Integrating macroecology with temporal and trait-based perspectives : toward better attribution of human drivers to diversity changes

Authors
Pierre Gaüzère[1*], Cyrille Violle[2], Franziska Schrodt[3], Matthias Grenié[1], Lucas Santini[4], Mickaël Hedde[5], Emmanuelle Porcher[6], Romain Goury[1], Miriam Beck[7] and Wilfried Thuiller[1]
[1]Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, 38000 Grenoble, France
[2]CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
[3]School of Geography, University of Nottingham, Nottingham, UK
[4]Department of Biology and Biotechnologies "Charles Darwin", Sapienza Università di Roma, Rome, Italy
[5]Eco&Sols, INRAE, IRD, CIRAD, Institut Agro, Montpellier, France
[6]Centre d'Ecologie et des Sciences de la Conservation (Cesco), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, 75005, Paris, France
[7]FRB-CESAB, Fondation pour la Recherche sur la Biodiversité – Centre de Synthèse et d'Analyse sur la Biodiversité, 5 rue de l'école de médecine 34000 Montpellier, France

*Corresponding author : pierre.gauzere@gmail.com

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Biosktech: The IMPACTS working group, founded by the CESAB FRB, aims to comprehensively assess the effects of human pressures on biodiversity. The project focuses on evaluating and refining existing data, indicators, and methodologies to establish best practices, complemented by a set of guidelines for assessing biodiversity impacts. Such frameworks will be applied to data from scientific inventories and participatory science initiatives, spanning both national and regional levels, and encompassing diverse taxonomic groups and biodiversity facets. Ultimately, the project seeks to quantify the sensitivity of various taxonomic groups to environmental changes, thereby illustrating the multifaceted impacts on biodiversity.

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Short title : Dynamic Macroecology for diversity changes

Abstract

The ongoing biodiversity crisis presents a complex challenge for ecological science. Despite a consensus on general biodiversity decline, identifying clear trends remains difficult due to variability in data, methodologies, and scales of analysis. To enhance our understanding of ongoing biodiversity changes and address discrepancies in biodiversity trend detection, we propose integrating macroecological theory with temporal and trait-based perspectives.

- First, analyzing temporal changes in macroecological patterns, such as species accumulation curves, can reconcile and synthesize conflicting observations of biodiversity change, enabling quantification of diversity shifts across scales.
- Second, diversity patterns across scales are linked to three proximate components: abundance, evenness, and spatial aggregation. Investigating temporal changes in these components provides deeper insights into how human activities directly influence biodiversity trends.
- Third, incorporating species traits into the analysis of these macroecological patterns improves our understanding of human impacts on biodiversity by elucidating the links between species characteristics and their responses to environmental changes.

We discuss the limitations and challenges of this integrative approach and highlight how it offers a comprehensive framework for understanding the drivers of biodiversity change across scales. This framework facilitates a more nuanced understanding of how human activities impact biodiversity, ultimately paving the way for more informed actions to mitigate biodiversity loss across spatial and temporal scales.

Keywords (6 max) : Diversity Trends, Macroecological theory, Global Change, Conservation, Traits

Declaration of interest : The authors declare no competing interests.

Introduction

Quantifying multiple aspects of the ongoing biodiversity crisis and delivering a comprehensive evaluation of its magnitude is a key challenge. Global empirical studies documenting species diversity changes show a complex picture (Cardinale *et al.*, 2018). First, global and regional decreases in species richness (gamma diversity) appear to contradict local observations of "no net loss" or increases in species number (alpha diversity) (Vellend *et al.*, 2013; Primack *et al.*, 2018; Boënnec *et al.*, 2023). Second, the reduction of diversity among communities (beta diversity), *aka* biotic homogenization, is recognized as a pervasive feature (Magurran *et al.*, 2015). This phenomenon might explain the apparent contradiction between alpha and gamma diversity trends by attributing local increases in species richness to expanding "winner" species, while regional or global decreases result from the extinction of "loser" species. However, this interpretation is difficult to test due to uncertainty regarding the spatial scale at which homogenization occurs and is increasingly challenged by empirical evidence (Buhk *et al.*, 2017; Blowes *et al.*, 2024). Despite improved clarity and guidance on the use of metrics to assess temporal biodiversity trends at different scales (McGill *et al.*, 2015), fundamental gaps remain. A key limitation is that the spatial scaling of diversity is not fully integrated in a continuous way, often merely comparing artificially defined local or regional scales, without providing a clear mechanistic connection between metrics and scales of diversity change.

Yet, macroecology has long stated that macroecological patterns result from invariant laws that depict changes in diversity across scales (Brown, 1995; Gaston & Blackburn, 2000; McGill & Collins, 2003; Azaele *et al.*, 2015). For instance, the well-known *Species Area Relationship* (SAR), *Species Accumulation Curve* (SAC), and *Distance Decay of Similarity* (DDS) integrate diversity across continuous scales, by describing changes in species richness or beta diversity with area, number of samples or geographic distance between samples. These laws define parametric functions that describe the expected change in diversity with scale. Macroecological patterns have been partly extended to address temporal biodiversity changes (Engen *et al.*, 2002; Harte *et al.*, 2021), in particular to quantify the effects of disturbance on species diversity (Petraitis *et al.*, 1989; Newman *et al.*, 2020; Franzman *et al.*, 2021). They thus offer the benefit of explicitly incorporating ecologically meaningful measures of scales which are relevant across ecosystems. An additional benefit of examining biodiversity dynamics through the lens of macroecological laws is that their variations are intrinsically linked to the total number of individuals (abundance), the distribution of abundance among species (evenness), and species spatial aggregation (McGill & Collins, 2003; Azaele *et al.*, 2015; Chase *et al.*, 2018). These three descriptors, commonly referred to as proximate components, bring a deeper understanding of diversity changes while integrating changes at the population scale, for which the average decline in population abundance appears as another critical aspect of biodiversity loss (Loh *et al.*, 2005; Leung *et al.*, 2022). Yet, the study of temporal diversity changes through the concept of "dynamic macroecological patterns" is still marginal. Only few empirical studies have attempted to integrate macroecological (spatial) patterns across time (White *et al.*, 2010), or have studied the temporal dynamics of macroecological patterns

(Blowes *et al.*, 2022; Terry & Rossberg, 2023; van Klink *et al.*, 2024) in the context of directional changes such as anthropogenic pressures.

