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Bridging macroecology and temporal dynamics to better attribute global change impacts on biodiversity

Short title : Dynamic Macroecology for diversity changes

Authors

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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.

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, analyzing temporal changes in diversity scaling relationships, such as species accumulation curves or distance decay, can reconcile and synthesize 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 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.

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; 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) (Boënnec et al., 2023; Primack et al., 2018; Vellend et al., 2013). 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 (Blowes et al., 2024; Buhk et al., 2017; Keck et al., 2025). Despite improved clarity and guidance on the use of metrics to assess temporal biodiversity trends at different scales (B. J. 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 development have leveraged the study of diversity scaling relationships for species (Azaele et al., 2015; Chase et al., 2019; Mcglinn 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 informs 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 (Azaele et al., 2015; Brown, 1995; Gaston & Blackburn, 2000; B. McGill & Collins, 2003). 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 (Franzman et al., 2021; Newman et al., 2020; Petraitis et al., 1989). 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 conspecific spatial aggregation (Azaele et al., 2015; Chase et al., 2018; B. McGill & Collins, 2003). 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 (Leung et al., 2022; Loh et al., 2005). Yet, the study of temporal diversity changes based on such approaches 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 (Adler et al., 2005; 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 link to ecosystem functions and services (Cadotte et al., 2011; Lavorel & Garnier, 2002). 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 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 synthesize 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 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 (Gonzalez et al., 2023; McGlinn et al., 2019).

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 “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 an herbaceous and 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 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 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 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 and illustrate our ideas using Species Accumulation Curves (SAC), 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 (for example with richness of fish species from 1970 to 1995, see Figure 1B) integrates changes continuously from local to global scales, and effectively summarizes diversity changes of numerous forms of diversity (B. J. 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 bends the SAC upwards at local scales and 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 (Chase et al., 2019; Leroy et al., 2023; Socolar et al., 2016). However, some combinations are likely to be impossible because of the link between alpha, gamma and beta diversity (Chao et al., 2023; Ricotta et al., 2019), 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 (B. J. 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 trends detection by avoiding the ambiguity inherent to interpreting and comparing trends when they are reporting diversity change at distinct but loosely defined scales.

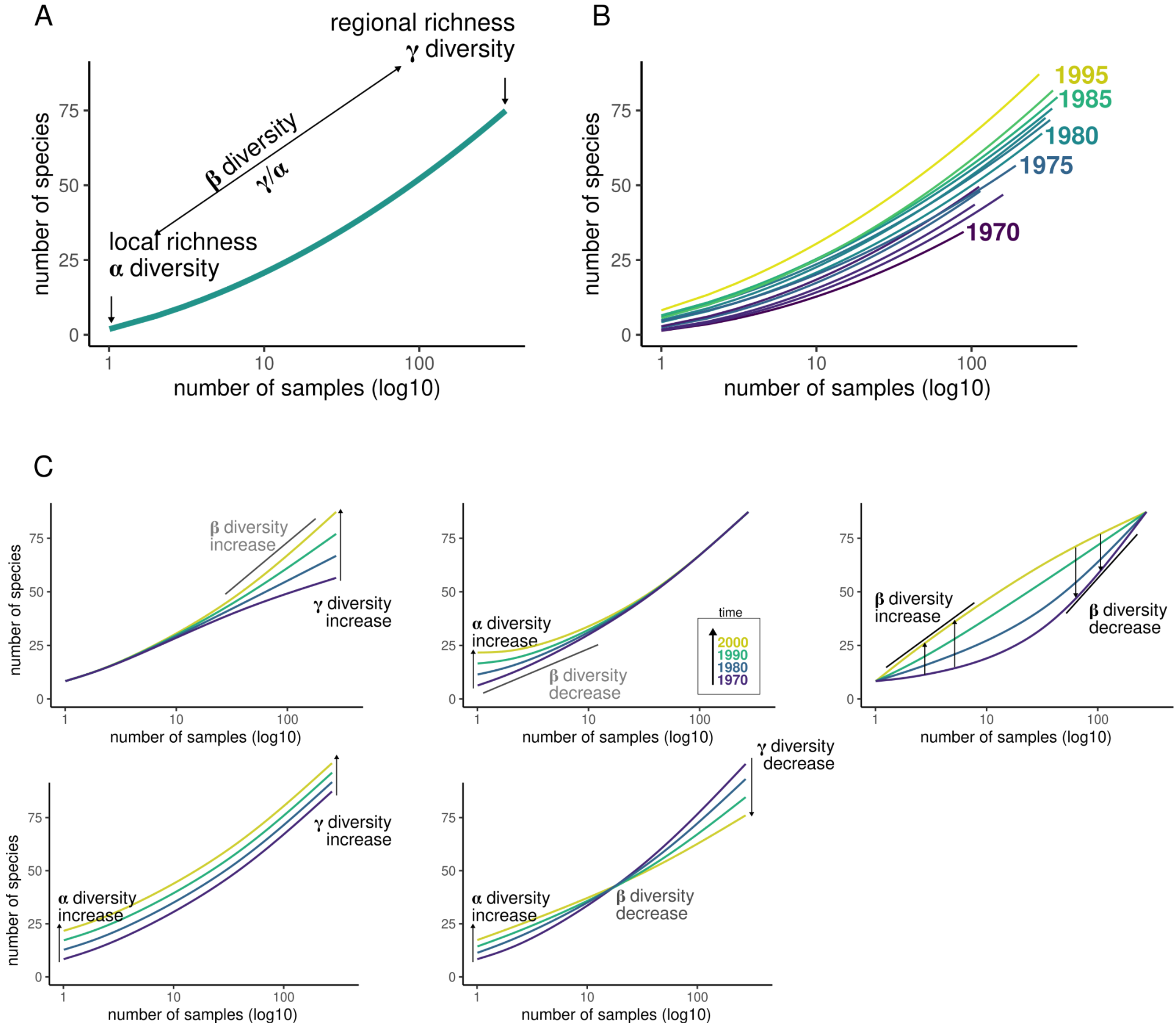

Figure 1. A. Species Accumulation Curves (SAC) describe how the number of species sampled increases with the number of samples *M*. **This macroecological pattern can describe biodiversity from small to large spatial extents depending on the number of samples M, and include any definition of 'local' (alpha-diversity) and 'regional' (gamma-diversity) scales, as long as M_local < M_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 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 (B. McGill & Collins, 2003; Storch et al., 2008). Subsequent application of this theory (Azaele et al., 2015; Blowes et al., 2022; Chase et al., 2018; Keil et al., 2021; McGlinn et al., 2021) has uncovered that diversity accumulation across scales is governed by three lower-level components (Figure 2): the total number of individuals in 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 (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 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 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).

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 & 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 (Species Abundance Distribution) 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 favoring 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 (Avolio et al., 2019; Blowes et al., 2022; Storch et al., 2018). 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 feedbacks is still to be explored with the proper methods and data, for example using empirical dynamic modeling (Chang et al., 2017; Ye et al., 2015) 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.

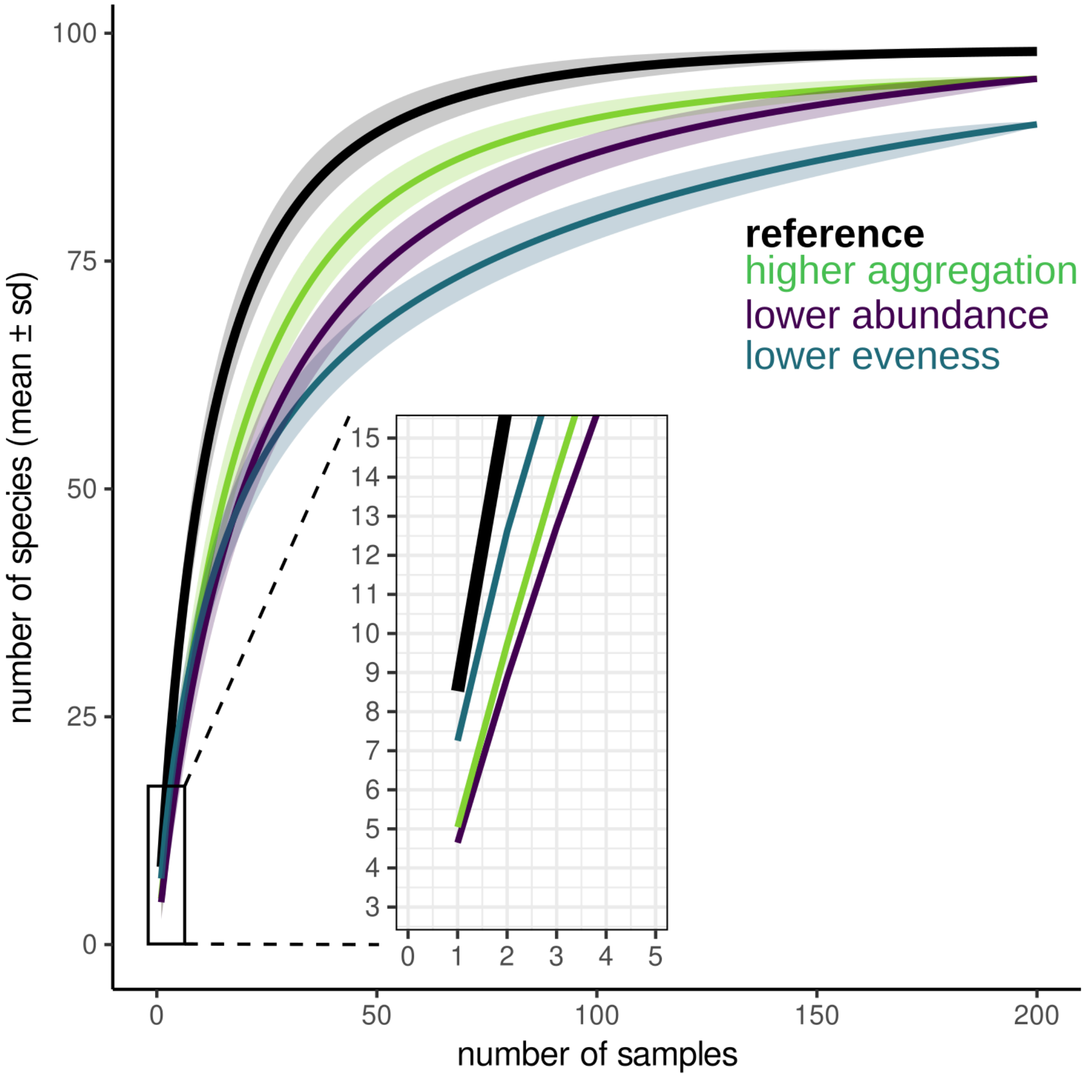

Figure 2. Variation in macroecological patterns are underpinned by change in proximate components of diversity across scales. Macroecology theory indicates that the abundance (total number of individuals), evenness (species - abundance distribution) and spatial aggregation jointly determine the shape 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), 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 *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 Species Abundance Distribution 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 sample-based rarefaction curve) for each simulation was computed using function specaccum() from *vegan* R package. In the x-axis, the number of samples refers to the number of plots sampled.

