Title: From environmental heterogeneity to stability: beta-diversity stabilises biomass across space

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Abstract

Understanding how biodiversity influences ecosystem stability across heterogeneous landscapes is a central challenge in ecology. The spatial insurance hypothesis proposes that turnover in species composition stabilises ecosystem processes in heterogeneous environments by allowing species to occupy the habitats where they perform best. Yet, empirical evidence remains mixed, partly due to confounding factors and overlooked causal mechanisms. We combined metacommunity simulations and a field experiment with marine benthic communities to test how β-diversity (species turnover) affects the spatial stability of biomass. The simulations, which varied the strength of selection via niche overlap, revealed that turnover enhanced spatial biomass stability in scenarios with low to medium niche overlap, but only when environmental heterogeneity was statistically accounted for. This stabilising effect weakened as niches overlapped more. In our field experiment, high turnover similarly mitigated the negative impact of environmental heterogeneity on spatial biomass stability. Together, these results provide strong support for the spatial insurance hypothesis, demonstrating that species turnover can stabilise ecosystem processes such as biomass production across heterogeneous landscapes. Crucially, failing to account for environmental heterogeneity can mask this effect, leading to the mistaken conclusion that turnover is neutral or destabilising. Our study highlights the importance of a causal framework that disentangles the effects of environmental heterogeneity and β-diversity, helping to resolve previous inconsistencies and advance a mechanistic understanding of biodiversity–stability relationships at landscape scales.

Introduction

Understanding how biodiversity shapes ecosystem processes across different spatial scales remains a central challenge in ecology (Gonzalez et al. 2020, Mori et al. 2021, Loreau et al. 2021, Le Provost et al. 2023, Ali 2023). Research has primarily focused on local scales, often intentionally striving to minimise the influence of environmental heterogeneity. Through hundreds of experiments, we have learned that biodiversity loss and associated changes in local species interactions generally have negative consequences for ecosystem processes (Cardinale et al. 2012). However, our knowledge of how biodiversity affects ecosystem processes at larger scales—the scales relevant for landscape management—is still limited (Gonzalez et al. 2020, Gamfeldt et al. 2023). Because many ecological analyses remain correlational (Franks et al. 2025), we adopt an explicitly causal framework from the outset to separate the role of turnover from environmental heterogeneity .

An increase in spatial scale is generally associated with increased spatial environmental heterogeneity (Hart et al. 2017). Typically, a larger landscape comprises more habitat types and ecological niches, creating a mosaic of environmental conditions across space. As species

respond differently to these spatially variable environmental conditions, a large landscape is expected to host more species than a smaller one, with distinct species compositions emerging between different habitat patches (Stein et al. 2014). High environmental heterogeneity is thus expected to promote high species turnover (i.e. replacement, an aspect of β-diversity). In the context of ecosystem processes (e.g., biomass production), species' different responses to the environment should ensure stability if different species drive a process in different environments–the spatial insurance hypothesis (Loreau et al. 2003, van der Plas 2019). It follows that, if β-diversity is reduced, the spatial stability (invariability) of ecosystem processes should decline. Yet, empirical testing of this prediction is inconclusive (van der Plas et al. 2023). Previous studies have shown mixed results, with some supporting the stabilising effect of β-diversity, e.g. Chen et al. (2022), while others indicate no relationship, e.g. Yang et al. (2022). This discrepancy in empirical findings indicates a gap that may stem from differing analytical approaches and from treating these relationships as correlational, which may obscure direction and magnitude of effects. Here we clarify mechanisms by quantifying environmental heterogeneity and modelling turnover as a mediating pathway to spatial stability (sensu causal mediation).

Spatial scale can fundamentally alter the balance among the core processes of community assembly—selection, drift, and dispersal (Vellend 2016). At larger spatial extents or in fragmented landscapes, dispersal limitation (e.g., barriers preventing high-functioning species from reaching suitable habitats) and demographic stochasticity (drift) can decrease the role of environmental filtering—the major cause of species sorting (Nekola and White 1999, Hubbell 2001, Chase 2010, Catano et al. 2025). Dispersal limitation and drift may thus generate patterns of species turnover decoupled from species' niche differences (Leibold et al. 2004, Vellend 2010). The spatial insurance hypothesis assumes that β-diversity relevant for stability is mainly the result of selection (i.e. species sorting)—where the local environment favours species that optimise ecosystem functioning. Selection-caused turnover is predicted to sort high functioning species into their respective environmental optima, thereby enhancing spatial stability of ecosystem processes across heterogeneous landscapes (Loreau et al. 2003). In contrast, turnover driven by drift or dispersal constraints may result in weak links between species traits and the environmental conditions, potentially weakening the spatial stability of ecosystem processes (van der Plas et al. 2023). Studies on β-diversity often conflate turnover caused by selection with that caused by neutral or dispersal-driven dynamics, explaining why empirical tests of spatial insurance remain equivocal (van der Plas et al. 2023). To clarify these scale-dependent mechanisms, it is important to disentangle how the shifting balance of assembly processes shapes β-diversity's consequences on ecosystem stability. Our study addresses this by testing whether turnover consistent with species sorting—not β-diversity per se—serves as the driver of spatial ecosystem stability.

Spatial β-diversity measures the difference in species composition between different sites in a metacommunity (Whittaker 1960, Anderson et al. 2011). To better isolate mechanisms, these compositional differences can be separated into two components: nestedness and turnover, which are driven by different mechanisms (Baselga 2010), see Figure 1. Nestedness captures abundance gradients and richness differences, whereby assemblages at one site can form

subsets of another. Turnover defines the replacement of species between sites, often driven by environmental filtering and niche differences (Vellend 2016). While both components contribute to overall β-diversity, turnover is the component most directly linked to the niche-based mechanisms underlying the spatial insurance hypothesis. Partitioning β-diversity (or focusing analysis on the turnover component) into these two components allows us to disentangle the relative contributions of nestedness and turnover to overall community variation (Baselga 2010, 2013). This approach can significantly improve our understanding of the relationship between community change and ecosystem processes by highlighting the mechanisms driving biodiversity patterns (Mori et al. 2018, Omidipour et al. 2021).

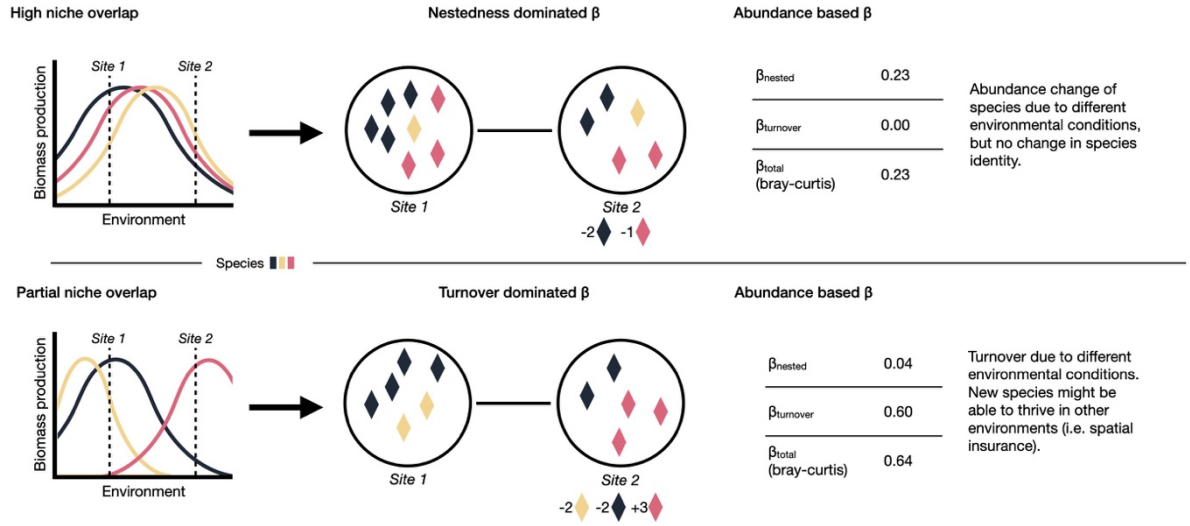

Figure 1: The Bray-Curtis distance shows the abundance-based total dissimilarity between the two communities. This can be partitioned into its turnover component (balanced variation in abundance between sites) and nestedness component (unidirectional abundance gradients). Similar patterns of species distribution could arise through drift and dispersal.

