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The Geography of Metacommunities: Landscape Characteristics Drive Geographic Variation in the Assembly Process through Selecting Species Pool Attributes

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abstract: The nonrandom association between landscape characteristics and the dominant life history strategies observed in species pools is a typical pattern in nature. Here, we argue that these associations determine predictable changes in the relative importance of assembly mechanisms along broadscale geographic gradients (i.e., the geographic context of metacommunity dynamics). To demonstrate that, we employed simulation models in which groups of species with the same initial distribution of niche breadths and dispersal abilities interacted across a wide range of landscapes with contrasting characteristics. By assessing the traits of dominant species in the species pool in each landscape type, we determined how different landscape characteristics select for different life history strategies at the metacommunity level. We analyzed the simulated data using the same analytical approaches used in the study of empirical metacommunities to derive predictions about the causal relationships between landscape characteristics and dominant life histories in species pools, as well as their reciprocal influence on empirical inferences regarding the assembly process. We provide empirical support for these predictions by contrasting the assembly of moth metacommunities in a tropical versus a temperate mountainous landscape. Together, our model framework and empirical analyses demonstrate how the geographic context of metacommunities influences our understanding of community assembly across broadscale ecological gradients.

Keywords: community assembly, dispersal, Janzen's hypothesis, niche breadth, mountains, Rapoport's rule.

Introduction

Community assembly theory studies the mechanisms by which species from a broader pool of potential colonizers assemble into local communities at finer scales (Hilleri-slambers et al. 2012). Metacommunity theory advances our understanding of a wide range of biodiversity patterns by extending community assembly theory to incorporate mechanisms such as dispersal limitation, environmental selection, and ecological drift (Mouquet and Loreau 2003; Vellend et al. 2014; Fournier et al. 2017; Koffel et al. 2022). Theoretical models have predominantly advanced our knowledge about the importance and links among these mechanisms by systematically manipulating parameters governing two distinct metacommunity components: (1) the attributes of species pools that form metacommunities (e.g., degree of species ecological specialization and dispersal ability) and (2) the characteristics of landscapes where metacommunity dynamics occur (e.g., environmental heterogeneity, connectivity). For instance, by independently manipulating species pool attributes and the environmental heterogeneity and connectivity of the landscape, one can simulate assembly dynamics corresponding to distinct metacommunity archetypes (e.g., Thompson et al. 2020; Suzuki and Economo 2021). Such theoretical frameworks produce insights into how distinct combinations of species pool attributes and landscape characteristics can generate the multitude of diversity patterns frequently observed in empirical metacommunities (e.g., Ovaskainen et al. 2019; Guzman et al. 2022).

However, the dominant life history strategies observed in species pools forming metacommunities are selected by the characteristics of landscapes where the assembly process occurs (Büchi and Vuilleumier 2014; Fournier et al. 2020). Indeed, this is a fundamental idea in spatial ecology (e.g., Peres-Neto et al. 2012) that also underlies well-established ecogeographic rules and macroecological hypotheses. For instance, Janzen's seasonality hypothesis states that latitudinal variation in the degree of spatial

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and temporal variation in landscape environmental conditions explains latitudinal clines in the degree of ecological specialization of species in the regional pools (Janzen 1967; Ghalambor 2006; Sheldon et al. 2018). Similarly, Rapoport's rule (i.e., the increase in species geographic ranges with latitude; Stevens 1989; Ruggiero and Werenkraut 2007) is assumed to be a consequence of the dominance of strong dispersers in temperate landscapes, where temporal variability in habitat conditions is high. While the nonrandom association between species pool attributes and landscape characteristics is a common pattern in nature (e.g., Sunday et al. 2011; Sheard et al. 2020), we have yet to determine its influence on our empirical understanding of metacommunity patterns and the relative importance of underlying assembly mechanisms. This understanding should be particularly relevant for generating insights into why broadscale empirical studies frequently report (bio)geographic variation in metacommunities (e.g., Qian and Ricklefs 2012; Myers et al. 2013; Henriques-Silva et al. 2015; Nishizawa et al. 2022).

In this study, we set out to determine how the dependence of species pool characteristics on landscape attributes influences the geographic context of metacommunity dynamics—that is, how it drives predictable variation in the relative importance of mechanisms that assemble different metacommunities distributed along broadscale ecological gradients, across biogeographic regions, or even at the global scale. Our conceptual framework can be described as a partial mediation model (fig. 1) in which landscape attributes (i.e., exogenous variables) determine the degree of specialization and dispersal ability of species that dominate species pools at the metacommunity scale (i.e., mediator variables). These two (model) compartments jointly dictate the relative importance of different assembly mechanisms (i.e., endogenous variables). Putting it in ecological terms, landscape attributes that vary across large-scale gradients (e.g., seasonality) should determine large-scale geographic changes in the dominant traits and life history strategies observed in species pools that form metacommunities (Peres-Neto et al. 2012; Henriques-Silva et al. 2015). As demonstrated in this study, these nonrandom associations between landscape characteristics and species pool attributes underpin geographic shifts in the relative importance of assembly mechanisms.
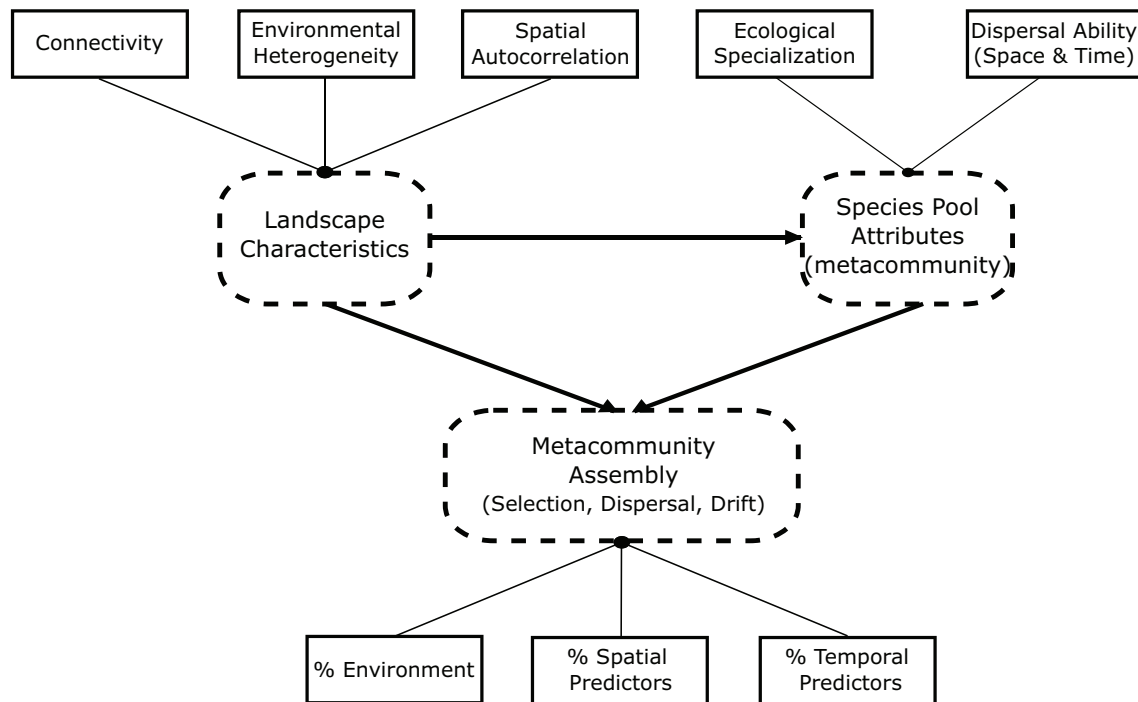

Figure 1: Mediation model for the geography of metacommunity assembly. The model incorporates the effects of both landscape (exogenous variables) and species pool (mediator variables) attributes on the relative importance of selection, dispersal, and drift (i.e., endogenous variable). Dashed round-edged boxes represent theoretical constructs, that is, components of the metacommunity theory that are inferred from measurable variables and patterns observed in empirical metacommunities (solid rectangles). The percent sign represents the amount of variation in community composition explained by environmental variables and spatial and temporal predictors. The variation explained by their covariation (i.e., joint contribution) is omitted. Species pools are defined at the metacommunity level (see "Species Pools and Metacommunity Dynamics" and the supplemental PDF for extended definitions.)