Integrating trait-based perspectives into temporal dynamics of macroecological patterns helps moving 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; Carmona et al., 2021; Chichorro et al., 2019). 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 (Cheung et al., 2013; Devictor et al., 2012; Gaüzère, Iversen, et al., 2020; Kampichler et al., 2012; Mouillot et al., 2013) 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 (Mazel et al., 2014; Ricotta et al., 2019; Smith et al., 2013). 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 analyzing 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 abundance of species with specific characteristics at the expense of others: common / widespread / generalist / small-bodied vs. rare / restricted / specialist / large-bodied species (Cardillo et al., 2005; Cooke et al., 2019; Purvis et al., 2000), 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 (Münkemüller et al., 2020; Smith et al., 2013). 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., (Hulshof & Umaña, 2023; Lamanna et al., 2014; Matthews et al., 2023). Functional Diversity Area Relationships (FDAR) extend the concept of species-area relationships 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 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, linking trait-based approaches and dynamic 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). 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.

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. motile species, 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 (Matthews et al., 2023; Mazel et al., 2014; Ricotta et al., 2019; Smith et al., 2013) 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.

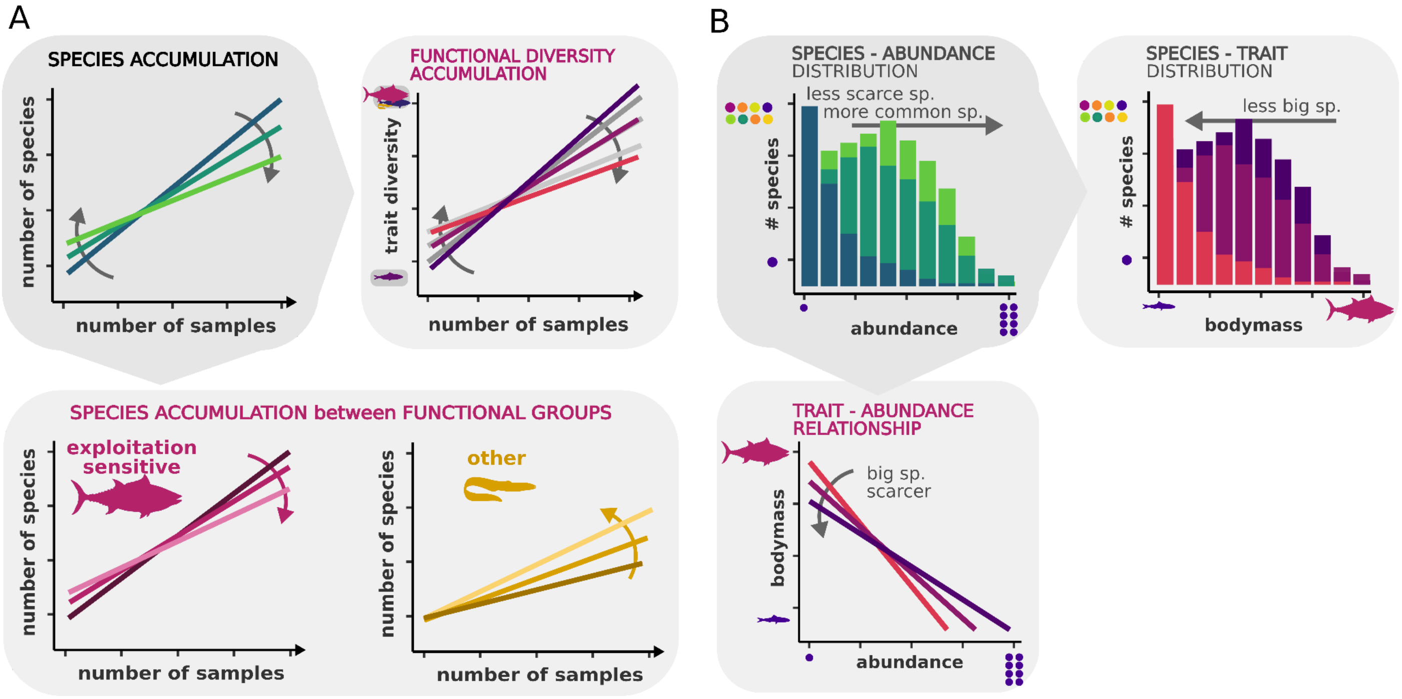

Figure 3. Integrating trait-based perspectives to dynamic macroecological patterns can be achieved by comparing temporal changes in SAC (A, top-left) between different functional groups (A, bottom), or by measuring temporal changes in functional diversity accumulation (A, top-right). Integrating trait-based 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 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 (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, 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 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 (Gonzalez et al., 2023; Laubach et al., 2021; 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 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.

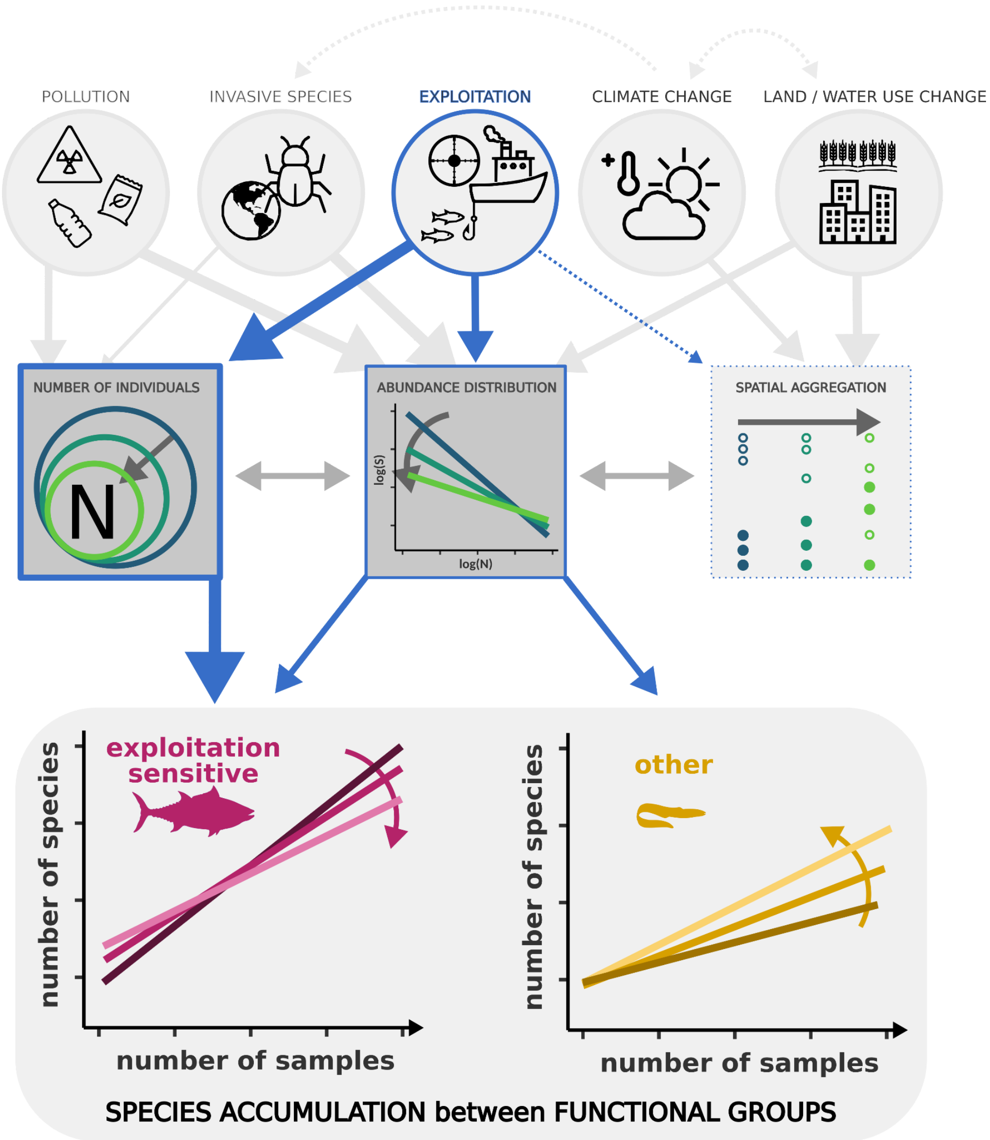

Figure 4. Graphical causal models integrating dynamic macroecological patterns with potential causal pathways from human drivers (top) to proximate components (middle) to trait-based dynamic macroecological patterns (bottom). All potential links across taxa and contexts are in gray. For example, in the 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, 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 decrease of large predatory species.

Case study

To illustrate the ideas of the previous sections, we analyzed 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 (Reif et al., 2024; Rigal et al., 2023), 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 macroecological 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.