Spatial stability, in the context of this study, is defined as spatial invariability of biomass production, quantified as the ratio of biomass production of two sites, similar to the inverse of the coefficient of variation used in other studies (Daleo et al. 2023). Because our focus is on purely spatial differences in ecosystem functioning at a single point in time, this provides a more direct and relevant metric than those incorporating temporal dynamics.

The term “stability” often carries a temporal connotation, as ecological stability is commonly assessed through temporal variability, where fluctuations in ecosystem properties over time determine resilience or resistance to change (Donohue et al. 2016, Gonzalez et al. 2020). Metrics such as spatial asynchrony extend this temporal framework by describing how out-of-phase temporal fluctuations among local communities stabilise ecosystem functioning at broader scales (Loreau et al. 2003, Loreau and de Mazancourt 2013, Wang et al. 2021, 2024, Qiao et al. 2023). Yet, these metrics require repeated time points or genuinely asynchronous

fluctuations across sites. If we only have data on ecosystem functioning at one time point, or if local communities are relatively stable over time, or if local communities respond synchronously to environmental variation in unison (e.g., a uniform growing season), spatial asynchrony metrics will not effectively capture purely spatial variations in ecosystem processes. Even when spatial asynchrony is high, sites may differ substantially in their mean levels of ecosystem functioning, a purely spatial property that asynchrony does not capture (Appendix S1: Figure S1 A). Given these limitations, spatial stability measured as invariability across space (Appendix S1: Figure S1 B) provides a more direct and appropriate metric for understanding how β-diversity influences the consistency of ecosystem functioning across a landscape.

In line with the insurance hypothesis, we predict that in landscapes characterised by significant environmental heterogeneity, high spatial turnover—driven by species sorting according to environmental niches—will facilitate spatial stability (of e.g. biomass production, which we use as our focal ecosystem function). This prediction only holds if species have different environmental optima (niches) where they are the superior competitors and their productivity is maximised (Loreau et al. 2021). When different species thrive under different conditions, they maintain biomass production at the landscape scale even though species composition varies across sites. Conversely, turnover caused by ecological drift or dispersal, such as the presence of sink populations or invasive species (Gilbert and Levine 2017), could decrease production by introducing species that are less adapted to local environmental conditions (Vellend 2016). Moreover, differences among local sites in resource availability and environmental conditions can directly decrease the spatial stability of biomass production. Productivity will be high at some sites and low in others, thereby causing high variation across a landscape. Because such differences may covary with the effect of β-diversity on spatial stability, failing to seperate them out could introduce omitted variable bias, leading to an inaccurate estimation of β-diversity's impact on biomass production stability (Rinella et al. 2020, Byrnes and Dee 2025), see Figure 2.

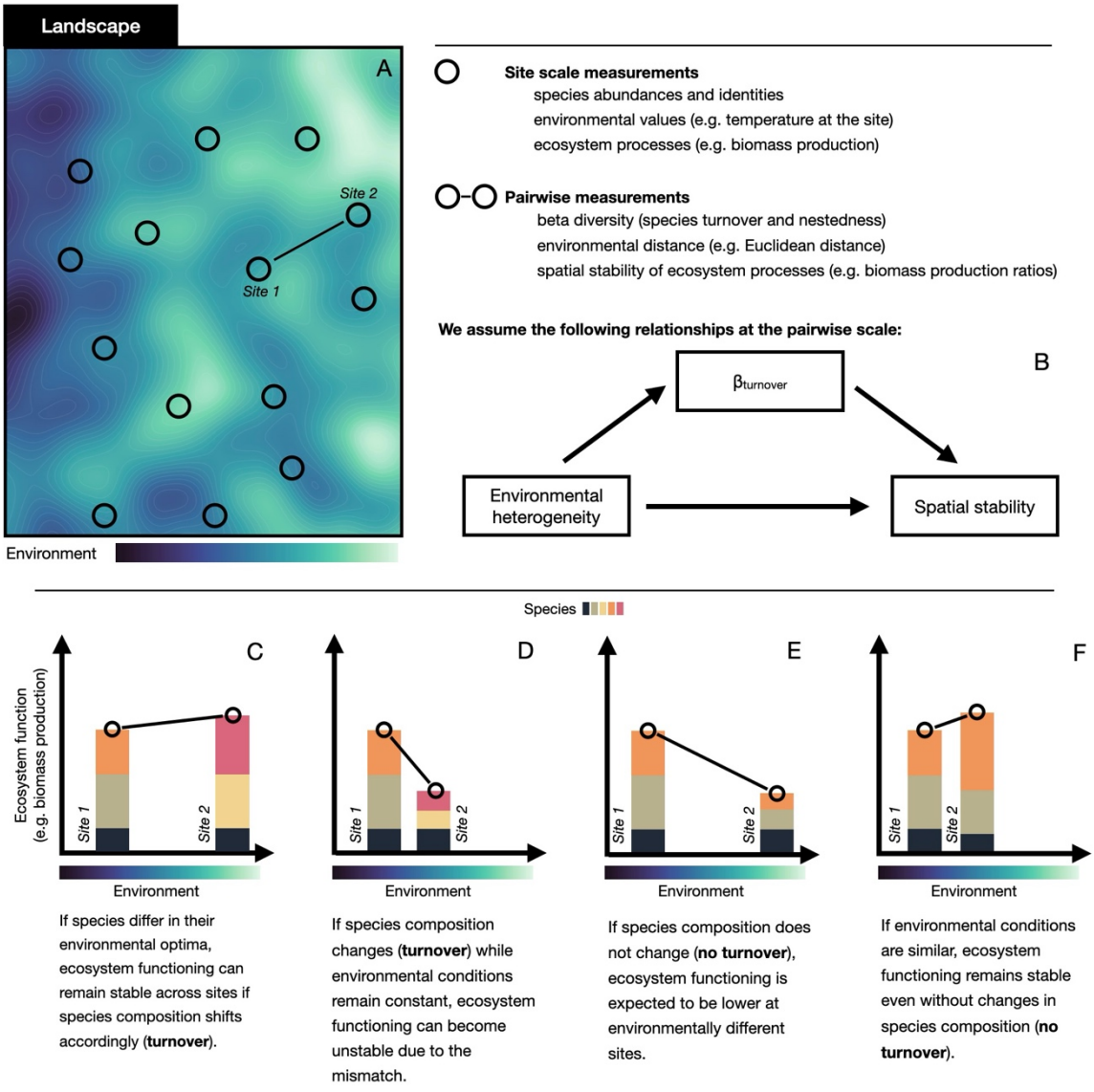

Figure 2: The effects of biodiversity on ecosystem stability can be measured at different scales. In A, a metacommunity consists of multiple sites, which can be aggregated in pairs to measure how β-diversity influences the spatial stability of ecosystem processes (e.g., biomass production) in the landscape. These sites differ in species identity and abundance, environmental conditions, and baseline levels of ecosystem processes. In B, we present a conceptual model illustrating the relationship between β-diversity (species turnover), environmental heterogeneity, and the spatial stability of ecosystem processes. To accurately assess the role of β-diversity, environmental heterogeneity must be accounted for statistically or experimentally, because the effect of β-diversity depends on environmental heterogeneity. In C, high turnover combined with high environmental heterogeneity can maintain high spatial stability in ecosystem processes. In D, high turnover under constant environmental conditions can lower spatial stability due to a mismatch between community composition and environmental conditions. In E, low turnover under high environmental heterogeneity reduces spatial stability across sites. In F, low turnover under low environmental heterogeneity results in high spatial stability in ecosystem processes.

We apply a causal framework for the spatial stability of biomass production with β-diversity serving as a mediator (Figure 2 B). Specifically, we measure environmental heterogeneity, β-diversity, and spatial stability at the same hierarchical level across the landscape (pairs of sites). This integrated approach enables us to disentangle the direct influence of β-diversity on spatial stability from the confounding effects of environmental heterogeneity, thereby minimising omitted variable bias. It is our aim to potentially elucidate some of the inconsistencies observed in previous empirical studies (see van der Plas et al. 2023) and contribute to a more robust foundation for predicting how changes in environmental heterogeneity and β-diversity affect the spatial stability of biomass production at larger spatial scales.

