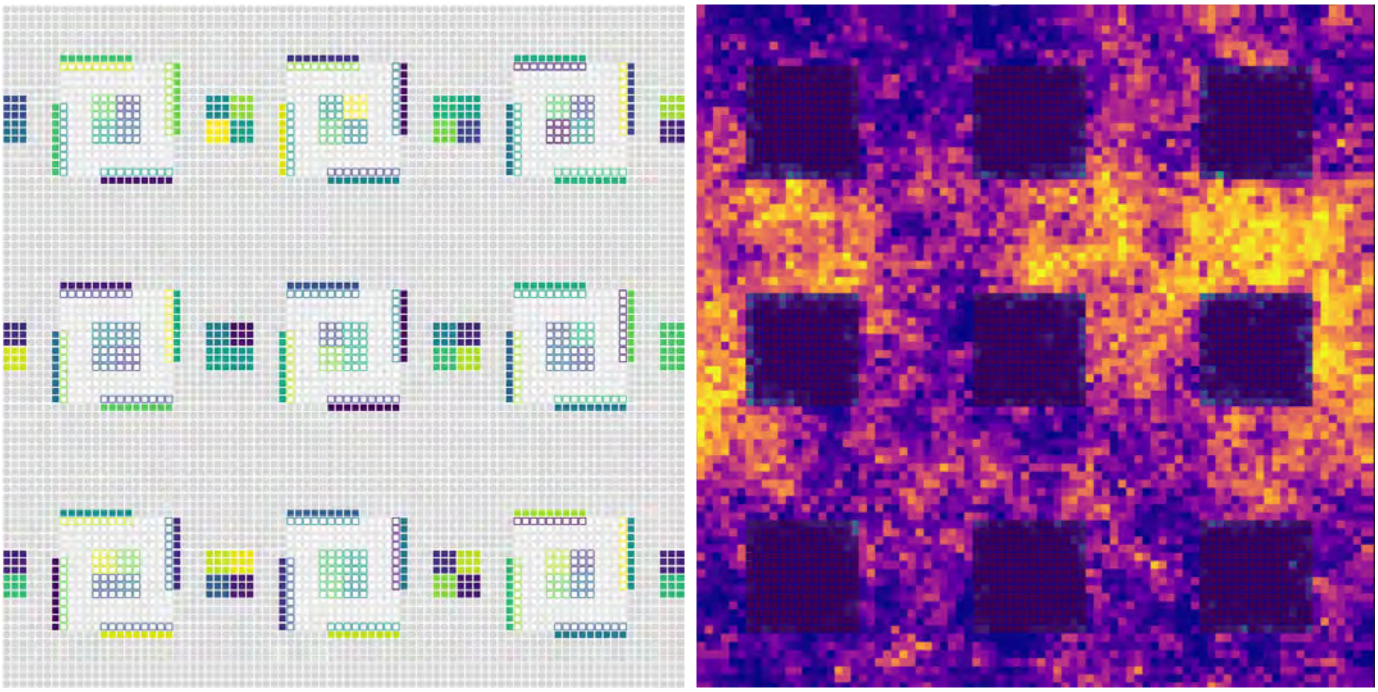
Thibault Kasprzyk

February 2026

Inferring mechanisms of community assembly from phylogenetic diversity.



DOCTORAL DISSERTATION

In Biology, Ecology and Evolution at the University of Liege
presented in order to obtain the grade of PhD in Sciences

Inferring mechanisms of community assembly from phylogenetic diversity.

Thibault Kasprzyk
February 2026

Thesis submitted in fulfilment of the requirements for the degree of Doctor in Sciences

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Department of Biology, Ecology and Evolution
University of Liege
February 2026

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For those who stay ...

ABSTRACT

The distribution of species is the result of past and present processes that shape the assemblage of their communities. Niche differentiation and competition are the two main ingredients of a trade-off between selection of traits for a given environment, enhancing fitness in the latter, and competition among closely related species. 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. This framework was later formalized by Chesson (2000) who explains species coexistence by two types of fundamental processes. **Equalizing** processes minimize fitness differences between species, so that coexisting species tend to share similar functional traits in a given habitat. In turn, **stabilizing** processes stabilize coexistence via negative density dependent selection, so that coexisting species tend to have dissimilar functional traits to avoid competition. Equalizing processes are thus expected, if adaptive traits are phylogenetically heritable, to generate communities with species more phylogenetically related to each other than expected by chance, a pattern known as phylogenetic clustering. Stabilizing processes, conversely, lead to the assemblage of communities with species less phylogenetically related to each other than expected by chance, a pattern known as phylogenetic overdispersion. The signature that assembly mechanisms leave in community phylogenetic structure has been used to infer community assembly mechanisms from patterns of phylogenetic diversity. Community assembly is, however, the result of a mixture 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.

Here, we re-assess the extent to which phylogenetic diversity can indeed be used as a proxy for mechanisms of community assembly. We implemented a novel, highly parametrizable and customizable spatially explicit model involving limited dispersal, drift, trait-based selection, and competition, to simulate community assembly under competing processes in a landscape with contrasted habitat connectivity. We subsequently implemented this approach to infer the evolutionary mechanisms underlaying one of the most pervasive biodiversity patterns, namely the latitudinal diversity gradient, using liverworts, a group of early land plants comprised of about 7000 species, as a model.

More precisely, we addressed the following questions (see graphical abstract):

1/ To what extent does the phylogenetic structure of communities vary under different assembly processes and combinations thereof (a), and to what extent do spatial and mass effects erode the signature of habitat selection and competition (b)? Can

phylogenetic diversity metrics associated with null models be used to infer community assembly mechanisms, and if so, with what associated rates of type-1 and type-2 errors (c)?

2/ How does liverwort phylogenetic diversity vary across latitudinal gradients at regional and worldwide scales (a), and to what extent does this variation correlate with environmental variation, pointing to phylogenetic niche conservatism (b)? What has been the role of the latter for shaping community phylogenetic structure throughout the evolutionary history of the group (c)?

The phylogenetic structure of simulated communities varied depending on assembly processes and the combination thereof, validating the assumption, seldom tested in a spatially explicit context, that different assembly processes indeed lead to significantly different patterns of community phylogenetic structure. While spatial effects may blur the phylogenetic structure of communities and decrease our ability to infer underlying processes, 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. Based on this, we provide guidelines to adequately infer assembly processes with the most suitable phylogenetic diversity metrics.

Our applications to the mechanisms of community assembly in liverworts along latitudinal gradients revealed that phylogenetic diversity significantly correlates with macroclimatic variation, pointing to macroclimatic niche conservatism, and, unlike species richness, increases with latitude. In contrast to the marked increase of angiosperm family diversity towards the tropics, the latitudinal diversity gradient evidenced at species level in liverworts decayed progressively at increasing phylogenetic level, suggesting that phylogenetic niche conservatism has played a much weaker role in liverworts than in angiosperms. The inverted latitudinal diversity gradient towards the deepest phylogenetic levels further lends support to the hypothesis that the earliest lineages diversified in extra-tropical conditions, explaining why, unlike in angiosperms, high species richness in the tropics is not associated with high phylogenetic diversity in liverworts. Our results highlight the extent to which a phylogenetically deconstructive approach allows for a better understanding of the accumulation of biodiversity through time.

RÉSUMÉ

La composition spécifique des communautés est le résultat de processus d'assemblage passés et présents. Parmi ceux-ci, la différenciation de niche et la compétition forment un compromis entre la sélection de traits pour un environnement, augmentant la fitness d'une espèce pour celui-ci, et la compétition entre espèces affines.

Darwin fut le premier à proposer une connexion entre différentiation de niche, compétition et distance phylogénétique entre espèces, offrant un cadre conceptuel permettant de mettre en lumière les différents processus d'assemblages à partir des patterns de diversité phylogénétique observés. Ce cadre conceptuel a été formalisé par Chesson (2000), qui propose d'expliquer la coexistence des espèces par deux types de processus fondamentaux. Les processus égalisateurs minimisent les différences de fitness entre espèces en limitant les différences de traits fonctionnels entre espèces cohabitantes au sein d'un même habitat. Les processus stabilisateurs permettent la coexistence des espèces par une sélection négative dépendante de la densité afin que les espèces présentent les traits fonctionnels les plus dissimilaires pour éviter la compétition. Les mécanismes égalisateurs vont donc générer des communautés avec des espèces plus proches phylogénétiquement qu'attendu aléatoirement, un pattern nommé clustering phylogénétique. Les processus stabilisateurs, quant à eux, génèrent des communautés composées d'espèces moins proches phylogénétiquement qu'attendu aléatoirement, un pattern nommé overdispersion phylogénétique. La signature de ces mécanismes d'assemblages sur la structure phylogénétique des communautés a largement été utilisée pour déterminer les processus qui y ont conduit. Cependant, l'assemblage des communautés est le résultat de multiples processus, en plus de potentiel facteurs confondant comme les limites dispersives ou les effets spatiaux. L'ensemble de ces processus et facteurs agissant simultanément remet en cause l'application de la diversité phylogénétique comme un estimateur des processus d'assemblage des communautés.

Dans ce travail, nous avons analysé si la diversité phylogénétique peut effectivement être utilisée comme un estimateur des mécanismes d'assemblages de communautés. Nous avons créé un nouveau modèle spatialement explicite d'assemblage des communautés. Ce modèle, hautement paramétrable, incorpore les processus ayant trait aux limites dispersives, à la dérive, à la sélection des traits et à la compétition pour simuler l'assemblage de communautés sous de multiples processus et diverses configurations spatiales. Nous avons poursuivi en appliquant cette approche pour déterminer les mécanismes évolutifs qui ont conduit à l'un des patterns de biodiversité les plus universels, le gradient latitudinal de diversité. Cette analyse a été conduite sur les hépatiques, un groupe basal de plantes terrestres qui contient environ 7000 espèces.

Plus précisément, nous avons adressé les questions suivantes (voir résumé graphique):

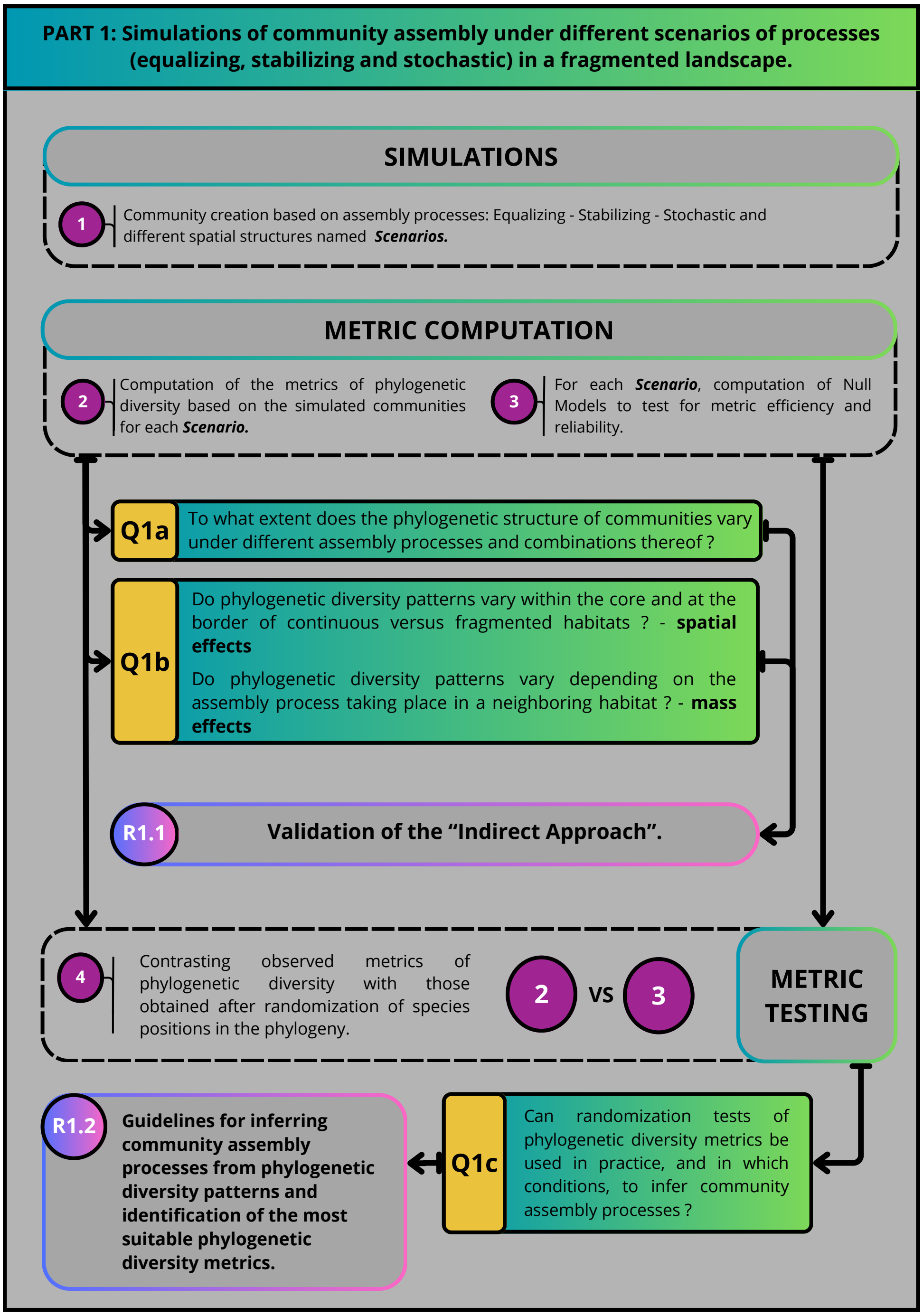
1/ Comment la structure phylogénétique des communautés varie-t-elle sous différents processus d'assemblages et leurs combinaisons (a) et dans quelle mesure les effets spatiaux affaiblissent-ils la signature de sélection par l'habitat et la compétition (b) ? Peut-on effectivement utiliser les métriques de diversité phylogénétique associées avec des modèles nuls pour inférer les mécanismes d'assemblage de communautés et, si tel est le cas, quels sont les erreurs de type 1 et type 2 associées (c) ?

2/ Comment la diversité phylogénétique des hépatiques varie-t-elle le long du gradient latitudinal à l'échelle régionale et globale (a), et dans quelle mesure cette variation est-t-elle corrélée avec la variation environnementale, pointant vers du conservatisme de niche phylogénétique (b) ? Quel a été le rôle de celui-ci dans la création de la structure phylogénétique des communautés des hépatiques tout au long de leur histoire évolutive (c) ?

Dans l'ensemble, la structure phylogénétique des communautés varie en fonction des processus d'assemblage et de leurs combinaisons, validant l'hypothèse encore peu testée dans un contexte spatialement explicite que différents processus d'assemblage produisent effectivement différents patterns de structures phylogénétiques. Bien que les effets spatiaux puissent brouiller la structure phylogénétique des communautés et diminuer notre capacité à inférer les processus sous-jacents, des résultats pertinents peuvent néanmoins être obtenus quand les comparaisons appropriées sont effectuées. En particulier, le clustering phylogénétique sous processus égalisateurs doit être testé avec des comparaisons entre habitats car ce sont les différences de sélection d'espèces entre habitats qui révèlent l'impact de ces processus. Grâce à ces résultats, nous fournissons des lignes directrices pour inférer les processus d'assemblage s'accompagnant de recommandations concernant les métriques de diversité phylogénétique les plus adéquates.

Notre étude des mécanismes d'assemblage des communautés d'hépatiques le long de gradients latitudinaux a révélé que, contrairement à la richesse spécifique, la diversité phylogénétique augmente avec la latitude et est corrélée significativement avec la variation macroclimatique, pointant vers du conservatisme de niche macroclimatique. Les patterns opposés de diversité phylogénétique et de richesse spécifique pointent vers une origine ancestrale des hépatiques en milieu extra-tropical suivie d'une diversification plus récente en milieu tropical. Contrairement à l'augmentation marquée de la diversité des familles d'angiosperme vers les tropiques, le gradient latitudinal de diversité observé au niveau spécifique pour les hépatiques disparait progressivement à plus haut niveau phylogénétique, suggérant que le conservatisme de niche phylogénétique a joué un rôle moindre chez les hépatiques que chez les angiospermes. Le gradient latitudinal de diversité inversé à plus haut niveau phylogénétique supporte l'hypothèse que les groupes les plus anciens se sont diversifiés sous conditions extratropicales, expliquant pourquoi, contrairement aux angiospermes, une haute richesse taxonomique dans les tropiques n’est pas associée avec une haute diversité phylogénétique chez les hépatiques. Nos résultats montrent à quel point une étude de la diversité phylogénétique à plusieurs niveaux taxonomiques permet une meilleure compréhension de l’accumulation de biodiversité au cours du temps.

PROCESSES ⟷ **PATTERNS**



PART 1: Simulations of community assembly under different scenarios of processes (equalizing, stabilizing and stochastic) in a fragmented landscape.

SIMULATIONS

1 Community creation based on assembly processes: Equalizing - Stabilizing - Stochastic and different spatial structures named ***Scenarios.***

METRIC COMPUTATION

2 Computation of the metrics of phylogenetic diversity based on the simulated communities for each ***Scenario.***

3 For each ***Scenario***, computation of Null Models to test for metric efficiency and reliability.

Q1a To what extent does the phylogenetic structure of communities vary under different assembly processes and combinations thereof ?

Q1b Do phylogenetic diversity patterns vary within the core and at the border of continuous versus fragmented habitats ? - **spatial effects**

Do phylogenetic diversity patterns vary depending on the assembly process taking place in a neighboring habitat ? - **mass effects**

R1.1 **Validation of the “Indirect Approach”.**

4 Contrasting observed metrics of phylogenetic diversity with those obtained after randomization of species positions in the phylogeny.

2 VS 3

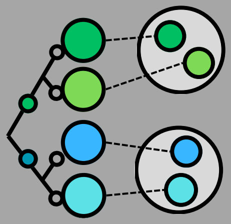
METRIC TESTING

Q1c Can randomization tests of phylogenetic diversity metrics be used in practice, and in which conditions, to infer community assembly processes ?

R1.2 **Guidelines for inferring community assembly processes from phylogenetic diversity patterns and identification of the most suitable phylogenetic diversity metrics.**

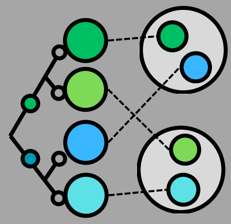
Characterization of the phylogenetic structure of communities

CLUSTERING



Species within communities are more **phylogenetically related** than expected by chance.

OVERDISPERSION



Species within communities are more **phylogenetically distant** than expected by chance.

PART 2:
Variation of phylogenetic diversity along latitudinal gradients.

5 Analyses of liverwort taxonomic and phylogenetic diversity patterns at both the regional and the global scale.

6 Correlation of liverwort diversity with environmental variables.

7 Correlation of liverwort diversity with environmental variables at increasing phylogenetic level.

Q2a How does liverwort phylogenetic diversity vary across latitudinal gradients at regional and worldwide scales ?

Q2b Is the diversity pattern driven by environmental variables, pointing to phylogenetic niche conservatism ?

Q2c What has been the role of the environment for shaping community phylogenetic structure throughout the evolutionary history of the group ?

R2

- **Increasing liverwort phylogenetic diversity towards the pole and inversion of the latitudinal taxonomic diversity gradient at increasing phylogenetic depth: evidence for an extra-tropical origin.**
- **Correlation between phylogenetic diversity and macroclimatic variation: the role of macroclimatic niche conservatism in shaping latitudinal species richness gradients.**

LIST OF CONTRIBUTIONS

The thesis is based on the following articles:

CHAPTER 1:

Kasprzyk, T., Dauby, G., Vanderpoorten, A., & Hardy, O. J. (2025). Mechanisms of Community Assembly through the Lens of Phylogenetic Diversity: A Critical Reappraisal. *Systematic Biology*, syaf062. https://doi.org/10.1093/sysbio/syaf062

CHAPTER 2:

Wang, J., Dai, Z., **Kasprzyk, T**., Yao, X., Hagborg, A., Söderström, L., Zhang, J., Vanderpoorten, A., & Collart, F. (2025). Inversion of the latitudinal diversity gradient at high taxonomic level in liverworts revealed by a phylogenetically deconstructive approach. *Annals of Botany*, mcaf051. https://doi.org/10.1093/aob/mcaf051

Qian, H., Vanderpoorten, A., Dai, Z., Kessler, M., **Kasprzyk, T.**, & Wang, J. (2024). Spatial patterns and climatic drivers of phylogenetic structure of regional liverwort assemblages in China. *Annals of Botany*, *134*(3), 427–435. https://doi.org/10.1093/aob/mcae080

SUPPORTING:

Shen, T., Corlett, R. T., Collart, F., **Kasprzyk, T.**, Guo, X. L., Patiño, J., Su, Y., Hardy, O. J., Ma, W. Z., Wang, J., Wei, Y. M., Mouton, L., Li, Y., Song, L., & Vanderpoorten, A. (2022). Microclimatic variation in tropical canopies: A glimpse into the processes of community assembly in epiphytic bryophyte communities. *Journal of Ecology*, *110*(12), 3023–3038. https://doi.org/10.1111/1365-2745.14011

Salces-Castellano, A*., **Kasprzyk, T***., Goffinet .B, Kiebacher, T., Patel, N., Liu, Y., Dong ,S ., Johnson, M., Guisan, A., Collart, F., & Vanderpoorten, A. Strong elevation-dependence of cross-taxon diversity patterns in plants. (Under Review).

*Equal contribution

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INTRODUCTION

COMMUNITY ASSEMBLY PROCESSES SIMULATIONS AND GRADIENTS

Bryophyte community recording along elevation gradients
Mt Brulé, Alt. 2500m, Valais, SUISSE
From left to right: Collart Flavien, Theunissen Kelly, Kasprzyk Thibault,
Guebel Léonie

GENERAL INTRODUCTION

Community assembly processes.

The question of how species communities are assembled has been fascinating ecologists for a long time (MacArthur R.H., 1965; Diamond, 1975; Connor & Simberloff, 1979; Hubbell, 2001). Defining a community as a “group of organisms representing multiple species living in a specified place and time”, community ecology is the “study of patterns in the diversity, abundance, and composition of species in communities, and the processes underlying these patterns” (Vellend, 2010), including the mechanisms by which local communities are formed from a larger regional species pool (Kraft & Ackerly, 2014). Over the years, many processes were hypothesized to explain community assembly and species coexistence without ever reaching a consensus (McGill, 2003). This multitude of potential processes as well as the intricate complexity and contingency of them have led scientists to colloquially consider community ecology as “a mess” (Lawton, 1999). To clean that mess, ecologists tried to unify these multitudes of processes into more integrative theories (McGill, 2010) and moved from narrow to broad frameworks (Simha et al., 2022).

Darwin (1859) was one of the first to hypothesize a connection between habitat selection, density-dependent selection, and the similarity among species. On the one hand, if habitat variation selects species depending on their adaptive traits, and if those traits are phylogenetically heritable (Blomberg, 2003), a mechanism known as phylogenetic niche conservatism (Losos, 2008; Wiens et al., 2010; Wiens & Graham, 2005), then species within communities are expected to be more closely related to each other than expected by chance, resulting in a pattern of phylogenetic clustering (Webb, 2000; Cavender-Bares, 2009). Species sharing the same adaptations for the same habitats are, however, also expected to compete for the same resources (Emerson & Gillespie, 2008; Violle et al., 2011) and are more likely to share parasites and diseases (Stephens et al., 2019, and references therein). To avoid competitive exclusion, parasite or predator transfer, a newly colonizing individual should, therefore, 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 & Graham, 2005; Anacker & Strauss, 2016). This paradox, known as “Darwin’s Conundrum” (Fan et al., 2023; Thuiller et al., 2010), reflects the relative importance of habitat filtering vs competition in community assembly.

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, while distinct habitats can select contrasted trait combinations. If, as the phylogenetic niche conservatism hypothesis posits, these traits are indeed heritable, then communities are expected to include closely related species sharing the same adaptations, and hence, to be phylogenetically clustered (Figure 1 A1-C1). **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 (Emerson & Gillespie, 2008; Violle et al., 2011), easy transfer of parasites (Stephens et al., 2019), or predator attraction, leading to a pattern of phylogenetic overdispersion (Figure 1 A2-C2).

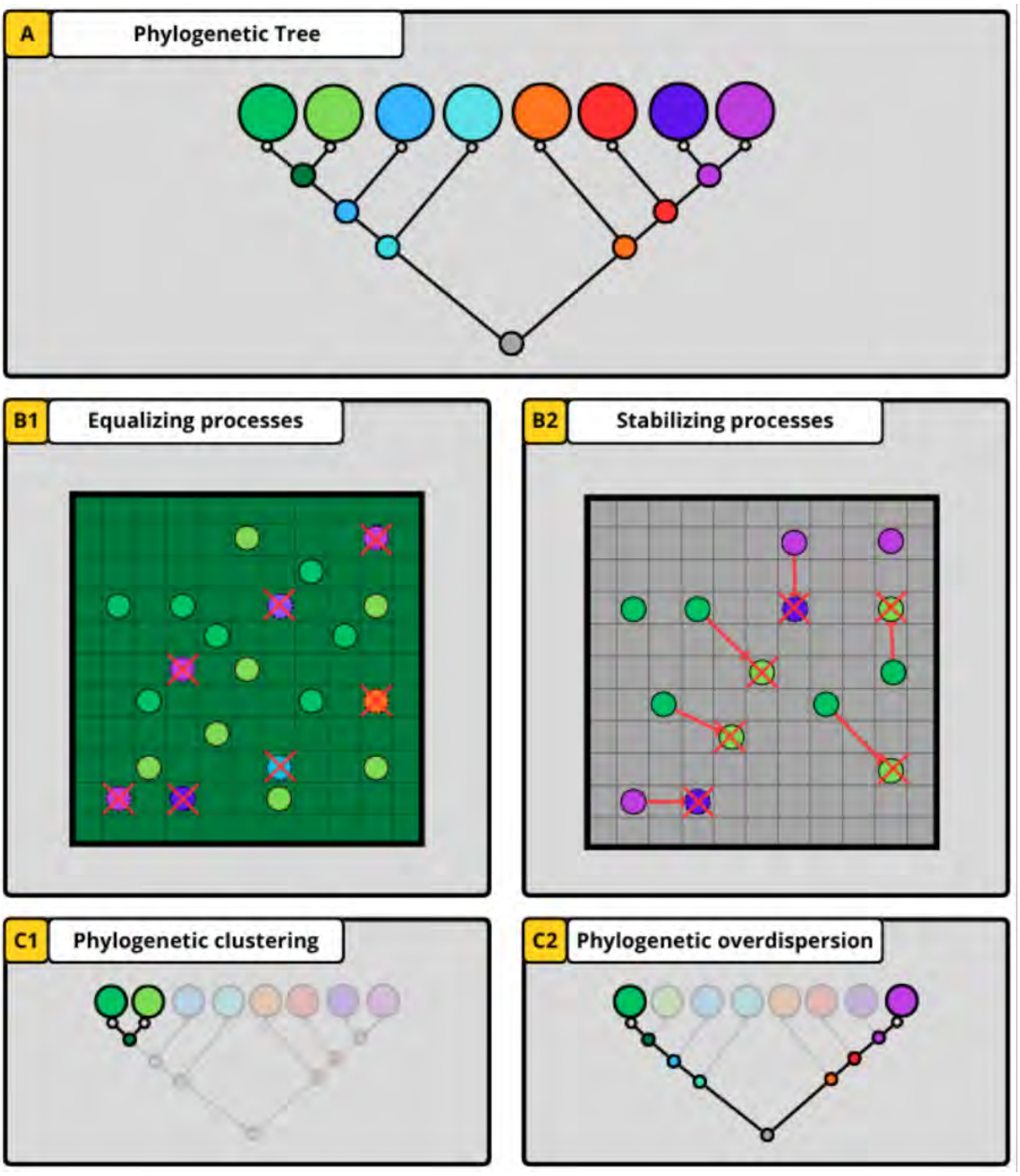


Figure 1: *Expected patterns of phylogenetic structure following community assembly processes described by Chesson (2000). Given a phylogeny (A) assumed to reflect the distribution of heritable niche traits among species (coloured dots), equalizing processes lead to the co-occurrence of closely related individuals (B1, C1). Under stabilizing processes conversely, competition between the phylogenetically closest species will lead to the elimination of one of them, leading to the co-occurrence of the most phylogenetically distant species (B2, C2).*

Equalizing and stabilizing processes, which regulate community assembly, are hence expected to leave a signature in the patterns of community phylogenetic structure, and hence, diversity. The analysis of community phylogenetic structure therefore appears as a promising tool to indirectly infer community assembly processes (Hardy, 2008; Münkemüller, 2012).

To do so, the observed phylogenetic diversity is computed and compared to values obtained following a null hypothesis of no phylogenetic pattern. An observed value of phylogenetic diversity that is significantly different (lower or greater) than expected by chance evidences phylogenetic clustering or overdispersion, which has been interpreted in terms of, respectively, habitat filtering and competition (Figure 2).

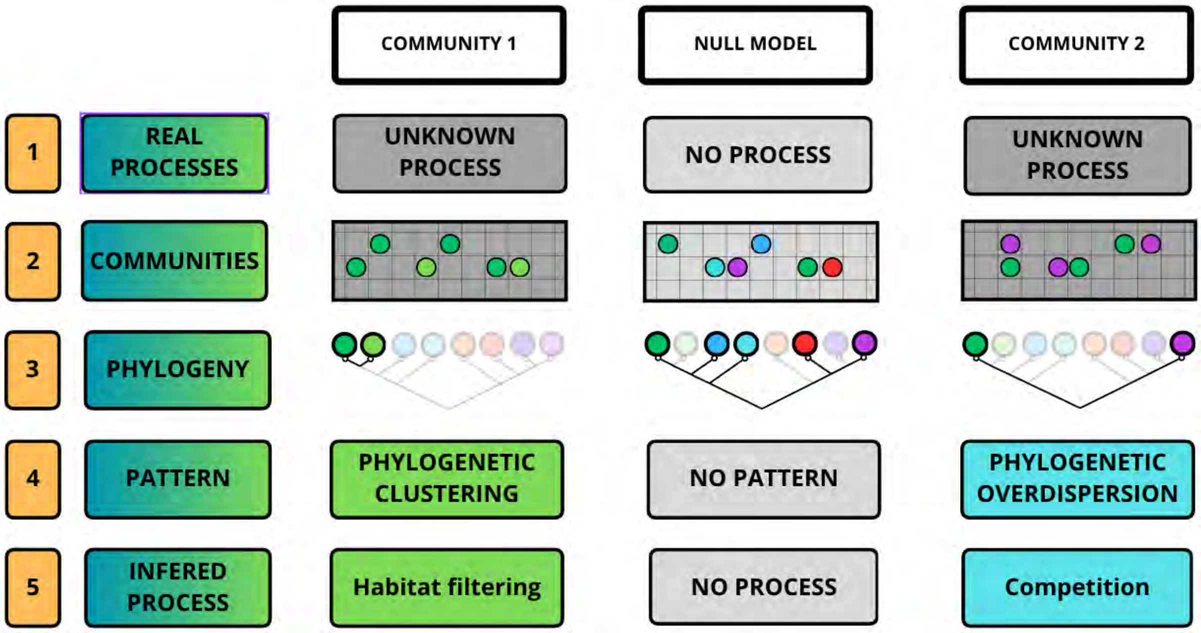


Figure 2: *Representation of the indirect approach, by which community assembly mechanisms can be inferred from their patterns of phylogenetic structure, and hence, diversity. Processes, such as environmental filtering and competition (1), determine the assembly of species in communities (2). Metrics of phylogenetic diversity are computed (3) and compared to those expected by chance under a null model, according to which phylogenetic relatedness is decoupled from species distribution patterns (4). If the observed phylogenetic diversity lays within the range of values expected under the null hypothesis, the hypothesis of a phylogenetically random species assembly cannot be rejected. If, conversely, the observed phylogenetic diversity is significantly higher or lower than expected under the null hypothesis, significant phylogenetic clustering or overdispersion is evidenced and can be interpreted in terms of assembly processes (5).*

Equalizing and stabilizing processes are, however, not the only processes shaping community assembly. In particular, niche and dispersal processes are 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 & Harms, 2009; Condit et al., 2012), the nature and strength of species interactions (Shurin & Allen, 2001; Chase et al., 2010), and environmental filtering (Réjou-Méchain & 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 & Hardy, 2011). Species co-occurrences thus quantitatively depend both on neighboring occupancy and local environmental conditions, which 'dilute' species/environment relationships (Shmida & Whittaker, 1981; Shmida & Wilson, 1985) and allows persistence of species outside their niche (Lerch et al., 2025). This phenomenon, known as "Mass Effect", can hinder assembly process recognition (Hernández-Ordónez et al., 2019) (Figure 3). In addition, neutral community simulations under limited dispersal can lead to high rates of false positives when inferring non-neutral processes (Hardy, 2008). It is therefore crucial to take spatial effects and dispersal limitations into account when inferring community assembly processes from community phylogenetic patterns (Wiegand et al., 2017).

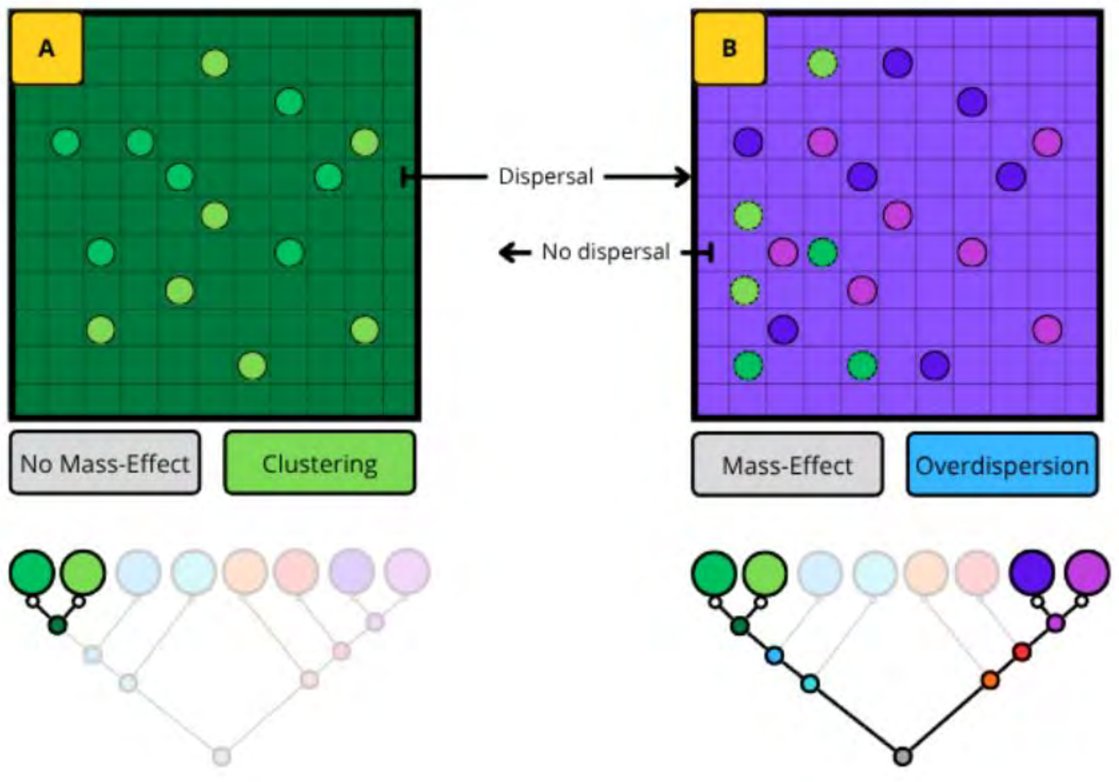


Figure 3: *Effects of dispersal limitations and mass-effects on patterns of community phylogenetic structure. Even if both communities are purely assembled by habitat filtering, continuous flow of maladapted individuals (dots) from A to B will induce a shift in community B from clustering to overdispersion, challenging the inference of the assembly process from community phylogenetic structure.*

Inferring assembly processes from diversity patterns is appealing but is far from straightforward (Münkemüller et al, 2020), even after testing the impact of each process and confounding factors (dispersal limitations, mass-effects) and relies on multiple assumptions. First, one-to-one equivalency between patterns and processes is most of the time assumed and niche conservatism and competition are thought to explain phylogenetic clustering and overdispersion respectively. Second, if multiple processes are at play simultaneously, whether one process will leave a stronger signature on community phylogenetic structure than the other processes, or whether the signal resulting from one process will be eroded by the other processes, is unknown.

Finally, a plethora of phylogenetic diversity metrics to describe the phylogenetic structure of communities has been developed (Tucker et al., 2017; Miller et al., 2017) and has been used across taxa and scales (see appendix 3 of Münkemüller (2012) for review). Whether these metrics accurately retrieve a significant phylogenetic structure under different community assembly mechanisms, and combinations thereof, and whether their variation also depends on confounding factors associated with spatial patterns and dispersal limitations, has also been seldom assessed. Miller et al. (2017) identified the best performing metrics in terms of statistical power and rate of false positives. Miller's et al. (2017) simulations, however, involved the placement of individuals based on their traits, regardless of dispersal limitations and spatial effects in community assembly.

In silico *simulations for testing the use of phylogenetic diversity as a proxy for assembly mechanisms.*

To test both the use of phylogenetic diversity as a proxy for assembly mechanisms and the reliability of different metrics, we cannot use empirical studies or experiments because we do not know the real processes that led to the observed patterns. Another option could be the use of microcosms to ensure a controlled environment, allowing to test for niche preference or competition (Liu & Salles, 2024), but does not allow to precisely test for other processes like dispersal limitation or mass-effects. Alternatively, this issue can be addressed by analysing communities created *in silico*. Ecological mechanistic models, used to recreate evolution of communities under modelized natural processes, received a lot of attention to confirm (or not) conceptual theory (Weiher et al., 2011; Webb et al., 2010) and paved the way for community simulation. These models have been used to test various hypotheses, such as the interplay of positive and negative species interactions across an environmental gradient (Travis et al., 2005), the effect of habitat heterogeneity (Ziv,1998), microclimates of tree tops (Lin et al., 2024) or coral reefs and disturbance (Langmead & Sheppard, 2004). In addition to being both time and cost efficient as no experiments are needed, simulations are highly repeatable and shareable between scientists. Therefore, the use of simulators, creating artificial species communities following known rules, is a valuable tool to assess both if ecological processes lead to the expected pattern and how metrics, or any other statistical tool (Minchin, 1987), will react. If correctly crafted, simulators allow to input any modelized processes with powerful parametrization of species characteristics to mimic natural communities at best. I will call this ensemble of parameters, leading to the creation of a distinct community, a *Scenario*.

In this context, the first part of the present thesis aimed at determining the extent to which specific assembly processes, and their combinations, indeed lead to expected patterns of community phylogenetic structure and diversity. Building on this theoretical approach, I applied phylogenetic diversity estimators to investigate the mechanisms underlaying one of the most pervasive biodiversity patterns, that is, the latitudinal diversity gradient (LDG).

The latitudinal diversity gradient.

The LDG has long been considered to be one of most recurrent patterns in ecology (Hillebrand, 2004; Mittelbach et al., 2007), with a remarkable consistency across space, habitats, taxonomic groups and time (Crane & Lidgard, 1989; Buckley & Jetz, 2007; Kreft & Jetz, 2007). Surprisingly, and despite the remarkable generality of the LDG and centuries of attention (Pianka, 1966), causes and processes responsible for the LDG are still under strong debate (Hillebrand, 2004; Jablonski et al., 2017; Etienne et al., 2019; Henriques-Silva et al., 2019; Saupe, 2023).

It is generally thought that the tendency of species to retain the ecological preferences of their ancestors (i.e. phylogenetic niche conservatism) determines which species in a regional species pool can occur in precise environmental conditions (Wiens & Donoghue, 2004). Because many extant lineages evolved and diversified during geological times when the Earth's climate was wet and warm (Wiens & Donoghue, 2004), traits associated with warm and wet climates are often considered ancestral for those clades, whereas traits that confer drought or cold tolerance evolved secondarily within a few clades (Wiens & Donoghue, 2004). Accordingly, many clades are still constrained to humid tropical climates, and few clades have made evolutionary breakthroughs into very cold and arid conditions (Wiens & Donoghue, 2004; Kellermann et al., 2012; Zanne et al., 2014). As a result of this tropical niche conservatism (Wiens & Donoghue, 2004; Qian et al., 2019), biological assemblages in areas with colder climates tend to possess more closely related species and to have lower species richness, whereas assemblages in tropical regions are more taxonomically and phylogenetically diverse.

Like numerous patterns in ecology and evolution, the LDG varies across phylogenetic levels (Graham et al., 2018). In vertebrates, the diversity in higher-level taxa (e.g. families, orders) increases towards the tropics. At shallower taxonomic levels, variation in diversity with latitude varies from one taxon to another (Worm & Tittensor, 2018). Many young clades show negative richness–temperature slopes, with the ages of these clades coinciding with the expansion of temperate climate zones in the late Eocene (Buckley et al., 2010). The subsequent spread and diversification of these lineages to higher latitudes provided the possibility of different latitudinal distributions, resulting in a decay of the LDG towards finer phylogenetic scales (Worm & Tittensor, 2018).

In this context, a deconstructive macroecological approach, looking at how biodiversity patterns vary among areas and across taxonomic levels, allows for a better understanding of how biodiversity has accumulated through time, but also through space (Marquet et al., 2004). Analysing the relationship between the different biodiversity dimensions in a geographical context may, in fact, unveil the occurrence of particular ecological and evolutionary mechanisms in some geographical places or specific clades (Vásquez-Restrepo et al., 2023). In particular, the strength of the LDG typically varies longitudinally, being shallower at intermediate longitudes (−20° to 60°) and strongest at extreme longitudes (Kinlock et al., 2018). For example, tropical plants are more species rich in East Asia and the Americas compared with Africa as a result of differences in past and current climatic conditions and higher speciation rates in South America and Southeast Asia than in Africa (Couvreur, 2015; Hagen et al., 2021; de Miranda et al., 2022). Despite the massive increase in phylogeny-based research over the last years, studies that systematically investigated how patterns and processes change with phylogenetic scale or use phylogenetic scale to examine the effects of aggregating or disaggregating taxa on global patterns are still relatively scarce (Worm & Tittensor, 2018; Chalmandrier et al., 2019; Vásquez-Restrepo et al., 2023).

Unveiling the mechanisms of the latitudinal diversity gradient in liverworts from analyses of the phylogenetic structure of their assemblages.

We focus on liverworts, a group of land plants including 7271 species (Söderström et al., 2016) that, together with mosses and hornworts, compose the bryophytes. Although an increase of species richness away from the tropics was evidenced regionally (Rozzi et al., 2008; Mateo et al., 2016), liverwort species richness peaks in tropical conditions at the worldwide scale (Wang et al., 2017). Liverworts are primarily wind dispersed by spores involved in chance transoceanic dispersal events (Patiño & Vanderpoorten, 2018). With increasing chances of a long-distance dispersal event during their evolutionary history, higher-level taxa are expected to exhibit larger distribution ranges. A decay of the LDG is therefore expected at increasing taxonomic depth, unless some lineages would have been restricted to specific environmental conditions. In particular, evidence for macroclimatic niche conservatism across liverworts floras worldwide (Collart et al., 2021) suggests that macroclimatic preferences are heritable, hampering tropical lineages from colonizing extra-tropical regions.

Objectives.

The present thesis addresses two main questions. To what extent can we infer community assembly processes based on observed community phylogenetic patterns? Based on this, what can phylogenetic diversity tell us on assembly processes in liverworts at large spatial scale throughout their evolutionary history?