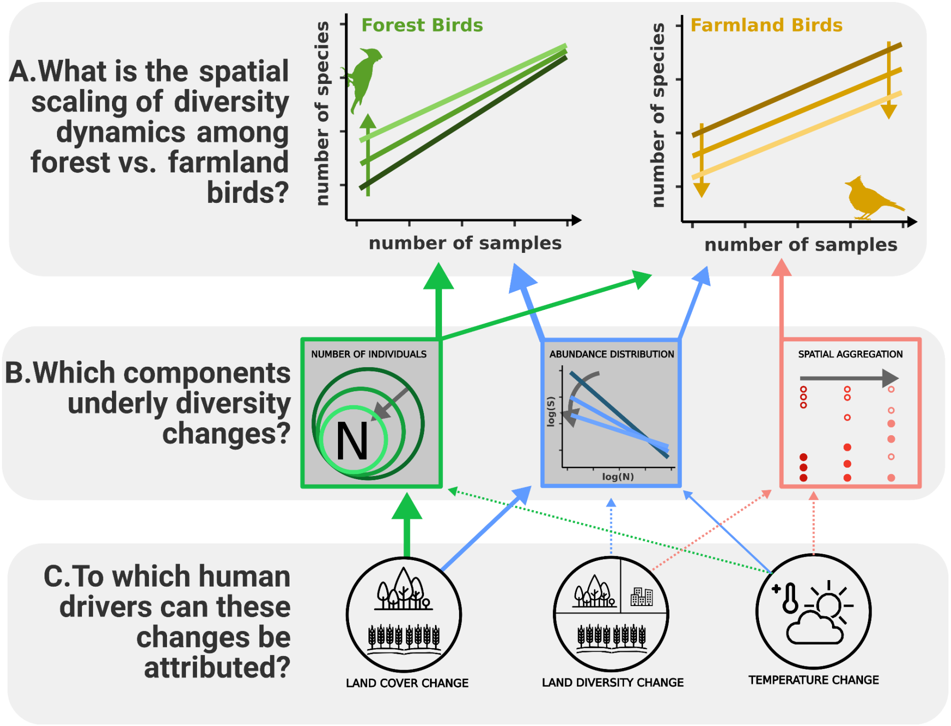

Figure 5. Conceptual description of the potential causal pathways from human drivers (bottom) to proximate biodiversity components (middle) to temporal changes in diversity scaling (top) of farmland and forest birds. Empirical effects of each arrow are shown in Figure 7, with corresponding letters (A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

Methods. We used data from the French Breeding Bird Survey (FBBS), a long-term monitoring program designed to assess the population dynamics of common passerine birds in France. Skilled volunteers conduct standardized 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 2002–2013 to analyze decadal changes which are less prone to nonlinear trends, while avoiding biases associated with the initial monitoring year (2001). Bird species were categorized 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 species accumulation curves and proximate components of species trends using the *mobr* R package (McGlinn et al., 2019). We quantified the contributions of changes in the total number of individuals (N), the relative abundance distribution (species abundance distribution [SAD]), and conspecific aggregation (agg) to species richness changes respectively by comparing three distinct types of species accumulation curves (for mode details, see supplementary or (McGlinn 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 analyzed this graph to detect potential confounder, mediators, and collider variables and adjusted the model structure accordingly (see supplementary - case study). 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 ~ cover_Forest + Temperature

SAD ~ cover_Forest + Habitat_diversity + Temperature

agg ~ Habitat_diversity + Temperature

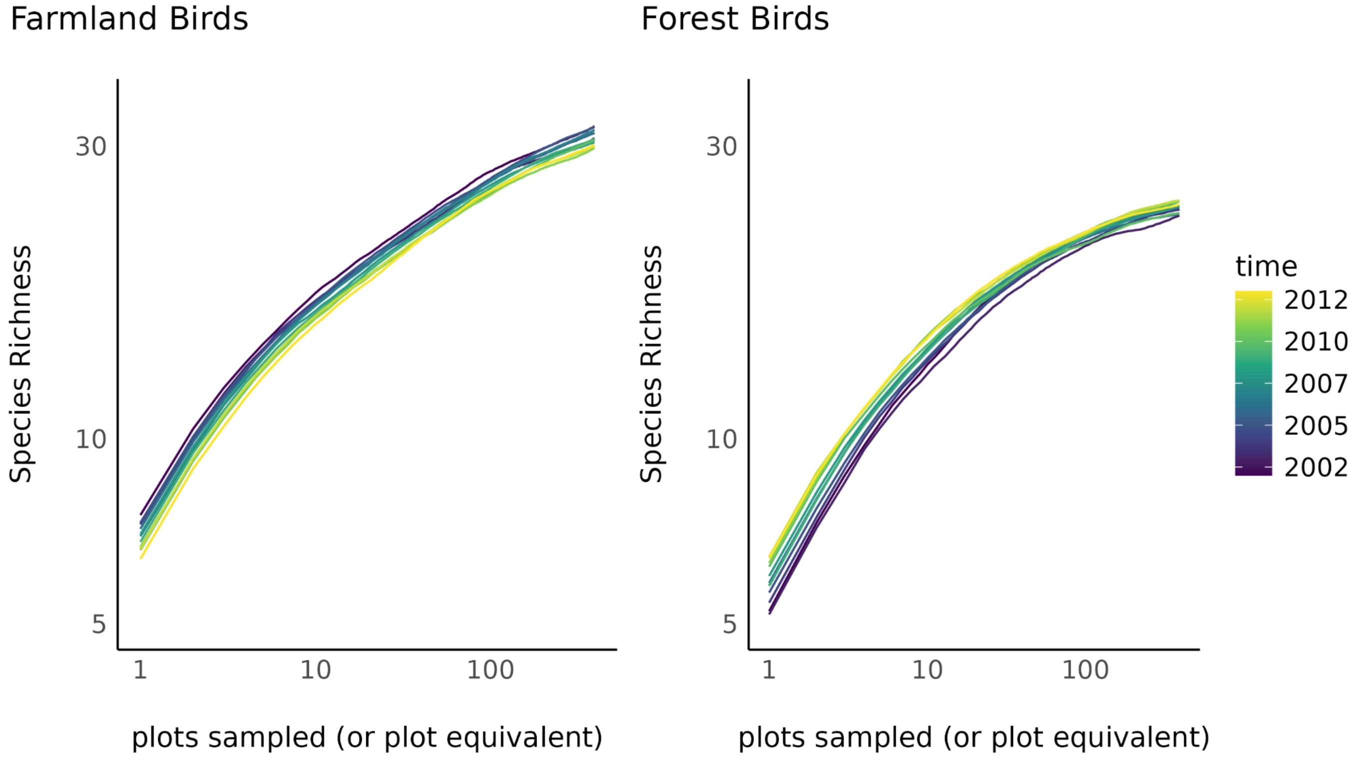

Figure 6. Spatially based species-accumulation curves for farmland birds (left panel) and forest birds (right panel) across multiple sampling years (2002–2013). The x-axis indicates the cumulative number of plots (or plot equivalents) sampled on a logarithmic scale, while the y-axis shows the corresponding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

Results. A first exploration of species accumulation curves across time (Figure 6) reveals small but divergent temporal changes in species accumulation. For farmland birds, species accumulation curves 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 plot 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.

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 difference in diversity change across sampling effort. For farmland birds, our analysis revealed spatially stationary decreases in species richness ranging from -0.15 sp.year^{-1} (between 1 and 150 plot sampled) to -0.2 sp.year^{-1} (at 400 plot 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 0.15 sp.year^{-1} for smaller number of samples (< 50 plot sampled), no significant trends between 100-150 plots sampled and a weak positive trend (0.075 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 1.C). 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 significant temporal change in diversity at any scales (results not shown).

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 fade away with increasing sampling effort, with only the positive effect of density driving the weak increase of species richness detected at large scale.

Human driver attribution. Scale-dependent attribution of human drivers to changes in components revealed scale-dependant 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 temporal decrease in agricultural cover over the study period led to 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 local scale. In contrast, the dynamics of habitat diversity and spring temperature appeared to contribute little to biodiversity changes, regardless of the components.

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 vs. forest birds, leading to different conclusions about the ongoing homogenization 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.