We tested the following three hypotheses:

1. High spatial turnover in species composition stabilises biomass production across local patches in heterogeneous environments.
2. The spatially stabilising effect of turnover is strongest when niche overlap is low and environmental heterogeneity is high.
3. Accounting for environmental heterogeneity is essential for accurately assessing the relationship between turnover and stability, and its influence will significantly alter the perceived effect.

We first employed metacommunity models (Thompson et al. 2020) to simulate scenarios with varying species niche widths. This approach allowed us to investigate how niche overlap influences the turnover-stability relationship in spatially heterogeneous environments. We then conducted a field experiment with marine benthic organisms–a system with strong environmental filters and high dispersal–to test the predictions from our models in a natural ecosystem. In this paper, we focus exclusively on spatial stability.

Methods

Metacommunity Simulations

We simulated metacommunities with several niche breadth scenarios (Table 1) using a Lotka–Volterra–based metacommunity model (Thompson et al. 2020), with each scenario repeated 100 times. This model includes density-independent abiotic responses of species to the environment, local density-dependent biotic interactions, and dispersal (Thompson et al. 2020). Each metacommunity consisted of 50 sites seeded with 20 species with different but evenly spread environmental optima (i.e. the environment where a species has its highest growth rate). The maximum growth rate for each species was drawn from a Poisson distribution $r_i \sim Poisson(\lambda = 5)$ to allow for high, but rare, growth rates. The simulations ran for 200 timesteps (generations) with a constant environment within a site (value between 0 and 1). This duration ensured that the local environment was the main driver of the species abundances, not initial abundances of the local site or adjacent sites. Dispersal probability–to

allow for species sorting–was set to 1% but ultimately depended on the distance between sites. We included the species' biomass (equal to the abundance) data and the environment at the last timestep at each site for further analysis. Using this data, we calculated the spatial environmental heterogeneity, spatial (between sites) biomass stability, and biomass-based turnover for pairs of sites (see *Data Analysis*).

Table 1: Four (A-D) scenarios for metacommunity simulations. The niche breadth is defined as the standard deviation of the Gaussian response to the environment (environment ranges from 0 to 1). Larger niche breadths result in a higher niche overlap.

ID	Scenario	Niche breadth	Number of simulations
A	Low niche overlap	0.1	100
B	Medium niche overlap	0.2	100
C	High niche overlap	0.5	100
D	Complete niche overlap	5.0	100

Experiment with marine benthic communities

The experiment was conducted between 7 July and 5 September 2022 in the Tjärnö archipelago on the Swedish west coast (58°52'30.0"N, 11°08'42.0"E). This archipelago is a shallow coastal environment situated in the northeastern arm of the Skagerrak, characterised by rocky shores, sandy beaches, and mudflats. The marine environment is characterised by variable salinity, generally ranging between around 15–30 PSU, and moderate water temperatures (ca. 15–20°C) during summer (University of Gothenburg 2023). Local hydrodynamic conditions create spatial heterogeneity in turbidity, wave exposure, and water flow, supporting a diverse benthic community typical of hard-bottom substrates (Berntsson and Jonsson 2003). Common sessile and sedentary animal species include barnacles (*Amphibalanus improvisus*), bryozoans (*Electra pilosa, Membranipora membranacea, Callopora rylandi*), ascidians (*Ascidiella scabra, Ciona intestinalis*), and hydrozoans (*Clytia sp., Laomedea flexuosa*). These organisms frequently colonise artificial structures such as boat hulls in addition to natural rocky habitats (Berntsson and Jonsson 2003).

A total of 150 polymethyl methacrylate (PMMA) panels (10 x 11 cm) were deployed across 50 sites (Figure 3). These sites were selected based on a priori geographical data to cover a

large portion of the environmental gradient in the archipelago. Environmental variables included water depth, turbidity, and wave exposure, with a minimum distance of 50 metres between sites. The exact positions of the sites were randomised. Settling panels were mounted on rigid frames suspended from surface buoys, maintaining a constant distance to the water surface of 3 m or 6 m at all sites. The two depth strata were used to increase environmental heterogeneity among sites with otherwise similar exposure and temperature. Each site received three settling panels, with additional panels for a different experiment. The panels were destructively sampled sequentially after 34, 47, and 60 days, with one panel collected at each sampling point. Environmental data were measured at each site and included the depth of the settling panels, the distance from the panels to the seabed, and the overall depth (distance from the surface to the seabed), water temperature (recorded hourly, with mean, minimum, maximum, and coefficient of variation), light intensity (hourly, with mean and coefficient of variation), salinity, oxygen concentration, Secchi depth for water clarity, and water flow. Water flow was approximated at three time points using gypsum block dissolution over approximately 30 hours (Muus 1968, Porter et al. 2000). Temperature and light were measured by deploying one light/temperature logger at each site (Onset MX2202 HOBO Pendant and Onset UA-002-64 HOBO Pendant).

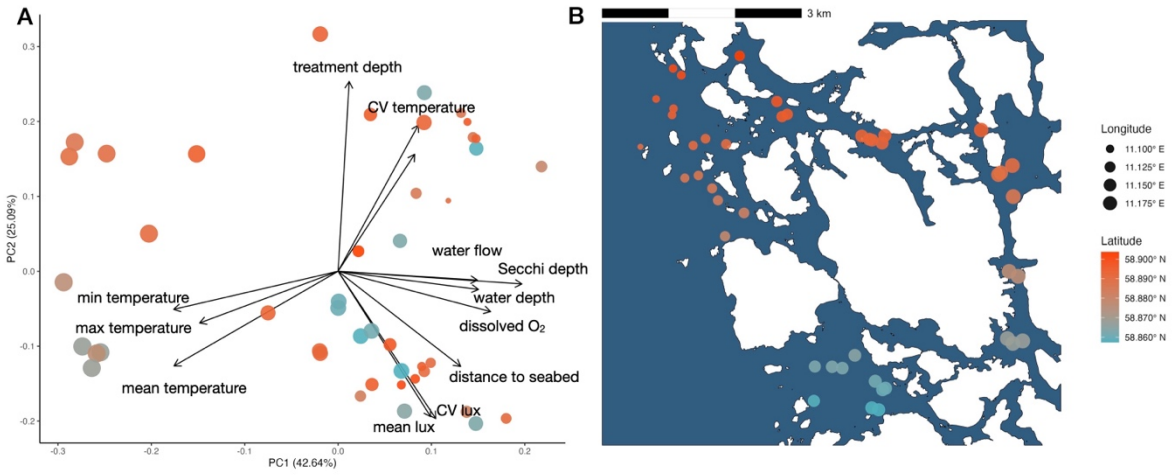

Figure 3: Principal component analysis of environmental variables (min: minimum observed value in; max: maximum observed value; CV: coefficient of variation of observed values) (A) and map of sites (B). The closer the points are on the PCA, the more similar their environments are. The colour and size of the points depict the position of the points on the map (longitude, latitude).

Benthic organisms from the surrounding environment naturally settled on the panels (Appendix S1: Figure S2). Organisms were identified visually to the highest taxonomic resolution feasible and grouped into five operational taxonomic units (OTUs): barnacles (mostly *Amphibalanus improvisus*), bryozoans (*Electra pilosa, Membranipora membranacea, Callopora rylandi*), *Ascidiella scabra*, hydrozoans (*Clytia sp., Laomedea flexuosa*), and *Ciona intestinalis*. After sampling, organisms were carefully scraped off the panels, sorted by

OTU, and weighed to assess wet, dry, and ash-free dry weights. To obtain dry weights, the organisms were dried in a drying oven at 60°C for 48 hours. Ash-free dry weights were determined by combusting the dry biomass at 500°C in a muffle furnace and subtracting the remaining ash weight from the dry weight, providing a reliable measure of organic matter and biomass energy content (Weil et al. 2019).