To provide theoretical validation and illustrate the utility of our conceptual framework, we built a process-based (simulation) metacommunity model wherein groups of species with the same initial distribution of continuous traits (here, ecological specialization and dispersal ability) were allowed to colonize and reach coexistence in landscapes with varying levels of spatiotemporal environmental heterogeneity, physical connectivity, and spatial structure (autocorrelated) of environmental (habitat) conditions. By evaluating the degree of ecological specialization and dispersal ability of the species that could persist and dominate the metacommunity (defined here as the metacommunity species pool sensu Fukami 2015) across various types of landscapes, we were able to understand how distinct landscape characteristics select for different dominant life history strategies. This modeling approach allowed us to understand how geographic clines in life history strategies, often attributed to broadscale variation in evolutionary and historical mechanisms (e.g., trait evolution/conservatism and speciation; Hua 2016), can also arise from ecological dynamics operating at the finer spatial and temporal scales of metacommunities (Henriques-Silva et al. 2015; Mittelbach and Schemske 2015).

To determine how the interdependences between species pool and landscapes influence inferences about metacommunity dynamics, we analyzed the resulting (simulated) metacommunities employing analytical approaches commonly used to infer the relative importance of assembly mechanisms in empirical metacommunities (discussed in "Methods"; for relevant conceptual and statistical limitations, see Gilbert and Bennett 2010; Peres-Neto and Legendre 2010). We then explored the causal links between landscape attributes, dominant life history strategies in species pools, and related inferences about community assembly through statistical models.

To provide empirical support for some of the theoretical predictions derived from our simulation framework, we analyzed empirical data on moth metacommunities in a tropical and temperate mountainous landscape. Tropical and temperate mountains are known to exhibit distinct patterns of spatial and temporal environmental heterogeneity (Zuloaga and Kerr 2017), making them suitable natural experiments for testing our theoretical predictions. For instance, a strong prediction derived from our simulation models (see below) posits that in landscapes where environmental variation is stronger in space than in time (e.g., tropical mountains), environmental specialists will predominate in species pools. Hence, empirical studies in these areas are likely to conclude that species-environment sorting is the primary driver of spatiotemporal variation in community composition. On the other hand, in regions where environmental variation is stronger in time than in space (e.g., temperate mountains), generalists should dominate species pools. As a result, mechanisms other than environmental selection (e.g., dispersal limitation or autocorrelation of demographic processes) are expected to play a greater role in affecting spatiotemporal variation in community composition. By contrasting the predictions generated by our conceptual model with the outcomes observed in these moth metacommunities, we demonstrated how our conceptual framework can serve as an inferential tool for investigating the geography of metacommunity dynamics.

Methods

Simulated Landscapes

For the sake of brevity, we only briefly describe how we simulated landscapes here. An extended description is found in the supplemental PDF. We generated a total of 216 types of landscapes considering a wide range of spatiotemporal heterogeneity levels (eight levels), physical connectivity (nine levels), and spatial distribution of environmental conditions (three levels; fig. 2). These landscape attributes have been shown to modulate the mechanisms underlying species coexistence, which in turn influence metacommunity dynamics (Büchi et al. 2009; Moritz et al. 2013; Fournier et al. 2017).

We randomly distributed 60 habitat patches in a geographic space defined by x- and y-coordinates ranging from 0 to 60. The environmental conditions in the landscape were set to range within the range [0, 5]. Three types of spatial distribution of environmental conditions were considered: random, autocorrelated, or linear gradient. Temporal variation in environmental conditions followed a sinusoidal function (plus a random error $\sim N(0, 0.1)$) with 100 periods (e.g., 100 years), each consisting of 12 time steps with distinct amplitudes to simulate different levels of landscape seasonality.

Landscape spatiotemporal environmental heterogeneity (SH/TH) was calculated as the log of the ratio between the average variance of the environment in space (SH) and the average variance of the environment through time (TH). $SH/TH > 0$ indicates spatially heterogeneous but aseasonal landscapes, $SH/TH \approx 0$ indicates similar levels of environmental heterogeneity in space and time, and $SH/TH < 0$ indicates spatially homogenous but highly seasonal landscapes.

The degree of physical connectivity (*Connectivity*) between pairs of patches was set as a negative exponential function of their distance (see eq. [SI-I]). Values of *Connectivity* below a threshold of 10^{-4} were truncated to zero to generate truly disconnected pairs of patches (as in Fournier et al. 2017). By varying the degree of exponential decay in connectivity but keeping this threshold constant,
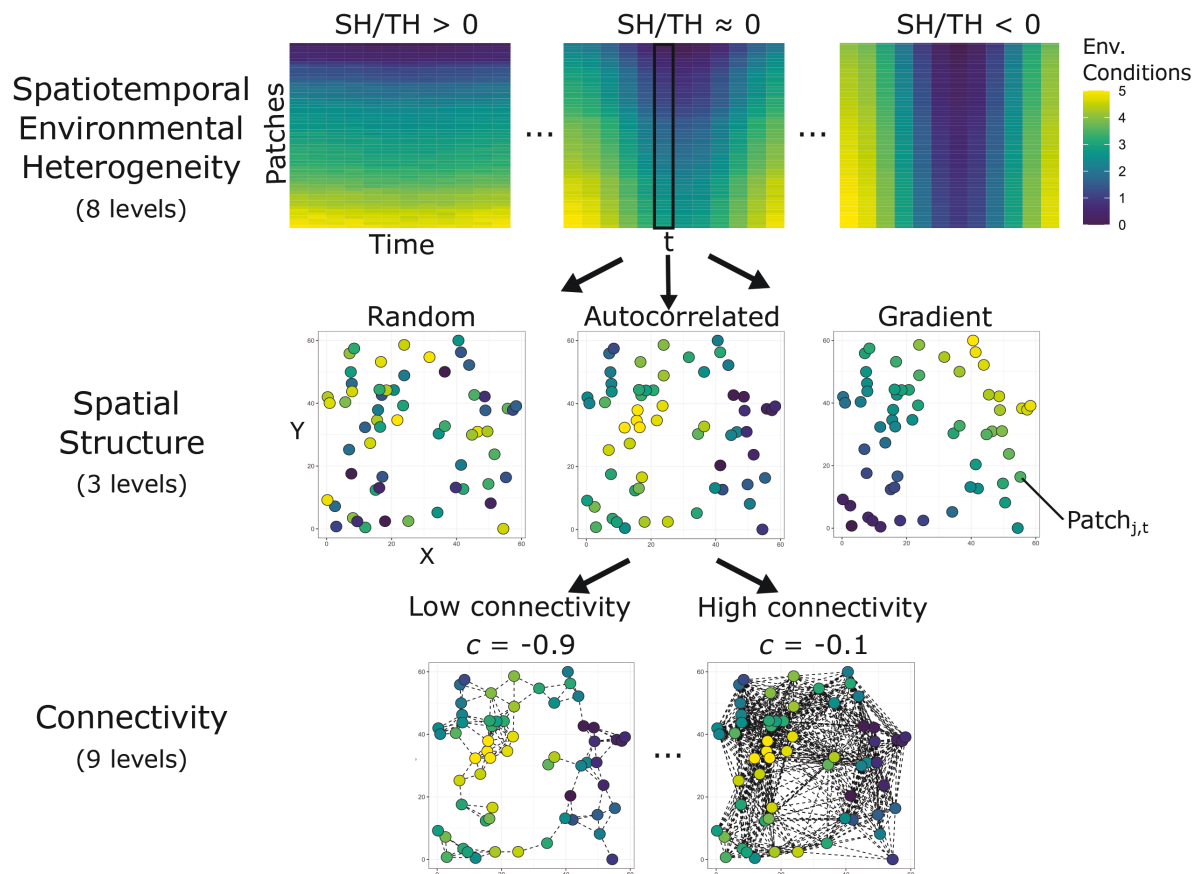
Figure 2: Schematic representation of simulated landscape characteristics. Spatiotemporal environmental heterogeneity SH/TH is calculated as the log of the ratio between the average variance of environmental conditions in space (SH) and the average variance of environmental conditions in time (TH). In the top heat maps, patches are ordered on the basis of environmental characteristics to aid in the visual comparison between spatial (vertical color variation) and seasonal (horizontal color variation) environmental heterogeneity. Spatial structure represents the type of spatial distribution of environmental conditions considered in the simulations—from totally random, through autocorrelated landscapes, to a linear gradient. Connectivity decayed exponentially with geographic distance between patches at rate c, and values below a fixed threshold were truncated to zero.

