



RESEARCH ARTICLE

In Situ Speciation of Dispersal-Limited Taxa Leads to Strong Phylogenetic Community Clustering

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ABSTRACT

Aim: Phylogenetic community structures have traditionally been interpreted through the lens of niche processes, such as environmental filtering and interspecific competition. However, these structures have been continuously shaped over evolutionary time by biogeographical dynamics, a process that is often overlooked. Here, we disentangled the influence of speciation and dispersal on spatial phylogenetic structures using neutral simulation models, while turning off niche-based processes.

Location: South America.

Taxon: Simulated clades.

Methods: We simulated biogeographical dynamics of individuals evolving under random speciation, dispersal and demographic processes. Each model incorporated different combinations of speciation and dispersal rates, and the phylogenetic structures of its communities were assessed using standardised effect sizes of Mean Phylogenetic Distances (SES_{MPD}). We evaluated the SES_{MPD} in response to varying degrees of speciation and dispersal rates, and its relationship with community isolation, using Ordinary Least Square (OLS) models.

Results: Increased speciation rates and reduced rates both contribute to higher phylogenetic clustering, leading to a higher co-occurrence of closely related species. While both variables independently influence phylogenetic structure, the extent of phylogenetic clustering is primarily determined by the increased ratio between speciation and dispersal rates. This trend toward phylogenetic clustering persisted even at smaller scales, albeit with reduced intensity. Clustering was more pronounced in isolated communities, with the effects intensifying based on the combination of speciation and dispersal rates.

Main Conclusions: Our study demonstrates that biogeographical dynamics can drive strong phylogenetic structures even in the absence of niche processes. Specifically, in situ speciation rates can enhance phylogenetic clustering by continuously adding species to community pools, such as through the exploitation of novel ecological opportunities. However, the extent of this clustering largely depends on the degree of geographical isolation and dispersal limitations experienced by the radiating lineages, which influence biotic interchange and phylogenetic homogenisation among community compositions.

1 | Introduction

Phylogenetic community structures have long been investigated to understand the processes underlying community assembly (Webb 2000; Kembel and Hubbell 2006; Si et al. 2022; Fourcade and Alhajeri 2025). Specifically, patterns of phylogenetic structure patterns are simultaneously influenced by the interplay of niche-based, historical and neutral processes (Cavender-Bares et al. 2009; Pinto-Ledezma et al. 2019). However, most studies interpret these phylogenetic structures exclusively through the lens of niche processes (Kraft et al. 2014), largely because niche-related traits tend to be strongly conserved phylogenetically (Wiens et al. 2010). Niche-based processes driving non-random phylogenetic structures are usually simplified as patterns driven by abiotic or biotic forces (i.e., environmental filtering or interspecific competition, respectively; Webb et al. 2002; Kembel and Hubbell 2006; Cavender-Bares et al. 2009). However, similar patterns of phylogenetic structure can result from different processes (see Kraft et al. 2014; Coelho et al. 2019). For instance, current phylogenetic structures have been continuously shaped by historical biogeographical dynamics (Cavender-Bares et al. 2009, 2018; Benício et al. 2021). Consequently, key historical dynamics like in situ speciation, limited dispersal and the colonisation of novel habitats by adaptive radiations can have a strong impact on community structures but are often overlooked (Kissling et al. 2012; Pinto-Ledezma et al. 2019; Si et al. 2022).

The phylogenetic relatedness among co-occurring species determines the phylogenetic structure within a given community (Cavender-Bares et al. 2009). This relatedness can be viewed as a continuum between phylogenetic clustering and overdispersion among the lineages present in a community. Phylogenetic clustering, characterised by the higher co-occurrence of closely related species, is often interpreted as evidence of environmental filtering selecting for phylogenetically conserved traits (Swenson et al. 2007; Wiens et al. 2010; Qian et al. 2024). Alternatively, phylogenetic overdispersion, where distantly related species coexist, suggests that interspecific competition favours ecologically distinct species to reduce the effects of competition (Kraft et al. 2014). However, phylogenetic and trait relatedness can commonly be independent of each other (Kluge and Kessler 2010; Cadotte and Tucker 2017; Fourcade and Alhajeri 2025), potentially overstating the roles of environmental filtering and interspecific competition in community assembly. For instance, environmental filtering could drive phylogenetic overdispersion if niche traits have evolved and converged among distant relatives (Kraft et al. 2014; Cavender-Bares et al. 2018). Alternatively, phylogenetic overdispersion could result from continuous colonisation by distant relatives rather than the extinction of close relatives due to competition (Li et al. 2015). Therefore, the role of historical biogeography, including speciation and dispersal dynamics, may be more crucial for understanding phylogenetic structure patterns than previously thought (Warren et al. 2014; Pinto-Ledezma et al. 2019; Benício et al. 2021).

