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Forum

Biodiversity change in light of succession theory

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Biodiversity is rapidly changing in the Anthropocene, but not all directional changes observed in biodiversity time series are anthropogenic. We discuss key research findings in global change ecology from the past decade, considering the possibility that natural succession contributes as a driving force of directional change. Succession theory suggests the possibility that: 1) accelerated rates of species temporal turnover could also reflect ecosystem recovery rather than global biodiversity redistribution; 2) natural changes in local diversity over time may not be zero, with successional diversity change being variable but often showing a positive temporal trend; 3) biotic homogenization may not only be driven by non-native species, but also by natural processes alone; and 4) successional dynamics may strongly modify the relationship between biodiversity and ecosystem functioning. We propose that a holistic integration of succession theory into global change ecology could provide a baseline for natural biodiversity change and allow us to better isolate the impact of anthropogenic drivers.

Keywords: accelerated species turnover, biodiversity ecosystem functioning, biodiversity redistribution, biotic homogenization, no net loss debate, non-natives

Succession as a baseline for biodiversity change

We are in the midst of a data revolution with a surge of global biodiversity monitoring networks and more ecological time series than ever before openly available (Culina et al. 2018, Díaz et al. 2019, Jetz et al. 2019). These temporal data provide critical insight into how anthropogenic global change (Glossary) affects ecological communities over time (Dornelas et al. 2013). But it is difficult to distinguish which changes are anthropogenic and which would occur even without humans under natural, baseline conditions. To estimate baseline levels of biodiversity change, global change ecologists commonly use stochastic and neutral null models (Dornelas et al. 2014, Magurran et al. 2018; see Glossary). Yet there is a century-long debate as to whether community assembly is stochastic or predictable (Clements 1916, Gleason 1926, Walker and Moral 2003, Prach and Walker 2011). The concept of ecological succession – a central theme throughout the history of ecology – posits that communities assemble, in part, predictably over time



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(Clements 1916, Chang and Turner 2019). Although the field of plant succession has moved away from the concept of a fully predictable and stable climax community (Clements 1916), many successional changes remain predictable, for example changes in community functional trait composition (Odum 1969, Prach et al. 1997). Considering such successional changes as baselines may provide complementary insights to stochastic biodiversity change, embracing the view that stochasticity and predictability can act simultaneously to shape community trajectories. Against a backdrop of a growing number of global-scale meta-analyses of biodiversity trends, we suggest there are broad opportunities for this field to draw from the rich literature on succession to inform baseline levels of biodiversity change.

Broad integration of the two disciplines is particularly pertinent given the long history of human activities (typically centuries to millennia; Ellis et al. 2013, 2021, Ostberg et al. 2015) and the successional legacies these can create in current biodiversity time series that cover only a limited time period (typically a few decades to a century; Verheyen et al. 2016, Dornelas et al. 2018, Jandt et al. 2022). The role of potential successional legacies is exacerbated by the way biodiversity is typically sampled. Time series, for example of plant communities, are predominantly recorded at sites where no major habitat alteration, such as clearcutting, has occurred between surveys (Verheyen et al. 2016 for selection criteria in forestREplot), and at sites where disturbance frequency has often even ceased (e.g. fire suppression, decline in traditional grazing regimes and management). This is likely to bias meta-analyses towards reflecting successional biodiversity change. Consequently, the assumption that directional biodiversity change could also reflect successional legacies should be a central null hypothesis in meta-analyses of biodiversity change.

Here, we take a look at four major themes in the literature on plant biodiversity change from the past decade through the lens of succession theory: 1) accelerated species turnover; 2) the 'no net loss' debate; 3) biotic homogenization; and 4) loss of ecosystem functioning under biodiversity loss. We do not aim to review the many detailed facets of biodiversity change, nor the plethora of successional theories, but to illustrate how closely succession can be interwoven with key facets of contemporary biodiversity change and why successional thinking should more fully permeate global change ecology.

Accelerated temporal species turnover

Temporal species turnover is the rate of species replacement over time, with fast turnover rates meaning that a high proportion of the original species in the community is replaced by novel species in a given time period (Glossary). An important finding in global change ecology from the last decade is that, although community species richness shows no directional temporal trend, rates of species turnover are accelerated in the Anthropocene (defined as from 1950; Zalasiewicz et al. 2017) in comparison to rates predicted from neutral and stochastic null models (Dornelas et al.