we generated landscapes with contrasting degrees of average connectivity among patches.

Species Pools and Metacommunity Dynamics

At the beginning of each simulation run (time step = 1), we generated 100 species with distinct environmental optima (μ), environmental tolerance (σ), and dispersal ability (η; i.e., here defined as emigration propensity). Values for μ, σ, and η were randomly drawn from continuous uniform distributions with ranges $[0, 5]$, $[0.1, 2]$, and $[0.01, 0.5]$, respectively (see the supplemental PDF for details about how these ranges were defined). This ensured that (1) all simulation runs were seeded with groups of species with the same initial trait value distributions and (2) different combinations of σ and η (i.e., different life

history strategies) were equally likely across all simulation runs (e.g., specialists and poor dispersers, specialists and strong dispersers, generalists and poor dispersers, and generalists and strong dispersers).

Species were allowed to colonize and reach stable coexistence in landscapes with distinct attributes (described above). The set of species that persisted in the metacommunity at the end of each simulation run (i.e., after reaching stable coexistence; see below) was the operational definition of "species pool" in this study. This operational definition aligns with the definition used in empirical studies in metacommunity ecology (Cornell and Harrison 2014)—that is, it refers to the set of all species sampled across local communities in a metacommunity. It also implies the assumption that changes in local communities driven by mechanisms operating at fine spatiotemporal

scales (here, environmental selection, dispersal, and demographic stochasticity) scale up to impact the size and composition of species pools directly (Fukami 2015). Refer to the supplemental PDF (fig. SI-I; figs. SI-I–SI-V are available online) for a detailed discussion about the assumptions associated with this operational definition of species pool.

Our model, largely inspired by Büchi and Vuilleumier (2014), Shoemaker and Melbourne (2016), and Thompson et al. (2020), generates metacommunity dynamics through a combination of density-dependent (intra- and interspecific competition) and density-independent (species-environment sorting) selection, spatial and temporal dispersal, and ecological drift (see schematic representation in fig. SI-I).

Considering $N_{i,j,t}$ to be the abundance of species i in patch j at time t, population dynamics were governed by

$$N_{i,j,t+1} = \text{Poisson}\left(N_{i,j,t} \times P_{i,j,t}\right) - \left(E_{i,j,t,\text{total}}\right) + \left(I_{i,j,t,\text{total}}\right).$$
(1)

The first term of equation (1) is a modified version of a Beverton-Holt model that equates discrete population growth as a function of selection and ecological drift (i.e., demographic stochasticity). The term $P_{i,j,t}$ is the local performance (i.e., growth rate) of species i when conditioned to competition and habitat selection in patch j at time t and is modeled as

$$P_{i,j,t} = R_{i,j,t} \times \frac{1}{1 + \alpha_{\text{intra}}N_{i,j,t} + \alpha_{\text{inter}}\sum_{k \neq i}^{\text{Sp}}N_{k,j,t}}, \quad (2)$$

where $R_{i,j,t}$ is the influence of local environmental conditions on species performance given by a Gaussian response:

$$R_{i,j,t} = u \times \frac{1}{\sigma_i\sqrt{2\pi}} \times \exp\left(\frac{-\left(\text{Env}_{j,t} - \mu_i\right)^2}{2\sigma_i^2}\right), \quad (3)$$

where $\text{Env}_{j,t}$ represents local abiotic conditions. The term $1/(\sigma_i\sqrt{2\pi})$ scales species responses to the environmental gradient, ensuring that in the absence of competition, all species that share the same environmental optima have identical cumulative growth rates along the environmental gradient regardless of their niche breadth (i.e., same areas below the performance-environment curves; see fig. SI-II; Büchi and Vuilleumier 2014). As such, any artificial advantages that may have influenced the persistence and dominance of either specialists or generalists in different landscapes were removed. The term u (set at 10 after pretrials showed that it allows the persistence of a larger number of species over time) is a scaling factor that ensures that all species were able to reach positive growth (i.e., $P_{i,j,t} > 1$) when local abiotic and biotic conditions were suitable.

The term on the right of equation (2) models the effects of density-dependent competition on population size at the intraspecific and interspecific levels; α_{intra} represents the per capita effects of species i on itself, whereas α_{inter} is the per capita effect of all other species on the local performance of i. Here, we assumed stabilizing competition in which $\alpha_{\text{intra}} > \alpha_{\text{inter}}$. This assumption is relevant because stabilizing competition favors coexistence by increasing the chances of locally rare species to keep positive population growth when locally dominant species have reached equilibrium at high abundances (i.e., the so-called invasibility criterion for coexistence; Chesson 2000; Grainger et al. 2019). By assuming stabilizing competition, we increased the chances of species with different life history strategies to coexist in suitable habitats and persist in the metacommunity (Thompson et al. 2020). We acknowledge that competition types other than stabilizing (e.g., equalizing: $\alpha_{\text{intra}} = \alpha_{\text{inter}}$; destabilizing: $\alpha_{\text{intra}} < \alpha_{\text{inter}}$) may be important to metacommunity dynamics, but evaluating their influence on the way landscapes and species pools are related is beyond our goals here (but see Thompson et al. 2020; Wisnoski and Shoemaker 2022). Across all simulations α_{intra} and α_{inter} were set to 1/400 and 1/800 (minimum values that allowed for species regional coexistence at high abundances based on pretrials), respectively.

We added ecological drift (demographic stochasticity) to local birth and survival by drawing the final local abundance of species i from a Poisson distribution (eq. [1]). This distribution's mean was determined by the deterministic influence of biotic density-dependent (here, competition) and abiotic density-independent (environment sorting) selection on population dynamics (following Shoemaker and Melbourne 2016; Shoemaker et al. 2022).