Understanding the cumulative effects of historical processes is crucial for interpreting the phylogenetic community structures (Cavender-Bares et al. 2018; Coelho et al. 2019; Benício et al. 2021). Past ecological opportunities may have spurred evolutionary processes that triggered in situ speciation, continuously adding lineages to the community pool over time (Kissling

et al. 2012; Polato et al. 2018; Kennedy et al. 2018). Increased in situ speciation can lead to greater phylogenetic clustering within these communities, though the extent of this clustering may depend on the degree of geographical or ecological isolation experienced by the lineages (Kissling et al. 2012; Pinto-Ledezma et al. 2019; Si et al. 2022). Dispersal limitations caused by isolation can shape phylogenetic community structure by influencing the degree of reproductive isolation among species populations (Cavender-Bares et al. 2009; Claramunt et al. 2011). Lineages with low dispersal ability are often geographically restricted, leading to higher chances of reproductive isolation and increased opportunities for speciation (Claramunt et al. 2011; Sobral and Cianciaruso 2015). Conversely, lineages with greater dispersal capacity can cover larger geographical areas but may experience reduced speciation due to increased gene flow (Claramunt et al. 2011; Sobral and Cianciaruso 2015). However, addressing the historical effects on phylogenetic structure is challenging due to the high uncertainty in inferring biogeographical events from extant phylogenies (Morlon et al. 2022). Moreover, empirical phylogenetic structures are intertwined with ecological processes, blurring the distinction of pure historical effects.

To tackle this challenge, we disentangled the influence of biogeographical forces on phylogenetic community structuring using a spatially explicit neutral model. By turning off niche-based processes, we isolated the effects of speciation and dispersal rates on phylogenetic structure to investigate their relationship and the magnitude of their impact. We assessed the phylogenetic community structures in our null models by computing standardised effect sizes of Mean Phylogenetic Distances (SES_{MPD} ; Webb 2000; Webb et al. 2002), while examining the impact of geographical isolation and scale on these patterns. Our findings show that variations in biogeographical dynamics—specifically speciation and dispersal rates—strongly influence phylogenetic community structures (Cavender-Bares et al. 2009). Increased speciation rates and reduced dispersal rates each drive communities toward higher phylogenetic clustering (i.e., higher co-occurrence of closely related species). Although both factors individually affect phylogenetic structure, the degree of phylogenetic clustering primarily depends on the increased ratio between speciation and dispersal rates. The effects of phylogenetic clustering intensify with the greater isolation of communities, with peripheral communities exhibiting more clustered than central ones. As expected, the scale of analysis reduces the observed phylogenetic structure within communities, but the general trend of clustering with increases in the ratio between speciation and dispersal rates notably persists.

2 | Methods

2.1 | Neutral Model

We implemented a spatially explicit neutral model to simulate the dynamics of individuals in space and time, without accounting for environmental dynamics. Our model simulated the biogeographical dynamics of individuals under random speciation, dispersal and demography within a bounded geographic domain. This geographic domain was represented by South America, divided into 561 regularly spaced grid cells to

assess the effects of biogeographical dynamics on phylogenetic community structure. Each grid cell represents a local community where, at each time step, a resident species can disperse and colonise one of its contiguous neighbouring cells (i.e., Moore neighbourhood). The connectivity between all pairs of cells was determined by their geographic distance, with dispersal allowed among adjacent cells based on a probability (m) (Boucher et al. 2014). Long-distance dispersal was not allowed for computational simplicity (enabling the use of sparse matrix methods), though different dispersal models could lead to similar patterns (see Dambros et al. 2015 for comparisons).

To set the initial conditions for the simulations, each community was populated with a fixed number of individuals (N_i , arbitrarily set to 10 in all cells) of an ancestral species. Neutral processes within the geographical domain were simulated following the approach of Boucher et al. (2014). At each time step, one individual was randomly selected from the entire geographical domain. This individual could either speciate, based on speciation probability (v), or die with probability ($1-v$). If the individual died, it left an empty spot in the domain, which could be colonised either by a descendant of a randomly chosen individual from the same community with probability ($1-m$), or by a random immigrant from an adjacent community with probability (m). In our simulation model, all species are equivalent, with no differences in their probabilities to speciate or disperse (Hubbell 2001).