2014, Magurran et al. 2018). This pattern, according to the prevailing hypothesis, reflects a rapid global redistribution of biodiversity in response to global change (Dornelas et al. 2014, Eriksson and Hillebrand 2019) and led to the question: at what point does elevated temporal turnover jeopardize community integrity (Magurran et al. 2018)?

During succession, plant life history trade-offs (e.g. colonizing ability/growth rate are inversely correlated with longevity/size at maturity (Drury and Nisbet 1973, Horn 1974)) and biotic reactions upon abiotic factors (e.g. light and nutrients (Clements 1916)) can influence turnover rates dramatically. Unlike in stochastic and neutral models, successional rates of species turnover frequently follow a distinct temporal pattern after disturbance; they tend to peak early and then decrease (Lichter 1998, Anderson 2007, Li et al. 2016). Consequently, high turnover rates during succession may reflect a process of ecosystem recovery in which community integrity is not compromised but restored (Clements 1916, Prach et al. 2016). Recently, global change meta-analyses have revealed that deforestation acts as a catalyst of global biodiversity change by accelerating turnover (Daskalova et al. 2020). Under a succession framework, this would be expected as a null hypothesis, as later successional stages tend to have lower turnover rates than earlier ones (Fig. 1a; Lichter 1998, Anderson 2007, Li et al. 2016). But rather than reflecting global biotic redistribution and a threat to ecosystem resilience, this turnover would be the very epitome of resilience, reflecting the dynamics of natural recovery.

We suggest that, in order to draw conclusions about the effects of global change on rates of species temporal turnover and its association to ecosystem resilience, turnover rates need to be compared, not among *different* successional stages, but among *similar*, e.g. early-successional ones (Fig. 1a–b). Comparisons of turnover rates among early-successional communities might indeed reveal slower turnover at high intensities of global change, considering that global change factors such as invasive species and reductions in regional seed pools of native species can slow successional rates (Walker and Wardle 2014). For example, invasive *Imperata* or *Dactylis* grasslands can slow turnover and inhibit forest succession and thus recovery in tropical and temperate regions, respectively (Connell and Slatyer 1977, D'Antonio and Vitousek 1992). Succession studies also find that species turnover rates can depend on natural environmental factors. For example, species replacement may be slow in the primary succession of an Arctic glacial foreland, but rapid in the productive and moist environments of tropical forests (Prach and Walker 2020, Poorter et al. 2021). Integrating these insights from succession may thus enhance our understanding of species temporal turnover in the Anthropocene, stimulating hypotheses such as that slowed rather than accelerated turnover following disturbance could jeopardize ecosystem resilience (Fig. 1c). Data synthesis work by research networks such as 2ndFOR (<https://sites.google.com/view/2ndfor/home>) to track ecosystem recovery after disturbance may provide new vantage points for studying such questions.