Individuals able to persist in any given local community after within-patch selection and local demographic stochasticity at time t could then disperse. To align our framework with recent developments in metacommunity ecology (e.g., Wisnoski et al. 2019; Wisnoski and Shoemaker 2022), we modeled two types of dispersal: spatial and temporal (Buoro and Carlson 2014). Here, we define temporal dispersal as any physiological (e.g., diapause, dormancy) or behavioral (e.g., hiding in refugia) strategies that buffer local extinctions. These strategies enable individuals to escape from short-term unfavorable conditions by avoiding costs related to reproduction and resource consumption. This was operationalized by temporally removing individuals from local communities and allowing them to return to the same patch in the future (see below). Temporal dispersal is relevant because, akin to spatial dispersal, it promotes local and regional coexistence when local abiotic and biotic conditions favor competing species in different periods (i.e., via temporal storage effects; Chesson 2000; Wisnoski and Shoemaker

2022). Therefore, dispersal in space and time can be understood as alternative risk-spreading strategies that can maximize species persistence in metacommunities under varying levels of spatial and temporal environmental heterogeneity (Buoro and Carlson 2014; Holyoak et al. 2020).

The total number of emigrants of species i leaving patch j at time t ($E_{i,j,t,\text{total}}$) is determined by binomial trials with a size equal to the outcomes of within-patch dynamics (first term of eq. [1]), and the probability of success is defined as the species-specific dispersal ability (η). Species with higher η were more propense to emigrate than species having lower η. To further explore the effects of spatial and temporal dispersal on the model outcomes, we created different scenarios wherein species would be more or less likely to undergo either type of dispersal. This was achieved by adjusting the values of the parameter *Dispersal Strategy*, which represents the probability of success in binomial trials used to determine the number of emigrants in $E_{i,j,t,\text{total}}$ that would undergo temporal dispersal ($E_{i,j,t,\text{time}}$). It follows that the number of spatial emigrants ($E_{i,j,t,\text{space}}$) is then given by $E_{i,j,t,\text{total}} - E_{i,j,t,\text{time}}$. We considered three different scenarios: in the "equal" dispersal scenario, species had an equal probability of emigrating through either spatial or temporal dispersal (*Dispersal Strategy* = 0.5), whereas in the "mainly temporal dispersal" and "mainly spatial dispersal" scenarios, *Dispersal Strategy* was set as very high (0.99) and very low (0.01), respectively, for all species.

The total number of immigrants of species i arriving at patch j at time t ($I_{i,j,t,\text{total}}$) was given by the sum of spatial ($I_{i,j,t,\text{space}}$) and temporal ($I_{i,j,t,\text{time}}$) immigrants. Spatial immigration was spatially explicit, meaning that individuals were more likely to immigrate to closer patches than distant ones. This was operationalized as follows. Consider the total number of spatial emigrants departing from patch h at time t ($E_{i,h,t,\text{space}}$). Let D_{space} be the set of potential destination patches (e.g., j) of each one of these individuals, and let P_{space} be the corresponding set of unequal sampling probabilities (scaled to sum to 1) of drawing any element in D_{space} in a random sampling process. These unequal probabilities were given by the degree of *Connectivity* between h and neighboring patches (which decayed exponentially with distance following eq. [SI-I]). Based on the probabilities in P_{space}, a random sampling process with replacement was repeated $E_{i,h,t,\text{space}}$ times to define the destination of spatial emigrants (see mathematical definition in the supplemental PDF). As such, the number of individuals of species i that left patch h and immigrated to patch j was then given by the number of times patch j was randomly drawn from D_{space}. It follows that $I_{i,j,t,\text{space}}$ is given by the sum of all individuals of species i that immigrated to patch j at time t coming from all other patches connected to j.

A similar procedure was used to determine temporal immigration. Consider $E_{i,j,t-x,\text{time}}$ to be the total number of individuals of species i that underwent temporal dispersal (e.g., entered dormancy) in patch j at time $t - x$. Let D_{time} be the set of potential moments in the future (e.g., t) when individuals can recover from dormancy and P_{time} be the set of probabilities of drawing each element in D_{time} in a random sampling process. Contrary to previous studies that assumed a constant recovery rate from "dormancy" over time (e.g., Wisnoski et al. 2019), we considered a more realistic temporal decay of recovery rates. For instance, individuals that underwent dormancy at time $t - x$ were more likely to recover from dormancy at time t if t is in the imminent future. This was operationalized by making the probabilities in P_{time} to be $\exp(-dt \times \Delta t)$, where Δt is the difference in time between t and $t - x$ (min = 1, max = 1) and dt is the rate of temporal decay. After pretrials where we tested different values for dt (not shown), we fixed it at 0.5 because it was the lowest value that allowed species persistence in highly seasonal and disconnected landscapes. Considering D_{time} and P_{time}, a sampling process with replacement was repeated $E_{i,j,t-x,\text{time}}$ times. The total number of individuals of species i that underwent dormancy in patch j at time $t - x$ and recovered from dormancy in the same patch at time t was given by the total number of times t was drawn from D_{time}. It follows that $I_{i,j,t,\text{time}}$ is the sum of all individuals of species i that underwent dormancy in patch j at a given moment in the past and recovered from dormancy at time t.

Simulation Iterations

For each parameter combination and dispersal scenario, we ran 20 independent replicates, yielding 12,960 simulations runs in total (20 replicates × 8 SH/TH levels × 9 connectivity levels × 3 types of the spatial structure of environment × 3 dispersal scenarios). Population dynamics of the 100 initial species in the regional pool were carried across all 60 patches over 1,200 time steps (i.e., 100 complete seasonal cycles). Between time steps 1 and 120, all patches were simultaneously seeded with species populations randomly drawn from a Poisson distribution (λ = 0.5). This allowed an opportunity for establishment and population growth for all species, provided that local abiotic and biotic conditions were suitable. The random placement of species populations across patches allowed those with similar habitat conditions to develop communities with dissimilar compositions due and priority effects (Thompson et al. 2020). To ensure that model summaries were carried out in stable rather than transient metacommunities, only communities in the last seasonal cycle (last 12 time steps) were analyzed. This decision was supported by sensitivity

analyses (not shown) that demonstrated stabilization of species pools (rate of regional extinctions close to zero) after approximately 700 time steps on average.

Analyzing Simulated Metacommunities

We determined the dominant life history of species in the regional pool (i.e., all species that persisted in the metacommunity in the last seasonal cycle) by calculating the regional relative abundance–weighted mean of niche breadth (hereafter, "metacommunity-weighted niche breadth") and dispersal ability (hereafter, "metacommunity-weighted dispersal ability") of each of the 12,960 simulations. By doing so, we could derive theoretical predictions underlying the life history strategies that maximized species persistence and dominance across different landscape types.

Our model was designed to generate insights into how landscape attributes and species pool characteristics influence inferences of the relative importance of different assembly mechanisms based on analytics commonly used to infer processes in empirical metacommunities (e.g., Cottenie 2005; Soininen 2014; Gálvez et al. 2022). To do so, we used variation partitioning (Borcard et al. 1992; Peres-Neto et al. 2006) to estimate the contribution of different groups of variables to the variation in community composition across simulated local communities. Since we used a simulation model that incorporates known processes and lacks missing predictors (such as unmeasured spatiotemporal environmental variables that influence species distribution), variation partitioning can draw direct inferences from the observed patterns, which may be challenging when using empirical data. Our simulations reproduced data commonly collected in metacommunity studies and were analyzed using the same inferential approach, enabling comparison and contextualization of our theoretical results with empirical findings (e.g., Nishizawa et al. 2022; see also "Empirical Support: The Assembly of Moth Metacommunities in Tropical and Temperate Mountainous Landscapes" below).