We defined a generation as the minimum number of time steps required to replace all individuals in the domain. Therefore, one generation (or number of time steps) in our simulation approximately equals the total number of individuals within the South America domain. The simulation continued until a specified number of generations was reached. At the end of the simulation, we created a matrix containing the presence (1) and absence (0) of each species in each grid cell and reconstructed a phylogeny based on the history of speciation events. The phylogeny was trimmed to include only those extant species. We ran models with different combinations of speciation (v) and dispersal (m) parameters, with speciation rates ranging from equal intervals between 0.00008 to 0.05 and dispersal rates from 0.00008 to 0.10. Each unique parameter combination of speciation and dispersal was simulated in 10 replicates. All neutral simulations were performed using the Delphi programming language to optimise computational performance, with the corresponding code available in Coelho et al. (2019).

2.2 | Speciation Modes

In all our simulations, each speciation event followed a probabilistic neutral process. Therefore, a new daughter species could emerge in the domain at each time step and is characterised by its initial species abundance (J_s). However, the final output of the simulation model can be influenced by the underlying speciation mode (Hubbell 2001; Boucher et al. 2014). To explore this, we modelled four different speciation modes to capture a broad and plausible range of ecological and evolutionary dynamics that could arise from them, each differing in the distribution of J_s and the spatial scale. Different speciation modes were selected to reflect a range of possible outcomes in terms of the initial population size of daughter species (J_s), which is a key factor

influencing model behaviour. Specifically, we chose modes that span from the smallest possible J_s s, where a single individual gives rise to a new species (i.e., Point Mutation), to larger-scale events where geographic barriers cause large portions of ancestral populations to diverge (i.e., Allopatric Speciation). This allowed us to explore the implications of speciation events that differ not only in spatial scale but also in the distribution and size of new species populations. Therefore, our simulations were conducted separately using (i) Point Mutation, (ii) Random Fission, (iii) Equal Split and (iv) Allopatric speciation modes to encompass diverse assumptions about how species emerge and to assess the robustness of the model outcomes across this variation.

The (i) Point Mutation speciation mode (Hubbell 2001) involved a sympatric speciation event occurring in an individual randomly chosen from the entire domain ($J_s=1$). In this case, a single daughter species emerges from one cell, occupying the ancestral range as a single individual. The (ii) Random Fission speciation mode (Hubbell 2001) was simulated by selecting one individual from the metacommunity. In this scenario, the species identity is recorded, and J_s individuals are drawn to undergo speciation within their respective grid cell. The value of J_s was determined by sampling a random integer ranging from 1 to half the species population size within the grid cell. The (iii) Equal Split speciation mode (Davies et al. 2011) is similar to Random Fission, but J_s is fixed as half of the species population size within the grid cell. Finally, the (iv) Allopatric speciation mode simulates an interior barrier with random orientation within the geographical domain. Unlike other modes, Allopatric speciation occurs at large scales, affecting the entire geographic domain and involving simultaneous speciation of individuals from multiple species. As a result, J_s varies among daughter species due to the random orientation of the barriers. Our implementation of allopatric speciation was based on the algorithms developed by Pigot et al. (2010) and Boucher et al. (2014).

2.3 | Phylogenetic Community Structure

To observe the degree of phylogenetic structuring within our simulated communities, we assessed their local phylogenetic relatedness. Specifically, the phylogenetic relatedness was assessed by computing the Mean Phylogenetic Distance (MPD) between all pairs of co-occurring species within each community (Webb et al. 2002). The choice of the MPD metric was based on its widespread acceptance and long-standing use as a surrogate for phylogenetic relatedness in community ecology studies (Kissling et al. 2012; Pinto-Ledezma et al. 2019; Fourcade and Alhajeri 2025). Since MPD measures are strongly influenced by species richness patterns, we adjusted for this effect by transforming MPD into standardised effect sizes (SES) using null models (Cavender-Bares et al. 2009). Specifically, for each simulated community we calculated:

$$||SES||_{MPD} = (||MPD||_{obs} - ||MPD||_{null}) / \sigma_{null}$$

where MPD_{obs} is the observed phylogenetic relatedness within the community, MPD_{null} is the mean of 999 randomizations that resample species identity in the phylogeny while maintaining constant community richness, and σ_{null} is the standard deviation of these randomizations. Positive values of SES_{MPD} (>0)

indicate a higher co-occurrence of distantly related species than expected by chance (i.e., phylogenetic overdispersion), while negative values of SES_{MPD} (<0) indicate a higher co-occurrence of closely related species than expected by chance (i.e., phylogenetic clustering; Webb 2000; Webb et al. 2002).

