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Opinion

# Cradles, museums, and disequilibria: reconciling biodiversity dynamics using equilibrium theory

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**Historical nonequilibrium processes are often considered the main drivers of global biodiversity patterns. We argue that while biodiversity is often out of equilibrium, the concept of equilibrium is still crucial for interpreting macroecological diversity patterns, and current confusion in the literature stems from misunderstandings concerning equilibrium dynamics. We demonstrate how an equilibrium-based framework, such as the 'Equilibrium Theory of Biodiversity Dynamics' (ETBD), illuminates diversity patterns in space and time, including the latitudinal diversity gradient, even in the out-of-equilibrium context. This framework has profound implications for understanding diversity dynamics during historical, current, and future climate changes, suggesting that while temperate diversity is probably below its equilibrium level, tropical biodiversity could be above its equilibrium, elevating extinction risk in tropical biomes.**

## Highlights

The classical distinction of biodiversity cradles and museums can be redefined with respect to biodiversity equilibria and out-of-equilibrium states, providing a useful framework for understanding past and future biodiversity changes.

The current species richness of a biome can lie above or below its biodiversity equilibria which has fundamental implications for future biodiversity dynamics.

The observed higher contemporary speciation rates in high-latitude biomes may be a consequence of both equilibrium and out-of-equilibrium dynamics.

Available fossil and phylogenetic evidence is fully compatible with an equilibrium framework.

The Equilibrium Theory of Biodiversity Dynamics is able to explain large-scale biodiversity patterns, including disequilibrium dynamics during the dramatic climate change in the Cenozoic.

## Historical and equilibrial interpretation of large-scale diversity patterns

Understanding the drivers of diversity patterns in space and time remains a fundamental pursuit of macroecological and macroevolutionary research [1,2]. The accumulation of phylogenetic data over the last few decades has facilitated the study of the evolutionary processes responsible for large-scale diversity patterns [3,4]. Using a combination of contemporary geographic distribution data and phylogenetic trees, researchers have sought to evaluate one of the prominent explanations for large-scale diversity variation: that species-rich regions have higher speciation rates leading them to be 'cradles' of diversity [5,6]. Although a positive link between species richness and speciation rate has been occasionally reported [7–9], many studies revealed that spatial diversity patterns are typically decoupled from geographic patterns of diversification [10–13], and speciation rates often seem higher in areas of low species richness [14–18]. An alternative explanation of large-scale diversity patterns thus posits that instead of having higher speciation rates, high diversity areas were historically older or have been colonized earlier, so that the lineages from these areas have had more time for speciation and species accumulation [19–21]. Highly diverse areas are then considered 'museums' of diversity, rather than cradles [5].

The idea that higher diversity has accumulated in biomes that were old, stable, and at the same time large enough to allow many lineages to speciate and adapt to them has become a prominent explanation for the major macroecological diversity pattern, the **latitudinal diversity gradient (LDG)** (see Glossary) [22–24]. It aligns well with our knowledge of the Earth's history during the **Cenozoic**, characterized by initially much warmer climates than today, so that most of the Earth's surface was tropical [25]. Many lineages, including major mammal orders, originated in the **Eocene** [55–35 million years ago (MYA)] [26], which was the warmest period. These lineages thus had enough opportunity to adapt to hot and humid environments, and, due to niche

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conservatism, it was only later that they colonized non-tropical environments, where they might not have enough time to generate high species richness. This overall narrative, subsumed under various names including 'age and area hypothesis' [27], 'niche conservatism hypothesis' [28,29] or 'time-for-speciation hypothesis' [19,20,28], has been considered to be supported by branching patterns of phylogenetic trees that seem to indicate older lineages in more diverse (typically tropical) regions [21,23,24,30].

The problem is that the metrics that have been largely used to infer the evolutionary age of the lineages and respective assemblages have several issues (Box 1), which prevent them from providing conclusive evidence of the role of age in large-scale diversity patterns [31]. Additionally, species richness patterns are typically more tightly linked to contemporary climate variables than to measures of **diversification rate**, speciation rate, and age [32–35]. Also, several large taxonomic groups appear to have originated in different regions than those in which they have highest diversity [36,37]. For example, the Carnivora is thought to have originated around 66 MYA in the East Palearctic and repeatedly dispersed south towards Africa, Southeast Asia, and South America where they now harbor greater species diversity [37]. Similarly, the oscines have a strong LDG in the New World despite having also colonized the Americas from the North around 15 MYA [36].

