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RECEIVED 24 October 2025

REVISED 16 January 2026

ACCEPTED 09 February 2026

PUBLISHED 27 February 2026

CITATION

Gent J, van Bodegom PM and Si Y
(2026) A conceptual framework
for the temporal dynamics of spatial
environmental heterogeneity–
biodiversity relationships.
Front. Ecol. Evol. 14:1731666.
doi: 10.3389/fevo.2026.1731666

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A conceptual framework for the temporal dynamics of spatial environmental heterogeneity–biodiversity relationships

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Environmental heterogeneity is an important spatial characteristic, the loss of which is thought to reduce biodiversity by decreasing the availability of niche space. The temporal dimension of the environmental heterogeneity–biodiversity relationship remains largely unexplored despite the increasing focus on anthropogenic change in ecology. To address this gap, we review peer-reviewed published studies to propose a first typology for the temporal dynamics associated with the terrestrial environmental heterogeneity–biodiversity relationship. We found a paucity of studies that address temporality, after filtering, just 23 papers met our search criteria. We propose three key temporal domains that require further research: short-term dynamics, long-term trajectories, and interactions with the spatial grain of observation which are essential for understanding biodiversity responses to environmental change.

KEYWORDS

biodiversity, environmental heterogeneity, long-term trajectories, sampling frequency, short-term dynamics, temporal dynamics, terrestrial ecosystems, environmental complexity

1 Introduction

Global biodiversity is in decline, driven in part by changes in the spatial characteristics of landscapes through land use change (Jaureguiberry et al., 2022; Maxwell et al., 2016). Land use change has accelerated from the late 19th century onwards as the intensity of terrestrial direct exploitation and its indirect effects increased (Ellis et al., 2021). This fast transition has a wide geographical scope as human activities have directly affected more than two thirds of the earth's land surface (Luyssaert et al., 2014). Therefore, investigating the pathways through which land use changes are altering patterns of biodiversity is key to any attempt to mitigate or reverse the trend.

Environmental heterogeneity describes the spatial variability present in an ecosystem in its biotic and abiotic elements and has been identified as a key spatial driver of biodiversity (Johnson and Simberloff, 1974; MacArthur and MacArthur, 1961; Stein et al., 2014; Tonetti et al., 2023; Udy et al., 2021). Changes to terrestrial land use that alter environmental heterogeneity are therefore important for understanding changes in biodiversity patterns. Environmental heterogeneity takes two key forms: compositional, which describes the variety of landscape elements present, and configurational, which describes their spatial arrangement (Li and Reynolds, 1995; Fahrig et al., 2011). Heterogeneity is thought to determine biodiversity through three mechanisms (Stein et al., 2014): increasing the

available niche space, promoting species coexistence (Potts et al., 2004; Regolin et al., 2020); providing refugia from environmental extremes, enabling species persistence (Fjelds  et al., 2012); and, over the long term, promoting speciation through niche space differentiation (Antonelli and Sanmart n, 2011). The implication of this relationship is that the temporal process of the temporal process of landscape simplification through the loss of heterogeneity will result in a loss of biodiversity.

However, increasing environmental heterogeneity may not always promote higher biodiversity. Temporal increases in environmental heterogeneity within a given area will eventually reach a point where the reduction in the amount of suitable space for individual species increases the likelihood of stochastic extinctions, referred to as an “area-heterogeneity trade-off” (Allouche et al., 2012). Therefore, at very high levels of heterogeneity, suitable habitat patches may be so fragmented that they cannot support viable populations resulting in overall fewer species present. Hence, biodiversity peaks at intermediate levels of environmental heterogeneity (Fahrig et al., 2011).

