

PERSPECTIVE

Bridging Macroecology and Temporal Dynamics to Better Attribute Global Change Impacts on Biodiversity

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ABSTRACT

Context: 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.

Ideas: 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, analysing temporal changes in diversity scaling relationships, such as species accumulation curves or distance decay, can reconcile and synthesise conflicting observations of biodiversity change, enabling quantification of diversity shifts from local to regional spatial scales. Second, diversity patterns across scales are linked to three proximate components: abundance, evenness and spatial aggregation of species. 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.

Case Study: We illustrate this integration in a case study of forest and farmland birds in France, highlighting how studying diversity changes across scales, and decomposing temporal change in different components can help to elucidate the mechanisms driving diversity change.

Conclusions: 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.

1 | 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; Keck et al. 2025). 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 recognised 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; Keck et al. 2025). 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 comparing artificially defined ‘local’ or ‘regional’ scales without providing a clear mechanistic connection between metrics and scales of diversity change. To address the challenge associated with scaling of biodiversity patterns, existing frameworks and their extension have provided valuable tools for assessing diversity changes across scales. In particular, recent developments have leveraged the study of diversity-scaling relationships for species (Azaele et al. 2015; Chase et al. 2019; McGlinn, Engel, et al. 2021; McGlinn, Xiao, et al. 2021) or traits (Mazel et al. 2014) with a focus on spatial differences or focused on temporal dynamics without considering multiple spatial scales (Dornelas et al. 2013). However, they often fail to integrate both temporal and trait-based perspectives, limiting their ability to uncover causal mechanisms of biodiversity change. Integrating the spatial and temporal components, but also integrating species traits into the analysis of temporal biodiversity trends, hence represent crucial steps forward. This integration serves a dual purpose: (1) changes in trait composition and diversity can inform about shifts in ecosystem functioning and community composition, and (2) trait-based approaches offer a mechanistic understanding of taxonomic diversity changes, allowing us to infer whether observed trends arise from processes such as environmental filtering, competition, or anthropogenic pressures. We here argue that explicitly bridging macroecological scaling laws with temporal dynamics and species traits approaches (via categorisation into functional groups or by using continuous traits) is a promising avenue to address these gaps and that it can be achieved by linking already existing frameworks.

Macroecology has long stated that macroecological patterns result from invariant laws that depict changes in diversity across scales (Brown 1995; Gaston and Blackburn 2000; McGill and 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 that 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 conspecific spatial aggregation (McGill and 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 based on such approaches is still marginal. Only a 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 (Adler et al. 2005; Blowes et al. 2022; Terry and 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 recognised that species trait characteristics bring a complementary and essential perspective to biodiversity thanks to their link to ecosystem functions and services (Lavorel and 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 jeopardise ecosystem functionality. In contrast, the loss of a single species may have little or no functional effect 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.

Our goal here is not to propose yet another biodiversity framework. Rather, we aim to synthesise and connect existing macroecological and trait-based concepts to stimulate new interpretations and applications in biodiversity change research. We first outline how temporal variation in macroecological patterns integrates 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 generalisation of such an approach

and how to better leverage dynamic macroecological patterns to attribute and quantify the potential effects of anthropogenic drivers on diversity changes across scales in the future (McGlenn 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.

2 | 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 “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 herbaceous and a woody species. Similarly, regional gamma-diversity is generally tightened to the study’s spatial extent, often without proper consideration of the actual area or the fraction of the regional species pool covered by observations. Consequently, the lack of clarity regarding the examined scales and their ecological relevance can affect the interpretation and comparability of biodiversity change across spatial scales. Importantly, it can also affect measures of beta diversity, often defined as the ratio or difference between regional (gamma) and local (alpha) diversity (see Figure 1), again due to inconsistent definitions of local and regional.

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 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 and 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 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 a single site (α species richness, i.e., often akin to local scales) to multiple sites (γ species richness at the maximum number of sampling sites), which can represent ‘regional’ or even global scales (in the case where the entire Earth is sampled); the pattern can be summarised 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 and illustrate our ideas using SACs, primarily due to their compatibility with

the spatially scattered sampling of most biodiversity monitoring schemes. But note that our central arguments regarding temporal dynamics apply equally to other diversity-scaling relationships (e.g., species–area relationships [SARs], rarefaction curves, or distance decay).

Looking at temporal changes in SAC (e.g., with richness of fish species from 1970 to 1995, see Figure 1B) integrates changes continuously from local to global scales and effectively summarises 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 in the SAC slope over time but no change in the intercept. In a second example, an increase in site-average α richness bends the SAC upwards at local scales and will be measured as a decrease in the SAC slope over time and an increase in the intercept (top middle in Figure 1C). In both examples, the resulting β diversity also changes at larger or smaller scales, respectively, for the first and second examples. 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, a 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 an increase in α richness and a 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 versus 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 diversity-scaling relationships along a spatial continuum. Altogether, such integration through continuous spatial scale can clarify diversity trend detection by avoiding the ambiguity inherent in interpreting and comparing trends when they are reporting diversity change at distinct but loosely defined scales.

3 | 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 distribution (SAD) within species’ geographic ranges (McGill and Collins 2003; Storch et al. 2008). Subsequent application of this theory (Azade et al. 2015; Chase et al. 2018; Keil et al. 2021; McGlenn, Engel, et al. 2021; McGlenn, Xiao, et al. 2021; Blowes et al. 2022) has uncovered that diversity accumulation across scales is governed by three lower-level components (Figure 2): the total number of individuals in

