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Mechanisms of Community Assembly through the Lens of Phylogenetic Diversity: A Critical Reappraisal

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ABSTRACT.—Darwin was one of the first to hypothesize a connection between niche differentiation and competition and species relatedness, offering an appealing framework to disentangle community assembly processes based on phylogenetic diversity patterns. Community assembly is, however, the result of several processes including potentially confounding factors associated with dispersal limitations and spatial effects, casting doubt about the application of phylogenetic diversity metrics to infer community assembly processes. We implemented a spatially explicit model involving limited dispersal, drift, trait-based selection, and competition to simulate community composition under competing assembly processes in a landscape with contrasted habitat connectivity. The phylogenetic structure of communities globally varied depending on assembly processes and the combination thereof, validating the assumption, made by a large number of studies but seldom tested in a spatially explicit context, that different assembly processes indeed lead to significantly different patterns of community phylogenetic structure. All the investigated alpha metrics exhibited a poor ability to detect overdispersion under stabilizing processes, and some even unduly recovered a signal of clustering. Some of the most widely used metrics, such as UniFrac, carry a redundant signal with non-phylogenetic metrics, and hence, poorly capture the phylogenetic signal in the data. We identified three metrics, namely Bst or Pst for abundance data and PIst for occurrence data, which best retrieved the correct signal of phylogenetic structure under different assembly processes. Spatial effects may blur the phylogenetic structure of communities and decrease our ability to infer underlying processes. However, meaningful results may be obtained when the appropriate comparisons are made. In particular, phylogenetic clustering under equalizing processes must be tested on inter-habitat comparisons because it is the differential filtering of species between habitats that reveals the impact of equalizing processes. Our simulations further suggest that a significant phylogenetic structure of communities can be retrieved even in species-poor communities, except when the communities being compared are dominated by a single, most abundant species. We therefore conclude with best practices to adequately infer assembly processes with useful phylogenetic diversity metrics. [Community assembly mechanisms; community simulation; phylogenetic diversity; phylogenetic metrics.]

A metacommunity is defined as a set of local communities where species coexistence depends on four main processes: niche differentiation, competition, drift, and dispersal (Leibold et al. 2004). The relative importance of these processes, which may operate simultaneously (Vellend 2010; Fournier et al. 2017), varies according to the capacity of species to disperse, experience their environment, and interact with other individuals (Livingston et al. 2012), but also depending on landscape connectivity and environmental heterogeneity.

Niche differentiation and competition are the two ingredients of a trade-off between selection of traits for a given environment, enhancing fitness in the latter, and competition among closely related species. This trade-off was formalized by Chesson's (Chesson 2000) integrative framework of species coexistence based on two fundamental processes. Equalizing processes minimize fitness differences between species, so that coexisting species tend to share similar functional traits in a given habitat, whereas distinct habitats can select contrasted trait combinations. Stabilizing processes stabilize coexistence via negative density-dependent selection, such as resource limitations, parasitism, and predation. Thus, coexisting species tend to have dissimilar functional traits to avoid competition for the same resources, easy transfer of parasites, or predator attraction (limiting similarity).

Darwin (1859) was one of the first to hypothesize a connection between habitat selection, density-dependent selection, and the relatedness among species. In fact, closely related species tend to share the same niche (phylogenetic niche conservatism (Wiens and Graham 2005; Losos 2008; Wiens et al. 2010). They hence compete for the same resources (Emerson and Gillespie 2008; Violle et al. 2011), but also are more likely to share parasites and diseases (Stephens et al. 2019, and references therein). To avoid competitive exclusion, parasite or predator transfer, the essence of stabilizing coexis-

Table 1. Simulations of community assembly under different processes and expected patterns of community phylogenetic structure

Process	Process in habitat (C)	Process in fragmented habitat (F)	Prediction or question
1/Stochastic	100% Stochastic (neutral)		No phylogenetic structure
2/Stabilizing	100% Stabilizing (competitive exclusion)		Phylogenetic overdispersion
3/Equalizing Specialist	100% Equalizing with specialist species (strong habitat filtering)		Strong phylogenetic clustering
4/Equalizing Generalist	100% Equalizing with generalist species (moderate habitat filtering)		Weak phylogenetic clustering
5/Mixed Specialist	Mixed specialist: equal contribution of equalizing and stabilizing processes with specialist species		Which process affects the most the phylogenetic structure?
6/Mixed Generalist	Mixed generalist: equal contribution of equalizing and stabilizing processes with generalist species		Which process affects the most the phylogenetic structure?
7/Mass Effect 1	100% Stochastic	100% Equalizing with specialist species	Does habitat filtering in habitat F affect the phylogenetic structure in habitat C?
8/Mass Effect 2	100% Equalizing with specialist species	100% Stochastic	Does habitat filtering in habitat C affect the phylogenetic structure in habitat F?

tence processes, a newly colonizing individual should be phylogenetically distant from the species already present in the community. Communities should thus include distantly related species, resulting in a pattern of phylogenetic overdispersion (Wiens and Graham 2005; Anacker and Strauss 2016).

Empirical evidence for this hypothesis has, however, been conflicting (Vamosi et al. 2009). This paradox, known as “Darwin’s Conundrum” (Thuiller et al. 2010; Fan et al. 2023), reflects the fact that an individual has better chances to establish within a community if its ecological niche is compatible with the environment of that community, the essence of equalizing coexistence processes. This happens if the colonizing individual shares the same adaptations for that environment with the species already established in the community, leading to a pattern of adaptive trait clustering and, indirectly, of phylogenetic clustering if these adaptations are phylogenetically conserved (Graham and Fine 2008).

Different phylogenetic patterns are therefore expected depending on the relative contribution of equalizing and stabilizing processes to community assembly (Lemoine et al. 2015). The analysis of community phylogenetic structure offers in this context an appealing framework to infer community assembly processes (Webb et al. 2002; Cottenie 2005; Graham and Fine 2008).

A large number of phylogenetic diversity metrics have been developed to characterize the phylogenetic structure of communities (Tucker et al. 2017) but have rarely been tested. Miller et al. (2017) identified the best performing metrics in terms of statistical power and rate of false positives. Their simulations, however, involved the placement of individuals based on their traits, regardless of dispersal limitations and spatial effects in community assembly. Niche and dispersal processes are, however, not independent from each other (Vilmi et al. 2021). Dispersal limitations lead to patchy communities assembled under neutral processes (Münkemüller et al. 2012), thus influencing the distribution of diversity (Cadotte 2006; Myers and Harms 2009; Condit et al. 2012), the nature and strength of species interactions (Shurin and Allen 2001; Chase et al. 2010), and environmental filtering (Réjou-Méchain and Hardy 2011). It was shown that the extent to which species are found in their optimal habitat is negatively correlated with the ratio between mean dispersal distance and the size of habitat patches (Réjou-Méchain and Hardy 2011). Species co-occurrences thus quantitatively depend on local environmental conditions, but also on neighboring occupancy. In particular, species abundant in one large habitat may invade a smaller neighbor habitat, where they are ill-adapted, due to the high number of dispersal events leading to rescue effects (i.e., the death of an ill-adapted individual is followed by its replacement by a new migrant). Such a phenomenon, known as the “mass effect,” “dilutes” species/environment relationships (Shmida and Wilson 1985).