While spatial aspects have been frequently explored (e.g. Moreno-Rueda and Pizarro, 2009; Chiron et al., 2010; Stein et al., 2014; Tonetti et al., 2023), the temporal dynamics have not received the same level of focus. We define the temporal dynamics of spatial environmental heterogeneity as changes through time in the variability of environmental variables across space. This is a separate concept to temporal heterogeneity which refers to variability through time that is experienced homogeneously across a spatial extent (Menge and Sutherland, 1976; Stein et al., 2014). Crucially, understanding these dynamics is fundamental to ecological theory as well as being important practical context for ecological interventions aiming to bend the curve of biodiversity loss. Among 100 key research questions in ecology, the influence of spatial and temporal environmental heterogeneity on diversity across scales remains unanswered (Sutherland et al., 2013). Despite this importance there are currently no systematic reviews addressing temporal dynamics of heterogeneity – biodiversity relationship based on longitudinal temporal studies.

Changes to spatial environmental heterogeneity through time present important shifts in niche space availability (MacArthur and Levins, 1967; Stein et al., 2014). Species-specific responses to these changes are mediated by traits including trophic level, dispersal ability, and life history (Hutchinson, 1957). The cumulative effect of these trait-mediated responses produces the community level biodiversity response to changes in environmental heterogeneity (McGill et al., 2006). Over multiyear time scales, meta-community processes such as dispersal, colonization, and local extinction will play a strong role in biodiversity responses alongside changes in niche availability (Leibold et al., 2004; Jarzyna et al., 2025). Conversely, short-term dynamics may be characterized by responses to sudden changes in heterogeneity, refugia from climatic extremes that promote species persistence, and seasonality, giving rise to interlinked spatial and temporal partitioning through storage effects (Ryo et al., 2019; Doxa et al., 2022; Chesson, 2000).

This gap in our current understanding of the effects of temporal environmental heterogeneity on biodiversity is an obstacle to enhancing ecological theory and hinders efforts to address the biodiversity crisis. In this study, we set out to determine the current state of knowledge regarding how temporal dynamics shape the spatial heterogeneity-biodiversity relationship and propose a conceptual framework to guide future research. We propose three priorities for future research: long-term trends, short-term dynamics, and interactions with spatial grain.

2 Methods

Following the PRISMA guidelines (Page et al., 2021), we conducted a comprehensive systematic literature search of Web of Science using a string capturing three key concepts: heterogeneity, biodiversity, and temporality (S1). We screened these results according to inclusion criteria that the study must be observational, original, and peer reviewed. It must also consider terrestrial ecosystems and not microorganisms. Either environmental heterogeneity and/or biodiversity must have been quantitatively sampled longitudinally, meaning at least two time points in the same place. In longitudinal studies, time is considered as an independent variable, allowing a deeper understanding of phenomena that are not observable with a cross-sectional approach (Lindenmayer et al., 2012). Longitudinal designs avoid the issues linked to space for time substitution studies that may lead to erroneous conclusions (Damgaard, 2019). The initial results of the search returned 2180 papers published between 1990 and 2024. After screening by title and abstract, 149 articles remained for full text screening, and a final group of 23 papers met the full screening criteria (Supplementary Figure S2).

Subsequently, we extracted the following key information from the selected papers: the spatial grain, the landscape type, the biodiversity metric used, along with the taxa studied and the timespan of biodiversity and heterogeneity sampling. Landscape types were categorized as agricultural, natural and semi-natural. Heterogeneity measures were categorized according to the typology outlined by Stein and Kref t (2015): vegetation, land cover, soil, topography, and climate. Spatial grains of heterogeneity analysis for each paper were harmonized to km. Where grain was reported as an area, the side length of the square plot or the diameter of the circle plot was recorded. The dates of biodiversity and heterogeneity samples were recorded where available.