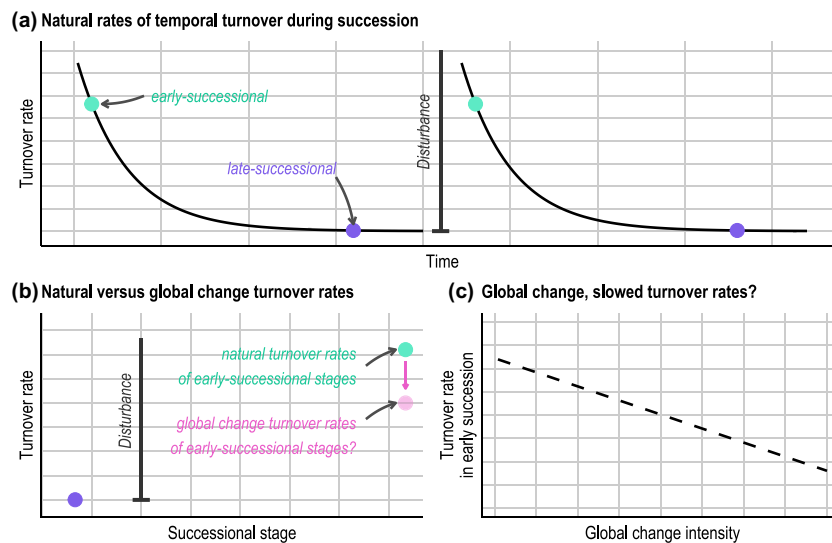


Figure 1. Succession theory suggests that accelerated temporal species turnover could also signal ecosystem recovery and thus need not be a threat per se to ecosystem resilience. (a) Turnover rates are naturally accelerated in early-successional stages and therefore, from a successional perspective, are a sign of recovery after natural or human disturbance. (b) To isolate human influence, turnover rates need to be compared not between different successional stages (e.g. late versus early) but between similar successional stages (e.g. an early successional stage in an environmentally comparable area with high versus low global change intensity). (c) This may lead to the hypothesis that some facets of global change could also lead to slowed turnover rates.

No net loss of local diversity

Over the past decade, several long-term studies of temporal changes in local plant diversity have found no evidence of systematic decline, despite the pervasive human impact on ecosystems worldwide (Verheyen et al. 2012, Vellend et al. 2013, Dornelas et al. 2014, Jandt et al. 2022). These findings are in stark contrast to space-for-time studies (Glossary) that demonstrate lower species richness in most land-use types other than primary and secondary vegetation, especially in areas intensively used by humans (Aronson et al. 2014, Murphy and Romanuk 2014, Newbold et al. 2015). These conflicting results sparked the ‘no net loss’ debate amongst ecologists, one that remains unresolved (Diekmann et al. 2014, Gonzalez et al. 2016, Vellend et al. 2017, Cardinale et al. 2018, Eichenberg et al. 2020, Pilotto et al. 2020, Jandt et al. 2022).

From the perspective of plant succession, temporal studies comparing resurveys to baseline surveys typically compare species richness of later- to earlier-successional stages. Again, this is because vegetation resurveys are mostly carried out in sites with no major disturbance since the baseline survey (Gonzalez et al. 2016, Verheyen et al. 2016). Per contra, space-for-time studies comparing disturbed to natural sites typically compare species richness of earlier- to later-successional stages, because disturbances shift later-successional stages to earlier ones (Clements 1916, Walker and Wardle 2014). If early-successional stages differ in species richness from later ones, this could help reconcile the contrasting trends in species richness between temporal and space-for-time studies (Fig. 2).

Succession studies find that species richness can have a negative, unimodal, fluctuating, positive or flat trend, with

synthesis tentatively suggesting that of these different trends, increases in species richness occur most frequently, in both primary and secondary successions in different habitats (Anderson 2007, Prach and Walker 2019). Some evidence also suggests that the high variability in successional richness trends may be due in part to spatial scale dependence (Meiners et al. 2015). While mean species richness in small plots may decline during succession because one shrub replaces several herbaceous species (Odum 1969), in large plots richness may increase, because minute natural disturbances at this scale are ubiquitous and, by nonuniformly resetting the successional clock, allow the coexistence of early- and late-successional species (Fig. 2a; Clements 1916). Thus, in large plots, space-for-time studies comparing disturbed to natural (i.e. early- to late-successional) sites may find that richness decreases, while studies using temporal data may find that richness increases (and vice versa in small plots; Fig. 2b–c). Although, of course, many other factors explain variation in successional diversity change, this example illustrates that conflicting results between temporal and spatial approaches may be expected under a succession framework. Considering successional richness trends may therefore help shed new light on the ‘no net loss’ debate. Successional diversity trends further suggest a need for null hypotheses that go beyond the usual ‘no change’ to contextualize contemporary trends in local diversity.

Biotic homogenization

The human-mediated breakdown of geographic dispersal barriers and other global change factors, such as habitat