2.4 | Analysis

We examined the changes in SES_{MPD} in relation to varying dynamics of speciation (v) and dispersal (m), and assessed how SES_{MPD} responds to isolation under these different dynamics. First, we calculated overall SES_{MPD} values for each combination of speciation and dispersal parameters. We then evaluated the SES_{MPD} response to changes in speciation and dispersal individually by fitting univariate linear models using Ordinary Least Squares (OLS). To capture the distinct SES_{MPD} responses to the interplay between speciation and dispersal, we fitted separate univariate models for each variable (e.g., speciation) across fixed parameters of the other variable (e.g., dispersal). Additionally, we fitted a univariate model to examine the SES_{MPD} response to relative changes in the square-root of the ratio of speciation and dispersal rates (v/m).

To account for the SES_{MPD} response to community isolation, we computed the eigenvector centrality of each grid cell within our studied domain. Each cell's centrality value ranged from 0 (i.e., more central) to 1 (i.e., more peripheral). We fitted nonlinear models to describe the relationship between SES_{MPD} patterns and cell centrality, given their observed asymptotic relationship. This nonlinear model differs from simple linear regression models by incorporating an exponential parameter to the predictor variable. We assessed SES_{MPD} responses to centrality effects across varying degrees of fixed speciation and dispersal parameter values. We explored patterns and relationships in the estimated model intercepts and slopes for different speciation and dispersal scenarios. Simulations with speciation or dispersal rates of 0.00008 were excluded due to overestimation in SES_{MPD} patterns. All models were fitted using the overall values from replicates of each parameter combination. All graphical results and model fitting analyses were conducted using the R programming environment (R Core Team 2024).

3 | Results

Phylogenetic structures, as measured by the standardised effect sizes of mean phylogenetic distances (SES_{MPD}), were lower than expected (i.e., phylogenetically clustered) for most combinations of speciation and dispersal rates (Figure 1). Specifically, the degree of phylogenetic clustering (i.e., lower SES_{MPD} values) increased with higher speciation rates and lower dispersal rates (see, respectively, the columns and rows in Figure 1), with a tendency for greater clustering in communities at the edges of the domain. However, the magnitude and nature of the effects of speciation and dispersal rates on phylogenetic community structures differed. While phylogenetic structures approached null expectations when dispersal was not limited (i.e., higher dispersal rates), reducing dispersal rates exponentially increased phylogenetic clustering (R^2 : 0.69; Figure S1a). Conversely, although weaker, increases in speciation rates linearly drove assemblages

toward higher phylogenetic clustering (R^2 : 0.18; Figure S1b). The spatial patterns of increased phylogenetic clustering with higher speciation rates and lower dispersal rates were consistent across different speciation modes (Figure S2).

The magnitude of the phylogenetic structuring response to dispersal and speciation rates depends on their combination (Figure 2). On one hand, the exponential effect of dispersal rate on phylogenetic structure scales linearly with increases in speciation rate, both in model intercepts ($r_{intercept}$: 0.97) and slopes (r_{slope} : 0.99; Figure S3a,b). On the other hand, the linear effect of speciation rate on phylogenetic structure scales logarithmically with increases in dispersal rates, in both model intercepts ($r_{intercept}$: 0.79) and slopes (r_{slope} : 0.87; Figure S3c,d). We found that the ratio between speciation and dispersal rates was the strongest driver of phylogenetic community structures (R^2 : 0.98; Figure 3a), more so than speciation or dispersal rates alone. Specifically, there is a linear increase in phylogenetic clustering (β : -3.47) with the square-root of the ratio between speciation and dispersal rates. This general trend of increased phylogenetic clustering with higher ratios between speciation and dispersal rates was consistently observed across null models performed in domains of varying scales (i.e., different number of communities; Figure S4). However, as expected, the magnitude of clustering decreased at smaller scales. Consequently, communities with higher clustering trends were classified as expected under null scenarios, even with higher speciation-dispersal ratios.