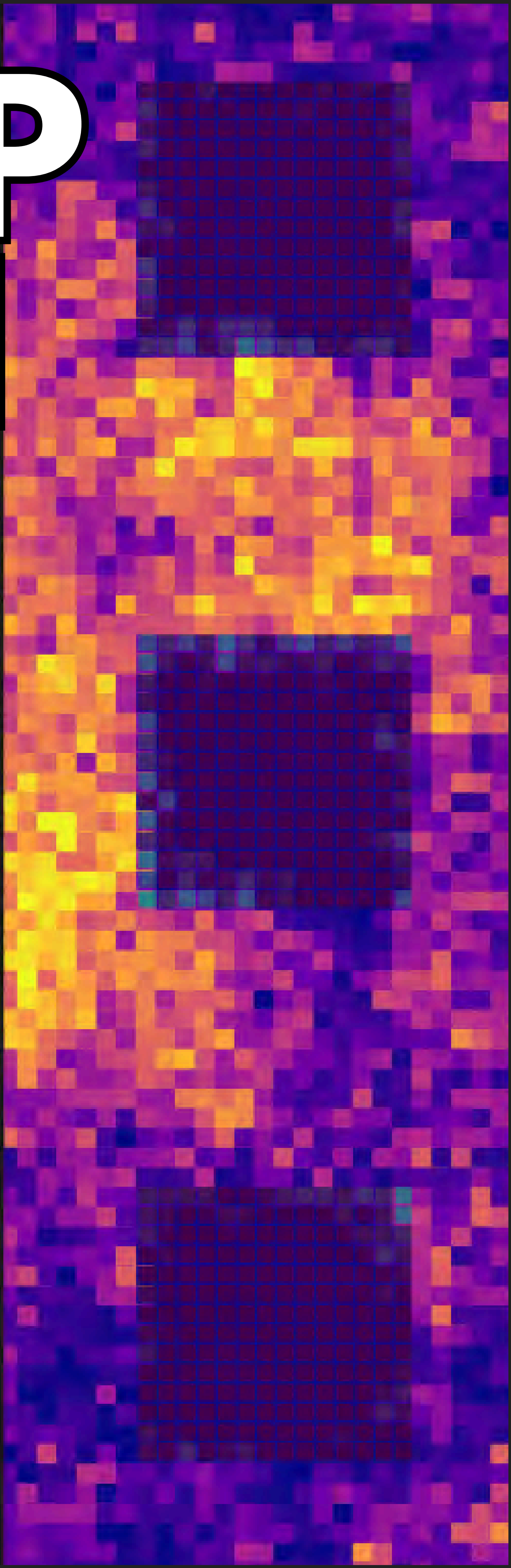
More precisely:

1/ To what extent does the phylogenetic structure of communities vary under different assembly processes and combinations thereof (a), and to what extent do spatial and mass effects erode the signature of habitat selection and competition (b)? Can phylogenetic diversity metrics associated with null models be used to infer community assembly mechanisms, and if so, with what associated rates of type-1 and type-2 errors (c) ?

2/ How does liverwort phylogenetic diversity vary across latitudinal gradients at regional and worldwide scales (a), and to what extent does this variation correlate with environmental variation, pointing to phylogenetic niche conservatism (b)? What has been the role of the latter for shaping community phylogenetic structure throughout the evolutionary history of the group (c)?

CHAPTER 1

IN SILICO SIMULATIONS AND INFERENCE OF COMMUNITY ASSEMBLY PROCESSES



Species abundance in a simulated grid of plots ranging from 0 (blue) to 50 (yellow) under equalizing processes.

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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

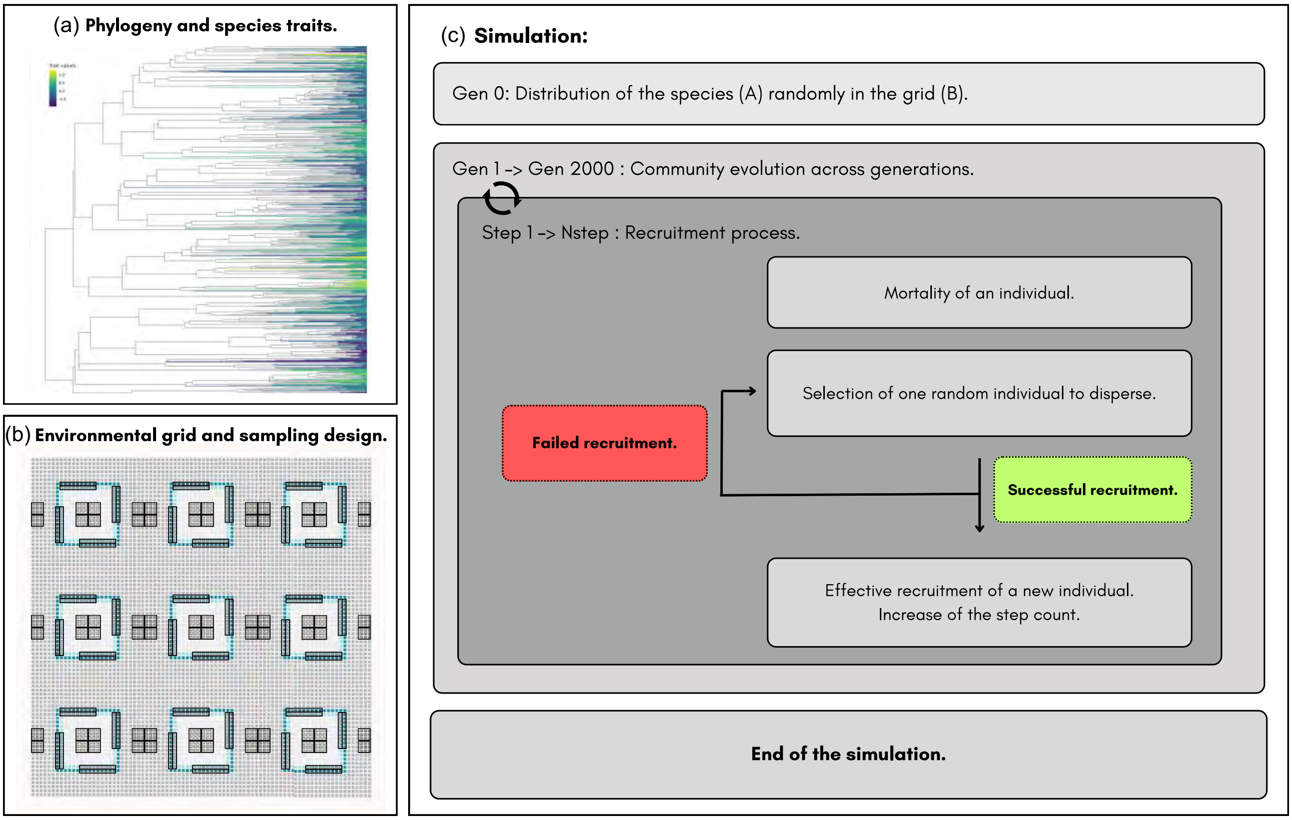

FIGURE 1. Illustration of the community assembly simulation framework under stochastic, equalizing, and stabilizing processes, and the combination thereof, in a fragmented landscape. (a) Simulation of a phylogeny, with nine species traits mapped on it following a Brownian evolutionary model (equalizing 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 ($84 \times 84 \times 50$ 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

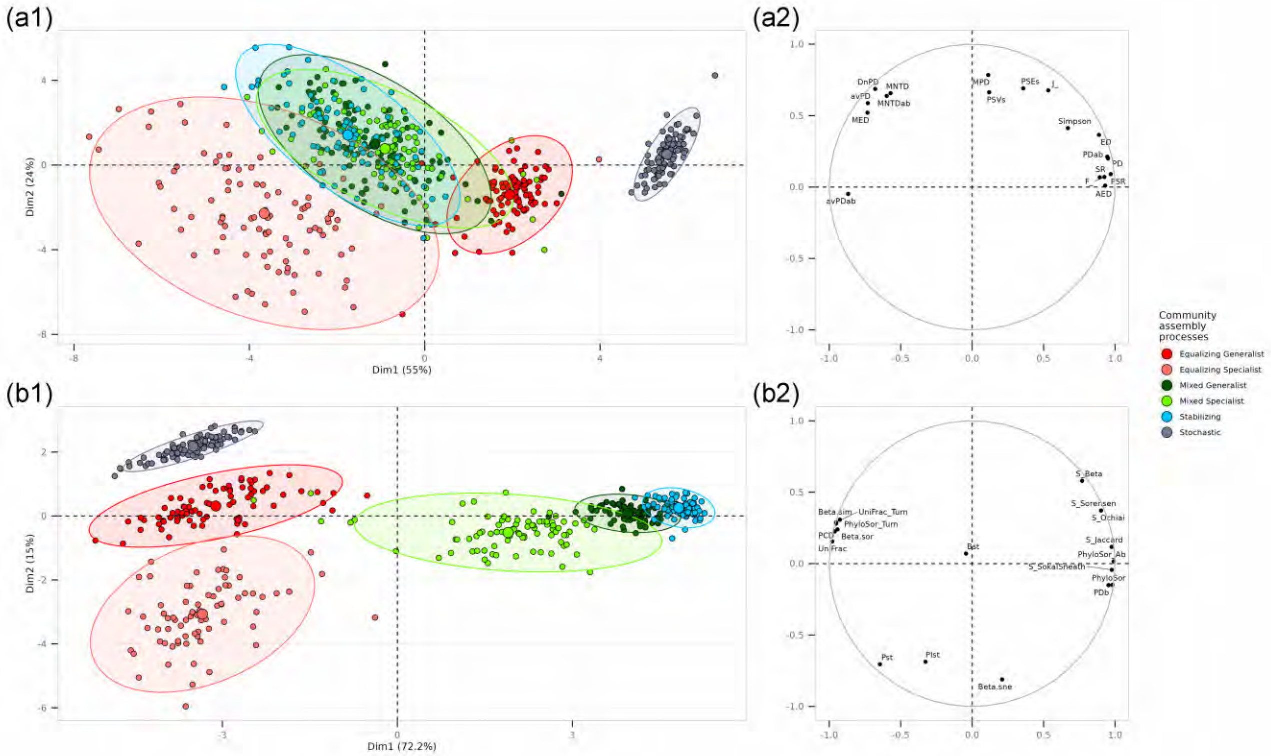

FIGURE 2. Principal Component Analysis of the communities assembled under different processes as a function of alpha (a1) and beta (b1) diversity metrics. Each dot represents one of 100 replicates of community assembly simulations per assembly process (stochastic, equalizing with specialist or generalist 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

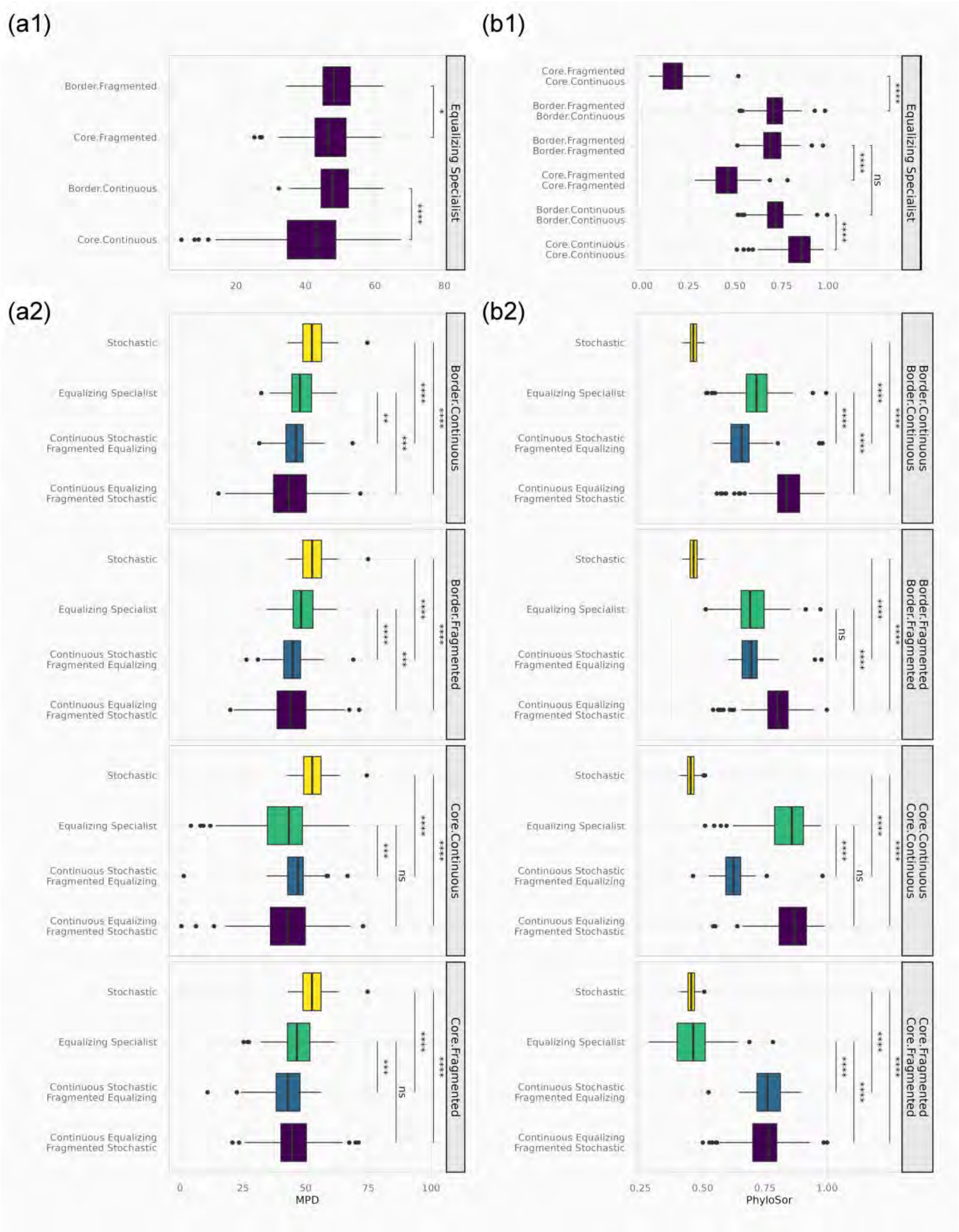

FIGURE 3. Impact of mass and spatial effects on community phylogenetic structure and diversity. Box plots (showing the 1st and third quartiles (upper and lower bounds), second quartile (center), 1.5∗ inter-quartile range (whiskers), and minima-maxima (beyond the whiskers) represent the variation of alpha 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.

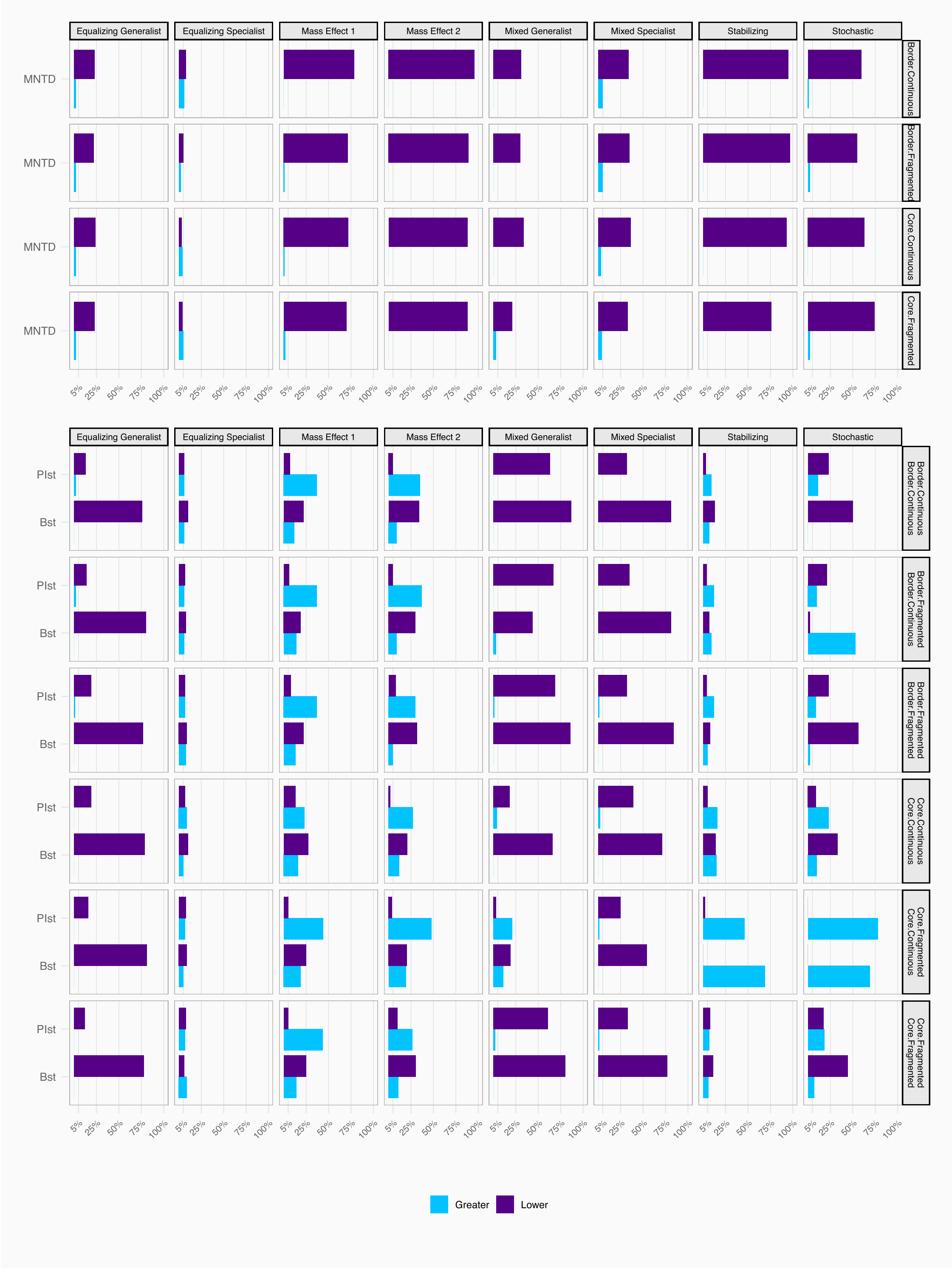

FIGURE 4. Performance, in terms of type 1 (false negative) and type 2 (false positive) errors, of selected metrics of phylogenetic diversity to retrieve the process under which communities were simulated. 1: stochastic, 2: stabilizing, 3–4: equalizing with specialist and generalist species, and combinations 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 cooccur 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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Supplementary Figures and Tables

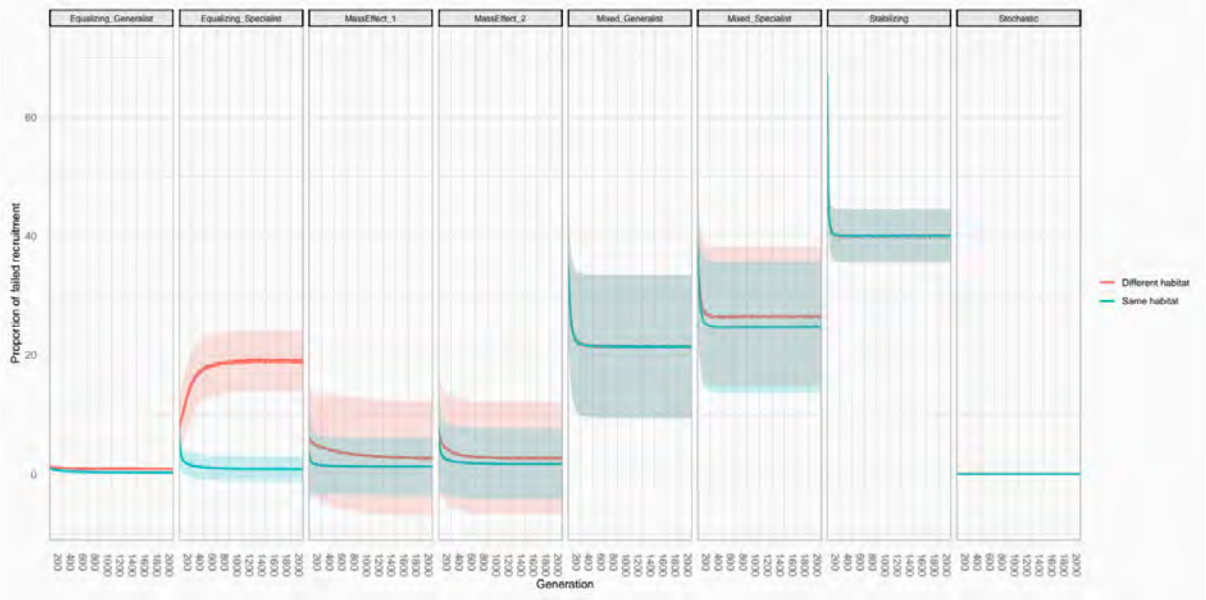

Figure S1: *Proportion of failed recruitments during the process of community assembly in a gridded landscape including one fragmented and one continuous habitat. Within this landscape, 196 pixels were sampled at each generation, one generation consisting of 352800 steps, during which one individual per plot 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, from the same (blue lines) or a different habitat (red line). Communities were assembled under contrasting processes, including stochastic, stabilizing, and equalizing processes for generalist and specialist species, and mixed processes. Two mixed processes were implemented: processes involving 50% of stabilizing and 50% of equalizing processes across the landscape, both for generalist (Mixed_generalist) and specialist species (Mixed_specialist) on the one hand, and equalizing processes for specialist species in the fragmented habitat but stochastic processes in the continuous habitat (MassEffect_1) and vice-versa (MassEffect_2).*

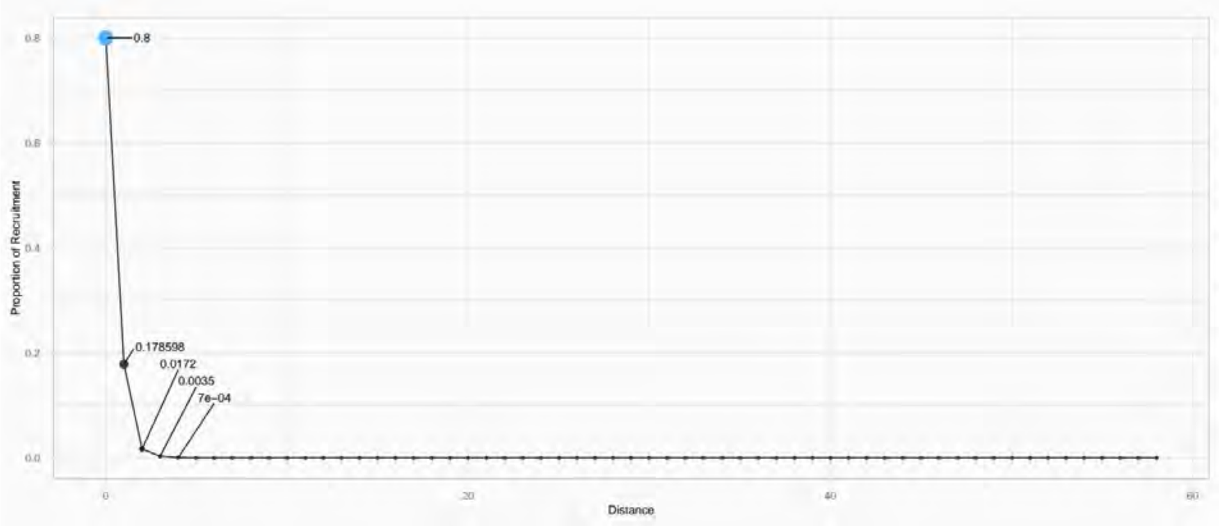

Figure S2: *Dispersal kernel implemented to simulate short-distance dispersal of individuals across a fragmented landscape.*

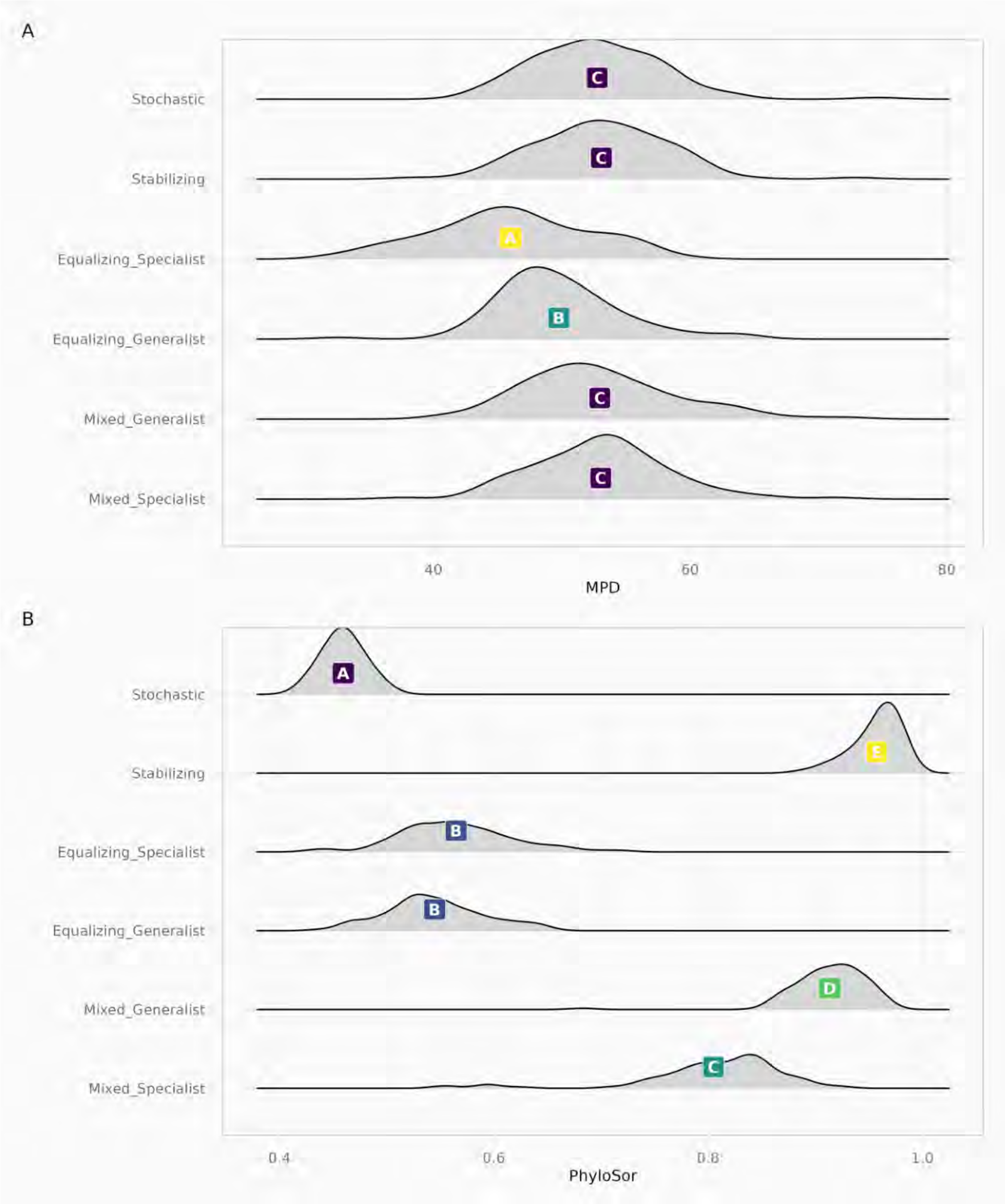

Figure S3: *Phylogenetic structure of communities simulated under competing assembly processes across a landscape including a continuous and a fragmented habitat. Distribution of average mean phylogenetic distance (MPD) values across all samples (A) and average PhyloSor values across all sample pairs (B) for 100 replicates of community simulations under contrasting assembly processes: stochastic, stabilizing, equalizing with specialist and generalist species, mixture of 50% of stabilizing processes and 50% of equalizing processes with specialist and generalist species. Letters indicate whether average MPD and PhyloSor significantly differ depending on assembly processes based on Dunn tests, the same letter being used for distributions with non-significantly different average values.*

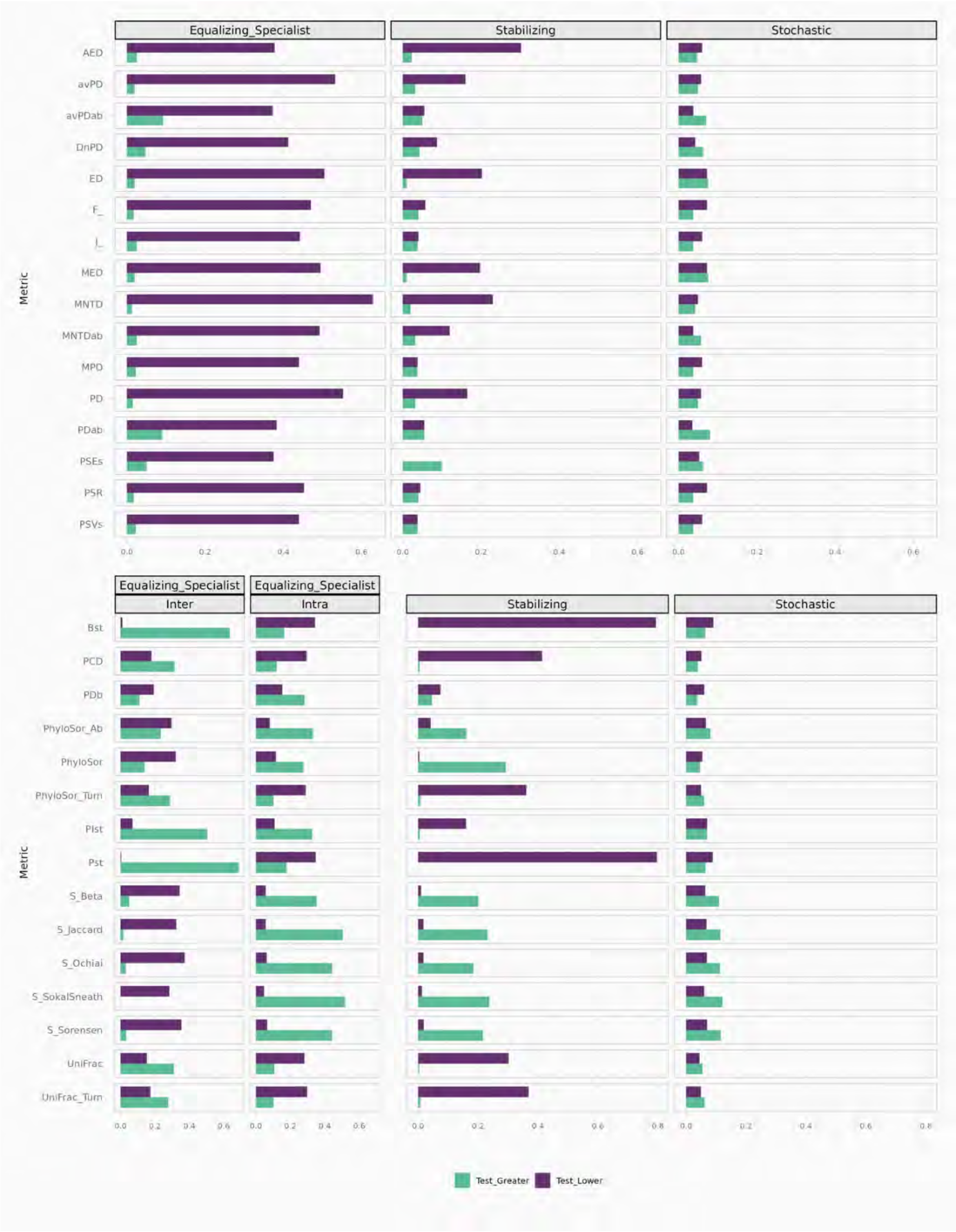

Figure S4: *Ability of alpha (above) and beta (below) metrics of phylogenetic diversity to retrieve phylogenetic clustering under equalizing processes (specialist species), phylogenetic overdispersion under stabilizing processes, and no phylogenetic structure under stochastic processes. For beta metrics under equalizing processes, the results within and among habitats are displayed.*

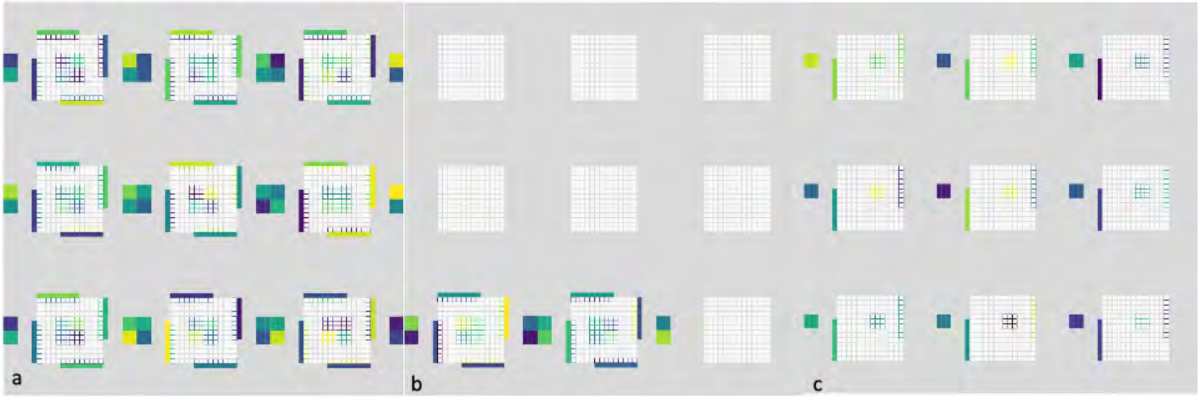

Figure S5: *Impact of the sampling design on the power of null models used to detect a significant community phylogenetic structure. (a) Sampling design of 36 samples per habitat, as originally implemented in this study. (b) Spatially-correlated design of 8 samples. (c) Sparse sampling, made of 9 samples for each habitat*

Table S1. *Probability of recruitment within communities under stochastic, stabilizing and equalizing processes.*

Process	Probability of recruitment $PR_{i,p}$ of an individual of species *i* in pixel *p*	Comment
Stochastic	$PRstoc_{i,p} = 1$	$PRstoc_{i,p} = 1$, as it does not depend on habitat type nor on the species composition of the target community.
Stabilizing	$PRst_{i,p}$ is a function of the Euclidean distance between the stabilizing traits of species *i* and those of the species *j* (*j=1…n*) already present in the pixel, $d_{i,j}$, relative to the largest distance between two species from the phylogeny, d_{max}. Considering 3 traits (*t*=1-3) involved in stabilizing processes (traits 1-3 simulated in §3.2): $PRst_{i,p} = \frac{\sum_{j=1}^{n} f_{j,p}\, d_{i,j}}{d_{max}}$	An individual has an increasing chance of successfully establishing in a community if it exhibits traits different from those of the species already present, thereby avoiding competition. It is worth noting that the habitat component is absent from this equation because habitat preference has no impact on stabilizing processes.
Equalizing	$PReq_{i,p}$, depends on the species *j* already present in the pixel and showing higher fitness values than *i*: $PReq_{i,p} = \sum_{j} f_{j,p}\, min\left(1, \frac{\omega_{i,h}}{\omega_{j,h}}\right)$ where $f_{j,p}$ is the relative frequency of species *j* in pixel *p*, $\omega_{i,h}$ is the fitness of species *i* in habitat *h,* which depends on the difference between species traits and optimal traits in the given habitat, considering the three traits (*t*=1-3) involved in equalizing processes (traits 4-6 simulated in §3.2): $\omega_{i,h} = \prod_{t=1}^{3} e^{-0.5\left(\frac{T_{t,i} - H_{t,h}}{\sigma_i}\right)^2}$ where $T_{t,i}$ is the value of trait *t* in species *i*, $H_{t,h}$ is the optimal value of trait *t* in habitat *h* (i.e. the trait value conferring highest fitness), and σ_i controls the degree of habitat specificity of species *i*, with σ_i= 2 or 5 to simulate habitat specialists or generalist species with weak habitat preferences, respectively.	The probability of establishment of an individual in habitat depends on its fitness compared to that of all the individuals already present in the pixel. This equation implies that $PReq_{i,p}$, = 1 if the propagule belongs to a species with a fitness higher or equal to all other species. We set $H_{t,h}$ at -0.5 and 0.5 for habitat 1 and 2, respectively. Habitat specificity was kept constant across species within each simulation run but varied between simulation runs.

Multiple Processes	When combining multiple processes in a same pixel, the establishment probability *Pe* is: $Pe = P_{stoch} + P_{equa}PReq_{i,p} + P_{stab}PRst_{i,p}$ where P_{stoch}, P_{equa} and P_{stab} are the relative importance of stochastic, equalizing and stabilizing processes during establishment ($P_{stoch} + P_{equa} + P_{stab} = 1$).

Table S2. *Classification of the phylogenetic diversity metrics implemented depending on their type (alpha vs beta metrics), nature (richness "R" vs divergence "D" level) and type of data (occurrence "O" vs abundance "A").*

Metric (reference)	**Definition**	**Nature**	**Type of data**
Alpha metrics			
PD (Faith, 1992)	Sum of total branch length connecting all the species together.	R	O
AvPD (Clarke & Warwick, 2001)	Sum of total branch length connecting all the species together, divided by species richness.	D	O
F (Izsák & Papp, 2000)	Sum of the phylogenetic distances between all pairs of species.	R	O
J (Izsák & Papp, 2000)	Expected difference/distance between two randomly chosen species (drawn with replacement).	D	O
PSV (Helmus et al., 2007)	Variability in an unmeasured neutral trait.	D	O
PSR (Helmus et al., 2007)	Variability in an unmeasured neutral trait multiplied by species richness.	R	O
PSE (Helmus et al., 2007)	Abundance weighted version of the PSV.	D	A
PDab (Vellend, 2010)	Sum of total branch length connecting all the species together where branches are scaled by proportional abundances of subtending species.	R	A
ΔnPD (DnPD) (Barker, 2002)	Sum of total branch length connecting all the species together where branches are scaled by abundances of subtending species.	R	A
AvPDab (Tucker et al., 2017)	Sum of total branch length connecting all the species together where branches are scaled by proportional abundances of subtending species, divided by the number of species.	D	A
MPD (Clarke & Warwick, 1998; Webb, 2000)	Mean phylogenetic distances between all pairs of species occurring within a site / Mean phylogenetic pairwise distance.	D	O
MNTD(Webb et al., 2008)	Mean phylogenetic distance to the nearest relative for all species occurring within a site.	D	O

MNTDab (Webb et al., 2008)	Mean phylogenetic distance to the nearest relative for all species occurring within a site, weighted by species proportions.	D	A
ED (Tucker et al., 2017)	Sum of species evolutionary distinctiveness.	R	O
AED (Tucker et al., 2017)	Sum of species evolutionary distinctiveness weighted by species abundance.	R	A
MED (Tucker et al., 2017)	mean evolutionary distinctiveness.	D	O
	Beta metrics		
Faith PDbeta (PDb) (Nipperess et al., 2010)	Measure of the resemblance in feature richness by using shared, unshared and absent branches between two assemblages.	R	O
PhyloSor(Bryant et al., 2008)	Proportional shared branch length between two communities. It ranges from indefinably close to 0 when only a small root is shared to 1 when the two communities are identical.	D	O
PhyloSorAb (Nipperess et al., 2010)	Proportional shared branch length between two communities weighted by species abundance.	D	A
PhyloSorTurn(Leprieur et al., 2012)	Turn-over component of PhyloSor.	D	O
UniFrac (Lozupone & Knight, 2005)	The fraction of the branch length of the tree that leads to descendants from either one environment or the other, but not both.	R	O
UniFracTurn (Leprieur et al., 2012)	Turn-over component of UniFrac.	R	O
S_Jaccard (Pavoine & Ricotta, 2014)	Generalization of the Jaccard Index.	R/D	O/A
S_Ochial (Pavoine & Ricotta, 2014)	Generalization of the Ochiai Index.	R/D	O/A
S_Sorensen (Pavoine & Ricotta, 2014)	Generalization of the Sorensen Index.	R/D	O/A
S_SokalSneath (Pavoine & Ricotta, 2014)	Generalization of the SokalSneath Index.	R/D	O/A
S_Beta (Pavoine & Ricotta, 2014)	Generalization of Rao's Dab index.	R/D	O/A
Pst (Hardy, 2008)	Local phylogenetic similarity excess between individuals.	D	A
Bst (Hardy, 2008)	Local phylogenetic similarity excess between non-conspecific individuals (Bst>0 under spatial phylogenetic clustering, Bst<0 under spatial phylogenetic overdispersion).	D	A
PIst (Hardy, 2008)	Local phylogenetic similarity excess between species (PIst>0 under spatial phylogenetic clustering, PIst<0 under spatial phylogenetic overdispersion).	D	O
PCD (Helmus et al., 2007)	How much of the variance among species in the values of a hypothetical non-selected trait in one community can be predicted by the known trait values of species in another community.	D	O

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CHAPTER 2

THE LATITUDINAL DIVERSITY GRADIENT

Bryophyte sampling mission
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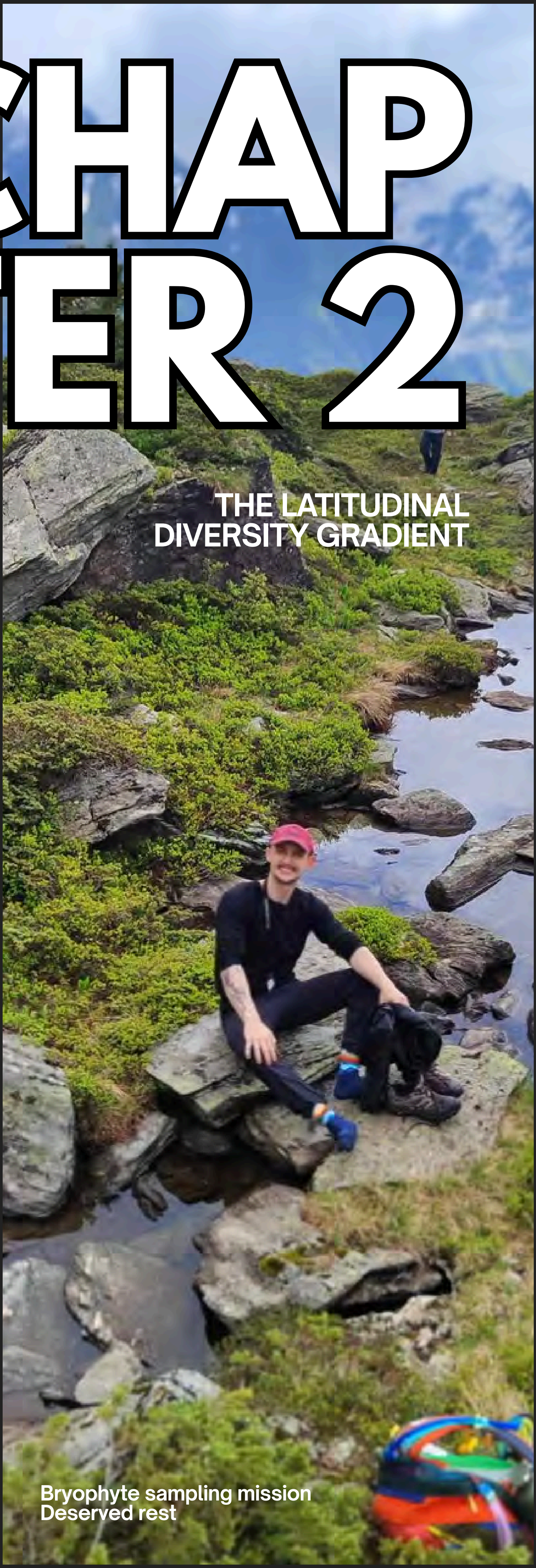
From left to right: Theunissen Kelly, Kasprzyk Thibault, Vanderpoorten Alain, Collart Flavien



Bryophyte sampling mission
Deserved rest

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REVIEW

Inversion of the latitudinal diversity gradient at high taxonomic level in liverworts revealed by a phylogenetically deconstructive approach

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- **Background and Aims** Like numerous patterns in ecology and evolution, the latitudinal diversity gradient varies across phylogenetic levels. Yet, studies that investigate systematically how patterns and processes change at different phylogenetic levels, from the tips to the root, are still relatively scarce. Here, we test the hypothesis that, despite the high long-distance dispersal capacities of liverworts, which would be expected to result in the homogenization of their distributions, an increase of diversity with latitude persists at increasing phylogenetic level owing to macroclimatic niche conservatism since the earliest evolutionary history of the group.
- **Methods** Liverwort distributions were scored for 450 operational geographical units worldwide. From the tips to the root, the phylogeny was sliced continuously to examine how taxonomic and phylogenetic diversity are correlated with latitude in a standardized way. Taxonomic diversity and mean phylogenetic distance among taxa were computed for each operational geographical unit at different phylogenetic levels and correlated with macroecological factors using spatial linear models.
- **Key Results** The correlation between taxonomic diversity and latitude shifted progressively from significantly negative at species level to non-significant, then significantly positive at the highest phylogenetic levels. Taxonomic diversity and mean phylogenetic distance were both significantly correlated with macroclimatic factors across all phylogenetic levels.
- **Conclusions** In contrast to the marked increase of angiosperm family diversity towards the tropics, the latitudinal diversity gradient evidenced at species level in liverworts decayed progressively at increasing phylogenetic level, suggesting that phylogenetic niche conservatism has played a much weaker role in liverworts than in angiosperms. The inverted latitudinal diversity gradient towards the deepest phylogenetic levels lends support to the hypothesis that the earliest lineages diversified in extra-tropical conditions, explaining why, unlike in angiosperms, high species richness in the tropics is not associated with high phylogenetic diversity in liverworts. Our results highlight the extent to which a phylogenetically deconstructive approach allows for a better understanding of the accumulation of biodiversity through time.