Species abundance and diversity alone do not fully capture the multifaceted nature of biodiversity. It has long been recognized that species trait characteristics bring a complementary and essential perspective to biodiversity thanks to their close link to ecosystem functions and services (Lavorel & Garnier, 2002; Cadotte *et al.*, 2011). For instance, the loss of functional diversity per unit of habitat loss (as measured from a functional diversity area relationship) is likely a more accurate predictor of ecosystem vulnerability than the loss of individual species. A decrease of a certain level of functional diversity—typically associated with specific combinations of functional traits—can jeopardize ecosystem functionality. In contrast, the loss of a single species may go unnoticed if other species with similar roles continue to thrive (Srivastava *et al.*, 2012) . Incorporating traits into macroecological laws is an active field of research (Mazel *et al.*, 2014), but the temporal aspect of these laws remains largely unexplored. Linking the temporal perspective of macroecological theory with trait-based approaches can illuminate our understanding of what drives biodiversity changes, and at which scales.

In this paper, we first outline how temporal variation in macroecological patterns integrate diversity change across spatial scales, then we explain how recent developments in macroecology theory can help to better understand changes in biodiversity. We then showcase how integrating species traits and dynamic macroecological patterns can link changes to drivers. We finally outline the current pitfalls limiting the generalization of such an approach, and how to better leverage dynamic macroecological patterns to attribute and quantify the potential effects of anthropogenic drivers to diversity changes across scales in the future (McGlinn *et al.*, 2019; Gonzalez *et al.*, 2023). By doing so, a path towards richer and more robust insights into how human activities affect biological diversity over time and space will emerge.

Dynamic macroecological patterns integrate diversity changes across time and space

Beyond data deficiency and statistical issues, the lack of explicit consideration and reporting of the scale at which diversity changes are estimated is a major issue when reporting and quantifying biodiversity changes (Estes *et al.*, 2018). Even when a specific scale such as local alpha diversity is the focus, the actual sampled area is often not clearly reported (Blowes *et al.*, 2024), and the definition of what is a “local” or “regional” changes significantly with the organism and biodiversity metric of interest. For example, even within a single taxonomic group such as vascular plants, the definition of local scale is likely to vary between a grassland and a forest. Similarly, regional gamma diversity is generally tightened to the study’s spatial extent, often without proper consideration of its actual area or how well it covers the regional species pool. Consequently, the lack of clarity regarding the examined scales and their ecological relevance can affect the interpretation and comparability of biodiversity change at local and regional scales. Importantly, it can also affects measures of beta diversity often defined as the ratio or difference between regional (gamma) and local (alpha) diversity (see Figure 1).

We argue that macroecological patterns that integrate diversity across an explicit spatial scale or sampling effort offer a valuable, theory-grounded solution to the aforementioned scaling issues. For example, the well-known Species–Area Relationship (SAR) describes the expected increase in the number of species with the area sampled, generally described as a simple function with two or three parameters (Connor & McCoy, 1979; Dengler, 2009). However, common biodiversity monitoring schemes rarely cover contiguous areas, but instead generally focus on scattered sampling units. In this case, the Species Accumulation Curve (SAC), describing the positive relationship expected between the number of species sampled in a group of sites and the number of sites, appears more suited (Figure 1A). This macroecological pattern can describe diversity continuously from the local scale (α species richness, i.e. within a single site), to regional scale (γ species richness at the maximum number of sampling sites), or even global scale (in the case where the entire earth is sampled) and can be summarized by a limited number of parameters (e.g intercept and slope) depending on the best model to fit the data. As the turnover of species, or β diversity, can be defined as γ/α, the SAC can also describe species turnover for any number of samples, called beta rarefaction (Ricotta *et al.*, 2019). We will thus further base our argumentation on the example of SAC but note that other macroecological patterns describing diversity along continuum of scales can equally be used.

Looking at temporal changes in SAC (for example with richness of fish species from 1970 to 1995, see Figure 1B) integrate changes continuously from local to global scales, and effectively summarize diversity changes of numerous forms of diversity (McGill *et al.*, 2015). In a first example, a temporal increase in γ richness will bend the SAC upwards at broad scales (top left in Figure 1C), which can be measured as an increase of the SAC slope over time but no change of the intercept. In a second example, an increase in site-average α richness bend the SAC upwards at local scales will be measured as a decrease of the SAC slope over time and increase of the intercept (top middle in Figure 1C). In both examples, the resulting β diversity also changes at larger or smaller scales, respectively for first and second example. Looking at change in the SAC allows a supplementary layer of understanding, as combinations of observed diversity changes across scales are underpinned by compositional changes in terms of species occupancy. In the second example, observed diversity changes can be interpreted by the replacement of range-restricted species by widespread species (Blowes *et al.*, 2024). In other cases, similar increase in α richness and γ richness will shift the SAC up without changing its slope (bottom left in Figure 1C), while a combination of increase in α richness and decrease in γ richness will change the slope of the SAC (temporal decrease in the slope of the SAC) without shifting its overall level (no change in intercept) (bottom middle in Figure 1C). Most combinations of SAC changes can be linked to temporal compositional changes of range-restricted vs. widespread species (Socolar et al. 2016; Chase et al. 2019; Leroy et al. 2023). However, some combinations are likely to be impossible because of the link between alpha, gamma and beta diversity (Ricotta *et al.*, 2019; Chao *et al.*, 2023), and mapping between compositional changes and changes in SAC parameters is not fully resolved and requires more research. It is thus possible to translate temporal changes in different forms of diversity arising from the combination of spatial scales and diversity metrics (McGill *et al*., 2015) in terms of changes in the parameters of macroecological patterns, along a spatial continuum. Altogether, such integration through continuous spatial scale can clarify diversity trends detection by avoiding the ambiguity inherent to interpreting and comparing trends when they are reporting diversity change at distinct but loosely defined scales.