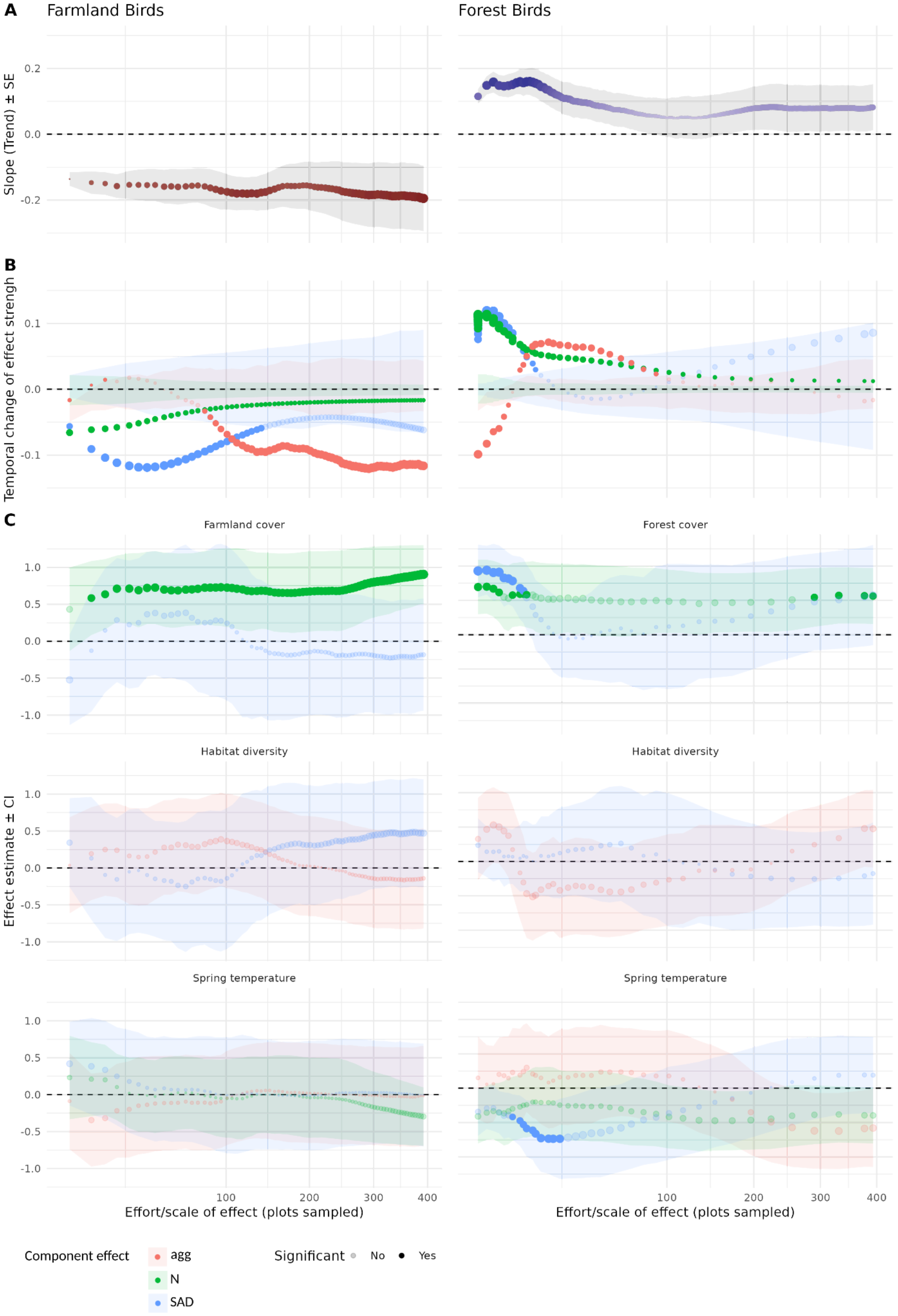

Figure 7. Diversity temporal changes (A), their underlying components (B), and estimated effects of drivers (C) along increasing scales (sampling effort, x - axis) for farmland (left) and forest birds (right). In A, point size shows the slope of the temporal trend (estimated by lm R function), and grey envelope the lower and higher confidence intervals, with non-significant slopes (at α = 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 components (estimated by 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.

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 (Boënnec et al., 2024; Cardinale et al., 2018; Primack et al., 2018), we support the study of dynamic macroecological patterns as a way to integrate diversity changes in a continuous and scalable manner (Connor & McCoy, 1979; Nekola & 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 standardized 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 analyzing 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 (Dornelas et al., 2013; Gotelli & Colwell, 2001; Magurran & Dornelas, 2010) (Magurran et al., 2010; Dornelas et al., 2013; Gotelli et al., 2022). 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; B. J. 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 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 (B. McGill & 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:

All data manipulation and analyses were conducted in R version 4.1.2. Key packages included `tidyverse` for data manipulation and visualization, `mobsim` (May et al., 2018) for simulations of Figure 2, `mobr` (Mcglinn et al., 2021) for species accumulation and component calculation, `broom` for extracting model results, supplemented with a few custom functions. The code and data are accessible at [repository link hidden to preserve anonymity].

Supplementary Case study

Context.
Numerous studies have documented substantial declines in the abundance and species richness of farmland birds. According to the European Bird Census Council (European Bird Census Council, BirdLife International, n.d.), farmland bird populations in Europe have decreased by approximately 20 - 50% since 1980. This decline is particularly pronounced in western and central Europe, where it is attributed to habitat degradation driven by intensive farming practices (Reif et al., 2024). In contrast, forest bird species tend to remain stable or even increase in abundance and numbers in western Europe since 2002 (PECBMS).

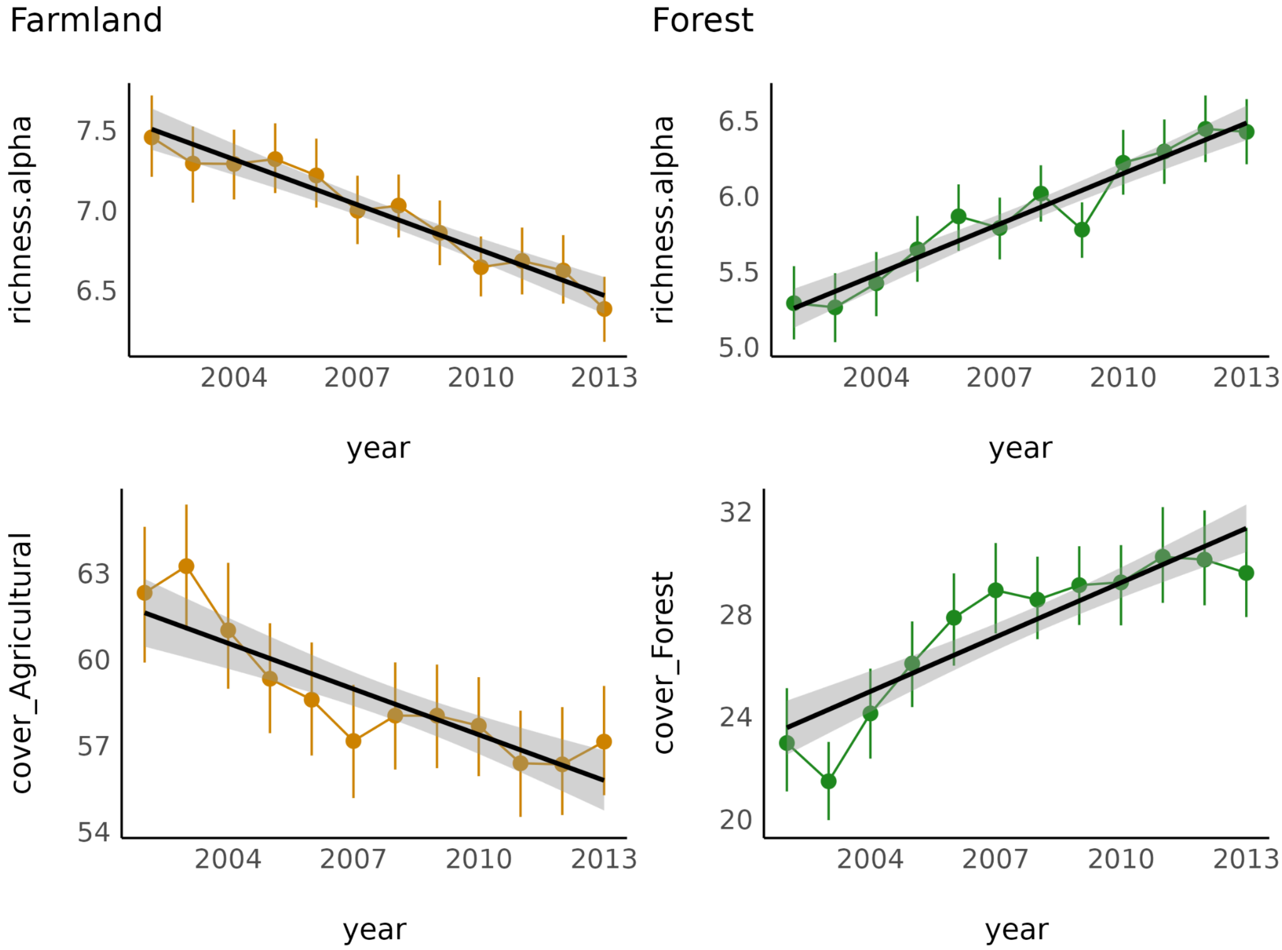

Figure 1. Top : Temporal trends in alpha diversity (richness) of farmland and forest bird species in France from 2000 to 2015. Left panel shows farmland bird species, and the right panel shows forest bird species. Bottom: Temporal trends in farmland (left) and forest (right) cover in % of site area (4km²) in France from 2002 to 2013. Points represent annual mean values, vertical lines represent standard errors, and black lines indicate fitted linear trends with 95% confidence intervals (shaded areas).

However, focusing solely on alpha diversity (species richness at individual sites) provides a limited perspective. Alpha diversity measures do not account for species composition differences between sites (beta diversity) or overall regional diversity (gamma diversity). This narrow focus can obscure important ecological dynamics, such as species turnover and community composition changes across landscapes. Therefore, while alpha diversity trends offer valuable insights, a comprehensive understanding of biodiversity patterns necessitates incorporating multi-scale diversity assessments to capture the full scope of ecological changes. We here used a dynamic macroecological approach, more specifically temporal changes in species accumulation curves, to assess diversity changes across a continuous scale, from alpha (one site) to gamma (~350 sites). We implemented the ideas discussed in this paper for improving detection and attribution of human drivers to diversity changes. **To investigate diversity changes across time and space**, we computed species richness accumulation along increasing sampling effort for each year of monitoring and estimated temporal richness changes at each scale/sampling effort. **To study how low-level biodiversity components underpin dynamics of macroecological patterns**, we applied the mobr framework to computed the effect of density, evenness and aggregation on species richness for each scale and year, allowing us to measure how temporal changes in richness are driven by temporal changes in each components. **To integrate trait-based perspectives** and move toward attribution of human drivers, we run the analyses on two contrasted groups defined by their habitat preference, here used as an integrative ecological trait. **To attribute diversity changes to anthropogenic drivers**, we built a causal diagram and applied time series analyses at each scale to uncover the effect of land cover change and climate change on the bird's richness trends via their underlying components.