We thus argue that the observed patterns, including those comprising phylogeny-based patterns of speciation, are actually compatible with an alternative scenario in which the differences in species richness among biomes or climate zones are shaped by different diversity equilibria [38], stemming from region-specific diversity-dependent rates of speciation and extinction (Figure 1). This view does not necessarily deny the role of Cenozoic history in macroecological diversity patterns, but is compatible with the increasing evidence that biological diversity cannot increase without bounds and there are region-specific diversity limits determined by the properties of the environment [39]. This evidence stems from several lines of arguments, ranging from fossil time series that indicate diversity-dependence of origination and extinction rates [40–42] to current diversity patterns [34,43–45], and provides a robust basis for understanding both the potential steady-state for **biodiversity** and the deviations from it due to continuous environmental change that can shift diversity out of equilibrium [46].

## Towards an equilibrium theory of biodiversity dynamics

To fully understand potential steady states of biodiversity as well as the deviations that reveal an effect of history, a proper theory is needed that encompasses the origin of the equilibria and more formal definitions of all the processes involved. We suggest that rather than speaking about diversity limits that imply some hard ceilings that cannot be overreached, it is useful to talk about particular diversity equilibria [47,48]. The situation is similar to population biology, where carrying capacity is actually a stable equilibrium of population dynamics, and populations can fluctuate both below and above a carrying capacity, or to the theory of island biogeography [49] in which equilibrium species richness on islands stems from a balance between colonization and extinction.

### Box 1. Muddled phylogenetic evidence for the time-for-speciation hypothesis

Evaluating the 'time-for-speciation' hypothesis requires estimating assemblage age – the amount of time an assemblage has had to diversify in its region – a task rife with potential pitfalls when relying on phylogenetic assemblages spatially confined within grid cells or biomes. Not properly accounting for extinction and colonization, incorrect use of phylogenetic metrics, and the intrinsic inseparability of diversification rates from age estimates lead to misleading findings, as illustrated in Table I. While many problematic methods remain popular, recent advances in phylogenetics have brought more robust modeling approaches that allow for the consideration of colonization and extinction when inferring ancestral states and diversification histories (e.g., state speciation and extinction models; [82]). Although these approaches are not without their own potential pitfalls [83,84] they offer promising solutions for overcoming many of the issues highlighted in Table 1.

### Glossary

**Biodiversity:** biological diversity, that is, all the variety of the living world. In this text, however, we use the term in a narrower sense, namely referring to a number of species of a given taxonomic group within a given region. For the purpose of this study, the terms biodiversity, diversity, and species richness are thus equivalent.
**Cenozoic:** Earth's current geological era, representing the last 66 million years of Earth's history. Tropical climates prevailed throughout the period, with the Eocene Thermal Maximum (approximately 50 MYA) followed by continuous cooling until app. 33 MYA. Another cooling followed the Middle Miocene Climatic Optimum (app. 15 MYA) and continues until today.
**Community abundance:** the total number of individuals across all species within a community. Note that we speak about communities of large regions (ecoregions, biomes within continents), comprising the whole biota of these regions, but practically we usually deal with an assemblage of a particularly defined clade, e.g. birds, mammals or angiosperms.
**Diversification rate:** the total rate of species production, that is, speciation minus extinction. Various measures and methods are devoted to inferring diversification or speciation rates from phylogenetic trees. The problem is that reliable assessment of extinction rates from phylogenetic trees of extant lineages work only under restrictive assumptions like homogeneity of extinction across regions or clades (which is especially problematic if the aim is to infer rate heterogeneity). Most reliable estimates thus include measures comprising tips of the phylogeny, that is, the most recent rates of diversification in which extinction presumably does not play a substantial role and diversification rate is thus roughly equivalent to speciation rate.
**Eocene:** the geological epoch that lasted between about 56 and 34 MYA. It was characterized by high temperatures (about 10–15$^{0}$C higher than today) and tropical climate across the majority of land. After the Eocene thermal maximum (about 50 MYA), the temperature began to decline, and the whole period ended by rapid global cooling linked to the glaciation of Antarctica.
**Equilibrium point:** the point in the phase space at which the forces

towards a movement in the phase space (e.g., speciation and extinction in the case of species richness) are balanced. If a small deviation from the equilibrium point leads to the movement back towards the equilibrium, we speak about stable equilibrium, and it represents an attractor of the dynamics.

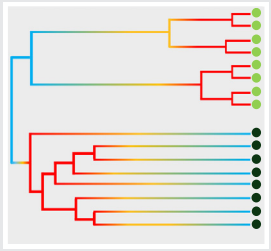
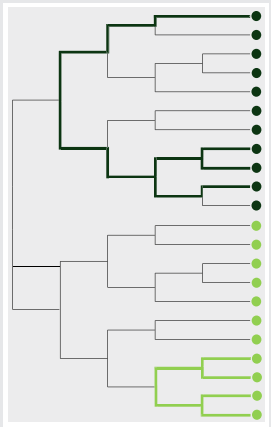
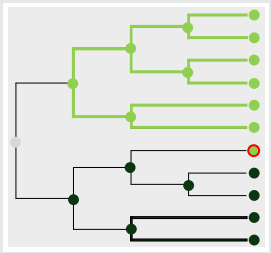
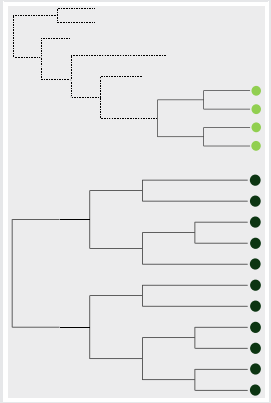
**Latitudinal diversity gradient (LDG):** the most pronounced spatial biodiversity pattern, characterized by the decreasing species richness from the equator to the poles.