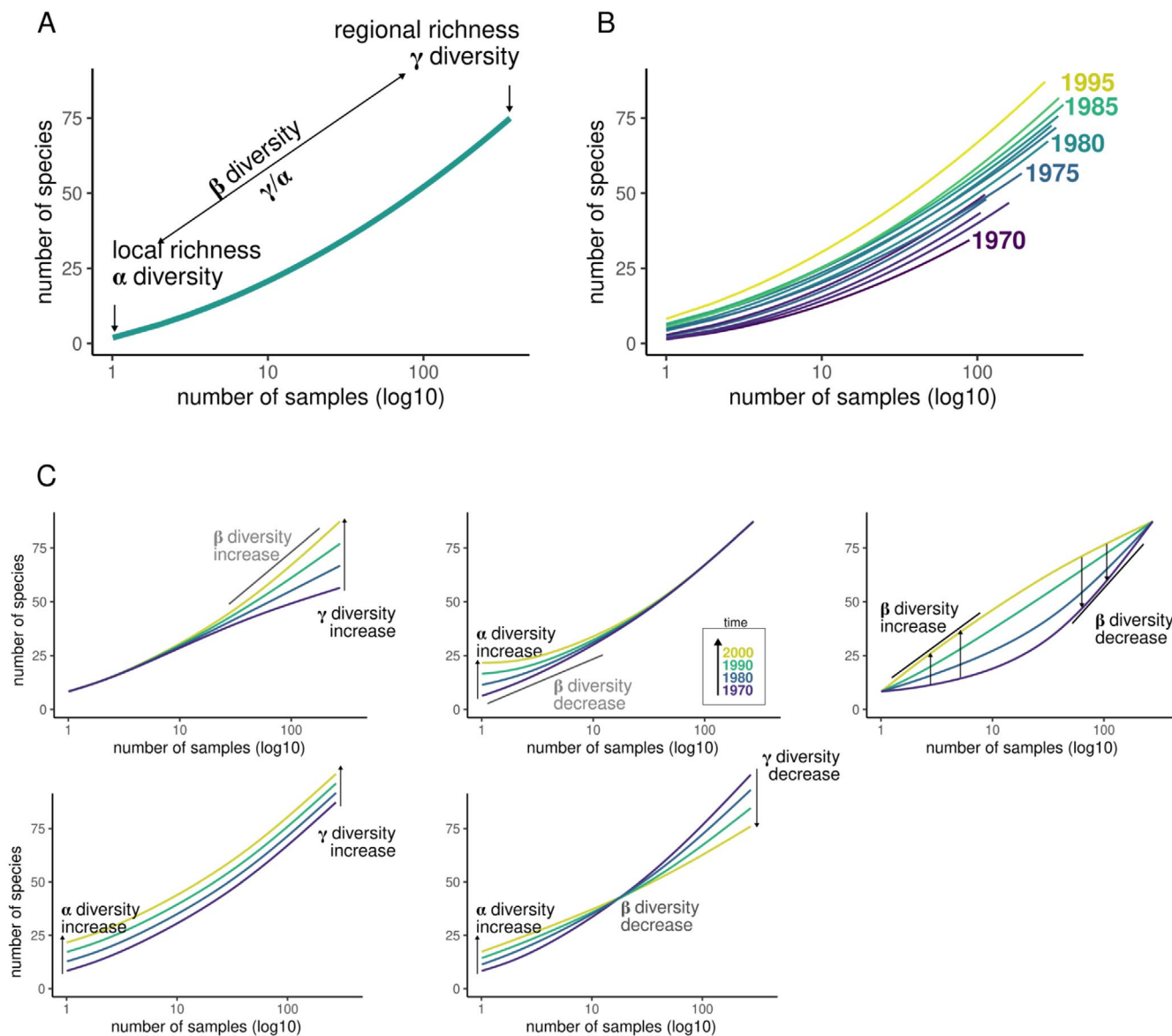


FIGURE 1 | (A) Species accumulation curves (SAC) describe how the number of species sampled increases with the number of samples M . This macroecological pattern can describe biodiversity from small to large spatial extents depending on the number of samples M , and include any definition of ‘local’ (alpha diversity) and ‘regional’ (gamma diversity) scales, as long as $M_{\text{local}} < M_{\text{regional}}$. For sake of readability, we depict the extreme case where local is a single sample and regional the maximum number of 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 visualisation at smallest scales.

communities (density), 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 (McGlenn et al. 2019). While the examination of proximate components to uncover spatial biodiversity patterns is already operational (McGlenn et al. 2019), it has mostly been used to compare the effect of specific drivers between spatial contexts or to separate treatment effects (Azaze 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 scales (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 turn these affect biodiversity