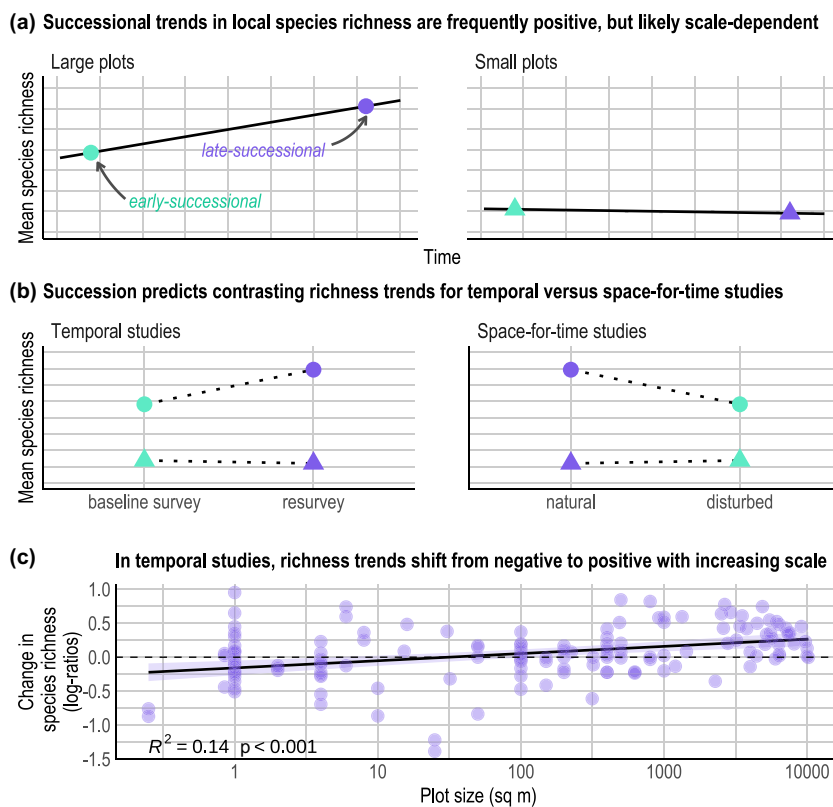


Figure 2. Successional thinking may reconcile contrasting local richness trends in temporal versus space-for-time global change studies. (a) Synthesis studies suggest that successional trends in local diversity are often positive but highly variable. Spatial scale may explain some of the variability, with negative trends in richness likely to be more prevalent in smaller than larger plots. (b) Thus, in large plots (circles), global change studies that use temporal data, comparing resurvey to baseline survey (i.e. later- to earlier-successional stages), may find that richness increases, whilst global change studies that use a space-for-time approach, comparing disturbed to natural sites (i.e. earlier- to later-successional stages), may find that richness decreases (and vice versa in small plots; triangles). (c) To estimate plot size at which richness may tend to decrease/increase over time, we use the [Vellend et al. 2013](#) data for forest resurveys that suggest positive temporal richness trends in plots above 100 m².

loss and eutrophication, are generally expected to lead to biotic homogenization ([McKinney and Lockwood 1999](#)). In this process, beta and gamma diversity (Glossary) is lost as spatially distant communities converge in species composition through the spread of relatively few widespread, often non-native species and the loss of many rare species ([Newbold et al. 2018](#), [Olden et al. 2018](#), [Staude et al. 2022](#)). There are increasing calls for stronger biosafety regulations for trade and transport to prevent floristic homogenization and a Homogocene ([Yang et al. 2021](#)).

Successional theory suggests the possibility of biotic homogenization and heterogenization by natural processes alone ([Clements 1916](#), [Margalef 1963](#), [Christensen and Peet 1984](#)). Empirical studies find that communities tend to converge in composition at the landscape scale and diverge in composition at the plot scale in successions of old fields ([Li et al. 2016](#)) and forests ([Frellich and Reich 1995](#)). One possible interpretation of these findings is that at the landscape scale, different seed banks, land-use legacies, environmental conditions, and thus priority effects initially favor dissimilarity. But, as slower-growing and more competitive,

taller plants become dominant, buffering against exogenous abiotic variation increases, and species pools become more predictable, stable, and similar between landscapes ([Fig. 3a](#); [Margalef 1963](#), [Fukami and Nakajima 2011](#), [Dini-Andreote et al. 2015](#), [Li et al. 2016](#)). At the plot scale, smaller community size may lead to stronger stochastic than deterministic competitive effects on beta diversity, and different species of woody plants can become monodominant in different plots, leading to heterogeneous vegetation mosaics that increase dissimilarity and nestedness between plots ([Orrock and Watling 2010](#), [Chase and Myers 2011](#), [Li et al. 2016](#)). As anthropogenic disturbances move mature systems to earlier-successional stages, successional beta diversity change could also imply that plot-level vegetation becomes more similar, while landscape-level vegetation becomes more heterogeneous under disturbance ([Fig. 3b](#)). Successional dynamics can therefore not only lead to pronounced directional beta diversity change over time, but also shape disturbance-driven beta diversity patterns. We therefore suggest successional beta diversity change deserves more consideration in our narrative of biotic homogenization.