**Nullclines:** (a.k.a., zero-growth isoclines) the curves in the phase plane that show the values at which the state variable is in equilibrium – that is, the variable is not expected to change if the other state variables are held constant. In a dynamical system, each state variable may have one or more nullclines.

**Phase plane:** dynamics is generally modeled as a movement in the phase space (or state space) defined by respective state variables. In the case of two variables, like species richness *S* and community abundance *J*, the phase space is two-dimensional, so we speak about the phase plane. Every point represents an assemblage with a particular *S* and *J*, which determines the vector of movement in the phase plane.

**Propensity for speciation or extinction:** region- or clade-specific tendency for speciation and extinction, respectively, determined by environmental factors (climate stability, topographic heterogeneity, temperature, seasonality etc.) or clade-specific properties (endothermy, body size, dispersal rate etc.). Speciation and extinction rates depend on the interaction of respective propensities and population sizes, which are, according to theory, dependent on species richness, leading to diversity-dependence of respective rates.

Table I. Examples with hypothetical phylogenetic trees showing how misleading inferences can result from phylogenetic estimates of assemblage age

| Tropical species | Temperate species |
|---|---|
|  | **Speciation and diversification rates confound estimates of assemblage age based on branch length**<br>Low speciation rates at tree tips (represented by cooler colors) lengthen terminal branches, resulting in misleadingly older assessments of assemblage age that are based on terminal branch length, despite the assemblages having similar ages. Other metrics like mean root distance (MRD; not depicted here) would reveal, in contrast, a positive relationship with diversification rate, since it measures the number of nodes separating the tip from the root in a lineage [34]. |
|  | **Evolutionary distances between lineages of an assemblage do not provide a measure of assemblage age**<br>Consider two clades, one found in the tropics (dark green) and the other in temperate regions (light green). Researchers have relied on measures of evolutionary distance such as mean phylogenetic distance (MPD; [85]) and phylogenetic diversity (PD; [86]) between all species within an assemblage, i.e. within a subtree for a particular site like a grid cell (thick lineages), to try to gage assemblage age. Here the tree for the particular tropical assemblage has a higher MPD value due to a distantly related extant species, even though the tropical clade has the same age as temperate one and extant species in both the assemblages originated recently. |
|  | **Colonization botches estimates of assemblage age based on maximum clade age**<br>Here the tropical and temperate assemblages have the same age – the first ancestors of both regions appear at similar positions on the tree. At some point, a tropical lineage left the tropics and colonized the temperate region (red circle with light green fill). Consequently, maximum clade age (a.k.a., oldest endemic age [23]) of the tropics (containing purely tropical species) is lowered and less than the temperate assemblage, because the entire tropical clade is not included in the estimate. |
|  | **Imbalanced extinction alters the estimated age of a phylogeny**<br>In this example, lineages have inhabited the temperate region for just as long as the tropical region, but have experienced more extinctions early in their history than the tropical region (dark green). The extinction imbalance leads to fewer extant old species in the temperate region, and consequently incorrectly younger estimates of temperate assemblage age, regardless of the phylogenetic age measure used. |