Key words: Bryophyte, latitudinal diversity gradient, phylogenetic niche conservatism, phylogenetic scale, taxonomic diversity, phylogenetic diversity.

INTRODUCTION

The increase of species richness towards the tropics, a pattern known as the latitudinal diversity gradient (LDG), has long been considered to be one of most recurrent patterns in ecology (Lomolino *et al.*, 2010), with a remarkable consistency across space, habitats, taxonomic groups and time (Crane and Lidgard, 1989; Buckley and Jetz, 2007; Kreft and Jetz, 2007). Like numerous patterns in ecology and evolution, the LDG varies across phylogenetic levels (Graham *et al.*, 2018).

In vertebrates, the diversity in higher-level taxa (e.g. families, orders) increases towards the tropics. At shallower taxonomic levels, variation in diversity with latitude varies from one taxon to another (Worm and Tittensor, 2018). Many young clades show negative richness–temperature slopes, with the ages of these clades coinciding with the expansion of temperate climate zones in the late Eocene (Buckley *et al.*, 2010). The subsequent spread and diversification of these lineages to higher latitudes provided the possibility of different latitudinal distributions, resulting in a decay of the LDG towards finer phylogenetic scales (Worm and Tittensor, 2018).

In this context, a deconstructive macroecological approach, looking at how biodiversity patterns vary among areas and across taxonomic levels, allows for a better understanding of how biodiversity has accumulated through time, but also through space (Marquet *et al.*, 2004). Analysing the relationship between the different biodiversity dimensions in a geographical context may, in fact, unveil the occurrence of particular ecological and evolutionary mechanisms in some geographical places or specific clades (Vásquez-Restrepo *et al.*, 2023). In particular, the strength of the LDG typically varies longitudinally, being shallower at intermediate longitudes (−20° to 60°) and strongest at extreme longitudes (Kinlock *et al.*, 2018). For example, tropical plants are more species rich in East Asia and the Americas compared with Africa as a result of differences in past and current climatic conditions and higher speciation rates in South America and Southeast Asia than in Africa (Couvreur, 2015; Hagen *et al.*, 2021; de Miranda *et al.*, 2022).

Despite the massive increase in phylogeny-based research over the last years, studies that systematically investigated how patterns and processes change with phylogenetic scale or use phylogenetic scale to examine the effects of aggregating or disaggregating taxa on global patterns are still relatively scarce (Worm and Tittensor, 2018; Chalmandrier *et al.*, 2019; Vásquez-Restrepo *et al*, 2023). Here, we examine how two complementary diversity metrics, namely taxonomic diversity and phylogenetic diversity, vary along a phylogenetic time scale. Phylogenetic diversity measures the extent to which species in a community are closely or distantly related to each other. Integrating the shared evolutionary history of species, phylogenetic diversity can depart from taxonomic diversity. For instance, recent radiations are characterized by low phylogenetic but high taxonomic diversity, while rare long-distance dispersal events may contribute little to taxonomic diversity but substantially increase phylogenetic diversity (Davies and Buckley, 2011). In the context of the LDG, phylogenetic diversity specifically allows us to test one of the main driving forces of the pattern, namely tropical conservatism. The tropical conservatism hypothesis (Wiens and Donoghue, 2004) posits, based on the fact that tropical regions were more extensive until the mid-Tertiary, that temperate clades include lineages that diverged recently from tropical ones and share adaptations to cold, resulting in phylogenetically clustered temperate lineages (Kerkhoff *et al.*, 2014).

We focus on liverworts, a group of land plants including 7271 species (Söderström *et al.*, 2016) that, together with mosses and hornworts, compose the bryophytes. Although an increase of species richness away from the tropics was evidenced regionally (Rozzi *et al.*, 2008; Mateo *et al.*, 2016), liverwort species richness peaks in tropical conditions at the worldwide scale (Wang *et al.*, 2017). Liverworts are primarily wind dispersed by spores involved in chance transoceanic dispersal events, but the number of those events is largely lower than that of intracontinental speciation events, suggesting that the speciation rate is higher than the transoceanic dispersal rate (Patiño and Vanderpoorten, 2018). With increasing chances of a long-distance dispersal event during their evolutionary history, higher-level taxa are expected to exhibit larger distribution ranges. A decay of the LDG is therefore expected at increasing taxonomic depth, unless some lineages would have been restricted to specific environmental conditions. In particular, evidence for macroclimatic niche conservatism across liverworts floras worldwide (Collart *et al.*, 2021) suggests that macroclimatic preferences are heritable, hampering tropical lineages from colonizing extra-tropical regions.

Specifically, we test the hypothesis that in liverworts, a latitudinal diversity gradient occurs at the species level and persists at increasing phylogenetic depth owing to macroclimatic niche conservatism, evidencing the role of the latter in shaping the observed patterns since the earliest evolutionary history of the group.

MATERIALS AND METHODS

Data sources

We scored species distributions in operational geographical units (OGUs) from the most comprehensive database of liverwort species distributions available to date, which has been built in the context of the Early Land Plants Today project (Söderström *et al.*, 2020). The distribution data are derived from a working database that, as of January 2019, included a bibliography of >11 000 references and >1 000 000 distribution records. Nomenclature follows Söderström *et al.* (2016). Based on this, we excluded 915 species, for which taxonomic evidence is conflicting (species with 'serious doubts', qualified with one star by Söderström *et al.*, 2016) and scored the presence/absence of 6331 accepted species names in 450 OGUs worldwide. Most of these units are defined by geopolitical boundaries, as commonly used in macroecological studies (e.g. Liu *et al.*, 2023; Qian *et al.*, 2024). They represent level-3 units (botanical countries) of the World Geographical Scheme for Recording Plant Distributions (https://www.tdwg.org/standards/wgsrpd), with the largest countries (e.g. USA, Canada, China, Brazil and Australia) divided into states or provinces (level-4 units).

The data are available from https://doi.org/10.6084/m9.figshare.22587199.v1.

Latitudinal variation in species richness was represented per band of 10°, including all the species recorded in the OGUs whose centroid was included in the band considered. Given that the proportion of land area decreases with increasing latitude in the Southern Hemisphere, we calculated species density for each latitudinal band as the number of species divided by the $\log_{10}$-transformed area (in kilometres squared) of the latitudinal band. To take the longitudinal variation of diversity patterns into account, we partitioned the data longitudinally into three main regions: New World (North and South America), western Old World (Europe and Africa) and eastern Old World (Asia and Oceania) (Condamine *et al.*, 2012).

We downloaded mean annual temperature (MAT) and mean annual precipitation (MAP) at 1-km resolution from CHELSA (https://chelsa-climate.org/bioclim). These data were complemented with information on the temporal variation of climate change, characterized by climate change velocity for MAT and MAP between Last Glacial Maximum (~21 000 years ago) and the present (1950–2000) at 2.5 arc-min resolution (Sandel *et al.*, 2011). For each variable, we computed the mean for each of the 450 OGUs.

Taxonomic and phylogenetic diversity

Taxonomic and phylogenetic diversity was computed for each OGU. Taxonomic diversity was computed by counting, for each OGU, the number of species or higher-level taxa. For phylogenetic diversity, we computed the mean phylogenetic distance (MPD) among taxa within an OGU. MPD measures the mean phylogenetic distance separating all the taxa within an OGU from each other (i.e. a tree-wide assessment of relatedness among co-occurring taxa) and thus quantifies the overall relatedness of the taxa within an OGU. Unlike other metrics, such as phylogenetic diversity, MPD is independent from taxonomic diversity (Miller *et al.*, 2017). An average value of the phylogenetic distance among taxa, MPD is a poor estimate of phylogenetic diversity when the number of taxa is low. In a global map of MPD among species across OGUs worldwide, some of the OGUs with the highest MPD are among the most species poor (Supplementary Data Fig. S1). This is particularly the case in some sub-Saharan African OGUs, which include only two, albeit highly divergent, species (one leafy and one thalloid species). Previous analyses showed that correlation patterns between phylogenetic diversity and environmental variation were similar when computed from datasets including all OGUs versus only OGUs with more than ten species, but with higher correlation coefficients with the reduced dataset (Collart *et al.*, 2021). Therefore, MPD was not computed for 35 OGUs with a species richness of less than ten to avoid spurious estimates of MPD attributable to the low number of species included.

Although a phylogenomic analysis of 151 liverwort genera based on 228 nuclear genes was published most recently (Bechteler *et al.*, 2023), we used the phylogeny of Laenen *et al.* (2014) based on the analysis of eight genes from all genomic compartments to compute MPD values. This phylogeny, whose topology is globally consistent with that of Bechteler *et al.* (2023), includes 303 genera, representing 84 % of the total extant generic diversity, i.e. the most densely sampled global liverwort phylogeny to date.

Given that the phylogeny includes a single species per genus, all congeneric species included in the distribution database were grafted onto the genus-level phylogeny. In the absence of well-resolved phylogenies at the species level, this approach has commonly been implemented in community phylogenetic analyses (for review, see Qian and Jin, 2021). Given that variation in the phylogenetic diversity of communities is driven mainly by ancestral branches (Hardy *et al.*, 2012), phylogenetic metrics derived from species-level phylogenies resolved at the genus level with species being attached to their respective genera as polytomies are highly correlated with those derived from a phylogeny fully resolved at the species level (Qian and Jin, 2021). Here, we attempted to take the uncertainty of the diversity metrics obtained after the grafting of species to their respective genus by generating 100 trees with randomly resolved relationships among congeneric species using the 'add.species.to.genus' function of the phytools package (Revell, 2012). Although far from covering the entire range of alternative phylogenies, this approach allowed us, instead of focusing on a single arbitrarily selected phylogeny or attaching species to their respective genera in the phylogeny as polytomies, to examine the impact of the random grafting of species within their genera across 100 trees. To assess further the extent to which this approach could lead to a bias in the patterns of diversity observed, we contrasted them with those obtained from the analysis of the genus-level phylogeny of Laenen *et al.* (2014). Here, MPD was not computed for 294 OGUs that included fewer than ten genera, for reasons detailed above.

To determine whether species (or higher-level taxa) within an OGU are more or less phylogenetically related than expected by chance, characterizing phylogenetic clustering and overdispersion, respectively, 100 MPD values were generated from each of the 100 phylogenies (thus for a total of 10 000 MPD values) whose species were randomized among the tips to build the distribution of the null hypothesis, then compared with the observed MPD values.

Statistical analyses

We determined how species and higher-level taxa are distributed along latitudinal gradients to test the hypothesis that a LDG can be characterized at different nested taxonomic levels (i.e. whether there is an increase of the diversity of genera, families etc. towards the tropics). Instead of computing the numbers of higher-level taxa per OGU, to avoid the problem that taxonomic ranks are arbitrarily defined (Avise and Johns, 1999; Kraichak *et al.*, 2017), we standardized the taxonomic level at which we characterize spatial diversity patterns by sampling taxa that are defined by a given age in the phylogeny. The regular levels at which the phylogeny was sliced do not, however, necessarily correspond to traditionally defined taxa, and we therefore refer hereafter to the phylogenetic level at which the analysis was conducted. To this end, we generated α-diversity-through-time profiles, analogous to the β-diversity-through-time framework (Groussin *et al.*, 2017) at arbitrarily defined intervals of 25 Myr along the phylogenetic time scale. From the tips to the root, the phylogenetic tree was sliced continuously, yielding, for each time period, clades that served as OTUs in downstream analysis. The phylogenetic tree was pruned to the desired depth by collapsing all descendent leaves of each of the branches encountered at 25 Myr periods. Accordingly, the branch lengths leading to these new terminal nodes progressively shortened and the number of OTUs progressively decreased towards the root (Supplementary Data Table S1). The geographical distribution of these branches was calculated as the union of the distributions of their descending leaves. For each 25 Myr period, we computed the correlation between taxonomic and phylogenetic diversity per OGU and the absolute value of the latitude of the centroid of each OGU.

To examine how taxonomic and phylogenetic diversity vary depending on macroclimatic variation, simultaneous autoregressive error (SAR) models, as implemented by the R package spatialreg (Bivand *et al.*, 2023), were used to take the effects of spatial autocorrelation into account (Kissling and Carl, 2008; Zhang *et al.*, 2013). We tested competing models involving all possible combinations of predictors. Competing models were compared on the basis of Akaike's information criterion (AIC) as proposed by Burnham and Anderson (2002), and the model with the lowest AIC was selected (Wagenmakers and Farrell, 2004). For the best-fitting model, we computed the relative importance of predictor variables by using the standardized partial regression coefficients for all predictor variables (Kissling and Carl, 2008; Zhang *et al.*, 2013, 2016). We assessed the importance of individual variables to the model by summing the AIC weights across all subset models in which the variable was included (Burnham and Anderson, 2002). Then, variation in taxonomic and phylogenetic diversity across OGUs, considering its spatial component, was entered as a new response variable to perform SAR models again and obtain the standardized coefficient for each predictor (Belmaker and Jetz, 2011). Finally, we computed the *P*-value of the variables remaining in the model to identify 'confusing' variables, i.e. variables that would be kept in the model based on the AIC criterion, but would have a P-value > 0.05 (Sutherland *et al.*, 2023). We summarized the standardized coefficients of variables in the best-fitting model and the weights of total variables together subsequently.

This analysis was repeated at increasing phylogenetic depth, i.e. at 25 Myr intervals along the phylogenetic tree. This approach does not account for the past distribution of climates when lineages arose, but simply seeks to determine whether current patterns of taxonomic and phylogenetic diversity at different phylogenetic levels vary depending on extant climatic conditions.

All statistical analyses were implemented in R v.4.2.3 (R Core Team, 2023), and the codes for all analyses implemented are available in the Appendix.

RESULTS

Taxonomic diversity at the species level (i.e. species richness) of liverworts among the 450 OGUs ranged from 2 to 819, with an average of 14 species (Fig. 1). There was a clear increase of species density (i.e. species richness weighted by area) towards the tropics, as expressed by the clear increase of species density per latitudinal band of 10° to the tropics (Fig. 2). This global pattern resulted from a strong increase of species density towards the tropics in the Americas and Asia/Oceania, whereas in Europe/Africa, species density strikingly decreased between 15° and 35°, corresponding to the Sahel region. MPD globally tended to decrease from the poles to the tropics, shifting from higher to lower values than expected by chance (Supplementary Data Fig. S2), hence from significant phylogenetic overdispersion to clustering, except across Europe/Africa (Figs 1B and 2B).

These patterns varied substantially at different phylogenetic levels (Fig. 3). The r^2 of the relationship between taxonomic richness per OGU and latitude decreased progressively at increasing phylogenetic level (Fig. 3C). The LDG globally collapsed from 50–75 Myr backwards, with most correlations between the number of lineages and latitude being insignificant across the 100 phylogenetic trees. About 100–125 Mya, the slope between taxonomic richness per OGU and latitude shifted from negative to positive (Fig. 3A). This shift was associated with a drastic increase of the r^2 in the Americas and Europe/Africa, but not in Asia/Oceania, to reach a value of 0.12 ($P < 0.001$) and 0.26 ($P < 0.001$) at 200 Mya, respectively (Fig. 3C). In contrast, the slope of the relationship between MPD and latitude remained positive across phylogenetic levels (Fig. 3B). The r^2 of this relationship tended to increase with phylogenetic depth in the Americas and Europe/Africa, but not in Asia/Oceania (Fig. 3D). The same patterns were recovered from the analysis using the genus-level phylogeny (Supplementary Data Fig. S3), evidencing the limited impact of the random grafting of species to their respective genus on the patterns of diversity observed.

Significant models between taxonomic diversity, MPD and macroclimatic predictors were obtained across all phylogenetic depths, with r^2 ranging between 0.29 and 0.36 and between 0.09 and 0.27 for taxonomic diversity and MPD, respectively (Table 1). Competing models did not always exhibit significant differences ($\Delta\text{AIC} > 2$), but yielded similar variable selections (Supplementary Data Table S2), with precipitation-related variables contributing globally more to models than temperature-related variables (Table 1).

DISCUSSION

Our analyses reveal a sharp increase in liverwort species richness towards the tropics, evidencing the presence of a latitudinal diversity gradient in a group wherein it has long been debated owing to regional departures of this pattern (Rozzi *et al.*, 2008; Mateo *et al.*, 2016). The increase of species richness towards the tropics varied longitudinally, with a clear pattern across the Americas and Asia/Oceania, but not across Europe/Africa. During the Last Glacial Maximum, the African rainforest area was reduced by ~84 %, i.e. to a much larger extent than its Amazonian counterpart, which probably shrank to 54 % of its present-day extent (Anhuf *et al.*, 2006). Extinction processes are, furthermore, expected to be stronger in Africa than in Amazonia because of the smaller African rainforest area (~249×10^6 ha in Africa vs. 668×10^6 ha in Amazonia), resulting in smaller population sizes, which, in turn, increases extinction risk (Parmentier *et al.*, 2007).

Such a clear latitudinal diversity pattern emerged despite the long-distance dispersal capacities of liverworts, which should have contributed to homogenize their distribution patterns. In fact, the significant correlation between phylogenetic diversity and macroclimatic variation that persisted through the entire phylogenetic time scale suggests, in line with previous evidence (Collart *et al.*, 2021), that macroclimatic niche conservatism took place in the early evolutionary history of liverworts and continuously shaped their distribution patterns. It is worth noting that significant correlations between liverwort

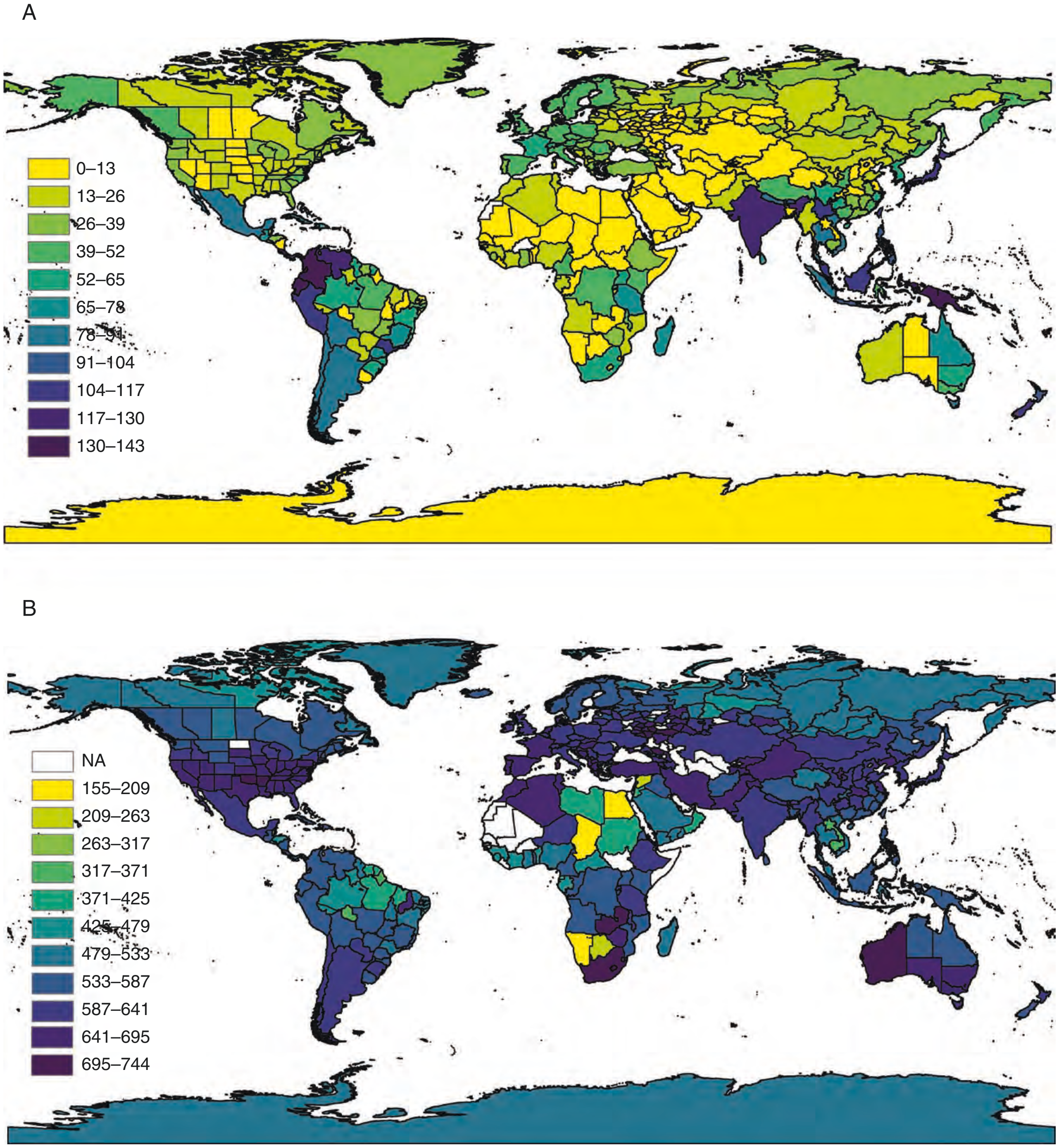

FIG. 1. Map of the species richness (A) and phylogenetic diversity [B; measured as the mean phylogenetic distance (MPD) among species] across 450 OGUs in liverworts. Abbreviation: NA, OGUs for which MPD was not computed owing to low species richness ($n < 10$).

phylogenetic diversity and macroclimatic conditions were revealed despite the fact that bryophytes are able to persist in microhabitats where a suitable microenvironment persists, long after the general climate of the region has changed (Schuster, 1983). As a result, bryophyte species distributions are typically disjunct (Patiño and Vanderpoorten, 2018). This suggests that, at a macroscale, such disjunctions associated with species microhabitat preferences do not prevent a global relationship between liverwort floras and macroclimatic conditions from emerging.

The latitudinal diversity gradient that emerged at the species level decayed progressively at increasing phylogenetic level, evidencing the wider range and weaker macroclimatic preference of high-level taxa. In fact, in our dataset, 41 % of liverwort species, but only 3 % of the genera and none of the families, exhibit a strictly tropical distribution. The erasure of

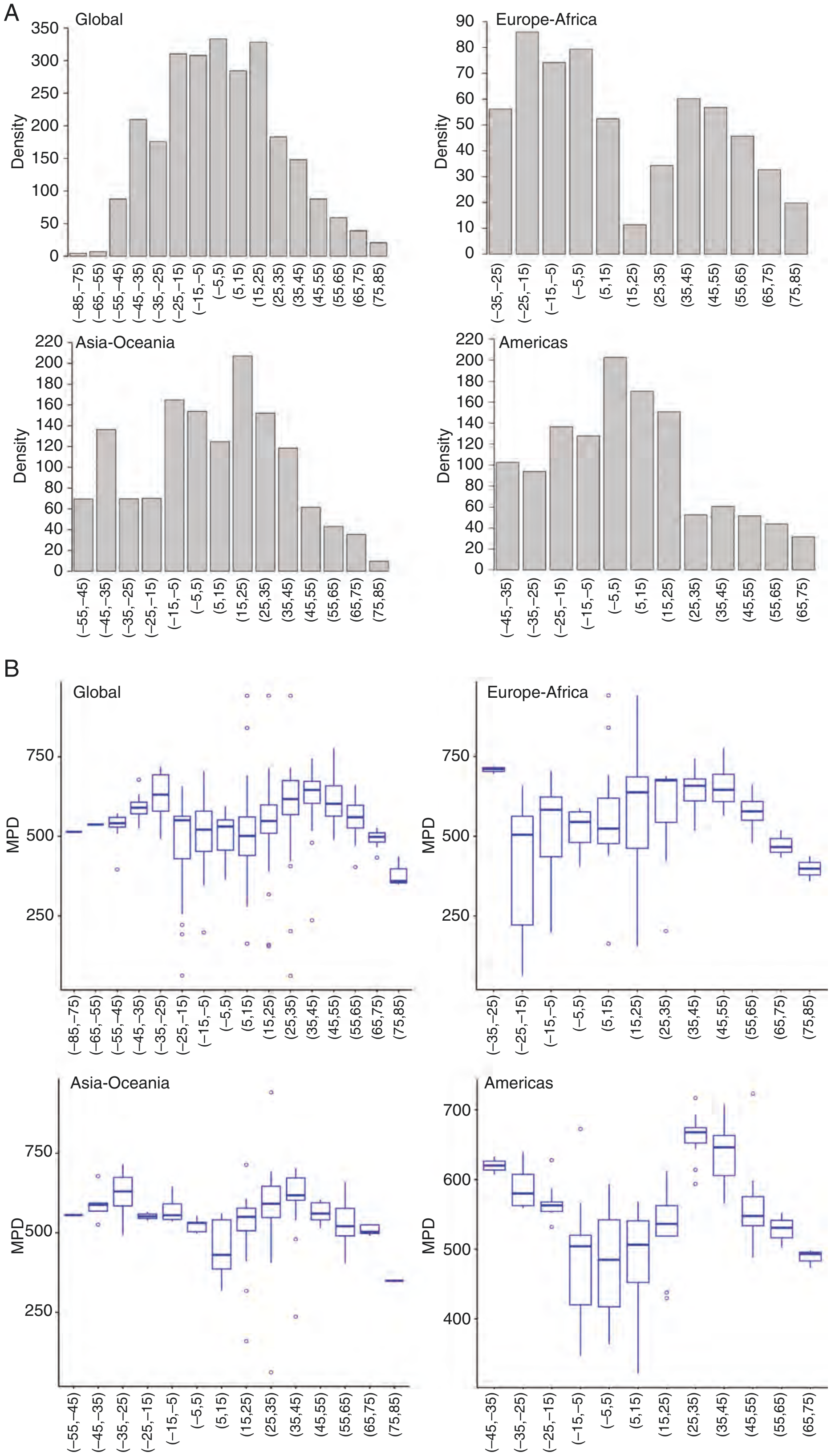

FIG. 2. Latitudinal patterns of liverwort species density (species richness per latitudinal band divided by the $\log_{10}$-transformed area; A) and mean phylogenetic distance (MPD) among species per OGU within each latitudinal band (B).

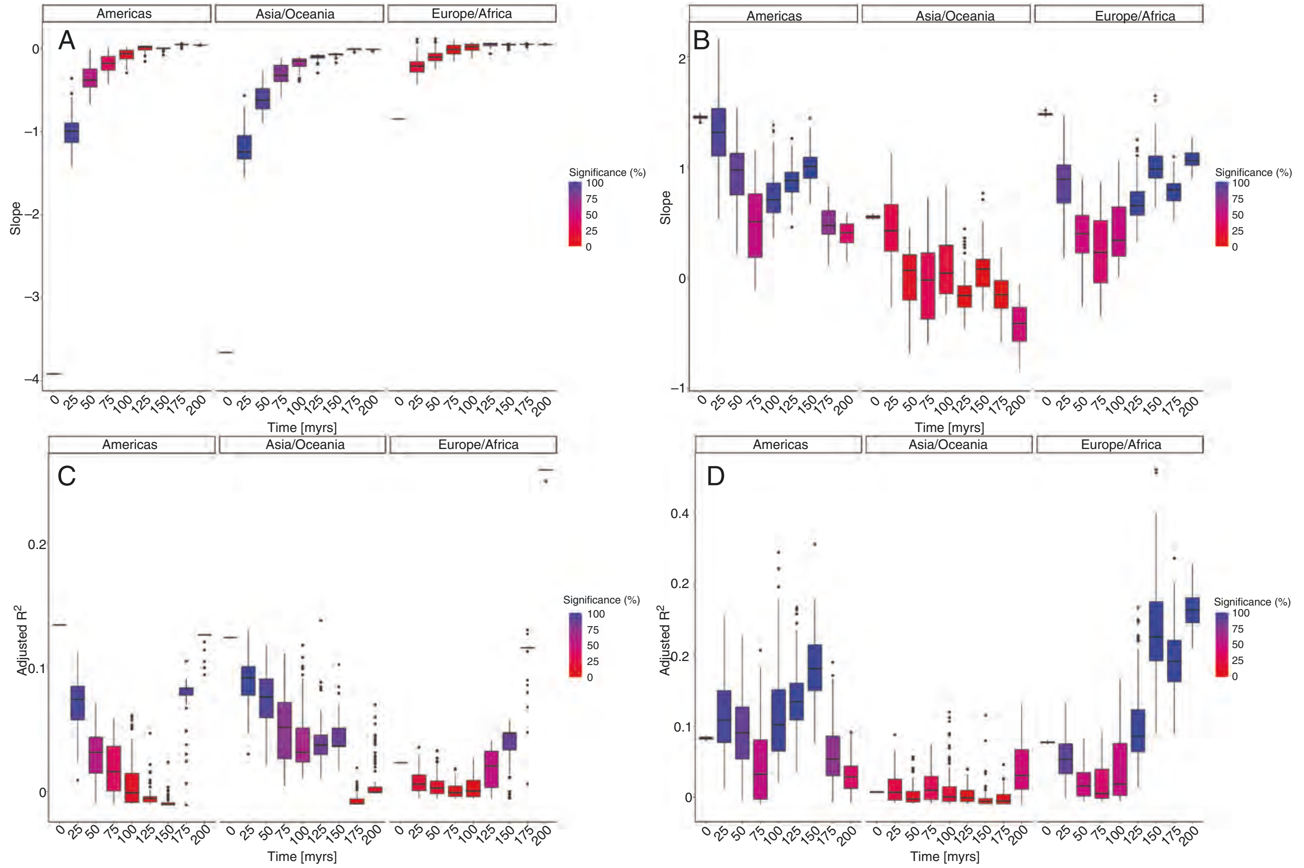

Fig. 3. Variation of the slope (A, B) and r^2 (C, D) of the relationship between liverwort taxonomic richness (A, C) and MPD (B, D) per OGU and latitude (as an absolute value) through a phylogenetic time scale. Box plots [showing the first and third quartiles (upper and lower bounds), second quartile (centre), 1.5 × interquartile range (whiskers) and minima–maxima beyond the whiskers] show the variation across 100 trees, for which species relationships within each genus were randomized, and the colour code reflects the proportion of replicates for which the slope was significant.

the latitudinal diversity gradient at genus and family level in liverworts contrasts with the marked increase of angiosperm family diversity towards the tropics, shaped by strong tropical niche conservatism (Ramírez-Barahona *et al.*, 2020). Although it has long been acknowledged that bryophytes exhibit higher long-distance dispersal capacities than spermatophytes (for review, see Patiño and Vanderpoorten, 2018), the rapid decay of the LDG in liverworts, together with the low, albeit significant, correlations between phylogenetic diversity and macroclimatic variation suggest that, by comparison with spermatophytes (Kerkhoff *et al.*, 2014), liverwort distributions are little constrained by tropical niche conservatism. Reconstruction of the ‘tropicality index’, which reflects the proportion of species latitudinal range that falls within the tropics minus the proportion of the latitudinal range that falls outside of it (Kerkhoff *et al.*, 2014), revealed, in fact, that many temperate lineages are phylogenetically clustered within tropical ones (Collart *et al.*, 2021), evidencing multiple instances of successful transition from tropical environments to temperate ones. For example, all temperate species of the most species-rich liverwort family, Lejeuneaceae, are nested in clades comprising mainly tropical species (Wilson *et al.*, 2007). Lejeunea, one of the largest liverwort genera, originated in the Neotropics and subsequently dispersed successfully into extra-tropical regions (Heinrichs *et al.*, 2013; Lee *et al.*, 2020), and the western European flora is composed largely of species of tropical origin (Patiño *et al.*, 2015).

Precipitation-related variables contributed more to the observed correlation between taxonomic and phylogenetic diversity and macroclimatic factors than temperature-related variables, pointing to the strong water dependence of liverworts. Phylogenetic diversity decreased with precipitation-related variables. We tentatively suggest that drought exerts a strong evolutionary pressure on lineages, which developed convergent adaptations among unrelated lineages, thereby resulting in the observed phylogenetic overdispersion in dry areas. For example, hot, xeric areas typically host a combination of xerophilic, specialist complex thalloid liverworts (in particular, Ricciaceae) and generalist leafy liverworts, accounting for the comparatively high phylogenetic diversity, but low taxonomic diversity values in desertic areas of sub-Saharan Africa. In contrast, leafy liverworts prevail in extremely humid environments. The dominance of some hyperdiverse families, such as the Lejeuneaceae, in tropical rainforests leads to high levels of taxonomic diversity but low levels of phylogenetic diversity.

Most interestingly, the diversity of higher-level lineages towards the deepest phylogenetic levels (200 Myr and older) increased with latitude. This inverted LDG is reminiscent of the pattern observed today at the species level in temperate regions

TABLE 1. *Variation of the relationship between liverwort taxonomic richness and mean phylogenetic distance (a) and as a function of macroclimatic predictors (b) across 450 OGUs worldwide at increasing phylogenetic level. Time slice represents the phylogenetic level (in million years) at which the analysis was conducted.* b *and* W *are the standardized coefficient index (slope) and the summed Akaike information criterion (AIC) weights for each predictor across all possible spatial linear models, respectively.* $^{*}P < 0.05$, $^{**}P < 0.01$ *and* $^{***}P < 0.001$. *Abbreviations: MAP, mean annual precipitation; MAT, mean annual temperature; TV and PV, climate change velocity for mean annual temperature and annual precipitation, respectively, between the Last Glacial Maximum and the present.*

Time slice	0		25		50		75		100		125		150		175		200	
	b	W	b	W	b	W	b	W	b	W	b	W	b	W	b	W	b	W
(a)																		
MAT	–	0.38	-0.15^{*}	0.81	-0.19^{**}	0.95	-0.24^{***}	0.99	-0.28^{***}	1.00	-0.35^{***}	1.00	-0.34^{***}	1.00	-0.44^{***}	1.00	-0.44^{***}	1.00
MAP	0.40^{***}	1.00	0.44^{***}	1.00	0.43^{***}	1.00	0.42^{***}	1.00	0.41^{***}	1.00	0.41^{***}	1.00	0.42^{***}	1.00	0.38^{***}	1.00	0.37^{***}	1.00
TV	–	0.48	–	0.33	–	0.29	–	0.30	–	0.35	–	0.42	0.12	0.49	–	0.40	0.17^{*}	0.65
PV	-0.12^{*}	0.64	-0.15^{**}	0.86	-0.16^{**}	0.92	-0.15^{**}	0.93	-0.15^{**}	0.92	-0.14^{**}	0.92	-0.19^{**}	0.92	–	0.56	-0.16^{*}	0.73
r^2	0.29		0.31		0.31		0.30		0.32		0.34		0.36		0.36		0.35	
(b)																		
MAT	–	0.39	–	0.43	–	0.31	–	0.31	–	0.40	–	0.38	–	0.29	–	0.27	–	0.42
MAP	−0.12	0.70	-0.14^{*}	0.58	-0.18^{**}	1.00	-0.16^{**}	0.96	-0.22^{***}	1.00	-0.27^{***}	1.00	-0.22^{***}	0.99	-0.22^{***}	0.99	−0.09	0.60
TV	0.20^{*}	0.78	0.17^{*}	0.64	0.13	0.52	0.14	0.63	0.12	0.55	0.11	0.57	0.17^{*}	0.80	–	0.33	0.13	0.54
PV	0.17^{*}	0.80	-0.17^{*}	0.76	-0.17^{*}	0.80	-0.19^{**}	0.87	-0.18^{**}	0.90	-0.24^{***}	0.99	-0.23^{***}	0.97	-0.12^{*}	0.80	-0.16^{*}	0.74
r^2	0.27		0.19		0.13		0.09		0.09		0.23		0.19		0.16		0.10	

Note: given that MAT was not included in the best-fitting model, there is no coefficient for it.

(southern South America, Rozzi *et al.*, 2008; and Europe, Mateo *et al.*, 2016) and, more globally, of the taxa that originated in cold conditions (Romdal *et al.*, 2013). Although reconstructions of ancestral distribution ranges at deep nodes in the liverwort phylogeny are challenged by recurrent long-distance dispersal events (Laenen *et al.*, 2018), it is tempting to see in the extra-tropical distributions of the centres of diversity of the basal lineages (e.g. Haplomitriaceae) an indication that such lineages originated in extra-tropical regions, where they would have become largely confined owing to macroclimatic niche conservatism. This is best exemplified by latitudinal gradients across South America, wherein a tropical-adapted 'modern' flora developed in the northern and central portions of the continent until at least mid-Tertiary, with few links to the flora of the southern part, which retained a large series of cool- and moisture-demanding Gondwanalandic elements (e.g. the families Haplomitriaceae and Blepharodophyllacaeae), largely shared with Australasia (Schuster, 1983). It is worth noting that although our analyses suggest that such taxa have been evolutionarily constrained by their macroclimatic niche, this does not necessarily mean that they persisted at locations where they are found today. Although this would be at odds with the high long-distance dispersal capacities of bryophytes, the distribution of continents, macroclimatic conditions and, most importantly, wind connectivity, which contributes more to bryophyte species distributions than geographical distance (Muñoz *et al.*, 2004), varied substantially in geological time, impacting dispersal.

The distribution of such Gondwanalandic taxa in southern South America accounts for the inverted gradient of phylogenetic diversity across South America. Thus, high species richness in the tropics is not associated with high phylogenetic diversity. This was also evidenced in woody spermatophytes, wherein phylogenetically distant gymnosperm species contributed substantially to the high phylogenetic diversity of high-latitude communities, to which the bulk of gymnosperm species would be confined owing to phylogenetic niche conservatism (Massante *et al.*, 2019).

The restriction of an inverse pattern of increasing MPD with latitude to the Americas raises the question of why the same pattern was not observed across Asia/Oceania, given that many Gondwanalandic taxa exhibit disjunct range disjunctions between southern South America and southern Australia and New Zealand (Schuster, 1983). In fact, comparatively high levels of MPD were observed in tropical Asia. This pattern corresponds to the occurrence of a series of isolated taxa of Gondwanalandic origin, such as the monogeneric, isolated family Delavayellaceae, which infused into the tropics via Indian plate migration and subsequently diversified following the elevation of the Himalaya (Schuster, 1983).

CONCLUSION

Liverworts exhibit striking variations of diversity through a phylogenetic time scale, highlighting how a deconstructive macroecological approach across phylogenetic levels allows for a better understanding of the accumulation of biodiversity through time. These changes highlight the fact that, even in organisms with high long-distance capacities, such as liverworts, changes in large-scale distribution patterns across phylogenetic levels, shaped by macroclimatic niche conservatism, are compatible with historical events associated with major diversification or extinction periods (Vanderpoorten *et al.*, 2010). Most importantly, they suggest that although the latitudinal diversity gradient can vary among taxa (Cerezer *et al.*, 2022), it can also vary substantially within the same taxon depending on the phylogenetic level investigated.

SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consist of the following.

Table S1: numbers of operational taxonomic units in the phylogenetic tree of liverworts sampled at genus level from Laenen *et al.* (2014) sliced at 25 Myr intervals. Table S2: model outputs of top three prediction models for mean phylogenetic distance (MPD) and species richness (SR). Abbreviations: AIC, Akaike's information criterion; Wr, Akaike weight. Figure S1: map of the phylogenetic diversity [measured as the mean phylogenetic distance (MPD) among species] across 450 operational geographical units in liverworts. Figure S2: phylogenetic structure, as expressed by mean phylogenetic distance (MPD), of liverwort communities per operational geographical unit, along a latitudinal gradient. Figure S3: variation of the slope and r^2 of the relationship between liverwort taxonomic richness (A) and MPD (B) per operational geographical unit and latitude (as an absolute value) through a phylogenetic time scale based on the original genus-level phylogeny of Laenen *et al.* (2014).

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AUTHOR CONTRIBUTIONS

Jian Wang: Conceptualization (lead); Data curation (lead); Investigation (lead); Funding acquisition (lead); Methodology (supporting); Project administration (lead); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). Zun Dai: Formal analysis (lead); Methodology (supporting); Visualization (lead); Writing – original draft (supporting); Writing – review and editing (supporting). Thibault Kasprzyk: Formal analysis (supporting); Visualization (supporting). Xue Yao: Data curation (equal); Writing – review and editing (supporting). Anders Hagborg: Data curation (supporting). Lars Söderström: Data curation (supporting). Jian Zhang: Conceptualization (lead); Methodology (lead); Writing – original draft (equal); Writing – review and editing (supporting). Alain Vanderpoorten: Conceptualization (lead); Methodology (supporting); Writing – original draft (lead); Writing – review and editing (lead). Flavien Collart: Data curation (supporting); Formal analysis (equal); Visualization (equal).

CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY

Liverwort species distribution data used in this study are available from the Figshare repository at https://doi.org/10.6084/m9.figshare.22587199. Molecular data sets and phylogenetic trees can be obtained from (http://purl.org/phylo/treebase/phylows/study/TB2:S15950?x-access-code=98d94511d8c016de8eae6f21c851826e&format=html). Climate data used in this study are available in the CHELSA climate database (https://chelsa-climate.org/bioclim). Other original data included in the article and the Supplementary Data.

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ORIGINAL ARTICLE

Spatial patterns and climatic drivers of phylogenetic structure of regional liverwort assemblages in China

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- **Background and Aims** Latitudinal diversity gradients have been intimately linked to the tropical niche conservatism hypothesis, which posits that there has been a strong filter due to the challenges faced by ancestral tropical lineages to adapt to low temperatures and colonize extra-tropical regions. In liverworts, species richness is higher towards the tropics, but the centres of diversity of the basal lineages are distributed across extra-tropical regions, pointing to the colonization of tropical regions by phylogenetically clustered assemblages of species of temperate origin. Here, we test this hypothesis through analyses of the relationship between macroclimatic variation and phylogenetic diversity in Chinese liverworts.
- **Methods** Phylogenetic diversity metrics and their standardized effect sizes for liverworts in each of the 28 regional floras at the province level in China were related to latitude and six climate variables using regression analysis. We conducted variation partitioning analyses to determine the relative importance of each group of climatic variables.
- **Key Results** We find that the number of species decreases with latitude, whereas phylogenetic diversity shows the reverse pattern, and that phylogenetic diversity is more strongly correlated with temperature-related variables compared with precipitation-related variables.
- **Conclusions** We interpret the opposite patterns observed in phylogenetic diversity and species richness in terms of a more recent origin of tropical diversity coupled with higher extinctions in temperate regions.

Key words: Bryophytes, environmental gradient, latitudinal diversity gradient, liverworts, phylogenetic diversity, phylogenetic niche conservatism, phylogenetic relatedness.