In this context, whether community phylogenetic structure truly reflects assembly processes has been increasingly questioned (Cadotte and Tucker 2017). First, species occurrence patterns are not only shaped by environmental filters, but also by biotic factors and dispersal limitations, which may interact in complex ways and result in patterns of community composition and phylogenetic structure that may erroneously be interpreted. Second, the link between phylogenetic clustering and environmental filtering, and between overdispersion and limiting similarity, is ambiguous (Cavender-Bares et al. 2006; Valiente-Banuet 2007).

Here, we implement numerical simulations integrating the key processes of dispersal, drift, and selection underlying the dynamics of local accumulation of biodiversity through time (Vellend 2016; Fournier et al. 2017) as well as the level of species habitat specialization. Our approach allows us to simulate species assembly across a continuum of scenarios, from purely neutral to niche-structured by stabilizing or equalizing processes, or combinations of them, while considering the importance of spatial effects in a fragmented landscape. In this

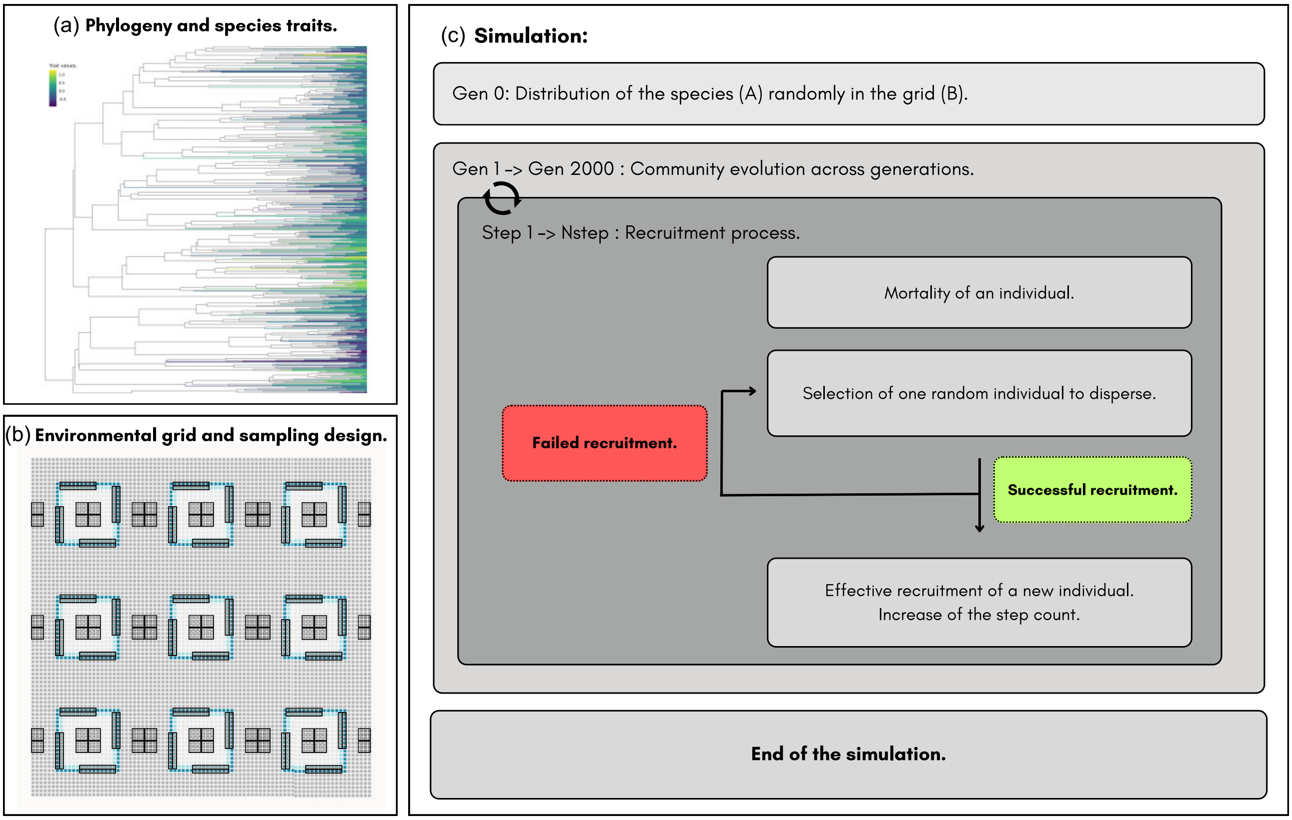

FIGURE 1. Illustration of the community assembly simulation framework under stochastic, equalizing, and stabilizing processes, and the combination thereof, in a fragmented landscape. (a) Simulation of a phylogeny, with nine species traits mapped on it following a Brownian evolutionary model (equalizing and stabilizing processes will depend each on three independent sets of three traits). (b) Landscape configuration and sampling design. Within a landscape of 84 by 84 pixels folded on a torus (i.e., opposite sides of the grid are adjacent to avoid border effects) projected onto a square grid for easier visualization, two types of habitats occur: a fragmented habitat (light gray) made of 9 patches including each 196 pixels is embedded in a continuous habitat (dark gray). Border pixels are highlighted in blue. Each pixel contains 50 individuals, whose species are randomly sampled among the species of the phylogeny at the beginning of the simulation (gen 0). At the end of the simulation, 144 plots combining 9 adjacent pixels (surrounded by a line) are used for analyses. We run 2000 generations where one generation consists of a number of steps equal to the total number of individuals (84 × 84 × 50 steps). Within each habitat, 36 core and 36 border plots are identified. (c) Community assembly over time and recruitment process. At each step, one individual dies and is replaced by another individual, either from the same pixel or from another pixel, with a probability and at a distance determined by a dispersal kernel. The probability Pr that the new individual establishes and replaces the dead individual depends on the process involved. Under neutral processes, $Pr = 1$. Under equalizing processes, Pr increases when the traits of the new individual approach optimal trait values for the habitat. Under stabilizing processes, Pr increases with the difference between the traits of the new individual and the traits of the other individuals from the pixel. One hundred replicates of 2000 generations are run for each of 8 scenarios involving an assembly process or combination thereof. Each replicate has a newly simulated metacommunity. The strength of selection for equalizing processes was high ("specialist species") or low ("generalist species"), depending on the scenario simulated.

framework, we address the following questions and test the following hypotheses (Table 1):

- To what extent does the phylogenetic structure of communities vary under different processes and combinations thereof (Q1)?
- To what extent does this structure vary depending on spatial and mass effects, that is, do phylogenetic diversity patterns vary within the core and at the border of continuous versus fragmented habitats (spatial effects) (Q2a), and within one habitat depending on the assembly process taking place in a neighboring habitat (mass effects) (Q2b), potentially blurring the relationship between assembly processes and phylogenetic structure?
- Can randomization tests of phylogenetic diversity metrics be used in practice, and in which conditions, to infer community assembly processes (Q3)?