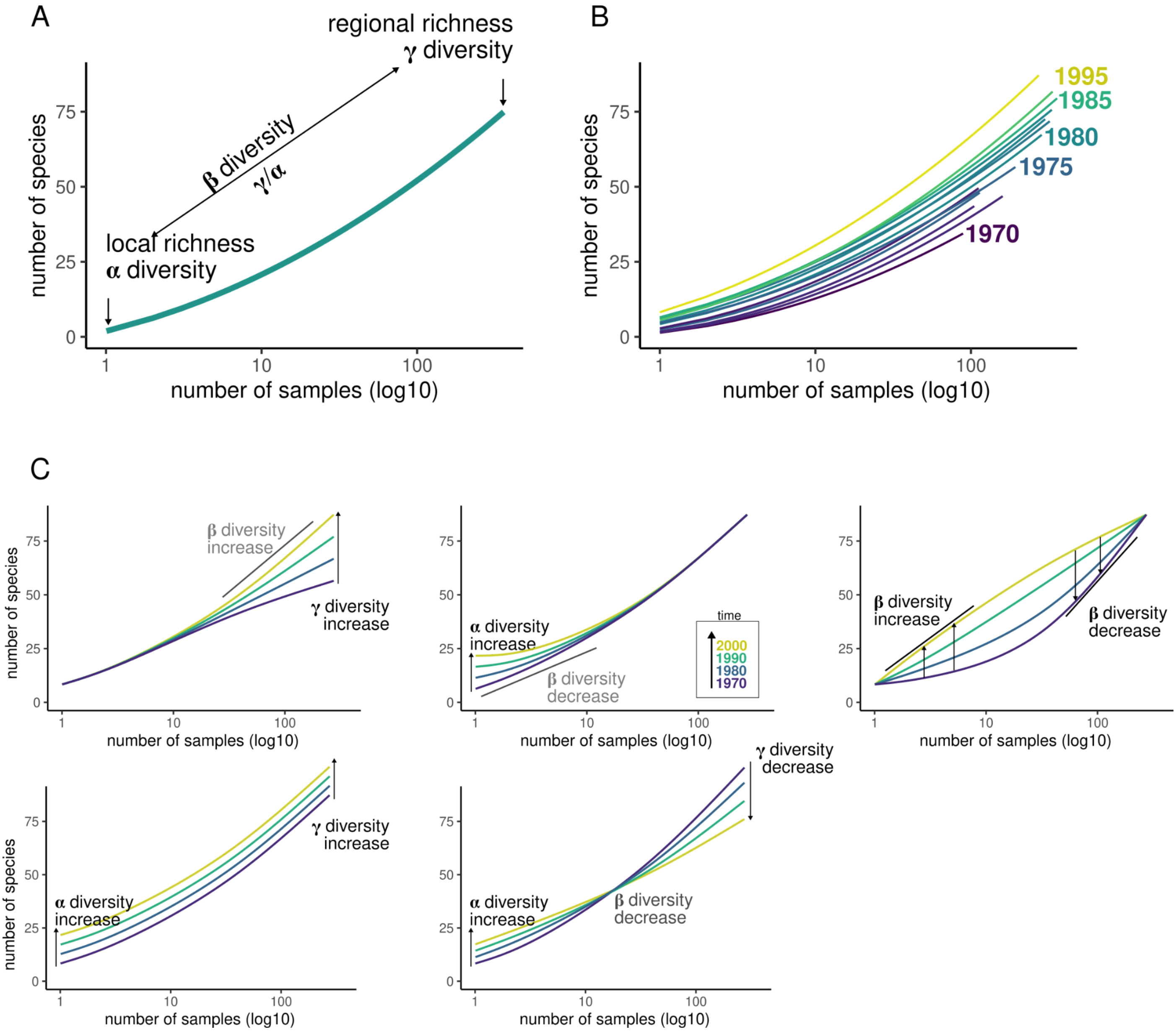

Figure 1. A. Species Accumulation Curves (SAC) describe how the number of species sampled increases with the number of samples **M**. This macroecological pattern can describe diversity from local scale (**α** diversity, **M** = one site sampled), to regional scale (**γ** diversity, **M** = maximum site samples). As *β* diversity can be defined as **γ/α**, the SAC can also describe species turnover for any **M**, called beta rarefaction. **B** When biodiversity is monitored in time, one can compute SAC for different times (from purple, 1970 to yellow = 2000), the change in the parameters of the SAC describes change in diversity from local to regional scale in a continuous way (for every **M** values). Here SAC are computed from fish monitoring (Biotime dataset #288). **C** Different possible forms of diversity changes can affect the shape of the SAC. The x-axis was log10 transformed in order to ease visualization at smallest scales.