Variation partitioning was applied to the final patch-by-species-by-time matrix. We started by calculating pairwise compositional dissimilarities matrices and then using generalized dissimilarity models (GDMs; Ferrier et al. 2007) to fit these as a function of environment, positive spatial autocorrelation (here represented by positive Moran's eigenvector maps [MEMs] calculated on the basis of the patch geographic xy-coordinates; Dray et al. 2006), and positive temporal autocorrelation (here represented by asymmetric eigenvector maps [AEMs]; Blanchet et al. 2008). Pairwise dissimilarities were calculated using the abundance-based Bray-Curtis index, which is widely used and underlies the link and variance functions of GDMs (see Ferrier et al. 2007). Traditionally, the amount of variation in pairwise

compositional dissimilarity matrices explained by environmental variables alone is considered a measure of the strength of species-environment sorting; the variation explained by spatial MEMs alone represents spatial autocorrelation in species distributions caused by the spatial signature of demographic events such as dispersal (Cottenie 2005; Beisner et al. 2006); the variation explained by temporal AEMs alone represents temporal autocorrelation in species dynamics associated with demographic events that are not related to extrinsic environmental factors (Legendre and Gauthier 2014). The variation explained by the covariation among variables (i.e., their joint contribution) was also estimated, although its association with specific ecological mechanisms is less clear, particularly in empirical data that often contain missing environmental variables in the model (but see Peres-Neto et al. 2012). Finally, we ranked the relative importance of each component (in ascending order) to facilitate comparisons across our 12,960 independent simulation rounds.

All simulations and statistical analyses described above and below were conducted using R (ver. 4.1.0; R Core Team 2023). AEMs and MEMs were generated using the adespatial package (Dray et al. 2022). We used the vegan package (Oksanen et al. 2020) to calculate compositional dissimilarities and the gdm package (Manion et al. 2018) to fit GDMs.

Identifying Interdependencies among Landscape Characteristics, Species Pool Attributes, and Assembly Mechanisms

We used path analysis to identify the causal interdependencies (pathways) among landscape attributes (i.e., exogenous variables: SH/TH, connectivity, and spatial structure of environment [ordinal; 1 = random, 2 = autocorrelated, 3 = linear gradient]), species pool characteristics (i.e., mediators: metacommunity-weighted niche breadth and metacommunity-weighted dispersal ability), and the variation partitioning components (i.e., endogenous variables) across the 12,960 simulation rounds. All predictors were standardized (mean = 0 and standard deviation = 1) prior to model fit to allow comparing fitted relationships. Pathways' direction (i.e., positive/negative) and magnitude (i.e., standardized estimates) represented the general theoretical predictions derived from our simulations. Given that we used simulated data, the P values of parameter estimates in the path models were not used to assess pathway significance because large simulation replications can yield low P values even with negligible effect sizes (see White et al. 2014). Refer to the "Results and Discussion" section for how we selected which pathways to interpret.

To assess whether theoretical predictions vary in direction (i.e., quantitatively) and/or magnitude (i.e.,

qualitatively) across dispersal scenarios (i.e., equal dispersal, mainly temporal dispersal, and mainly spatial dispersal), we contrasted the outcomes of a path analysis that combined all dispersal scenarios (global model) with the results of separate path analyses for each dispersal scenario. We used the Akaike information criterion corrected for small sample sizes to evaluate the fit of path models that considered different combinations of the linear and quadratic terms of predictors. The models that considered only linear terms (simplest) were identified as the best-fitting path models in most cases. We used the piecewiseSEM R package (Lefcheck 2020) to fit the path models across dispersal scenarios.

Empirical Support: The Assembly of Moth Metacommunities in Tropical and Temperate Mountainous Landscapes

To generate empirical support for the core theoretical predictions derived from our conceptual and simulation model (see below), we analyzed published data on moth metacommunities in two mountainous landscapes: the tropical Mount Cameroon (MTC; Maicher et al. 2019) and the temperate H. J. Andrews Experimental Forest (AEF; Miller and Jones 2005; Highland et al. 2013).

Moths in both datasets were collected using light traps along an elevational gradient (MTC: from 35 to 2,000 m asl; AEF: from 400 to 1,400 m asl). Sampling was carried out at different moments of the reproductive season in each region (AEF: we used data from May 2004 to October 2004; MTC: we used different moments of the dry season and the transition between dry to wet and wet to dry seasons; see more details in references and the supplemental PDF). Because moths are generally good spatial dispersers when adults and can persist in the landscape through prolonged juvenile diapause (Lees and Zilli 2019), both spatial and temporal dispersal are likely to influence the structure of moth metacommunities.

To estimate and contrast the degree of spatiotemporal environmental heterogeneity (SH/TH), we used sample coordinates to extract monthly temperature (mean, maximum, and minimum monthly values) and precipitation data at 1 km × 1 km resolution (CHELSA data; Karger et al. 2017). We then performed a principal component analysis on the temperature variables and log-transformed precipitation (standardized to mean = 0 and standard deviation = 1) and used the sample scores on the first two principal component (PC) axes as a proxy of the climatic conditions of each site across different time periods of the year. In both the MTC and the AEF, PC1 explained a substantial portion of the climate data variance at 76.2% and 74.2%, respectively, while PC2 accounted for 22.1% and 20.7%, respectively,

resulting in cumulative proportions of 98.3% and 94.9%, respectively.

We estimated the climatic tolerance of each species through the tolerance index of Dolédec (2000) using the package ade4 (Thioulouse et al. 2018). This index estimates species-specific climatic tolerance (i.e., niche breadth) on the basis of the dispersal of samples that contain the target species in the multivariate climatic space. We pooled together data on moths and climate variables of both mountainous landscapes to estimate climatic tolerance in the same multivariate space. By doing so, we could directly contrast the degree of ecological specialization of species observed in both datasets. Last, we inferred the relative importance of different assembly mechanisms in both landscapes using variation partitioning (following the same steps described in "Analyzing Simulated Metacommunities"). This was done by estimating the variation in the community composition data explained by climate (PC1 and PC2), space (spatial MEMs), and time (temporal AEMs).

To consider how differences in sample design (e.g., the length of elevational range sampled in each mountain) of both datasets could influence our inferences, we rerun the analyses described above after removing samples in the MTC dataset so that it would span the same elevational range as the AEF dataset (i.e., approximately 1,000 m asl). Given that the results remained qualitatively the same (see fig. SI-V), here we report only the results considering the complete elevational gradient in the MTC.

Results and Discussion

Because of qualitative similarities in the results of path models fitted considering each dispersal scenario separately (see tables SI-I–SI-IV, available online), we report only the results considering data on all dispersal scenarios pooled together. However, we also highlight and discuss cases in which there were differences in the direction of pathways across dispersal scenarios. For purposes of tractability and synthesis, we focused our discussion on the pathways with the highest importance in the fitted path models. That is, only pathways (minimum of two per mediator and endogenous variables) with partial coefficients higher than the median coefficient across all relationships among exogenous (landscape characteristics), mediators (species pools attributes), and endogenous variables (i.e., the isolated contribution of environment, spatial MEMs, and temporal AEMs to variation partitioning) are discussed and reported here. Nonetheless, the complete set of numerical relationships estimated by path analyses across all dispersal scenarios and considering the full set of variation partitioning components can be found in the supplemental PDF.

Theoretical Predictions: Landscape Attributes Influence the Degree of Ecological Specialization and Dispersal Ability of Dominant Species in the Regional Pool

Our simulation clearly showed that seasonality (measured as the ratio between spatial and temporal heterogeneity, SH/TH) was the most important factor determining the degree of ecological specialization of the dominant species in the regional pool (figs. 3, 4). Ecological specialization was favored in aseasonal landscapes where environmental heterogeneity was higher in space than in time (SH/TH > 0). Conversely, ecological generalization was favored in highly seasonal landscapes where environmental heterogeneity is higher in time than in space (SH/TH < 0). Notably, we observed an increase in the persistence of ecological specialists in seasonal landscapes when we considered the mainly temporal dispersal scenario (see fig. SI-III). These findings highlight the impor-

tance of temporal dispersal to the coexistence of specialists and generalists in (temporally) fluctuating environments (Chesson 2000; Wisnoski and Shoemaker 2022).