MATERIAL AND METHODS

Simulating Communities under Contrasting Assembly Processes

We simulated the assembly of theoretical communities that meet the expectations of stochastic, equalizing, and stabilizing processes. An overview of the procedure is presented in Figure 1.

Species phylogeny and traits.— For each replicate, a different metacommunity was generated following a Fisher's log series (but assuming identical species abundances) with an expected species count of 800 (function *fisher.ecosystem* of package *untb*; Hankin 2007). A phylogenetic tree for these species was simulated under a pure Birth process with a speciation rate of 0.2 and an extinction rate of 0 with the *TreeSim* package (Stadler 2009, 2011). The evolution of nine continuous traits was simulated on that tree under a Brownian motion model with a random deviation of 0.1 with the function *rtraitcont* of the *ape* package (Paradis and Schliep 2019).

Community simulations.— The simulation of a community starts by randomly assigning each of the 50 individuals of each pixel to one of the species from the simulated phylogeny. Then, 2000 generations are simulated to ensure that key parameters, such as species richness and proportion of failed recruitment, reach a plateau (Supplementary Fig. S1), each generation including a number of death-recruitment steps equal to the size of the total community (number of pixels × number of individuals per pixel = 352,800). Each step was divided into three phases: the death of one individual chosen at random across all pixels, the random selection of a new individual from the same or another pixel according to a dispersal kernel, and the establishment probability of this new individual to replace the dead one according to an assembly process.

Dispersal processes and establishment probability. The new individual had a probability of (1) 0.0001 to originate from the initial species pool (long-distance dispersal); (2) 0.7999 to originate from the same pixel as the dead individual (reproduction); and (3) 0.2 to originate from a surrounding pixel following an exponential dispersal kernel with a mean dispersal distance of 1 grid unit (distance between two adjacent pixels) (short-distance dispersal). Accordingly, 80.2% of the new individuals originated from the same pixel (reproduction) and the longest dispersal distance was 4 grid units, with a probability of 7.10^{-4} (Supplementary Fig. S2). The probabilities of recruitment Pr under the different processes are detailed in Supplementary Table S1. When the probability of recruitment $Pr < 1$, a random number, R, is drawn between 0 and 1 and the new individual effectively establishes if $R \leq Pr$. Otherwise, a new individual is chosen following the dispersal process described above, until a successful recruitment takes place, ending the step.

Simulations of community assembly. We ran 100 replicates of 2000 generations for each of eight processes of community assembly (Table 1). At the end of a simulation, the community was sampled for further data analyses, using plots made of 9 adjacent pixels (450 individuals per sample). Within the core and border of each habitat type, we used 36 plots of core continuous habitat, core fragmented habitat, border continuous habitat, and border core habitat for a total of 144 plots (Fig. 1b).

Computation of Phylogenetic Alpha and Beta Diversity Metrics

An array of phylogenetic diversity metrics has been proposed. These metrics can be classified based upon a series of properties (Pavoine and Bonsall 2011; Tucker et al. 2017). Alpha metrics characterize a single community, whereas beta metrics quantify differences between communities. Metrics can further be differentiated depending on the type of data involved (occurrence vs. abundance) and their nature, that is, whether they characterize a richness (e.g., sum of phylogenetic distances among species) or a divergence level (e.g., mean phylogenetic distance between species) (Tucker et al. 2017). Here, we selected 31 of these metrics to cover the range of metric types (Supplementary Table S2).

For each scenario, we computed phylogenetic diversity metrics for each of the 100 replicates. Alpha metrics were computed for each sample within core habitat and border type, resulting in 14,400 values per scenario across the 100 replicates. Beta metrics were computed for each pair of plots from the same habitat and border type (intra-core and intra-border comparisons), and from different habitats and border types (inter-core and inter-border comparisons), resulting in 10,296 values per scenario per replicate.

Statistical Analyses

To determine whether diversity metrics vary significantly depending on assembly processes and the combination thereof (Q1), we computed, for each simulation replicate, the average value across plots ($n = 144$) (alpha metrics) and the average values among pairs of plots (n = 10,296) (beta metrics). We then sought for significant differences among community assembly processes across the 100 replicates per process using Dunn tests due to the non-homoscedasticity of the data and their departure from a normal distribution, as evidenced by Shapiro–Wilk and Brown–Forsythe tests, respectively.

To summarize the variation of phylogenetic structure, as reflected by the different metrics, under different assembly processes and in different environments (Q1), we implemented a Principal Component Analysis (PCA) ordinating replicates in the space of metrics, including both taxonomic and phylogenetic diversity metrics to characterize the communities. For alpha diversity, taxonomic metrics included species richness and Simpson's diversity index. For beta metrics, we included the two components of beta diversity, namely turnover (measured by Simpson's similarity index, βsim) and nestedness (βsne) (Baselga 2010).

To determine whether community phylogenetic structure varied among assembly processes within continuous versus fragmented habitats and at their borders (Q2a), we used Dunn tests to determine whether there was a significant difference in the average metric value across the 100 replicates between the continuous and fragmented habitat, contrasting core and border habitats. To determine whether variation in community assembly in one habitat could affect community phylogenetic structure in the other habitat (Q2b), we also used Dunn tests to determine whether there was a significant difference in the average metric value in the continuous habitat when the fragmented habitat was under stochastic versus equalizing processes, respectively, and vice versa.

Finally, we assessed whether phylogenetic diversity metrics can be used in practice to detect phylogenetic clustering or overdispersion (Q3). To do so, we implemented null models to determine whether the observed value of a metric is significantly higher or lower than expected by chance. The distribution of the null hypothesis (i.e., the distribution of the metric value expected in communities without any phylogenetic structure) was generated by reshuffling species positions among the tips of the phylogeny 100 times, keeping only species actually sampled from the metacommunity.

Results

The community assembly simulation model is depicted in Figure 1, and descriptive features of the resulting communities in terms of variation in species distribution patterns, trait values, abundance, and diversity patterns under eight assembly processes (Table 1) are detailed in Supplementary Appendix 1.

Variation of Phylogenetic Diversity Metrics under Different Processes

We selected mean phylogenetic distance (MPD) and PhyloSor, two of the most widely used metrics of alpha and beta phylogenetic diversity, respectively, to illustrate variations in phylogenetic structure resulting from different assembly processes. Average MPD was significantly lower under equalizing processes (reaching lower values with specialist than with generalist species) than under all other assembly processes (Supplementary Fig. S3a). PhyloSor was maximum under stabilizing processes, minimum under stochastic processes, and did not significantly differ, on average, between specialist and generalist species under equalizing processes (Supplementary Fig. S3b).