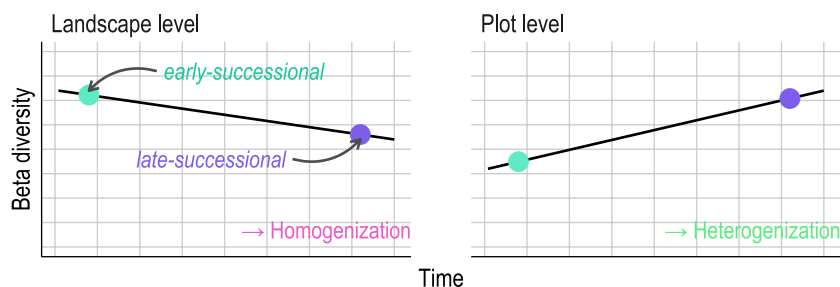
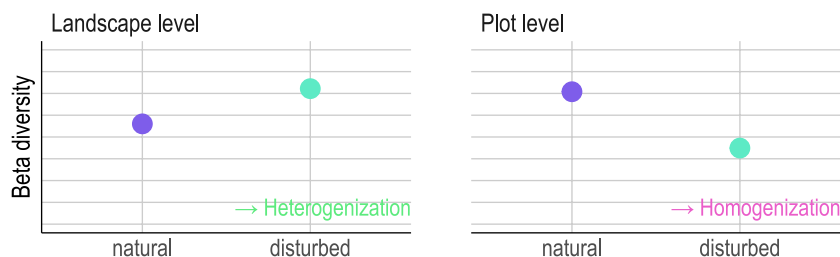
(a) Beta diversity between landscapes and between plots during succession**(b) Beta diversity change upon disturbance as predicted from succession**

Figure 3. Vegetation can become more homogeneous or heterogeneous in species composition by natural succession. (a) Empirical evidence suggests successional beta diversity trends may be scale-dependent. Successional processes can homogenize floristic composition between landscapes but differentiate vegetation between plots over time. (b) Because anthropogenic disturbance can push natural habitats back to earlier successional stages, successional models predict that disturbance will increase beta diversity between landscapes and decrease beta diversity between plots. Changes, particularly declines, in beta-diversity over time and due to disturbance are typically attributed in the global change literature to global reshuffling of species rather than successional processes.

Although other successional changes in beta diversity are conceivable (c.f. Nishizawa et al. 2022), the succession studies above raise the possibility that 1) changes in beta diversity, as in homogenization, may not be exclusively human-caused or negative, but could also reflect the formation of mature ecosystems, and that 2) preventing the spread of non-native species may not suffice to halt floristic homogenization. To illustrate, if human activities ceased in central Europe, cultivated land would return to forest (Cotta 1865), whereby successional processes may homogenize the heterogeneous flora that is sustained through human activities (Vera 2000, Martins et al. 2022). Given the confounding role of succession in biotic homogenization, quantifying the relative contributions of natural and anthropogenic processes is critical. We suggest that quantifying the extent to which beta diversity is due to gains/losses in widespread/rare species and what fraction of these are early-/late-successional, may help to better isolate the role of humans. For example, if gains in widespread species are primarily due to gains in late-successional native species (e.g. trees can have large geographic ranges) rather than non-native species, humans may play a lesser role in floristic homogenization. The role of non-native species in the decline of beta diversity is consistently highlighted in the scientific literature, but the fact that succession can also be an important component of this biodiversity change is often overlooked. This potential role of succession is underscored by recent meta-analyses, which show that forest species are on the rise, coinciding with patterns of few winners versus more loser species (Jandt et al. 2022, Staude et al. 2023).