INTRODUCTION

The composition of species in biological assemblages in any area is determined by the interplay of evolutionary and ecological processes (Ricklefs, 1987; Rosenzweig, 1995). Environmental filtering is thought to play an important role in determining the composition of species in an area at a broad spatial scale, and species that are not able to survive and reproduce in the environment of the area are excluded (Qian *et al.*, 2019). Biological interactions such as competition among species, in contrast, play little role at broad spatial scales, particularly in plants (Qian and Sandel, 2022). It is generally thought that the tendency of species to retain the ecological distributions of their ancestors (i.e. phylogenetic niche conservatism) determines which species in a regional species pool can occur in a particular environmental condition (Wiens and Donoghue, 2004), and that species that have common evolutionary history tend to tolerate similar conditions of environment. Because many extant lineages evolved and diversified during geological times when the Earth's climate was wet and warm (Wiens and Donoghue, 2004), traits associated with warm and wet climates are often considered ancestral for those clades, whereas traits that confer drought or cold tolerance evolve relatively slowly (Wiens and Donoghue, 2004). Accordingly, many clades are still constrained to humid tropical climates, and few clades have made evolutionary breakthroughs into very cold and arid conditions (Wiens and Donoghue, 2004; Kellermann *et al.*, 2012; Zanne *et al.*, 2014). As a result of this phylogenetic niche conservatism, biological assemblages in areas with colder climates tend to possess more closely related species and to have lower species richness, whereas assemblages in tropical regions are more phylogenetically diverse, which is often termed the 'tropical niche conservatism' hypothesis (Wiens and Donoghue, 2004; Qian *et al.*, 2019).

The hypothesis of tropical niche conservatism has gained support from many empirical studies focusing on taxa that evolved in tropical climate conditions. For example, the fossil record suggests that angiosperms evolved in tropical or tropical-like climates during the Cretaceous and Cenozoic (Takhtajan, 1969; Wolfe, 1997; Berendse and Scheffer, 2009). Regional assemblages of angiosperms tend to have stronger phylogenetic relatedness in areas of colder climates (e.g. Lu *et al.*, 2018). The same pattern has been observed in polypod ferns, which are the largest clade of ferns (including 80 % of all extant fern species worldwide) and diversified more or less in parallel with the angiosperms (Qian *et al.*, 2021).

Liverworts, including ~7300 extant species worldwide (Söderström *et al.*, 2016), originated ~500 million years ago (Ma) (Morris *et al.*, 2018), during a greenhouse (warm) period (635–450 Ma). However, because liverworts have experienced several cycles of greenhouse and icehouse periods during the past ~500 million years (Voosen, 2019), tropical climates may not necessarily be ancestral niches for the extant clades of liverworts. Considering that mosses, which are sister to liverworts, likely diversified in temperate climate conditions (Shaw *et al.*, 2005; Wu *et al.*, 2022), one might propose that liverworts also likely originated under these conditions. Indeed, the first significant burst in liverwort diversification has been dated in a globally cool period at ~150–200 Ma (Laenen *et al.*, 2014). Furthermore, although their species richness increases towards the tropics, very much like the patterns reported in angiosperms, the diversity centres of the basal lineages of liverworts are not located in tropical regions (Wang *et al.*, 2017; Qian *et al.*, 2023*a*), suggesting that temperate, rather than tropical, climate might be an ancestral niche in liverworts. Accordingly, one would expect that phylogenetic relatedness in liverworts is higher in regions with high temperatures than those with low temperatures.

Previous studies have demonstrated that temperature and precipitation, and variables related to them, are among the major climatic factors influencing species richness and metrics of phylogenetic structure at regional scales, and that variables related to temperature play a greater role than variables related to precipitation in angiosperms and ferns (e.g. Qian *et al.*, 2019, 2023*b*). Because liverworts are poikilohydric (Patiño and Vanderpoorten, 2018), one might hypothesize that variables related to precipitation are more important drivers of phylogenetic diversity and relatedness in liverworts, compared with variables related to temperature. Furthermore, the ecological impacts of climatic factors are generally not determined by the commonly used long-term means, but rather by climatic variability and climatic extremes, where occasional strong frost or drought events may be crucial in limiting the distributions of species (Qian *et al.*, 2019, 2022*b*). Physiologically, climatic seasonality is also challenging for plant species, since it requires adaptations to a broad range of different climate conditions (Qian *et al.*, 2022*b*). However, the relative influences of climatic seasonality versus climatic extremes on biological assembly remain poorly explored (Qian *et al.*, 2021, 2023*b*).

Here, we assess the relationships of metrics of phylogenetic structure (phylogenetic diversity and phylogenetic relatedness) with macroclimatic conditions in province-level floras of liverworts in China. We specifically test the following hypotheses: (1) assemblages from extra-tropical regions have higher phylogenetic diversity due to the contribution of the most anciently diverging lineages, and phylogenetic relatedness increases with increasing temperature due to phylogenetic niche conservatism, assuming that liverworts evolved and diversified in temperate climate conditions, as noted above; (2) climatic variables related to precipitation are more important than climatic variables related to temperature in driving phylogenetic structure in liverworts, partly because liverworts are poikilohydric and partly, as shown in Qian and Chen (2016), because liverwort species richness in China is more strongly associated with annual precipitation compared with mean annual temperature; and (3) climate extreme variables are more important, compared with climate seasonality variables, in driving phylogenetic structure in liverworts, because this pattern has been frequently observed for angiosperms in China and across the world (e.g. Qian *et al.*, 2019, 2024).

We focus on liverworts in China for several reasons. First, a well-resolved phylogeny including nearly all liverwort families and the vast majority of liverwort genera in China is available (Laenen *et al.*, 2014). Second, the species composition of regional liverwort floras has been well documented in China (Qian and Chen, 2016; Jia, 2018; Qian *et al.*, 2023*a*). Third, China covers a great geographic extent with relatively long climatic gradients, which facilitate tests of climate-based hypotheses. Fourth, the phylogenetic structure of ferns, gymnosperms and angiosperms in regional and province-level floras in China have already been investigated (Lu *et al.*, 2018; Qian *et al.*, 2019, 2021), allowing comparison of patterns of phylogenetic structure of liverworts with those observed in other plant groups within the same geographic and ecological contexts.

MATERIALS AND METHODS

Liverwort floras

China was divided into 28 province-level regions (as shown in Supplementary Data Fig. S1), an approach used in previous studies (e.g. Qian and Chen, 2016; Qian *et al.*, 2022*a*). We used the data in Catalog of Life China (https://data.casearth.cn/thematic/Catalogue_of_Life_China), Collart *et al.* (2021), and additional sources (e.g. Jia and He, 2013; Qian and Chen, 2016; Jia, 2018) to generate species lists of native liverworts for each of the regions. We used the package U.Taxonstand (Zhang and Qian, 2023) to standardize liverwort names according to Bryophyte Nomenclator (Brinda and Atwood, 2023). We combined infraspecific taxa (e.g. subspecies) with their parental species. A total of 1125 species in 172 genera and 64 families of liverworts were included in the present study (Fig. 1).

Reconstruction of phylogenetic tree

We used the chronogram of Laenen *et al.* (2014), which was built based on the lower bound for the root node set at 475 Ma (Edwards *et al.*, 2014), as a backbone to generate a phylogenetic tree for the liverwort species included in this study. Of the

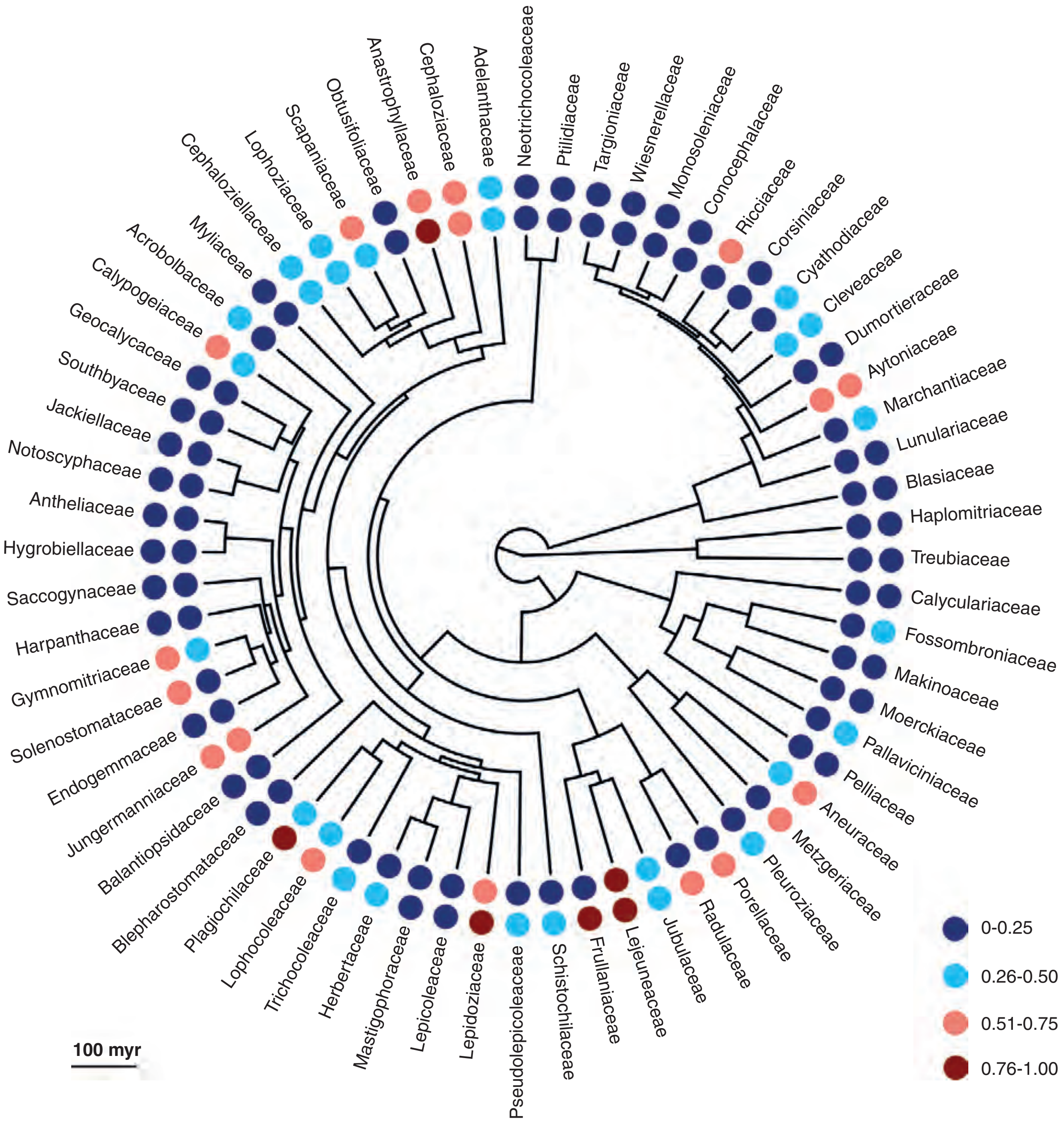

Fig. 1. Distribution of genus (inner circle) and species (outer circle) richness of Chinese liverworts among families. Genus richness ranged from 1 to 28, and species richness ranged from 1 to 253. Richness of genera or species in a family was first $\log_{10}$-transformed, and then standardized to vary from 0 to 1 among the families.

172 liverwort genera in our study, 150 (87 %) were present in the phylogeny backbone. The 22 remaining genera were grafted onto the phylogeny based on most recent evidence about their phylogenetic position (Supplementary Data Table S1). Since the backbone phylogeny of Laenen *et al.* (2014) included one species per genus, we used the functions build.nodes.1 and Scenario 3 in the package U.PhyloMaker (Jin and Qian, 2023) to graft all congeneric species in our dataset onto the genus-level phylogeny backbone. Lehtonen *et al.* (2015) and Qian and Jin (2021) have shown that values of a phylogenetic metric derived from phylogenetic trees resolved fully at the species level are nearly perfectly correlated to those derived from a phylogenetic tree resolved only at the genus level, so that the results of our study based on the phylogenetic tree derived from a genus-level phylogeny backbone should be robust. The phylogenetic tree was pruned to only retain the tips with species present in China.

Phylogenetic metrics

We used three metrics of phylogenetic structure in this study: mean pairwise distance (MPD), the standardized effect size of phylogenetic diversity (PD_{ses}) and the standardized effect size of mean pairwise distance (MPD_{ses}), which reflect different evolutionary depths of phylogenetic structure (Mazel *et al.*, 2016). MPD is the mean phylogenetic distance (i.e. branch length) among all pairs of species within an assemblage (Webb, 2000). MPD_{ses} measures the phylogenetic relatedness of the more basal structure of the phylogenetic tree, whereas PD_{ses} reflects the phylogenetic relatedness of the more terminal structure of the phylogenetic tree (Mazel *et al.*, 2016). In both PD_{ses} and MPD_{ses}, a positive value reflects relative phylogenetic overdispersion of species whereas a negative value reflects relative phylogenetic clustering of species. MPD is mathematically independent of species richness (Miller *et al.*, 2017), and MPD_{ses} and PD_{ses} both are richness-standardized indices (Cadotte *et al.*, 2010; Weigelt *et al.*, 2015). We used the package PhyloMeasures (Tsirogiannis and Sandel, 2016) to calculate these phylogenetic metrics.

Data for climatic variables

Climatic variables identified to shape plant and animal distributions included minimum temperature of the coldest month (T_{min}), mean annual temperature (T_{mean}), temperature seasonality (T_{seas}), precipitation during the driest month (P_{min}), annual precipitation (P_{mean}), and precipitation seasonality (P_{seas}) (e.g. Kooyman *et al.*, 2012; Weigelt *et al.*, 2015; Qian *et al.*, 2019). We related the phylogenetic metrics to these six climatic variables. We obtained data for these climatic variables from the CHELSA database (located at https://chelsa-climate.org/bioclim) (Karger *et al.*, 2017). We calculated the mean value for each of the climate variables within each province-level region using data at the resolution of 30 arc-seconds.

Statistical analysis

We investigated the relationships of MPD, PD_{ses} and MPD_{ses} with the six variables of climate using spatial simultaneous autoregressive error models (Kissling and Carl, 2017) as implemented in Spatial Analysis in Macroecology (Rangel *et al.*, 2010; www.ecoevol.ufg.br/sam/). We also assessed their relationships with latitude, because many previous studies on phylogenetic relatedness included latitude, and therefore including it in the present study eases comparisons between the results of this and other studies. We regressed each of MPD, PD_{ses} and MPD_{ses} on latitude and each of the six climatic variables; we assessed the relationship between pairwise variables according to standardized coefficients derived from regressions. We conducted two sets of variation partitioning analyses for each phylogenetic metric to determine the relative importance of each group of climatic variables to the phylogenetic metric. One set of analyses determined whether variables related to temperature (T_{min}, T_{mean} and T_{seas}) or variables related to precipitation (P_{min}, P_{mean} and P_{seas}) are more important in shaping the phylogenetic metric, and the other set of analyses determined whether variables representing climate extreme (T_{min} and P_{min}) or variables representing climate seasonality (T_{seas} and P_{seas}) are more important in shaping the phylogenetic metric.

RESULTS

Species richness and species density (i.e. species richness divided by log-transformed area) of liverworts in regional floras decreased with increasing latitude in China (Fig. 2). In contrast, all the three phylogenetic metrics examined in this study

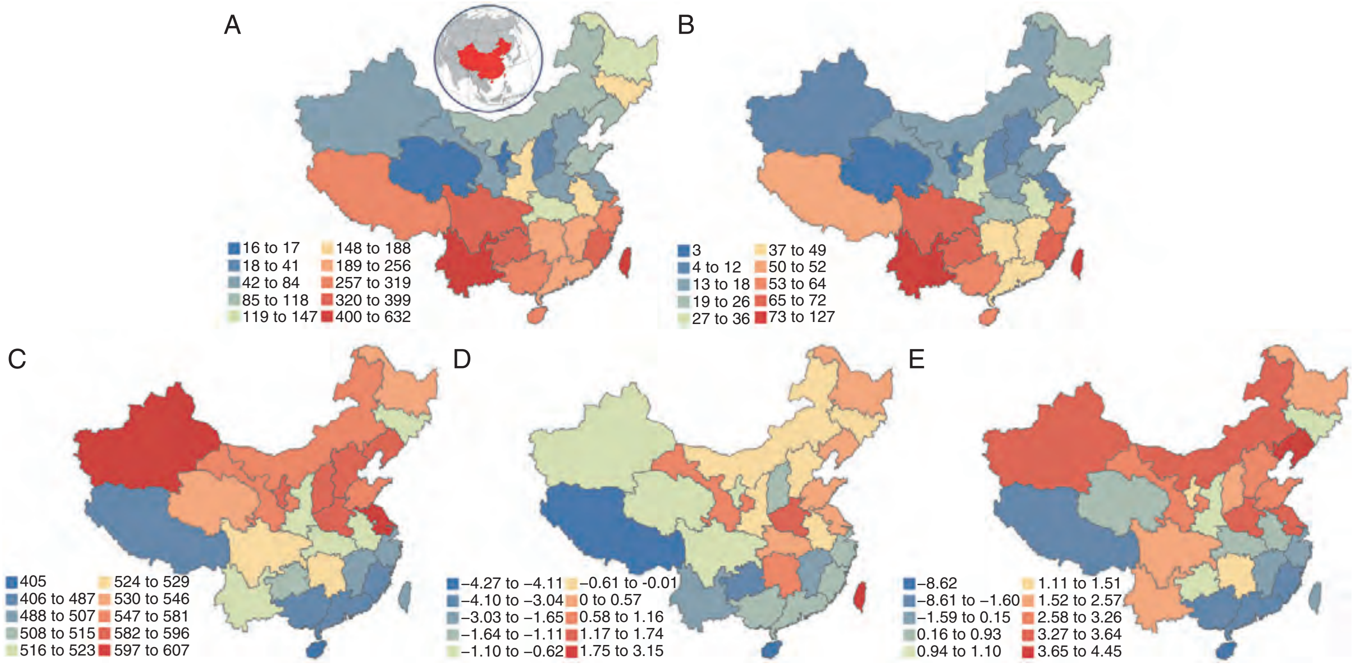

FIG. 2. Geographic patterns of (A) species richness, (B) species density (i.e. species richness divided by $\log_{10}$-transformed area in square kilometres), (C) mean pairwise distance (MPD), (D) standardized effect size of phylogenetic diversity (PD_{ses}), and (E) standardized effect size of mean pairwise distance (MPD_{ses}) for regional liverwort floras in China. Chinese islands that were not included in this study are not shown.

(i.e. MPD, PD_{ses} and MPD_{ses}) increased with increasing latitude (Figs 2 and 3).

Patterns of the relationships of MPD with climatic variables were similar to those for MPD_{ses} (Fig. 4). Specifically, MPD and MPD_{ses} increased with increasing P_{seas} and T_{seas}, and decreased with increasing T_{min}, T_{mean}, P_{mean}, and P_{min}. Nine of the 12 relationships were significant ($P < 0.05$; Fig. 4). However, none of the relationships of PD_{ses} with the climatic variables were significant ($P > 0.05$ in all cases; Fig. 4).

The six climatic variables together explained 73, 33 and 60 % of the variation in MPD, PD_{ses} and MPD_{ses}, respectively. Temperature-related variables explained more variation in MPD and MPD_{ses} but less variation in PD_{ses}, compared with precipitation-related variables (Fig. 5A). Similarly, climate extreme variables explained more variation in MPD and MPD_{ses} but less variation in PD_{ses}, compared with climate seasonality variables (Fig. 5B).

DISCUSSION

This study shows that phylogenetic diversity of liverwort communities in China increases from the tropics northwards and that phylogenetic relatedness is higher in regions with wetter and warmer climates. These patterns are contrary to the hypothesis of tropical niche conservatism but consistent with the notion that liverworts likely evolved and first diversified in temperate climates, as in mosses (Shaw *et al.*, 2005; Wu *et al.*, 2022). This finding is consistent with the timing of the first

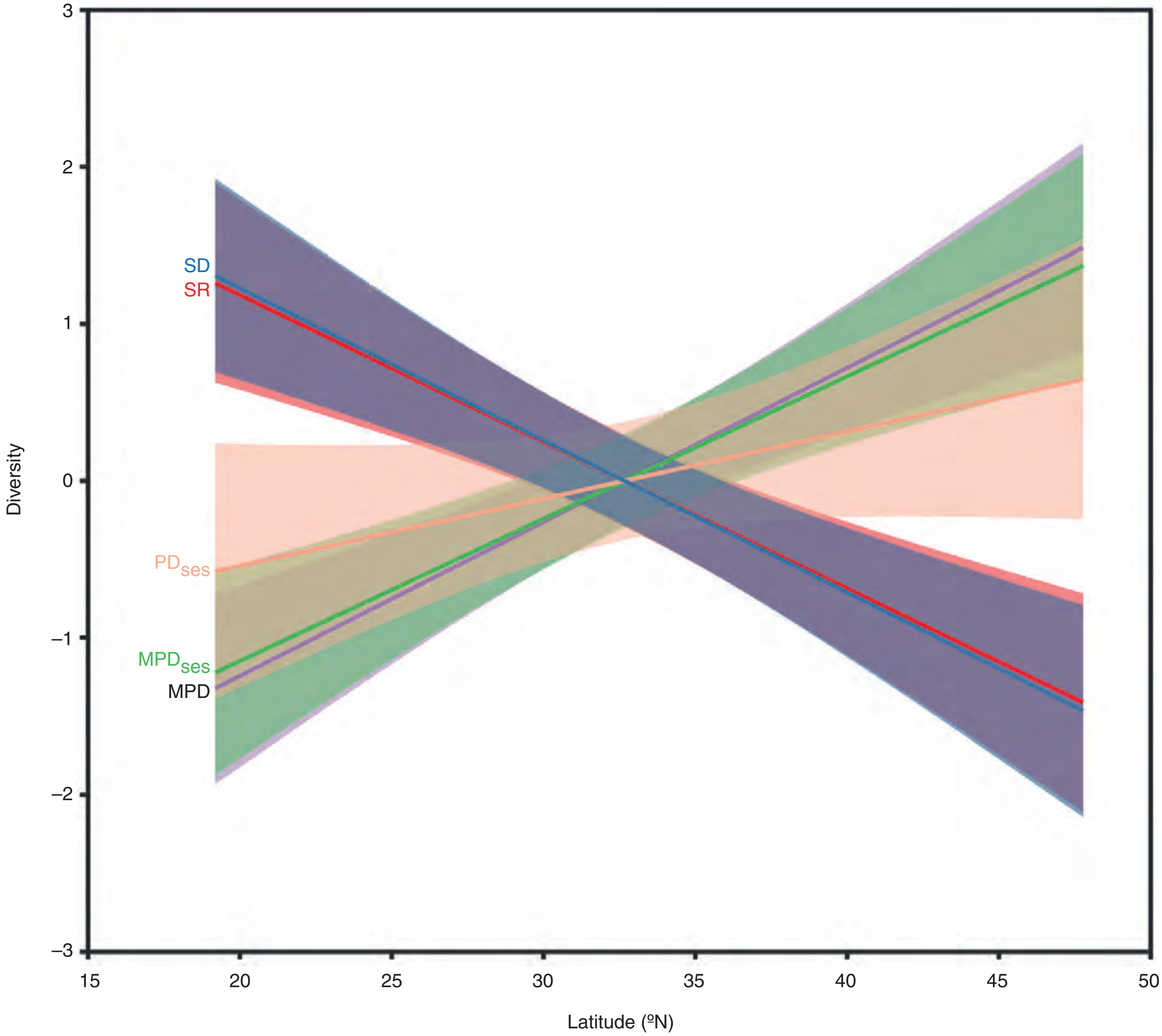

Fig. 3. Relationships between latitude and metrics of diversity (SR, species richness; SD, species density, which is species richness divided by log-transformed area; MPD, mean pairwise distance; PD_{ses}, standardized effect size of phylogenetic diversity; and MPD_{ses}, standardized effect size of mean pairwise distance). Each of the five metrics of diversity was standardized to zero mean and unit variance. Lines indicate best-fit linear regressions with 95 % confidence intervals. Four of the five relationships were significant ($P < 0.001$) and the other (PD_{ses}) was marginally significant ($P = 0.089$).

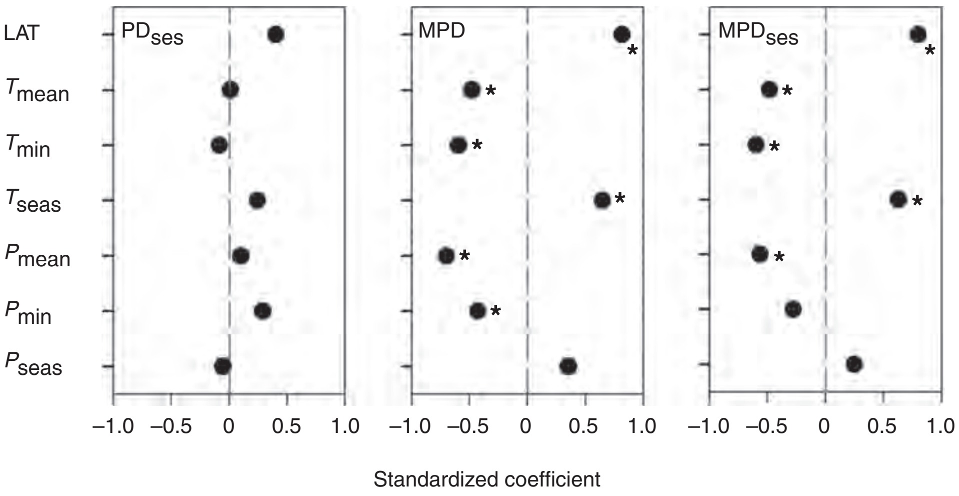

FIG. 4. Relationships (standardized coefficient) between each of the three phylogenetic metrics for regional liverwort floras in China and each of the explanatory variables. Phylogenetic metrics are mean pairwise distance (MPD), standardized effect size of phylogenetic diversity (PD_{ses}), and standardized effect size of mean pairwise distance (MPD_{ses}). Explanatory variables are latitude (LAT), mean annual temperature (T_{mean}), minimum temperature of the coldest month (T_{min}), temperature seasonality (T_{seas}), annual precipitation (P_{mean}), precipitation during the driest month (P_{min}) and precipitation seasonality (P_{seas}). $^*P < 0.05$.

significant burst in liverwort diversification rates ~150–200 Ma (Laenen *et al.*, 2014), a period during which the global climate was much colder than the one that prevailed ~100 Ma (Voosen, 2019), when ferns and angiosperms underwent their major radiation burst (Qian *et al.*, 2019, 2021, 2023*b*). The patterns for liverworts demonstrated in this study are in sharp contrast with those patterns reported in angiosperms and polypod ferns in China and elsewhere, which conform to the expectations of the hypothesis of tropical niche conservatism (Qian and Sandel, 2017; Lu *et al.*, 2018; Qian *et al.*, 2019, 2021, 2023*b*).

As we mentioned above, liverworts originated during a greenhouse period. One might ask why the relationship of phylogenetic structure with temperature in liverworts is contrary to the hypothesis of tropical niche conservatism, which was proposed for clades originating and diversifying in warm climates. One possible answer to this question might be that although a greenhouse period was generally warm worldwide, there were places with temperate climate conditions (Voosen, 2019), in which some clades might originate. Furthermore, even if liverworts indeed originated under tropical climatic conditions, because they experienced three icehouse periods through their evolution, some of the major extant liverwort clades might have originated under temperate climates during these icehouse periods. Because the fossil record in liverworts is scarce, it is not possible to test these hypotheses at the present time.

It appears to be at odds that in liverworts, phylogenetic diversity is highest and phylogenetic relatedness is lowest at temperate latitudes, as observed in this study, whereas species richness exhibits a typical increase from high to low latitudes (Wang *et al.*, 2017), which is a typical pattern for most groups of organisms (Rosenzweig, 1995). Two processes may help reconcile apparently conflicting patterns of a higher phylogenetic diversity in temperate regions and higher clustering in the subtropics and tropics, but higher species richness of liverwort communities in the subtropics and tropics.

First, the pattern of the increase in species richness but decrease in phylogenetic diversity towards the tropics could be explained in terms of a more recent origin of tropical diversity coupled with higher extinctions in temperate regions. In fact, tropical liverwort genera show significantly higher net diversification rates compared with extra-tropical genera; this suggests that the latitudinal diversity gradient results from higher extinction rates in extra-tropical lineages and/or higher speciation rates in the tropics (Laenen *et al.*, 2018). In fact, the same pattern has been found along tropical elevational gradients, where phylogenetic diversity of liverworts peaks in cool and moist cloud forests at mid-elevations, whereas tip diversification rates are highest in the tropical lowlands (K. Maul, M. Kessler *et al.*, unpubl. data). The increase in phylogenetic relatedness and decrease in phylogenetic diversity among liverwort species towards tropical regions is reminiscent of similar patterns reported in pteridophytes, wherein a few ancient, phylogenetically isolated clades (e.g. Equisetaceae, Osmundaceae and Ophioglossaceae), which have a rich fossil record revealing substantial past diversity but are represented today by a few, species-poor genera, are well represented in regions of temperate climate but either absent or species-poor in regions of tropical climate (Qian *et al.*, 2021).

The hypothesis that tropical liverworts experienced bursts of diversification is compatible with the fact that the most species-rich families of liverworts, such as the Frullaniaceae and Lejeuneaceae, radiated concomitantly with the development of megathermal angiosperm forests, offering a sudden increase in habitat complexity and availability in these mostly epiphytic families during the late Cretaceous (Feldberg *et al.*, 2014). The analyses of our study on basal- versus tip-weighted metrics of phylogenetic relatedness reveal, however, that the diversification of tropical liverworts has been relatively more ancient than that in angiosperms. In fact, while a significant correlation emerged between basal-weighted metrics of phylogenetic relatedness (i.e. MPD_{ses}) and macroclimatic conditions, this was not the case with tip-weighted metrics of phylogenetic relatedness (i.e. PD_{ses}). In angiosperms, conversely, the relationships between tip-weighted metrics of phylogenetic

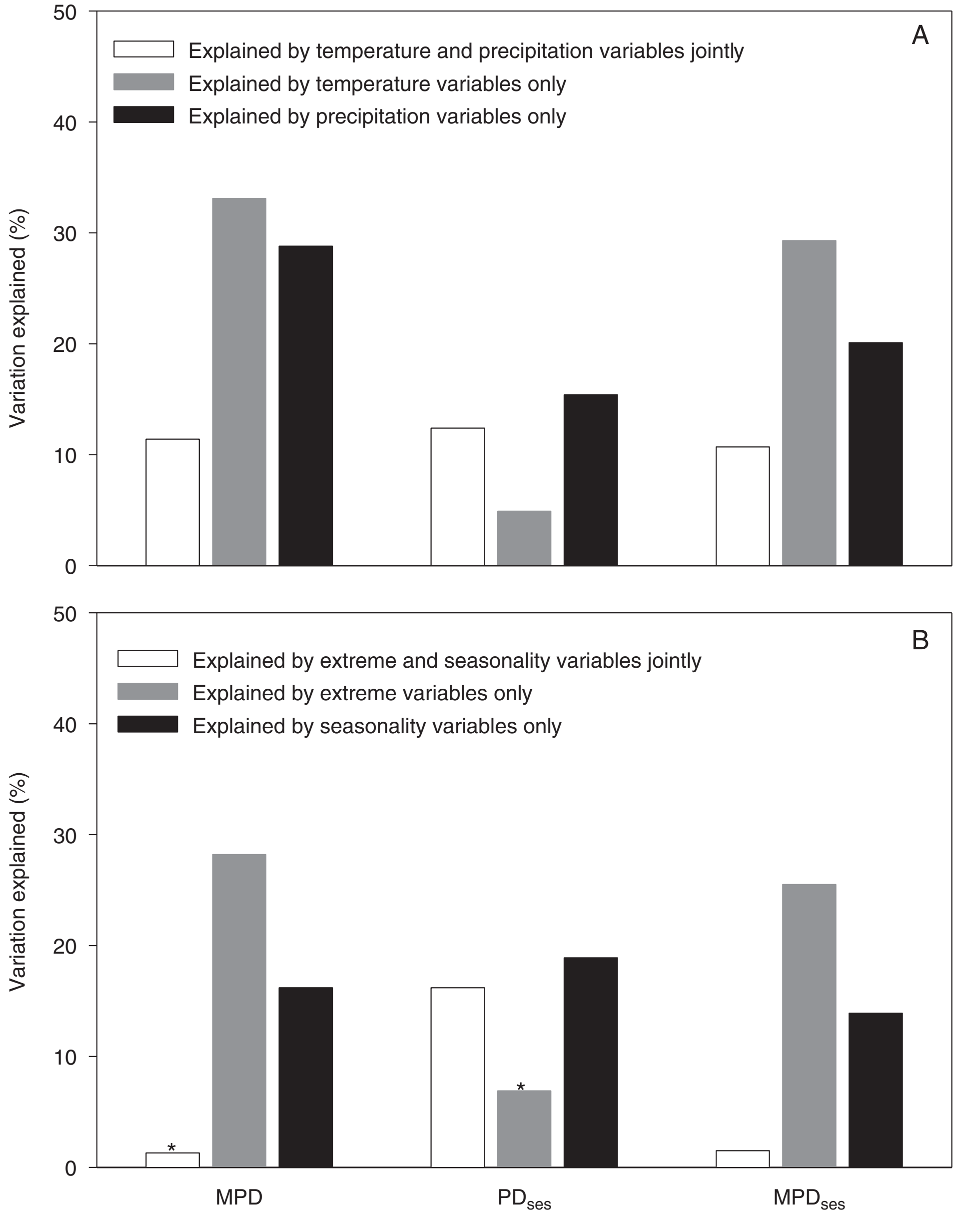

Fig. 5. Variation in each of the three phylogenetic metrics for regional liverwort floras in China explained (A) by temperature- versus precipitation-related variables, and (B) by climate extreme versus seasonality variables. The phylogenetic metrics are mean pairwise distance (MPD), standardized effect size of phylogenetic diversity (PD_{ses}) and standardized effect size of mean pairwise distance (MPD_{ses}). Temperature-related variables included T_{mean}, T_{min} and T_{seas}, and precipitation-related variables included P_{mean}, P_{min} and P_{seas}. Climate extreme variables included T_{min} and P_{min}, and climate seasonality variables included T_{seas} and P_{seas}. An asterisk indicates a negative value resulting from the variation partition (for statistical interpretation of a negative value, see Legendre and Legendre, 2012).

relatedness and climatic variation in China are strong and significant (Lu *et al.*, 2018; Qian *et al.*, 2019). This discrepancy suggests that older branches of the liverwort phylogeny contribute more strongly to the correlation between phylogenetic diversity and macroclimatic variation compared with younger branches in the angiosperm phylogeny, emphasizing differences in the timing of diversification of these two groups as a response to macroclimatic variation.

Second, our analyses suggest that the differences in liverwort species richness along the latitudinal gradient caused by more recent diversifications in tropical areas and extinctions in extra-tropical ones are maintained by macroclimatic niche conservatism. The macroclimatic control of the spatial variation in phylogenetic diversity evidences macroclimatic niche conservatism, both from temperate to tropical regions and vice versa, and serves to explain why diversity patterns in liverworts have not been balanced during the evolutionary history of the group, despite the high capacities of long-distance dispersal of its species. The results of this study are thus in line with mounting evidence for the role of macroclimatic conservatism as an important driver of present-day distribution patterns of plant diversity (Crisp *et al.*, 2009; Segovia *et al.*, 2020).

Finally, we found that, among the macroclimatic drivers of phylogenetic diversity, climatic variables related to temperature explained more variation than did climatic variables related to precipitation, and the climate extreme variables explained more variation compared with the climate seasonality variables. A key role for temperature- rather than precipitation-related variables in driving large-scale patterns of phylogenetic community structure has also been found for ferns and angiosperms (Qian *et al.*, 2021, 2023b). Moles *et al.* (2014) and Lancaster and Humphreys (2020) also found that temperature is a more important driver of the variation in distribution and tolerance for vascular plants compared with precipitation. We suggest that while precipitation-related variables are indeed the most important driving force of current patterns of species richness and community composition of liverworts, phylogenetic community structure was shaped during major historical climate change events at geological time scales, during which dramatic temperature changes resulted in massive extinctions while acting as a severe filter for colonization under new climatic conditions, resulting in the strongly clustered phylogenetic patterns reported here. Our initial expectation was that the poikilohydric nature of liverworts would relate their diversity to climatic parameters emphasizing water availability, but in fact poikilohydry is also physiologically favourable under cold conditions, since dehydrated plant tissue, in which no ice crystals can form, is less damaged by frost (Dilks and Proctor, 1975; van Zuijlen *et al.*, 2024).

Concluding, our study shows that in addition to the well-documented pattern of land plants originating and diversifying in high-temperature tropical or tropical-like climates during the Cretaceous and Cenozoic (Takhtajan, 1969; Wolfe, 1997; Berendse and Scheffer, 2009), for some lineages of land plants that diversified earlier during globally cooler temperatures, such as liverworts and some early-diverging fern families, a hypothesis of low-temperature niche conservatism may be more appropriate. Other plant lineages for which this hypothesis may be tested include the remaining major bryophyte groups (mosses, hornworts) and the three lycophyte families (Isoetaceae, Lycopodiaceae, Selaginellaceae).

SUPPLEMENTARY DATA

Supplementary data are available at Annals of Botany online and consist of the following. Figure S1: map showing 28 province-level regions in China. Table S1: genera that were included in this study but absent from Laenen *et al.* (2014).

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY

Liverwort species distribution data are available at Catalog of Life China (http://www.sp2000.org.cn/CoLChina) and Liverwort species lists (https://doi.org/10.6084/m9.figshare.22587199). Climate data used in this study are available at the CHELSA climate database (https://chelsa-climate.org/bioclim). Data used to yield the results reported in this article are available at https://github.com/ISMRCC/liverwort-1.

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DISCUSSION

Plagiochila asplenioides (L.) Dumort. (swissbryophytes 49393)
habitus, plante humide © swissbryophytes / Ralf Schmiede
Deutschland, Landkreis Goslar, Herbier Ralf Schmiede
ventral

Barbilophozia hatcheri (A.Evans) Loeske
(swissbryophytes 34277)
habitus, plante humide © Michael Lüth
Schweden, Lappland

GENERAL DISCUSSION

Phylogenetic diversity metrics have been massively used to infer community assembly processes (Jia et al., 2022; Kluge & Kessler, 2011; Montaño-Centellas et al., 2020; Galvàn-Cisneros et al., 2023). However, the reliability of this "indirect approach" remained to be tested before its use in empirical settings. Indeed, while the performance of the metrics was already studied (Tucker et al., 2017), the impact of competing assembly processes, and the combination thereof, on the phylogenetic diversity of communities in a spatially-explicit context was still unclear. To address this question, I took advantage of a new simulator of community assembly we developed that allows the implementation of equalizing, stabilizing, and stochastic processes, and the combination thereof, in a contrasted landscape where individuals experience dispersal limitations. After checking that the simulated communities exhibited the expected properties in terms of species richness, abundance, turnover, and distribution, I determined the extent to which, and under which conditions, phylogenetic diversity can be used as a proxy for assembly mechanisms. I concluded this first part of the thesis by providing guidelines regarding which metrics to use, and in which conditions reliable conclusions can be drawn. I finally applied this approach to investigate the mechanisms underlaying the latitudinal diversity gradient in liverworts.

Descriptive features of the communities simulated under contrasting assembly processes.

Based on the protocol described in Chapter 1, different communities were simulated under contrasted assembly processes (equalizing, for an initial species pool comprised of species with either broad or narrow habitat preferences, stabilizing and stochastic), and the combination thereof, in a landscape comprised of a fragmented habitat within the matrix of a continuous habitat.

Species distributions in communities simulated under stochastic processes were patchy (Figure 4C), reflecting a spatial clustering associated with an isolation-by-distance pattern. Communities simulated under stochastic processes included on average 28 ± 2 species (26±0.8 and 30±0.7 species in core and border habitats, respectively) per plot, which was the highest species richness as compared to that of communities simulated under other processes (Figure 5A and B). A peak of species richness under stochastic processes was also reported by Overcast et al. (2021). This pattern, which contrasts with the notion that competition is important for maintenance of biodiversity (Tilman, 1994), could be explained here by the fact that, under stabilizing processes, a few species with specific, often extreme trait values, were most abundant, decreasing species richness. Communities simulated under stochastic processes were also characterized by a strong spatial turnover (mean total beta diversity βtot, as estimated by Sorensen index between samples= 0.81 ± 0.01) resulting from limited dispersal and high species richness.

In contrast, while all c. 800 species were equally likely to spread in the community under stochastic processes, a small proportion had adequate habitat adaptive traits to spread in one of the habitats under equalizing processes. As a result, specialist species were restricted to their preferred habitat, where the best adapted ones were dominant, although with a clearly patchy distribution reflecting dispersal limitations (Figure 4A). A similar pattern, with more 'fuzzy' species distributions, was observed in the case of generalist species due to the lower habitat specificity of the latter (Figure 4B). Species richness was therefore expectedly lower under equalizing processes (5.5 ± 3.5 and 17 ± 3 with specialist and generalist species respectively) than under stochastic processes. In the case of species with narrow habitat preferences, species turnover between habitat cores was very strong between the two habitat types (βtot = 0.95 ± 0.04), low within the continuous habitat (βtot = 0.23 ± 0.13) and moderate within the fragmented habitat (βtot = 0.79 ± 0.06). Similar patterns, but with lower turnover values, were observed in the case of species with broad habitat preferences.

Under stabilizing processes, a few species with specific, often extreme trait values exhibited the highest abundance levels, generating a trait-abundance pattern that departed from the balanced species abundances, regardless of trait values, under stochastic processes. Thus, only a few combinations of species showing very divergent competitive traits (Figure 6) were able to coexist, reducing species richness to an average of 8 ± 2 species per sample. Accordingly, a few dominant species were scattered across the landscape (Figure 4G), and there was nearly no species turnover (βtot = 0.07 ± 0.03) because the same combination(s) of locally coexisting divergent species were systematically observed. Species turnover between borders was smaller than between cores for corresponding pairs of habitats, and mixtures of processes led to species turnover patterns intermediate between those of the corresponding pure processes. Species abundance distribution according to these processes can be seen in Figure 4.