A PCA ordinating simulation replicates in the space of diversity metrics showed that pure processes generate different patterns of community phylogenetic structures, especially when characterized with beta metrics (Fig. 2). Communities simulated under stabilizing processes were well-characterized in the space of beta metrics (Fig. 2b1), but not in the space of alpha metrics (Fig. 2a1), where they overlapped with communities simulated under mixed processes. Phylogenetic metrics such as PD, AED, and PSR were highly correlated with species richness (Fig. 2a2). No phylogenetic beta metric was correlated with the difference in species richness among communities (βsne), but a series of phylogenetic beta metrics, including UniFrac, PhylosSor_turn, and PCD, were redundant with species turnover (βsim) (Fig. 2b2). Pst, Bst, and PIst were uncorrelated to all other beta metrics (Fig. 2b2), potentially expressing complementary patterns.

Impact of Mass and Spatial Effects on Phylogenetic Structure and Diversity

Patterns of phylogenetic diversity were substantially affected by mass and spatial effects when equalizing processes were involved (Fig. 3). Alpha diversity estimated by the MPD index was significantly lower in core habitats than at their borders (Fig. 3a1). At the limit between two habitat types indeed, both well- and ill-adapted species, whose presence is influenced by the neighboring community composition, occur. The same effects explain why MPD was significantly lower in both the core and border of one habitat when the other habitat was under stochastic rather than equalizing processes (Fig. 3a2), as equalizing processes maintain phylogenetic divergence among species from different habitats. Similarly, when one habitat was under stochastic processes, MPD was lower when the other habitat was under equalizing processes (Fig. 3a2) because species selected in one habitat freely disperse into the other habitat.

Among intra-habitat comparisons, beta diversity quantified by the PhyloSor index was the lowest in core fragmented habitat comparisons and the highest in core continuous habitat comparisons (Fig. 3b1), but, due to spatial effects, these differences were eroded in border habitats. This was evidenced by the fact that (1) average PhyloSor at the border of the continuous habitat did not significantly differ from average PhyloSor at the border of the fragmented habitat and (2) average PhyloSor was significantly higher in inter-border than in inter-core habitat comparisons (Fig. 3b1). PhyloSor was significantly higher within one habitat when communities in the other habitat were assembled under a different process except in the case of the core continuous and border fragmented habitats under equalizing processes (Fig. 3b2).

To What Extent Can We Retrieve Community Assembly Processes from Phylogenetic Diversity Metrics Associated with Null Models?

The performance of 31 diversity metrics associated with a null model shuffling species among the tips of

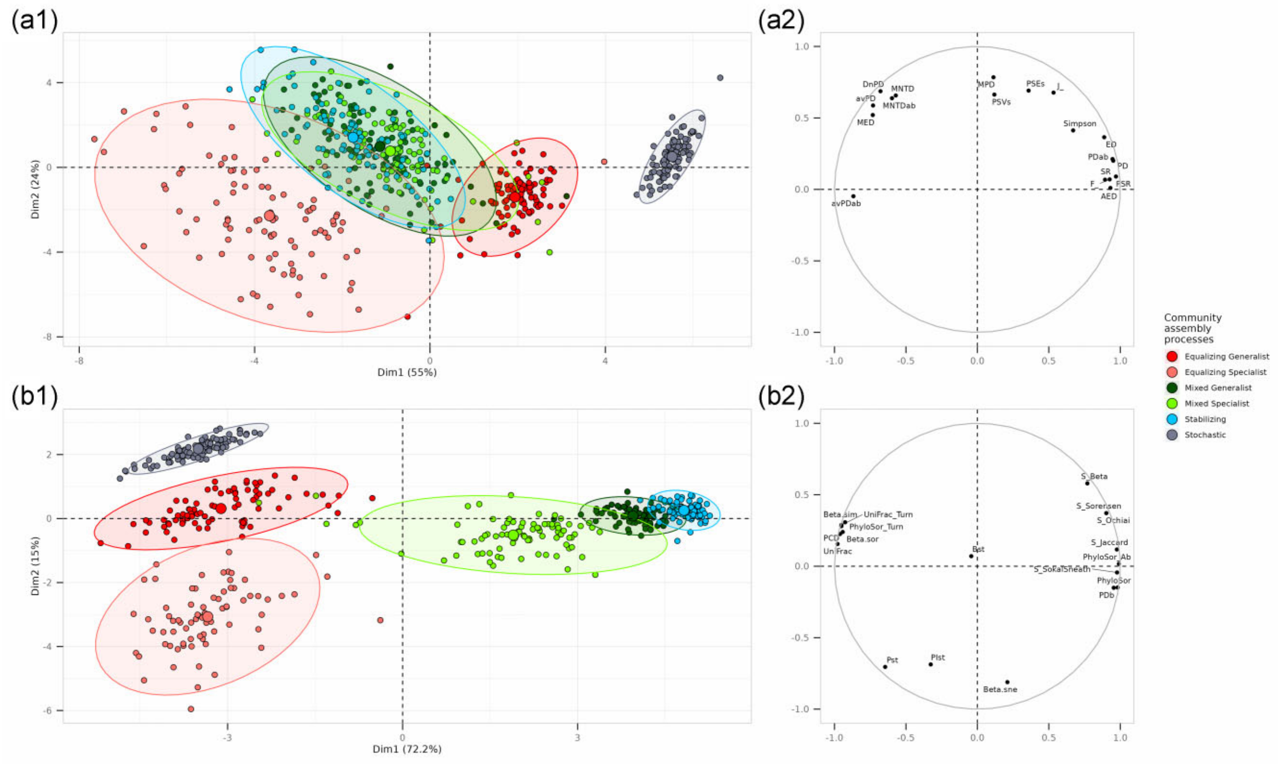

FIGURE 2. Principal Component Analysis of the communities assembled under different processes as a function of alpha (a1) and beta (b1) diversity metrics. Each dot represents one of 100 replicates of community assembly simulations per assembly process (stochastic, equalizing with specialist or generalist species, stabilizing, and mixed equalizing, with specialist or generalist species)/stabilizing processes. The inserts (a2 and b2) show the correlation between alpha and beta metrics, respectively, and the axes (see Supplementary Table S2 for abbreviations).

the phylogeny to identify the correct assembly process is illustrated in Supplementary Figure S4. The percentage of significant tests under stochastic processes (type 1 errors) was generally <10% across all but "S" metrics. All alpha metrics failed to retrieve overdispersion under stabilizing processes, with significant overdispersion found in <10% of the simulations. Worst, alpha metrics retrieved, on average, 5–25% of significant clustering under stabilizing processes (Supplementary Fig. S4a). Alpha metrics evidenced significant clustering under equalizing processes for specialist species in 37–64% of the simulations, with the highest rates with MNTD.