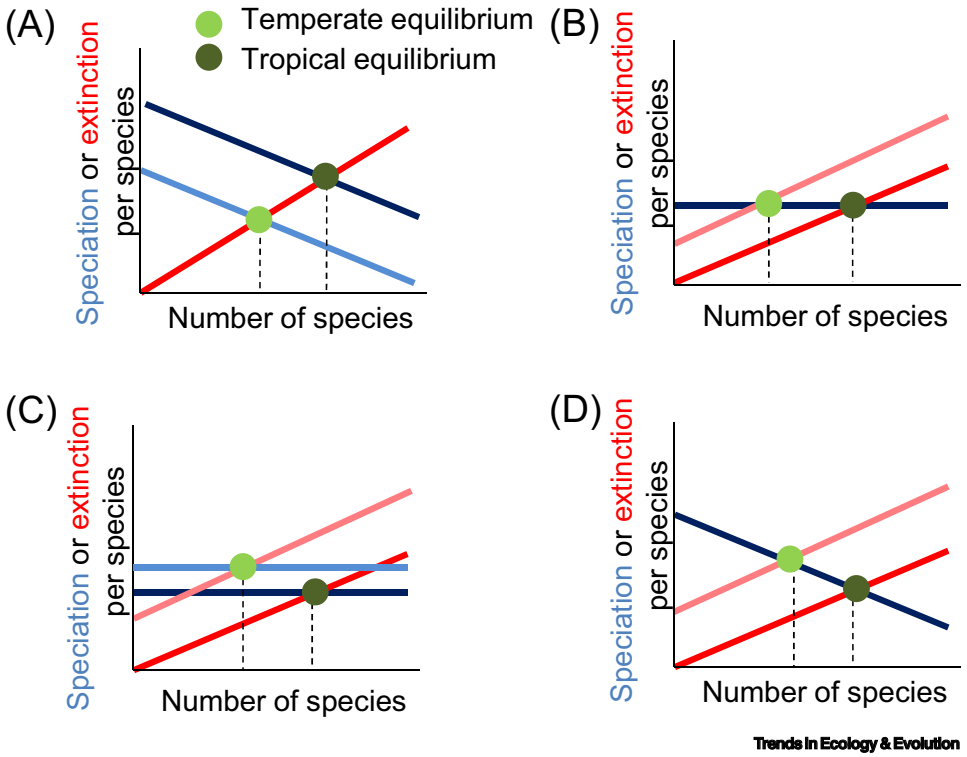



Figure 1. Non-trivial consequences of the diversity-dependence of origination and extinction rates. Diversity-dependence of speciation (blue) and extinction (red) rates can lead to various relationships between equilibrium species richness and observed speciation rate, since the realized rates depend on both rate propensity (position of respective line) and diversity-dependence. (A) Both speciation and extinction rates may be diversity-dependent, but if the regions differ only in their propensity of speciation (the position of respective lines differ; dark colors depict the tropics, light colors the temperate zone), while extinction rate increases with species richness in the same way in both regions, higher species richness is always associated with higher speciation rate. The reason is that in such a case all diversity equilibria lie along the unique increasing extinction line. (B) If, however, regions differ in their extinction lines (i.e., extinction propensities - the temperate region is, for instance, less stable, which elevates extinction rate for given mean population sizes), speciation as well as extinction rate may be equal across regions if speciation rate is diversity-independent and constant across regions. (C) If extinction propensity differs (as in B) and speciation propensity is diversity-independent but higher in temperate regions, higher species richness may be associated with lower speciation rates. (D) This negative relationship between diversity and speciation rate is also expected when speciation propensity does not vary across regions, but speciation rate is negatively diversity-dependent, which is expected when speciation probability depends positively on population size. Note that extinction rate is generally expected to depend positively on diversity due to a negative effect of population size on extinction probability (Box 2).

The multiple theories that address equilibrium diversity dynamics at large scales (i.e., for regions like biomes, ecoregions or continents) [49–51] all share some common and universal components. The first key property of equilibrium dynamics (analogously to population dynamics) is a negative diversity-dependence of diversification rate resulting from an increase of extinction rate and/or decrease of speciation rate with increasing species richness [52]. It is reasonable to assume that these dependencies are mediated by population size-dependencies of at least one of these rates [47,53]. Species with larger populations have lower extinction probability [54–56] and simultaneously may have a higher speciation probability due to typically larger geographic ranges, larger genetic variability, and a faster accumulation of genetic incompatibilities [57,58]. As the number of species increases, population sizes must decrease for a given amount of utilized resources, resulting in a faster increase of extinction rate than speciation rate, and consequently in the negative diversity-dependence. Ultimately, as already pointed out by Charles Darwin [59],

increasing species richness must lead to the situation in which most species have such small populations that extinction rates overreach origination rates, and diversity cannot grow any more.

The second essential component of any Equilibrium Theory of Biodiversity Dynamics comprises the links between resources, species richness and **community abundance** (i.e., total number of individuals of a given taxon within the region). One option would be just to assume that a given amount of resources (e.g., energy available to a given taxon or functional group) is directly translated to community abundance which then drives the diversity-dependence due to the abovementioned mechanism [60]. However, a general theory of biodiversity dynamics should avoid unrealistically strict assumptions about the link between resources and community abundance and should include the possibility that the addition of species can increase the spectrum of utilized resources or the efficiency of resource utilization [38,53,61], ultimately increasing community abundance, albeit in a decelerating rate. Addressing such biodiversity effects on community abundance would reconcile two apparently opposing views on biodiversity dynamics, both of which have substantial experimental, observational, and theoretical support, namely the assumption that diversity limits do exist [39,47] and the observation that an increasing number of species may expand the spectrum of utilized resources [62,63].