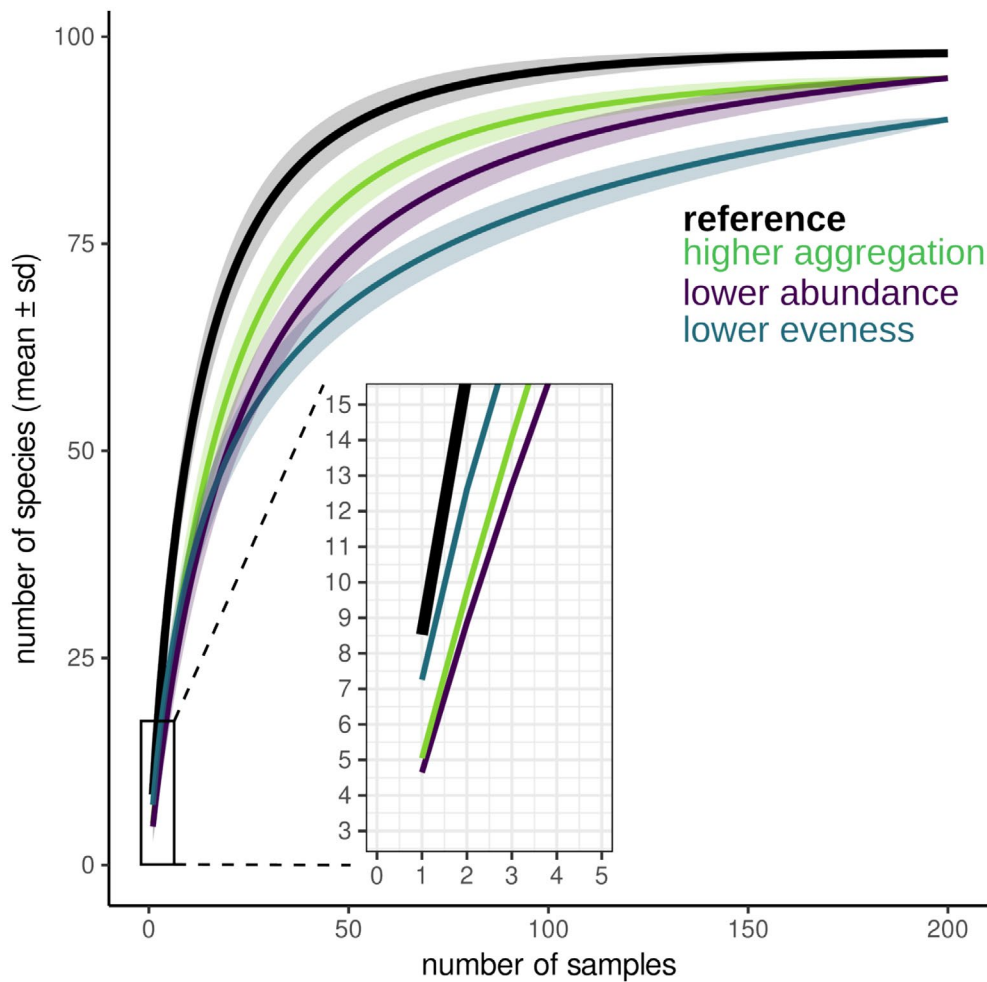


FIGURE 2 | Variation in macroecological patterns is underpinned by change in proximate components of diversity across scales. Macroecology theory indicates that the abundance (total number of individuals), evenness (species-abundance distribution, SAD) and spatial aggregation jointly determine the shape of the species accumulation curve (SAC). 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), while keeping a constant species pool of 100 species and randomly sampling 200 virtual plots (area=0.005). Each independent change in a 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 the *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 “lower evenness” simulation with a steeper SAD `sad_coef*5`, and in green, the “higher aggregation” simulation with a higher spatial clustering of individuals with `sigma/2`. The species accumulation (also called the sample-based rarefaction curve) for each simulation was computed using the function `specaccum()` from the *vegan* R package. In the x-axis, the number of samples refers to the number of plots sampled.

change. Indeed, it is likely that human activities directly influence proximate components, rather than diversity per se (van Klink et al. 2024).

Direct human exploitation—such as hunting, fishing, or harvesting—represents a clear driver of temporal changes in total species abundance. For instance, intensive fishing practices have led to pronounced declines in fish abundance globally (Myers and Worm 2003). Temporal changes in species abundance also reflect changes in demographic processes, such as survival, reproduction and migration (Keil et al. 2025), which can be linked to altered resource availability and habitat quality. For instance, a decline in overall abundance within bird communities has frequently been associated with reduced habitat quality due to agricultural intensification (Donald et al. 2001, 2006). Conversely, an increase in abundance might reflect

habitat restoration or expansion, such as reforestation, which increases resource availability and breeding opportunities for forest-dwelling species (Thomas et al. 2012). Changes in conspecific spatial aggregation might often result from altered habitat structure, connectivity, or landscape fragmentation. Increasing aggregation typically occurs when suitable habitats become fragmented, forcing species into smaller, isolated patches (Fahrig 2003). Conversely, decreased aggregation might reflect improved habitat connectivity or the spread of invasive or generalist species (Simberloff et al. 2013). Changes in evenness (SAD) provide insights into shifts in community composition and dominance patterns. Reduced evenness, resulting from dominance by fewer species, might indicate habitat degradation or anthropogenic disturbances favouring common species at the expense of rare or specialist species, thus reducing the overall ecological complexity and resilience of communities

(Hillebrand et al. 2008). Increased evenness might occur when disturbance regimes or conservation management actions reduce competitive dominance, allowing coexistence of more species and potentially indicating more stable or recovering ecosystems (Blowes et al. 2020).

Currently though, some limitations still prevent a more general elucidation of the effects of proximate components on diversity changes. 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 need to be clarified. Such likely existence of dynamic feedbacks is still to be explored with the proper methods and data, for example, using empirical dynamic modelling (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 SAD (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 standardised monitoring protocols allowing the estimation of simultaneous changes in abundance and spatial aggregation.

4 | Integrating Trait-Based Perspectives Into Temporal Dynamics of Macroecological Patterns Helps Move Toward Attribution of Diversity Changes to 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 constant species richness may hide strong species turnover driven by human-induced environmental changes, which can involve stark alteration in trait composition (Barnagaud et al. 2017). In other cases, changes in species composition might not involve changes in trait composition (McLean et al. 2019). We argue that advancing species-based approaches (such as the one described above) thanks to trait-based approaches can allow for a more sensitive attribution of diversity changes to human drivers and a more nuanced understanding of community responses to threats and disturbances (Mouillot et al. 2013; Parmesan et al. 2013).

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, Iversen, et al. 2020) 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). Trait distributions and/or functional diversity provide a complementary perspective to taxonomic richness by highlighting shifts in community composition that may be masked in taxonomic assessments alone. For instance, changes in functional diversity can indicate shifts in species interactions or environmental filtering (Münkemüller et al. 2020), even when decoupled from taxonomic richness changes (McLean et al. 2019). Conversely, observed taxonomic diversity changes may be better explained by analysing how functional diversity is restructured over time in response to environmental pressures. This approach has been successfully used, for example, to determine whether human activities increase the abundance of species with specific characteristics at the expense of others: common/widespread/generalist/small-bodied versus 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 via physical barriers or 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 is thought to vary as a function of spatial scale and should thus be expected to leave a variable imprint on functional diversity depending on scale (Gaüzère et al. 2023). Over the last decade, several studies have recast macroecological laws from a functional trait perspective (e.g., Lamanna et al. 2014; Hulshof and Umaña 2023; Matthews et al. 2023). Functional diversity area relationships (FDAR) extend the concept of SAR by linking functional trait diversity to habitat size, helping disentangle the effects of biotic competition and environmental filtering (Mazel et al. 2014). Functional rarefaction extends the context of SAC to traits (Ricotta et al. 2012). Similarly, distance decay of functional similarity (FDDS) enables a spatial assessment of trait-based ecological similarity, providing a more nuanced understanding of biodiversity responses to environmental gradients (Graco-Roza et al. 2022). FDAR, for example, identifies the scale-dependence of environmental versus 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, linking trait-based approaches and dynamic macroecological patterns offers promising means to better identify the influence of global change drivers on diversity dynamics (Chapin et al. 2000; Violle et al. 2014). Note that we do not aim to introduce a new framework to assess trait-based diversity changes but propose two methods to integrate existing trait-based perspectives into the temporal dynamics of diversity-scaling relationships. By linking species traits—such as life history, morphology and habitat preferences—to macroecological dynamics, we highlight how trait-based macroecological patterns provide a more sensitive lens for detecting human impacts on biodiversity.