The spatial structure of the environment also influenced the overall niche breadth of species pools, but this relationship was relatively weak (figs. 3, 4; table SI-I). When environmental conditions were randomly distributed across the landscape, an increase in the dominance of generalists in the regional pool was observed. Reduced spatial structure (autocorrelation) in habitat conditions increased the chances of environmental specialists being isolated in patches surrounded by unsuitable habitat conditions (Büchi and Vuilleumier 2014; Fournier et al. 2017). Since isolation increases populations' chances of becoming locally extinct due to demographic stochasticity, the lack of spatial structure in environmental conditions should increase isolation and, consequently, local and regional extinction of ecological specialists.
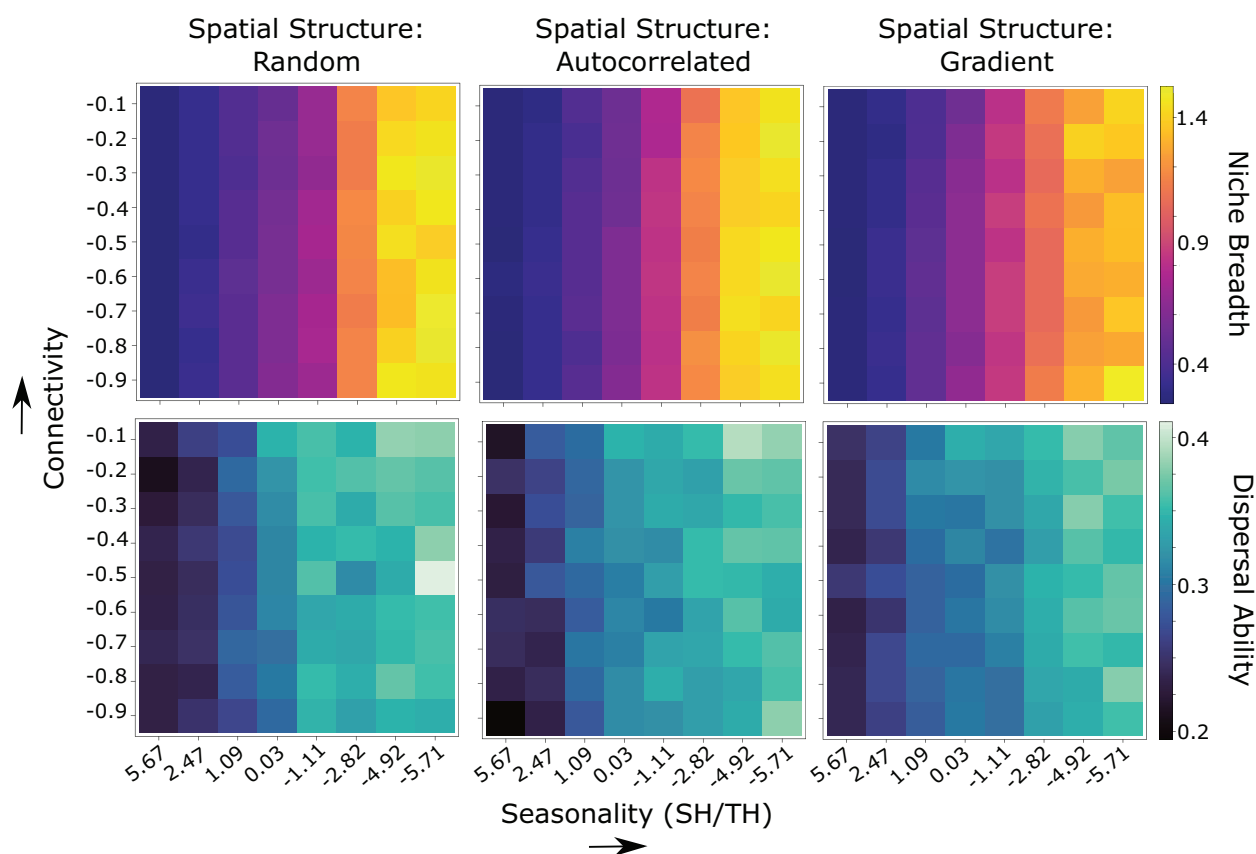

Figure 3: Landscape attributes determine the dominant life history strategies in species pools. Among landscape attributes, variation in landscape seasonality was the main driver of variation in metacommunity-weighted niche breadth and dispersal ability (also see fig. 4). Aseasonal landscapes (SH/TH > 0) selected for environmental specialists (i.e., narrow niche breadth) that were also weak dispersers (i.e., low dispersal ability). Seasonal landscapes (SH/TH < 0) favored the dominance of environmental generalists that were also strong dispersers. These are the results reported for the equal dispersal scenario, where species were equally likely to disperse spatially and temporally. The results for the mainly spatial and mainly temporal dispersal scenarios are reported in figures SI-II–SI-V.
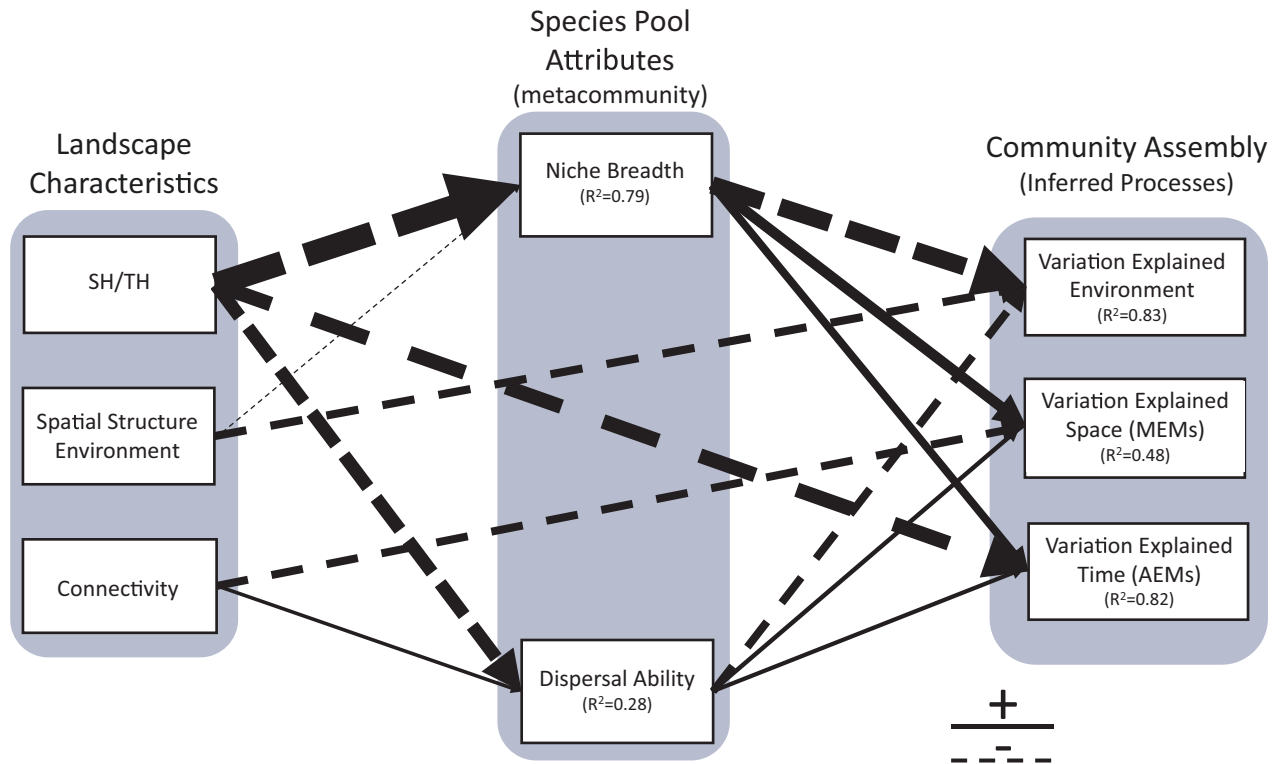
Figure 4: Theoretical predictions derived from path analysis considering the relationships among landscape characteristics (exogenous variables), the dominant life history strategies in species pools (mediators), and the variation partitioning components (endogenous variables). For purposes of tractability and synthesis, only pathways with effect sizes higher than the median absolute effect sizes across all relationships among exogenous variables (landscape characteristics), mediators (species pool attributes), and endogenous variables (variation partitioning assembly) are reported here. Arrow widths are proportional to the effect sizes estimated. The SH/TH index is given by log of the ratio between spatial and temporal environmental heterogeneity. It has positive values in landscapes where spatial environmental variation is stronger than seasonal variation but negative values in landscapes where spatial environmental variation is weaker than seasonal variation. Results reported considering all dispersal scenarios pooled together. The numerical results obtained from path analyses considering each dispersal scenario pooled together and separately are reported in tables SI-I–SI-V.