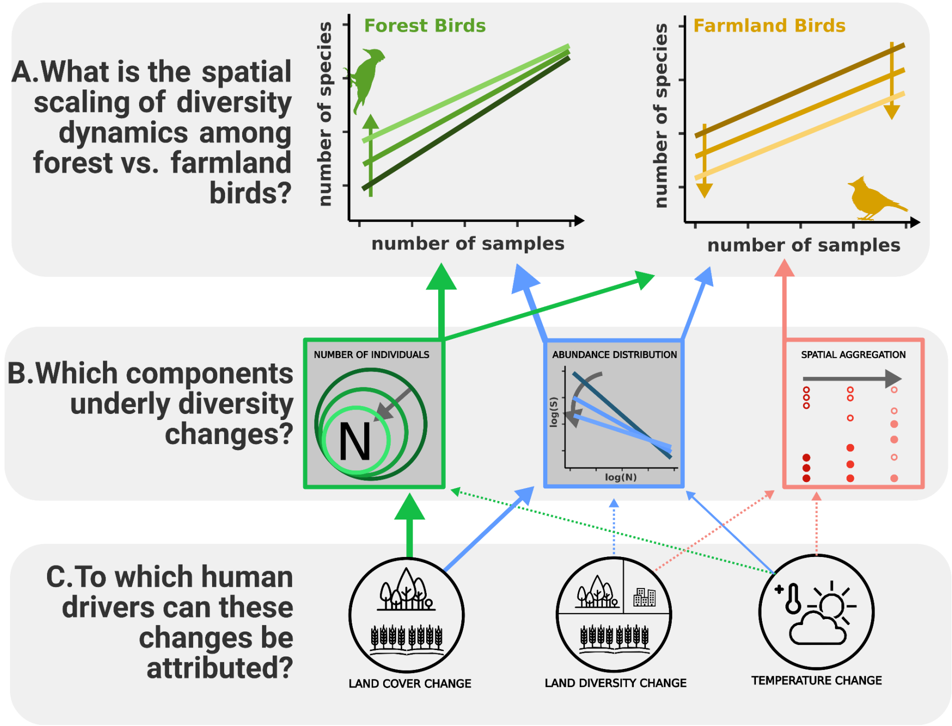

Figure 2. Conceptual description of the potential causal pathways from human drivers (bottom) to proximate biodiversity components (middle) to temporal changes in diversity scaling (top) of farmland and forest birds. Potential links are in grey, estimated links are in black and colors for each component. Empirical effects of each arrow are shown in Figure 7, with corresponding letters (A : diversity changes, B: diversity components, C: driver effects).

Data.

Bird community data were from the French Breeding Bird Survey. The French breeding bird survey was designed to monitor population dynamics of common passerine bird species in France. In this survey, skilled volunteer ornithologists count birds at a given site, following a standardized protocol, at the same site, year after year (Jiguet et al., 2012). Species abundances are recorded across 2792 sites, each covering a 4km² area. Volunteers provide their home locality to the national coordinator, and a 2×2 km site is randomly selected from within a 10 km radius (out of 80 possible sites) by the coordinator. Each spring, volunteers carry out 10 point counts separated by at least 300 m within the selected site, for a fixed period of five minutes. Two sampling sessions are carried out from 1 April to 8 May, and then from 9 May to the end of June, to detect both early and late breeders, with a gap of 4–6 weeks between sessions. Counts are repeated annually on approximately the same date (±7 days) and at dawn (1–4 h after sunrise) by the same observer, in the same order. The highest count from these two sessions is used as the measure of point-level species abundance. We sub-selected sites that were monitored between 2002 and 2013, in order to avoid the first year of the restructured monitoring scheme (i.e 2001), and to limit our analyses to linear trends, more likely to characterize decadal dynamics. We used the latest PECBMS classification (https://pecbms.info/) to classify farmland and forest species according to their pre- dominant habitat.

Climatic data were extracted from CHELSA (https://chelsa-climate.org/, v.2.1) for each site and each sampling year. We computed the average daily temperature and precipitation during the bird breeding season (April - August). **Land cover data** were extracted from CORINE Land Cover (European Environment Agency, 2010). Percentage land covers within FBBS site were computed by taking the habitat class area (in square meters) and dividing it by the total area of the site. Because CLC data were available only for 2000, 2006, 2012 and 2018, some FBBS site-year combinations were not covered by the dataset. In this case, we attributed site land cover for the uncovered year to the last year for which we had CLC data available (for example, sites monitored in 2001 were attributed land cover from CLC 2000). More specifically, we focused on two aggregated CLC classes, agricultural areas and forests.

Analyses.

Species accumulation curves and proximate components of species trends were calculated for each year using the mobr R package (McGlinn et al., 2019). We quantified the contributions of changes in the total number of individuals (N), the relative abundance distribution (species abundance distribution [SAD]), and species aggregation (agg) to species richness changes. These contributions were estimated using three distinct types of species accumulation curves, each capturing different combinations of the components (N, SAD, and aggregation, see Figure 2). Temporal changes in differences between accumulation curves of the same type are used to estimate temporal change in the effect of each component on species richness changes, according to the following steps :

1. Compute three rarefaction curves that capture different information on the influence of N, the SAD, and aggregation for each sampling effort and year: IBR, nsSBR, and sSBR.
2. Compute the differences between rarefaction curves at each site each year. N effect = nsSBR - IBR; aggregation effect = sSBR - nsSBR. SAD effect is calculated directly from the IBR (equal to S for a given sampling effort at a given year).
3. Model the relationship between the estimates of the SAD, N, and aggregation effects and years.
4. Examine how the temporal rate of change of each effect (i.e., slope of model) varies with sampling effort.
5. Compare the observed results to randomization- based null models for each component of community structure (i.e., SAD, N, and aggregation) to examine if the effects and their temporal change relationship are different than expected from a null expectation.

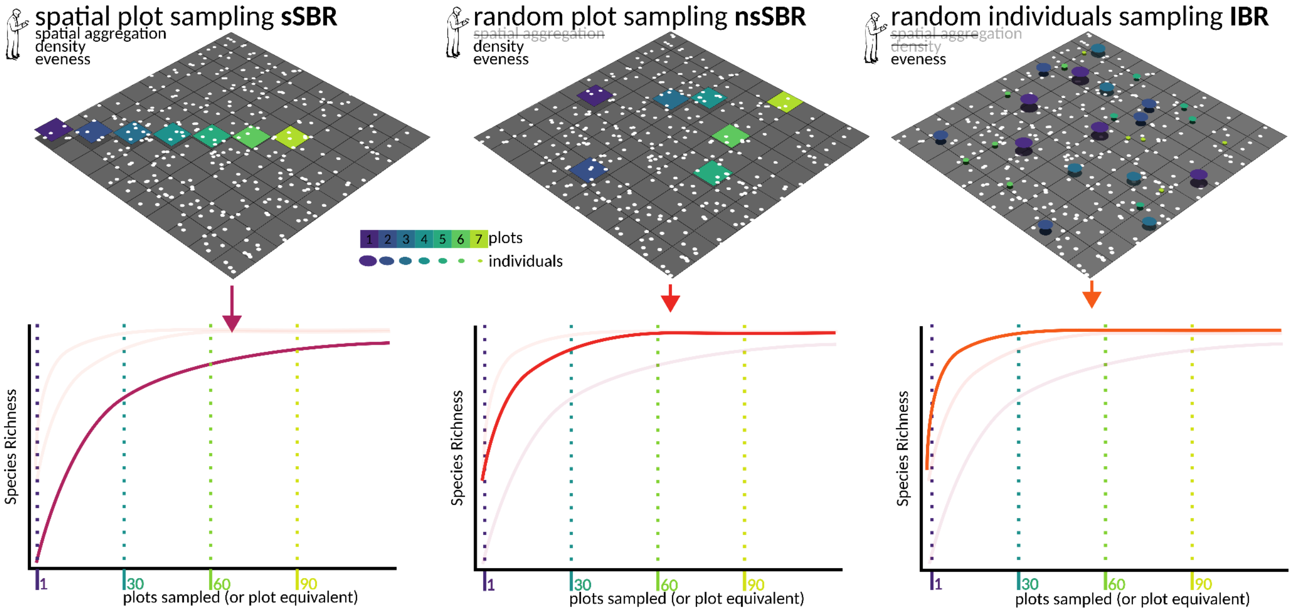

Figure 3. Diagram sketching the different accumulation of species that incorporate or not different biodiversity components, used to calculate their effect across scales.

Causal drivers effects on proximate component dynamics were estimated across spatial scales using a stepwise approach. First, we build a simple causal diagram linking a limited set of predictors to each component based on our expertise and literature. For the sake of simplicity, we only used spring temperature, agricultural cover, forest cover, and habitat diversity for potential drivers of richness changes. We acknowledge that a real study would require more potential drivers, and discuss this point later.

Change in density are positively related to change in the cover of their habitat (more cover leads to higher density, via increase in resource availability) and temperature (more temperature leads to higher density, via increased productivity).

Change in evenness is negatively related to habitat diversity (more diversity leads to lower evenness, i.e more abundant generalist species) and positively related to temperature (higher temperature leads to mower evenness via more generalist species) and habitat cover (more cover leads to more forest specialist species).

Change in aggregation is positively related with habitat diversity (more diversity leads to more aggregation) and temperature, as more generalist species can increase dominance patterns.

Habitat diversity increases with increasing forest cover, and decreases with increasing agricultural cover. Hence, habitat diversity effect can be ultimately influenced by cover change. However, to avoid but is not explicitly tested here.
Land cover change influenced habitat diversity because composition and diversity of land cover in the FBBS sites can't be independent. In the case of attributing the effect of habitat diversity change on evenness, the influence of land cover on habitat diversity acts as a confounder variable as it can influence both the habitat diversity and the evenness (see the fork pattern in grey, Figure 4). We thus included land cover change as a covariable in the model testing the effect of habitat diversity change on evenness change.