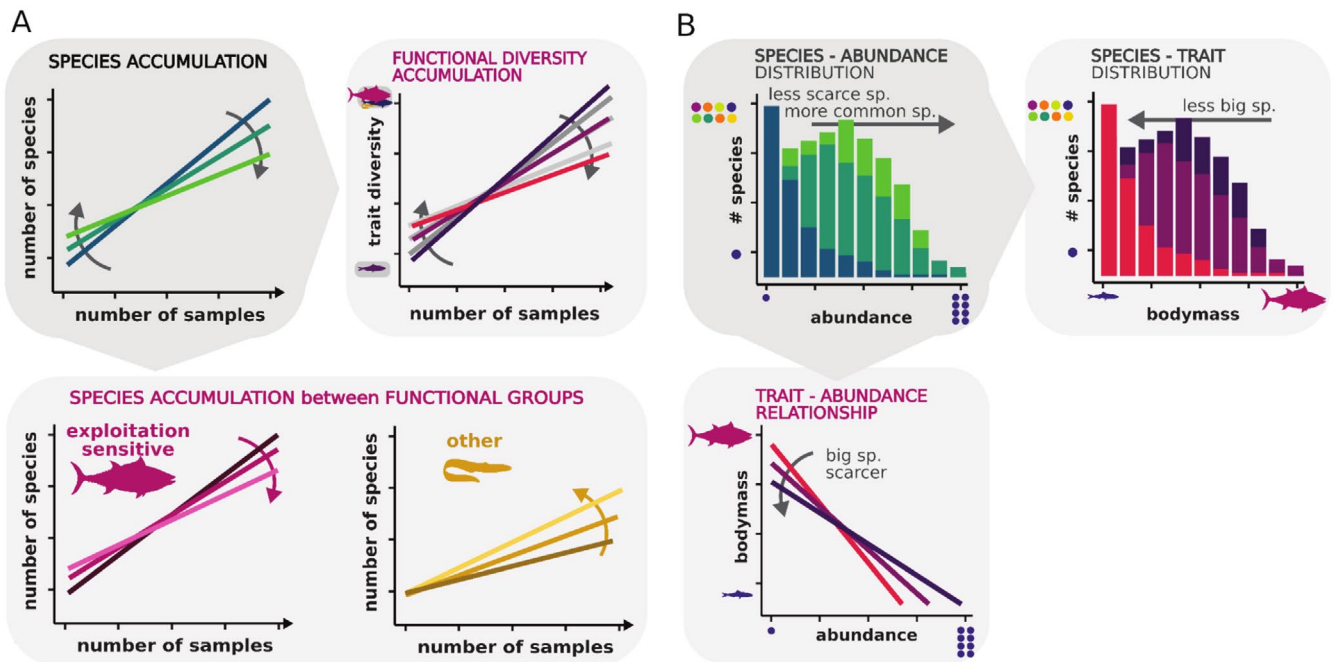


FIGURE 3 | Integrating trait-based perspectives into dynamic macroecological patterns can be achieved by comparing temporal changes in SAC (A, top-left) between different functional groups (A, bottom) or by measuring temporal changes in functional diversity accumulation (A, top-right). Integrating a 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 colour per species).

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 versus large organisms, cold versus hot dwellers, sessile versus motile species and those with varying mating systems, genome sizes and longevity (Staab et al. 2023). This approach has proven useful to attribute fisheries impact on diversity differences between protected and unprotected areas (Blowes et al. 2020). 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 the aforementioned emerging trait-based equivalents (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). Note

that recent studies have also shown the fundamental relationships linking traits-abundance distribution and richness-productivity relationships (Pigot et al. 2025), opening exciting perspectives for trait-based macroecology.

By building on established methods and extending them to trait-based macroecological patterns, we here delineate a roadmap to better quantify and interpret human-induced changes in biodiversity at multiple scales (Figure 3).

5 | 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 thought 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