Three low-level biodiversity components underpin dynamics of macroecological patterns

Macroecology theory acknowledges that scaling of diversity emerges due to the spatial structuring of species abundance distributions within species' geographic ranges (McGill & Collins, 2003; Storch *et al.*, 2008). Subsequent application of this theory (Azaele *et al.*, 2015; Chase *et al.*, 2018; Keil *et al.*, 2021; McGlinn *et al.*, 2021; Blowes *et al.*, 2022) has uncovered that diversity accumulation across scale is governed by three lower-level components (Figure 2): the total number of individuals in communities (abundance), the distribution of abundance among species (evenness), and the aggregation of individuals in space. As such, these building blocks of biodiversity patterns are defined as "proximate" components governing parameters of macroecological patterns, because they differ from ultimate drivers such as climate, or direct human species extirpations / introductions (McGlinn *et al.*, 2019).

While the examination of proximate components to uncover spatial biodiversity patterns is already operational (McGlinn *et al.*, 2019), it has mostly been used to compare the effect of specific drivers between spatial contexts or to separate treatment effects (Azaele *et al.*, 2015). While promising, only a few studies using it actually integrate the temporal dimension to better understand species diversity trends (Blowes *et al.*, 2022). We thus call for a more general application of this approach on dynamic data. Detecting and quantifying the role played by proximate components on the temporal dynamics of macroecological patterns would provide a supplementary layer of understanding of diversity changes across scales and metrics. We claim that it also has direct implications in terms of conservation actions, as it represents a relevant opportunity to gain insights into how anthropogenic drivers impact diversity dynamics across scale (Blowes *et al.*, 2020). Instead of focusing on the direct effect of humans on diversity, conservationists should rather focus on the direct effect of humans on species abundance, evenness and aggregation, and how in turns these affect biodiversity change. Indeed, it is likely that human activities directly influence proximate components, rather than diversity per se (van Klink *et al.*, 2024). Currently though, some limitations still prevent a more general elucidation of the effects of proximate components on.

First, the intricate interdependence between proximate components is not elucidated (Storch *et al.*, 2018; Avolio *et al.*, 2019; Blowes *et al.*, 2022). Whether and how much abundance, evenness, and spatial aggregation influence each other, and how they might themselves be influenced by diversity patterns still needs to be clarified. Such likely existence of dynamic feedback is still to be explored with the proper methods and data, for example using empirical dynamic modeling (Ye *et al.*, 2015; Chang *et al.*, 2017) applied to dynamic data. Second, the appropriate metrics and the scale at which these proximate components should be quantified remain open questions, in particular for Species Abundance Distribution (Avolio *et al.*, 2019) and spatial aggregation (Keil *et al.*, 2021). In any case, this change of perspective calls for a more systematic monitoring of species abundance (or density) and traits (see next section), and more standardized monitoring protocols allowing the estimation of simultaneous changes in abundance and spatial aggregation.