During the experiment, six sites were lost due to buoy detachment, reducing the number of sites from 50 to 44 prior to the first time point. Another site was lost between the second and third time point, decreasing the number to 43. To quantify environmental heterogeneity between the sites, principal component analysis (PCA) was conducted using all measured environmental variables, excluding those used for a priori site selection. We summarised correlated environmental variables with PCA and computed Euclidean distances in the first three PC axes (PC1: 43%, PC2: 25%, PC3: 10%; 78% cumulative) to minimise collinearity and emphasise dominant environmental gradients relevant to assembly. Multivariate dispersion was then calculated from these distances. Each sampling point (at 34, 47, and 60 days) was analysed independently, as the focus of this study was on spatial variability rather than temporal dynamics.

To visualise species' realised environmental niches, we fitted generalised additive models (GAMs) for each OTU with ash-free dry weight as the response and environmental PC1–PC3 as predictors. A hurdle approach was used to account for zero-inflated biomass (binomial presence model combined with a Tweedie biomass model). Expected ash-free dryweights were predicted across PC1 and PC2 while holding PC3 at its median and shown as heatmaps.

Data Analysis

All statistical analyses were conducted using R version 4.4.2 (2024). We investigated the relationships among spatial stability of biomass, turnover, and environmental heterogeneity in both simulated and experimental metacommunities using the same statistical methods. We computed pairwise measures for all possible pairs of sites within each metacommunity to assess how differences in community composition and environmental conditions relate to spatial stability.

To derive these pairwise measures, we employed a distance-based approach using the upper triangle of the distance matrix. By restricting our analysis to the upper triangle, we ensured that each pair of sites was only included once, thereby avoiding redundancy in the data. This method provided us with 1225 unique site pairings for the simulated metacommunities (with 50 sites) and 903 or 946 pairings for the experimental metacommunities (with 43 or 44 sites, respectively).

Because individual sites were represented in multiple pairwise measures, our approach introduced pseudoreplication (Arnqvist 2020). We addressed this issue by incorporating Bayesian mixed-effects regression models with multi-membership random effects (Bürkner 2018, Park and Beretvas 2020, Wurz et al. 2024). This modelling strategy accounts for the non-independence of observations, as each pair involves two sites that may appear in other

comparisons, ensuring that our parameter estimates, uncertainty of estimates, and inference on the relationships among spatial biomass stability, β-diversity, and environmental heterogeneity remain robust.

Since we were interested in purely spatial effects, we fitted separate models for each time point.

β-Diversity and Turnover

We calculated the balanced variation component of the Bray–Curtis dissimilarity (i.e., the abundance-based turnover component) for each pair using the *betapart* package in R (Baselga et al. 2023). This metric quantifies the extent of species turnover between two sites while considering species abundances, thereby capturing changes in community composition attributable to species replacement rather than differences in total abundance. The partitioning of the Bray–Curtis dissimilarity d_{BC} is given by Equation 1.

Equation 1:

$$d_{BC} = d_{BC\ balanced\ variation} + d_{BC\ abundance\ gradient}$$

where $d_{BC\ balanced\ variation}$ is the balanced variation (turnover) component and $d_{BC\ abundance\ gradient}$ is the abundance gradient (nestedness) component (Baselga 2013). In our analysis, we focused on $d_{BC\ balanced\ variation}$ to directly assess species turnover (Anderson et al. 2011).

We selected this abundance-based turnover metric for two primary reasons. First, by separating species replacement from overall abundance differences, we avoid confounding the effect of turnover with simple gains or losses in total community abundance, aligning better with the mechanisms of the spatial insurance hypothesis. Second, unlike metrics based on presence/absence data (e.g., the Jaccard index), $d_{BC\ balanced\ variation}$ utilises species abundance information, making it more sensitive and appropriate for detecting compositional turnover where changes in relative abundance are significant while species identities overlap largely between places.

Environmental Heterogeneity

Environmental heterogeneity between sites was quantified using multivariate dispersion. For the experimental data, we conducted a Principal Component Analysis (PCA) on the measured environmental variables—excluding those used for initial site selection—to reduce dimensionality and identify the main environmental gradients. The first three principal components (PC1: 43%, PC2: 25%, PC3: 10%) were retained as they captured the majority of environmental variation. We then calculated the Euclidean distances between sites in this reduced environmental space using the *vegan* package (Oksanen et al. 2024). This approach ensures our heterogeneity metric reflects the dominant environmental gradients driving community structure across the archipelago. These distances served as our measure of environmental heterogeneity for each pair. For the simulated metacommunities, each site was assigned a single environmental value ranging from 0 to 1. We calculated environmental

heterogeneity between sites using the same Euclidean distance function. In this univariate case, the Euclidean distance is equivalent to the absolute environmental difference between two sites.

Spatial Biomass Stability

We quantified spatial stability as the ratio of the smaller to the larger biomass value in each site pair. For each site, total biomass was calculated by summing the abundances (in simulations) or the ash-free dry weights (in the experiment) of all species present. Spatial stability was computed using Equation 2.

Equation 2:

$$Spatial\ stability\ = \frac{min(B_i, B_j)}{max(B_i, B_j)}$$

where B_i and B_j represent the total biomass at site *i* and site *j*, respectively. This metric reflects variability in biomass between sites and is bounded between 0 and 1. This bounded nature makes it suitable for Beta regression. The metric is strongly related to the inverse of the coefficient of variation (Wang and Loreau 2014, 2016). A higher value indicates lower variability in total biomass between sites, reflecting greater stability of ecosystem processes at the regional scale.

Statistical Modelling

To investigate relationships among spatial stability, environmental heterogeneity, and turnover, we employed Bayesian mixed-effects regression models using the brms package in R (Bürkner, 2018). All continuous predictors were standardised (z-transformed) to a mean of 0 and a standard deviation of 1, facilitating convergence and comparability of effect sizes.

Because our response variable, *spatial stability*, is continuous and constrained between 0 and 1, we employed a Beta regression framework to capture its distribution appropriately.

We fitted two main models for each of the three time points:

1. **Full Model:**
   spatial stability ~ turnover × environmental heterogeneity + (turnover × environmental heterogeneity | mm($site_i$, $site_j$))
   This model evaluates the interactive effects of turnover and environmental heterogeneity on spatial stability. The multi-membership random effects structure, indicated by *mm($site_i$, $site_j$)*, accounts for the fact that each observation involves a pair of sites ($site_i$ and $site_j$), which can appear in multiple pairwise comparisons.
2. **Confounded Model:**
   spatial stability ~ turnover + (turnover | mm($site_i$, $site_j$))
   This model assesses the effect of turnover on spatial stability without including environmental heterogeneity.

For both models, we employed the default flat priors provided in brms (Bürkner, 2018). Pairwise comparisons involve two sites—$site_i$ and $site_j$—that can appear in multiple pairs, which introduces pseudoreplication if treated as independent observations. To address this, we specified a multi-membership random effects structure using the mm() function. This approach assigns random intercepts and slopes to both sites within each pair, thereby accounting for the non-independence inherent in our pairwise data (Browne et al. 2001, Park and Beretvas 2020). Posterior predictive checks and leave-one-out cross-validation (LOO) were conducted to assess model fit and verify that the models adequately captured the underlying structure of the data (Vehtari et al. 2017). Additionally, we analysed other regression paths (e.g. stability ~ environmental heterogeneity) using the same method for a complete mediation analysis.

Aggregation of Simulation Results

Each simulation of the metacommunity model incorporated stochastic variables, including random maximum growth rates r_i, species environmental optima, interspecific competition coefficients, and dispersal influenced by inter-site distances (Thompson et al. 2020). For each replicate, we fitted statistical models to the simulation output to estimate key coefficients. To account for variability across replicates and obtain robust parameter estimates, we pooled the posterior samples for these coefficients from all 100 simulation replicates within each scenario (as defined in Table 1). From these combined posterior distributions, we calculated the mean and 90% highest density interval (HDI) as the credible interval (CI) for each coefficient, providing a comprehensive summary of the estimate and its associated uncertainty.