Based on these two key components, we have recently formulated a general theory of biodiversity dynamics [38,64] (Equilibrium Theory of Biodiversity Dynamics [ETBD]; Box 2) that illuminates how changes in resource levels (including those linked to global climate changes) affect diversity equilibria and dynamics at large spatial scales (evolutionary arenas sensu [65] or biogeographic provinces [66]). Importantly, according to the theory, species richness equilibria and their potential shifts may be affected by three principally different factors: (i) total resource abundance (in general, energy availability of a given region), (ii) the speciation-extinction balance (determined by the species richness-independent **propensity for speciation and extinction**, specific for particular regions and clades), and (iii) the way species richness affects energy utilization, and consequently total community abundance (Box 2). All these factors may change in the course of history, changing the positions of biodiversity equilibria. Historical changes in species richness can then reflect either the changes in equilibrium biodiversity itself or a shift of diversity that is temporarily out of the equilibrium towards a new equilibrium.

To illustrate the relevance of total resource abundance and the speciation-extinction balance for diversity equilibria and dynamics, consider a biota (or a subset of it, comprising a well-defined higher taxon within a region) that has recently experienced a rapid increase in total energy availability, whether from an enlarged area or augmented ecosystem productivity. The resulting increase in its total number of individuals $J$ (a.k.a., community abundance) is accompanied by an increase in each species' population size $N$. This leads, according to the theory, to a temporary drop in per species extinction rate, due to the larger populations having lower extinction probabilities. Because of the lowered extinction rate, however, the biota's species richness, $S$, subsequently increases through time. Since average population size is $J/S$, this increase of species richness is accompanied by a decline in the number of individuals per species, returning extinction rate to a higher level at which total extinction rate is balanced by total speciation rate. The biota has now settled on a new stable **equilibrium point** and has higher species richness than before the increase in total energy availability. Similarly, if two different regions differ in their resource availability and total number of individuals, the theory demonstrates that these underlying dynamics would also cause the region with higher resource availability to support a higher species richness equilibrium point.

## Interpretation of global biodiversity changes using the equilibrium theory

Let us now apply this theoretical framework to global diversity dynamics during the Cenozoic. Here, for simplicity, we distinguish just two major zones, tropical and temperate (in which we

## Box 2. Cornerstones and predictions of the Equilibrium Theory of Biodiversity Dynamics (ETBD)

ETBD addresses the dynamics and dependencies of species richness $S$ on extinction, speciation, and resource availability (see derivations and evidence using species richness and abundance data in [38]) Unlike other theories, such as neutral theory, it recognizes that $S$ may itself influence community abundance $J$ via effects on resource utilization and thus that it is necessary to concomitantly address the dynamics of $J$. To elucidate the general dynamics of $S$ and $J$, ETBD develops inferences and derivations of the **nullclines** for $S$ and $J$ in the system's **phase plane** (Figure I). According to ETBD, the population size-dependence of extinction and/or speciation generates a stabilizing linear *S-nullcline* (blue line in Figure I) in the S-J phase plane – since the probability of extinction (and perhaps speciation) depends on population size, there must exist a mean population size at which total rates of extinction and speciation are balanced. This S-nullcline thus denotes values of $J$ for a given S where communities have this equilibrium mean population size $\widehat{N} = J/S$, and all communities on the right from the S-nullcline reveal higher extinction than speciation rate due to mean population size being lower than $\widehat{N}$ (and vice versa). Importantly, while theories like neutral theory implicitly assume a stabilizing J-nullcline that is invariant of $S$, ETBD accommodates a stabilizing J-nullcline that increases with $S$ (orange curve in Figure I) with a ceiling determined by total energy availability $E$ and mean individual metabolic rate $B$. This leads to two-way feedbacks between $S$ and $J$ that shape biodiversity patterns and dynamics. ETBD demonstrates the universal existence of a stable equilibrium point, which occurs at the S-nullcline and J-nullcline's intersection (black circle).

ETBD makes various predictions, including curves in Figure I. According to [38], probabilities of extinction $P_x(N)$ and speciation $P_v(N)$ scale with population abundance $N$ as $P_x(N) \propto x_0 N^{-x_1}$ and $P_v(N) \propto v_0 N^{v_1}$, where $x_0$ and $v_0$ determine the probabilities for a given $N$ (i.e., extinction and speciation propensities), respectively, and $v_1$ and $x_1$ quantify their dependence on $N$; the J-nullcline follows $J = \left(\frac{E}{B}\right) cS^{\beta}$, where $c$ sets the fraction of $E$ used by one-species communities and $\beta$ quantifies the biodiversity effect on community abundance. For communities on the J-nullcline, it follows from Equation 13 of [38] that per species rates of extinction and speciation are, respectively, $\boldsymbol{V_{TOT}/S = v_0 c^{v_1} (E/B)^{v_1} S^{-v_1(1-\beta)}}$ and $\boldsymbol{X_{TOT}/S = x_0 c^{-x_1} (E/B)^{-x_1} S^{x_1(1-\beta)}}$, demonstrating that: (i) population size-dependencies cause per species extinction and speciation rates to be diversity-dependent, (ii) the J-nullcline mediates this diversity-dependence, and (iii) $E$ and $B$ affect the rates.