In addition to influencing overall patterns of phylogenetic clustering, the combinations between dispersal and speciation rates also shaped the spatial organisation of phylogenetic structuring. Specifically, communities in the peripheral regions of the South American domain exhibited greater phylogenetic clustering (i.e., lower SES_{MPD}) compared to those in central areas (Figure 3b). The degree of clustering in the central regions and the greater clustering toward the periphery were both influenced by dispersal and speciation rates (Figure S5). Phylogenetic clustering in the central regions increased exponentially with decreasing dispersal rates ($r_{intercept}$: 0.55; Figures S5a and S6a), leading to a higher concentration of closely related species. Similarly, clustering in central regions increased linearly with higher speciation rates ($r_{intercept}$: -0.95; Figures S5b and S6c). Clustering toward the periphery could be pronounced under very low dispersal rates ($\beta_{0.005}$: 9.80), but generally, this effect increased linearly with higher dispersal rates (r_{slope} : 0.88; Figure S6b). Consistent with the effects of dispersal rates, the increase in phylogenetic clustering from central to peripheral communities also scaled linearly with speciation rates (r_{slope} : 0.48; Figure S6d).

4 | Discussion

Most ecological studies interpret non-random patterns of phylogenetic community structure as evidence of environmental filtering or intensified competition (Kraft et al. 2014; Warren et al. 2014). However, these patterns have been shaped over evolutionary time and continually reshaped by biogeographical dynamics (Cavender-Bares et al. 2009, 2018; Coelho et al. 2019). By using null simulation models to tease apart the effects of pure biogeographical factors on community assembly, our study demonstrates that variations in speciation and dispersal dynamics can