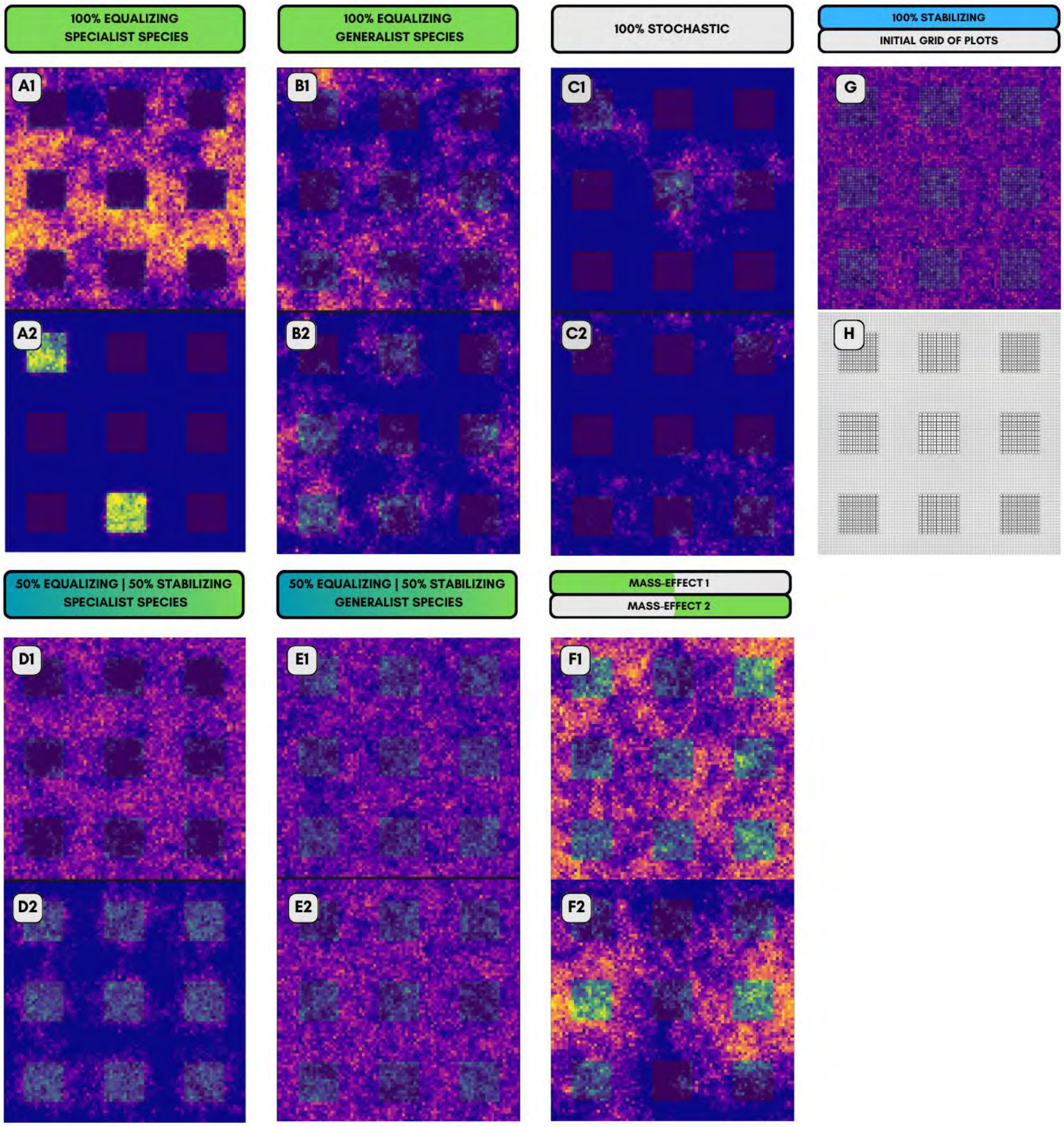


Figure 4: *Abundance of the most abundant species per pixel of 50 individuals in each of a fragmented and continuous habitat at the end of a process of community assembly under stochastic, stabilizing, and equalizing processes for generalist and specialist species, and mixed processes. Two mixed processes were implemented: processes involving 50% of stabilizing and 50% of equalizing processes across the landscape, both for generalist and specialist species on the one hand, and equalizing processes for specialist species in the fragmented habitat but stochastic processes in the continuous habitat (Mass-Effect 1) and vice-versa (Mass-Effect 2). When the most abundant species was the same in both habitats, only one heatmap is displayed. The abundance of the most abundant species ranges from 0 in dark blue to 50 in bright yellow.*

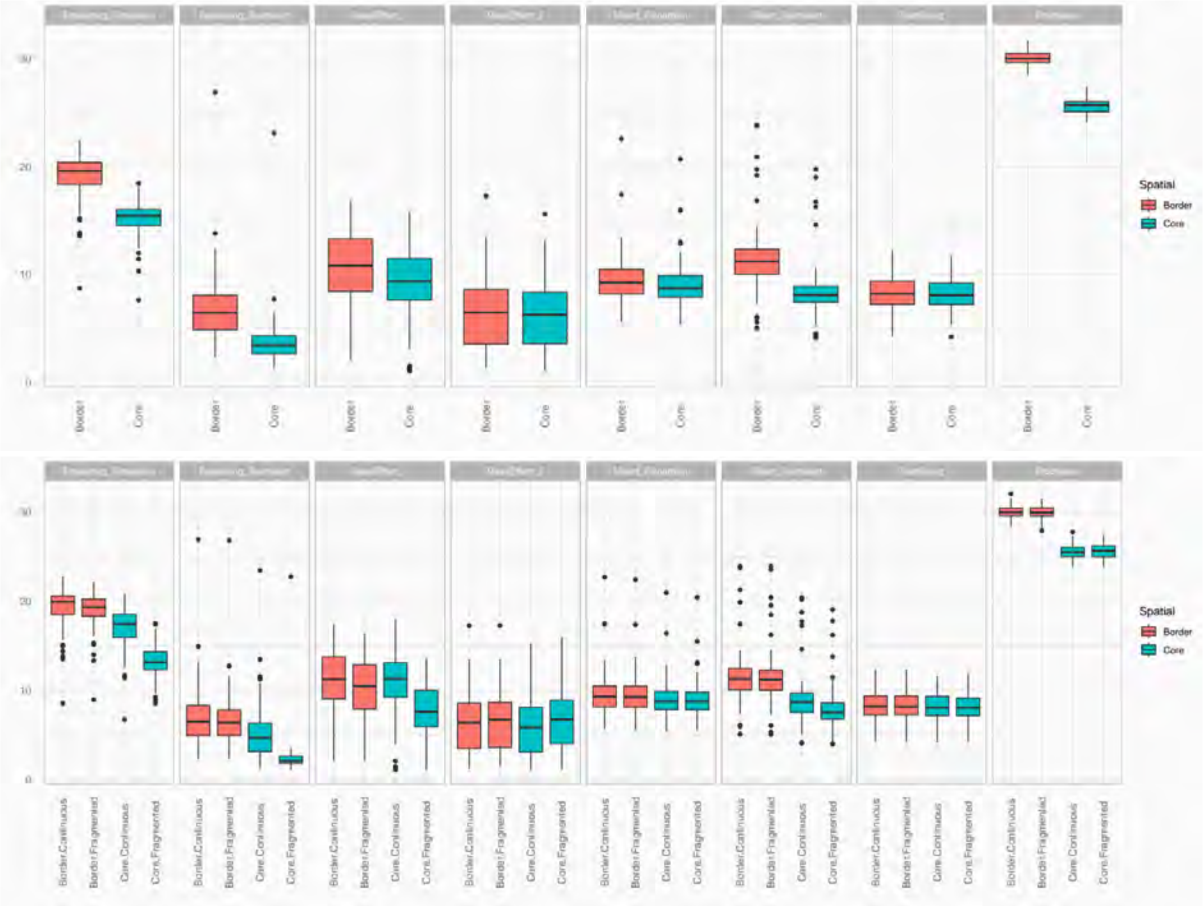


Figure 5: *Species richness per plot at the end of a process of community assembly under competing assembly processes in a gridded landscape including one fragmented and one continuous habitat. Box-plots (showing the 1st and 3rd quartiles (upper and lower bounds), 2nd quartile (centre), 1.5* interquartile range (whiskers) and minima-maxima beyond the whiskers) represent the range of species richness under stochastic, stabilizing, and equalizing processes for generalist and specialist species, and mixed processes. Two mixed processes were implemented: processes involving 50% of stabilizing and 50% of equalizing processes across the landscape, both for generalist (Mixed_generalist) and specialist species (Mixed_specialist) on the one hand, and equalizing processes for specialist species in the fragmented habitat but stochastic processes in the continuous habitat (MassEffect_1) and vice-versa (MassEffect_2).*

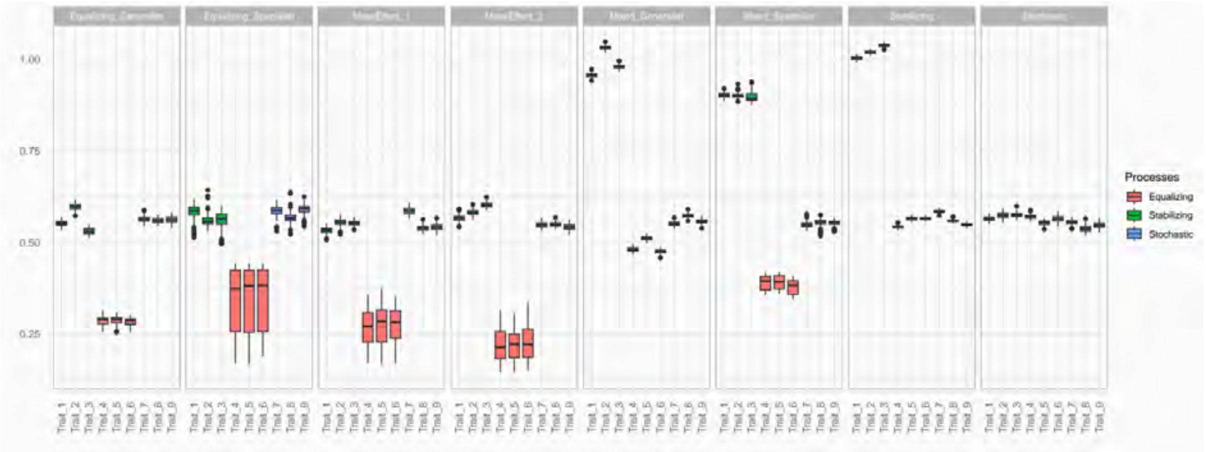


Figure 6: *Standard deviation of nine continuous traits simulated by a Brownian motion model at the end of a process of community assembly under stochastic, stabilizing, and equalizing processes for generalist and specialist species, and mixed processes in a gridded landscape including one fragmented and one continuous habitat. Two mixed processes were implemented: processes involving 50% of stabilizing and 50% of equalizing processes across the landscape, both for generalist (Mixed_generalist) and specialist species (Mixed_specialist) on the one hand, and equalizing processes for specialist species in the fragmented habitat but stochastic processes in the continuous habitat (MassEffect_1) and vice-versa (MassEffect_2). Box-plots (showing the 1st and 3rd quartiles (upper and lower bounds), 2nd quartile (centre), 1.5* interquartile range (whiskers) and minima-maxima beyond the whiskers) represent the variation of the standard deviation of traits. Traits 1-3, 4-6, and 7-9 represent the traits that are selected under equalizing, stabilizing, and stochastic processes, respectively.*

Can we use phylogenetic diversity as a proxy for assembly processes?

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 & Jiang, 2014; Zhang et al., 2018; Li et al., 2018; Galván-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 (Figure 7). 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.

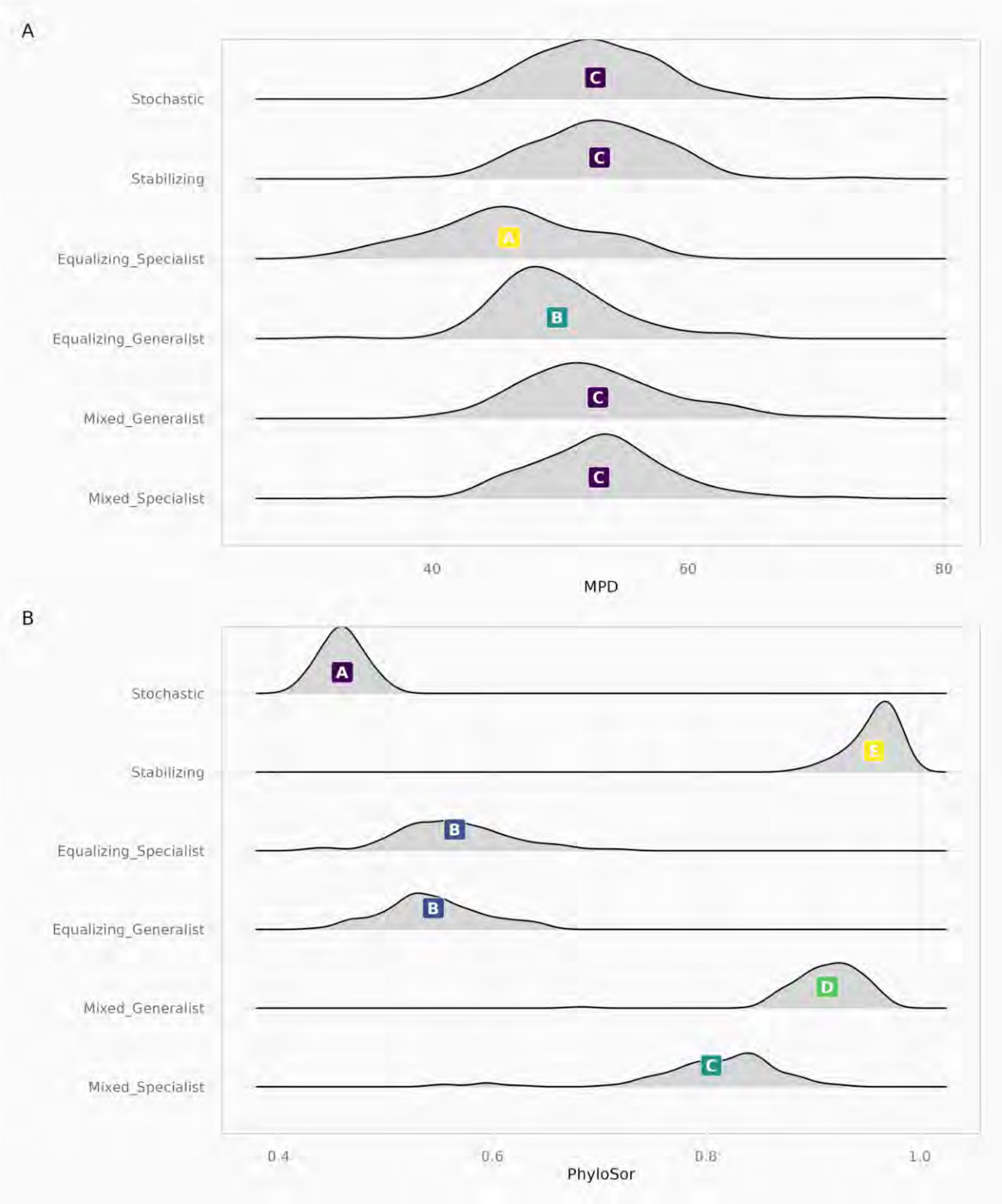


Figure 7: *Phylogenetic structure of communities simulated under competing assembly processes across a landscape including a continuous and a fragmented habitat. Distribution of average mean phylogenetic distance (MPD) values across all samples (A) and average PhyloSor values across all sample pairs (B) for 100 replicates of community simulations under contrasting assembly processes: stochastic, stabilizing, equalizing with specialist and generalist species, mixture of 50% of stabilizing processes and 50% of equalizing processes with specialist and generalist species. Letters indicate whether average MPD and PhyloSor significantly differ depending on assembly processes based*

on Dunn tests, the same letter being used for distributions with non-significantly different average values.

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 (Webb et al., 2008) and AED (Tucker et al., 2017) 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). 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-Dukát & Czúcz, 2016; Blanchet et al., 2020), the metrics that exhibited the highest statistical power under stabilizing processes were Bst and Pst (Hardy, 2008). 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 (Lozupone & Knight, 2005), 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. To emphasize this issue, Vellend (2010) quoted the link between processes and patterns "the black box of community ecology". Analyses of community patterns (phylogenetic or trait) to infer processes is dampered by pitfalls ecologist must avoid (reviewed by Münkemüller et al., 2020), especially when linking one pattern to one process. Despite the non-one-to-one equivalency between pattern and processes and the lack of generalization, it is still of high importance (Simberloff, 2004) and possible to disentangle all these processes by completing different analyses as supports. As examples, when phylogenetic clustering is observed, in field transplantation could help disentangle the effects of niche filtering or dispersal limitations (Rinas & Vellend, 2024)

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 & 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 (with a Yule process in Palm Trees (Couvreur et al., 2011) or a pure birth process but different diversification rates in Coleoptera (Trizzino et al., 2011), 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 & 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 (Figure 8b) versus one sample out of each of the nine clusters of four samples (Figure 8c) (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 (Figure 9, upper). 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 (Figure 9, lower). This suggests that sparse sampling could help enhancing statistical power.

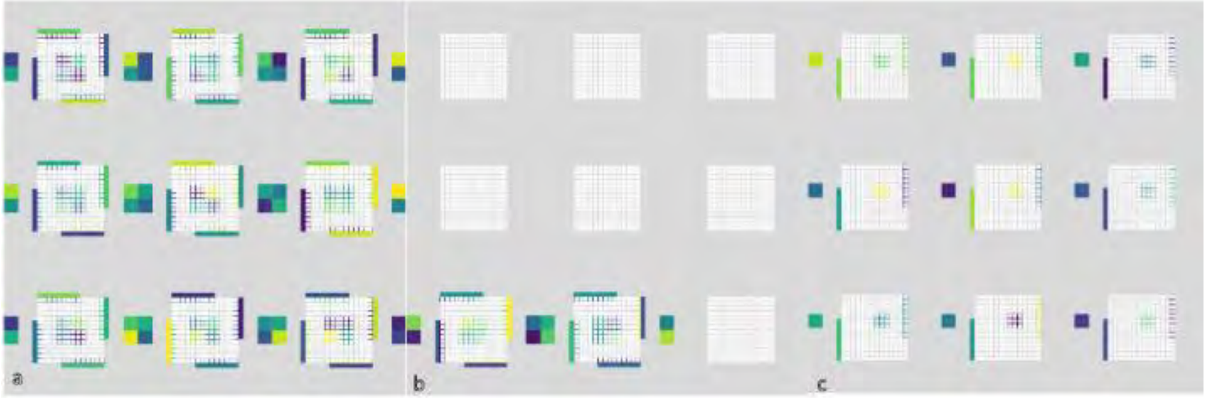


Figure 8: *Impact of the sampling design on the power of null models used to detect a significant community phylogenetic structure. (a) Sampling design of 36 samples per habitat, as originally implemented in Chapter 1. (b) Spatially-correlated design of 8 samples. (c) Sparse sampling, made of 9 samples for each habitat*

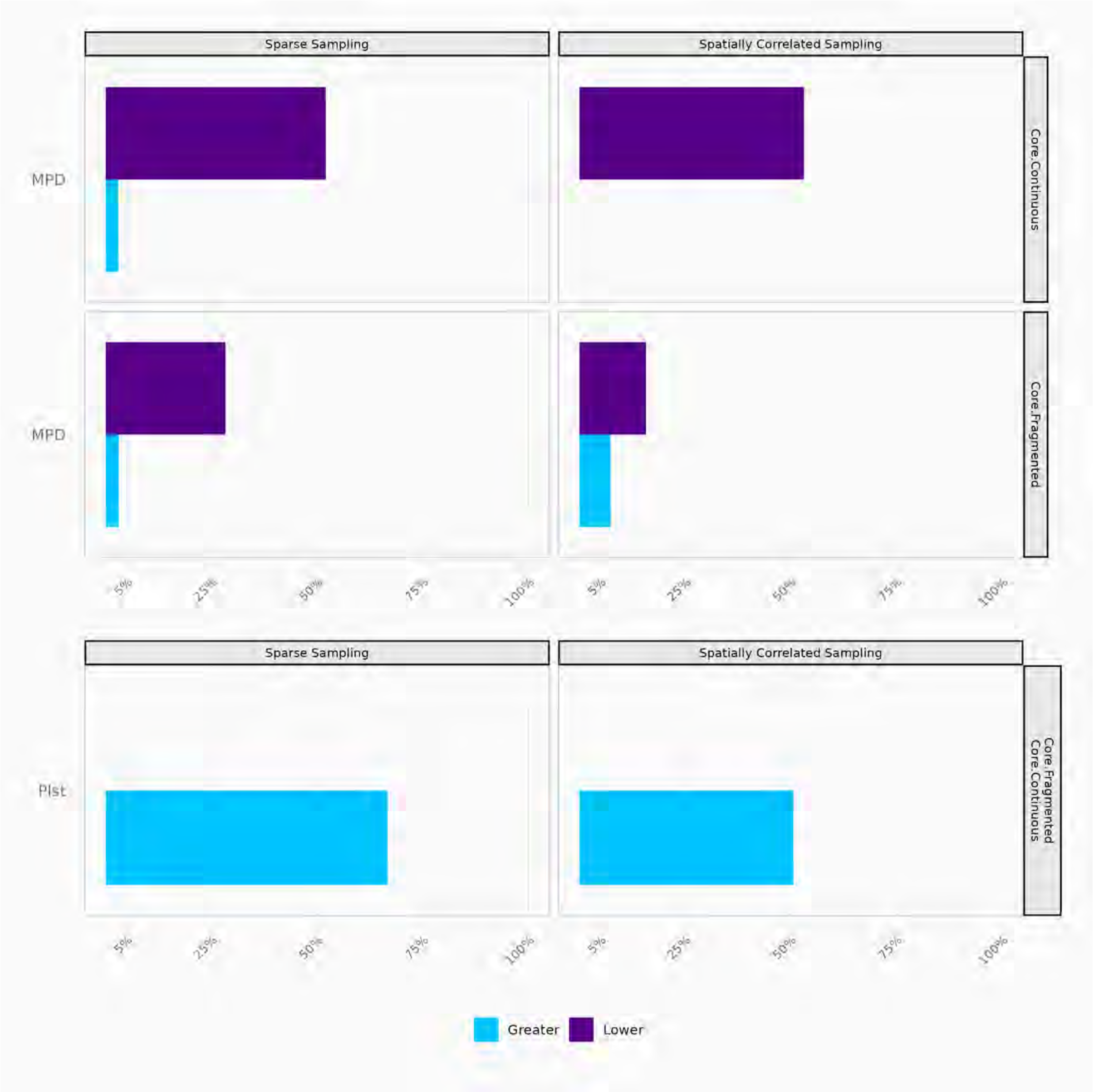


Figure. 9. *Ability of MPD and PIst to retrieve phylogenetic clustering under equalizing processes with specialist species within (MPD) and among habitats (PIst) under different sampling schemes. Left: spatially-correlated sampling. Right: sparse sampling. Bars represent the percentage of tests for which the statistic was significantly higher (in blue) or lower (in violet) across 100 replicates.*

Inferring mechanisms of community assembly in liverworts along a latitudinal gradient based on analyses of spatial phylogenetic structure.

At both regional and global scales, the analyses presented here revealed a sharp increase in liverwort species richness towards the tropics, evidencing the presence of a latitudinal diversity gradient in a group wherein it has long been debated owing to regional departures of this pattern (Rozzi et al., 2008; Mateo et al., 2016). The increase of species richness towards the tropics varied longitudinally, with a clear pattern across the Americas and Asia/Oceania, but not across Europe/Africa. During the Last Glacial Maximum, the African rainforest area was reduced by ~84 %, i.e. to a much larger extent than its Amazonian counterpart, which probably shrank to 54 % of its present-day extent (Anhuf et al., 2006). Extinction processes are, furthermore, expected to be stronger in Africa than in Amazonia because of the smaller African rainforest area (~249 × 106 ha in Africa vs. 668 × 106 ha in Amazonia), resulting in smaller population sizes, which, in turn, increases extinction risk (Parmentier et al., 2007).

In contrast, phylogenetic diversity increased from the tropics northwards while phylogenetic relatedness was higher in regions with wetter and warmer climates. These patterns are contrary to the hypothesis of tropical niche conservatism but consistent with the notion that liverworts, like mosses (Shaw et al., 2005; Wu et al., 2022), likely evolved and first diversified in temperate climates. This interpretation is further supported by three lines of evidence. First, the timing of the first significant burst in liverwort diversification rates dates back to ~150–200 Ma (Laenen et al., 2014), a period during which the global climate was much colder than the one that prevailed ~100 Ma (Voosen, 2019), when ferns and angiosperms underwent their major radiation burst (Qian et al., 2019, 2021, 2023a, 2023b). Second, the analyses of our study on basal versus tip-weighted metrics of phylogenetic relatedness revealed that the diversification of liverworts has been relatively more ancient than that in angiosperms. In fact, while a significant correlation emerged between basal-weighted metrics of phylogenetic relatedness (i.e. MPDses) and macroclimatic conditions, this was not the case with tip-weighted metrics of phylogenetic relatedness (i.e. PDses). In angiosperms, conversely, the relationships between tip-weighted metrics of phylogenetic relatedness and climatic variation in China are strong and significant (Lu et al., 2018; Qian et al., 2019). This discrepancy suggests that older branches of the liverwort phylogeny contribute more strongly to the correlation between phylogenetic diversity and macroclimatic variation compared with younger branches in the angiosperm phylogeny, emphasizing differences in the timing of diversification of these two groups as a response to macroclimatic variation. Third, our deconstructive analysis of the patterns of taxonomic diversity at increasing phylogenetic depth revealed that the diversity of higher-level lineages towards the deepest phylogenetic levels (200 Myr and older) increased with latitude. This inverted LDG is reminiscent of the pattern observed today at the species level in temperate regions (southern South America, Rozzi et al., 2008; and Europe, Mateo et al., 2016) and, more globally, of the taxa that originated in cold conditions (Romdal et al., 2013). Although reconstructions of ancestral distribution ranges at deep nodes in the liverwort phylogeny are challenged by recurrent long-distance dispersal events (Laenen et al., 2018), it is tempting to see in the extra-tropical distributions of the centres of diversity of the basal lineages (e.g. Haplomitriaceae) an indication that such lineages originated in extra-tropical regions, where they would have become largely confined owing to macroclimatic niche conservatism. This is best exemplified by latitudinal gradients across South America, wherein a tropical-adapted 'modern' flora developed in the northern and central portions of the continent until at least mid-Tertiary, with few links to the flora of the southern part, which retained a large series of cool- and moisture-demanding Gondwanalandic elements (e.g. the families Haplomitriaceae and Blepharodophyllacaeae), largely shared with Australasia (Schuster, 1983). It is worth noting that although our analyses suggest that such taxa have been evolutionarily constrained by their macroclimatic niche, this does not necessarily mean that they persisted at locations where they are found today. Although this would be at odds with the high long-distance dispersal capacities of bryophytes, the distribution of continents, macroclimatic conditions and, most importantly, wind connectivity, which contributes more to bryophyte species distributions than geographical distance (Muñoz et al., 2004), varied substantially in geological time, impacting dispersal.

The opposite latitudinal gradients in liverwort species richness and phylogenetic diversity reported here could be explained in terms of a more recent origin of tropical diversity coupled with higher extinctions in temperate regions (Figure 10). In fact, tropical liverwort genera show significantly higher net diversification rates compared with extra-tropical genera. This suggests that the latitudinal diversity gradient results from higher extinction rates in extra-tropical lineages and/or higher speciation rates in the tropics (Laenen et al., 2018). The hypothesis that tropical liverworts experienced bursts of diversification is compatible with the fact that the most species-rich families of liverworts, such as the Frullaniaceae and Lejeuneaceae, radiated concomitantly with the development of megathermal angiosperm forests, offering a sudden increase in habitat complexity and availability in these mostly epiphytic families during the late Cretaceous (Feldberg et al., 2014). The same pattern has been found along tropical elevational gradients, where phylogenetic diversity of liverworts peaks in cool and moist cloud forests at mid-elevations, whereas tip diversification rates are highest in the tropical lowlands (Maul et al., 2023). The increase in phylogenetic relatedness and decrease in phylogenetic diversity among liverwort species towards tropical regions is reminiscent of similar patterns reported in pteridophytes, wherein a few ancient, phylogenetically isolated clades (e.g. Equisetaceae, Osmundaceae and Ophioglossaceae), which have a rich fossil record revealing substantial past diversity but are represented today by a few, species-poor genera, are well represented in regions of temperate climate but either absent or species-poor in regions of tropical climate (Qian et al., 2021).

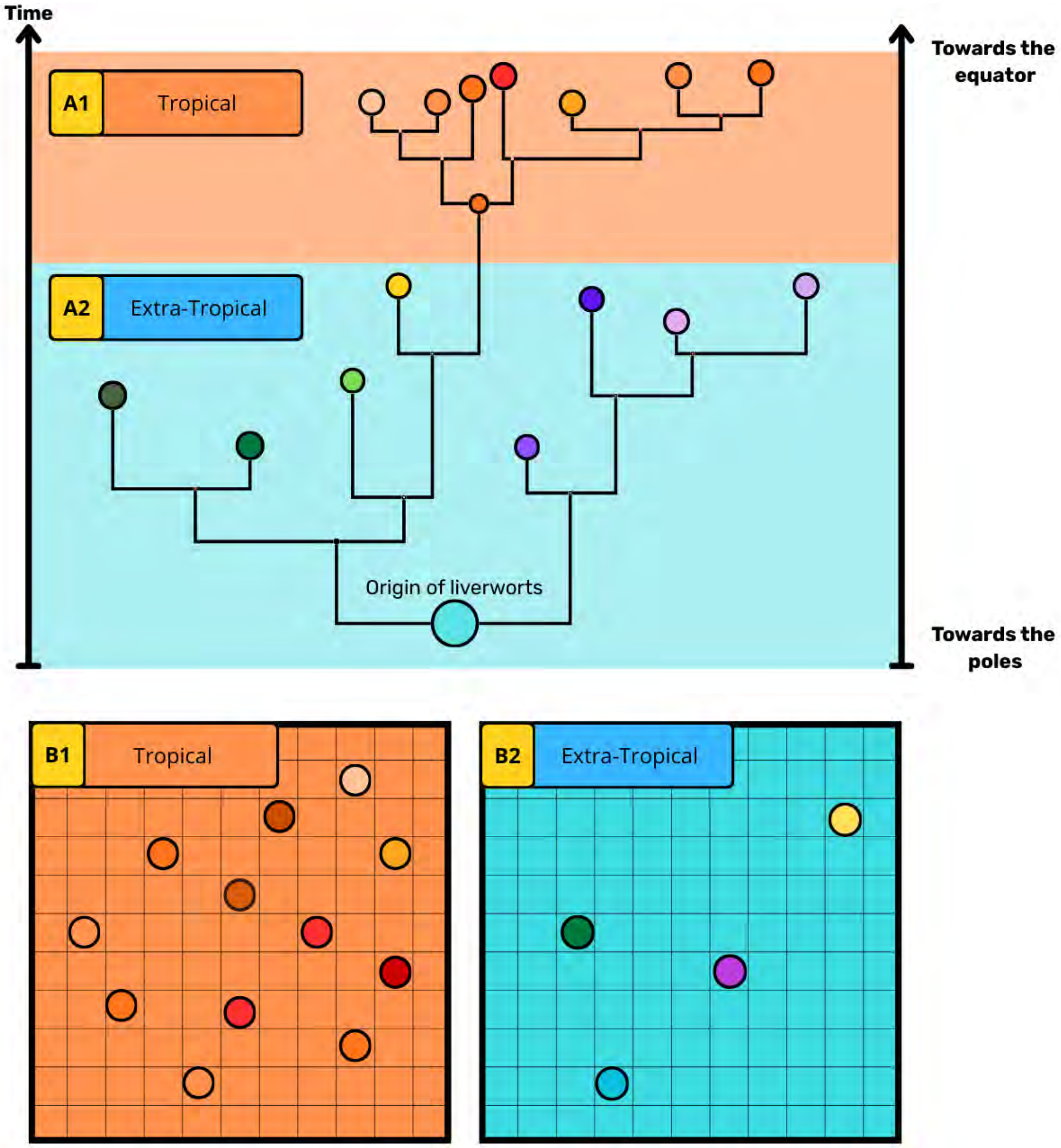


Figure 10. *Hypothesis for the opposite pattern of species richness and phylogenetic diversity along a latitudinal gradient for liverworts. Liverworts likely originated and primarily diversified in extra-tropical regions, creating a phylogenetically diversified group (A2). Few adapted taxa migrated to tropical regions where a radiative burst*

primarily diversified in extra-tropical regions, creating a phylogenetically diversified group (A2). Few adapted taxa migrated to tropical regions where a radiative burst occurred (A1). This higher net diversification rate in tropical region, associated with either higher speciation rates in the tropics and/or higher extinction rates in extra-tropical areas, would have led to phylogenetically clustered species rich communities in tropical region (B1) and phylogenetically overdispersed species poor communities in extra-tropical regions (B2).

Finally, the macroclimatic control of the spatial variation in phylogenetic diversity evidenced here suggests that macroclimatic niche conservatism, both from temperate to tropical regions, and vice versa, serves to explain why diversity patterns in liverworts have not been balanced during the evolutionary history of the group, despite the high capacities of long-distance dispersal of its species. The results of this study are thus in line with mounting evidence for the role of macroclimatic conservatism as an important driver of present-day distribution patterns of plant diversity (Crisp et al., 2009; Segovia et al., 2020).

Our analyses at increasing phylogenetic depth reveal, however, that the latitudinal diversity gradient that emerged at the species level decayed progressively at increasing phylogenetic level, evidencing the wider range and weaker macroclimatic preference of high-level taxa. In fact, in our dataset, 41 % of liverwort species, but only 3 % of the genera and none of the families, exhibit a strictly tropical distribution. The erasure of the latitudinal diversity gradient at genus and family level in liverworts contrasts with the marked increase of angiosperm family diversity towards the tropics, shaped by strong tropical niche conservatism (Ramírez-Barahona et al., 2020). Although it has long been acknowledged that bryophytes exhibit higher long-distance dispersal capacities than spermatophytes (for review, see Patiño & Vanderpoorten, 2018), the rapid decay of the LDG in liverworts, together with the low, albeit significant, correlations between phylogenetic diversity and macroclimatic variation suggest that, by comparison with spermatophytes (Kerkhoff et al., 2014), liverwort distributions are less constrained by tropical niche conservatism. Reconstruction of the ‘tropicality index’, which reflects the proportion of species latitudinal range that falls within the tropics minus the proportion of the latitudinal range that falls outside of it (Kerkhoff et al., 2014), revealed, in fact, that many temperate lineages are phylogenetically clustered within tropical ones (Collart et al., 2021), evidencing multiple instances of successful transition from tropical environments to temperate ones. For example, all temperate species of the most species-rich liverwort family, Lejeuneaceae, are nested in clades comprising mainly tropical species (Wilson et al., 2007). *Lejeunea*, one of the largest liverwort genera, originated in the Neotropics and subsequently dispersed successfully into extra-tropical regions (Heinrichs et al., 2013; Lee et al., 2020). In addition, the western European flora is composed largely of species of tropical origin (Patiño et al., 2015).

CONCLUSION

Species abundance in a simulated grid of plots ranging from 0 (blue) to 50 (yellow) under mass-effect.

Kasprzyk Thibault discovering what is the meaning of a field mission.
Near the botanical garden of Pont de Nant.
September 2018

CONCLUSION AND PERSPECTIVES

We validated the use of community phylogenetic patterns to infer assembly processes, and we provided guidelines to do so, notably on which metrics to use. 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. Based on empirical evidence in liverworts along a latitudinal gradient, we have found that these assembly processes were influenced by phylogenetic scale, with a significant impact of climatic variables, evidencing macroclimatic niche conservatism as the main driver underlaying the currently unbalanced distribution of species richness from the tropics to the poles.

A new community assembly model: premises to an innovative ABC approach in community ecology.

To perform the first theoretical part of this work and legitimate the empirical analyses that followed, we developed a new mechanistic, spatially explicit model of community assembly based on the framework of Chesson (2000), combining equalizing, stabilizing and stochastic processes. Some spatially-explicit, mechanistic models of community evolution over time were previously built by Münkemüller et al. (2012) or Chave et al. (2002) but did not allow for competition between individuals within communities. In addition, to our knowledge, no pre-existing simulators allowed the mixing of different processes (but see Overcast et al., 2021; Munoz et al., 2018). The effects of multiple processes simultaneously acting were still unknown. We therefore created a new model accounting for these issues based on a grid design to test for spatial and dispersal effects while allowing the mixing of processes. This model mimics a mechanistic assembly of communities from generation to generation under explicit processes and combination thereof while taking dispersal limitation and spatial effects into account. More precisely, we focused on processes that were highlighted by Darwin's conundrum to verify that one can effectively discriminate between the main possible explanations of community assembly (habitat filtering or competition) by describing phylogenetic patterns (clustering or overdispersion). We included a high number of parameters so that users can modify the processes at play, the number of species and their abundance, the shape and size of the grid (influencing the spatial effects) or the degree of specialization of each species.

Modelling, however, comes with inherent problems. First, the degree to which the results are transposable in natural settings are unknown and all the results can only be interpreted in the context of our own simulator (Van Nes & Scheffer, 2005). Second, many assumptions were made to facilitate the use of the simulator when information is not available. For example, all species were characterized by the same dispersal kernel. If available, one could use real values from empirical datasets to better mimic the data of interest. Approaching real data sets could also be improved by implementing a variety of new parameters to make our simulator more flexible. A non-restrictive list of examples of these possible enhancements includes:

- the possibility of implementing more than two habitats, with each of them containing their own assembly processes and combination thereof;
- a flexible grid to reflect real geographic features based on the acquisition of a map, as done in spatially explicit coalescent models (Dellicour et al., 2017) (Figure 11);
- adding in situ speciation to complete the sets of the “Big four” types of processes proposed by Vellend (2010), the three other types, namely selection, drift, and dispersal, being already implemented in the simulator;
- various other possible parameters for tree topology (e.g., modifying branch lengths to mimic radiative bursts) or trait evolution (other than Brownian Motion models) or null models used to test significance (Hardy, 2008).

The null models, however, possess a statistical power that substantially varies among metrics and depending on the assembly processes involved, impeding the reliability 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 one that were actually observed in natural communities best correspond, would represent a much appealing way to move forward (Figure 12). 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). The number of parameters to be estimated in such simulations represents, however, one of the major challenges in such approaches (Bertorelle et al., 2010), and this would especially be true in community ecology, wherein the number of parameters to be assessed exceeds the already large number of parameters in coalescence analyses (e.g., effective population sizes, migration rates…). 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., Nait Saada et al., 2023), and could provide the solution to address this challenge. This improvement is to be pursued to provide biologists with the first tool of this kind to infer assembly processes. Technical constraints must first be tackled as these analyses, already computationally heavy when traditionally used in coalescent analysis with a low number of parameters, would represent a very time-consuming process without proper optimization and parameter variability choice.

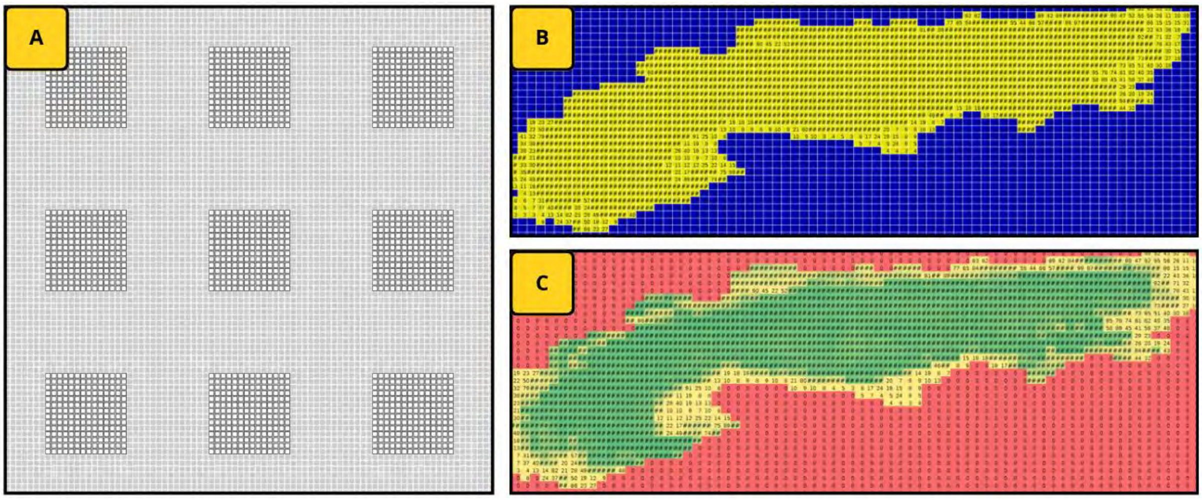
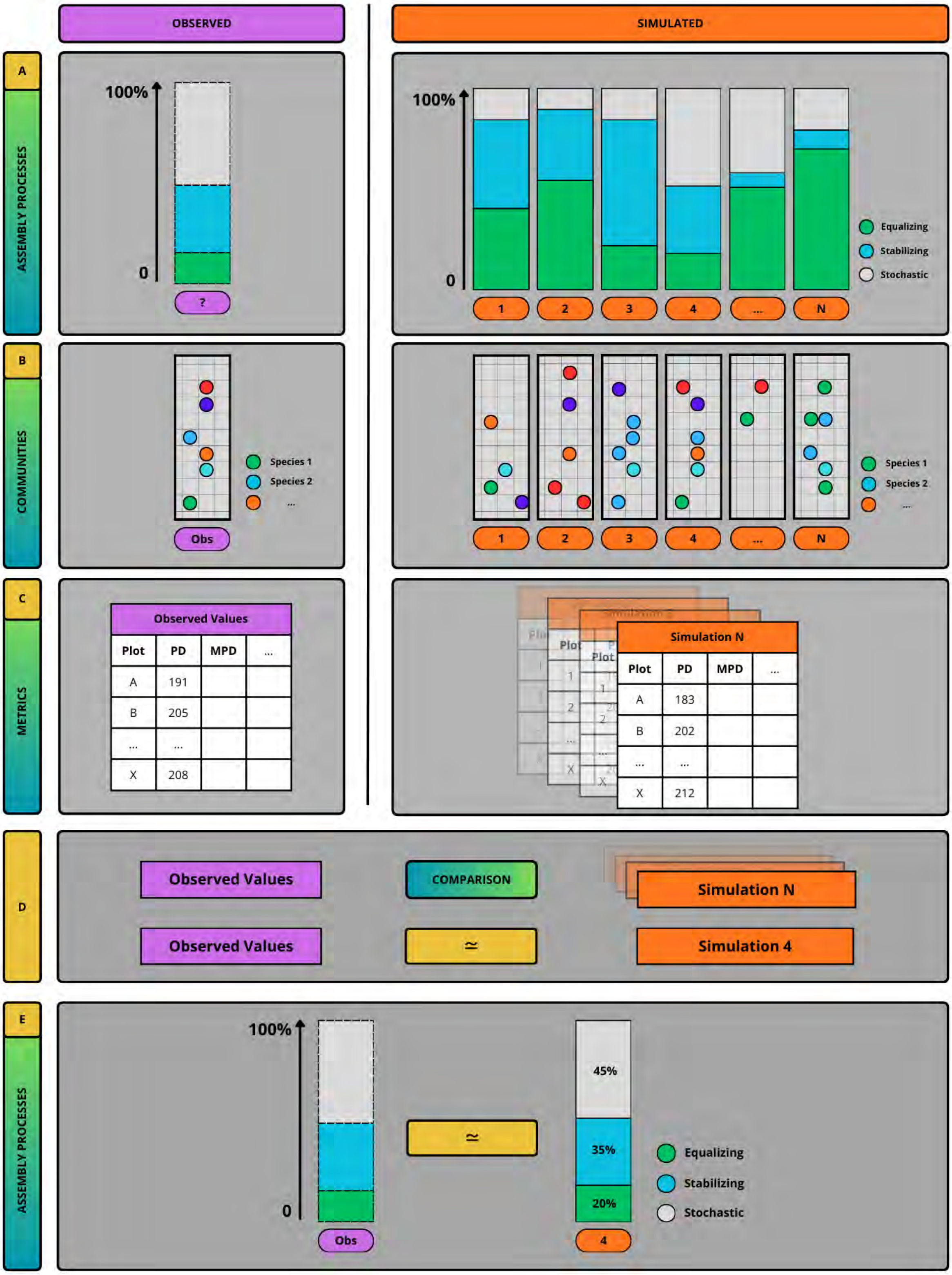


Fig. 11. *The actual grid of plots used in the simulator (A) and possible improvements proposed as a grid of two (B) or more (C) habitats (represented by different colors) representing real geographic areas, such as the Alps depicted here.*



Observed Values

Plot	PD	MPD	...
A	191		
B	205		
...	...		
X	208		

Simulation N

Plot	PD	MPD	...
A	183		
B	202		
...	...		
X	212		

Fig. 12. *Proposed ABC approach for the simulator proposed in this work to assess the assembly processes at play in natural communities by comparing their phylogenetic diversity to the phylogenetic diversity of simulated communities following known assembly processes. To find the assembly processes leading to the observed community of interest, multiple replicates of starting parameters of different assembly*

processes are created to cover a wide range of possibilities (A). From these parameters of assembly processes, communities are simulated (B). A selection of phylogenetic diversity metrics is computed for both the observed and the simulated communities for each community (plot) simulated (C) to be compared against each other (D) The ensemble of diversity metrics simulated that shows the highest similarity with the observed diversity metrics will reveal the most plausible assembly processes that led to the observed community of interest (E).

Practical recommendations for inferring assembly processes from analyses of phylogenetic diversity.