Results

Simulations

Across 100 simulations for each scenario (Table 1), we found that the spatially stabilising effect of turnover was dependent on both niche overlap and environmental heterogeneity (Figure 4, top 4 rows). In scenarios with low niche overlap (Table 1, scenario A), we observed a strong positive interaction between turnover and environmental heterogeneity on biomass stability (mean aggregated coefficient: 0.24, 90% credible interval: [-0.06, 0.62]), alongside a positive main effect of turnover (0.33, 90% CI: [-0.08, 0.80]). This stabilising interaction weakened progressively as niche overlap increased. In the scenario with complete niche overlap (Table 1, scenario D), both the main effect of turnover (0.07, 90% CI: [-0.05, 0.19]) and the interaction with environmental heterogeneity (0.00, 90% CI: [-0.05, 0.06]) were negligible. Crucially, when environmental heterogeneity was omitted from the model (the biased model), the estimated effect of turnover was biased toward zero and failed to capture this critical interaction, particularly in the low and medium niche overlap scenarios (Figure 4, right column). Notably, the variation in effect sizes among individual metacommunity realisations was high (Figure 4, grey dots), underscoring the importance of aggregating results from multiple stochastic simulations.

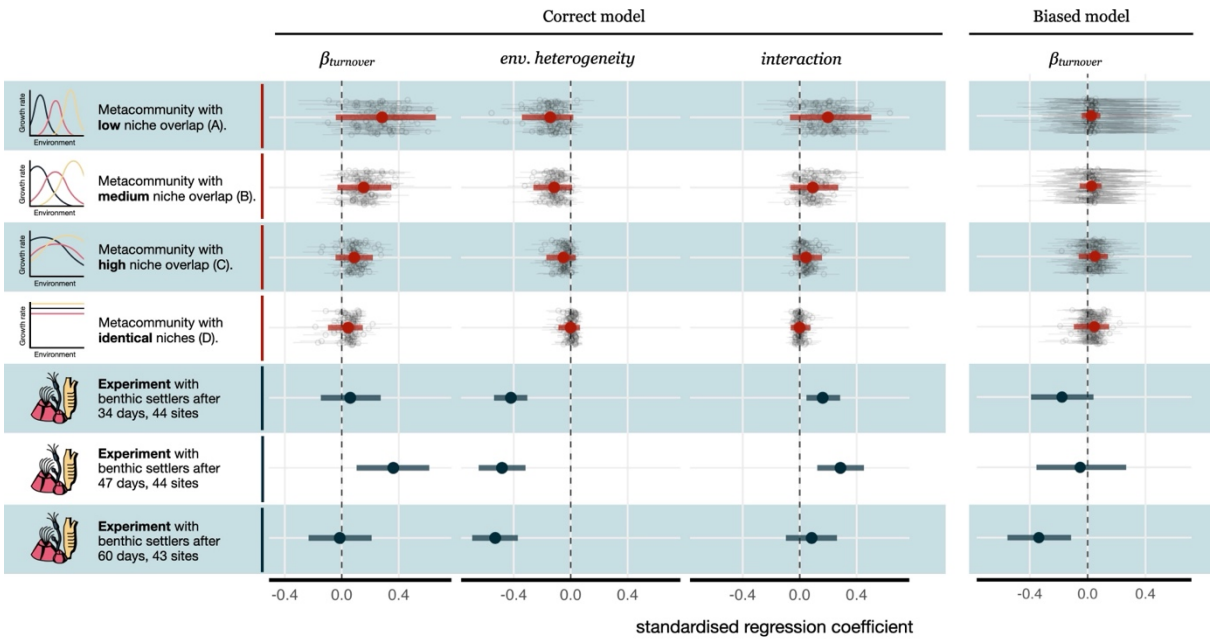

Figure 4: Effects of turnover, environmental heterogeneity, and their interaction on the spatial stability of ecosystem processes in simulated metacommunities and in a field experiment. The simulations represent four niche width scenarios described in Table 1 (A: low overlap, B: medium overlap, C: high overlap, D: identical niches). Coloured points represent mean standardised regression coefficients (± 90% CI) under the correct model (including turnover, environmental heterogeneity, and their interaction), while grey points represent individual model fits to the metacommunity simulations. The biased model (right) excludes environmental heterogeneity and its interaction, leading to incorrect estimates of the effect of turnover. Experimental results are shown for benthic settler communities after 34 days (44 sites), 47 days (44 sites), and 60 days (43 sites). Each time point was analysed independently.

To illustrate the causal pathways underlying these results, we examined a single representative metacommunity from the medium niche overlap scenario (Figure 5). In this iteration, the confounded effect of turnover on stability (effect a) was minimal (0.04, 90% CI: [-0.01, 0.08]). After accounting for environmental heterogeneity, the direct effect of turnover (effect c) became strongly positive (0.14, 90% CI: [0.01, 0.27]), accompanied by an additional interaction term (0.08, 90% CI: [-0.02, 0.19]). Environmental heterogeneity had a strong positive effect on turnover (effect b: 0.98, 90% CI: [0.81, 1.15]) but a negative direct effect on stability (effect d: -0.06, 90% CI: [-0.15, 0.03]). The resulting total effect of heterogeneity on stability was close to zero (0.02, 90% CI: [-0.02, 0.07]; effect e). This mediation analysis reveals how failing to account for the dual role of environmental heterogeneity, which both generates turnover and directly destabilises biomass, can mask the true, positive contribution of turnover to spatial stability.