Extracted relationships were grouped into five categories based on their primary significant direction, grounded in established ecological theory as shown in Figure 1c. “Positive” relationships were identified where at least one spatial or temporal scale showed a positive association, a result generally expected under niche theory (Stein et al., 2014). Conversely, “negative” relationships, defined by a negative association at one or more scales, were expected due to the area-heterogeneity trade-off where extreme fragmentation increases stochastic extinction (Allouche et al., 2012; Fahrig et al., 2011). Results were labeled non-significant when no significant associations

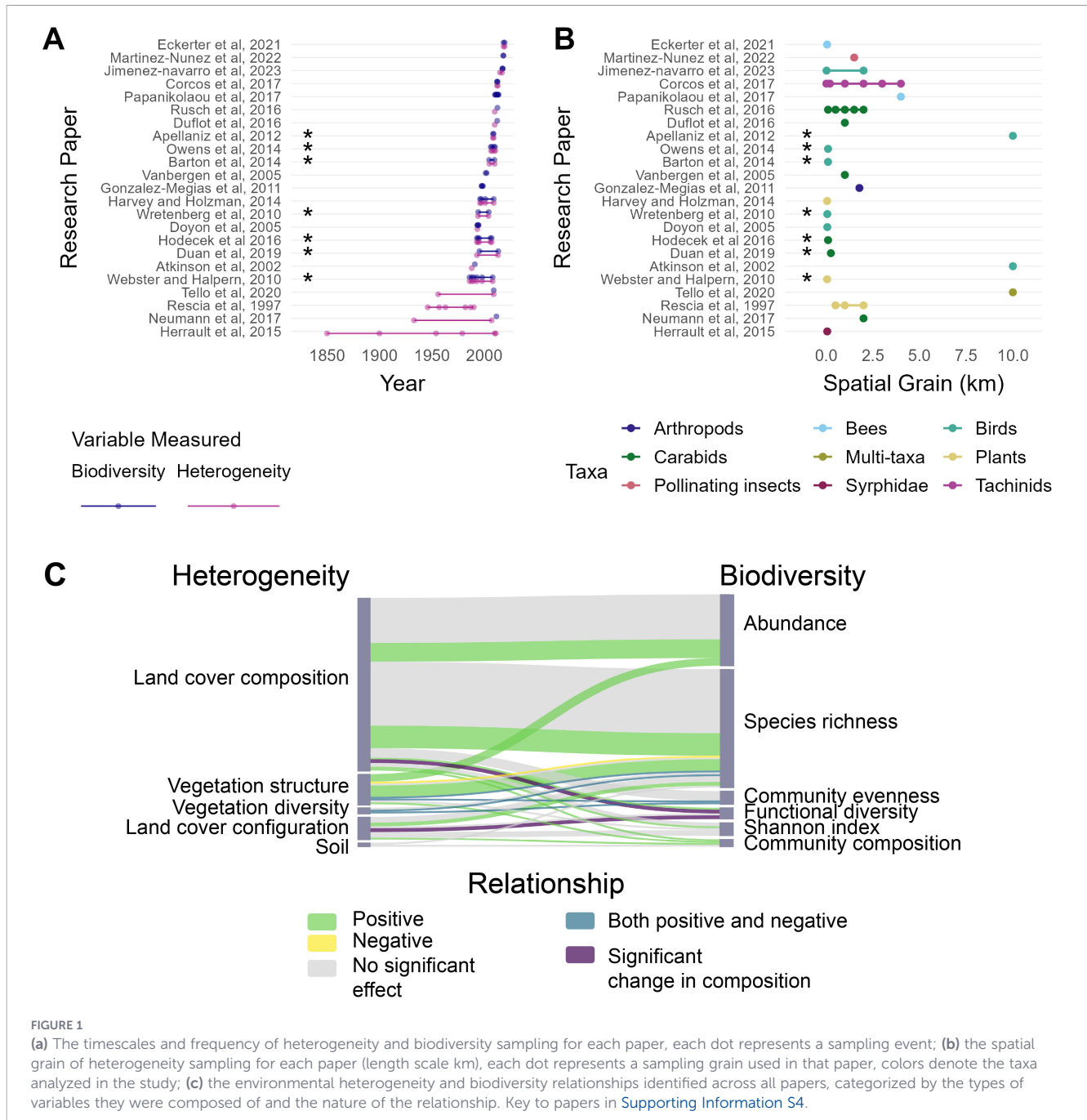


FIGURE 1

(a) The timescales and frequency of heterogeneity and biodiversity sampling for each paper, each dot represents a sampling event; (b) the spatial grain of heterogeneity sampling for each paper (length scale km), each dot represents a sampling grain used in that paper, colors denote the taxa analyzed in the study; (c) the environmental heterogeneity and biodiversity relationships identified across all papers, categorized by the types of variables they were composed of and the nature of the relationship. Key to papers in Supporting Information S4.

emerged across any scale, potentially indicating a spatiotemporal mismatch or response lag (Ryo et al., 2019). Finally, studies were categorized as “both positive and negative” where directions varied across scales, or “significant change in composition” where richness remained stable.