Dispersal ability was influenced by seasonality and the level of connectivity in landscapes (figs. 3, 4), although the strength of these relationships varied across dispersal scenarios (see tables SI-I–SI-IV). When metacommunity dynamics were primarily driven by spatial dispersal (i.e., the mainly spatial dispersal scenario), dispersal ability increased at intermediate levels of seasonality but increased linearly with physical connectivity. This finding suggests that highly connected landscapes reduce the risks associated with spatial dispersal by increasing the likelihood of species successfully tracking suitable patches when environmental heterogeneity is equally strong in space and time (see Kubisch et al. 2014 and references within). In contrast, when species mainly dispersed over time (the mainly temporal dispersal scenario) or had equal chances of dispersing in space and time (the equal dispersal scenario), the landscape's spatiotemporal environmental heterogeneity (which is negatively correlated with season-

ality) emerged as the most important landscape attribute selecting for species with weak dispersal abilities. This implies that species' ability to disperse in time is critical to their persistence in highly seasonal landscapes. Additionally, these results illustrate that spatial and temporal dispersal are risk-spreading strategies favored by different levels of spatial environmental heterogeneity (Buoro and Carlson 2014).

Collectively, our findings provide theoretical support for macroecological hypotheses and ecogeographic rules invoked to explain latitudinal clines on species' ecological specialization and dispersal ability. For instance, Janzen's seasonality hypothesis posits that the high elevational stratification of climate and the low seasonality of tropical mountainous landscapes should favor the dominance of environmental specialists whose spatial distributions are restricted to different types of climate (Janzen 1967). Conversely, strong seasonality in temperate regions should

favor the dominance of species that have broad physiological tolerances and are less sensitive to spatial variation in climate (Sheldon and Tewksbury 2014). Previous studies have demonstrated that niche evolution through a mutation-selection process is critical to the patterns predicted by Janzen's hypothesis (e.g., Hua 2016). Our study expands on this understanding by demonstrating that latitudinal clines in niche breadth can arise due to metacommunity dynamics at fine temporal scales where speciation and trait evolution is expected to play a minimal role in community assembly.

Our model successfully replicated the expected relationship between temporal variability in the environment and the optimal level of dispersal ability in the regional pools that shape metacommunities (e.g., Jocque et al. 2010; Sheard et al. 2020). We found that weak dispersers that are also highly specialized in local conditions dominate local communities and increase their persistence in the regional pool when the environment is temporally homogenous. In contrast, high temporal variability of environmental conditions favored species with increased dispersal ability that can escape from temporally unsuitable local conditions (fig. 3). Given that (i) dispersal ability can contribute substantially to geographic ranges (Alzate and Onstein 2022; but see Lester et al. 2007) and (ii) the strength of seasonality (particularly in temperature) increases from the equator to the poles, our model was able to re-create the underlying conditions that lead to an increase in range size as a function of latitude, as predicted by Rapoport's rule (Stevens 1989).

Theoretical Predictions: Landscape and Species Pool Attributes Influence Inferences about the Relative Importance of Assembly Mechanisms

Our theoretical framework allowed us to generate a mechanistic understanding of how landscape characteristics and species pools can influence empirical inferences about the relative importance of assembly mechanisms in metacommunities (fig. 4). The unique contribution of the environment (via variation partitioning) captures the importance of species-environment sorting in community assembly (Cottenie 2005; Ovaskainen et al. 2019). Path analyses applied to the combined results of all dispersal scenarios indicate that the strength of species-environment sorting on community composition is reduced when landscapes are composed of large clusters of suitable habitat conditions. They also indicate that species-environment sorting increases when species pools are dominated by environmental specialists that are weak disperses (i.e., the species-sorting paradigm).

However, the direction of the relationship between dispersal ability and the contribution of environmental variables in the variation partitioning was not constant across dispersal scenarios (see tables SI-I–SI-IV). When spatial dispersal occurs as frequently as or more frequently than temporal dispersal (i.e., the equal and mainly spatial dispersal scenarios), dispersal ability increased the relative importance of environmental selection in community assembly. This suggests that the influence of the environment on community composition can intensify with spatial dispersal when it increases the likelihood of specialists reaching and persisting in large numbers of suitable patches. Conversely, this relationship becomes negative when dispersal is constrained to be mostly temporal (i.e., under the mainly temporal dispersal scenario). This pattern suggests that "seed banks" buffer the extinction of populations in unsuitable local conditions, decreasing the strength of the match between community composition and environment (Wisnoski et al. 2019).

The importance of the unique contribution of space (spatial MEMs) is typically associated with the influence of dispersal limitation in community assembly (Cottenie 2005; Beisner et al. 2006). We observed that community composition became more spatially structured as niche breadth and dispersal propensity increased but decreased with landscape connectivity (fig. 4). This suggests that spatial autocorrelation in community composition unrelated to the spatial structure of the environment arises when species with weak responses to environmental gradients are constrained to dispersing to neighboring patches.

The proportion of variation in the community matrix explained by the unique contribution of temporal variation (AEMs) is usually linked to temporal autocorrelation in population dynamics unrelated to environmental variation (Legendre and Gauthier 2014). Our simulations indicate that this type of autocorrelative pattern tends to increase when temporal environmental variation is weak (i.e., aseasonal landscapes) and generalists with strong dispersal capacity dominate metacommunities (fig. 4). Under these conditions, stochastic events of colonization and local extinctions outweigh the influence of species-environment sorting in generating temporal autocorrelation in population dynamics. These results are aligned with previous empirical studies demonstrating that the stochastic signature of temporal changes in community composition increases in aseasonal landscapes where environmental heterogeneity is stronger in space than in time (e.g., Khattar et al. 2021).

In summary, our model demonstrates that landscape attributes and species pool characteristics are strongly associated and should not be considered as independent axes in the assembly process. It also demonstrates that this link can lead to variation in the relative importance of assembly mechanisms along broadscale gradients that encompass variation in key landscape attributes.

Empirical Support

While our model should not be interpreted as an attempt to scale directly with the dynamics of any given real metacommunity, it generated testable predictions on empirical data (fig. 5). For instance, a strong prediction derived from our model is that in landscapes where environmental heterogeneity is relatively greater in space than in time (aseasonal landscapes, $SH/TH > 0$), species pools should be dominated by specialists (figs. 3, 4). Consequently,

environmental selection should be the primary mechanism driving community assembly in these landscapes. Conversely, generalists should dominate species pools in landscapes where environmental conditions change relatively more in time than in space (seasonal landscapes, $SH/TH < 0$). As such, it is reasonable to infer that mechanisms beyond environmental selection alone likely play a significant role in driving community assembly.