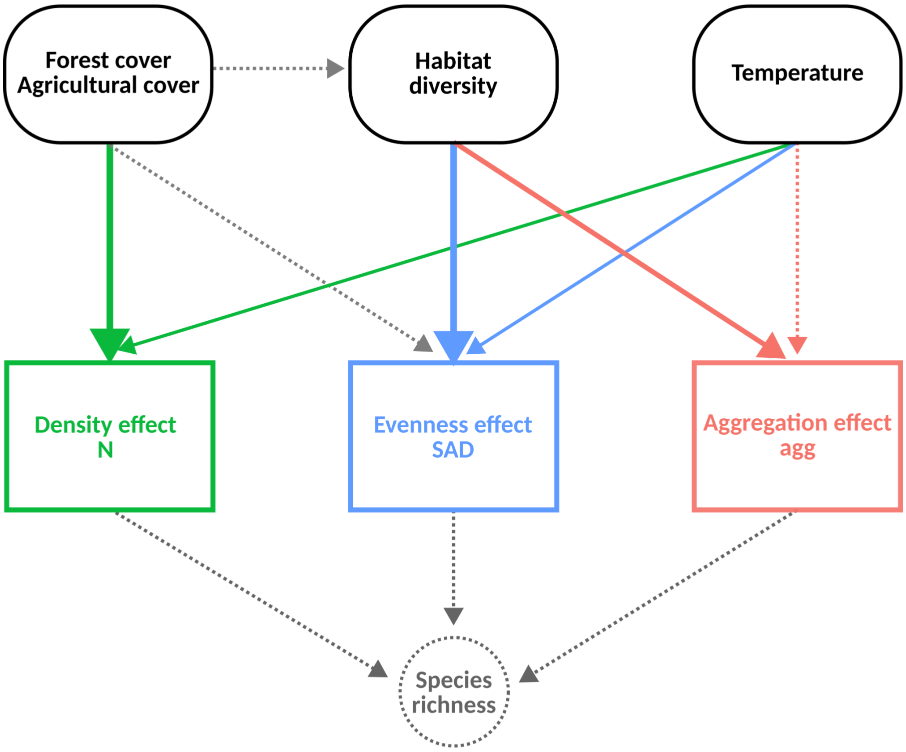

Figure 4. Causal graph representing the potential causal link hypothesized for our analyses.

Second, we computed the accumulation of each predictor variable (e.g., farmland cover, forest cover, temperature, and diversity indices) at scales. For each scale, the accumulated value of the variables was calculated by progressively aggregating data over an increasing number of spatial units (corresponding to one used above), ensuring that the scale-dependent relationships between predictors and response variables could be captured effectively. To assess the relationships between accumulated variables and biodiversity metrics, we fitted a series of linear models at each spatial scale. The dependent variables included **effect_N**, **effect_SAD**, and **effect_agg.** Each dependent variable was regressed against combinations of predictor variables (scaled across spatial scales): forest cover (`sc_cover_Forest`), temperature (`sc_temp`), and species diversity (`sc_div`). The specific models run at each scale were:

effect_N ~ sc_cover_Forest + sc_temp
effect_SAD ~ sc_cover_Forest + sc_div + sc_temp
Effect_agg ~ sc_div + sc_temp

The models were iteratively fitted using scale-specific subsets of the data for each sampling effort, allowing us to estimate the scale-dependent relationships between predictors and component changes in time. At each scale, we extracted the following metrics from the model outputs: coefficient estimates, Standard errors (SE), Confidence intervals (95%) z-statistics, and p-values for each predictor, and the R^2 for each model. The script iteratively applied the models and combined the outputs into a single dataset for further analysis and plotting.

Software and Packages. All data manipulation and analyses were conducted in R (version X.X.X). Key packages included `tidyverse` for data manipulation and visualization, `mobr` (Mcglinn et al., 2021) for species accumulation and component calculation, `broom` for extracting model results,, supplemented with a few custom functions. The code and data are accessible at:

A.What is the spatial scaling of diversity dynamics among forest vs. farmland dwelling birds ?

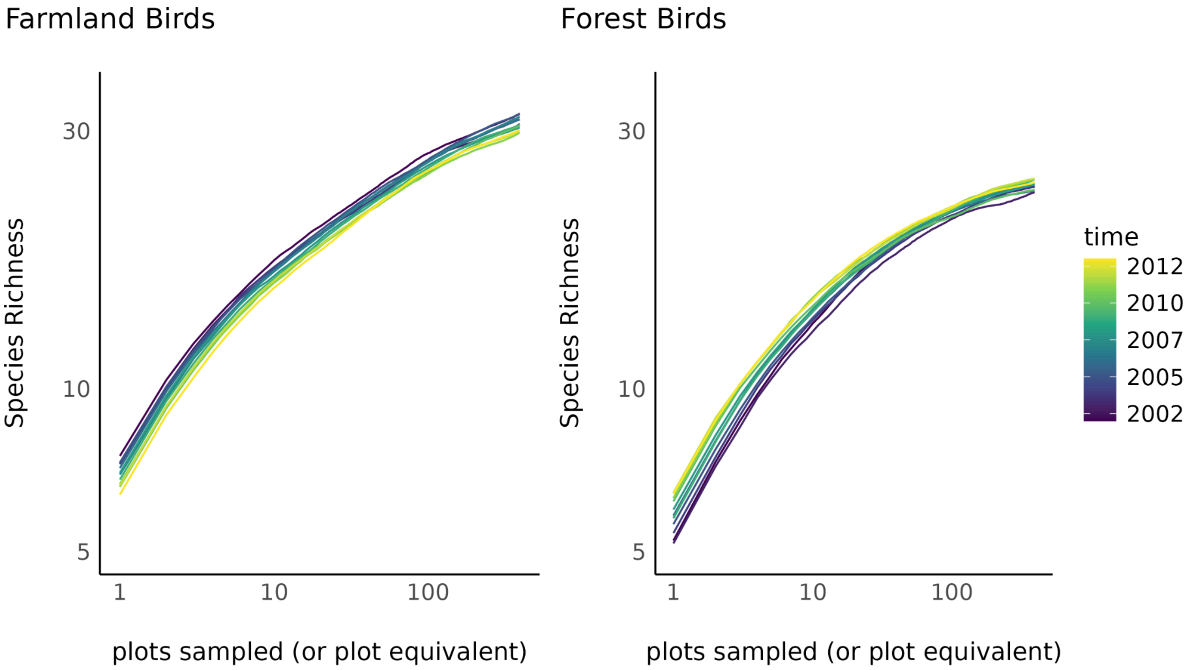

Figure 5. Spatially based species-accumulation curves for farmland birds (left panel) and forest birds (right panel) across multiple sampling years (2002–2013). The x-axis indicates the cumulative number of plots (or plot equivalents) sampled on a logarithmic scale, while the y-axis shows the corresponding total species richness. Each colored line represents a different sampling year (ranging from 2002 in purple to 2013 in yellow).

Farmland bird assemblages tend to reach slightly higher overall richness (right panel), whereas forest assemblages exhibit a more moderate increase yet display consistently higher richness in more recent sampling years (Figure 5, left panel). The gradual shift in curve position over time suggests that species richness decreases at all scales during the period (dark lines are always on top of the bright lines), while for forest birds the species richness increase at small scales is less marked at larger scales. To further enhance interpretation, species accumulation data can also be visualized using surface plots. In these plots, each cell represents a unique combination of sampling effort and year, with cell color depicting difference in species richness relative to 2002, where red signifies negative anomalies and blue indicates positive anomalies, expressed as the number of species detected

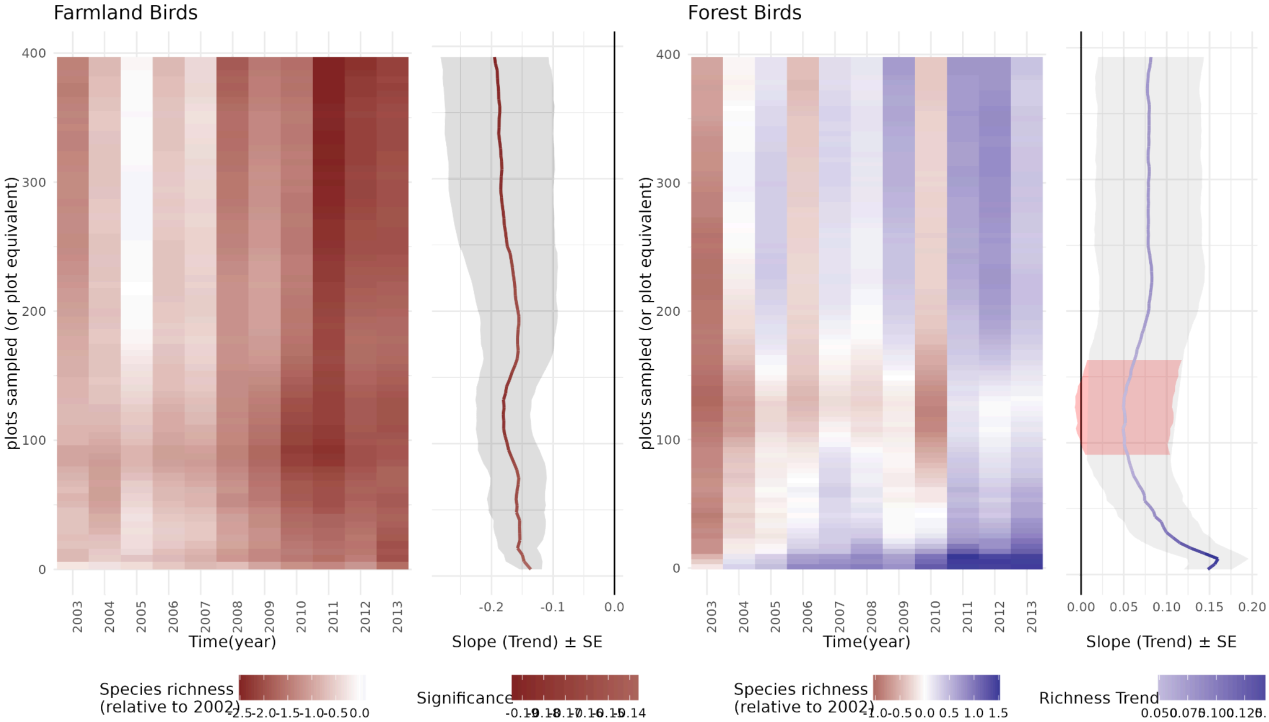

Figure 6. Heatmap representation of species-accumulation dynamics, where each cell corresponds to a unique combination of sampling effort (number of plots) and year. The color scale indicates the *change in species richness* (relative to 2002), with red tones signifying lower richness than 2002 (negative anomalies) and blue tones signifying higher richness than 2002 (positive anomalies). Thus, darker red values reflect greater declines, while darker blue values represent greater gains in species numbers.