3 Results

We found just eight papers that measured both biodiversity and heterogeneity through time, 12 measured just biodiversity through time, and 3 only sampled heterogeneity temporally. Among the 23 that passed screening, there was a deficit of studies considering both

longer biodiversity and heterogeneity datasets. However, this seems to be driven by a broader pattern of a lack of long-term biodiversity data rather than historical heterogeneity data (Figure 1a).

Across the 20 of 23 papers that measured biodiversity through time, the independent variables fell into 3 categories: time since disturbance/intervention (Barton et al., 2014; Harvey and Holzman, 2014; Hodecek et al., 2016; Owens et al., 2014; Webster and Halpern, 2010; Eckarter et al., 2021; Doyon et al., 2005), seasonality (Apellaniz et al., 2012; Atkinson et al., 2002; Corcos et al., 2017; Dufflot et al., 2016; Gonzalez-Megias et al., 2011; Jimenez-Navarro et al., 2023; Martinez-Nunez et al., 2022), and long-term temporal intervals utilizing sampling years or intervals (Duan et al., 2019; Wretenberg et al., 2010; Papanikolaou et al., 2017; Rusch et al., 2016; Herrault et al., 2016; Vanbergen et al., 2005). Within these studies, the specific

environmental heterogeneity metrics used as independent variables included land cover composition (e.g. Shannon-Weaver index of land use), vegetation structure (e.g. coefficient of variation of stem density), and landscape configuration (e.g. ecological connectivity index) as shown in Figure 1c. We clarify that only the subset of eight studies re-measured heterogeneity metrics at each time point, they are identified with an asterisk in Figure 1.

Among all 23 papers, 5 heterogeneity datasets looked at time periods longer than 20 years compared to just 1 biodiversity dataset of that time scale. Conversely, 12 of the biodiversity datasets used were less than one year in duration, compared to only 1 heterogeneity dataset of that length. Figure 1a shows the frequency of biodiversity and heterogeneity sampling for all 23 papers. For studies that measured both variables longitudinally, apart from (Webster and Halpern, 2010), most had sparse sampling between the start and end of the study. For some studies, particularly (Duan et al., 2019) and (Barton et al., 2014), the sampling of each variable category did not take place simultaneously.

The spatial grain used to quantify heterogeneity also varied significantly, studies using plot-based designs varied in size from 0.01km to 10km (Figure 1b). However, it should be noted that the 10km grain seems to be an outlier, and the two papers that consider this scale both looked at vertebrate species. Across the 23 papers, only four papers looked at more than one spatial grain of environmental heterogeneity. Five papers based their analysis grain on the dispersal ability of the response taxa, two conformed to the resolution of the biodiversity data. However, this means that 12 out of the 23 papers did not give a specific justification for their chosen spatial grain for measuring heterogeneity.

Across all 23 papers, including the multi-taxa study by Tello et al. (2020), 8 papers analyzed birds, making them the most frequently studied taxon. Notably, this meant that of the 8 studies that considered both heterogeneity and biodiversity temporally, 4 used birds as their study taxa. The majority (14) of the studies were situated in agricultural landscapes, 4 semi-natural landscapes, 5 were based in natural landscapes.