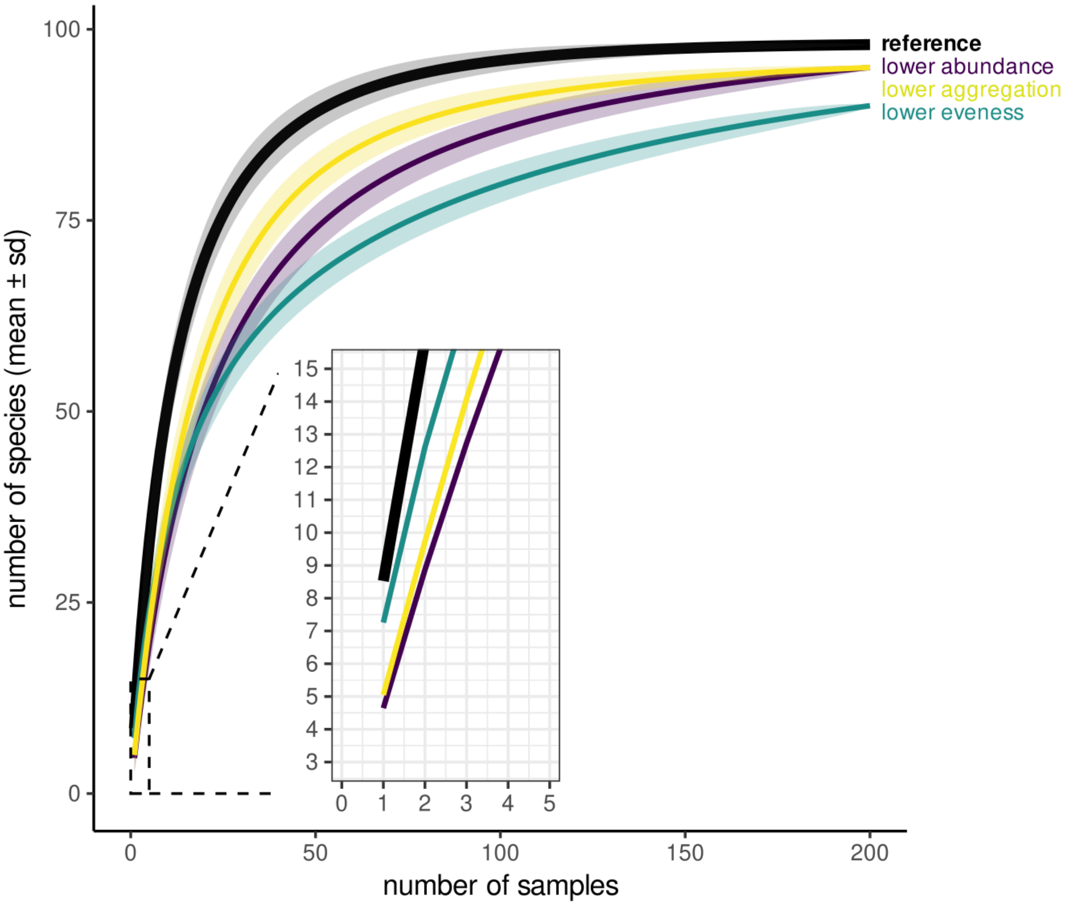

Figure 2. Variation in macroecological patterns are underpinned by change in proximate components of diversity across scales. Macroecology theory indicates that the abundance (total number of individuals), evenness (species - abundance distribution) and spatial aggregation jointly determine the shape of Species Accumulation Curve. In this simulation run using the *mobsim* R package, a reference SAC (e.g at t0) is compared to SAC (e.g at t1) after a decrease in the total abundances (purple), a decrease in spatial aggregation of individuals (yellow), or a decrease in evenness (green). Ecah independent change in proximate component has a different influence on the SAC, either on the intercept (see inner zoom) or on the slope coefficient.
Simulations were performed using the sim_thomas_community() function from mobsim R package. In black, the reference simulation was run with s_pool = 100 n_sim = 1000, sad_type = "lnorm", sad_coef = 1, and sigma = 0.1. In purple the “lower abundance” simulation with n_sim/3, in green the “less evenness” simulation with a steeper Species Abundance Distribution sad_coef *5, and in yellow the “more aggregated” simulation with a higher spatial clustering of individuals with sigma / 2. The species accumulation curve for each simulation using function specaccum() from vegan R package.

Integrating trait-based perspectives into temporal dynamics of macroecological patterns helps moving toward attribution of human drivers

Following a clear detection of trends in diversity across scales, a subsequent step, called “attribution”, lies in evaluating the contributions of potential drivers (Gonzalez *et al.*, 2023). Taxonomic approaches have inherent limitations for (human) drivers attribution because species identity itself is not related to its susceptibility to a given driver. In some cases, local species richness may not change but hide strong species turnover driven by human-induced environmental changes, which can involve stark alteration in trait composition. We argue that advancing species-based approaches (such as the one described above) thanks to trait-based approaches will allow for a more sensitive attribution of human drivers, and a more nuanced understanding of community responses to threats and disturbances.

The first reason is that species traits, encompassing characteristics of life history, morphology, habitat or climatic preferences, can be robust indicators of species' susceptibility to anthropogenic impacts (Cardillo *et al.*, 2005; Chichorro *et al.*, 2019; Carmona *et al.*, 2021). Because traits are linked to species responses to global changes, community recomposition can also be measured by change in trait composition, making it possible to dissect and understand the nuanced recomposition of communities under various threats (Devictor *et al.*, 2012; Kampichler *et al.*, 2012; Cheung *et al.*, 2013; Mouillot *et al.*, 2013; Gaüzère *et al.*, 2020b) that may remain unnoticed by taxa-based metrics alone (Villéger *et al.*, 2010). Considering species traits in conjunction with dynamic macroecological patterns thus has a high potential to enlighten the mechanisms behind ecological responses across diverse taxa (Smith *et al.*, 2013; Mazel *et al.*, 2014; Ricotta *et al.*, 2019). This approach has been successfully used, for example, to determine whether human activities increase abundance of species with certain characteristics at the expense of others: common / widespread / generalist / small-bodied vs. rare / restricted / specialist / large-bodied species (Purvis *et al.*, 2000; Cardillo *et al.*, 2005; Cooke *et al.*, 2019), or affect the spatial aggregation of individuals and species : physical barriers due to human settlements, landscape configuration (Tucker *et al.*, 2018, 2021).

The second reason is that patterns of trait diversity can reveal key insights into community assembly processes (Weiher *et al.*, 2011): low functional diversity (relative to random expectation) can result from environmental filtering or biotic hierarchical competition, while high functional diversity can indicate interspecific competition (Smith *et al.*, 2013; Münkemüller *et al.*, 2020). Interestingly, the influence of community assembly processes are thought to vary as a function of spatial scale, and should thus be expected to leave variable imprint on functional diversity depending on scale. Over the last decade, several studies have recast macroecological laws from a functional trait perspective (e.g., (Lamanna *et al.*, 2014; Hulshof & Umaña, 2023; Matthews *et al.*, 2023). Trait diversity accumulation over space has been explored with Functional Diversity Area Relationships (FDAR), the trait-based equivalent to SAR (Mazel *et al.*, 2014), Functional rarefaction, the trait-based equivalent of SAC (Ricotta *et al.*, 2012), or Distance Decay of Functional Similarity (FDDS), (Graco-Roza *et al.*, 2022). FDAR, for example, identifies the scale-dependence of environmental vs. biotic filtering (Smith *et al.*, 2013), while FDDS deciphers the relative effect of pure dispersal from environmental and biotic filtering depending on the spatial scale (Graco-Roza *et al.*, 2022). As such, trait-based macroecological patterns offer promising means to better identify the influence of global change drivers on diversity dynamics (Chapin *et al.*, 2000; Violle *et al.*, 2014). However, the theoretical foundations of these laws are still developing. One obvious reason is that the shape of trait-based macroecological patterns depends on the traits under consideration, even though recent studies indicate a low-dimensional evaluation of functional spaces may capture the primary dimensions of organismal functioning across taxonomic groups (Mouillot *et al.*, 2021).