Biodiversity and ecosystem functioning

The last decades have seen a surge of experiments and observational studies creating new or exploiting existing plant diversity gradients, respectively, to test the relationship between biodiversity and ecosystem function (BEF relationship; Cardinale et al. 2012, van der Plas 2019; see Glossary). The vast majority of studies report positive relationships between plant diversity and various ecosystem functions (Cardinale et al. 2012, van der Plas 2019), most commonly examining the relationship between species richness and biomass, productivity, and temporal stability of these functions (van der Plas 2019). Positive relationships are hypothesized to result mechanistically from functional complementarity and selection effects (van der Plas 2019). However, most experimental studies assemble random communities, treat biodiversity facets as independent variables, and control species composition to maintain diversity gradients (Huston 1997, Huston et al. 2000, van der Plas 2019). Even in observational studies, the extremes of the diversity gradients, i.e. monocultures or highly diverse mixtures, often result from human interference (Ratcliffe et al. 2017). The dominant signal of positive BEF relationships thus emerges from systems with altered community assembly dynamics and conditions untypical for natural succession (Srivastava and Vellend 2005, Laure et al. 2009).

During succession, the shape of the temporal trajectories of species diversity and ecosystem functioning depends on a wide range of factors, including the mode of succession

(primary versus secondary), the type, severity, and timing of disturbances initiating succession, the environmental template, chance effects and spatial scale (Perry et al. 2008, Wirth and Lichstein 2009). BEF patterns in successional series are therefore likely to carry a mixed signature of successional mechanisms and classical BEF mechanisms and their mutual interaction. To illustrate, we will present a scenario for successional trends of biodiversity and primary productivity after a large and severe disturbance, such as stand- and seed-destroying fire or agriculture on rich soil (Kinzig and Pacala 2001; Fig 4). Early- and late-successional species overlap to create a mid-successional diversity peak, and as fast-growing pioneer species are replaced by slow-growing late-successional species, productivity declines (colonization–competition trade-off; Tilman 1990; Fig 4a). This would lead to a progression from negative BEF relationships during early succession – in contrast to predictions from experimental evidence – to positive relationships during late succession (Fig. 4b; Lasky et al. 2014). The scenario further suggests that the relative importance of selection effects, i.e. positive BEF relationships arising from a higher probability and dominance of productive species in diverse communities, may decrease during succession. Per contra, complementarity effects, i.e. positive BEF relationships arising from resource partitioning, abiotic facilitation, or biotic interactions (Barry et al. 2019), may be independent from successional dynamics and moderate BEF relationships during early and late succession (Fig. 4b). Note that the above scenario is only one of many possibles – for example, plant diversity could drop in mid-succession due to competition while productivity is high (e.g. in temperate forest secondary successions; Hilmers et al. 2018, Lanta et al. 2023), or diversity could increase asymptotically while

productivity declines (e.g. in tropical forest secondary successions; Magnabosco Marra et al. 2018, Rozendaal et al. 2019), leading to a similar decoupling of changes in diversity and functioning. We therefore suggest that succession can play an important role in shaping BEF relationships in observational studies (Mori et al. 2017).

This logic may also extend to other ecosystem functions and to dynamic attributes of ecosystems, such as stability with its components of resistance and resilience. According to Margalef (1963, 1975), maturing ecosystems are characterized by an increase in vertical structure, structural complexity, and biomass, all of which buffer environmental fluctuation and thus increase resistance to perturbations. In contrast, the highly productive species in early-successional systems recover quickly from disturbances, thus lending resilience to the system (Horn 1974). Again, these contrasting features are due to the colonization–competition trade-off between fast-growing pioneers and slow-growing but tall-statured competitors dominating late-successional stages (Tilman 1990). And although diversity may have a direct effect on the successional pattern of stability responses (Sakschewski et al. 2016, Craven et al. 2018, Schnabel et al. 2021), they can also be explained by successional shifts in species composition. Succession deserves greater consideration when studying the consequences of biodiversity loss on ecosystem function in real-world systems.