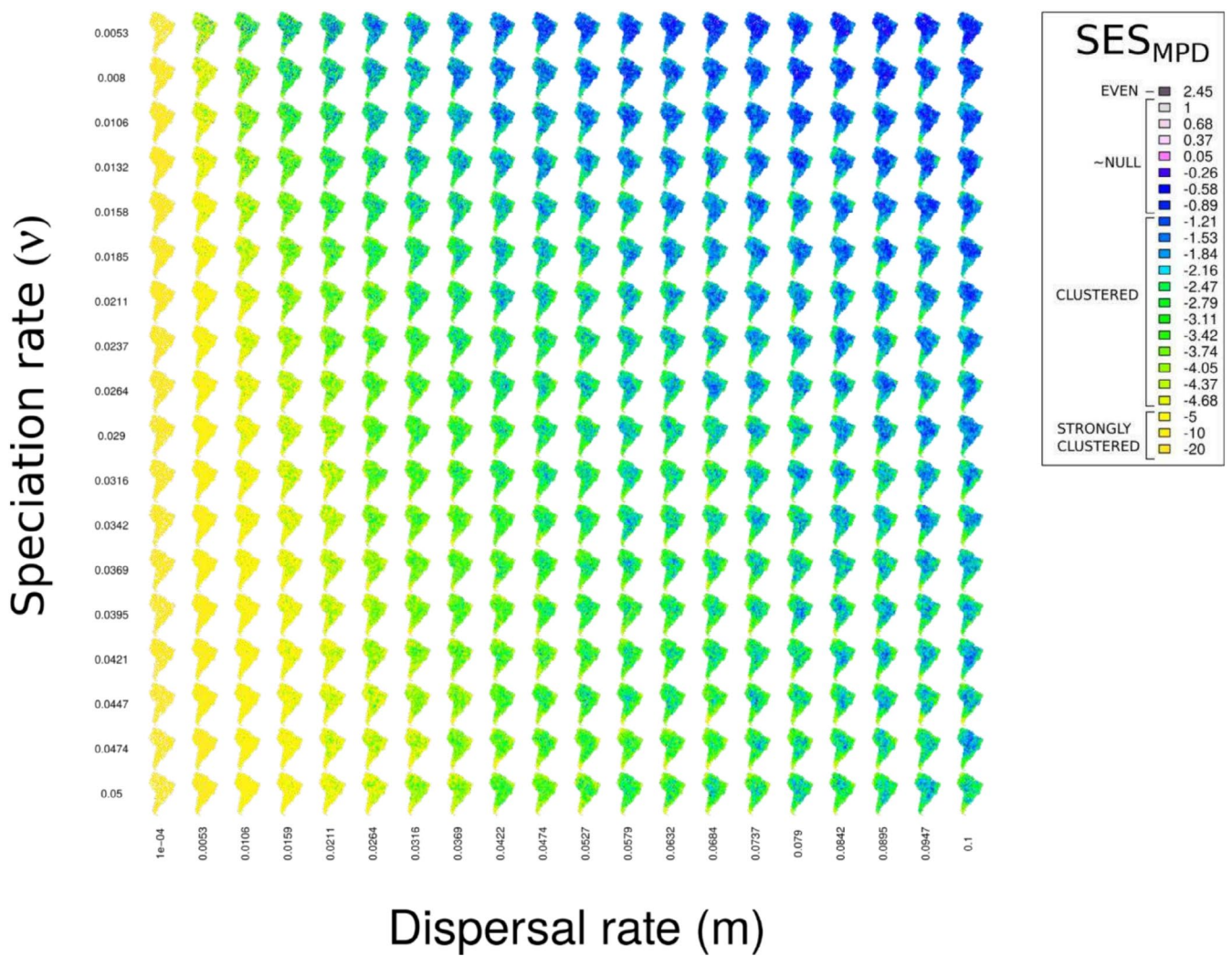


FIGURE 1 | Spatial patterns of the standardised effect size of Mean Phylogenetic Distances (SES_{MPD}) from neutral models. Each panel represents a null model performed using different configurations of speciation and dispersal rates within the South American domain. Rows indicate increasing dispersal rates (from left to right), while columns represent increasing speciation rates (from top to bottom). The models were run using the Point Mutation speciation mode, with dispersal allowed only between neighbouring cells (i.e., Moore neighbourhood).

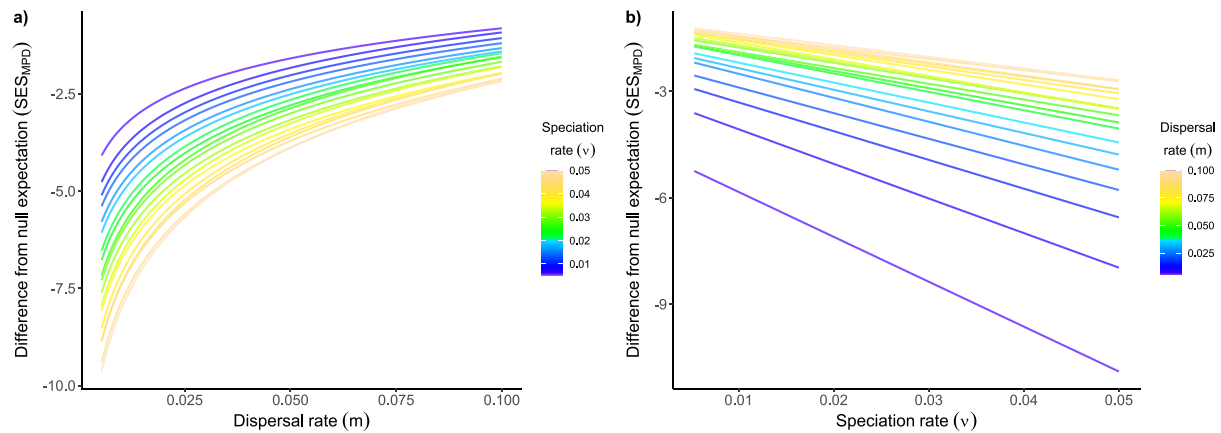


FIGURE 2 | Fitted regression models showing the relationship between the overall standardised effect size of the mean phylogenetic distances (SES_{MPD}) and different rates of (a) dispersal (m) and (b) speciation (v). Regressions between SES_{MPD} and dispersal rates (m) were computed separately for each speciation rate (v) parameter to assess its effect on the relationship. Similarly, regressions between SES_{MPD} and speciation rate (v) were assessed separately for each parameter of dispersal rate (m). Changes in speciation and dispersal rates during model fitting are indicated in the respective panel legends.