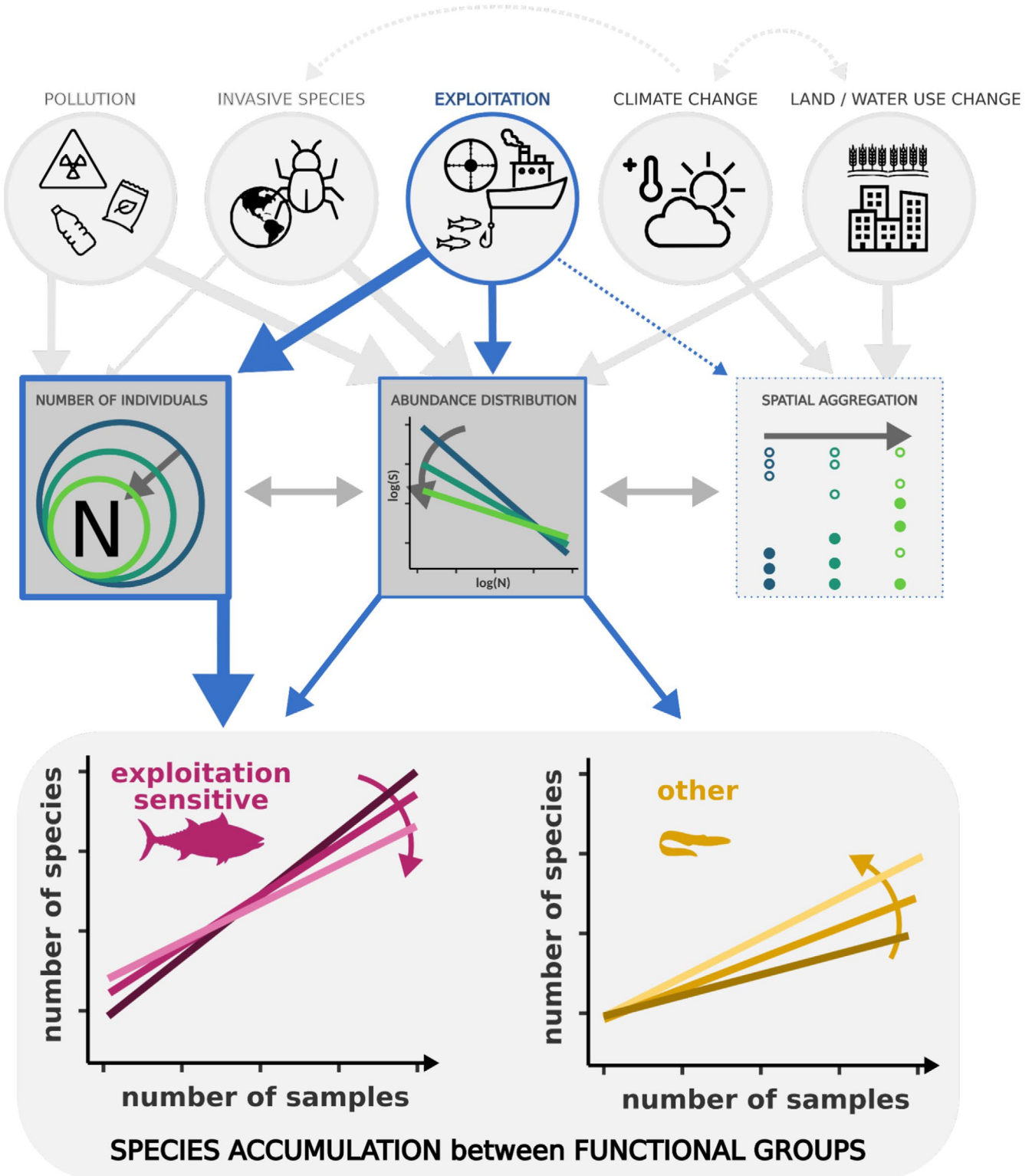


FIGURE 4 | Graphical causal models integrating dynamic macroecological patterns with potential causal pathways from human drivers (top) to proximate components (middle) to trait-based dynamic macroecological patterns (bottom). All potential links across taxa and contexts are in grey. For example, in the case of diversity changes in exploited marine ecosystems, expert knowledge might contribute to specifying a causal pathway where changes 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 changes in SAD (for all species). We emphasise this pathway to exemplify a potential, much simplified 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 the decrease of large predatory species.

(Powell et al. 2013). Second, diversity measures focused on species identity alone are inherently limited in linking specific drivers to spatio-temporal patterns in 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 and intercorrelated (Bowler et al. 2020) and interact with each other (Gaüzère, Barbaro, et al. 2020). 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 modelling (Arif and 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 visualise 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 and 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” perspective described above by integrating it with the structural causal modelling framework for causal attribution. Studying the proximate components of biodiversity change (abundance, evenness, spatial aggregation, Figure 2) in the context of structural causal modelling allows identification of direct causal pathways from (ultimate) human drivers via change in proximate components to change in macroecological patterns, thus enabling better understanding of 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 hypothesise 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 SADs. In practice, switching from qualitative causal graphs to (quantitative) causal models fitted to empirical time series can be achieved using a structural equation modelling (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 1), causal graphs and SEM enable

BOX 1 | 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 drive the shape of SAC, making it a valuable tool to understand the intrinsic links between proximate components and macroecological patterns. Although not primarily designed to study the temporal dynamics of macroecological pattern, current developments are going toward the extension of the capabilities of *mobsimr* (<https://github.com/sRealmWG>).

Empirical analyses of macroecological patterns

- *Rarefy* R package (Thouvenot et al. 2020) summarises 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 SACs), hence measuring spatial autocorrelation in species composition among plots along an a priori defined spatial, temporal or environmental gradient.
- *mobr* R package (McGlinn, Engel, et al. 2021; McGlinn, Xiao, et al. 2021) performs analyses of biodiversity data at various spatial scales and quantifies 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; McGlinn, Engel, et al. 2021; McGlinn, Xiao, et al. 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 computing and comparing different measures of spatial aggregation (<https://github.com/petrkeil/spasm/tree/1.4>).
- Keil and 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 modelling

- *DAGitty* is a browser-based environment for creating, editing and analysing causal diagrams (also known as directed acyclic graphs or causal Bayesian networks). The focus is on the use of causal diagrams for minimising 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 R. The package allows for performing structural equation models (SEM) on many types of statistical models, such as generalised linear, phylogenetic least-square, and mixed effects models, and as such can handle random effects and temporal autocorrelation: https://jslefeche.github.io/sem_book/.

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.

6 | Case Study

To illustrate the ideas of the previous sections, we analysed diversity changes across scales for farmland and forest birds in France between 2002 and 2013. The temporal trends of birds, particularly the decline of farmland birds in Europe, have been well studied (Rigal et al. 2023; Reif et al. 2024), but primarily through the lens of species abundance and at a local scale. Thus, our goal is to demonstrate how integrating a temporal perspective with diversity-scaling relationships between different functional groups can provide novel insights into a well-studied system. This case study is thus meant as a simplified toy example. Indeed, many aspects of the interpretations below would benefit from more comprehensive analyses informed by a mechanistic understanding of avian biodiversity change in France.

In this case study, we specifically address three main questions, following the four sections of the paper (Figure 5). To assess diversity changes over time and space, we analysed avian species richness accumulation across sampling efforts (1–400 sites) per year and estimated temporal richness changes at each scale. We then assessed how low-level biodiversity components (density,

evenness and aggregation) underpin the dynamics of macro-ecological patterns. To integrate trait-based perspectives, we conducted separate analyses for two functional groups based on habitat preference. Finally, we constructed a causal graph and used temporal anomalies to evaluate the effects of land cover and climate change on the components driving avian richness changes.