4 Discussion

Despite claims of its importance, our understanding of the impacts of temporal dynamics of environmental heterogeneity on biodiversity is scattered and limited. The limited extent of literature meeting our criteria echoes a wider neglect of temporality in ecology in comparison to work that focusses on spatial phenomena (Ryo et al., 2019). The consequences of such gaps are captured by the term the “invisible present” which describes the shortsightedness that emerges without long-term research into processes that occur on timescales imperceptible to anecdotal observations (Magnuson, 1990). He suggested that “in the absence of the temporal context provided by long-term research, serious misjudgments can occur not only in our attempts to understand and predict change in the world around us, but also in our attempts to manage our environment”.

The gap in temporal data limits our ability to test how environmental heterogeneity–biodiversity relationships unfold through time. For example, an intervention predicted to increase

biodiversity on a spoil heap in Czechia through adding topsoil and planting trees resulted in lower functional diversity than naturally colonized areas when monitored over a 14-year period (Hodecek et al., 2016). This outcome underscores how essential temporal monitoring is to validate ecological predictions. Our framework allows evaluating long-term dynamics in the relationships, that cannot be captured by static predictions.

The main limitation preventing the inclusion of papers was inadequate quantification of heterogeneity. Of the 125 studies excluded during the full text screening, 72 were rejected on this basis. Frequently, the relationship between heterogeneity and biodiversity was only implied by extrapolation in the discussion of the paper. For example, studies investigating landscape-scale patterns often focus on different environmental factors, such as fire history or grazing intensity. However, these factors are frequently studied in a chrono-sequence of patches as a proxy for succession through time e.g (Hovick et al., 2015). Furthermore, many forestry and succession studies used treatment prescriptions as proxies for heterogeneity rather than taking quantitative measurements after intervention.

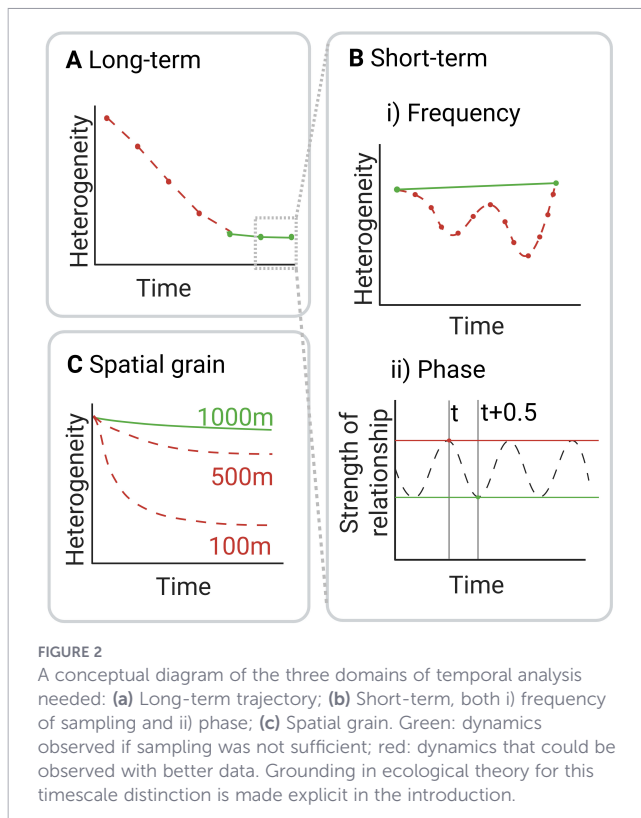
Despite limited literature, we found that between the same two variables the relationship between environmental heterogeneity and biodiversity varied significantly across different spatial and temporal scales (Figure 1c). While it is too early to draw firm conclusions, this reinforces the importance of investigating our three suggested domains of temporal dynamics as a structured way to address the knowledge gap.

What could a well-designed investigation into the temporal dynamics of the environmental heterogeneity biodiversity relationship reveal? With appropriate sampling and analysis, we would observe important differences in temporal behavior between study systems. There is a spatial precedent for context-dependent patterns. Despite a prediction of maximum biodiversity at intermediate levels of heterogeneity, specific systems are expected to display a variety of patterns depending on their taxonomic focus and scales of analysis (Allouche et al., 2012). The same ecological processes that give rise to spatial variation also govern how these systems behave through time. It is therefore plausible that they may also shape temporal dynamics.