Conclusion and way forward

In addition to recent calls to account for multiple biases in temporal biodiversity data and establish representative global

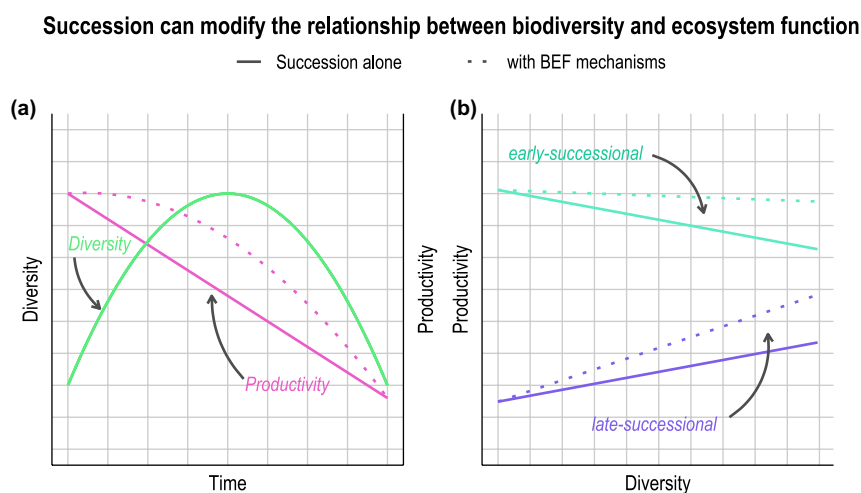


Figure 4. One exemplar scenario under which biodiversity loss may not always lead to loss of ecosystem functions. Despite a possible consistent diversity effect on productivity (solid versus dotted line), the relationship between diversity and productivity may change slope during succession. During succession, primary productivity may decline and coincide with an initial increase in diversity (leading to a negative biodiversity–ecosystem function (BEF) relationship in early succession) and later with a decline in diversity (leading to a positive BEF relationship in late succession), suggesting that additional processes can generate patterns that deviate from classical BEF relationships observed in experiments. Similar deviations from classical BEF relationships are expected for diversity–stability relationships, with resistance increasing and resilience decreasing during succession. Note that various trajectories for species diversity and ecosystem function are possible. The scenario illustrated does not aim to suggest generalities, but rather a possible case in which successional processes can strongly alter BEF relationships.

biodiversity monitoring networks to estimate biodiversity trends (Gonzalez et al. 2016, Díaz et al. 2019, Jetz et al. 2019, Mentges et al. 2021), we believe another priority is to better integrate and extend our knowledge on how biodiversity naturally changes over time. A century of studies on succession can provide an empirical and conceptual basis to disentangle the relative influence of human and natural drivers of biodiversity change. Whilst we focus on plants in this article, we suggest successional dynamics will also be relevant for other groups of organisms, not least because their dynamics are often coupled with vegetation changes (Siemann et al. 1999, Anderson 2007). Succession theory suggests the possibility that: 1) accelerated species turnover rates reflect ecosystem recovery rather than global biodiversity redistribution, with the possibility that turnover rates may in fact slow owing to global change; 2) successional trends in local diversity may reconcile conflicting findings of temporal and space-for-time studies on local diversity change; 3) biotic homogenization can result from natural processes alone, without requiring the presence of non-native species to explain patterns of community convergence; and 4) successional dynamics are likely to impact the relationship between biodiversity and ecosystem functioning. We provide a research prospectus to motivate a broader integration of successional thinking in global change ecology (Box 1: Motivating questions).

Putting this integration into practice analytically is, however, not trivial. Whilst the qualitative nature of successional null hypotheses may be fairly clear, it can be difficult to quantify the precise magnitude of successional change over time for a given system and biodiversity facet. Different types of successional studies, i.e. chronosequential and temporal, may yield different successional trajectories for the same system, where reliance on chronosequential studies to determine baseline successional changes may give a false sense of predictability (Johnson and Miyanishi 2008). Furthermore, controlling for successional stage can be challenging, given the general paucity of data on historical land use preceding the baseline survey. But similar to stochastic null models, there are successional models (Pacala et al. 1996, Wirth and Lichstein 2009, Zakharova et al. 2019) that can provide quantitative insights into baseline-level biodiversity change from succession. To estimate the successional stage at baseline, plant functional traits may help classify species and communities along a continuum of early- to late-successional, which can be complemented with reconstructed land use maps (Hurt et al. 2020, Winkler et al. 2021) and local knowledge. For example, if determined, based on local knowledge, that a given system was early-successional at baseline, existing empirical data (Prach et al. 1997, Poorter et al. 2021) could be used to predict the magnitude of compositional change in functional traits that may occur naturally over a given period of time. If the magnitude of observed change (e.g. no change in plant height) is much less than predicted from succession (e.g. increase in plant height), this could indicate a jeopardized recovery process. More importantly, however, succession must be taken into account in the formulation of research questions and conclusions of global change studies. For