Beta metrics exhibited contrasting behavior and performances (Supplementary Fig. S4b). Under stabilizing processes, only Pst and Bst indicated significant phylogenetic overdispersion in a majority of replicates (80%). Under equalizing processes for specialized species, Pst, Bst, and PIst were also the only metrics detecting significant phylogenetic clustering in a majority of replicates (52–68%) when comparing pairs of samples from different habitats.

Based on his, we selected one of the alpha metrics (MNTD) and two beta metrics (Bst for abundance data and PIst for presence–absence data) that best performed in terms of their ability to detect significant phylogenetic community structure under different assembly processes. We examined the performance of these metrics under different combinations of assembly processes and spatial configurations (Fig. 4). MNTD correctly retrieved clustering under equalizing processes with generalist species at rates >90% in the core continuous and border habitats, and 75% in the core fragmented habitat (Fig. 4). The performance of MNTD was unexpectedly slightly lower in the case of specialist species. When one habitat was under equalizing process and the other one under stochastic process, MNTD retrieved clustering in both habitats at rates of >70%. The performance of MNTD was poor under stabilizing processes, retrieving significant clustering instead of overdispersion in about 25% of the simulations. Under mixed equalizing/stabilizing processes, MNTD retrieved significant clustering in about 25% of the simulations.

Abundance-based beta metrics had a higher statistical power compared with presence-based metrics. For instance, Bst recovered overdispersion under stabilizing processes at 80%, whereas the equivalent metric using occurrence data (PIst) returned a rate of only 15%.

Bst and PIst recovered clustering under equalizing processes with both generalist and specialist species at about 75% in inter-core habitat comparisons. When

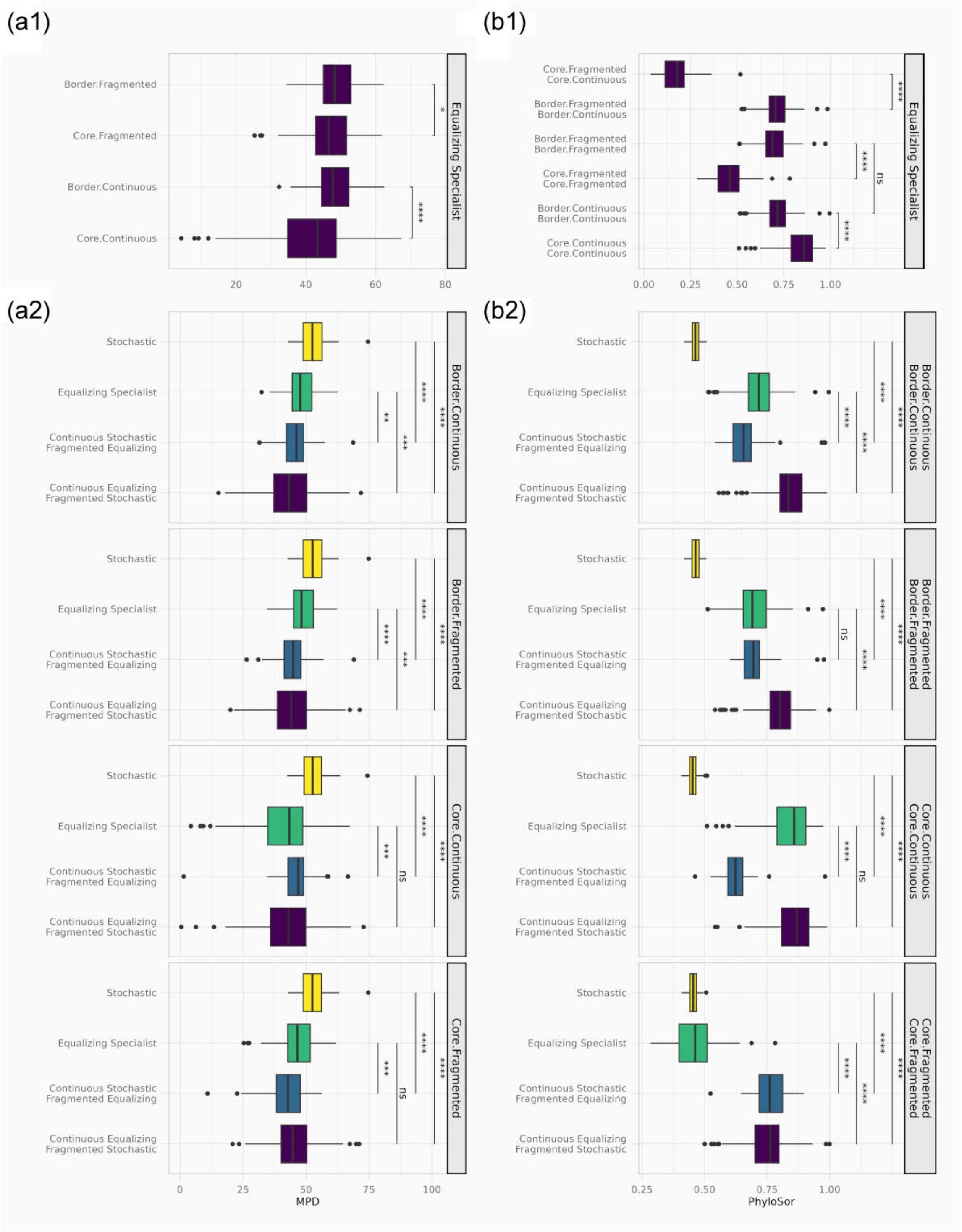

FIGURE 3. Impact of mass and spatial effects on community phylogenetic structure and diversity. Box plots (showing the 1st and third quartiles (upper and lower bounds), second quartile (center), 1.5∗ inter-quartile range (whiskers), and minima-maxima (beyond the whiskers) represent the variation of alpha diversity (quantified by MPD) (a) and of beta diversity (quantified by Phylosor) (b) in the core and border of each habitat when communities in both habitats are assembled under the same versus different processes (stochastic vs. equalizing for specialist species). The upper (a1 and b1) panel represents comparisons among habitat samples (core and border continuous, core and border fragmented) under equalizing processes. The lower (a2 and b2) panel compares the impact of different processes (with different colors) for each type of habitat sample. ns, ∗, ∗∗, and ∗∗∗ indicate whether selected comparisons are not significant or significant at the 0.05, 0.01, and 0.001 level, respectively, based on Dunn tests.