Informed by our preliminary body of literature we identify three key domains, based on the ecological processes identified in the introduction, within which differences are expected (see Figure 2): (a) long-term trends, (b) short-term trends, and (c) differences across spatial grains. Where long-term trends refer to a cumulative trajectory defined by statistical properties such as trend stationarity, short-term dynamics are events that occur within the period of a trajectory (Ryo et al., 2019). Distinguishing between systems based on these temporal variables would allow us to better understand and predict the effects of past changes and forecast the impacts of future changes and interventions.

4.1 Long-term trends

Identifying the trajectory, the long-term variability of a system, is crucial to understanding big picture changes taking place in ecosystems (Ryo et al., 2019). There is evidence for long term changes in environmental heterogeneity, such as increasing



heterogeneity since the 1870s in lowland Czech Republic along with simultaneously decreasing heterogeneity at higher elevations (Sychrová et al., 2024). Identifying how these trends are associated with biodiversity trends would clarify an important explanatory variable for biodiversity conservation. This association can be complex, we identified emerging evidence for an effect of historical heterogeneity on current biodiversity (Herrault et al., 2016; Neumann et al., 2017). The observation of lag effects, and extinction debt, operating on the over decades significantly expands the timescale that we need to consider relevant when describing biodiversity patterns related to heterogeneity (Kuussaari et al., 2009). This also suggests that the effects of current conditions will play a strong role in determining the success of restoration efforts in the future. Going forward, sampling needs to take place over decades long time scales in the same study system so that we have a temporally continuous record of changes.

4.2 Short-term dynamics

Looking into the intermediate time points of a process of change with more frequent sampling enables us to better understand the paths taken in processes of transition, or the complexity of a stable system. Furthermore, frequent sampling allows us to uncover patterns that are cyclical in nature and the potential differences in the environmental heterogeneity biodiversity relationship between phases. We found that where the heterogeneity-biodiversity relationship was sampled intra-annually, a seasonal variability often emerged, particularly in agricultural landscapes (Apellaniz et al., 2012; Atkinson et al., 2002; Corcos et al., 2017; Dufлот et al., 2016; Gonzalez-Megias et al., 2011; Jimenez-Navarro et al., 2023;

Martinez-Nunez et al., 2022). In these studies, the yearly cycle of agriculture is likely to be interacting with changes in the resource requirements of taxa and seasonal shifts in resource availability. For example, Apellaniz et al. (2012) found that species richness of insectivorous birds related to primary productivity in spring and autumn, whereas richness of seed-eaters only showed a positive association with habitat heterogeneity during the spring. They hypothesized that when grain is plentiful in autumn, seed-eaters may focus on more favorable sites and therefore do not need to diversify their feeding and associate with heterogenous landscapes. However, the crop landscape can also be perceived by some insects as hostile in the summer due to crop harvest, highlighting that the effect depends on whether a species is more reliant on crops or the matrix (Corcos et al., 2017). Over a seasonal timescale spatial environmental heterogeneity seems to generate temporal niche opportunities, linking spatial and temporal partitioning through storage effects (Chesson, 2000).

Testing this effect in agriculturally less intensive areas would be important to establish whether there is a similarly large seasonal influence without agricultural cycles. Importantly, these patterns can only be observed with frequent sampling within the time frame of one year. Not only does this capture intra-annual changes but also increases the likelihood of sampling the phase of an annual cyclical process in which a relationship is apparent. If for instance Apellaniz et al. (2012) had only sampled annually during spring, the positive autumnal relationship between seed-eating birds and habitat heterogeneity would not have been observed.