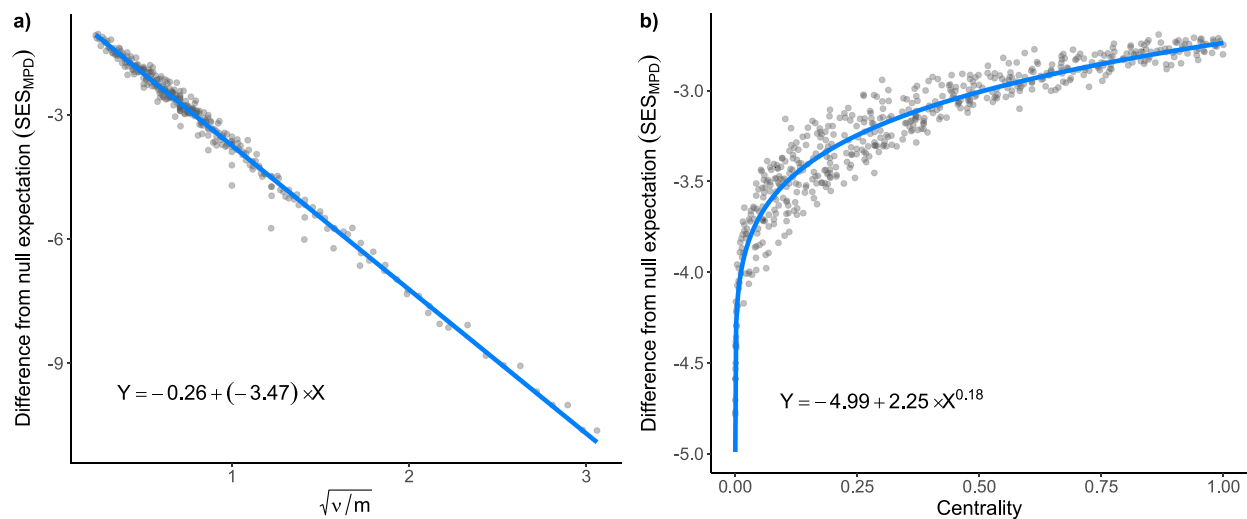


FIGURE 3 | Scatterplot with fitted regression lines (in blue) showing the relationship between the overall standardised effect size of the mean phylogenetic distances (SES_{MPD}) of all simulations and the (a) square-root of the ratio between speciation (v) and dispersal rates (m), and the (b) degree of centrality measured for each community cell. Centrality values range from 0 (i.e., peripheral cells) to 1 (i.e., central cells).

drive strong phylogenetic structures even in the absence of niche processes (e.g., environmental filtering). Specifically, increased speciation rates lead to a continual addition of closely related species into community pools, resulting in a higher phylogenetic clustering (Hubbell 2001; Economo and Keitt 2010; Dambros et al. 2015). Conversely, higher dispersal rates, which reduce dispersal limitations, tend to drive communities toward random phylogenetic structuring due to increased homogenisation in their composition (Hubbell 2001; Vellend 2010; Claramunt et al. 2011). Together, the combined effects of speciation rates and dispersal limitation contribute significantly to the phylogenetic structures observed today at various scales, yet these mechanisms have been largely overlooked and poorly understood until now.

Speciation contributes to phylogenetic community structure by adding new species to communities. Elevated speciation rates promote a higher co-occurrence of closely related species, leading to increased phylogenetic clustering within communities (Kissling et al. 2012; Si et al. 2022). Scenarios of higher speciation are often found in regions offering higher availability of ecological opportunities (Rabosky and Hurlbert 2015), independently of ecological filters. For instance, speciation rates may be higher in recently colonised regions with previously unexplored ecological opportunities (e.g., isolated islands; Pinto-Ledezma et al. 2019; Si et al. 2022). Alternatively, ecological opportunities can be achieved from the evolution of traits that allow lineages to exploit novel niche resources (Kennedy et al. 2018; Marki et al. 2019). The utilisation of these new resources often reduces competition and triggers in situ speciation, driving communities toward phylogenetic clustering (Kennedy et al. 2018; Benício et al. 2021). In the same way, the development of key traits that enable survival in harsher climates may facilitate species exploration of opportunities in regions under strong environmental filtering (Qian et al. 2024). Although the phylogenetic scale can strongly affect clustering patterns, as different clades may exploit different niche aspects (Cavender-Bares et al. 2018; Graham et al. 2018), this rationale is supported by neutral simulations

showing that speciation dynamics can lead to the emergence of trait conservatism (Coelho et al. 2019). Thus, while environment strongly filters influence species colonisation, in situ speciation of pre-adapted ancestral lineages exploiting ecological opportunities in these harsh environments may be the primary mechanism driving patterns of phylogenetic clustering and trait conservatism within these regions (Wiens et al. 2010; Cavender-Bares et al. 2018; Qian et al. 2024).