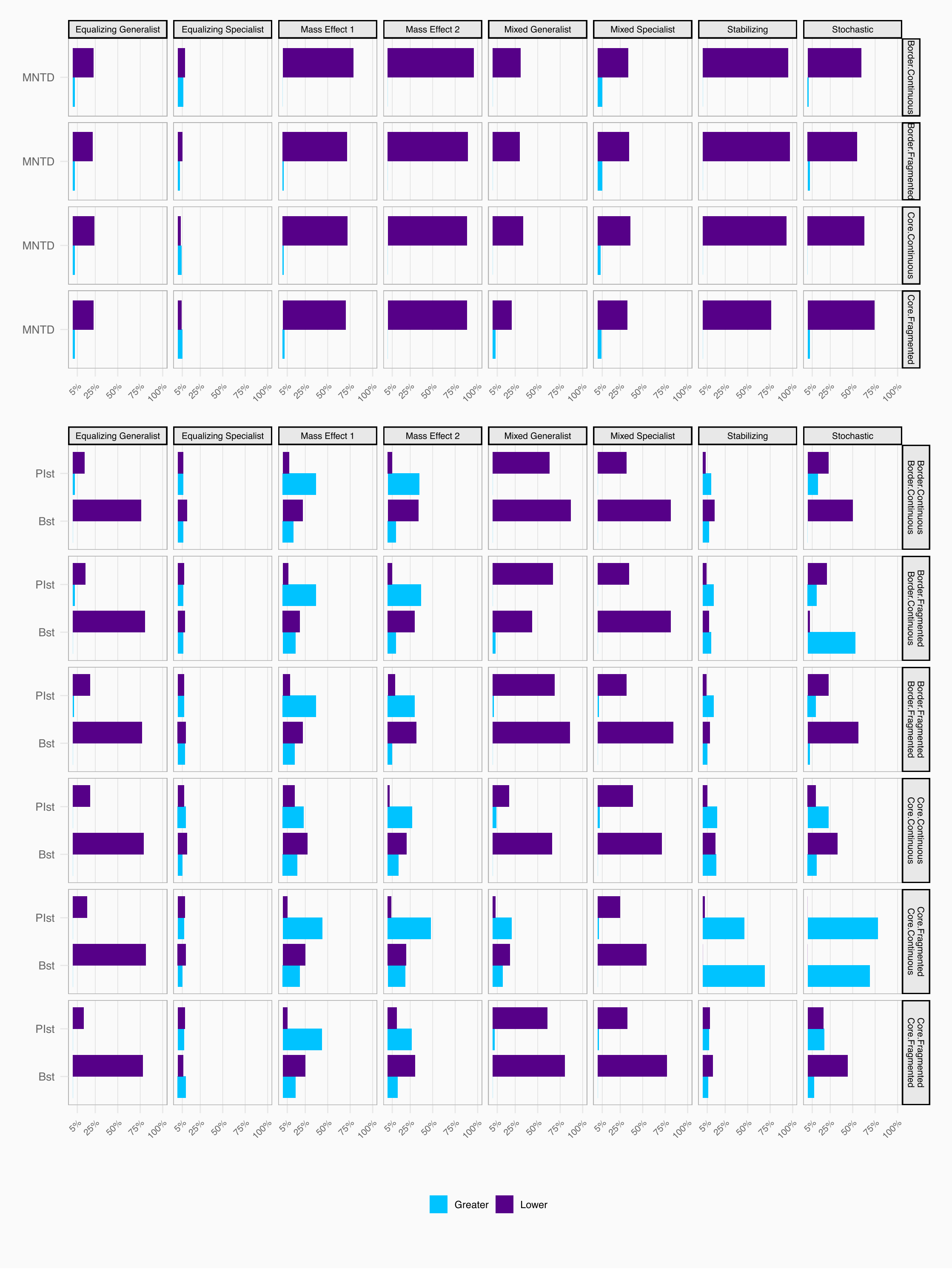

FIGURE 4. Performance, in terms of type 1 (false negative) and type 2 (false positive) errors, of selected metrics of phylogenetic diversity to retrieve the process under which communities were simulated. 1: stochastic, 2: stabilizing, 3–4: equalizing with specialist and generalist species, and combinations thereof (equal contribution of equalizing and stabilizing processes with specialist (5, Mixed Specialist) and generalist (6, Mixed Generalist) species, respectively; stochastic processes in the continuous habitat, equalizing processes in the fragmented habitat (7, Mass Effect 1) and vice versa (8, Mass Effect 2) (see Table 1) in a landscape composed of a fragmented and a continuous habitat and depending on neighboring occupancy (mass effects), whose impacts are examined within core and border plots. Bars represent the percentage of tests for which the statistic was significantly higher (in blue) or lower (in violet) across 100 replicates.

mixed stabilizing/equalizing processes were at play, Bst and PIst consistently recovered significant overdispersion at >75% or between 30% and 75%, respectively, in intra-core habitat comparisons. In intra-border habitat comparisons, Bst retrieved clustering at 80% in the case of both generalist and specialist species, whereas PIst recovered significant clustering at rates of 30% for generalist species and slightly less than 75% for specialist species. Both metrics failed to detect a significant phylogenetic structure in inter-core habitat comparisons for mixed scenarios with specialist species.

Mass effects played a substantial role by eroding or even modifying the phylogenetic structure in one habitat depending on the process at play in the other habitat. Under equalizing processes with generalist species, Bst and PIst among habitats both characterized strong phylogenetic clustering among core plots but almost no signal among border plots. Under equalizing processes with specialist species, the proportion of significant Bst values dropped from about 75% to about 50%, but PIst shifted from a strong signal for clustering to a weak signal of overdispersion. When the two habitats were simulated under different assembly processes (stochastic vs. equalizing), PIst retrieved a signal of clustering at the border and within the core of the two habitats. Bst retrieved a signal of overdispersion at the border and within the core of the two habitats.

Discussion

Community Phylogenetic Structure under Different Assembly Processes

The phylogenetic structure of communities globally varied under equalizing, stabilizing, and stochastic processes, and the combination thereof. This validates the assumption, made by a large number of studies aiming at disentangling the importance of competition and habitat filtering (Qian and Jiang 2014; Zhang et al. 2018; Li et al. 2022; Galvan-Cisneros et al. 2023), but seldom tested in a spatially explicit context (Münkemüller et al. 2012), that different assembly processes indeed lead to significantly different patterns of community phylogenetic structure. Unlike previous simulations of community assembly that focused on pure processes, our results further revealed that combinations of processes more likely to occur in real communities also leave identifiable patterns of phylogenetic structure.

Performance of Phylogenetic Diversity Metrics to Retrieve Phylogenetic Structure under Competing Assembly Processes

Whether different processes left a strong signature on phylogenetic diversity patterns varied among metric kinds and processes. Our results confirm that different metrics of phylogenetic diversity exhibit very contrasting performances to detect phylogenetic clustering and overdispersion, and hence, indirectly, infer assembly processes (Münkemüller et al. 2012; Miller et al. 2017), and further highlight under which conditions which metrics are most appropriate.