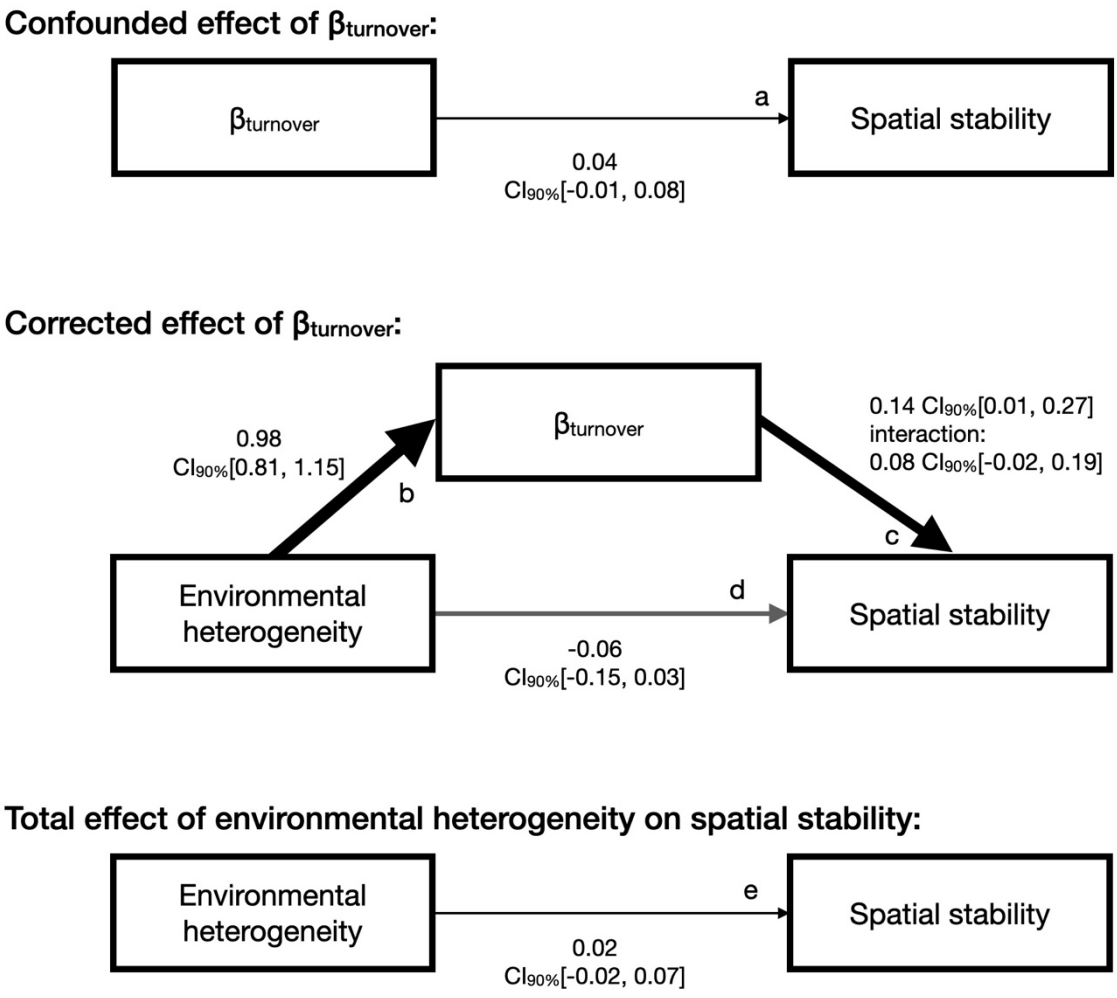

Figure 5: A mediation analysis on a single metacommunity model from scenario B, with medium niche overlap, reveals significantly different effects between the confounded effect of β-diversity and the corrected effect of β-diversity. The numbers represented are standardised regression coefficients. The size and colour of the arrows indicate the strength and direction of the effect. The arrows depict (a) the confounded effect of turnover on biomass stability, which should not be interpreted, (b) the effect of environmental heterogeneity on turnover, (c) the effect of turnover on stability while correcting for environmental heterogeneity, (d) the direct effect of environmental heterogeneity on biomass stability, i.e., not considering turnover, and (e) the total effect of environmental heterogeneity on biomass stability, including turnover.

Experiment

To evaluate whether the dominant taxa differed in their environmental responses, we fitted generalised additive niche models for each OTU. These heatmaps (Appendix S1: Figure S3)

show distinct biomass optima across the main environmental gradients (PC1 and PC2). Species having different environmental optima is a prerequisite for species sorting.

Our experiment with marine benthic communities demonstrated a positive interaction effect between turnover and environmental heterogeneity, consistent with our simulation results (Figure 4, rows 5 to 7). The interaction coefficient was 0.16 (90% CI: [0.05, 0.28]) after 34 days and 0.29 (90% CI: [0.12, 0.45]) after 47 days. After 60 days, the estimate was similar in direction but with greater uncertainty (0.08, 90% CI: [-0.10, 0.26]). This consistent interaction suggests that turnover mitigated the negative impact of environmental heterogeneity on community stability, as stability decreased with environmental differences when turnover was low. The main effect of turnover on stability was positive after 47 days (0.36, 90% CI: [0.11, 0.62]), while the credible intervals for 34 days (0.06, 90% CI: [-0.15, 0.27]) and 60 days (-0.01, 90% CI: [-0.23, 0.21]) overlapped zero.

We analysed the three time points separately since we were interested in spatial stability. Since we sampled destructively and measured environmental variables at each sample date, the three time points are independent. As predicted, the sites showed highly correlated changes in biomass over time (Appendix S1: Figure S4 A), with a median pairwise site correlation of 0.89 (Appendix S1: Figure S4 B). In addition, the median pairwise correlation of biomass over time demonstrates that biomass responses were highly synchronous among sites.

In contrast, the confounded model that omitted environmental heterogeneity severely underestimated the effect of turnover, yielding negative coefficients at 34 days (-0.18, 90% CI: [-0.39, 0.04]) and 60 days (-0.34, 90% CI: [-0.56, -0.12]). This shows that failing to account for environmental heterogeneity can lead to the erroneous conclusion that turnover is destabilising. The focus on spatial stability was justified by the highly synchronous increases in biomass observed across sites (median pairwise temporal correlation = 0.89; Appendix S1: Figure S4).

Discussion

Our study provides strong evidence that species turnover stabilises biomass production across heterogeneous environments, but this effect is dependent on the strength of species sorting. By combining theoretical simulations with experimental data from marine benthic communities, we demonstrate that species turnover can buffer against the destabilising effects of environmental heterogeneity, supporting the spatial insurance hypothesis (Loreau et al. 2003, Wilcox et al. 2017, van der Plas 2019). Unlike some prior correlational studies, our causal framework explicitly separates the effects of turnover from those of environmental heterogeneity, resolving potential ambiguities in earlier work and advancing a mechanistic understanding of biodiversity-stability relationships.

The simulations reveal that the positive interaction between turnover and environmental heterogeneity on spatial stability of biomass is strongest in scenarios with low to medium

niche overlap (Table 1, Figure 4). This finding aligns with the theoretical predictions of the spatial insurance hypothesis, which posits that species' differential responses to environmental conditions contribute to maintaining ecosystem processes across multiple sites in a metacommunity (Yachi and Loreau 1999, Loreau and de Mazancourt 2013). Critically, this mechanism depends on niche overlap: when species have distinct environmental optima (low niche overlap), turnover reflects species sorting, which has a stabilising effect on biomass production. As niches overlap completely, this insurance effect vanishes.

Our experiment broadly supports the findings from the simulations. We observed a positive interaction between turnover and environmental heterogeneity at all sampling dates, validating the theoretical predictions in a natural ecosystem. In addition, the main effect of turnover on stability was generally neutral to positive, although the uncertainty of these effects was higher in the experimental scenario. This discrepancy between simulations and the experiment may be attributed to priority effects—a phenomenon well documented in shallow marine benthic systems (Fraschetti et al. 2002, Irving et al. 2007, Vieira et al. 2018). Priority effects refer to the strong influence of early arriving species on community development. They can lead to alternative stable states and potentially alter the expected relationship between diversity and stability (Fukami 2015). Within Vellend's (2016) framework, such priority effects highlight the importance of historical contingency (see also Chase 2003), where the sequence of species arrival (dispersal) and initial establishment success (potentially involving ecological drift) shapes subsequent community development, often leading to alternative states maintained by positive frequency-dependent selection. In our study, priority effects could occur if barnacles or bryozoans dominated the panels early on, thereby preventing later-arriving species from establishing. Specifically, such early dominance might have reduced the overall level of species turnover achieved during the experiment, potentially masking the full stabilising effect of turnover on biomass production that was evident in the simulations where community assembly was more controlled. Overall, our results suggest that species turnover buffers the negative impact of environmental variability on the spatial stability of community biomass. However, the role of stochastic processes like priority effects in modulating this relationship in natural systems should not be overlooked.

Our analysis underscores that controlling for environmental heterogeneity is essential when assessing the impact of β-diversity on ecosystem stability, especially if we assume environmental variation between sites and the differential responses of species (Stein et al. 2014). In our simulations, failure to account for heterogeneity led to a clear underestimation of the effect of turnover on spatial stability in low and medium niche overlap scenarios, and this bias was also evident across all experimental settings. In contrast, this underestimation was not observed in high or full niche overlap simulations, where such bias is not expected. This discrepancy highlights the potential for omitted variable bias (Rinella et al. 2020, Byrnes and Dee 2025) to contribute to inconsistent results in previous studies (van der Plas et al. 2023). Our comparison between the full model (including heterogeneity) and the confounded model (excluding it) starkly illustrates this point: failing to account for heterogeneity can mask or even reverse the perceived effect of turnover, as visualized in our mediation analysis

(Figure 5) and regression results (Figure 4). While many biodiversity-ecosystem functioning experiments have intentionally minimised environmental heterogeneity (Gonzalez et al. 2020, 2023), our results align with studies like Daleo et al. (2023). There, controlling for environmental heterogeneity was achieved implicitly by independently analysing heterogeneous and homogeneous environments (i.e. as categorical variables, yielding similar results as in our study). In their study, β-diversity had a destabilising effect in homogeneous environments but no effect on stability in heterogeneous environments—a pattern that is consistent with our findings.

It is important to acknowledge the limitations of our study. While our simulations offered valuable theoretical insights, they only partially capture the dynamics of natural communities. Although no single metric can fully reflect every ecological function, our focus on biomass ratios naturally emphasises only one dimension of ecosystem functioning. Moreover, quantifying environmental heterogeneity poses a considerable challenge; ideally, it should reflect the specific gradients to which species respond. In our experiment, the choice of environmental metrics was informed by prior knowledge of the system, and we applied a PCA to reduce the dimensionality of correlated variables and focus on the dominant environmental gradients. Consequently, restricting site comparisons to ecologically relevant spatial boundaries helps maintain comparable species pools and environmental conditions (Burley et al. 2016). Ultimately, more comprehensive studies across a variety of ecosystems are essential to clarify the wider applicability of our findings.