Farmland birds (left panel). Across all spatial scales (from low to high sampling effort), farmland bird richness exhibits a consistent declining trend over time, as indicated by the predominantly red coloration. The lack of any blue zones suggests that local decrease (Figure 6) propagates to larger spatial scales, indicating a relatively uniform loss of species across scales. Computing the linear trend over the study period showed substantial and significant decreases in species richness ranging from -0.15 sp.year^{-1} at local scale to -0.2 sp.year^{-1} at larger scale.

Forest birds (right panel). In contrast, forest bird richness presents a more complex “mosaic” pattern in space and time. At small spatial scales (low sampling effort), there is an evident increase in species richness over time (blue shading near the bottom of the heatmap), aligning with the positive alpha-diversity trend noted in Figure 1. However, these gains quickly diminish at intermediate to larger spatial scales (~100 plots sampled). Some areas in the plot showing net losses (red areas) between 2003 and 2010. This contrast indicates that local-scale increases in forest bird assemblages do not necessarily translate into increases at larger scales. Computing the linear trend over the study period showed substantial and significant increases in species richness at local scale (0.15 sp.year^{-1}), no significant trend at intermediate scales (100-150 plots sampled) and weaker positive trend at larger scale (0.075 sp.year^{-1}).

Implications of multi-scale biodiversity assessment. Taken together, these results highlight the importance of examining biodiversity trends at multiple spatial scales. Farmland bird communities show spatially stationary declines while forest gains at small scales are not reflected regionally, suggesting that local increases do not propagate into larger-scale biodiversity benefits, hence leading to spatial homogenization.This multi-scale perspective underscores the need to consider both local and regional along a continuum of spatial scale to fully capture the dynamics of bird diversity.

B.Which proximate components underlie these changes ?

Using the **mobr** package, we decomposed observed changes in species richness across time and sampling scales into three key components: (1) **Density (N)**, reflecting changes in the total number of individuals, (2) **Aggregation (agg)**, indicating how individuals are clustered or dispersed in space, and (3) **Species Abundance Distribution (SAD)**, which captures shifts in the evenness or dominance structure of the community.

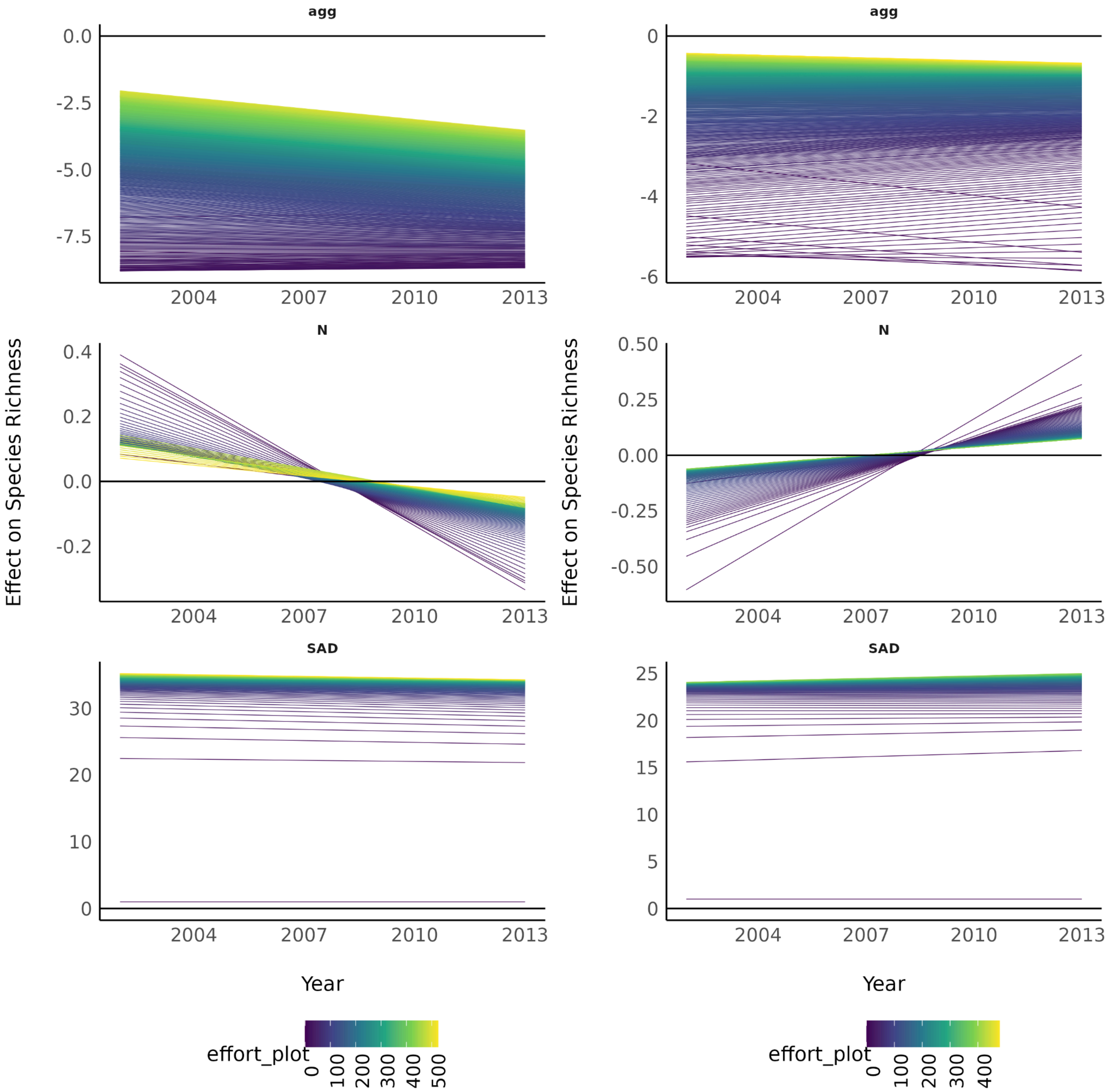

Figure 7. Temporal linear trends in the effect of each component on overall species richness of farmland (left) and forest (right) birds, with darker hues denoting results at smaller (local) scales and lighter hues indicating progressively larger spatial scales.

Farmland Birds (Left Panels).

Aggregation (agg, top-left panel). The aggregation effects were negative, indicating species richness was lower than expected due to spatial aggregation (Figure 7). At local scale, aggregation effects increase through time (purple slopes), but decrease with time for larger scales, which indicates that farmland birds are experiencing increased spatial clustering through the study period, leading to decreasing species richness at intermediate and large scales.

Density (N, middle-left panel). Farmland birds exhibit a decrease in N effect over time at all scales, with stronger decrease at local scales. This pattern indicates that decrease in species richness across the study period is driven by declining bird abundance, in particular at local scale.

Species-Abundance Distribution (SAD, bottom-left panel). SAD effects were strongly positive, but weakly decreased during the study period, indicating that the strong positive effect of evenness decreased though time. This implies that evenness or patterns among farmland species changed from toward relatively more common than scarce species.

Forest Birds (Right Panels).

Aggregation (agg, top-right panel). Although also negative in sign, the aggregation effect for forest birds tends to be less intense than for farmland birds. The spatial aggregation showed temporal decrease at the very local scale (1 or 2 plot samples), then temporal increase at intermediate scale, then weak decrease at larger scale. This suggests that, while there is some degree of spatial increasing aggregation, it is not as strongly driving richness declines as in farmland systems.

Density (N, middle-right panel). In contrast to farmland birds, *N* for forest birds increased over time, especially at local scales. This indicates an overall increase in abundance forest driving an increase in species richness.

Species-Abundance Distribution (SAD, bottom-right panel). Forest communities exhibited increasing *SAD* values at local and regional scale, implying that abundance values may have become more evenly distributed among species.

To ease interpretation of how temporal changes of component effects vary along the continuum of spatial scales, the coefficients of temporal slopes were plotted for each sampling effort, and confronted to the null expectation.

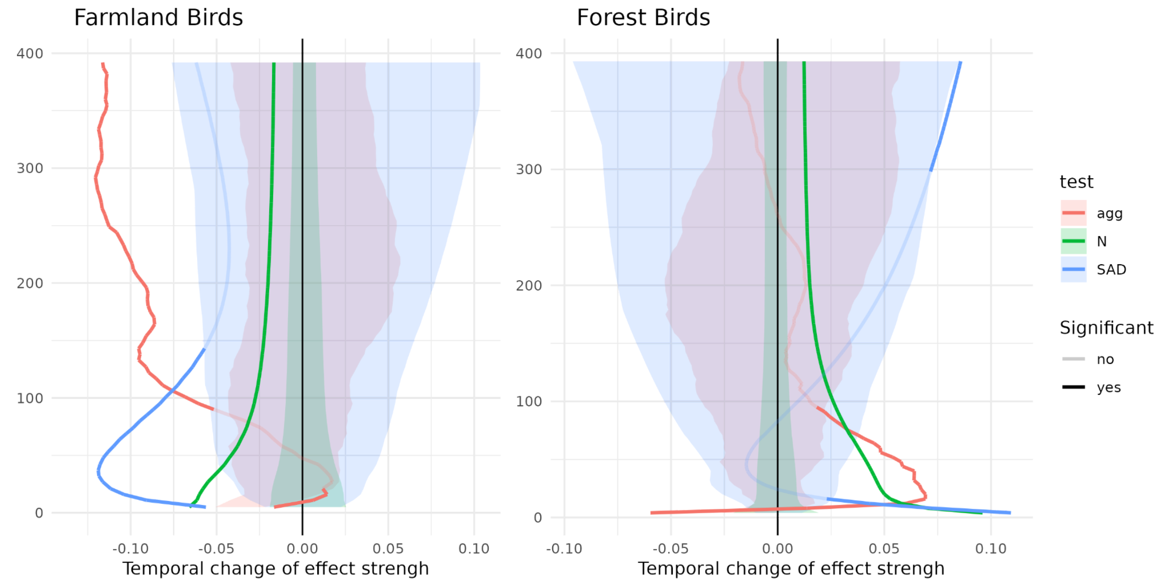

Figure 8: Temporal changes in the strength of diversity change components for Farmland Birds (left) and Forest Birds (right). The x-axis represents the rate of temporal change in effect strength, and the y-axis shows the scale (sampling effort). Three components —density (N, green), evenness (SAD, blue), and spatial aggregation (agg, red)—are displayed with corresponding null expectations (95% CI, shaded areas).