As typically observed in tropical mountains (fig. 5*A*), climate (PC1 scores) varied more across elevations than
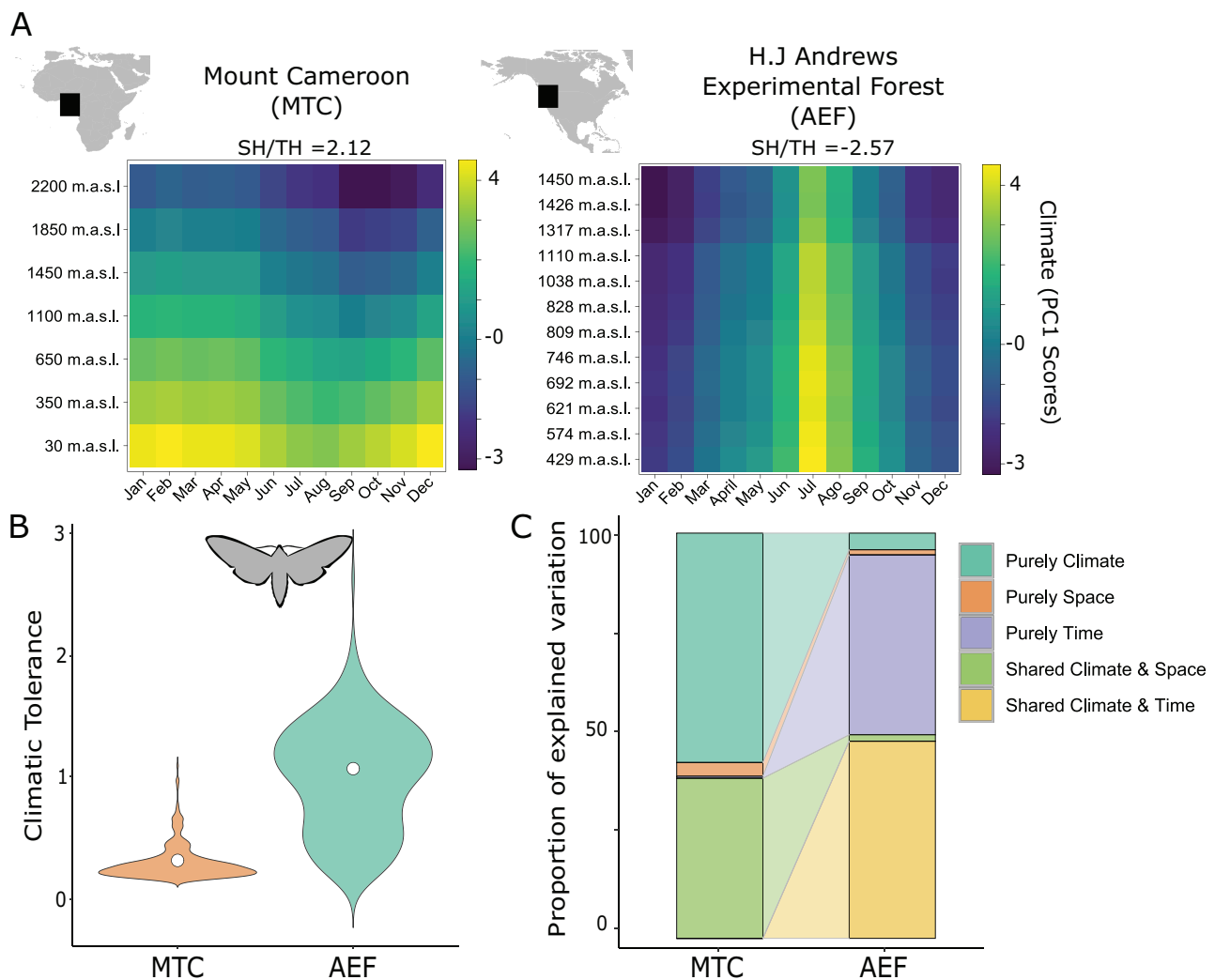

Figure 5: We analyzed the assembly of moth metacommunities in two different mountainous landscapes (*A*): the tropical and relatively aseasonal Mount Cameroon (MTC; $SH/TH > 0$) and the temperate and relatively seasonal H. J. Andrews Experimental Forest (AEF; $SH/TH < 0$). In the MTC, the regional pool is dominated by climate specialists, while climate generalists dominate the regional pool in the AEF (*B*). As such, deterministic species-environment sorting is the primary driver of community assembly in the MTC, whereas temporal autocorrelation on population dynamics and the temporal structure of climate are the main drivers of variation in community composition in the AEF (*C*). White circles in *B* represent estimated metacommunity-weighted climate tolerances. Shared contributions of climate, space, time, and time and space were extremely small in both metacommunities (<0.1%) and therefore were omitted from the plot in *C*.

over time in MTC (SH/TH = 2.12). Conversely, climate varied more in time than across elevations in the temperate AEF (SH/TH = −2.56). In figure 5*B*, we contrasted the degree of climatic tolerance of the dominant species in the regional pool of both landscapes. As anticipated, the aseasonal MTC exhibited a species pool dominated by climate specialists (i.e., metacommunity-weighted mean climatic tolerance = 0.21), while the seasonal AEF favored the prevalence of climate generalists in its pool (metacommunity-weighted mean climatic tolerance = 1.23).

As predicted (fig. 5*C*), variation in community composition in the aseasonal MTC (where specialists dominated the species pool) was mostly explained by climate variation alone. This pattern suggests a strong influence of species-environment sorting in community assembly in aseasonal landscapes. In contrast, variation in community composition in the highly seasonal AEF (where generalists dominate the species pool) was mainly explained by temporal autocorrelation in community composition underpinned by endogenous demographic mechanisms and their association with climate (Legendre and Gauthier 2014).

Conclusions, Assumptions, and Future Directions

In this study, we proposed a conceptual framework for metacommunity assembly that acknowledges the dependency of species pool attributes on landscape characteristics and elucidates how their combined and individual contributions determine the relative importance of different assembly mechanisms. By doing so, we derived testable predictions underlying geographical patterns of metacommunity assembly when inferred from empirical data.

While we recognize that our conceptual framework and theoretical model did not consider other aspects of landscapes that are known to influence the coexistence of specialists and generalists, these could be incorporated in future model versions. For instance, recent empirical studies have shown that the spatial frequency of climate conditions at large scales and patch heterogeneity are relevant factors determining the degree of ecological specialization of species pools (Fournier et al. 2020).

Last, our framework for the geography of metacommunities assumes that species pool dynamics are primarily influenced by mechanisms operating at the landscape scale while intentionally disregarding the effects of evolutionary and historical mechanisms operating at biogeographic scales. Nevertheless, our proposed framework proves valuable in advancing syntheses to explore the substantial variation in the relative importance of mechanisms observed in empirical metacommunities across different parts of large-scale ecological gradients. Future studies could explore how evolutionary processes mediate the relationships among dominant life history strategies, landscape attributes, and assembly mechanisms at the metacommunity level (e.g., Mittelbach and Schemske 2015).

Statement of Authorship

G.K. and P.R.P.-N. conceptualized the study; G.K. developed simulation models, analyzed the data, and led the writing of the original draft of the manuscript; and both authors contributed substantially to the editing and writing of the final manuscript.

Data and Code Availability

Data and R code are available on Figshare (https://doi.org/10.6084/m9.figshare.24535018.v1; Khattar and Peres-Neto 2023).

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