6.1 | Methods

We used data from the French Breeding Bird Survey (FBBS), a long-term monitoring programme designed to assess the population dynamics of common passerine birds in France. Skilled volunteers conduct standardised bird counts at the same 4 km² sites annually, which are randomly selected within a 10 km radius of their home locality. For this study, we focused on data from 2002 to 2013 to analyse decadal changes that are less prone to nonlinear trends while avoiding biases associated with the initial monitoring year (2001). Bird species were categorised as farmland or forest species using the PECBMS classification. We incorporated environmental data, including temperature during the bird breeding season (sourced from CHELSA; Karger et al. 2017) and habitat composition and diversity (using CORINE Land Cover; European Environment Agency 2010). We calculated SAC and proximate components of species trends using the *mobr* R package (McGlenn et al. 2019). We quantified the contributions of changes in the total number of individuals (N), the relative abundance distribution (SAD) and conspecific aggregation (agg) to species richness changes, respectively, by comparing

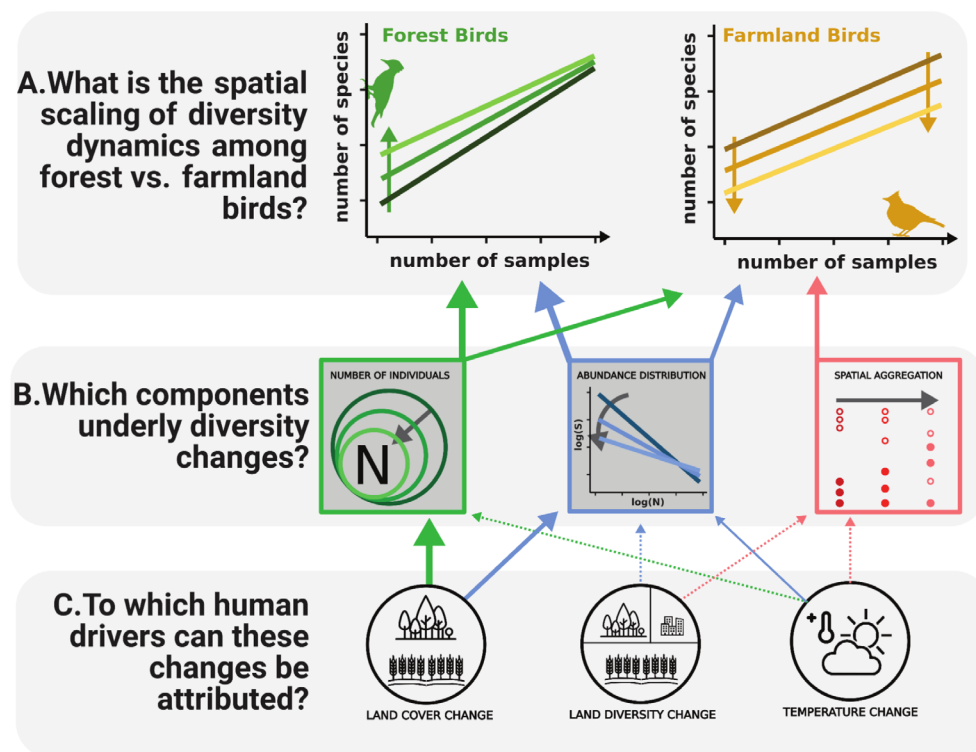


FIGURE 5 | Conceptual description of the potential causal pathways from human drivers (bottom) to proximate biodiversity components (middle) to temporal changes in diversity scaling (top) of farmland and forest birds. Empirical effects of each arrow are shown in Figure 7, with corresponding letters (A: Diversity changes, B: Diversity components, C: Driver effects).

three distinct types of SACs (for more details, see Appendix S1 or McGlinn, Engel, et al. 2021; McGlinn, Xiao, et al. 2021). We then estimated the effects of habitat cover, habitat diversity and temperature on the resulting N, SAD and agg effects for each sampling effort. We first drew a causal graph linking each predictor to each component based on our expertise and literature (Figure 5). We analysed this graph to detect potential confounders, mediators and collider variables and adjusted the model structure accordingly (see Appendix S1). For each year of monitoring, we computed the accumulated sum of each predictor variable along sampling effort, ensuring that the scale-dependent relationships between predictors and response variables could be captured effectively. To assess the effect of predictors on each component, we fitted three linear models (N , SAD, agg) at each sampling effort to estimate the relationship between each component effect value and temporal anomalies ($n = 12$ years) of driver values (i.e., scaled to zero mean and unit variance), as follows:

$$N \sim \text{cover_Forest} + \text{Temperature}$$

$$\text{SAD} \sim \text{cover_Forest} + \text{Habitat_diversity} + \text{Temperature}$$

$$\text{agg} \sim \text{Habitat_diversity} + \text{Temperature}$$

6.2 | Results

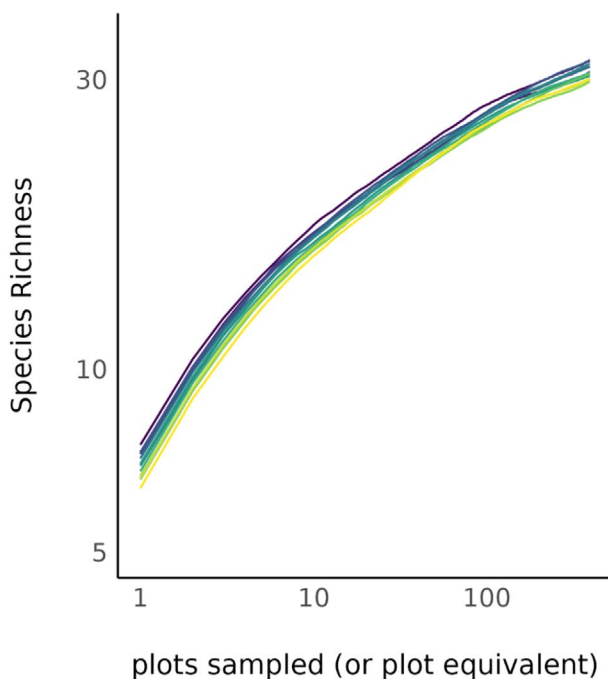
A first exploration of SACs across time (Figure 6) reveals small but divergent temporal changes in species accumulation. For farmland birds, SACs got consistently lower through time (yellow lines below purple lines regardless of spatial

scale), revealing a spatially stationary decrease in species richness through time. For forest birds, accumulation curves were higher through time at lower scales (i.e., between 1 and 20 plots sampled, yellow lines are above purple lines), but not at larger scales where curves cross each other, revealing an increase in richness at lower scales but no temporal trends at larger scales.