4.3 Trends at different spatial grains

Analyses undertaken at inappropriate spatial grains may give rise to results that are artifacts rather than real system dynamics (Rescia et al., 1997). Within studies, we identified different trends through time at different spatial scales. Rescia et al. (1997) found that configurational heterogeneity was the most important factor in explaining woody plant diversity at their smallest spatial grain of analysis, a 250m radius, and increased through time. However, at a 1km radius heterogeneity decreased through time and was not linked to biodiversity. Similarly, different effects on insect biodiversity were observed with different spatial scales by Corcos et al. (2017). In this instance, interactions with seasons increased with increasing spatial grain. Species perceive spatial environmental heterogeneity according to their specific characteristics of mobility, resource use, and life history (Wiens, 1989; Levin, 1992). It follows that the composition of the ecological community, and the specific species response grains, will determine the complex response of biodiversity as a whole.

This also means that selecting just one spatial grain can limit the explanatory power of a study. For example, (Webster and Halpern, 2010) used a small spatial grain of 0.1km², which they suggest could have limited their ability to capture broader patterns. This was also noted by Wretenberg et al. (2010) who suggested that the effects of landscape heterogeneity operate at larger spatial scales than they investigated. By contrast, Atkinson et al. (2002) struggled to identify the mechanism driving the association of bird species to mixed agricultural landscapes due to their 10km-by-10km scale of analysis being very coarse. The inclusion of temporal dynamics gives us an

extra lens with which to distinguish the specific differences in the environmental heterogeneity biodiversity relationship between ecosystems at different spatial grains.

4.4 Implications

Together, these three domains show temporal dynamics are key to understanding environmental heterogeneity biodiversity relationships. We can draw a parallel with the insights gained from the area-heterogeneity trade off theory. Understanding the limits and contingencies of the environmental heterogeneity biodiversity relationship can allow for appropriate conclusions to be drawn for specific systems (Lawton, 1999; Linquist et al., 2016). Assuming a positive linear spatial relationship between environmental heterogeneity and biodiversity could lead to environmental heterogeneity maximization being prioritized and unintended deleterious consequences (Fahrig et al., 2011; Allouche et al., 2012). Similarly, by understanding how temporal characteristics of the environmental heterogeneity biodiversity relationship vary we can be more specific with interventions and avoid unintended outcomes (Hodecek et al., 2016).

The importance of spatiotemporal monitoring of environmental heterogeneity has been highlighted by Schmeller et al. (2018) as one of eight Essential Biodiversity Variables (EBVs). Environmental heterogeneity could soon be operationalized as an early warning variable for environmental change driving biodiversity loss. We suggest that our typology of three temporal domains can help prioritize research efforts with long running high resolution remote sensing products. Looking to the future, we can identify remote sensing products with currently limited temporal extent that will become useful once sufficient sampling has accumulated. It would be prudent to also establish localized higher resolution heterogeneity data collection in sites already dedicated to long term biodiversity monitoring. Intra-patch heterogeneity sampling at finer resolution such as identifying vegetation structure changes is harder to achieve with remote sensing products. In these cases, long term on the ground monitoring will be needed to establish time series data. If coordinated as a spatial network with a nested structure, a variety of spatial grains across a spatial extent that includes many different ecologies could be monitored.

5 Conclusion

We found a paucity of studies that sampled biodiversity and heterogeneity longitudinally through time, reflecting a wider neglect of temporality in ecology. Nevertheless, where research addressed these issues, we observed complex temporal dynamics that distinguish ecological systems from each other. Our typology suggests that short-term dynamics, long-term trajectories, and the temporal interaction with spatial grain are fruitful avenues for future investigation. Exploring these complexities further will not only provide additional insight into ecological theory but also inform practical interventions in conservation and management, ensuring we can adequately understand the changes that have already occurred and predict those to come.

Author contributions

JG: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing, Project administration. PMVB: Conceptualization, Supervision, Writing – original draft, Writing – review & editing. YS: Conceptualization, Funding acquisition, Project administration, Supervision, Writing – original draft, Writing – review & editing.

Funding

The author(s) declared that financial support was received for this work and/or its publication. This work was supported by the CML Impact Fund.

Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declared that generative AI was not used in the creation of this manuscript.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2026.1731666/full#supplementary-material>

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