We have shown that not all metrics are equal when it comes to recover phylogenetic clustering or overdispersion. Some of the most widely used diversity metrics like PD (Faith, 1992; Cardillo, 2023; Hu et al., 2021), MPD (Webb, 2000; Webb et al., 2002), and PhyloSor (Bryant et al., 2008, Dvorak et al., 2025, González-Caro et al., 2021) behaved poorly in our simulations. As examples, PD and MNTD typically found clustering at a 20% rate under stabilizing mechanisms while MPD and PhyloSor were overall lacking statistical power. Furthermore, some metrics are, in fact, mathematically identical (as found by Miller et al. (2017), e.g., MPD (Webb, 2002) and Δ+ (Warwick & Clarke, 1995), or highly correlated, like UniFrac and PhyloSor (Leprieur et al., 2012). Therefore, results of hundreds of papers concluding to clustering must be taken with caution or, at best, be reevaluated with more robust metrics.

Following our results, we favor the use of beta metrics with, if available, abundance rather than occurrence data (Estrada & Arroyo, 2012; Waldock et al., 2022, Nipperess et al., 2010) such as Bst as metrics of phylogenetic diversity to infer assembly processes. Furthermore, we highlight the importance of realizing the computation inter-habitat rather than intra-habitat to evidence patterns of phylogenetic diversity.

Even when all methodological aspects are taken into account, ecologists should be aware of other aspects impacting the results, such as striking variations of diversity through changes in phylogenetic scale. We therefore encourage ecologists to carefully design their analyses both by the methods and tools chosen and nuance the conclusions made from the patterns they observe. By taking into account the spatial scale and the phylogenetic level they are working with, researchers can produce highly valuable results for explaining community assembly that were at work in the past. The importance of highlighting how communities were assembled gives clues of how they will react in the future: will they be able to keep up with climate change (Sanz-Martín et al., 2024, Burrows et al., 2014), adapt to it (Piatkowski et al., 2023), be outcompeted by new competitors (Lyu & Alexander, 2024) or simply vanish, along with the disappearance of their niche they evolved in for thousands years (Lomolino, 2023)?

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RESEARCH ARTICLE

Microclimatic variation in tropical canopies: A glimpse into the processes of community assembly in epiphytic bryophyte communities

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Abstract

1. Epiphytic communities offer an original framework to disentangle the contributions of environmental filters, biotic interactions and dispersal limitations to community structure at fine spatial scales. We determine here whether variations in light, microclimatic conditions and host tree size affect the variation in species composition and phylogenetic structure of epiphytic bryophyte communities, and hence, assess the contribution of environmental filtering, phylogenetic constraints and competition to community assembly.
2. A canopy crane giving access to 1.1 ha of tropical rainforest in Yunnan (China) was employed to record hourly light and microclimatic conditions from 54 dataloggers and epiphytic bryophyte communities from 408 plots. Generalized Dissimilarity Modelling was implemented to analyse the relationship between taxonomic and phylogenetic turnover among epiphytic communities, host-tree characteristics and microclimatic variation.
3. Within-tree vertical turnover of bryophyte communities was significantly about 30% higher than horizontal turnover among-trees. Thus, the sharp vertical variations in microclimatic conditions from tree base to canopy are more important than differences in age, reflecting the likelihood of colonization, area, and

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habitat conditions between young and old trees, in shaping the composition of epiphytic bryophyte communities.

4. Our models, to which microclimatic factors contributed most (83–98%), accounted for 33% and 18% of the variation in vertical turnover in mosses and liverworts, respectively. Phylogenetic turnover shifted from significantly negative or non-significant within communities to significantly positive among communities, and was slightly, but significantly, correlated with microclimatic variation. These patterns highlight the crucial role of microclimates in determining the composition and phylogenetic structure of epiphytic communities.
5. *Synthesis*. The mostly non-significant phylogenetic turnover observed within communities does not support the idea that competition plays an important role in epiphytic bryophytes. Instead, microclimatic variation is the main driver of community composition and phylogenetic structure, evidencing the role of phylogenetic niche conservatism in community assembly.

KEYWORDS

beta diversity, biotic interactions, environmental filters, epiphytic bryophytes, forest canopy, microclimates, niche conservatism, phylogenetic constraints

1 | INTRODUCTION

The relative influence of community assembly mechanisms varies depending on spatial and temporal scales (Kneitel & Chase, 2004; Kraft & Ackerly, 2014). In Grime's competitive, stress-tolerant, ruderal (CSR) theory of plant ecological strategies (Grime, 1977), community composition is controlled by selection for traits depending on levels of competition, stress and disturbance. Along a gradient of decreasing habitat filtering, community composition is expected to shift from a dominance of stress-tolerant species to competitive and ruderal species (Escobedo et al., 2021). At larger spatial scales, and hence, as variation in environmental conditions increases, community composition is conversely increasingly driven by environmental filtering (Powell et al., 2015). The contribution of environmental and biotic filters to community assembly is, however, often confounded (Cadotte & Tucker, 2017), especially at small spatial scales, at which both processes may occur (Xu et al., 2021).

In this context, phylogenetic turnover, which characterizes the phylogenetic structure of communities, offers an appealing framework to disentangle the processes involved in community assembly (Graham & Fine, 2008). While taxonomic turnover measures the extent to which some species are replaced by others along environmental gradients, phylogenetic turnover measures the extent to which species replacement is phylogenetically constrained, so that species within a community are more or less phylogenetically related to each other than expected by chance.

Positive phylogenetic turnover occurs when species in a community are more closely related to each other than species from different communities. A clumped phylogenetic distribution of taxa (phylogenetic clustering) indicates that habitat-use is a conserved trait within the pool of species in the community, and hence, evidences phylogenetic niche conservatism (Webb et al., 2002). The application of the phylogenetic niche conservatism hypothesis has substantial ecological and evolutionary implications because it makes it possible to determine whether niche preferences are evolutionarily labile or, to the reverse, are phylogenetically constrained, potentially hampering the chances of species to respond to climate change.

Negative phylogenetic turnover (phylogenetic overdispersion) occurs when species from the same community are more phylogenetically distant than species from different communities. While phylogenetic overdispersion points to non-random species assemblages, its interpretation has been controversial. In line with Darwin's competition-relatedness hypothesis, which posits that closely related species compete more strongly than distantly related ones (Cahill et al., 2008), phylogenetic overdispersion has primarily been interpreted in terms of competition among related species sharing limited resources within the same niche (Anacker & Strauss, 2014; Wiens & Graham, 2005). Phylogenetic overdispersion may, however, also result from niche convergence (Cavender-Bares et al., 2004) or facilitation (Valiente-Banuet & Verdu, 2007) among phylogenetically unrelated species.

Epiphytes appear as an interesting model to address the question of the factors shaping community structure at small spatial scales (Adams et al., 2017, 2019; Méndez-Castro et al., 2020). For epiphytes, host-trees typically function as habitat islands, exhibiting, like oceanic islands but at much smaller spatial scales and shorter time frames, sharp spatio-temporal variations in their abiotic environment (Adams et al., 2017; Hidasi-Neto et al., 2019; Itescu, 2019; Taylor & Burns, 2015).

The ecological conditions that prevail along a vertical gradient, from the base to the uppermost canopy, typically vary in terms of extrinsic (e.g. air humidity, light intensity, temperature) and intrinsic (physical properties of the substrate, such as bark texture and physico-chemistry, branch orientation and diameter) features (Cornelissen & ter Steege, 1989). In the outer canopy, the high light intensity and extremely low humidity, high wind exposure and daily variation in temperature and relative humidity, exert strong selection pressure for traits similar to those seen in desert habitats, such as leaf succulence, small stature, slow growth rate, water and nutrient storage capabilities and UV protection (Spicer & Woods, 2022). Progressing towards the tree base, physical stability of the support and relative humidity (RH) increases, while light, temperature and the daily variation in microclimatic conditions decrease, resulting in a more stable environment inhabited by species that are less tolerant of drought and high light intensity (Cornelissen & ter Steege, 1989; Freiberg, 1996; Watkins et al., 2007; Woods et al., 2015).

These conditions further vary along horizontal gradients not only due to differences among host-tree species in terms of branching architecture, bark texture and physico-chemistry (Hidasi-Neto et al., 2019) but also due to age differences among host trees. As the likelihood of colonization increases with time, old trees typically exhibit a higher epiphytic species richness than young ones (Taylor & Burns, 2015). Old trees also have a larger area for colonization and a higher diversity of micro-habitats than young ones (Paillet et al., 2019).

In this context, Grime's CSR theory of plant ecological strategies (Grime, 1977) allows us to make predictions on the importance of interactions among epiphytes depending on the ontogenetic stage of their host-tree and the habitat they occupy (Spicer & Woods, 2022). On a tree, competition is expected to increase from the canopy, characterized by large variations in light and microclimatic conditions, to tree base, with more buffered environmental variations. Competition is also expected to increase from young to old host-trees, as pioneer species progressively accumulate before entering competition with specialized competitors (Ellis & Ellis, 2013).

Despite these expectations, where and when competition and facilitation dominate, if at all, remains relatively unexplored in epiphyte ecology (Francisco et al., 2018; Spicer & Woods, 2022). Furthermore, while the vertical structures of epiphyte communities (Gehrig-Downie et al., 2013; Mota de Oliveira et al., 2009; Mota de Oliveira & ter Steege, 2015; Zotz, 2016) and, to a lesser extent, associated variations in microclimatic conditions (Murakami et al., 2022; Stuntz et al., 2002; Toivonen et al., 2017), have long been documented, no analysis has, to our knowledge, examined the relationship between microclimatic variation and species composition in a spatially explicit framework. In fact, although forest canopy science has been an active discipline since the 19th century, its progress has been slow, partly due to the limited accessibility of canopies (Nakamura et al., 2017) and the limited availability of fine-scale microclimatic data (De Frenne et al., 2021), a critical issue for canopy epiphytes (Murakami et al., 2022).

Bryophytes represent an important component of epiphytic floras, to which they contribute up to 75% of the biomass, and hence, play a key role in nutrient and water cycles (Gradstein et al., 2010). Bryophytes are poikilohydric and rely on rainfall or moisture in the atmosphere for water uptake. They are hence ideal models to investigate the impact of microclimatic variation on community composition, which strikingly varies from the base to the canopy (Mota de Oliveira & ter Steege, 2015; Sporn et al., 2010). Although mounting evidence points to the relevance of climatic niche conservatism for the assembly of bryophyte floras over large spatial and evolutionary time scales (Collart et al., 2021; Piatkowski & Shaw, 2019; Wilson & Coleman, 2022), whether shifts in community composition along vertical microclimatic gradients and along horizontal gradients in host-tree size are structured phylogenetically, that is, whether niche conservatism could operate at such micro-scales, remains to be tested.

Furthermore, it has been suggested that bryophytes may not compose communities similar to those of vascular plants, but instead, that the distributions of individual species would be driven by niche preferences and dispersal capacities, regardless of other species (Wilson et al., 1995). The unbounded relationship between epiphytic species richness and tree age has been interpreted in terms of the unrestricted increase in species richness in the absence of competition in unsaturated communities (Boudreault et al., 2000; Fritz, Brunet, & Caldiz, 2009). In line with this hypothesis, a significantly lower evenness, which could reflect weaker competition, was reported in bryophyte communities compared with those formed by vascular plants (Steel et al., 2004). Results from common garden experiments conversely revealed that competition is more important than temperature for the performance of bryophyte species (Greiser et al., 2021). The role of competition in bryophyte communities has, thus, long been questioned (Rydin, 2009). Wilson et al. (1995) concluded that there is community structure among bryophytes, in that species exclude each other to the same degree as higher plants do in their communities. They failed, however, to identify groups of species within a community that are mutually exclusive because of similarity in resource use, leading them to conclude that bryophyte species all form one guild.

Taking advantage of one of the world's 22 canopy cranes, the goal of the present study is to determine whether variations in light, microclimatic conditions and host tree size affect the variation in species composition and phylogenetic structure of epiphytic bryophyte communities, and hence, assess the contribution of environmental filtering, phylogenetic constraints and competition to community assembly. More precisely, we address the following questions: Is variation in species composition among epiphytic communities more important vertically, reflecting within-tree changes in microhabitat and microclimatic conditions, or horizontally, reflecting differences in age, and hence size and microhabitat diversity, among trees (Q1)? To what extent are these changes in community composition phylogenetically constrained (Q2)? Among communities, we test the hypothesis of an increasingly positive phylogenetic turnover along microclimatic gradients, pointing to phylogenetic niche conservatism (H1). Within communities, we test the hypotheses that species exhibit increasingly competitive interactions, and hence, increasing phylogenetic overdispersion, from the canopy to the base, and from young to old trees (H2).

2 | MATERIALS AND METHODS

2.1 | Study site and sampling design

This study took place in a 1.44 ha square plot in a lowland (643–700 m) seasonal rain forest (101°34′59.1′′E, 21°37′2.6′′N) in Mengla, one of the five subdistricts that together form Xishuangbanna National Natural Reserve (Yunnan, SW China). Mean monthly RH and mean monthly temperature recorded by dataloggers from 12 trees at 2 m during 2017–2019 were 95.3% and 20.8°C, respectively, with the coldest month in January (15.8°C) and the warmest month in June (25.2°C). This site was selected because it is equipped with an 81 m-high canopy crane (TCT7015-10E, Zoomlion Heavy Industry, Changsha, China) whose 60 m-long arm provides access to the canopy within a 1.1 ha circular area (Figure 1c).

Xishuangbanna National Natural Reserve covers an area of 242,510 ha that comprises the largest tropical forest area in China. The region experiences a typical monsoon climate with a 6-month dry season from November to April and a rainy season from May to October. In a 20-ha plot of tropical seasonal rainforest of Xishuangbanna, 468 tree species in 213 genera and 70 families were recorded. The tallest trees attain 70 m, and there are 4791.70 stems and a total basal area of 42.34 m^2 per hectare (Lan et al., 2012). Within the 1-ha plot investigated, the canopy layer (height > 30 m) is dominated by *Parashorea chinensis* (Dipterocarpaceae), which contributes 19.5% of the trees with a diameter at breast height (DBH) ≥ 5 cm and most of the tallest trees. It is accompanied by *Canarium album*, *Pometia tomentosa*, *Sloanea tomentosa* and *Semecarpus reticulata*. The sub-canopy layer (16–30 m) is dominated by *Ficus langkokensis*, *Litsea dilleniifolia*, *Barringtonia fusicarpa*, *Diospyros atrotricha* and *Pseuduvaria indochinensis*, and the understorey layer (6–16 m) by *Pittosporopsis kerrii*, *Baccaurea ramiflora*, *Diospyros xishuangbannaensis*, *Cleidion brevipetiolatum* and *Mitrephora maingayi*.

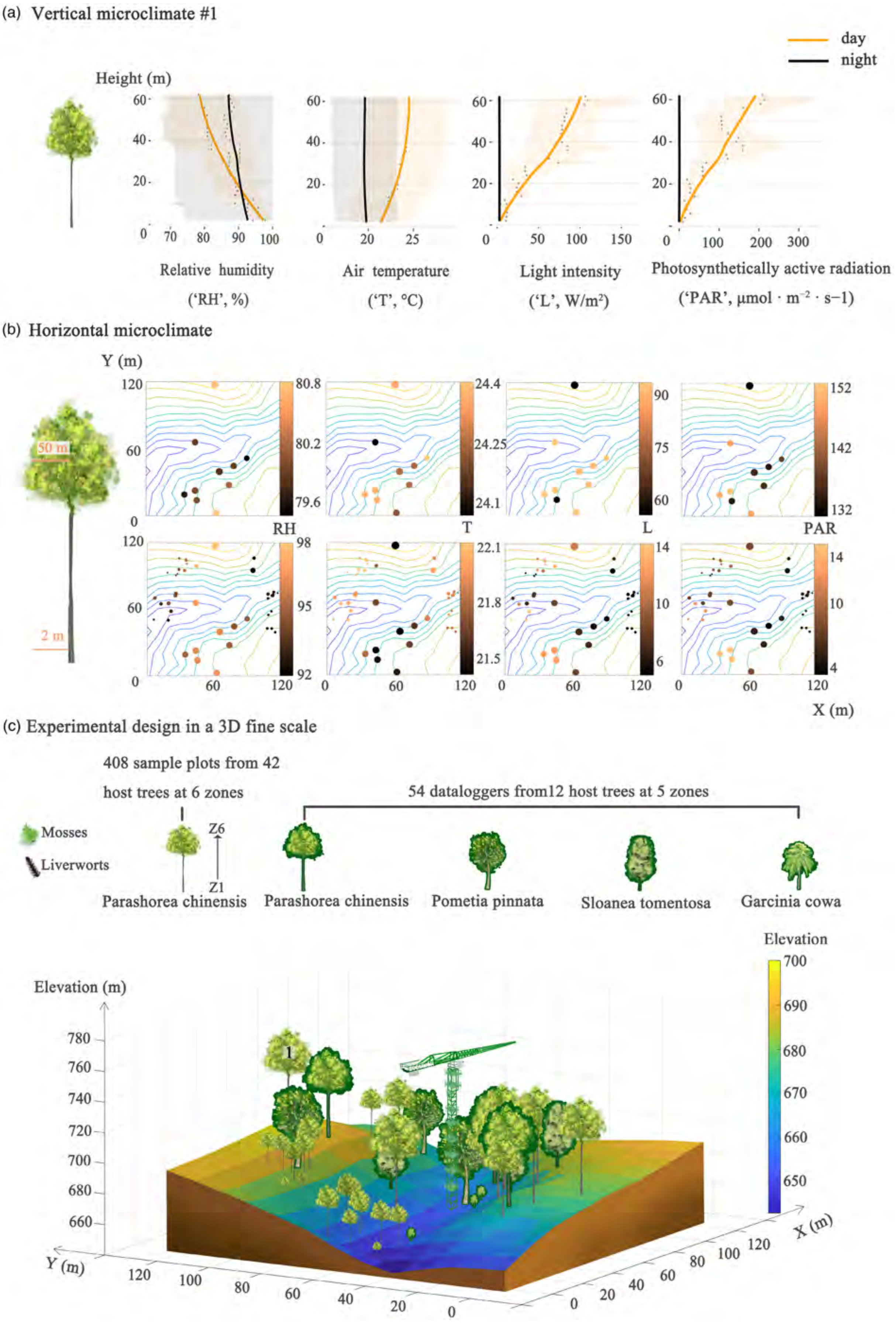
Epiphytic bryophytes were recorded only on the dominant host-tree species, *Parashorea chinensis*, to control for host specificity (González-Mancebo et al., 2003; Guan et al., 2017; Schmitt & Slack, 1990). *Parashorea chinensis* is an evergreen species, characterized by large buttresses, and hosts abundant epiphytic bryophytes (Shen et al., 2018). Although our analyses were restricted to the communities found on *P. chinensis*, these are representative of the entire epiphytic bryophyte community of the area. 102 epiphytic bryophyte species we found on 42 tree individuals, that is, slightly more than the 90 species reported from 69 individual trees belonging to 14 different tree species in the same plot in a previous investigation (Shen et al., 2018).

Trees with a DBH < 5 cm or covered by vines and lianas were discarded, resulting in a total of 42 with a DBH ranging from 5.4 to 135 cm. Each tree was divided into six height zones based on a slightly modified version of Johansson's (1974) zonation scheme (see e.g. Figure 7.11 in Zotz, 2016), which is not based on absolute height, but on tree architecture, as follows: tree base (zone 1), <2 m and corresponding to the buttresses; lower trunk (zone 2), between zone 1 and middle height of the trunk; upper trunk (zone 3), between the middle height of the trunk and the first ramifications of the canopy; inner, middle, and outer canopy (zones 4–6), corresponding to the lowest, middle and upper thirds of the canopy.

For each height zone, two plots were haphazardly located vertically. From the 504 initial plots, 96 had no bryophyte species, leading us to focus on 408 plots (see Shen (2021a) for individual plot coordinates) with at least one species, suitable for analyses of beta diversity (see below). Although orientation typically plays a limited role in explaining variation in epiphytic community composition in tropical cloud forests (Song et al., 2011), we controlled for this factor by sampling, for each plot, four sub-plots of 20 × 20 cm (as measured with a tape) on the trunk or branches (zones 1–4). These four sub-plots were organized in pairs, with the two plots of a pair being diametrically opposed and the pairs being perpendicular to each other. At zone 5, branches may be narrower than 20 cm, and we recorded epiphytes within a shape of 80 × 5 cm. At zone 6, we recorded an area of *c.* 400 cm^2 of twigs. This led to a total of 1632 sub-plots, 1156 of which had bryophytes.

Within each sub-plot, a complete species inventory was conducted. Representative specimens of each species were sampled in each sub-plot, resulting in 1156 collections that were subsequently analysed in the laboratory using relevant microscopic techniques and monographs (Shen et al., 2018). In some instances, the material available was too scanty to allow for an identification at the species level, and sometimes, even at the genus level. This was the case for six moss taxa, labelled as sp1–6, respectively (Table S4). Voucher specimens of each of the species included in the 1156 collections are kept at the Herbarium of the University of Liège (LG). The observations performed at the level of each sub-plot were then merged to produce presence-absence data for each of the moss and liverwort communities at the level of each plot (data available at https://doi.org/10.6084/m9.figshare.17057615.v8).

FIGURE 1 Experimental design and 3D microclimatic modelling of temperature (T), relative humidity (RH), photosynthetically active radiation (PAR) and light intensity (L) in a 1.44 ha tropical canopy crane facility, Yunnan, SW China. (a) Vertical profile of day (orange line) and night (black line) monthly averages (and standard deviation, grey ribbon) of T, RH, PAR and L modelled at the level of Tree #1; (b) topographic map of the study area representing the position of the 42 sampled trees in a x-y space and the modelled horizontal variation in monthly average of day T, RH, PAR, and L at 2 m ($n = 50$) and at 50 m ($n = 10$) height, respectively; (c) experimental design. Circle diameters in (b) are proportional to tree DBH.


(a) Vertical microclimate #1

(b) Horizontal microclimate

(c) Experimental design in a 3D fine scale

2.2 | Geographic and environmental variables

Nine ecological and geographic variables were recorded at each plot and were used to derive differences in ecological and geographic conditions among plots for subsequent analyses (Figure 2a).

The *X*–*Y* coordinates of each tree (Shen, 2021a) were used to compute the horizontal distance (hereafter, 'GeoDist', ranging between 0 and 114.82 m) among tree bases and the relative position between two treesin the *x*–*y* space (distance to a reference point, 'TreePos'). Tree height and plot height on the tree (*Z* coordinate) were measured with a tape from the hanging basket of the canopy crane. DBH of each tree was measured at 1.3 m above ground. The difference in DBH (hereafter, 'ΔDBH') was computed among all pairs of trees. We measured the elevation at 10 m intervals via the autopilot vehicle (LiAIR VUX-1350) equipped with VUX-1UAV Laser (RIEGL Laser Measurement Systems GmbH) and generated a 10 m resolution map with the measurements as pixel centroids using the RASTER package (Hijmans, 2021). The difference

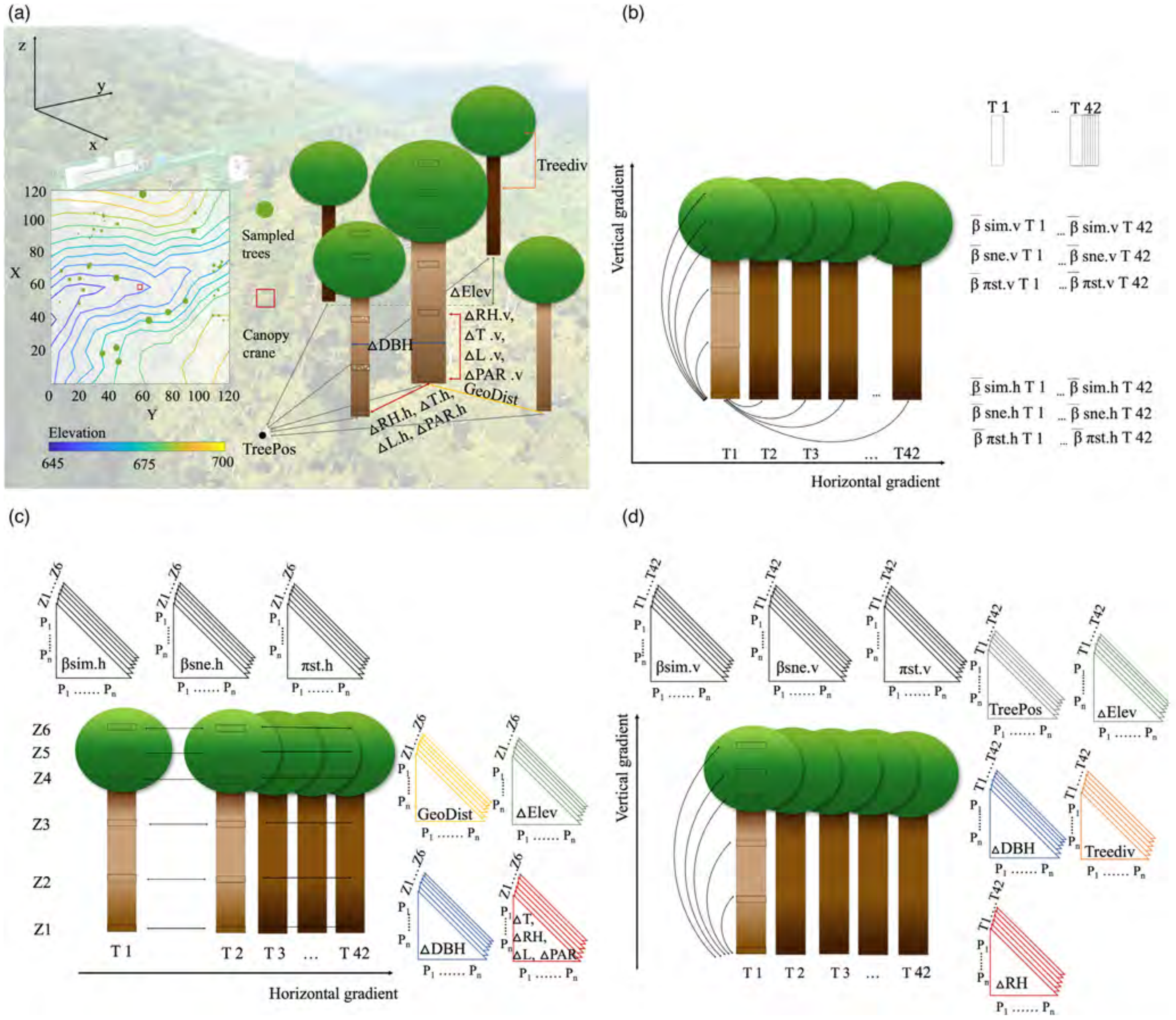


FIGURE 2 Statistical design implemented for the analysis of the turnover (βsim) and nestedness (βsne) components of beta diversity and the phylogenetic turnover (πst) among epiphytic moss and liverwort communities. (a) Factors used in the analyses. Ecological and geographic distances among plots used as predictors include the horizontal (.h) and vertical (.v) differences in relative humidity (ΔRH), temperature (ΔT), light (ΔL), photosynthetically active radiation (ΔPAR), microtopography (relative difference in elevation among trees), ΔElev, derived from a topographic map of the area (insert), a variable accounting for within vs among trunk/canopy comparisons (Treediv), a variable reporting the relative position between two trees in the *x*–*y* space (distance to a reference point, TreePos), difference in DBH among trees (ΔDBH), the geographic distance among trees (GeoDist); (b) comparisons of the vertical (.v) and horizontal (.h) variation in βsim, βsne and πst; (c) horizontal variation in βsim, βsne and πst within each of the six height zones (Z1–Z6) as a function of differences in ΔRH, ΔT, ΔL, ΔPAR, ΔDBH and GeoDist; (d) vertical variation in βsim, βsne and πst among height zones within trees as a function of ΔRH, ΔDBH, ΔElev, TreePos and Treediv.

in elevation ('ΔElev') was then computed among all pairs of trees. To characterize the main habitat difference between the trunk and the canopy, a binary variable ('Treediv') was used to describe whether plots were both located on the trunk or in the canopy. In pairwise plot comparisons, two plots located on the trunk or the canopy had a 'Treediv' of 0, whereas pairs of plots including one plot from the trunk and the other plot from the canopy had a 'Treediv' of 1. Finally, we generated a binary variable indicating whether pairs of plots being compared are located on the same tree (0) or on different trees.

Air temperature ('T', °C), relative humidity ('RH', %), photosynthetically active radiation ('PAR', μmol m^{-2} s^{-1}) and light intensity ('L', W m^{-2}) were used to characterize light and microclimatic environmental conditions. T and RH were measured by HYS15 air temperature and relative Moisture Sensors, Unism, China. PAR and L were measured by LI-190R Quantum Sensor, LI-COR Biosciences (Figure S1). These variables were recorded by 54 dataloggers every hour during 30 months from July, 2017 to December, 2019, to document the spatio-temporal variation of microclimates and calibrate microclimatic models (see below). To cover the range of vertical and horizontal microclimatic variation within the 1.44 ha plot, these dataloggers were located at regular height intervals on 12 trees scattered across the study area (Table S1). Because of datalogger failures, for instance during storm events, data could not be collected by all the dataloggers over this entire time period. To avoid missing data, we therefore averaged the values recorded for the same hour and month across years (data available at https://doi.org/10.6084/m9.figshare.17057624).

2.3 | Spatial microclimate modelling

To predict the light and microclimatic conditions at each of the 408 plots from the data collected by the 54 dataloggers, we modelled hourly variation in T, L, RH and PAR in an *X*–*Y*–*Z* space (thus including tree height and elevation) using Random Forest (Liaw & Wiener, 2002) as implemented by the RANDOMFOREST package in R v4.0.4 (R Development Core Team, 2021). Random forest is an efficient technique to model complex interactions among predictor variables (Cutler et al., 2007) and non-linear responses (Arulmozhi et al., 2021), which has increasingly been used in climatic modelling (Arulmozhi et al., 2021; Ellis & Eaton, 2021; Su et al., 2021). 80% and 20% of the data were used to train and assess the models, respectively. The models were tuned by searching the best hyperparameter values after 10-fold cross-validation (see Figure S2 for a flow chart of the protocol used). Model predictions were used to compute the Euclidian distance (ΔT, ΔRH, ΔL, ΔPAR) of the hourly difference in predicted microclimatic conditions between each pair of plots.

2.4 | Taxonomic and phylogenetic beta diversity

Taxonomic beta diversity was partitioned into nestedness (βsne) and turnover (here represented by Simpson's dissimilarity index, βsim) with the BETAPART package (Baselga & Orme, 2012). Nestedness occurs when species found at the poorest plots represent a subset of the species pool found in the richest plots (Baselga, 2010), reflecting, for example, the accumulation of species on trees with time. Species turnover, in turn, reflects the shift in species composition that typically occurs along ecological gradients, and is expected here among communities from the base to the canopy.

Phylogenetic turnover was quantified through the πst statistics, which is a measure of the average phylogenetic distance among species within versus among plots (Hardy, 2008; Hardy et al., 2012). To determine whether there was a significant phylogenetic overdispersion (πst < 0) or clustering (πst > 0) of epiphytic communities (Q2), we computed an average πst from all pairwise comparisons of plots, both within and among height zones and DBH classes. We determined whether πst was significantly lower or higher than expected by chance by comparing the distribution of observed πst values with that obtained with 100 randomized phylogenies among the tips to build the distribution of the null hypothesis. For each of the 100 randomly resolved phylogenetic trees, we re-computed the pairwise πst values among plots, which served to generate the distribution of 100 average πst among plots that would be expected if phylogenetic relationships among species were random. An observed average πst was significantly lower or higher than expected by chance if it was lower or higher than 95% of the values obtained after phylogeny permutations.

Phylogenetic distances among species pairs were computed from the moss and liverwort chronograms produced by Laenen et al. (2014). These chronograms resulted from large-scale analyses using genera as sampling units and including a single species per genus. The liverwort phylogeny was derived from the analysis of eight genes from all genomic compartments and includes 303 genera, representing 84% of the total extant generic diversity. The moss phylogeny was based on the analysis of one nuclear, one mitochondrial and one chloroplast gene and includes genera representing 64% of the total extant generic diversity of mosses. Phylogenetic trees were pruned to only keep the tips corresponding to observed species to generate suitable distributions of the null hypothesis (Hardy & Senterre, 2007). Twelve genera, which were not sampled in the phylogenies, were assigned to their closest genus based on phylogenetic evidence (Table S2). Since the phylogenies included a single species per genus, all congeneric species included in the present dataset were grafted onto the genus-level phylogeny, ensuring that phylogenetic relationships and branch lengths within genera were random and that the ages of genus crown nodes ranged between time present and the age of their stem node. In total, 100 trees with randomly resolved relationships among congeneric species were generated and separately analysed to take phylogenetic uncertainty into account. Taxa which could not be identified at the genus level were omitted from the analysis.

2.5 | Statistical analyses

Comparing vertical and horizontal patterns in βsim, βsne and πst (Q1) involves the inclusion of the same plot multiple times, violating the assumption that the observations are independent from each other. We therefore computed, for each tree, the average βsim, βsne and πst among plots on the same tree, avoiding comparisons among plots located within the same height zone. This generated a distribution of 42 average vertical βsim, βsne and πst (Figure 2b). We then computed, again for each tree, the average βsim, βsne and πst among plots between the focal tree and all other trees, making sure to restrict the comparisons among plots from the same height zone and to trees that belong to the same DBH class to avoid non-homologous comparisons (e.g. plots from the canopy of a 9 m and 70 m tree). The categories considered were small trees (DBH of 5.4–19.6 cm, $n = 16$), medium trees (DBH of 20.3–39.6 cm, $n = 15$), and large trees (DBH of 66.9–135 cm, $n = 11$). This generated 42 average horizontal βsim, βsne and πst distributions (Figure 2b). The vertical and horizontal distributions of average βsim, βsne and πst significantly departed from normality (Kolmogorov–Smirnov test, $p < 0.001$) and homoscedasticity (Bartlett's test, $p < 0.001$) for both mosses and liverworts. We therefore applied a paired Wilcoxon rank test to test the hypothesis that, on average, vertical βsim, βsne and πst are larger than horizontal βsim, βsne and πst values.

To disentangle the contribution of the factors affecting βsim and βsne along horizontal and vertical gradients, we implemented Generalized Dissimilarity Modelling (GDM; Ferrier et al., 2007). Because the GDM program needs values in the biological dissimilarity matrix ranging between 0 and 1, πst values were rescaled accordingly in these analyses. For horizontal gradients, we generated six matrices (Figure 2c), each of which encompassed all pairwise comparisons among plots located within the same height zone within and among trees. Predictors included GeoDist, ΔDBH, ΔElev, ΔT, ΔRH, ΔL and ΔPAR among each pair of plots. For the vertical patterns, we focused on pairs of plots located on the same tree and generated a matrix including all pairwise plot comparisons within the 42 trees (Figure 2d). Predictors included ΔT, ΔRH, ΔL, ΔPAR and Treediv. To inform the model of the structure in the data, wherein only within-tree comparisons were allowed, we added the variable TreePos.

To circumvent collinearity among predictors, we computed, for each analysis, the correlation between environmental predictors as well as the variation inflation factor (VIF). If any of the predictors exhibited a VIF >5, the predictor with the highest VIF was removed. The VIF of the remaining variables was re-computed, and so on until all predictors had a VIF <5 (Akinwande et al., 2015). We then performed variable significance testing with 50 permutations per step until only significant ($p < 0.05$) variables remained in the model. We finally estimated the contribution of each variable to the model using the gdm.varImp function (Fitzpatrick et al., 2021).

To determine how πst varies along environmental gradients, we performed analyses at the level of average πst within and among communities and pairwise πst among plots. We visualized the variation of average πst per DBH class and height zone as a function of an ordinal ecological distance, computed as the number of height zone difference between communities. The significance and strength of this relationship was assessed with a Mantel test (VEGAN package, Oksanen et al., 2020). We then performed a second series of analyses using pairwise plot comparisons using the GDM framework described above.

3 | RESULTS

3.1 | Microclimatic modelling

Microclimatic conditions exhibited substantial vertical variations (Figure 1a). Between 2 and 62 m above ground, day (8 am–7 pm) RH ranged between 53.6% and 99.9% (monthly average 79.7–93.5%), day temperature between 12.0 and 31.7°C (monthly average 17.8–27.8°C), light intensity between 2.3 W m^{-2} and 208.0 W m^{-2} (monthly average 27. 8–51.0 W m^{-2}), and PAR between 0.0 μmol m^{-2} s^{-1} and 407.6 μmol m^{-2} s^{-1} (monthly average 41.4–94.0 μmol m^{-2} s^{-1}). Average variations ± standard deviation (SD) in the day between 2 m and 50 m were of 2.4 ± 1.6°C for temperature, −16.7 ± 10.2% for RH, 85.0 ± 47.3 W m^{-2} for light intensity, and 128.0 ± 77.1 μmol m^{-2} s^{-1} for PAR. Horizontal variation was more subtle (Figure 1b), with average maximum variations (differences between maximum and minimum) in the day at 2 m and at 50 m reaching, respectively, 0.9 ± 0.5°C and 0.5 ± 0.3°C for temperature, 4.4 ± 1.9% at and 3.3 ± 2.1% for RH, 13.1 ± 13.5 W m^{-2} and 24.2 ± 18.0 W m^{-2} for light, 12.7 ± 12.4 μmol m^{-2} s^{-1} and 48.9 ± 40.4 μmol m^{-2} s^{-1} for PAR. This variation was captured by Random Forest models, with R^2 ranging from 0.96 for PAR to 0.99 for temperature (Figure S3; Table S3).

3.2 | Species richness and composition

Totals of 50 moss and 52 liverwort species were recorded (Table S4). The base (zone 1) was dominated by *Circulifolium microdendron*, *Caduciella mariei* and *Claopodium prionophyllum*. Along the trunk (zones 2–3), *Plagiochila parviramifera* and *Plagiochila fordiana* prevailed on small trees, and *Frullania monocera*, *Mastigolejeunea repleta* and *Caduciella mariei* on large trees. The most representative species were *Erythrodontium julaceum* and *Groutiella tomentosa* in the inner canopy of large trees, *Lejeunea flava*, *Cheilolejeunea eximia* and *Groutiella tomentosa* in the inner canopy of medium and large trees, and *Frullania ericoides*, *Acrolejeunea recurvata* and *Sematophyllum subhumile* in the outer canopy of large trees. The most frequent epiphylls were *Caudalejeunea reniloba*, *Cololejeunea planissima* and *Leptolejeunea subacuta*.

In mosses, species richness decreased from the base, with an average ± (SD) of 4.5 ± 1.5 species per plot (14.5 ± 3.3 species per DBH class) to 2.6 ± 1.0 species per plot (4.5 ± 2.5 species per DBH class) in the outer canopy of large trees. In liverworts in contrast, species richness increased from the base (small trees), with 1.4 ± 0.5 species per plot (7.6 ± 2.7 species per DBH class), to the outer canopy, with 2.9 ± 1.3 species per plot (12.3 ± 6.9 species per DBH class) on large trees (Figure 3).

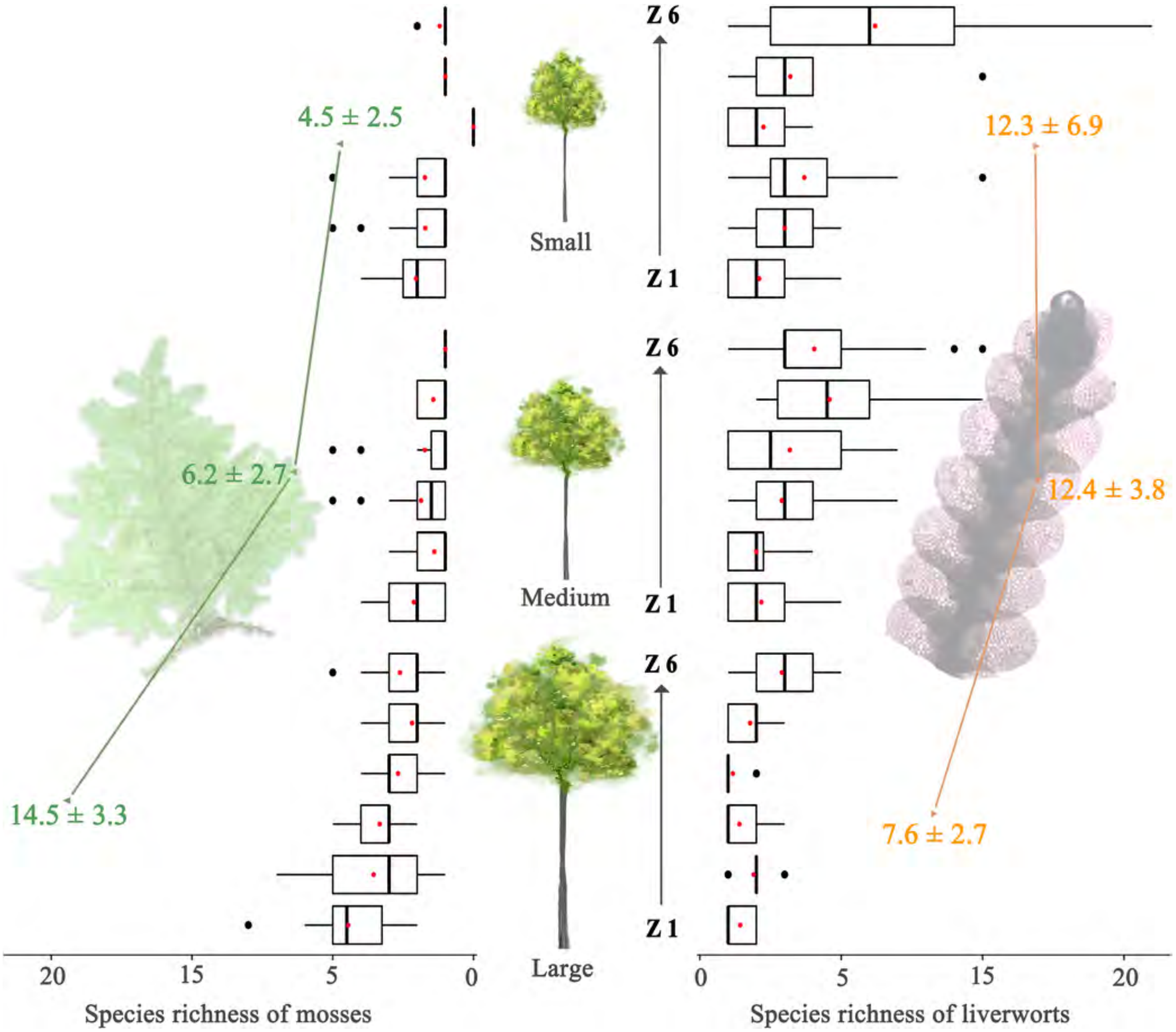


FIGURE 3 Vertical variation in species richness of epiphytic mosses (left) and liverworts (right) in a 1.44 ha tropical canopy crane facility, Yunnan, SW China. The box-plots [showing the first and third quartiles (upper and lower bounds), second quartile (center), average (red dots), 1.5* interquartile range (whiskers) and minima–maxima beyond the whiskers] represent species richness per height zone on small (DBH of 5.4–19.6 cm, $n = 16$), medium (DBH of 20.3–39.6 cm, $n = 15$) and large (DBH of 66.9–135.0 cm, $n = 11$) *Parashorea chinensis* individuals. The line represents the average (mean ± SD) of moss (green triangles) and liverwort (orange triangles) species richness per DBH class.

3.3 | Taxonomic beta diversity

Turnover contributed about three- to fivefold more to taxonomic beta diversity than nestedness (Figure 4). Vertical turnover of moss and liverwort communities was significantly higher than horizontal turnover (average ± SD of vertical βsim = 0.59 ± 0.25 and 0.66 ± 0.24, average horizontal βsim = 0.42 ± 0.20 and 0.50 ± 0.16 in mosses and liverworts, respectively, $p < 0.001$ for the differences between vertical and horizontal βsim in both mosses and liverworts). Nestedness exhibited the reverse pattern (average horizontal βsne = 0.15 ± 0.07 and 0.14 ± 0.06, average vertical βsne = 0.11 ± 0.09 and 0.14 ± 0.06 in mosses and liverworts, respectively, $p < 0.001$ for the differences between vertical and horizontal βsne in both mosses and liverworts).