example, when examining the drivers of accelerated turnover, one might find a correlation between high turnover and non-native species and conclude these act as catalysts for biodiversity change, whereas it may simply be that such time series are early-successional and therefore naturally with high turnover. Integrating successional thinking into our research questions, null hypotheses, and conclusions will ultimately help us gain a deeper understanding of contemporary biodiversity change and the role of humans therein.

Box 1: Motivating questions

To what extent does accelerated temporal species turnover in ecological time series reflect global biodiversity redistribution compared to ecosystem recovery? High turnover during succession is typical of early-successional stages and reflects a process of recovery and not necessarily a global re-shuffling of biodiversity.

How does anthropogenic global change affect post-disturbance recovery trajectories? Studies on successional rates suggest that high intensities of several global change factors can slow rates of temporal turnover. This reduced, rather than accelerated turnover, may signal a threat to ecosystem resilience.

To what extent do successional changes confound the direction and magnitude of temporal trends in local diversity? Synthesis studies tentatively suggest predominantly positive local diversity trends during succession that need to be taken into account when interpreting contemporary biodiversity trends.

To what extent are changes in beta diversity in time series exacerbated by successional dynamics? Studies suggest floristic convergence can occur naturally during succession. Successional convergence may reflect a trend towards longer-lived species and the forming of carbon sinks rather than biodiversity loss per se.

How does community composition change with respect to rare versus widespread (and specialist versus generalist) species during succession? Successional studies suggest the composition of species functional traits and range sizes may change markedly during succession, partially due to the competition–colonization trade-off.

To what extent can succession explain variability in the direction and strength of BEF relationships? Successional models suggest the possibility that BEF relationships may reverse direction during succession, creating scenarios in which biodiversity loss may not necessarily lead to loss of ecosystem function.

Glossary

Global change ecology: studies investigating directional changes in biodiversity that are due to human activities, such as anthropogenic changes in land use, nutrient status,

climate, biological invasions, natural disturbance regimes (e.g. fire, weather extremes, diseases), and extinctions.

Stochastic and neutral null model: generates null expectations through random sampling that assigns species fixed parameters for colonization and extinction probability (stochastic) or treating organisms of a community identical in their per capita probabilities of giving birth, dying, migrating, and speciating (neutral); excludes biological mechanisms such as species interactions and changing environments.

Ecological succession: ubiquitous process of vegetation development by which structure, function, and species composition can progressively change over time. Differs from community assembly by the temporal scale of focus. Plant succession studies are typically between decades to centuries, whereas community assembly studies focus on the relatively short-term processes of biodiversity.

Turnover rate: the speed at which species change occurs, often quantified as the rate of change in community similarity over time, or as species exchange ratio between two consecutive time periods (i.e. the proportion of species gained (G) plus species lost (L) of the total number of different species (S_T) in both time periods $(G + L)/S_T$).

Space-for-time studies: space-for-time substitution analyzes contemporary spatial phenomena using static spatial data sets (e.g. comparing biodiversity between natural and disturbed habitat) to infer temporal ecological processes (e.g. how does biodiversity change due to human activities).

Beta diversity: the degree of community differentiation across space and environmental gradients, in its simplest form defined as the ratio between regional (γ) and local (α) diversities.

BEF: the biodiversity and ecosystem functions (BEF) research field aims to understand the causal effects and consequences of biodiversity loss on ecosystem functions such as biomass production. The vast majority of studies report positive BEF relationships, with complementarity and selection effects presumed to be the mechanistic basis for positive BEF relationships.

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Author contributions

Ingmar R. Staude: Conceptualization (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Alexandra Weigelt:** Conceptualization (supporting); Visualization (supporting); Writing – original draft (supporting). **Christian Wirth:** Conceptualization (supporting); Visualization (supporting); Writing – original draft (supporting).

Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study. The R code to reproduce the figures is available on GitHub: <https://zenodo.org/record/8247222>.

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