In line with the fact that stabilizing processes generated alpha diversity patterns that could not be distinguished from those generated under mixed processes, all the investigated alpha metrics exhibited a poor ability to detect overdispersion under stabilizing processes. Even worse, metrics such as MNTD and AED recovered a signal of clustering. This contrasts with previous findings that alpha metrics based on mean relatedness, such as MPD, are most powerful for detecting phylogenetic overdispersion due to competitive exclusion (Miller et al. 2017). In Miller's et al. (2017) simulations in fact, individuals were placed on a grid based on their traits, thereby forcing unrelated species to co-occur under stabilizing processes. Communities simulated based on an actual assembly process taking dispersal limitations into account may not include the most distantly related species, highlighting the crucial importance of spatially explicit simulations when assessing the responses of biological communities to assembly processes (Wiegand et al. 2017).

Compared with alpha metrics, some of the beta metrics performed extremely well in recovering overdispersion under stabilizing processes. In line with evidence that species abundance data, but not occurrence data, carry information regarding species interactions (Botta-Dukat and Czucz 2016; Blanchet et al. 2020), the metrics that exhibited the highest statistical power under stabilizing processes were Bst and Pst. These abundance-based metrics in fact substantially outperformed equivalent metrics based on occurrence data, such as PIst.

Altogether, two lines of evidence lead us to recommend, among beta metrics available, the application of Bst or Pst and PIst for abundance and occurrence data, respectively. First, although most beta phylogenetic metrics range between 0 and 1, the actual value of Bst and PIst is informative regarding the identity of the process at play. Indeed, Bst and PIst can be negative, indicating spatial phylogenetic overdispersion, or positive, indicating spatial phylogenetic clustering. Second, unlike divergence metrics, which are based on average distance among species within versus among communities, richness metrics, which sum up the proportion of shared branch lengths between two communities (Tucker et al. 2017), were correlated with their taxonomic counterpart (species turnover). This suggests that such metrics differentiate communities assembled under different processes due to the different patterns of species richness and composition generated by those processes, but that the signal included in those metrics is not driven by the phylogenetic structure of communities. Such phylogenetic metrics are thus redundant with their taxonomic counterparts. We therefore suggest that metrics such as UniFrac, although one of the most widely used in analyses of community phylogenetic structure (Jin et al. 2015; Shooner et al. 2018; Lazzaro et al. 2020), could usefully be replaced by other metrics, such as Bst and PIst, which carry a signal that is independent from that of the taxonomic metrics.

Can Community Assembly Processes Be Unambiguously Inferred from Phylogenetic Diversity Patterns?

Our simulations revealed that specific assembly processes lead to expected patterns of phylogenetic clustering under habitat filtering and overdispersion under limiting similarity when appropriate metrics are employed. Inferring assembly mechanisms from community phylogenetic structure requires, however, a careful interpretation because phylogenetic clustering or overdispersion is not a synonym of environmental filtering and limiting similarity, respectively. In fact, other processes than competition, for instance niche convergence (Cavender-Bares et al. 2004) or facilitation (Valiente-Banuet 2007) among phylogenetically unrelated species, can also lead to phylogenetic overdispersion, challenging the interpretation of the latter.

Unexpectedly, overdispersion (negative Bst or Pst statistics) was detected under equalizing processes with specialist species in intra-habitat comparisons. We observed these patterns when the effective number of species per sample (i.e., the inverse of the sum of squares of species frequencies) was very low, about <2.5. In those conditions, one or a few closely related adapted species dominate the two samples being compared, along with a few rare, ill-adapted species brought by immigration or mass effect. Hence, the negative Bst or Pst values observed in such conditions results from the comparison of random mean abundance-weighted phylogenetic distances among species within each sample and low mean abundance-weighted phylogenetic distance among species among samples. This means that, to be able to detect equalizing processes, Bst and PIst must thus be tested on inter-habitat comparisons (i.e., habitats must filter species traits on distinct optima), because it is the differential filtering of species between habitats that reveals the impact of equalizing processes. In those conditions, meaningful results may be obtained, according to our empirical evaluation, in species-poor communities, that is, much below the minimum of 10 species per samples imposed by Miller et al. (2017), except when the communities being compared are dominated by a single, most abundant species.

Regarding the ability of the investigated metrics to recover phylogenetic clustering under equalizing processes, the alpha metrics that performed best in our simulations, such as MNTD, consistently recovered phylogenetic clustering under equalizing processes, with a similar power with regard to the spatial configuration of the habitat (border vs. core habitat). By comparison, the beta metrics that performed best in our simulations, such as Bst, Pst and PIst, recovered phylogenetic clustering in the case of generalist species at a much lower rate in inter-border habitat than in inter-core habitat comparisons. Worst, metrics based on occurrence data such as PIst further exhibited a low statistical power at recovering phylogenetic clustering in inter-border habitat comparisons, even under stringent equalizing processes involving specialist species. Such metrics thus appear highly sensitive to the homogenization of the communities among habitats, either due to low species specialization levels and/or spatial configurations favoring the migration of poorly adapted species (mass effects). The apparent high ability of alpha metrics such as MNTD to recover phylogenetic clustering, whatever the spatial configuration of the habitat, must, however, be interpreted with caution. In fact, MNTD erroneously recovered a signal of clustering in habitats under stochastic processes when the other habitat was under equalizing processes, whereas beta metrics ambiguously recovered both significant clustering and overdispersion at low rates (<25%), characterizing a complex situation.

Limitations of the Simulation Framework

As in all simulations, the conclusions made in the present study apply within the range of a series of explicit assumptions based on the choices made at each step. A first assumption was made by generating a regional species pool with an expected species count of 800. The size of the species pool is an important parameter because, with a small number of species either included in the community or excluded by the assembly process, the probability of any given combination of taxa arising by chance in the null model is high (Kraft et al. 2007). Here, 800 represented a trade-off between a large number, increasing computation time, and a low number resulting, in the most stringent simulations, in a too low species richness in the local communities. With a species richness of 800 in the metacommunity, 13.4 plots out of a total of 144 had already to be removed, on average across 100 replicates, from the analysis under equalizing processes with specialist species for hosting a single species. The ca. 800 species included in the regional species pool exceed by a factor of 2–3 the species pool implemented by Kraft et al. (2007), who reported that the statistical power decreases with increasing pool size for communities simulated by competition. In the present analyses, however, the selected metrics (Bst and Pst) had a somewhat higher statistical power to retrieve overdispersion under stabilizing processes than clustering under equalizing processes. In addition, when mixed processes were implemented, stabilizing processes left a stronger imprint on community phylogenetic structure than equalizing processes. In fact, phylogenetic overdispersion was retrieved when both stabilizing and equalizing processes were at work in all habitat comparisons, whereas clustering in inter-habitat comparisons would have been expected.