In GDM analyses focusing on the horizontal variation in taxonomic turnover within the same height zone, which accounted, on average, for 19.3 ± 21.8% (mosses) and 11.1 ± 2.6% (liverworts) of the explained deviance across height zones, the difference in DBH among trees was the best predictor, with a relative contribution ranging between 64.7% and 99.8% across height zones (Table S5). For horizontal nestedness, no model was significant except for liverworts in height zone 2 (Table S5).

In analyses focusing on the vertical variation in beta diversity (Figure S4), models contributed to 33.3% and 17.8% of the total deviance of species turnover in mosses and liverworts, respectively. Difference in RH among plots was the most important variable in the model, contributing to 98.8% and 83.0% of the deviance in species turnover of mosses and liverworts, respectively, while Treediv

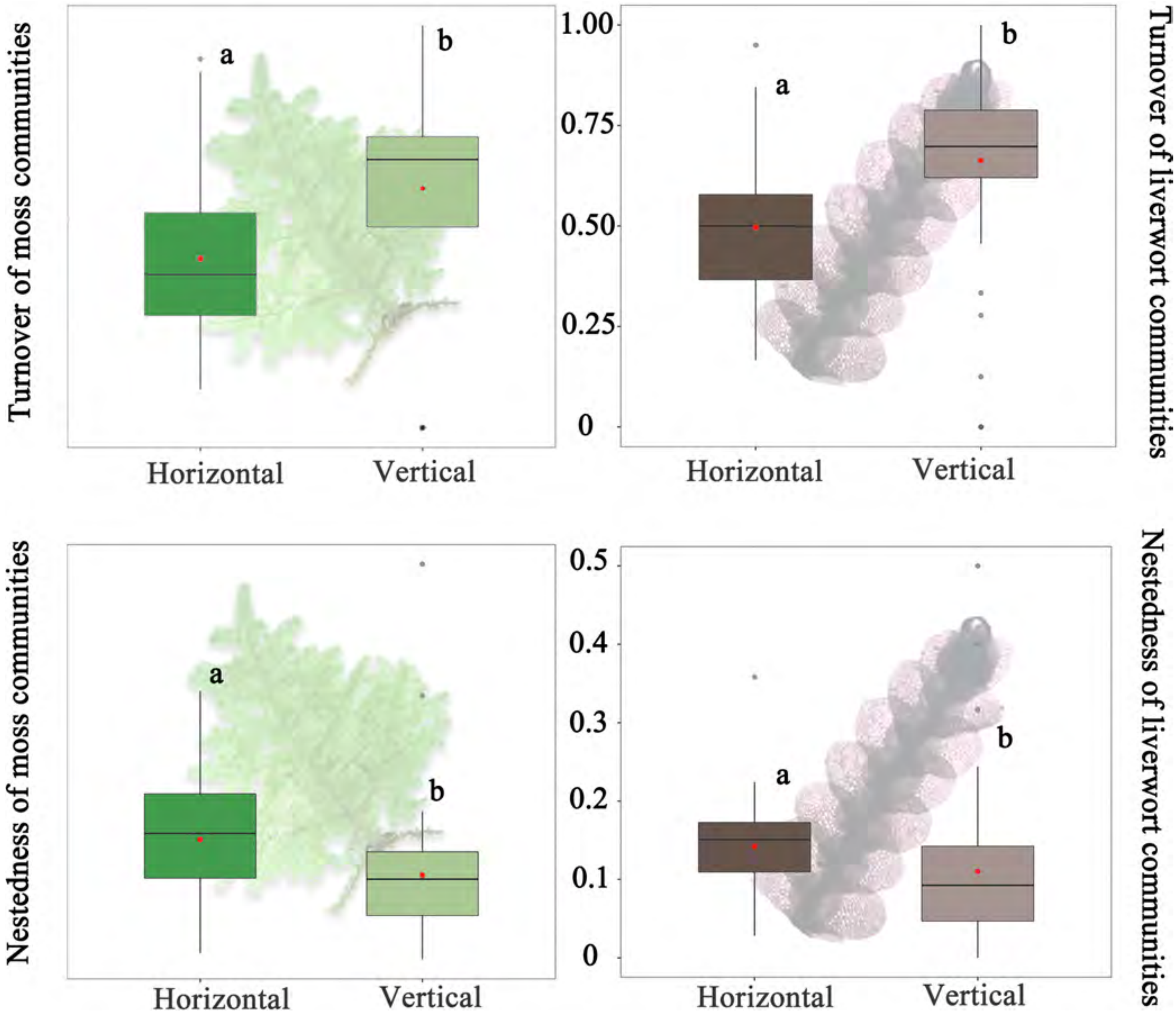


FIGURE 4 Vertical and horizontal patterns of turnover and nestedness in epiphytic mosses and liverworts on *Parashorea chinensis* in a 1.44 ha tropical canopy crane facility, Yunnan, SW China. Box-plots [showing the first and third quartiles (upper and lower bounds), second quartile (center), average (red dots), 1.5* interquartile range (whiskers) and minima-maxima beyond the whiskers] represent the vertical turnover, nestedness for pairs of plots on the same tree and horizontal turnover, nestedness within the same height zone and among trees belonging to the same class of diameter at breast height (DBH; small trees, DBH of 5.4–19.6 cm, medium trees, DBH of 20.3–39.6 cm, and large trees, DBH of 66.9–135 cm) of moss and liverwort epiphytic communities. Letters above each box-plot indicate which comparisons significantly differ.

contributed to less than 1% and 15%. No model was significant for the vertical variation in nestedness.

3.4 | Phylogenetic turnover

Average πst per height zone and DBH class significantly increased ($r = 0.25$, $p < 0.001$ for liverworts and $r = 0.09$, $p < 0.001$ in mosses) and shifted from mostly non-significant or rarely significantly negative (at the base of small trees in both mosses and liverworts and in the outer canopy of large trees in mosses, Table S6) to consistently significantly positive along a gradient of height zone differences (Figure 5).

In pairwise plot comparisons, horizontal phylogenetic turnover could not or could marginally be predicted from horizontal variation in microclimatic conditions and differences in DBH among trees (Table S5). For vertical phylogenetic turnover (Figure S5), the GDM accounted, on average across the 100 phylogenetic trees randomly resolved among congeneric species, for 6.6 ± 0.3% and 11.5 ± 0.7% of the total deviance in mosses and liverworts, respectively. In mosses, the best predictor was RH, which contributed to more than 99% of the explained deviance. A different pattern was observed in liverworts, where the variable accounting for within versus among trunk/canopy comparisons accounted for 65.6 ± 3.3% of the explained deviance, while the position of each individual tree in the

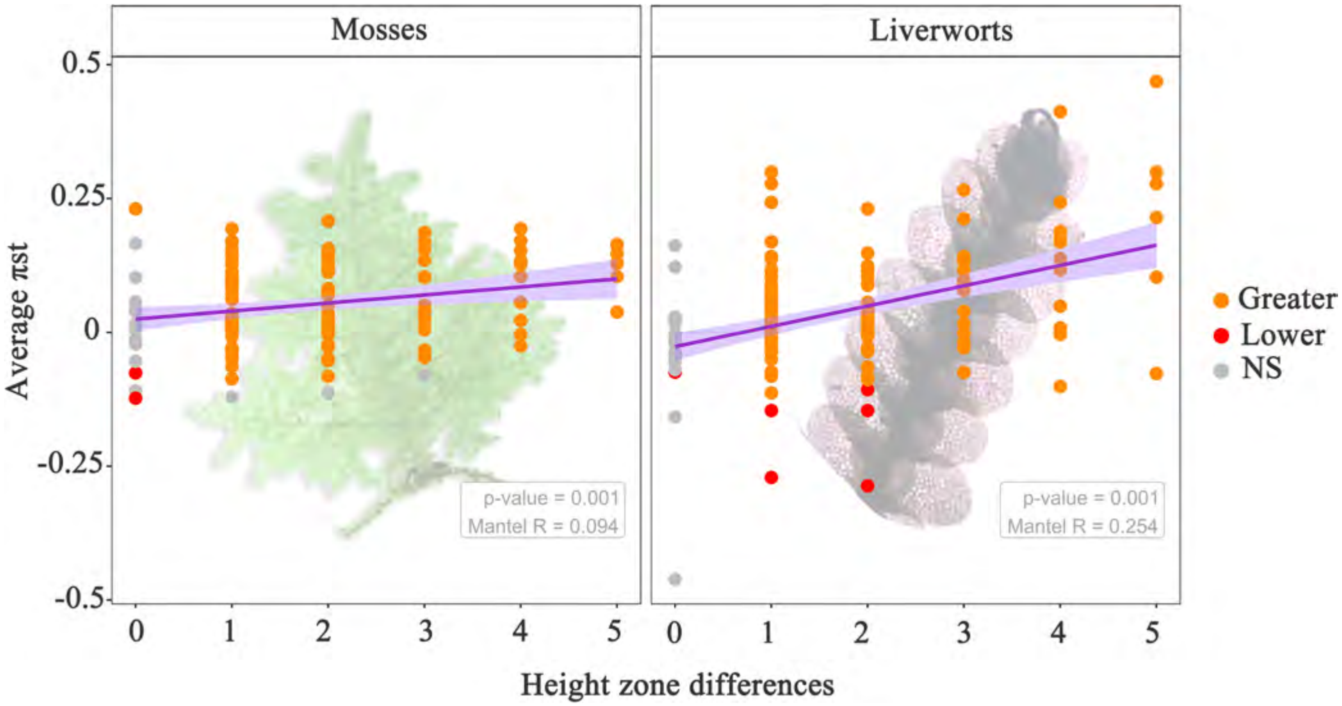


FIGURE 5 Variation of average phylogenetic turnover within epiphytic moss and liverwort communities from the same height zone and on trees from the same DBH class in a lowland dipterocarp forest (Xishuangbanna, Yunnan, SW China) along a gradient of height zone difference. Average πst for a given environmental distance class that were significantly greater, significantly lower, and non-significantly (NS) different than expected by chance, are represented by orange, red and grey dots, respectively.

x-y space and RH each contributed to less than 20% of the explained deviance.

4 | DISCUSSION

The microclimatic data reported here and their three-dimension modelling help to fill a gap in our knowledge of the spatial variation of forest microclimates and to address the question of how microclimatic variation within and below tree canopies impacts community species richness and composition (De Frenne et al., 2019; Ellis & Eaton, 2021; Murakami et al., 2022). In line with previous assessments of microclimatic variation within canopies (see Murakami et al., 2022 and references therein), variations in temperature and RH were progressively buffered from the canopy to the tree base, with a substantially higher day/night difference in temperature and RH in the canopy. Monthly average temperatures of 28.9°C were recorded in the upper canopy and 26.1°C at the base, in line with previous reports of a mean difference of 4°C between forest understory and open ground due to the absorption of solar radiation by the canopy and increased evapotranspirative cooling (De Frenne et al., 2019).

The much wider range of vertical versus horizontal variation in microclimatic conditions explains why vertical species turnover is significantly higher than horizontal species turnover, despite the large differences in habitat conditions between young and old trees in terms of bark texture and chemistry (Fritz & Heilmann-Clausen, 2010; Fritz, Niklasson, & Churski, 2009; Wagner et al., 2015) as well as the effect of time, reflected by age differences among host trees, which impacts on the likelihood of colonization (Hidasi-Neto et al., 2019). Due to the prevalence of vertical microclimatic gradients, the contribution of nestedness to vertical beta diversity is negligible because specialist species segregate among height zones. In Amazonian rainforests for instance, more than half of the epiphyte species are height-zone specialists (Mota de Oliveira et al., 2009). Consequently, communities from the canopy share almost no species with communities from the tree base, preventing any nested pattern from emerging.

Our models accounted for 33% and 18% of the variation in vertical turnover in mosses and liverworts, respectively, and the predominant contributions of microclimatic factors (83–98%) to this pattern evidences their crucial role in determining the composition of epiphytic communities. The similar explanatory power of microclimatic conditions for moss and liverwort species turnover hides, however, opposite patterns of species richness in the two groups, with moss richness decreasing and liverwort richness increasing from the base to the canopy. Horizontal turnover in the two groups was similarly explained by the same factor, that is, tree size, but moss species richness peaked on large trees, while liverwort species richness peaked on small trees. Epiphytic moss and liverwort community composition thus responded in an opposite way to the same gradients, highlighting substantial differences in niche preferences between them. In vascular epiphytes, large, old trees tend to host a higher epiphytic richness than young ones due to the larger amount of time for colonization, larger space availability and greater diversity of microhabitats (Mayumi Francisco et al., 2021; Patiño et al., 2018; Zotz & Schultz, 2008; Zotz & Vollrath, 2003), and have therefore been a major focus for conservation (Adhikari et al., 2021; Wang et al., 2017). Our results suggest that epiphytic bryophyte diversity assessments in tropical forests must also include small, understorey trees (Sporn et al., 2010), which should also be considered for conservation.

Despite a comprehensive set of environmental variables, our models accounted for only 1/5–1/3 of the variation in species turnover, within the range of similar analyses for vascular epiphytes (0.10–0.57, Zotz & Schultz, 2008; Woods et al., 2015). Although additional variables characterizing microhabitat conditions, such as bark texture and chemistry, branch diameter, or percentage cover of canopy humus (Woods et al., 2015), would certainly increase model accuracy, we interpret the large proportion of unexplained variance in terms of stochasticity associated with dispersal limitations. Although epiphytes need to track patches of suitable trees (or leaves in the case of epiphylls) in a dynamic landscape for persistence (Snäll et al., 2005), mounting evidence suggests that dispersal capacity is counter-selected in epiphytic bryophytes. Epiphytic bryophytes typically exhibit spatially clustered distributions (Löbel et al., 2006; Snäll et al., 2003; Wagner et al., 2015) and their fine-scale patterns of genetic variation are strongly spatially structured (Ledent et al., 2020; Vanderpoorten et al., 2019), pointing to important effects of isolation-by-distance. These patterns are paralleled by morphological adaptations counter-favouring dispersal. For instance, the peristome, a ring of hygroscopic teeth that enhance spore dispersal in mosses, and the seta, which elevates the capsule above the substratum, are typically reduced in epiphytic species (Hedenäs, 2012). Peristome reduction is itself significantly associated with hygrochasy, i.e., the release of spores under wet conditions (Zanatta et al., 2018), further decreasing chances of long-distance dispersal but enhancing rates of establishment (Johansson et al., 2016).

The shift between negative or non-significant average phylogenetic turnover to consistently significant clustering that was observed along a gradient of height zone differences suggests that phylogenetic constraints further contribute to shaping the assembly of epiphytic bryophyte communities. The slight, but significant correlation between this trend for an increasing phylogenetic clustering with variation in microclimatic conditions adds to emerging evidence for the role of phylogenetic niche conservatism in community assembly through time (Saladin et al., 2019; Segovia et al., 2020), including at the much smaller spatial scales of epiphytic communities. Phylogenetic niche conservatism in epiphytic bryophyte communities, along with mounting evidence for niche conservatism in vascular epiphytes (Müller et al., 2017), shows that the specialization for vertical niches and their associated microclimatic conditions is phylogenetically inheritable, and hence, that species may be limited in their ability to shift among niches. The deep phylogenetic level (genus-level phylogeny), at which the analysis was conducted, further points to deeply nested phylogenetic constraints, which may have evolved during the burst of diversification of epiphytic lineages triggered by the development of large, humid, megathermal angiosperm forests (Feldberg et al., 2014).

The fact that there was no significant horizontal phylogenetic clustering of liverworts communities, and that the horizontal phylogenetic clustering observed in moss communities was not explained by differences in DBH among trees, conversely suggests that the succession of communities on a tree depending on its age is not phylogenetically constrained. Typically, early pioneers are short-lived organisms with a high reproductive effort, whereas late-colonizers have a longer lifespan and are characterized by limited reproductive investment (During, 1992). Although restricted to a set of 42 trees in a specific 1.44 ha plot, our results thus suggest that these life-history strategies arose multiple times during the evolutionary history of epiphytes.

The negative πst observed at tree base in mosses and liverworts is consistent with the expectation that competition in epiphytic communities should occur at levels characterized by lower variation of daily and seasonal microclimatic conditions rather than high-up in the canopy (Spicer & Woods, 2022). Although even strong competition levels can leave no trace in community phylogenetic structure (Bennett et al., 2013), the non-significant phylogenetic turnover that mostly characterized communities from the same height zone and trees of the same DBH class does not support the idea that competition plays an important role in shaping epiphytic bryophyte communities. In vascular epiphytes of lowland rain forests, which use only a small proportion of the available bark surface, the importance of competition has been similarly questioned (Zotz, 2016; Zotz & Vollrath, 2003). Competition could, however, be more important in montane forests, where epiphytes are typically much more abundant (Burns & Zotz, 2010). Instances of niche displacement were already reported among epiphytic bryophytes (Wiklund & Rydin, 2004), raising a series of questions on how species may shift niche to avoid competition.

5 | CONCLUSIONS

We provide here, through the spatially-explicit modelling of microclimatic conditions in a tropical forest, explicit support for the long-held notion that vertical variation in light, temperature and humidity conditions are the main driver of epiphytic species turnover along a tree. Epiphytic bryophyte communities were phylogenetically clustered, and the low, but significant correlation between phylogenetic turnover among communities and vertical microclimatic variation evidences fine-scale phylogenetic niche conservatism. Despite the comprehensive description of the host-tree environment, our analyses captured, however, only 1/5–1/3 of the floristic variation among communities, calling for further improvements and opening the door to new research perspectives. First, our analyses did not allow us to assess the potential role of positive interactions. In vascular epiphytes, positive co-occurrence patterns suggest potential facilitation (Burns & Zotz, 2010; Ceballos et al., 2016), as a dense clumping of epiphytes could enhance temperature and drought stress, which is expected to increase towards the outer canopy (Spicer & Woods, 2022). Second, our analyses failed to consider bryophyte-vascular epiphyte interactions, whose role in the structuring of bryophyte communities should be further investigated as vascular and bryophytic epiphytes significantly co-occur (Lu et al., 2020; Zotz & Vollrath, 2003).

The tight link between community composition and microclimatic conditions, as well as evidence for niche conservatism, raise questions about the ability of epiphytic bryophyte communities to move down along the trunk to track the shift of their niche in the context of climate change. How macroclimatic changes will impact the changes within canopies remains, however, uncertain. While the statistical modelling of microclimatic conditions as we implemented here may successfully capture the spatial variation of microclimatic conditions, the potential of such approaches to forecast novel conditions is somewhat questionable, calling for the development of mechanistic models based on first-principles physics (Maclean & Klinges, 2021).

AUTHOR CONTRIBUTIONS

A.V., T.S., L.S., R.T.C. conceived the study. T.S., L.S., W.-Z.M., J.W., Y.--M.W., L.M. and Y.L. collected the data. T.S., F.C., T.K., Y.S. and L.M. performed the analyses. F.C., X.L.G., J.P. and O.H. provided suggestions throughout the process. A.V., T.S., R.T.C. and L.S. wrote the paper with the assistance from all co-authors.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The raw information on each individual tree and epiphytic species distribution data are available at https://doi.org/10.6084/m9.figshare.17057615.v8 (Shen, 2021a). The microclimatic data are available at https://doi.org/10.6084/m9.figshare.17057624 (Shen, 2021b).

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Strong elevation-dependence of cross-taxon diversity patterns in plants

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Abstract:	Cross-taxon congruence, the degree of similarity in the diversity patterns across different taxonomic groups, raises the fundamental question of what processes shape biodiversity, and hence has substantial implications for developing conservation strategies. Cross-taxon congruence is expected due to biotic interactions or the sharing of similar responses to environmental variation among taxa, but varies depending on spatial resolution and diversity metrics. Here, we examine how the strength of the cross-taxon correlation and its underlaying mechanisms vary among major plant lineages at fine resolution along a 375 to 3210m elevation gradient. A database of bryophyte and spermatophyte species distributions and environmental conditions in 413 plots of 4m² in the Western Swiss Alps was combined with phylogenomic data to compute

taxonomic and phylogenetic α and β diversity metrics. Spatial error simultaneous autoregressive models were employed to analyze the variation of the cross-taxon correlation with regard to variation in topography, climatic conditions, soil conditions and land cover across the entire elevation gradient and within each elevation belt. Cross-taxon congruence was much higher for taxonomic than phylogenetic diversity, indicating that similar ecological processes or direct interactions shape species richness and community composition among land plant taxa, but that the evolutionary mechanisms shaping the phylogenetic structure of their communities differ along an elevation gradient. Global patterns of cross-taxon correlations across the entire gradient hid elevation-dependent variations. The strength of the correlation between moss and spermatophyte species richness increased with elevation. The high cross-taxon correlation in species richness above the treeline remained significant and its strength dropped by about 1/3 when controlling for environmental variation, pointing to the contribution of both shifts towards common environmental factors and direct biotic interactions in shaping the observed cross-taxon correlation patterns. Cross-taxon correlations of species turnover also varied in strength with elevation but exhibited a hump-shape pattern reflecting the peak of species turnover displayed by mosses and spermatophytes at mid-elevation. The differences in the ecological and evolutionary mechanisms shaping diversity patterns among groups depending on environmental conditions warrant taxon-specific approaches, casting doubts about the usefulness of spermatophytes as surrogates of bryophytes in conservation planning.

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Keywords: bryophytes; cross-taxon congruence; elevation gradient; phylogenetic diversity; species richness; species turnover; spermatophytes.

Open Research statement: The bryophyte and spermatophyte distribution data matrices are available at http://doi.org/10.6084/m9.figshare.22778636. The abiotic conditions in each plot were characterized by 68 variables of topography, climatic conditions, soil conditions and land cover at a spatial resolution of 2–25 m (data matrix available at http://doi.org/10.6084/m9.figshare.22778636). The phylogenomic data are currently being submitted to NCBI.

Abstract.

Cross-taxon congruence, the degree of similarity in the diversity patterns across different taxonomic groups, raises the fundamental question of what processes shape biodiversity, and hence has substantial implications for developing conservation strategies. Cross-taxon congruence is expected due to biotic interactions or the sharing of similar responses to environmental variation among taxa, but varies depending on spatial resolution and diversity metrics. Here, we examine how the strength of the cross-taxon correlation and its underlaying mechanisms vary among major plant lineages at fine resolution along a 375 to 3210m elevation gradient. A database of bryophyte and spermatophyte species distributions and environmental conditions in 413 plots of $4m^2$ in the Western Swiss Alps was combined with phylogenomic data to compute taxonomic and phylogenetic α and β diversity metrics. Spatial error simultaneous autoregressive models were employed to analyze the variation of the cross-taxon correlation with regard to variation in topography, climatic conditions, soil conditions and land cover across the entire elevation gradient and within each elevation belt. Cross-taxon congruence was much higher for taxonomic than phylogenetic diversity, indicating that similar ecological processes or direct interactions shape species richness and community composition among land plant taxa, but that the evolutionary mechanisms shaping the phylogenetic structure of their communities differ along an elevation gradient. Global patterns of cross-taxon correlations across the entire gradient hid elevation-dependent variations. The strength of the correlation between moss and spermatophyte species richness increased with elevation. The high cross-taxon correlation in species richness above the treeline remained significant and its strength dropped by about 1/3 when controlling for environmental variation, pointing to the contribution of both shifts towards common environmental factors and direct biotic interactions in shaping the observed cross-taxon correlation patterns. Cross-taxon correlations of species turnover also varied in strength with elevation but exhibited a hump-shape pattern reflecting the peak of species turnover displayed by mosses and spermatophytes at mid-elevation. The differences in the ecological and evolutionary mechanisms shaping diversity patterns among groups depending on environmental conditions warrant taxon-specific approaches, casting doubts about the usefulness of spermatophytes as surrogates of bryophytes in conservation planning.

Introduction

Cross-taxon congruence refers to the degree of similarity or correlation in the diversity patterns across different taxonomic groups (Serrana et al., 2025, and references therein). Whether diversity patterns are congruent across taxa raises the fundamental question of what processes shape biodiversity, and hence, has substantial implications for developing conservation strategies. Cross-taxon congruence indeed suggests that well-studied taxa can serve as surrogates for other taxa, making it possible to design simplified, standardized and efficient tools for biodiversity monitoring and conservation planning (Larrieu et al., 2018).

In practice, cross-taxon congruence analyses have yielded very contrasting results (Westgate et al., 2014; Larrieu et al., 2018). Cross-taxon congruence strongly depends on spatial scale, which determines the factors shaping the variation of diversity patterns (Toranza & Arim 2010; Ekroos et al., 2013). At large scales, cross-taxon congruence has been recurrently reported because certain factors, in particular macroclimatic conditions, act as common drivers of diversity patterns through their control over the availability of water and energy. At finer scales in contrast, competitive interactions may lessen the congruence of cross-taxon diversity patterns (van Rensburg et al., 2002; Rahbek, 2005).

Three main hypotheses have been proposed to explain the variation of the cross-taxon congruence among taxa (Toranza & Arim, 2010). Cross-taxon congruence typically occurs when one taxon has a direct impact on another taxon through biotic interactions, for instance, when one taxon provides food resources or shelter for another taxon. Cross-taxa congruence may also occur as a result of shared biogeographic history among taxa. Finally, different taxa may share common diversity patterns because they exhibit similar responses to environmental variation.

Cross-taxon congruence also largely varies depending on the metrics of diversity employed. Three levels of species diversity can be distinguished in biological communities: species richness within communities (α diversity), the extent of change among communities (β diversity), and the species diversity of a number of community samples (γ diversity), resulting from both the α diversity within each sample and the β diversity among them (Whittaker, 1960). These three levels of diversity can be quantified based on species composition (taxonomic diversity), the variation of traits (functional diversity) or the degree of phylogenetic relatedness among species (Le Bagousse-Pinguet et al., 2019), which can provide insight into community assembly processes (Webb et al., 2002). Phylogenetic clustering occurs when species within communities are more phylogenetically similar to each other than expected by chance, pointing to shared adaptations to local environmental conditions, and hence, to phylogenetic niche conservatism (Webb et al., 2002). Conversely, phylogenetic overdispersion occurs when species from the same community are more phylogenetically distant than expected by chance, pointing to competition among related species sharing limited resources within the same niche (Anacker & Strauss, 2014; Wiens & Graham, 2005).

Mounting evidence has revealed more inconsistency in cross-taxon congruence patterns as measured by α diversity (Vessby et al., 2002; Santi et al., 2010) than by β diversity (McMullan-Fisher et al., 2009; Westgate et al., 2017). In fact, factors influencing the α diversity of different taxa might operate independently or through different mechanisms, whereas environmental heterogeneity between sites may have a common influence on the patterns of pairwise dissimilarities of species composition (Serrana et al., 2025). Fewer studies employed phylogenetic diversity to measure cross-taxon congruence (Franke et al., 2020), revealing considerable differences among taxa in the same area (Zupan et al., 2014; Franke et al., 2020).

Elevational gradients offer an appealing framework to analyse cross-taxon diversity patterns and determine their underlaying mechanisms (Ramos et al., 2024). Elevation gradients span several climatic zones across short distances, thereby maximizing the strength of the environmental filter over spatial effects on diversity patterns (Graham et al., 2014). The increasingly harsh conditions that prevail towards high elevation suggest that the composition of high-elevation communities is under stronger environmental control than that of lowland communities (Pottier et al., 2013; Klanderud et al., 2015). In turn, the stress gradient hypothesis posits that biotic interactions shift from competition to facilitation under harsh conditions (Soliveres & Maestre, 2014), raising the hypothesis that vegetation architecture plays an increasing role to explain community composition towards high elevation. Furthermore, the large body of studies on diversity patterns along an elevation gradient offers a suitable framework to develop a hypothetical framework for cross-taxon correlations. Species richness along elevational gradients typically decreases or exhibit a hump-shaped relationship (McCain & Grytnes, 2010), with an optimum elevation that varies among taxa (Grau et al., 2007). In contrast, different patterns of phylogenetic diversity (expressed as average phylogenetic dispersion of the species within the community, thus independently from species richness) along elevational gradients have been reported, involving either an increase (Hawkins et al., 2014; Li et al., 2014; Liang et al., 2023; Banares-de-Dios et al., 2024), a decrease (Shooner et al. 2018; Di Musciano et al., 2024), or a (multi) modal relationship (Rana et al., 2019; Li et al., 2022) of phylogenetic relatedness among species within communities.

A substantial literature on the variation of gamma diversity along an elevation gradient has relied on distribution data obtained by populating elevation bands based on published species elevation ranges (Rana et al., 2019; Li et al., 2022; Di Musciano et al., 2024; Qian et al., 2024). This approach offers a macro-ecological perspective of diversity patterns along elevation gradients, but assumes that all species automatically occupy all the bands within their elevation range, and thus de facto generates a strong relationship between γ diversity and elevation, regardless of local environmental variation, spatial effects and biotic interactions. Most importantly, a macro-ecological approach does not allow for an evaluation of the variation of the strength of the cross-taxon correlation depending on elevation and its underlaying mechanisms along an elevation gradient.

Here, we examine the extent to which bryophyte and spermatophyte diversity patterns at fine resolution are spatially correlated within and among elevation belts along an elevation gradient. The ambiguity of previous reports on the correlation of species richness patterns between bryophytes and spermatophytes (Pharo et al., 2000; Bagella, 2014; Jiang et al., 2024) may reflect two opposite trends. On the one hand, bryophytes differ from tracheophytes in a series of morphological (and in particular, size) and ecophysiological traits, such as poikilohydry, strong reliance on rainfall for water uptake, large tolerance to freezing but high sensitivity to long periods of drought and high temperatures (see He et al., 2016, for review). On the other hand, the microenvironmental variation encountered within the bryophyte layer is mediated by the presence and structure of overlying tracheophytes. There is a trade-off between the shade provided by herb cover, protecting the underlying moss layer from desiccation, and the competition with dense herbaceous layers (Bergauer et al., 2022). Several studies demonstrated the persistence of cross-taxon congruence when the environmental effects on taxa diversity have been controlled, supporting the idea that vegetation structure contributes to correlated cross-taxon diversity patterns (Toranza & Arim, 2010).

Based on an extensive fine resolution plot sampling across land plants along an elevation gradient and phylogenomic data for mosses and liverworts, we address the following questions:

To what extent are bryophyte and spermatophyte diversity patterns correlated at fine resolution along an elevation gradient (Q1a), and how does the strength of theses cross-taxon correlations vary with increasing elevation (Q1b)? Is the congruence of the diversity patterns among taxa explained by their common response to environmental drivers and/or by direct nursing effects of one taxon on the other (Q2a), and how does the contribution of these factors to cross-taxon diversity patterns vary from low to high elevation (Q2b)?

2. Material and methods

2.1. Study area, vegetation sampling and environmental data

This study took place in the Vaud Alps (Western Switzerland) within an area of approximately 700 km^2 with an elevation ranging from 375 m to 3210 m. The area was selected because of the availability of a wide range of biotic and abiotic information collected in the framework of Rechalp (http://rechalp.unil.ch), a geodatabase of scientific metadata including detailed information on soil, climate and topography. The survey was limited to open, non-woody vegetation only, including grasslands, meadows, rocks and screes, and followed a random-stratified sampling design based on elevation, slope and aspect (Hirzel & Guisan, 2002).

Complete bryophyte and spermatophyte inventories for 413 plots of 2 x 2 m, selected to cover the entire study area and elevation gradient and encompass a similar number of plots within each of six elevational bands (≤1000;]1000–1400];]1400–1800];]1800–2000];]2000–2200]; > 2200), were used. Plots were separated from each other by a minimum distance of

200 m to minimize spatial autocorrelation (Randin et al., 2009a). Pteridophytes were not included due to their very limited diversity among our plot samples. Spermatophytes and bryophytes were recorded between 2002 and 2022 (Randin et al., 2009b; Buri et al., 2017; Dubuis et al., 2011, and ongoing sampling) and between 2017 and 2021 (Collart et al., 2024), respectively. The bryophyte and spermatophyte distribution data matrices are available at http://doi.org/10.6084/m9.figshare.22778636. The abiotic conditions in each plot were characterized by 68 variables of topography, climatic conditions, soil conditions and land cover at a spatial resolution of 2–25 m (data matrix available at http://doi.org/10.6084/m9.figshare.22778636).

2.2. Diversity metrics

Four diversity metrics of taxonomic and phylogenetic α and β diversity were computed. A diversity metrics included species richness and the mean phylogenetic distance (MPD) among species within a plot. β diversity metrics included taxonomic turnover, quantified by Simpson's dissimilarity index βsim (Baselga, 2010), and phylogenetic turnover, quantified by PIst (Hardy, 2008; Hardy et al., 2012). βsim and PIst were computed using the package *Betapart* (Baselga et al., 2012) and *spacodiR* (Eastman et al., 2011), respectively. Both metrics are uncorrelated to species richness (Baselga, 2010; Kasprzyk et al., 2025). All the phylogenetic diversity metrics employed are independent from taxonomic diversity (Kasprzyk et al., 2025) and were initially computed for each plot (MPD) or pair of plots (PIst) with at least two species. Nevertheless, these metrics can exhibit large ranges of variation in species-poor communities. For example, a plot including only one thalloid and one leafy liverwort, would exhibit a large value of MPD. We therefore recomputed the phylogenetic diversity metrics, setting the minimum number of species per plot to 5 and 8 (Appendix 1)

Phylogenetic diversity metrics for spermatophytes were computed from the time-scaled phylogeny of Zanne et al. (2014). Although, with 32,223 species, this phylogeny includes a less comprehensive species sampling than subsequent megaphylogenies for angiosperms, such as that of Janssen et al. (2020), which included 36,101 species, it was based on a larger (7 vs 2 genes) molecular sampling and included a higher proportion of species recorded in the plots surveyed (67.6%, 485 out of a total of 718). The largest moss (Cox et al., 2010) and liverwort (Laenen et al., 2014) phylogenies available in terms of taxon sampling included a single species per genus and were based on a limited sampling of 3 and 8 genes, respectively. To decrease the uncertainty due to such a limited taxon and molecular sampling, we produced here novel moss ('true' mosses, excluding Sphagnopsida and Polytrichopsida) and liverwort phylogenies, specifically targeting the species occurring in the 413 surveyed plots. The protocols for the target capture of 894 nuclear genes in liverworts and 770 nuclear genes in mosses are described in Appendix 1. For mosses, phylogenomic data were produced for 117 out of 221 species present in the plot metacommunity (Appendix 2). We further assigned another 73 species, for which no sequence could be produced, to their congeneric sequenced species (Appendix 2). In total, 86% of moss species present in the plot metacommunity were included in the phylogeny while the remaining 14% were excluded from phylogenetic distance computations. For liverworts, phylogenomic data were produced for 36 out of 63 species and sequences for another four species were downloaded from the National Center for Biotechnology Information. Twelve species, for which no sequence could be produced, were assigned to their congeneric sequenced species (Appendix 2). In total, 83% of liverwort species present in the plot metacommunity were included in the phylogeny and the remaining 17% were excluded from phylogenetic distance computations.

To build the phylogenies of mosses and liverworts, the concatenated nucleotide alignments were analyzed under maximum likelihood (ML) following Liu et al. (2019) and Bechteler et al. (2023). Using the parallel version of RAxML-NG v1.2.0 (Kozlov et al., 2019), the ML trees were first inferred under the GTR+Γ model with default parameters and a partition by genes (894 genes for liverworts and 770 genes for mosses). Branch support was assessed by standard non-parametric bootstrapping (MRE-based bootstopping test every 50 replicates and default cutoff value). Bootstrap support values were mapped onto the most likely tree using the Transfer Bootstrap Expectation support metric (Lemoine et al., 2018; Zaharias et al., 2023). Finally, the timetrees were built using the RelTime-ML option (Mello, 2018) in MEGA v11.0.8 (Tamura et al., 2021), computing relative times under the GTR+Γ model.

2.3 Statistical analyses

Due to essential differences of the nature of α and β diversity metrics, the former characterizing the diversity patterns per plot while the latter characterizing differences between plots, specific suites of analyses were implemented. Analyses were implemented across the entire elevation gradient on one hand and within each elevation belt on the other. In liverworts, the limited numbers of plots with at least two species (110 plots across the entire gradient, but only 11 and 13 at 1000-1400m and above 2200m, respectively), did not warrant analyses within elevation belts, which therefore focused on mosses and spermatophytes.

Alpha diversity

To determine the extent to which moss, liverwort and spermatophyte α diversity patterns are correlated along the elevation gradient (Q1a), we first analyzed for each taxon the relationship of species richness and MPD per plot with the elevation-using spatial error simultaneous autoregressive (SAR) models (Kissling & Carl, 2008) to control for spatial autocorrelation. We then implemented SAR models to determine how species richness and MPD co-vary between pairs of taxa across plots. To evaluate whether the strength of the correlation of the diversity patterns between mosses, liverworts and spermatophytes varies from low to high elevation (Q1b), we recomputed the above SAR models within each of the 6 defined elevation belts. To determine whether the congruence of the diversity patterns among taxa is explained by their common response to environmental drivers and/or by direct nursing effects of one taxon on the other (Q2a) and whether the contribution of these environmental factors vary from low to high elevation (Q2b), we first regressed, within each elevation belt, the diversity of one taxon against environmental variation. The residuals of this model were then regressed against the residuals of this model for a different taxon. To reduce the number of environmental predictors and avoid overfitting, we summarized the variation included within each of the environmental predictor categories (topography, climatic conditions, soil conditions and land cover) using Principal Component Analyses (PCA). The first two PCA axes of each category were retained.

Beta diversity

To determine the extent to which moss, liverwort and spermatophyte β diversity patterns correlated along the elevation gradient and the variation of theses cross-taxon correlations at increasing elevation (Q1), we first implemented Mantel tests to correlate beta diversity (βsim and PIst) between each pair of plots with their elevation difference. We then implemented Mantel tests to determine how βsim and PIst co-vary between pairs of taxa across plots, across the entire elevational gradient (Q1a) and within each of the 6 elevational belts (Q1b). To determine whether the congruence of the diversity patterns among taxa is explained by their common response to environmental drivers and/or by direct nursing effects of one taxon on the other (Q2a) and whether the contribution of these environmental factors vary from low to high elevation (Q2b), we first implemented Generalized Dissimilarity Models (GDM, Ferrier et al., 2007), as implemented by the 'gdm' R package (Fitzpatrick et al., 2021), to regress β diversity among plots for one taxon against matrices of environmental distances (i.e., the Euclidian distance between the environmental PCA scores for each pair of plots). The correlation between the residuals of this analysis and the residuals among plots for another taxon was then assessed using Mantel tests. All Mantel tests were implemented using Moran spectral randomization (Crabot et al., 2019) with the packages *ade4* (Bougeard & Dray, 2018), *adespatial* (Dray et al., 2020) and *spdep* (Bivand, 2002) to control for spatial autocorrelation.

3. Results

Per-taxon diversity patterns of land plants along an elevation gradient in the Vaud Alps

The species pool included 222 moss, 42 liverwort and 718 spermatophyte species. Species richness per 4m² plot across 413 plots of open vegetation in the Vaud Alps averaged 8.4 ± 6.3, 1.2 ± 1.9, and 35.8 ± 20.9 species in mosses, liverworts, and spermatophytes respectively. Phylogenetic trees for liverworts, mosses and spermatophytes are displayed in Fig. S1-3. The moss and liverwort tree topologies conform to those of Bechteler et al. (2023), except for the relationships of *Marchantia* and *Preissia* within complex thalloids.

Alpha diversity. For all the taxa, species richness exhibited a significant hump-shaped relationship with elevation (Fig. 1A1-3). The relationship was stronger for spermatophytes ($r^2=0.29$, $p<0.001$) than for liverworts ($r^2=0.16$, $p<0.001$) and mosses ($r^2=0.17$, $p<0.001$). The mode of the relationship between species richness and elevation occurred at lower elevation (1111m) in spermatophytes than in liverworts (1985m) and mosses (1827m). The strength of the correlation between MPD and elevation, although significant, was lower than with species richness, and the shape of the relationship differed among lineages. For mosses, the U-shaped relationship, with a mode at 1079m (Fig. 1B1, $r^2=0.07$, $p<0.001$), contrasted with the hump-shape relationship, with a mode at 1468m, observed in spermatophytes (Fig. 1B3, $r^2=0.08$, $p<0.001$). In liverworts, MPD decreased with elevation (Fig. 1B2, $r^2= 0.06$, $p = 0.007$).

Beta diversity. For all taxa, taxonomic turnover was consistently correlated with elevation difference (mosses: $r^2 = 0.14$, $p<0.001$; liverworts: $r^2 = 0.07$, $p<0.001$; spermatophytes: $r^2 = 0.23$, $p<0.001$). In contrast, elevation difference was an extremely poor predictor of phylogenetic turnover in all taxa ($r^2=0.01$, $p = 0.01$ in spermatophytes, $r^2=<0.01$, $P=0.90$, in mosses, and $r^2<0.01$, $P=0.95$ in liverworts). Average taxonomic turnover per elevation band exhibited a hump-shape relationship with elevation with a mode at 1400-2000m in mosses and spermatophytes (Fig. 2). No trend in the variation of average phylogenetic turnover per elevation band with elevation was observed (Fig. 2).

Cross-taxon diversity patterns among land plants along an elevation gradient

Taxonomic diversity. Species richness and taxonomic turnover were significantly correlated among taxa (Fig. 1A4-6, Table 1), and this correlation, although lower, remained significant after controlling for environmental variation (Table 1).

Phylogenetic diversity. Phylogenetic diversity patterns (MPD and phylogenetic turnover, Fig. 1B4-6 and Table 1) poorly correlated among taxa, except for a significant relationship of the phylogenetic turnover between spermatophytes and liverworts that did not decrease after controlling for environmental variation (Table 1).

Cross-taxon diversity patterns among land plants per elevation band

Alpha diversity. The correlation of moss and spermatophyte species richness shifted from non-significant or marginally significant values below 2000m to significant values with r^2 reaching 0.32 and 0.67 between 2000 and 2200m and above 2220m, respectively (Fig. 3, Table 2). The same pattern persisted after controlling for environmental variation, with a drop of the r^2 to 0.24 and 0.40 between 2000 and 2200m and above 2220m, respectively. Conversely, MPD patterns between mosses and spermatophytes did not significantly correlate at any of the elevational belts.

Beta diversity. The correlation of taxonomic turnover between mosses and spermatophytes globally increased from low (0-1400 m) to mid- (1400-2000 m) elevations, to drop above 2200m, a pattern that persisted, although with a substantial drop of r^2 values that remained significant at mid-elevation only, after controlling for environmental variation (Table 2). Phylogenetic turnover exhibited a similar trend, with much lower r^2 values that reached marginal significance at mid-elevation only (1800-2000 m) in both analyses, without and with control for environmental variation.

Discussion

The significant cross-taxon correlation between species richness patterns among land plants reflects a common hump-shape relationship with elevation that has been recurrently reported in all groups (Grau et al., 2007; McCain & Grytnes, 2010; Dubuis et al., 2011; Hernández-Hernández et al., 2017). The strength of this correlation varies, however, with spatial resolution. The cross-taxon correlation (r^2) in species richness of 0.21 between mosses and spermatophytes, of 0.51 between mosses and liverworts, and of 0.14 between liverworts and spermatophytes, are comparable to those reported among the same groups in alpine environments at the same (2 × 2m) resolution (Odland et al., 2014), but substantially lower than those documented for γ diversity at coarser (entire elevation belts) scale. By comparison, these r^2 values were 0.54, 0.79 and 0.35, respectively, in land plant communities across elevational belts in the Himalaya (Grau et al. 2007). As we move to finer resolution indeed, the role of chance in community composition increases, and other factors than macroclimatic elevation gradients, including local environmental conditions (e.g. soil, land use) and biotic interactions play an increasing role (Gazol and Iba´n˜ez, 2010; Laliberté et al., 2009; Lewis et al., 2014; Pearson and Dawson, 2003; Wisz et al., 2013). Nevertheless, the significance of the variation of moss and liverwort species richness with elevation at fine resolution conflicts with the hypothesis that the dependence of bryophyte communities on fine scale environmental heterogeneity (micro-habitats) prevents the emergence of a macro-ecological signal of elevation (Grytnes et al., 2006).