A first, straightforward and easy way to integrate the trait-based perspective into the dynamic macroecological patterns is to compare dynamics between groups of species with contrasting traits or requirements across groups. For example, one might anticipate distinct responses between endotherms and ectotherms, small vs.large organisms, cold vs. hot dwellers, sessile vs.mobile species, those with varying mating systems, genome sizes and longevity (Staab *et al.*, 2023). A second approach is to use quantitative trait values to build trait-based macroecological patterns. This could entail switching from traditional macroecological measures (SAR, DDS, SAD) to before mentioned trait-based equivalents that are emerging (FRAR, FDDS, TAD) (Figure 4). Both approaches only require knowledge about species' mean trait values, which is more and more accessible from databases for many taxonomic groups, thus facilitating the construction of "trait-based" dynamic macroecological patterns (Smith *et al.*, 2013; Mazel *et al.*, 2014; Ricotta *et al.*, 2019; Matthews *et al.*, 2023) and offering a more comprehensive understanding of biodiversity dynamics in the face of global change (Graco-Roza *et al.*, 2022; Koffel *et al.*, 2022).

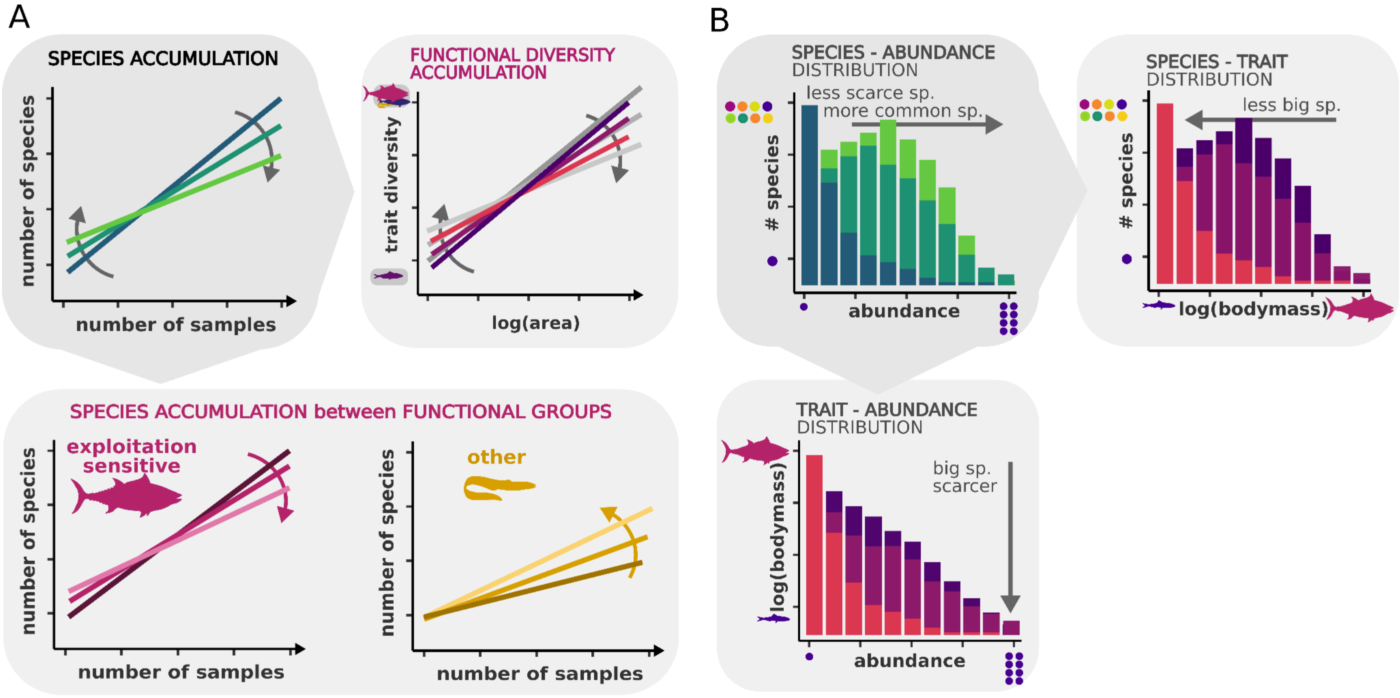

Figure 3. Integrating trait-based perspectives to dynamic macroecological patterns can be achieved by comparing temporal changes in SAC (A, top-left) between different functional groups (A, bottom), or by measuring temporal changes in functional diversity accumulation (A, top-right). Integrating trait-based perspective with proximate diversity components can be achieved by moving from species abundance distribution (B, top-left) to species trait distribution describing the variations in the number of species holding a particular trait value (B, top-right), or via trait-abundance distribution describing the abundance of species holding particular trait values (B, bottom-left). Here exemplified using species biomass. Dots are individuals from different species (one color per species).

Attributing detected diversity changes to anthropogenic drivers using (trait-based) dynamic macroecological patterns

While changes in diversity can be detected and quantified with large spatio-temporal inference, causally attributing them to ultimate (human) drivers is rarely accomplished. Yet, many temporal diversity changes are believed to be driven by anthropogenic impacts on the environment. Land and sea use change, climate change, pollution, invasive species and direct exploitation are all thought to have predominantly negative effects on diversity (Díaz et al., 2020), while land protection and biodiversity restoration actions are thought to have a positive effect (Kail et al., 2015; Meli et al., 2017). Three main factors make the attribution of diversity changes to human drivers challenging. First, human drivers impact diversity patterns differently depending on the spatial scale. Here, we have seen that a dynamic macroecological pattern approach, which considers continuous scale dependence can clarify which human drivers influence diversity along an explicit scale continuum (Powell et al., 2013). Second, diversity measures focused on species identity alone are inherently limited in linking specific drivers to diversity. As outlined in the previous section, trait-based dynamic macroecological patterns can provide a complementary, functional perspective. Third, human drivers' effects on diversity are complex, intercorrelated (Bowler et al., 2020), and interact with each other (Gaüzère et al., 2020a). Such intrications can lead to confounding effects and biases when trying to measure their influence on biodiversity patterns, particularly if the influencing variables are not available or incorrectly related. A way to address this third issue is to rely on structural causal modeling (Arif & MacNeil, 2023). A graph model represents qualitative causal relationships as a directed graph where variables of interest are nodes related by edges that represent potential directional influence. Such graphs can be used to clearly set and visualize assumptions about the cause-and-effect relationships between anthropogenic drivers and diversity changes and to identify the role of variables (i.e. confounder, mediator) when targeting a causal effect. Graphs can be built from expert knowledge alone, or with the help of causal discovery algorithms that look for causal signatures in the data (Glymour et al., 2019). This allows assessing the need for statistical adjustments (i.e. in case of confounders) which is especially relevant when causal relationships are determined from observational data (for more explanations, see (Arif & MacNeil, 2023). Such a priori identification of the role of potential driver variables offers a more comprehensive and relevant expectation of human impacts on biodiversity (Laubach et al., 2021; Gonzalez et al., 2023; Runge, 2023; Runge et al., 2023).