ETBD also predicts how equilibrium $S$ and $J$ scale with energy and other parameters, predicting $S = c^{1/(1-\beta)} (x_0/v_0)^{1/[(x_1+v_1)(\beta-1)]} (E/B)^{1/(1-\beta)}$ and $J = c^{1/(1-\beta)} (x_0/v_0)^{\beta/[(x_1+v_1)(\beta-1)]} (E/B)^{1/(1-\beta)}$ [38], as well as that at equilibrium $\boldsymbol{X_{TOT}/S = V_{TOT}/S = v_0^{x_1/(x_1+v_1)} x_0^{v_1/(x_1+v_1)}}$ (derived here from Equations 13 and 18 of [38]).

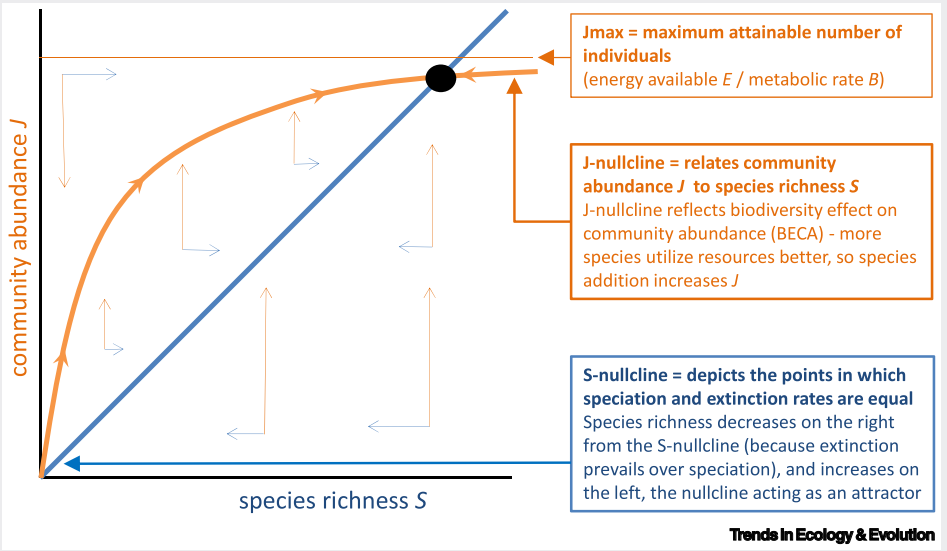



Figure I. The phase plane of ETBD, showing how the J-nullcline and S-nullcline govern biodiversity trajectories and equilibria. Communities can be out of equilibrium due to a perturbation knocking communities away from their equilibria, or an abrupt change in a nullcline (e.g., due to a shift in energy availability or speciation or extinction parameters). Due to evolutionary rates being slower than rates of population change, out-of-equilibrium communities generally follow trajectories rapidly converging on the J-nullcline, moving faster in the vertical (abundance) direction (orange vectors) than the horizontal (richness) direction (blue vectors). They then move along the J-nullcline towards the equilibrium point. Consequently, most communities are expected to be positioned relatively close to the J-nullcline.

include the Arctic). In the earlier periods of the Cenozoic, namely the Eocene, the larger area and productivity of tropical biomes would be expected to augment their biodiversity equilibria compared to temperate regions, via elevating total community abundance $J$ (Figure 2). Additionally, other attributes of the tropics could augment speciation propensity (e.g., temperature) or lower extinction propensity (e.g., reduced seasonality), further elevating tropical species richness equilibria [7,67]. The subsequent global cooling has decreased the area of tropical biomes and enlarged the area of temperate biomes [68] (including novel biomes like temperate steppes), shifting in opposite directions their biodiversity equilibria, their extinction rates, and potentially their speciation rates [67,69] (Figure 2). These equilibria shifts could comprise all terrestrial and marine regions, depending on their distance from the equator. The reason is that, due to the spherical shape of the Earth, shifting the cold climatic zones from high latitudes towards the equator expands their area, while the warm zones close to the equator necessarily shrink in the course of cooling.