6.3 | Spatial Scaling of Diversity Dynamics

Computing the linear trend of species richness along a continuum of scales for farmland (Figure 7A left) or forests (Figure 7A right) showed marked differences in diversity change across sampling effort. For farmland birds, our analysis revealed spatially stationary decreases in species richness ranging from $-0.15 \text{ sp year}^{-1}$ (between 1 and 150 plots sampled) to $-0.2 \text{ sp year}^{-1}$ (at 400 plots sampled), i.e., indicating a relatively uniform loss of species across scales. In contrast, for forest birds our analysis revealed scale-dependence of diversity changes, with substantial and significant increases in species richness of $0.15 \text{ sp year}^{-1}$ for a smaller number of samples (< 50 plots sampled), no significant trends between 100 and 150 plots sampled, and a weak positive trend ($0.075 \text{ sp year}^{-1}$) for larger sampling effort (> 200 plots sampled). Hence, small-scale increases in forest bird assemblages do not translate into increases at larger scales and instead lead to spatial homogenisation (decrease in beta diversity at intermediate scales) (see Figure 1C). Note that when performed on all bird species from our dataset (i.e., without separating “functional groups” based on habitat), the same analyses showed an absence of any

Farmland Birds



Forest Birds

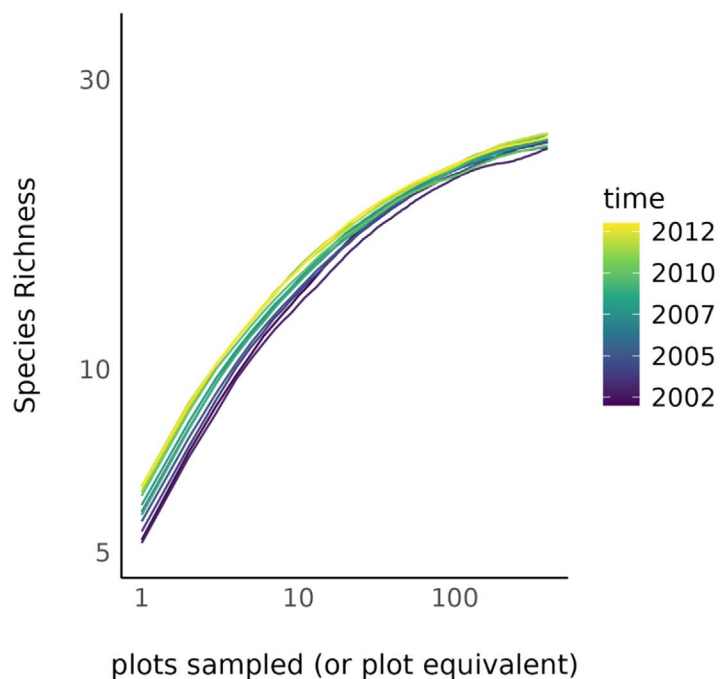


FIGURE 6 | Spatially based species-accumulation curves for farmland birds (left panel) and forest birds (right panel) across multiple sampling years (2002–2013). The x-axis indicates the cumulative number of plots (or plot equivalents) sampled on a logarithmic scale, while the y-axis shows the corresponding species richness. Each coloured line represents a different sampling year (ranging from 2002 in purple to 2012 in yellow).

