafauna had been partially substituted by fine-grained traditional agriculture, which prevented overgrowth by a homogeneous forest during the Neolithic and later on (Bocherens 2018). However, this positive human effect disappeared with the advent of industrial large-scale agriculture and the allowance of shrub and forest regrowth (Buitenwerf et al. 2018, Dobrovodská et al. 2019). Maintenance of species-rich forestless mid-latitude northern habitats thus requires simulation of the processes

that maintained it during the last millennia, either via permanent human intervention or reintroduction of large herbivores (rewilding).

This example, so typical for the European countryside, illustrates an important point. Although the concept of biodiversity equilibria may seem at first glance quite similar to the concept of ecosystem climax, it is substantially different. Climax is a final stage of ecological succession, a single outcome of various successional pathways, i.e. an attractor of the ecosystem dynamics. The concept of climax assumes that for a given climate only one such ecosystem stable state exists; however, our theoretical framework shows that an ecosystem may have multiple equilibria with different biodiversity levels, depending on the exact balance of the processes of species origination and extinction modulated by resource availability and the effect of species composition (including the keystone species) on resource utilization. Within this framework, we can interpret two potential states of the dominant European landscape as two alternative equilibria. One such equilibrium is (in prevailing European conditions) a closed forest (the climax), the other equilibrium involves a fine-grained mosaic of trees, grasses and shrubs, which are more species-rich due to the keystone species which change competitive hierarchies and the distribution of individual sizes, as well as population abundances, by preventing dominance by a few functional groups and species of plants, and thus depressing extinction rates.

Life in the Anthropocene means, among many other things, that people make decisions as to which equilibrium states are maintained. Closed forest is not by any means more or less natural than savanna-like open mosaics. It is a free decision whether we prefer closed forest or open habitat mosaics. People cannot at all, even in the Anthropocene, completely determine the natural world – it is not possible to maintain any possible state of an ecosystem, as most of these states do not represent stable equilibria. However, people can make decisions between alternative stable states. These decisions may be based on various criteria. One possibility is to keep the stable state which maintains maximum species richness, but there may be other considerations, including human needs or the necessity to protect endangered species or a specific ecological phenomenon. Ecological restoration requires deciding which of the alternative stable states to maintain and then management of the conditions necessary for the maintenance of the processes that determine the desired equilibrium state.

Concluding remarks

Recent findings indicate that biodiversity dynamics has its attractors, i.e. stable equilibria, even though it does not mean that nature is exactly in equilibrium – it can oscillate around it or even remain out of equilibrium for a long time if the equilibrium itself is moving. This view does not preclude the existence of multiple equilibria, i.e. alternative stable states, which may be, according to the ETBD, driven by non-linear effects of diversity on resource utilization and consequently community size and ecosystem functioning. In the Anthropocene, a period in which human activities transform countless features of the Earth system, it is natural to expect that human activities can also modify equilibrium diversity levels by changing resource levels, the diversity–ecosystem function relationship and rates of species migration, speciation and extinction. Viable ecological restoration must be based on a prior decision regarding which equilibrium to maintain, and the management of conditions necessary for the maintenance of the processes determining that equilibrium. Both these steps require a well-grounded understanding of the system, specifically the positioning and characteristics of different equilibria. Often these features cannot be easily predicted solely from general theory, requiring local studies and management experiments to develop system-specific models of biodiversity dynamics. Even when management is optimized, shifts in biodiversity equilibria are expected, e.g. due to changing climate.

Some biodiversity changes are inevitable, but there are some general principles that can be used to maintain relatively high equilibrium biodiversity levels. Given the predicted non-linear effects of resource supply on diversity equilibria, restoration actions should highly value nurturing the resource fluxes necessary for the maintenance of stable total community abundance and biomass production (e.g. water levels in wetlands or deadwood in forests). Emphasis should also be placed on ensuring the presence of trophic interactions that control dominant competitors, in order to encourage efficient resource partitioning (namely key predators and/or large herbivores), as well as the presence of ecosystem engineers which facilitate resource utilization and thus ensure the maintenance of sufficiently high community biomass and diversity. Searching for and refining these principles is a crucial direction for future research in biodiversity and conservation science.

Author contributions

David Storch: Conceptualization (lead); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Project administration (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Irena Šímová**: Conceptualization (equal); Investigation (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Jan Smyčka**: Conceptualization (equal); Formal analysis (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Eliška Bohdalková**: Investigation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Anna Toszogyova**: Conceptualization (supporting); Investigation (equal); Writing – review and editing (equal). **Jordan G. Okie**: Conceptualization (equal); Formal analysis (equal);

Investigation (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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