We propose to leverage the “dynamic (trait-based) macroecological pattern” framework described above by integrating it with the structural causal modeling framework for causal attribution. Studying the proximate components of biodiversity change (abundance, evenness, spatial aggregation, Figure 2) in the context of structural causal modeling allows identification of direct causal pathways from (ultimate) human drivers via change in proximate components to change in macroecological patterns, thus enabling to better understand the underlying drivers (and potentially mechanisms) through which human drivers impact species diversity over time and across spatial scales. We can extend causal graphs by explicitly including proximate components to hypothesize specific paths of action for different contexts (Figure 4). For example, in the case of wild capture fisheries, a causal graph might indicate how this human activity drives changes in aquatic animal diversity mainly indirectly through selective effects on the total number of individuals and species abundance distributions. In practice, switching from qualitative causal graphs to (quantitative) causal models fitted to empirical time series can be achieved using a Structural Equation Modeling (SEM) approach. These models can estimate the effects of the proximate components as well as the direct and indirect effects of potential (human) drivers on SAR and DDS parameters (DeMalach *et al.*, 2019), while handling the dynamic nature of time-series data using, for example, Latent Growth Curve (LGC) models or ARMA-based SEMs, (Fan *et al.*, 2016). Compared to already existing frameworks (e.g mobr, see Box 2) causal graphs and SEM enable the integration of several drivers and thus to consider their interaction, which is essential for (many) real-world scenarios. This enhanced understanding of causal pathways from human activities to diversity changes across scales could then be used to propose concrete control policies aimed at impacting particular components (Blonder *et al.*, 2023) in order to achieve effective prevention and mitigation of diversity loss.