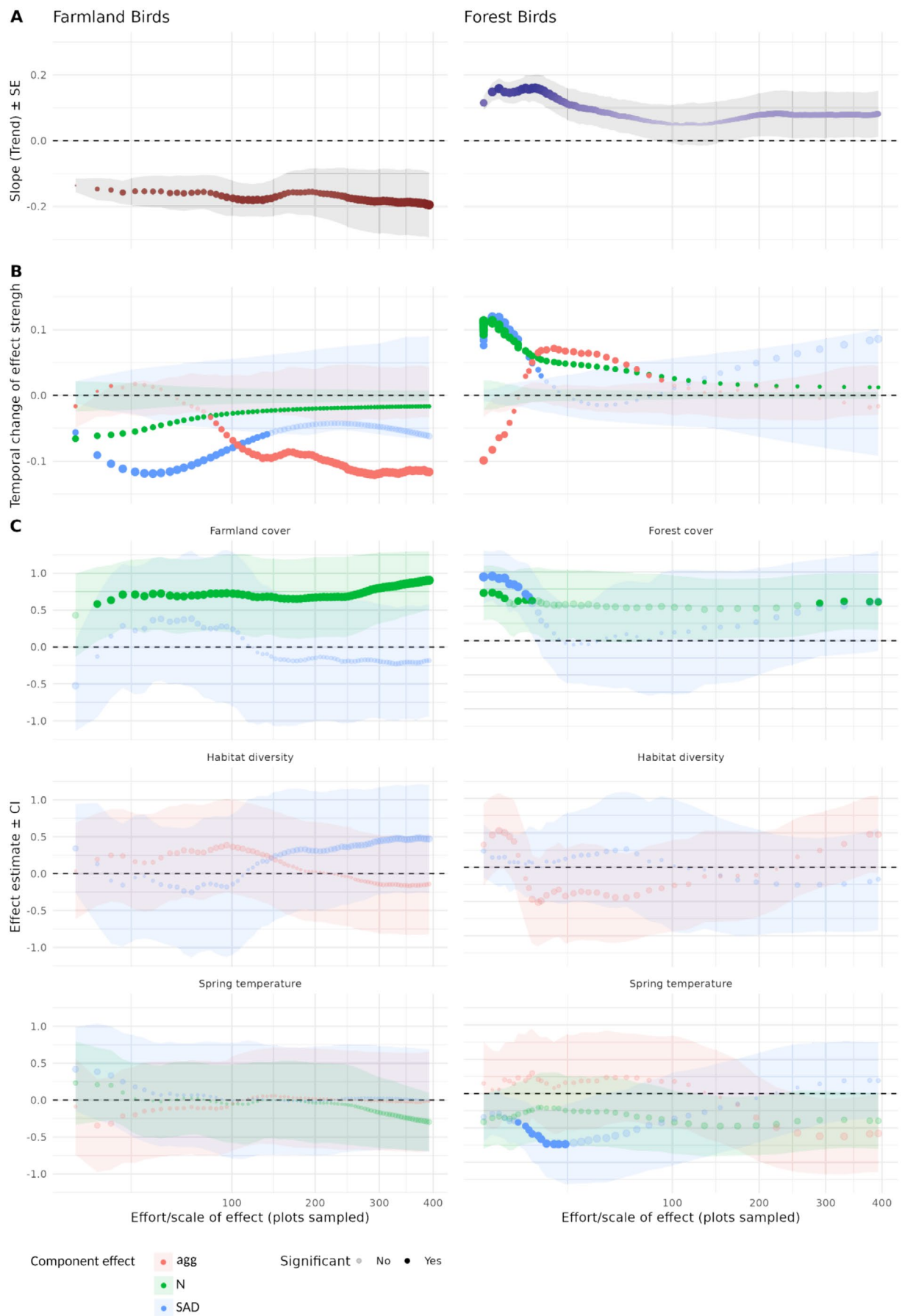


FIGURE 7 | Legend on next page.

FIGURE 7 | Diversity temporal changes (A), their underlying components (B) and estimated effects of drivers (C) along increasing scales (sampling effort, x-axis) for farmland (left) and forest birds (right). In A, point size shows the slope of the temporal trend (estimated by the lm R function), and the grey envelope shows the lower and higher confidence intervals, with non-significant slopes (at $\alpha = 0.05$) being shown as transparent points. In B, point size shows the size of the effect for each component (red = aggregation “agg”, green = density “N”, blue = evenness “SAD”, and envelopes show expectation from null models, with non-significant effects being shown as transparent points). In C, point size shows the effect of each predictor on each component (estimated by the lm R function) and envelopes the lower and higher confidence intervals of each effect, with non-significant effects (at $\alpha = 0.05$) being shown as transparent points.

significant temporal change in diversity at any scales (results not shown).

6.4 | Lower-Level Biodiversity Components

The contribution of the three components (density *N*, spatial aggregation *agg* and evenness *SAD*) to diversity changes varied with scale and functional groups. For farmland birds (Figure 7B left), species richness decrease was driven by density (fewer individuals, in green) across all scales, combined with evenness (relatively fewer rare species, in blue) around 50–150 plots sampled, and higher spatial aggregation (in red) for large sampling effort. For forest birds (Figure 7B right), increasing species richness at small scales was driven by density (more individuals, in green) and evenness (more similar species abundances). These effects faded away with increasing sampling effort, with only the positive effect of density driving the weak increase in species richness detected at a large scale.

6.5 | Human Driver Attribution

Scale-dependent attribution of human drivers to changes in components revealed scale-dependent effects of land cover and climate change on diversity dynamics. For farmland birds (Figure 7C left), our analyses revealed a positive dynamic relationship between agricultural cover and density across all scales; i.e., a temporal decrease in agricultural cover over the study period led to a decrease in density (less farmland → fewer individuals). For forest birds (Figure 7C right), our analyses revealed a positive dynamic relationship between increasing forest cover and increasing density (more forest → more individuals) and evenness (more forest → more similar species abundances) at a local scale. In contrast, the dynamics of habitat diversity and spring temperature appeared to contribute little to biodiversity changes, regardless of the components.

6.6 | Discussion

Bridging macroecology and temporal dynamics in a well-studied system and dataset, we showed that novel insights can be gained in comparison to an approach focused on local-scale diversity dynamics only. First, behind an apparent no net change when all species were pooled, studying and comparing diversity between species “functional groups” defined by their habitat revealed temporal changes in diversity. Second, integrating these changes along a continuum of scales exhibited distinct scaling patterns for farmland versus forest birds, leading to different conclusions about the ongoing homogenisation of biodiversity.

Our results highlight that diversity changes within a single (functional) group are influenced by different components depending on the spatial scale, suggesting that distinct processes drive diversity dynamics at each scale. This decomposition of diversity dynamics provides a more nuanced analysis and interpretation of the underlying processes and drivers of diversity change. We identified that a substantial part of the observed increase in forest species richness at the local scale—attributable to increased density and evenness—can be attributed to the expansion of forest cover in France. In contrast, the decline in farmland bird species richness was only partially explained by loss of agricultural land cover via its effect on density, suggesting that other drivers are at play too. For instance, some aspects of habitat alteration or fragmentation not taken into account in our analyses may have disproportionately impacted specialist farmland bird species, leading to reduced evenness. These structural changes in agricultural landscapes likely also contribute to decreased spatial aggregation at broader scales. Collectively, our findings underscore the value of integrating diversity components and scaling perspectives for disentangling the complex drivers of cross-scale biodiversity changes and identifying targeted conservation strategies.

7 | Concluding Remarks

To date, research on diversity change detection has mainly focused on separate discrete spatial scales without embracing its scale-dependence fully 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 here we focused on SAC because it is one of the most studied patterns due, among others, to its suitability to handle data from most existing standardised biodiversity monitoring, the potential of using dynamic macroecological patterns to understand diversity changes across scales is not limited to this specific example. We acknowledge that the feasibility of analysing temporal dynamics in diversity-scaling relationships ultimately depends on the quality and availability of empirical data, the consistency in survey methodologies and sampling effort, among others (Magurran and Dornelas 2010; Dornelas et al. 2013; Gotelli and Colwell 2001). However, the use of rarefaction curves specifically helps address variability in sampling effort across time and space, thereby reducing potential biases and improving comparability in biodiversity assessments.

(Chao et al. 2014; McGill et al. 2015). While data quality remains a central limitation for temporal biodiversity analyses, employing these methodological safeguards can allow robust interpretations even in the presence of inherent variability.

Macroecological patterns provide bridges from observed diversity to ecological processes (Grilli 2020), while effectively synthesising 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 that 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 a 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.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data manipulation and analyses were conducted in R version 4.1.2. Key packages included tidyverse for data manipulation and visualisation, mobsim (May et al. 2018) for simulations of Figure 2, mobr (McGlinn, Engel, et al. 2021; McGlinn, Xiao, et al. 2021) for species accumulation and component calculation, and broom for extracting model results, supplemented with a few custom functions. The code and data are accessible at <https://doi.org/10.5061/dryad.cnp5hqcq9>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.