A second assumption involved the use of a pure Birth process for simulating phylogenies and of a Brownian model to map trait evolution on them. The Brownian model of trait evolution involves that traits continuously evolve along branches at a constant rate and without directionality (Elliot and Mooers 2014). Although being the most common model for the evolution of continuous characters, this model does not accurately describe the evolution of traits under selection, and hence, exhibiting directional tendencies, or of traits under punctuated evolution. Although other models could be implemented, we suggest that the specific evolutionary model is not critical for our results as long as it leads to a phylogenetic signal so that, although trait convergence among unrelated species may occur by chance (Hardy and Pavoine 2012), the degree of trait sharing is proportional to that of phylogenetic relatedness.

A third strong constraint imposed in the present simulations was the implementation of a short-tail dispersal kernel. Dispersal can have a strong effect on community phylogenetic structure, generating non-random patterns under stochastic processes (Kembel 2009). Implementing dispersal kernels with fatter tails would most likely increase the likelihood of colonization of ill-adapted species. Although this would decrease community phylogenetic structure and hence, affect statistical power, this would not necessarily affect the relative performance of different metrics to retrieve phylogenetic structure under different assembly processes.

Fourth, the choice of the null model may also substantially impact type 1 error rates (Kembel 2009; Miller et al. 2017). The null model implemented here (1s in Hardy 2008) was among the ones producing the lowest type 1 error and the most robust under limited dispersal. Moreover, it allows testing specifically whether the phylogenetic relationships among species affect the phylogenetic diversity metrics while keeping intact the spatial patterns of species distribution.

Finally, the sampling design may also impact the statistical power of the tests. To decrease the degree of spatial autocorrelation in the data, sparse sampling could be implemented. We compared the statistical power of the tests under equalizing processes for specialist species, selecting eight spatially correlated samples (Supplementary Fig. S5b) versus one sample out of each of the nine clusters of four samples (Supplementary Fig. S5c) (sparse sampling). The proportion of significant MPD values across replicates was 53% and 28% for sparse sampling and 52% and 16% for spatially correlated sampling in continuous and fragmented habitats, respectively. With PIst among core continuous and core fragmented habitats, 67% and 50% of the tests based on sparse versus spatially correlated sampling, respectively, retrieved significant clustering. This suggests that sparse sampling could help enhancing statistical power. Investigating the impact of the sampling design on the power of the tests of phylogenetic structure would, however, require a thorough investigation. In this perspective, all the parameters fixed in the present study (e.g., models of trait evolution, dispersal kernels . . .), as well as the sampling design, can be changed to perform new simulations under different sets of assumptions based on the code available from Dryad: https://doi.org/10.5061/dryad.mcvdnck92

Range of Applications

Different biological systems involving species dispersal in a fragmented landscape (e.g., epiphytes, arthropod communities associated with bird-nest ferns, woodlands in a matrix of open habitat . . .) could correspond to the setting of the present simulations. We suggest that species-rich forest tree communities would represent a typical example of application (see, e.g., Hardy et al. 2012). Each pixel could represent a 0.1–1 ha forest patch containing 50 reproducing trees within a landscape of tens to hundreds square kilometers hosting several hundreds of tree species. This is, for example, the case of tropical rainforests. In Amazonia, 3–357 (121 on average) tree species per ha () and 829 tree species across 21 0.9–2.5 ha plots within a 400 km^2 area (Pitman et al. 1999) have been reported, mimicked by the 2–30 species per plot and the 800 species included here in the metacommunities. In such environments, seed dispersal is typically extremely limited, with median dispersal distances of <1 to >80 m (Dalling et al. 2002) and about 80% of established progeny remaining within the same 1 ha patch of the mother tree (Hardy et al. 2019; Angbonda et al. 2021; Bhasin et al. 2024), as modeled by the dispersal kernel implemented in our simulations. Under the 100% stochastic scenario, all tree species are equally adapted to the forest environment, which is uniform. This could mimic a diverse tropical rainforest showing very low environmental variation through space, and assuming that neutral processes prevail (Latimer et al. 2005).

Under scenarios involving equalizing processes, only the species having specific combinations of environmental adaptation traits survive and reproduce in one of the two habitat types. Here, these traits filtered by the environment could represent, for example, a position along a trade-off between drought and waterlogging tolerance. The two simulated habitats could be analogous to the mosaic formed by a continuous *terra firme* forest (habitat 1) interrupted with patches of swamp forest occurring in topographic depression, or of white sand forests (habitat 2), which typically occur as habitat islands hosting specialized species assemblages across the Amazonian rainforest (Fine and Bruna 2016).

Under scenarios involving stabilizing processes, species compete locally (one-hectare scale) for resources if they have similar resource acquisition traits. These traits could correspond to a position along the trade-off between slow-growing shade-tolerant and fast-growing light-demanding strategies, favoring species with the most original resource acquisition traits in the species pool. The simulated community receives random migrants from the species pool, which is comparable to the seed rain landing in a forest after occasional long-distance dispersal events from similar or dissimilar plant communities occurring in the same region.

Conclusions and Perspectives

Our simulations formalize the idea that equalizing and stabilizing processes leave a distinct signature in the phylogenetic structure of communities, which can provide insights into community assembly processes. With real data, the actual underlying assembly process is, however, unknown. This makes it necessary to implement null models, with a statistical power that substantially varies among metrics and depending on the assembly processes involved, to determine whether the phylogenetic structure observed in the data is indeed stronger than expected by chance. Simulating communities expected under competing assembly processes, generating the corresponding range of expected phylogenetic diversity metrics, and determining to which of these simulated phylogenetic diversity metrics the ones that were actually observed in natural communities best correspond, would represent a much appealing way to move forward. Such an approach is frequently used in phylogeographic studies, wherein coalescence simulations are implemented within an Approximate Bayesian Computation (ABC) framework to determine the historical scenario that best fits with observed patterns of genetic variation (Collin et al. 2021, and references therein). The number of parameters to be estimated in such simulations (e.g., effective population sizes, migration rates . . .) represents, however, one of the major challenges in such approaches (Bertorelle et al. 2010). The problem would be worst in community ecology, wherein the number of parameters to be assessed exceeds the already large number of parameters in coalescence analyses. In this context, recent advances in machine learning have increasingly facilitated the development of simulation-based inference (Cranmer et al. 2020) with mounting applications in population genetics (e.g., Saada et al. 2023), and could provide an appealing solution to address this challenge.

SUPPLEMENTARY MATERIAL

Data available from the Dryad Digital Repository: https://datadryad.org/dataset/doi:10.5061/dryad.mcvdnck92

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AUTHOR CONTRIBUTION

T.K., G.D., and O.J.H. performed the analyses. All authors conceived the project and contributed to the manuscript.

DATA AVAILABILITY

The codes and data sets used to perform the simulations and compute the diversity metrics are available from Dryad: https://datadryad.org/dataset/doi:10.5061/dryad.mcvdnck92

CONFLICT OF INTEREST

None declared

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