Determining species' niches and the degree to which they overlap is non-trivial, yet it is key to inferring the strength of species sorting and thus the underlying causes of turnover. The supplementary niche models (Appendix S1: Figure S3), although based on realised niches after competition, illustrate that the focal taxa occupy distinct optima along the main environmental gradients, supporting this assumption in our study. The fundamental niche—which represents the range of environmental conditions a species can tolerate in the absence of competitors (Hutchinson 1957)—is often estimated under simplified conditions or from incomplete field data, leading to potential biases that may not reflect how a species actually performs under competition (Germain et al. 2018). Competition and other biotic interactions usually constrain species to their realised niches (Soberón and Arroyo-Peña 2017, Germain et al. 2018, Schrofner-Brunner et al. 2023). When species share highly similar fundamental niches, competition can lead to dominance by a few species, and any observed turnover may reflect these dynamics rather than from distinct environmental optima. In contrast, if species have different environmental optima, turnover is more likely linked to shifts in abiotic conditions. Recognising these different pathways to turnover—and how they relate to niche overlap—is essential for interpreting observed community patterns.

Spatial asynchrony—i.e. out-of-phase temporal fluctuations in biomass among local communities—is widely recognised as a key stabilising factor in ecosystems (e.g. Qiao et al., 2023; Wang et al., 2021, Wilcox et al., 2017). Yet, spatial asynchrony does not directly address differences in mean functioning levels across sites. For example, two sites can show asynchronous biomass fluctuations (thus stabilising aggregate biomass over time) yet differ

substantially in their long-term mean biomass due to environmental heterogeneity (Appendix S1: Figure S1 B). However, strong temporal synchrony can also arise in systems with relatively short time windows or pronounced environmental gradients, where spatial differences in mean biomass exceed the magnitude of temporal fluctuations (Lubchenco 1980, Körner 2007, Sporn et al. 2010, van der Wal et al. 2010, Defriez and Reuman 2017). Because our aim was to isolate purely spatial effects—and because species' biomasses increased relatively synchronously—we focused on spatial stability, quantified as invariability of the average functioning across sites. This approach provides a complementary perspective to spatiotemporal studies and a more direct test of the spatial insurance hypothesis in relation to environmental heterogeneity (Loreau et al., 2003). Nevertheless, future research could benefit from integrating both spatial and temporal metrics to gain a more comprehensive understanding of how biodiversity mediates ecosystem functioning across scales.

Our study provides strong evidence for the spatially stabilising effect of turnover in species composition on biomass production in heterogeneous environments. It also highlights the complexity of this relationship in natural systems. By demonstrating the importance of niche overlap, the causes of turnover, and controlling for environmental heterogeneity in analyses of β-diversity effects, we contribute to resolving ongoing debates in the field (van der Plas et al. 2023) and provide a methodological framework for future research. Our framework involves (1) explicitly measuring and accounting for environmental heterogeneity across sites, (2) considering the potential role of niche overlap in mediating the effects of turnover, and (3) acknowledging the influence of stochastic processes. Moreover, these insights underscore the critical role of biodiversity in buffering ecosystem processes, providing practical guidance for management decisions such as establishing species-specific niches in restoration efforts (Holl et al. 2022).

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Author Contributions

BSB led the manuscript writing, with all authors contributing to revisions and comments. BSB, JGH, and LG conceptualised the experiment. Fieldwork was conducted by BSB, JH, JMM, LCM, PP, and ESB. Simulations and data analysis were performed by BSB, and data curation and analysis involved BSB, JGH, JMM, LCM, PP, and JH. All authors reviewed and approved the final manuscript.

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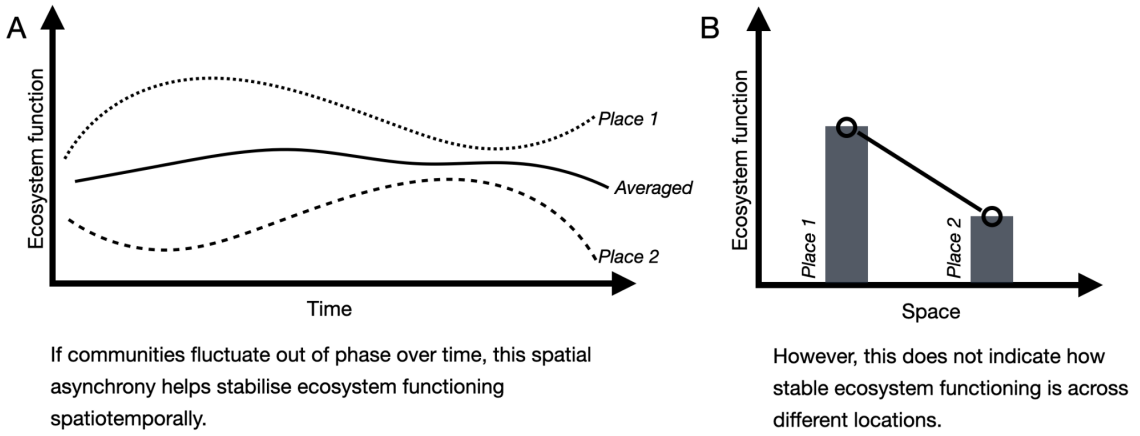
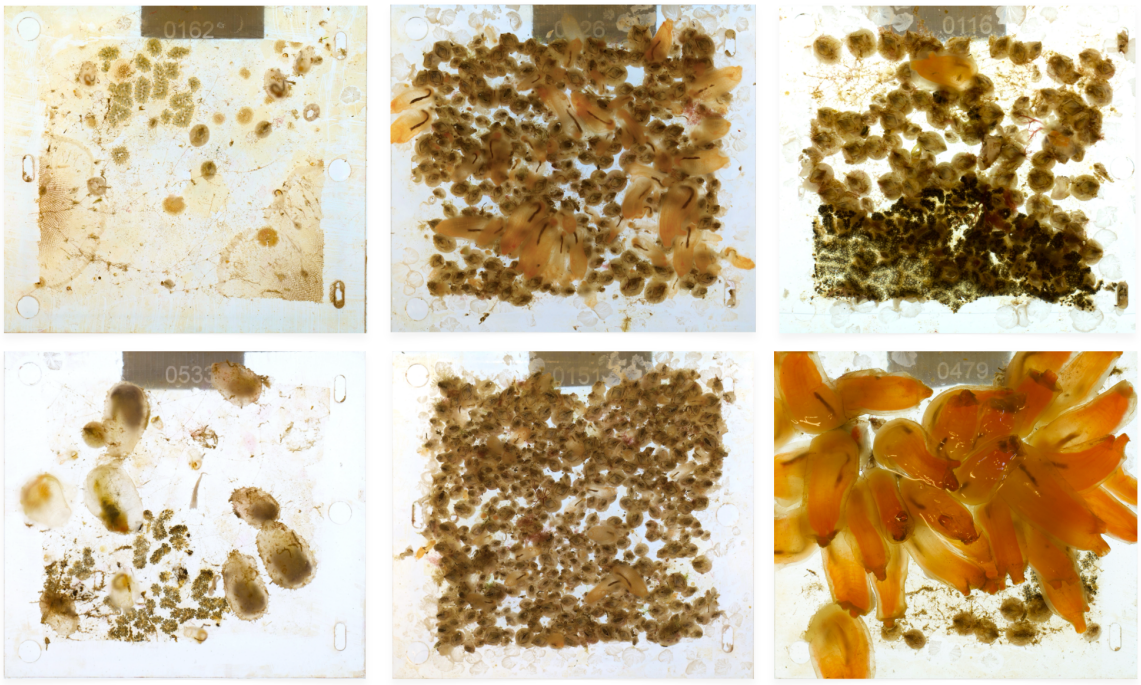
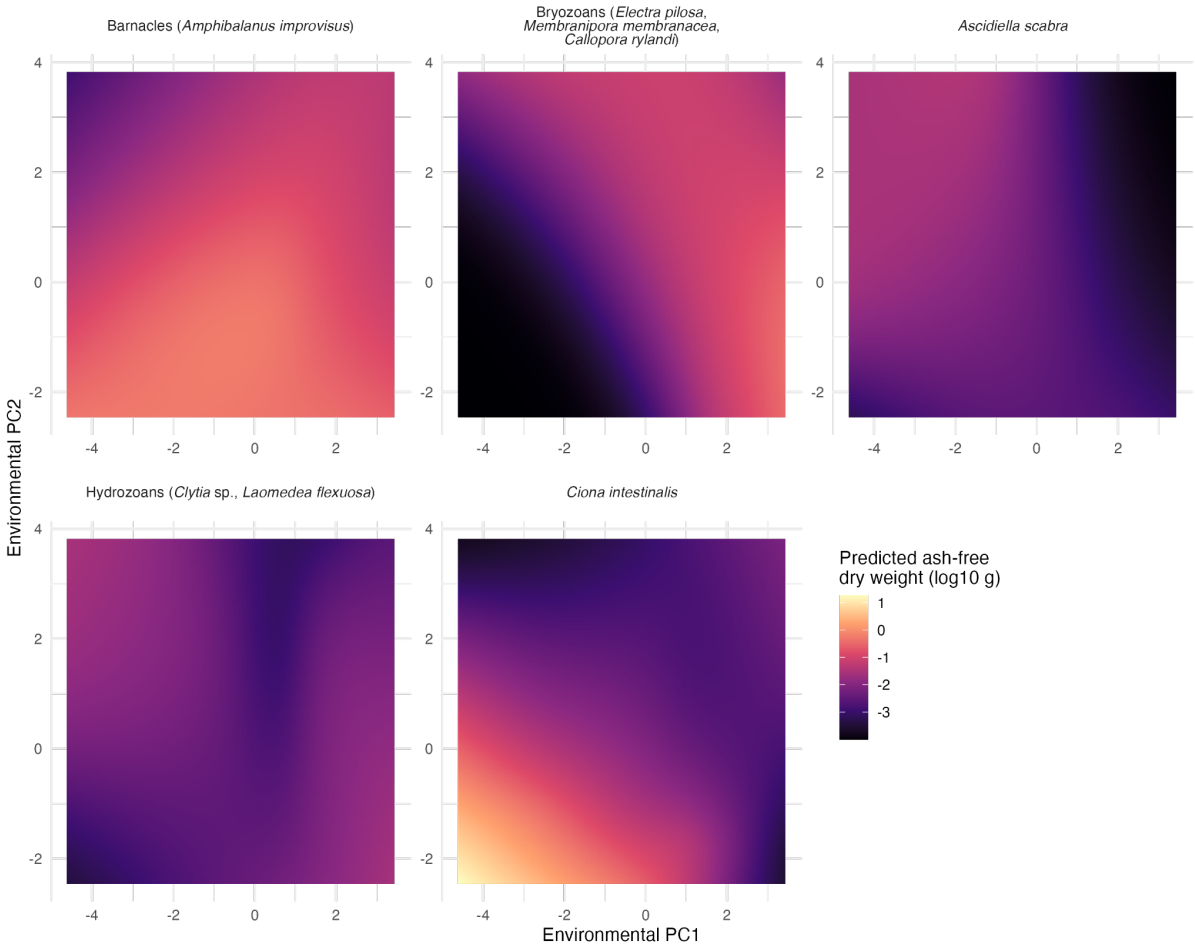
Appendix S1:



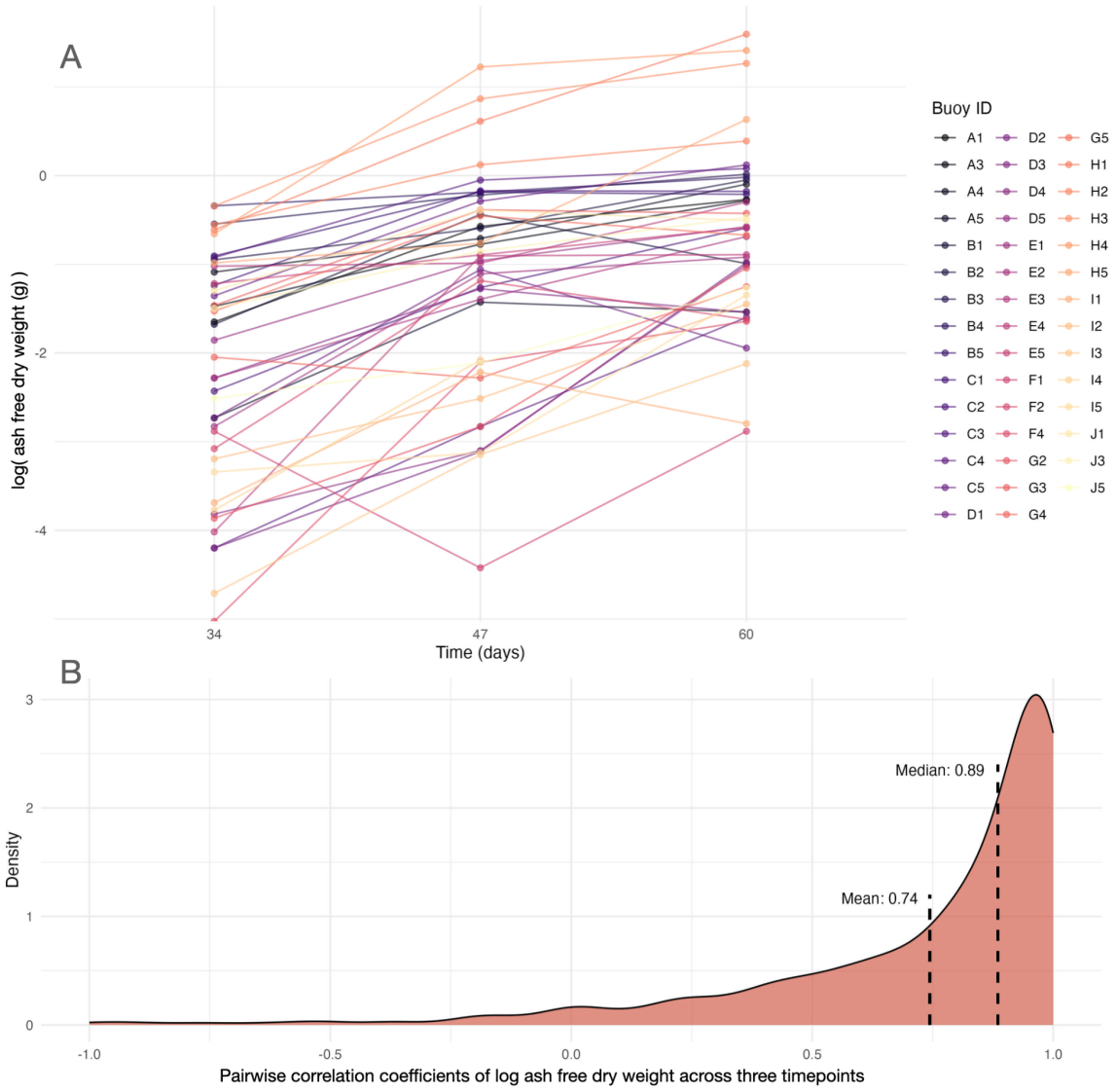
Appendix S1: Figure S1: Spatial asynchrony can stabilise community responses spatiotemporally (A, solid line). However, spatial asynchrony does not indicate how variable ecosystem functioning is across locations (i.e., comparing the average functioning of both places, B).



Appendix S1: Figure S2: Example communities from different sites with species from the surrounding environment settling on PMMA panels.



Appendix S1: Figure S3: Generalised additive model (GAM) predictions ash-free dryweight (g) across environmental gradients of PC1 and PC2, with PC3 held at its median. Panels show barnacles (Amphibalanus improvisus), bryozoans (Electra pilosa, Membranipora membranacea, Callopora rylandi), Ascidiella scabra, hydrozoans (Clytia sp., Laomedea flexuosa), and Ciona intestinalis. These niche models illustrate that the taxa occupy different environmental optima, consistent with species sorting along environmental gradients.



Appendix S1: Figure S4: A: Log of ash-free dry weight (g) coloured by site (n=44). B: Density plot of pairwise (each site pair) correlation of ash-free dry weight over time as synchrony measure.