Figure 8 confirms patterns from figure 7, showing that Farmland birds small scale decrease in species richness is driven by decrease in density and evenness, while the decrease at larger scale is driven by increasing spatial aggregation. These results show that different underlying components dynamics are influencing diversity trends depending on the scale. Forest birds' richness increase at local scale was related to increase of density, evenness, and increase in spatial aggregation. At larger scale, evenness and aggregation effects disappeared were not significantly different from null expectations, while the density effect increase stayed positive and significant at larger scale. Overall, the temporal decrease in farmland birds richness was driven by a combination of decreasing densities and community evenness at lower scales (1 to 100 plots sampled), but these effects were replaced by an increase in spatial aggregation driving declines in species richness across scales at larger scale (200-400 plots sampled). By contrast, the temporal increase in forest bird communities at local scale was driven by the combination of decreasing aggregation, density and evenness, while none of the components had significant effect at larger scale, in line with the weak trends in species richness detected previously.

C.Which human drivers can be attributed to changes ?

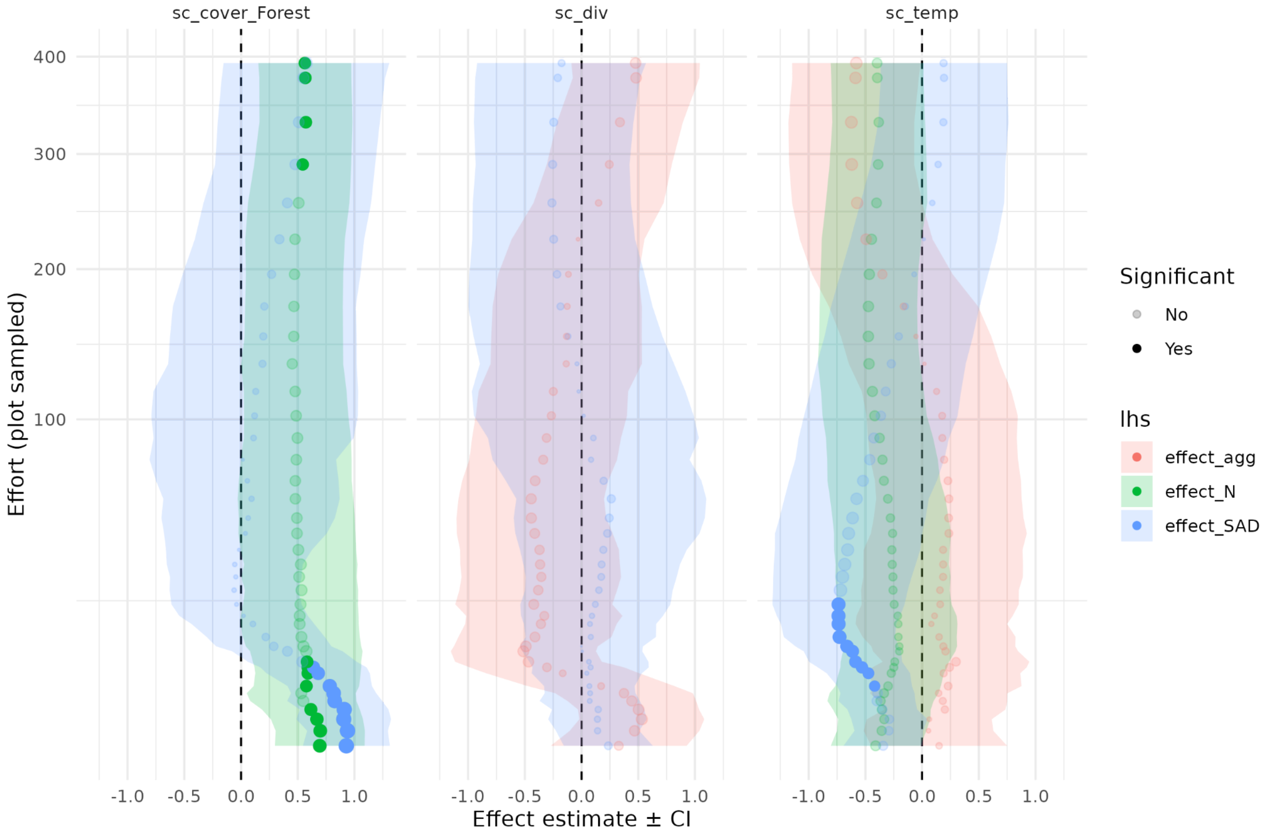

Figure 9: Effects of forest cover, habitat diversity and temperature change (x-axis) on the temporal effects of three components —density (N, green), evenness (SAD, blue), and spatial aggregation (agg, red) at each scale (y-axis). Model estimates are shown by points (size corresponding to effect magnitude), and 95% confidence intervals are displayed by shaded areas. Non significant effects are transparent, significant effects are not.

Increasing cover forest consistently drove increasing density effect (N) at all scale, and increasing evenness effect at local scale. Decreasing habitat diversity decreased spatial aggregation (agg) at intermediate scales

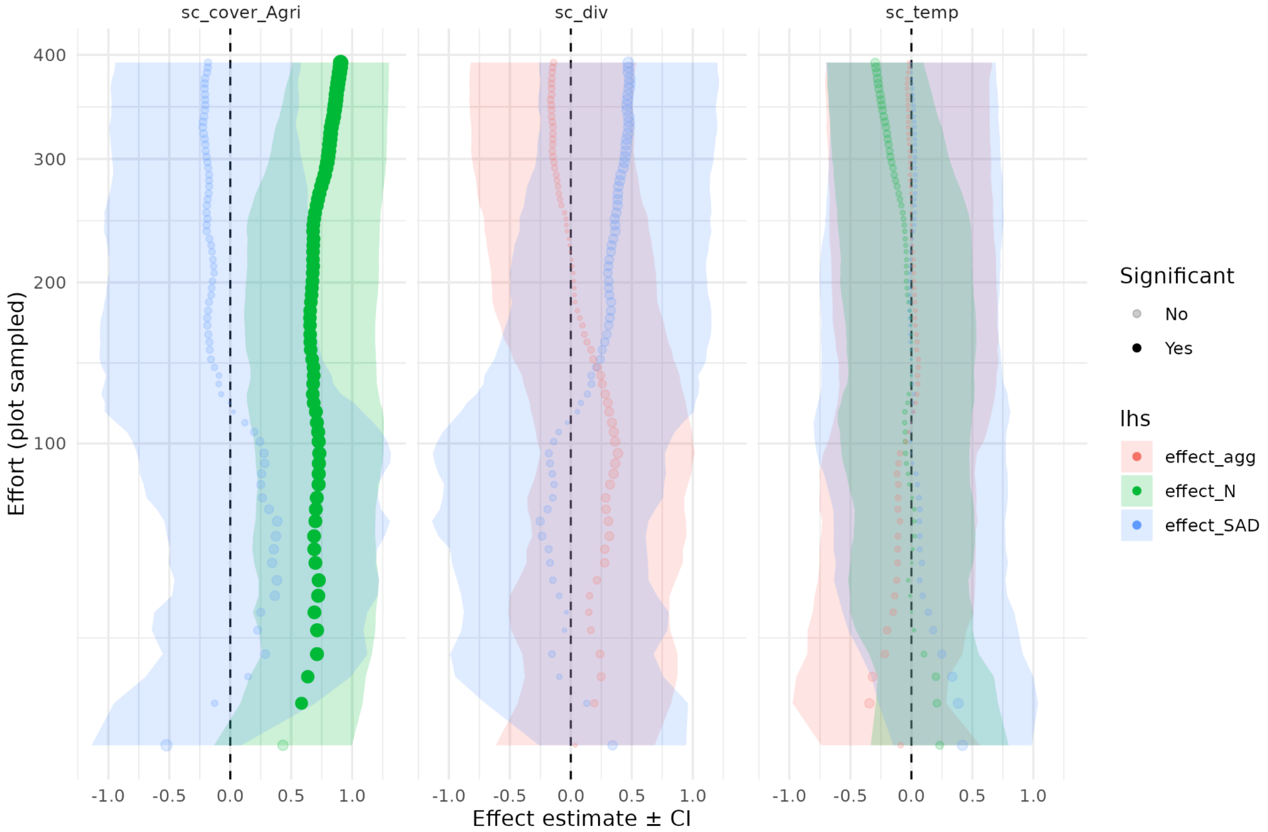

Figure 10: Effects of Agricultural cover, habitat diversity and temperature change (x-axis) on the temporal effects of three components —density (N, green), evenness (SAD, blue), and spatial aggregation (agg, red) at each scale (y-axis). Model estimates are shown by points (size corresponding to effect magnitude), and 95% confidence intervals are displayed by shaded areas. Non significant effects are transparent, significant effects are not.

Discussion

By integrating changes in biodiversity across spatial scales into a well-studied system and dataset, we demonstrated that novel insights can be gained, revealing the complexity obscured by solely focusing on local-scale diversity dynamics. Specifically, we found that changes in diversity for farmland and forest birds exhibit distinct scaling patterns, leading to fundamentally different conclusions about the ongoing homogenization of biodiversity. Our results highlight that diversity changes within a single 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 causal analysis and interpretation of the drivers of biodiversity change. For instance, we identified that a substantial part of the observed increase in forest species richness at the local scale—attributable to increased density and evenness—correlates strongly with the expansion of forest cover in France. In contrast, the decline in farmland bird species richness cannot be explained by a reduction in agricultural land cover, indicating that other drivers are at play. Decomposing diversity changes into proximate components further revealed that the decline in farmland bird richness primarily results from decreases in density and evenness, which are likely linked to the intensification of agricultural practices rather than changes in land area. In particular, the increasing use of pesticides has been identified as a significant pressure, likely exerting direct effects on bird population density.

Additionally, habitat fragmentation and alteration, such as the removal of hedgerows, 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 biodiversity change and identifying targeted conservation strategies.