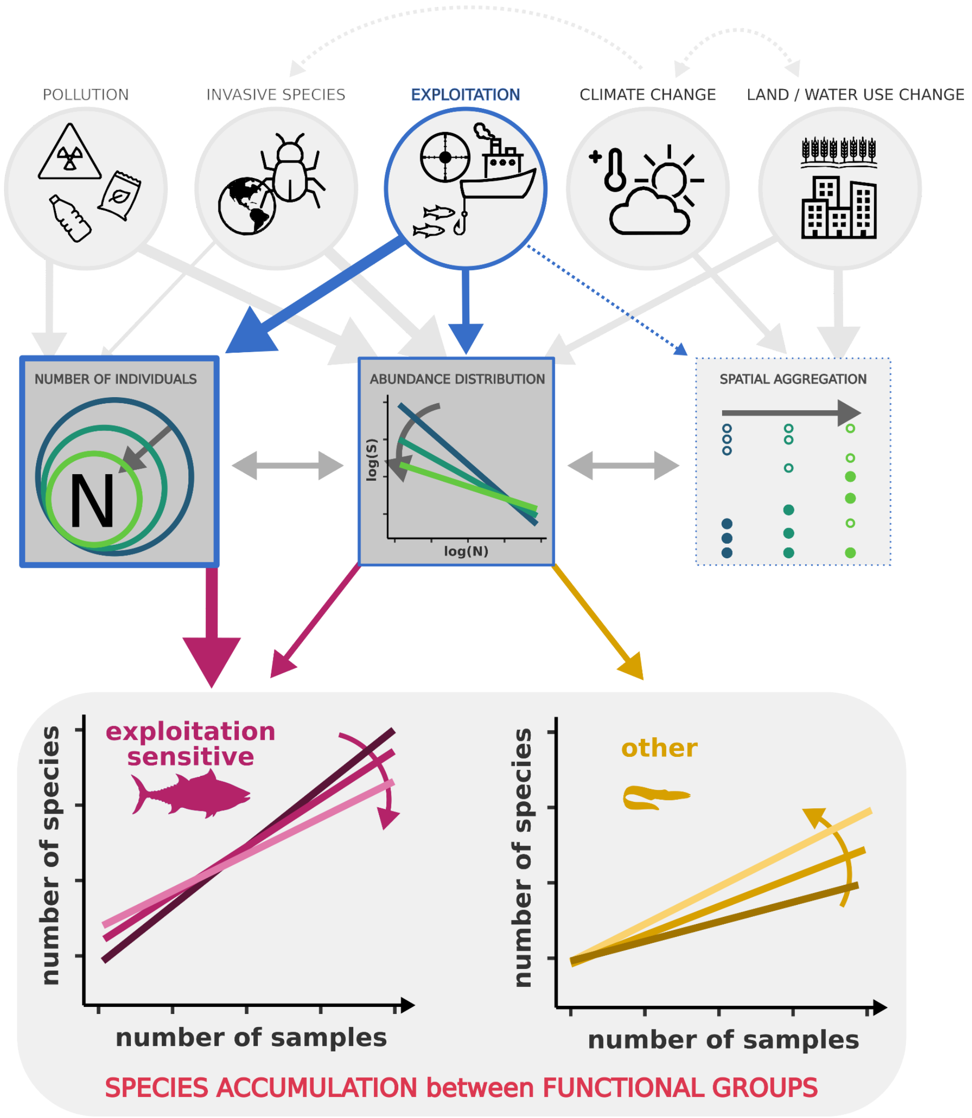

Figure 4. Graphical causal models integrating Dynamic macroecological patterns potential causal pathways from human drivers (top) to proximate components (middle) to trait-based dynamic macroecological patterns (bottom). All potential links across taxa and contexts are in gray. In the case of diversity changes in exploited marine ecosystems, expert knowledge might contribute to specify a causal pathway where change in species richness across scales in response to exploitation (wild capture fisheries) could be mediated by the effect of fisheries on the total number of individuals, particularly on exploitation-sensitive fishes (Blowes *et al*., 2020), and to change in species abundance distribution (for all species). We emphasize this pathway to exemplify a potential case, which is not supposed to reflect reality. Moreover, it does not incorporate possible compensation effects leading to the increase in abundance and size of small species in response to decrease of large predator species.

Concluding remarks

To date, research on diversity change detection has mainly focused on separate discrete spatial scales without embracing its scale dependence and without accounting for the linkage between different metrics, which often produces conflicting “diversity trends” that cannot easily be reconciled. In response to the need for a coherent framework that embraces complexities in biodiversity trends observed at different scales (Cardinale et al. 2018; Primack et al. 2018; Boënnec et al. 2024), we support the study of dynamic macroecological patterns as a way to integrate diversity changes in a continuous and scalable manner (Connor and McCoy 1979; Nekola and White 1999).It is important to note that although we here focused on SAC because it is one of the most studied patterns due among others to its suitability to handle data from most existing standardized biodiversity monitoring, the potential of using dynamic macroecological patterns to understand diversity changes across scales is not limited to this specific example. Macroecological patterns provide bridges from observed diversity to ecological processes (Grilli, 2020), while effectively synthesizing varying forms of diversity change, and providing a clear (albeit more complex) picture of biodiversity dynamics. Beyond improving the detection of diversity trends, we outlined the importance of studying proximate components of biodiversity changes which are pivotal for understanding diversity dynamics (McGill and Collins 2003; Storch et al. 2008).

We argue that such understanding is essential for accurately interpreting biodiversity trends and their underlying causes. One of the strengths of this approach is that most of the required tools are already available (Box - metrics and methods for Dynamic Macroecological Patterns) and only need to be "tweaked" to accommodate temporal data. Furthermore, we discuss how integrating trait based perspective and causal graphical models approach into this framework represents two important steps towards attributing biodiversity changes to specific anthropogenic drivers. This integration will enable a more nuanced understanding of how human activities impact biodiversity at various scales (Bowler *et al.*, 2020; Gonzalez *et al.*, 2023). In summary, dynamic and trait-based macroecological patterns not only enhance our ability to quantify diversity changes across scales, but also provide a powerful tool for identifying, preventing and mitigating the impacts of human activities on ecological systems. It advocates for policies that are informed by a deeper understanding of the intricate mechanisms driving biodiversity changes.

Box 2. Methods for Dynamic Macroecological Patterns

Simulations of macroecological patterns

- **mobsimr** (May *et al.*, 2018) is an R package designed for simulating the abundances and spatial distribution of different species. This package is particularly useful for deriving biodiversity patterns and simulating sampling of biodiversity. It enables researchers to study how abundance, evenness, and aggregation drives the shape of SAC, making it a valuable tool to understand the intrinsic links between proximate components and macroecological patterns. Although not primarily design to study temporal dynamics of macroecological pattern, current development are going toward extension of the capabilities of mobsimr (https://github.com/sRealmWG)

Empirical analyses of macroecological patterns

- **Rarefy** R package (Thouverai *et al.*, 2020) summarize directional and non-directional species accumulation (Chiarucci *et al.*, 2009) and multi-site beta diversity (Ricotta *et al.*, 2019) as a function of sampling effort (i.e. via species accumulation curves), hence measuring spatial autocorrelation in species composition among plots along an a-priori defined spatial, temporal or environmental gradient.
- **mobr** R package (Mcglinn *et al.*, 2021) performs analyses of biodiversity data at various spatial scales, and quantify the roles of proximate components (evenness, density, and aggregation) in shaping macroecological patterns, based on the Measurement of Biodiversity framework (Chase *et al.*, 2018; McGlinn *et al.*, 2019, 2021).

- (Keil *et al.*, 2021) test and compare approaches to quantify interspecific spatial associations on empirical and simulated data, and provide recommendations for how to use and interpret them in biodiversity science. The R package **spasm** allows to compute and compare different measures of spatial aggregation (https://github.com/petrkeil/spasm/tree/1.4)
- (Keil & Chase, 2022)proposes a machine learning approach to estimate biodiversity changes over time by allowing for the interpolation of biodiversity data across spatial scales while accounting for variations in data availability and completeness.

Causal graph building and modeling

- **DAGitty** is a browser-based environment for creating, editing, and analyzing causal diagrams (also known as directed acyclic graphs or causal Bayesian networks). The focus is on the use of causal diagrams for minimizing bias in empirical studies in epidemiology and other disciplines : https://dagitty.net/
- **piecewiseSEM** R package (Lefcheck, 2016) is an implementation of confirmatory path analysis for the R. The package allows to perform Structural Equation Models (SEM) to many types of statistical models such as generalized linear, phylogenetic least-square, and mixed effects models, and as such can handle random effects and temporal autocorrelation: https://jslefche.github.io/sem_book/

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Data Accessibility Statement:

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