While dispersal may not influence patterns of phylogenetic trait conservatism (Coelho et al. 2019), it plays a key role in shaping phylogenetic structure by modulating the effects of isolation and dispersal limitations on community composition. More accessible communities can host lineages from different pools (i.e., higher biotic interchange), leading to less phylogenetically structured patterns (Kissling et al. 2012; Li et al. 2015; Si et al. 2022). In contrast, isolated communities are less accessible to foreigner species due to dispersal filtering (e.g., islands or peripheral cells), resulting in higher phylogenetic clustering as they remain confined to their own lineage pool (Kissling et al. 2012; Si et al. 2022). Therefore, a lineage's dispersal capacity is crucial in determining the extent of structuring effects driven by isolation. Lineages presenting high dispersal capacity and broad distribution can reduce phylogenetic structuring by homogenising the communities species compositions (Hubbell 2001; Sobral and Cianciaruso 2015). While high dispersal capacity can promote speciation through geographic expansion (Kennedy et al. 2018), it primarily inhibits speciation by maintaining higher gene-flow among species populations (Claramunt et al. 2011). Conversely, species with lower dispersal capacity often have restricted geographical distributions and reduced population gene-flow, making them more susceptible to speciation due to isolation (Claramunt et al. 2011). Thus, lower dispersal capacity can confine entire radiations to their area of origin, promoting strong phylogenetic clustering within the region (Si et al. 2022). However, environmental barriers related to niche conservatism can also limit dispersal and produce similar phylogenetic structures regardless of lineage dispersal capacity

(Wiens et al. 2010; Kraft et al. 2014), which must be carefully considered (Eiserhardt et al. 2013; Pinto-Ledezma et al. 2019).

Even though speciation and dispersal dynamics have independent effects on phylogenetic structure patterns (Cavender-Bares et al. 2009), they operate simultaneously and amplify each other's effects. As a rule, increased ratio between speciation and dispersal rates enhances phylogenetic clustering and amplifies the effects of geographical isolation. While speciation rates determine the number of new lineages added to a species pool, dispersal rates influence whether these lineages remain in their region of origin (i.e., increasing clustering) or disperse to other regions (i.e., decreasing clustering). Therefore, dispersal limitation is potentially the strongest biogeographical force driving clustered phylogenetic structures at macroecological scales (Kissling et al. 2012). For instance, species with lower dispersal capacities (e.g., vagile species) are more likely to remain within their region of origin, with the degree of clustering increasing as higher are their speciation rates (Cavender-Bares et al. 2018; Si et al. 2022). These biogeographical processes continue to influence phylogenetic structure at smaller scales, though they become harder to detect as the scale decreases (Cavender-Bares et al. 2009; Graham et al. 2018). This difficulty arises because biogeographical dynamics operate at larger spatial-temporal scales, while smaller scales often share similar environmental constraints and biogeographical histories (Kissling et al. 2012; Benício et al. 2021). Thus, although biogeographical dynamics may still impact phylogenetic structure at smaller scales, other factors begin to play a more significant role in shaping them (e.g., biotic interactions and microclimate; Benício et al. 2021).

Studies of phylogenetic community structures often overlook the historical processes underlying these patterns (but see Pigot and Etienne 2015). Historical elements can leave strong phylogenetic structure in current community assembly patterns, which could potentially be misinterpreted as evidence of niche processes (Cavender-Bares et al. 2018; Pinto-Ledezma et al. 2019; Coelho et al. 2019). Specifically, biogeographical dynamics, driven by different rates of speciation and dispersal, can generate pronounced phylogenetic clustering independent of niche processes (Cavender-Bares et al. 2009; Cadotte and Tucker 2017). Our simulation models do not account for speciation driven by the occupation of novel ecological opportunities (Kennedy et al. 2018), nor for dispersal limitations caused by environmental barriers (Eiserhardt et al. 2013). We acknowledge that species traits significantly influence their ability to exploit new ecological opportunities, while niche conservatism can impose strong physiological constraints on range expansion (Wiens et al. 2010; Benício et al. 2021). However, even though we recognise that future studies should address these niche aspects, we emphasise the importance of our simulation to understand complex historical dynamics that are challenging to estimate empirically. Estimating biogeographical events often involves high uncertainty due to challenges in estimating extinction rates from extant phylogenies (e.g., due to incomplete species records, fossils gaps and taphonomic biases; Morlon et al. 2022). Therefore, we recommend that future research considers the impact of phylogenetic scale on structure patterns, as different clades may exhibit unique niche constraints and dispersal capacities that strongly influence their currently observed patterns (Cavender-Bares et al. 2018; Benício et al. 2021).

Author Contributions

M.T.P.C., N.J.G., R.C., T.F.R. and C.D.S. jointly conceived the ideas for the paper. M.T.P.C. constructed the simulation models, while both M.L.A. and C.S.D. conducted the formal analysis and wrote the first draft of the manuscript. M.L.A., M.T.P.C., N.J.G., R.C., T.F.R. and C.D.S. revised and approved the final manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data generated within this study and its analysis can be found at <https://doi.org/10.6084/m9.figshare.28464227.v1>. Delphi scripts for running the simulations could be found cited throughout the manuscript.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.