The extent to which realized species richness followed these equilibria shifts depends on the speed of the respective processes, namely climate change, speciation, extinction, and the rate of coloni-

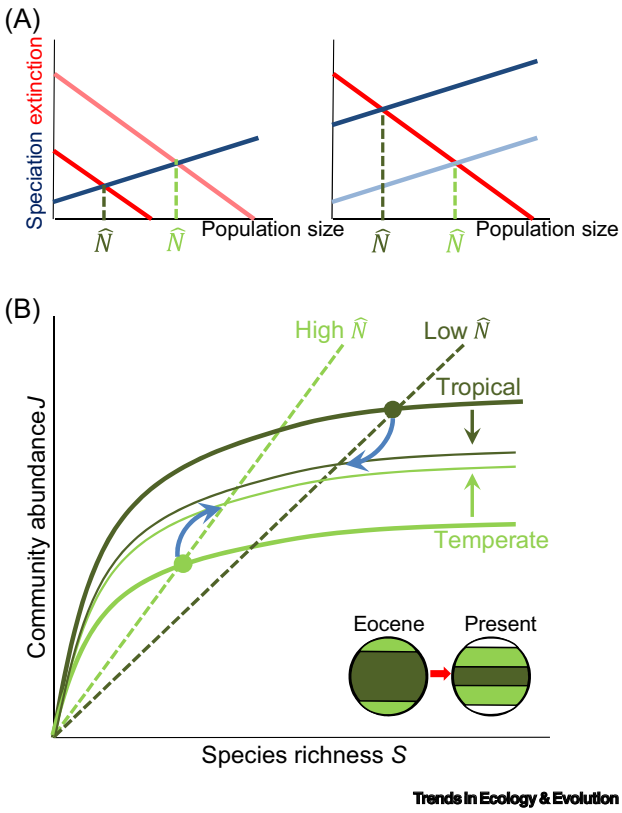



Figure 2. Application of the Equilibrium Theory of Biodiversity Dynamics (ETBD) to understand the consequences of shifting global climate during the Cenozoic. (A) If tropical (darker color) extinction rates are lower (left panel) or speciation rates are higher (right panel) than respective temperate rates (lighter colors) for a given population size, equilibrium mean population size $\widehat{N}$ is lower in the tropics (dark green dashed line). (B) Due to lower tropical mean equilibrium population sizes, the tropical S-nullcline has a shallower slope. The Eocene situation comprises a large tropical region (dark green) and a very small temperate zone (light green), and correspondingly elevated nullclines for community abundance $J$ (J-nullclines, solid lines). Global cooling since the onset of the Oligocene (inset) has led to the shrinkage of the tropics and expansion of the temperate zone. Note that due to sphere geometry, this expansion holds even if the latitudinal extent of the temperate zone does not change. Therefore, original (Eocene) equilibria for both regions (full circles) that reflected the different total amount of resources of the two zones move due to the shifts of respective J-nullclines (green arrows towards the thin lines) into new equilibria which might not yet be reached. The system dynamics is depicted by blue arrows: in the out-of-equilibrium situation, $J$ changes quickly (as population dynamics is faster than extinction-speciation dynamics) and the new J-nullcline is soon reached, but the shift in species richness to new equilibria is much slower. Note that here we assume that the regions differ in their speciation–extinction balance as depicted in (A), but the assumption is not necessary, as the equilibria would shift even if both tropical and temperate S-nullclines were identical, i.e. if the balance of speciation and extinction rates did not differ between the regions. Additionally, if speciation probability depends positively on population size, speciation rate can readily increase in the temperate zone and be higher than the tropical zone while decreasing in the tropical zone due to the temporary out-of-equilibrium positions (see Box 2 predictions).

zation of newly available habitats. Due to tropical niche conservatism, and also relatively low rates of speciation (typically about one speciation event per lineage during a few million of years [70]), it is possible that biodiversity change has lagged behind the change of biodiversity equilibria, and current biodiversity levels are out of equilibrium. In such a case, tropical assemblages are expected to still have higher diversity than their current lowering equilibria, and consequently higher extinction than speciation rates (leading to negative diversification rates, as often observed in the fossil record [67,71]). In contrast, temperate assemblages are expected to have relatively larger population sizes, due to species richness now being lower than equilibrium richness, and so would have lower extinction rates relative to their speciation rates, leading to positive diversification rates (Figure 2).

In this respect, we can reinterpret the classical distinction between biodiversity cradles and museums: the contemporary tropics would represent 'museums' of biodiversity, as it contains species from the past higher equilibrium, while temperate areas would be contemporary biodiversity 'cradles', as their speciation rates prevail over extinction rates. Additionally, because of the positive diversity-dependence of extinction, the out-of-equilibrium temperate biota could have lower contemporary extinction rates than the tropical biota, despite having lower diversity. Regardless of whether the biota are in equilibrium or not, if speciation rate is negatively dependent on species richness – which is expected when speciation probability increases with population size (Box 2) – temperate regions could have higher speciation rates than tropical biota in a variety of scenarios (e.g., Figure 1D). Current findings that many extratropical lineages reveal higher speciation rates than tropical lineages [14–18] can be thus explained by the differences in equilibria between the regions, regardless of whether or not the biota have reached their equilibria (Figures 1D and 2).

Although the equilibrium framework is compatible with the observed phylogenetic patterns, the time-for-speciation hypothesis, which assumes diversification is effectively unbounded, can also be compatible with observed patterns if it is additionally assumed that due to the recent expansion of temperate biomes or recovering from past disturbances, temperate lineages diversify faster than tropical ones. However, this view does not address the possibility that tropical diversity is actually above its contemporary equilibrium, so that it is no longer increasing, and may be actually decreasing in the course of global cooling [67,71]. These different scenarios cannot be distinguished using just phylogenetic trees, as the observed branching patterns are compatible with all of them. One possible way to resolve them involves using fossil data [72], although this approach is not straightforward due to the fragmentary nature of the fossil record and especially a strong geographical bias (namely, a much poorer fossil record in the tropics). We contend that recent pieces of evidence comprising fossil time series [40–42], as well as the strong signal of contemporary climate [32,73] (in contrast to various measures of historical processes) provide support for the equilibrial view, but more research is needed to reconcile these views.

## Concluding remarks: biodiversity past and future

It is possible that whether observed biodiversity patterns are attributable to differences in their equilibria or the time for species accumulation depends on the taxon, phylogenetic and temporal scale, and rates of environmental change [46,74,75] (see Outstanding questions). Still, we argue that it is vital to consider biodiversity equilibria to understand the full spectrum of processes which are responsible for biodiversity patterns in space and time. The advocates of the non-equilibrial view on biodiversity patterns often argue that diversity limits or equilibria may exist, but current diversity levels are well below these limits [76,77]. However, deeper theoretical considerations that do not focus just on the ultimate upper hard limits of diversity but rather on equilibria determined by the negative diversity-dependence of diversification [47,78], as well as a closer analysis of the observed patterns [45,79], indicate that biota can often be rather close to biodiversity equilibria.

### Outstanding questions

Which data and approaches are necessary to test the equilibrium theory and reconcile the equilibrium view with the time-for-speciation hypothesis? Both of these views may generate similar predictions comprising phylogenetic patterns, but the equilibrium theory makes specific statements about patterns of community abundance, population size, and diversity-dependence of respective rates. Since ETBD explicitly addresses abundance dynamics, good large-scale abundance data would be vital, but those are scarce and often inaccurate.

What is the role of species movement (range shifts) between regions in generating and maintaining large-scale biodiversity patterns? Typically, movement out of the tropics does not seem to prevail over opposite movements, but climate changes certainly lead to substantial range shifts that could affect biodiversity equilibria as well as out-of-equilibrium dynamics.

When should disturbances, including large-scale extinction events, be understood as forces pushing diversity out of equilibrium, in contrast to taking disturbances as environmental factors affecting extinction rates?

How can phylogenetics, the fossil record, statistics, and eco-evolutionary models be better integrated and leveraged to more reliably estimate extinction rates? Phylogenetic trees can be used for inferring extinction rates only under restrictive assumptions and the fossil record is fragmentary and incomplete, hindering a proper evaluation of the equilibrium framework.

How can the ETBD be integrated with local-scale (meta) community dynamics, characterized by a different set of important processes and a crucial role of spatial dynamics?

How can equilibrium biodiversity theory be applied to different spatial, phylogenetic, and temporal scales? At large-scales, stable equilibria emerge via a negative feedback between species richness and population size, but other feedbacks could also occur, especially at smaller scales and in specific groups, leading to additional equilibria and tipping points.

Biodiversity changes can relatively tightly follow the shifts of equilibria rather than continuously approaching them [46,73], and some regions of biomes can even be temporarily above the equilibrium diversity level.

If this is the case for most tropical biomes, it implies that tropical biota is even more endangered than what we infer just from known anthropogenic pressures, and is more sensitive to any changes in habitat area or resource availability, environmental stability or rearrangements of community structure. It might appear that current global warming could have a positive effect in this respect, as it apparently returns the climate towards past levels linked to higher tropical biodiversity equilibria. Indeed, it has been shown using fossil time series that extinction rates were lower when short-term climate changes went against the prevailing long-term climatic trend [80]. However, contemporary global changes are extremely fast, and rather than progressive shifts towards a more tropical Earth, they represent a series of disturbances, increasing not only long-term temperature mean, but also temporal environmental variation, which increases extinction rates, decreasing equilibrium biodiversity levels or moving biodiversity farther out of the equilibrium [81]. Without concrete measures that would help to elevate tropical diversity equilibria, tropical areas are expected to face an extinction crisis of an unprecedented extent.

What do the biodiversity equilibria and out-of-equilibrium states imply for predictions of biodiversity dynamics in the Anthropocene and conservation and ecosystem management? Understanding biodiversity dynamics has crucial implications for predicting how biodiversity will respond to current environmental changes, including climate change and habitat loss.

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## Declaration of interests

No interests are declared.

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