The 2 to3 fold higher cross-taxon correlation between species richness patterns of bryophyte lineages (r^2=0.51) than between the latter and spermatophytes (r^2=0.14-0.21) highlights that the responses of moss and liverwort species richness to macro-ecological variation along an elevation gradient are more similar than that of spermatophytes. In fact, species richness peaked, in line with previous reports on land plant species richness patterns along elevational gradients (Grau et al., 2007; McCain & Grytnes, 2010; Dani et al., 2023), at higher elevations for bryophytes (1800-2000m) than for spermatophytes (1000-1200m) This pattern may be best explained by the significant differences of ecophysiological attributes among these groups, with mosses and liverworts sharing a strong reliance on atmospheric precipitation for water uptake, comparatively lower temperature optima and larger cold tolerance than their spermatophyte counterparts (Patino & Vanderpoorten, 2018).

In contrast, cross-taxon congruence in phylogenetic diversity was virtually absent despite apparently opposed patterns of MPD along an elevation gradient. In mosses, MPD tended to reflect a shift from phylogenetic clustering (low MPD) to overdispersion (high MPD) towards high elevation, in line with an origin of bryophytes in cold environments (Laenen et al., 2018; Maul et al., 2025), so that cold-adapted lineages would contribute more phylogenetic diversity at high elevation than more recently evolved, warm-adapted ones at low elevation (Qian & Kessler, 2024; Qian & Grau, 2024; Wu et al., 2022). In spermatophytes, the reverse pattern was observed, in line with an origin of the group during warm geological periods, with few lineages that diversified in cool environments, forming clusters of closely related species and reducing phylogenetic diversity towards high elevation (Hawkins et al., 2006; Buckley et al., 2010; Qian et al., 2019, Li et al., 2022). Although significant, the strength of the correlation between phylogenetic diversity and elevation was extremely weak for all taxa (mean $r^2 = 0.07$ for MPD and non-significant for Pist) and, as Liang et al. (2025) also noticed, much lower than that between taxonomic diversity and elevation. Consequently, phylogenetic diversity among lineages was uncorrelated along the elevation gradient. Previous reports on the variation of phylogenetic diversity along elevation gradients were conflictual and their outcome depends on spatial resolution. Strong correlations between phylogenetic diversity along elevation were revealed by analyses utilizing entire elevation bands as sampling units and generating species distributions by continuously filling bands based upon species elevation ranges (Li et al., 2022; Qian & Kessler, 2024). In contrast, analyses at finer resolution revealed much weaker correlations between phylogenetic than taxonomic diversity and elevation (Liang et al., 2025), or failed to evidence a significant community phylogenetic structure (Ndiribe et al., 2013) and a clear pattern of phylogenetic diversity along an elevation gradient (Shooner et al., 2018). Such differences may reflect the impact of a series of factors such as stochasticity, dispersal limitations, disturbance regimes and biotic interactions at fine resolution, which may blur the correlation between phylogenetic diversity and elevation along the entire gradient. At such fine resolution in particular, competition among phylogenetically related species may result in phylogenetic overdispersion, counteracting phylogenetic clustering resulting from the sharing of adaptive traits among phylogenetically related species (Kembel & Hubbell, 2006; Mayfield & Levine, 2010).

Although MPD and PIst are two metrics independent from species richness (Miller et al., 2016, Kasprzyk et al., 2025), this lack of signal could also result from a large variance of the phylogenetic diversity estimates associated to the low species richness due to the small size of the investigated plots. This interpretation is, however, weakened by the fact that the patterns persisted when setting the minimum number of species per plot to 2, 5 or 8. Furthermore, the same patterns were also obtained in spermatophytes, a much more speciose group than bryophytes and wherein average species richness per plot reached 26. In addition, significant phylogenetic structures were detected in species-poor communities (3-10 species per plot) along steep environmental gradients, both under simulated (Kasprzyk et al., 2025) and empirical (Shen et al., 2022) conditions. Thus, the absence of a strong variation of phylogenetic structure of bryophytes and spermatophytes along an elevation gradient may reflect a weak selection pressure for the adaptation to cold environment. This hypothesis potentially applies to bryophytes, which exhibit high intrinsic levels of cold tolerance (Segreto et al., 2010, and references therein), but not to spermatophytes. Alternatively, the weak phylogenetic structure revealed here along the elevational gradient could also originate from the lack of phylogenetic signal in the traits involved in cold adaptation, i.e., to the phylogenetic non-heritability of these adaptations. At a macro-evolutionary scale, this hypothesis is at odds with the notion that angiosperms originated in the tropics and that adaptation to cold occurred within a subset of derived lineages (Kerkhoff et al., 2014). As Körner (2023) noticed, however, alpine plants are morphologically, anatomically and physiologically extremely diverse, and there is no ‘archetype’ alpine plant (Körner, 2021). In herbaceous plants at elevation above 3000 m in the Alps for example, dry matter allocation (how much mass is invested in roots, storage organs, shoots and foliage) covers the entire possible spectrum (Körner & Renhardt, 1987; Körner, 1991). This, coupled with the fact that adaptations to alpine environments may also result from convergence rather than heritability, so that distant relatives may co-occur in the same habitats (Read et al., 2014), also contributes to weaken the phylogenetic structure of the communities.

Global patterns of cross-taxon correlations across the entire gradient hid fine-scale, elevation-dependent variations. Indeed, the correlation between moss and spermatophyte species richness patterns strikingly increased above 2000m. These cross-taxon correlations in species richness remained significant and their strength dropped by about 1/3 when controlling for environmental variation, pointing to the role of both the influence of common environmental factors and biotic interactions at high elevation. Two factors may thus account for the striking increase of the cross-taxon correlation in species richness among bryophytes and spermatophytes above the treeline of 2000m. On one hand, size differences between mosses and spermatophytes decrease with elevation, increasingly exposing them to the same environmental factors. As Körner (2023) noticed, plants above the climatic treeline are small ‘by design’. The restriction of alpine plant life to these low-stature architectures is the outcome of evolutionary selection. Tall species are aerodynamically coupled to the atmosphere (Körner & Hiltbrunner, 2021) and are hence exposed to large temperature ranges and lethally cold temperatures in the winter. In contrast, smaller species experience buffered microclimatic near-ground conditions, especially in winter-time, during which their buds are protected by snow cover (Körner et al., 2022; Körner, 2023).

On the other hand, in line with the stress gradient hypothesis (Soliveres & Maestre, 2014), facilitation is expected to play an increasing role in community composition towards high elevation. In fact, the architecture of the vascular vegetation was shown to play a substantial role in alpine environments (Wietrzyk-Pełka et al., 2021) and its contribution to account for variation in bryophytes community composition increases from low to high elevation (Collart et al., 2024). In turn, the increase of vascular plant diversity with moss-cushion area and layer depth suggests that mosses can also act as nurse plants for vascular plants in alpine environments (Gavini et al., 2019).

Cross-taxon correlations of species turnover also varied in strength with elevation, but in contrast to species richness, exhibited a hump-shape pattern with a peak at mid-elevation (1400-2000 m). This pattern of elevation-dependent cross-taxon correlation in species turnover mirrored the typically displayed hump-shape variation of species turnover along latitudinal gradients (Koleff et al., 2003; McFadden et al., 2019) and most recently reported along elevational gradients, along which species turnover in both mosses and spermatophytes peaked at mid-elevation (Chen et al., 2025; Liang et al., 2025). Kraft et al. (2011) proposed that the size of species pools directly impacts the extent of species turnover. While such an explanation would potentially hold true in mosses, wherein the peak of species richness and turnover coincided at 1400-1800m, this was not the case for spermatophytes, wherein the peak in species richness occurred at lower (1000-1200m) elevation. In contrast to theories linking species richness and turnover (Stevens, 1989; Koleff et al., 2003), recent evidence suggests that local richness and turnover are independent biological patterns associated with distinct climatic conditions (Sonne & Rahbek, 2024). In fact, conditions favourable for the highest species richness may not necessarily coincide with those favouring highest levels of turn-over, which correlate with areas characterized by the most variable environmental conditions (Sonne & Rahbek, 2024) and variable disturbance. In the present study, however, the peak of species turnover did not occur at the elevation belt exhibiting the highest range of environmental conditions (Fig. S4). The peak of species turnover correlates with climatic factors (Chen et al., 2025), but how these factors determine the observed variation of species turnover needs to be further investigated.

Conclusion

Cross-taxon congruence of diversity patterns between bryophytes and spermatophytes along an elevational gradient was much higher for taxonomic than phylogenetic diversity, indicating that similar ecological processes or direct interactions shape species richness and community composition among land plant lineages, but that the evolutionary mechanisms shaping the phylogenetic structure of their communities differ along an elevational gradient. The strength of the cross-taxon correlation for species richness increased with elevation, reaching maximum values above the treeline as a reflection that alpine bryophytes and spermatophytes compose communities exposed to similar environmental conditions, but probably also display direct interactions. The variation of the cross-taxon correlation for species turnover exhibited a different pattern, peaking at mid-elevation and reflecting the hump-shape variation of species turnover with elevation shared by mosses and spermatophytes. The fact that the strength of the correlation of the diversity patterns between mosses and spermatophytes is strongly elevation-dependent, explains why previous studies on the use of spermatophyte diversity as a surrogate of bryophyte diversity yielded controversial results (Bagella, 2014; Carter et al., 2022). In practice, our results cast doubts about the usefulness of spermatophytes as surrogates of bryophytes in conservation planning because while variations in species richness largely correspond to each other in the two groups above the treeline, this is not the case for community composition. In addition, the evolutionary mechanisms shaping phylogenetic diversity vary among groups. Therefore, evolutionary responses to ongoing environmental changes are likely multifaceted and warrant taxon-specific consideration and research.

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Data. Raw genomic data for mosses and liverworts generated by target-capture sequencing are available at ...

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Table 1: Cross-taxon beta diversity patterns (taxonomic turnover βsim, phylogenetic turnover PIst) among land plants along an elevation gradient. The partial R² represents the strength of the correlation after controlling for variation in abiotic factors. *, **,***, correspond to a *p*-value <0.05, 0.01, 0.001, respectively.

	βsim		**PIst**	
	R²	Partial R²	R²	Partial R²
Mosses/ Spermatophytes	0.25^{***}	0.02^{***}	<0.01	<0.01
Mosses/ Liverworts	0.14^{***}	0.06^{***}	<0.01	<0.01
Liverworts/ Spermatophytes	0.12^{***}	0.03^{***}	0.12^{***}	0.12^{***}

Table 2: Cross-taxon variation of taxonomic (βsim) and phylogenetic (PIst) turnover between spermatophytes and mosses within each of six elevation belts. The partial R^2 represents the strength of the correlation after controlling for variation in abiotic factors. *, **,***, correspond to a *p*-value <0.05, 0.01, 0.001, respectively.

Elevation belt	**βsim**		**PIst**	
	R^2	Partial R^2	R^2	Partial R^2
[0;1000[	0.04**	<0.01	<0.01	<0.01
[1000;1400[	0.07***	<0.01	0.02	<0.01
[1400;1800[	0.15***	0.06***	<0.01	<0.01
[1800;2000[	0.16***	0.01	0.02	0.02*
[2000;2200[	0.10***	0.06***	<0.01	<0.01
>2200	<0.01	<0.01	<0.01	<0.01

Figure 1. Variation and co-variation of species richness (A) and Mean Phylogenetic Distance (B) among land plant lineages along an elevation gradient based on 4m² plots (n=413) in the western Alps. 1-3: variation depending on elevation, with optimum values indicated. 4-6: cross-taxon correlations (4: mosses vs spermatophytes; 5: liverworts vs spermatophytes; 6: liverworts vs mosses).

Figure 2. Variation of βsim and PIst among 4m² plots (n=413) in mosses, liverworts and spermatophytes per elevation belt along an elevation gradient in the western Alps. Box-plots (showing the 1st and 3rd quartiles (upper and lower bounds), 2nd quartile (centre), 1.5* interquartile range (whiskers) and minima-maxima beyond the whiskers) represent the range of variation among pairs of 4m² plots within each of six elevation belts.

Figure 3. Cross-taxon variation of species richness and Mean Phylogenetic Distance in spermatophytes and mosses 4m² plots (n=413) within each of six elevation belts in the western Alps. Trend lines shown for significant relationships.

Figure S1. Timetree from 894 concatenated nuclear single-loci sequences of liverworts based on RAxML and RelTime-ML (MEGA v11.0.8) analyses. All branches maximally supported (i.e. 100% bootstrap frequencies) unless otherwise marked (Transfer Bootstrap Expectation support metric).

Figure S2. Timetree from 770 concatenated nuclear single-loci sequences of mosses based on RAxML and RelTime-ML (MEGA v11.0.8) analyses. All branches maximally supported (i.e. 100% bootstrap frequencies) unless otherwise marked (Transfer Bootstrap Expectation support metric).

Figure S3. Megaphylogeny of angiosperms (Zanne et al. (2014) restricted to include the 485 species recorded in the 413 plots of 4m^2 of the present survey and used to compute molecular diversity patterns.

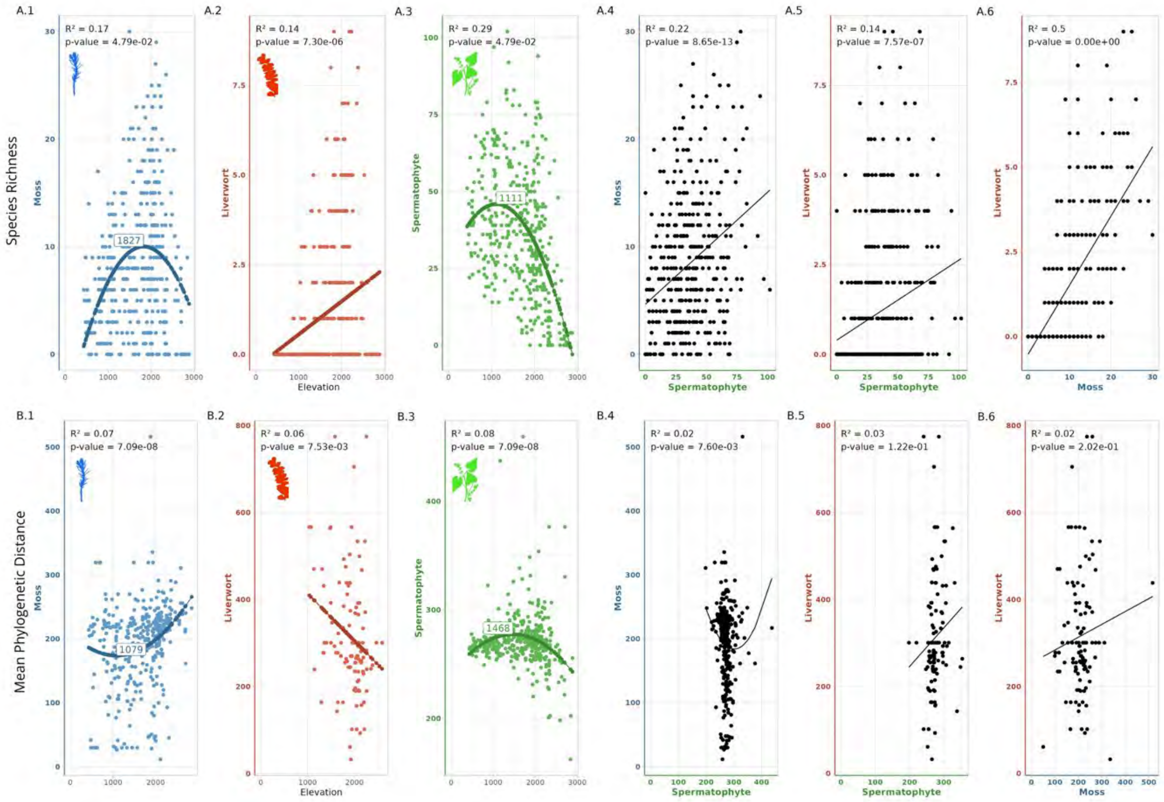
A.1
R² = 0.17
p-value = 4.79e-02
Species Richness
Moss
1827
A.2
R² = 0.14
p-value = 7.30e-06
Liverwort
Elevation
A.3
R² = 0.29
p-value = 4.79e-02
Spermatophyte
1111
A.4
R² = 0.22
p-value = 8.65e-13
Moss
Spermatophyte
A.5
R² = 0.14
p-value = 7.57e-07
Liverwort
Spermatophyte
A.6
R² = 0.5
p-value = 0.00e+00
Liverwort
Moss
B.1
R² = 0.07
p-value = 7.09e-08
Mean Phylogenetic Distance
Moss
1079
B.2
R² = 0.06
p-value = 7.53e-03
Liverwort
Elevation
B.3
R² = 0.08
p-value = 7.09e-08
Spermatophyte
1468
B.4
R² = 0.02
p-value = 7.60e-03
Moss
Spermatophyte
B.5
R² = 0.03
p-value = 1.22e-01
Liverwort
Spermatophyte
B.6
R² = 0.02
p-value = 2.02e-01
Liverwort
Moss

Figure 1

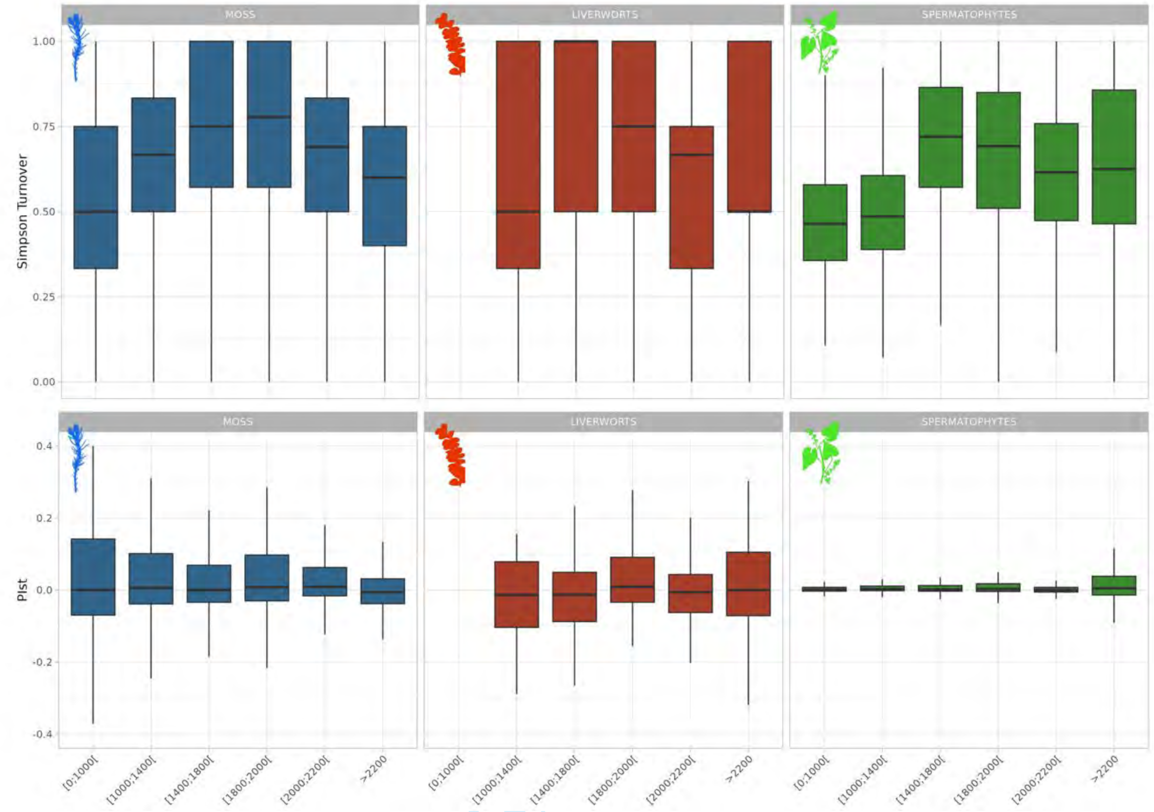
MOSS
LIVERWORTS
SPERMATOPHYTES
Simpson Turnover
1.00
0.75
0.50
0.25
0.00
MOSS
LIVERWORTS
SPERMATOPHYTES
PIst
0.4
0.2
0.0
-0.2
-0.4
[0;1000[
[1000;1400[
[1400;1800[
[1800;2000[
[2000;2200[
>2200
[0;1000[
[1000;1400[
[1400;1800[
[1800;2000[
[2000;2200[
>2200
[0;1000[
[1000;1400[
[1400;1800[
[1800;2000[
[2000;2200[
>2200

Figure 2

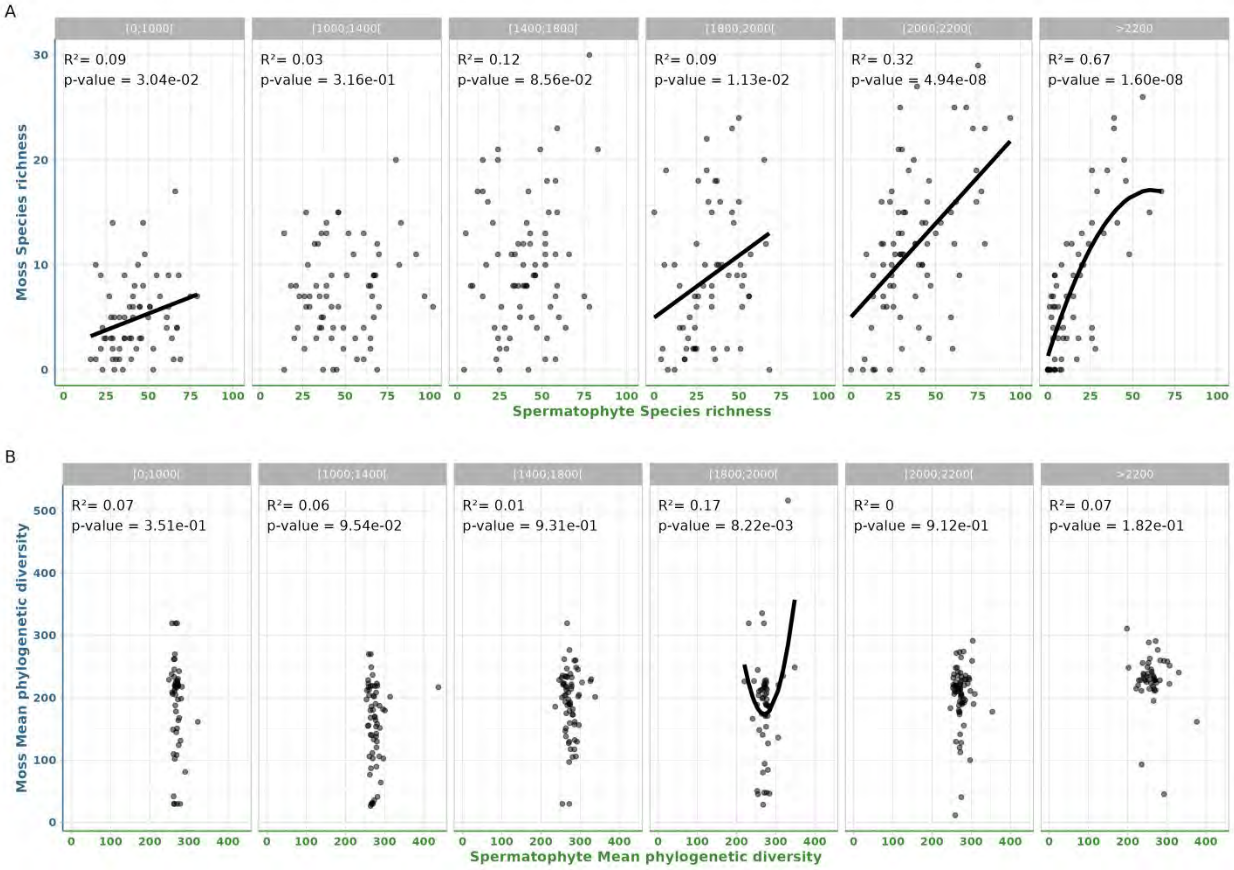
A
[0;1000[
[1000;1400[
[1400;1800[
[1800;2000[
[2000;2200[
>2200
R²= 0.09
p-value = 3.04e-02
R²= 0.03
p-value = 3.16e-01
R²= 0.12
p-value = 8.56e-02
R²= 0.09
p-value = 1.13e-02
R²= 0.32
p-value = 4.94e-08
R²= 0.67
p-value = 1.60e-08
Moss Species richness
0
10
20
30
0
25
50
75
100
Spermatophyte Species richness
B
[0;1000[
[1000;1400[
[1400;1800[
[1800;2000[
[2000;2200[
>2200
R²= 0.07
p-value = 3.51e-01
R²= 0.06
p-value = 9.54e-02
R²= 0.01
p-value = 9.31e-01
R²= 0.17
p-value = 8.22e-03
R²= 0
p-value = 9.12e-01
R²= 0.07
p-value = 1.82e-01
Moss Mean phylogenetic diversity
0
100
200
300
400
500
0
100
200
300
400
Spermatophyte Mean phylogenetic diversity

Figure 3

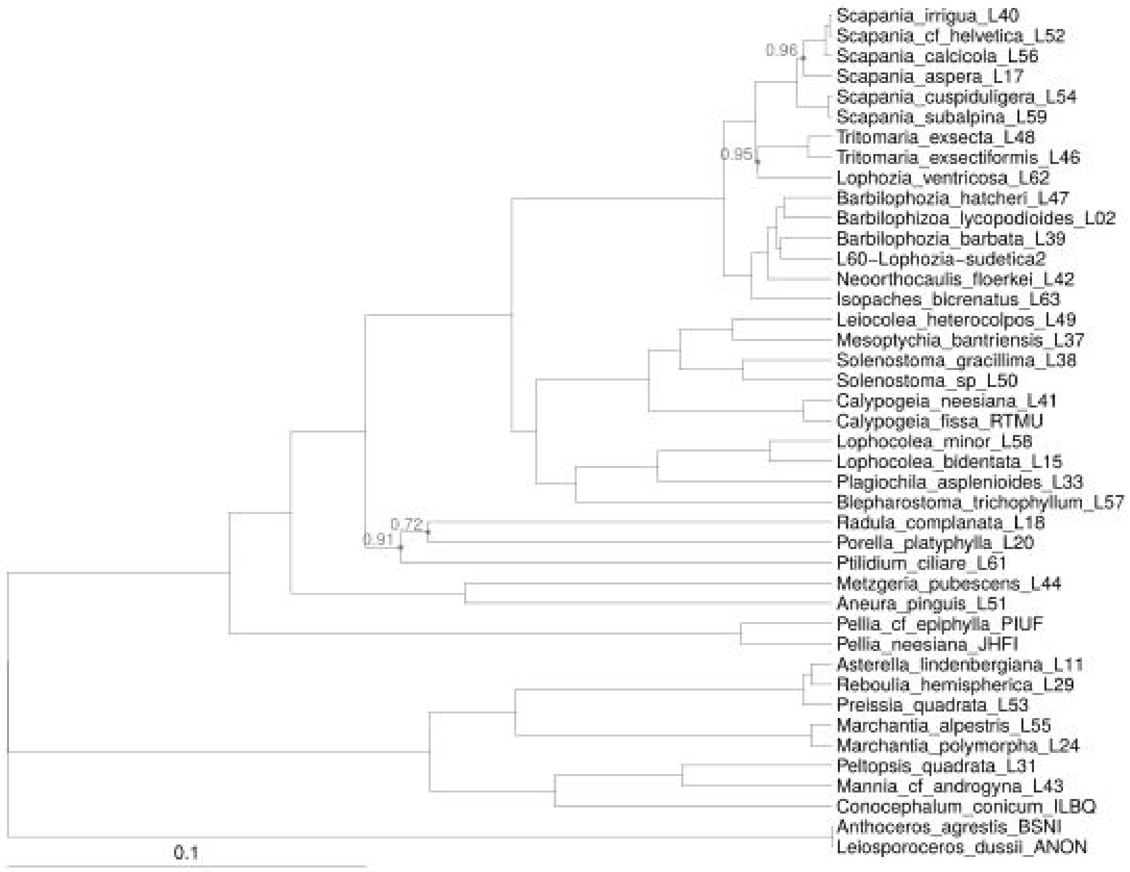
Scapania_irrigua_L40
Scapania_cf_helvetica_L52
Scapania_calcicola_L56
Scapania_aspera_L17
Scapania_cuspiduligera_L54
Scapania_subalpina_L59
Tritomaria_exsecta_L48
Tritomaria_exsectiformis_L46
Lophozia_ventricosa_L62
Barbilophozia_hatcheri_L47
Barbilophizoa_lycopodioides_L02
Barbilophozia_barbata_L39
L60-Lophozia-sudetica2
Neoorthocaulis_floerkei_L42
Isopaches_bicrenatus_L63
Leiocolea_heterocolpos_L49
Mesoptychia_bantriensis_L37
Solenostoma_gracillima_L38
Solenostoma_sp_L50
Calypogeia_neesiana_L41
Calypogeia_fissa_RTMU
Lophocolea_minor_L58
Lophocolea_bidentata_L15
Plagiochila_asplenioides_L33
Blepharostoma_trichophyllum_L57
Radula_complanata_L18
Porella_platyphylla_L20
Ptilidium_ciliare_L61
Metzgeria_pubescens_L44
Aneura_pinguis_L51
Pellia_cf_epiphylla_PIUF
Pellia_neesiana_JHFI
Asterella_lindenbergiana_L11
Reboulia_hemispherica_L29
Preissia_quadrata_L53
Marchantia_alpestris_L55
Marchantia_polymorpha_L24
Peltopsis_quadrata_L31
Mannia_cf_androgyna_L43
Conocephalum_conicum_ILBQ
Anthoceros_agrestis_BSNI
Leiosporoceros_dussii_ANON
0.96
0.95
0.72
0.91
0.1

Figure S1

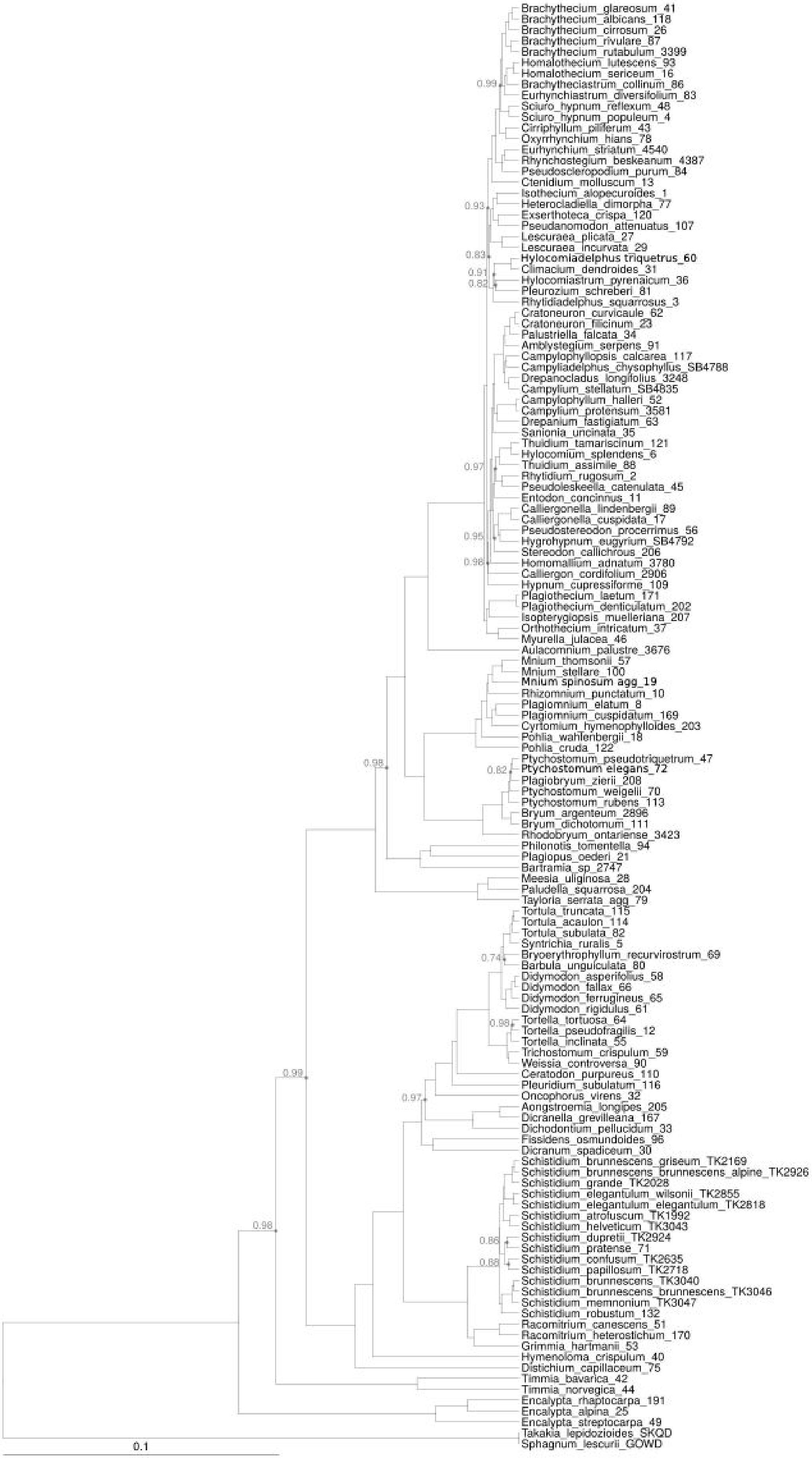
Brachythecium_glareosum_41
Brachythecium_albicans_118
Brachythecium_cirrosum_26
Brachythecium_rivulare_87
Brachythecium_rutabulum_3399
Homalothecium_lutescens_93
Homalothecium_sericeum_16
0.99
Brachytheciastrum_collinum_86
Eurhynchiastrum_diversifolium_83
Sciuro_hypnum_reflexum_48
Sciuro_hypnum_populeum_4
Cirriphyllum_piliferum_43
Oxyrrhynchium_hians_78
Eurhynchium_striatum_4540
Rhynchostegium_beskeanum_4387
Pseudoscleropodium_purum_84
Ctenidium_molluscum_13
Isothecium_alopecuroides_1
0.93
Heterocladiella_dimorpha_77
Exsertheca_crispa_120
Pseudanomodon_attenuatus_107
Lescuraea_plicata_27
Lescuraea_incurvata_29
0.83
Hylocomiadelphus triquetrus_60
0.91
Climacium_dendroides_31
0.82
Hylocomiastrum_pyrenaicum_36
Pleurozium_schreberi_81
Rhytidiadelphus_squarrosus_3
Cratoneuron_curvicaule_62
Cratoneuron_filicinum_23
Palustriella_falcata_34
Amblystegium_serpens_91
Campylophyllopsis_calcarea_117
Campyliadelphus_chysophyllus_SB4788
Drepanocladus_longifolius_3248
Campylium_stellatum_SB4835
Campylophyllum_halleri_52
Campylium_protensum_3581
Drepanium_fastigiatum_63
Sanionia_uncinata_35
Thuidium_tamariscinum_121
Hylocomium_splendens_6
0.97
Thuidium_assimile_88
Rhytidium_rugosum_2
Pseudoleskeella_catenulata_45
Entodon_concinnus_11
Calliergonella_lindenbergii_89
Calliergonella_cuspidata_17
Pseudostereodon_procerrimus_56
0.95
Hygrohypnum_eugyrium_SB4792
Stereodon_callichrous_206
0.98
Homomallium_adnatum_3780
Calliergon_cordifolium_2906
Hypnum_cupressiforme_109
Plagiothecium_laetum_171
Plagiothecium_denticulatum_202
Isopterygiopsis_muelleriana_207
Orthothecium_intricatum_37
Myurella_julacea_46
Aulacomnium_palustre_3676
Mnium_thomsonii_57
Mnium_stellare_100
Mnium spinosum agg_19
Rhizomnium_punctatum_10
Plagiomnium_elatum_8
Plagiomnium_cuspidatum_169
Cyrtomium_hymenophylloides_203
Pohlia_wahlenbergii_18
Pohlia_cruda_122
0.98
Ptychostomum_pseudotriquetrum_47
0.82
Ptychostomum elegans_72
Plagiobryum_zierii_208
Ptychostomum_weigelii_70
Ptychostomum_rubens_113
Bryum_argenteum_2896
Bryum_dichotomum_111
Rhodobryum_ontariense_3423
Philonotis_tomentella_94
Plagiopus_oederi_21
Bartramia_sp_2747
Meesia_uliginosa_28
Paludella_squarrosa_204
Tayloria_serrata_agg_79
Tortula_truncata_115
Tortula_acaulon_114
Tortula_subulata_82
Syntrichia_ruralis_5
0.74
Bryoerythrophyllum_recurvirostrum_69
Barbula_unguiculata_80
Didymodon_asperifolius_58
Didymodon_fallax_66
Didymodon_ferrugineus_65
Didymodon_rigidulus_61
0.98
Tortella_tortuosa_64
Tortella_pseudofragilis_12
Tortella_inclinata_55
Trichostomum_crispulum_59
Weissia_controversa_90
0.99
Ceratodon_purpureus_110
Pleuridium_subulatum_116
0.97
Oncophorus_virens_32
Aongstroemia_longipes_205
Dicranella_grevilleana_167
Dichodontium_pellucidum_33
Fissidens_osmundoides_96
Dicranum_spadiceum_30
Schistidium_brunnescens_griseum_TK2169
Schistidium_brunnescens_brunnescens_alpine_TK2926
Schistidium_grande_TK2028
Schistidium_elegantulum_wilsonii_TK2855
Schistidium_elegantulum_elegantulum_TK2818
Schistidium_atrofuscum_TK1992
0.98
Schistidium_helveticum_TK3043
0.86
Schistidium_dupretii_TK2924
Schistidium_pratense_71
0.88
Schistidium_confusum_TK2635
Schistidium_papillosum_TK2718
Schistidium_brunnescens_TK3040
Schistidium_brunnescens_brunnescens_TK3046
Schistidium_memnonium_TK3047
Schistidium_robustum_132
Racomitrium_canescens_51
Racomitrium_heterostichum_170
Grimmia_hartmanii_53
Hymenoloma_crispulum_40
Distichium_capillaceum_75
Timmia_bavarica_42
Timmia_norvegica_44
Encalypta_rhaptocarpa_191
Encalypta_alpina_25
Encalypta_streptocarpa_49
Takakia_lepidozioides_SKQD
Sphagnum_lescurii_GOWD
0.1

Figure S2

Figure S3

Journal name: Ecological Monographs

Manuscript title: Strong elevation-dependence of cross-taxon diversity patterns in plants.

Authors:

Antonia Salces-Castellano, Thibault Kasprzyk , Bernard Goffinet , Norman Wickett, T. Kiebacher, Nikisha Patel , Yang Liu , Shanshan Dong , Antoine Guisan, Flavien Collart, Alain Vanderpoorten

Appendix 1: Plant diversity patterns per 4m^2 plot in the western Alps based on plots with at least 5 and 8 species

Table 1: Number of plots from the 413 initial plots with at least 5 and 8 species of spermatophytes, mosses and liverworts.

Taxa	N>4	N>7
Spermatophytes	380	368
Mosses	275	188
Liverworts	19	2

Table 2: Cross-taxon variation of taxonomic (βsim) and phylogenetic (PIst) turnover among land plants along an elevation gradient, based on plots of $4m^2$ containing at least five species. The partial R^2 represents the strength of the correlation after controlling for variation in abiotic factors. *, **,***, correspond to a *p*-value <0.05, 0.01, 0.001, respectively.

	βsim		**PIst**	
	R^2	Partial R^2	R^2	Partial R^2
Mosses/ Spermatophytes	0.31***	0.08***	0	0
Mosses/ Liverworts	0.25***	0.25***	0.09*	0.05*
Liverworts/ Spermatophytes	0.03**	0.06*	0.01	0.07

Table 3: Cross-taxon variation of taxonomic (βsim) and phylogenetic (PIst) turnover among land plants along an elevation gradient, based on plots of $4m^2$ containing at least eight species. The partial R^2 represents the strength of the correlation after controlling for variation in abiotic factors. *, **,***, correspond to a *p*-value <0.05, 0.01, 0.001, respectively.

	βsim		**PIst**	
	R^2	Partial R^2	R^2	Partial R^2
Mosses / Spermatophytes	0.28***	0.11***	0	0
Mosses / Liverworts	/	/	/	/
Liverworts / Spermatophytes	/	/	/	/

Table 4: Cross-taxon variation of taxonomic (βsim) and phylogenetic (PIst) turnover between spermatophytes and mosses within each of six elevation belts, based on plots of $4m^2$ containing at least five species. The partial R^2 represents the strength of the correlation after

controlling for variation in abiotic factors. *, **,***, correspond to a *p*-value <0.05, 0.01, 0.001, respectively.

Elevation belt	**βsim**		**PIst**	
	R^2	Partial R^2	R^2	Partial R^2
[0;1000[	0.08**	0.02*	0	0
[1000;1400[	0.17***	0.02*	0.09*	0
[1400;1800[	0.22***	0.12***	0	0
[1800;2000[	0.17***	0.03*	0	0.02
[2000;2200[	0.13***	0.10***	0	0
>2200	0	0.02*	0	0.05*

Table 5: Cross-taxon variation of taxonomic (βsim) and phylogenetic (PIst) turnover between spermatophytes and mosses within each of six elevation belts, based on plots of $4m^2$ containing at least eight species. The partial R^2 represents the strength of the correlation after controlling for variation in abiotic factors. *, **,***, correspond to a *p*-value <0.05, 0.01, 0.001, respectively.

Elevation belt	**βsim**		**PIst**	
	R^2	Partial R^2	R^2	Partial R^2
[0;1000[	0.35**	0.16*	0.01	0.03
[1000;1400[	0.36***	0	0.25**	0
[1400;1800[	0.31***	0.26***	0	0
[1800;2000[	0.22***	0.03*	0.01	0.02
[2000;2200[	0.11***	0.10***	0	0
>2200	0	0.02	0	0.01

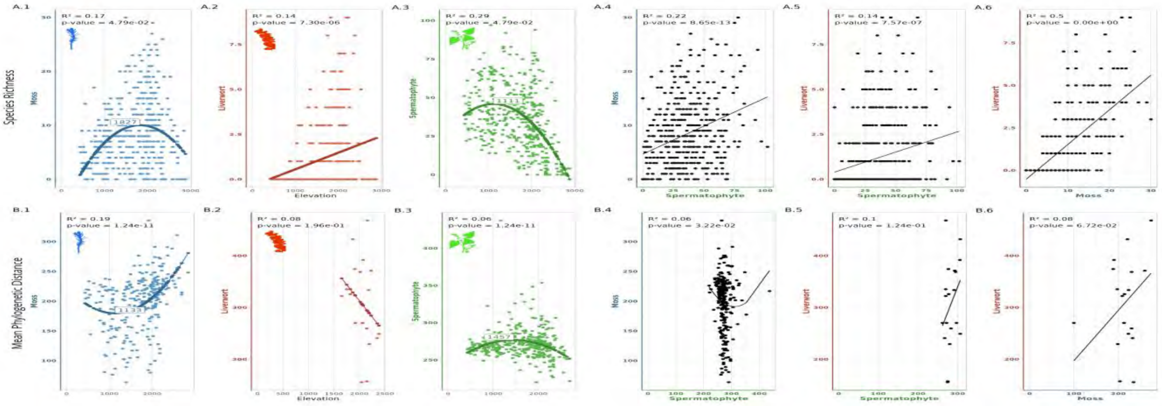

Figure 1. Variation and co-variation of species richness (A) and Mean Phylogenetic Distance (B) among land plant lineages along an elevation gradient based on 4m² plots containing at least five species (number of plots depending on taxa and metrics, see Table 1) in the western Alps. 1-3: variation depending on elevation, with optimum values indicated. 4-6: cross-taxon correlations (4: mosses vs spermatophytes; 5: liverworts vs spermatophytes; 6: liverworts vs mosses).

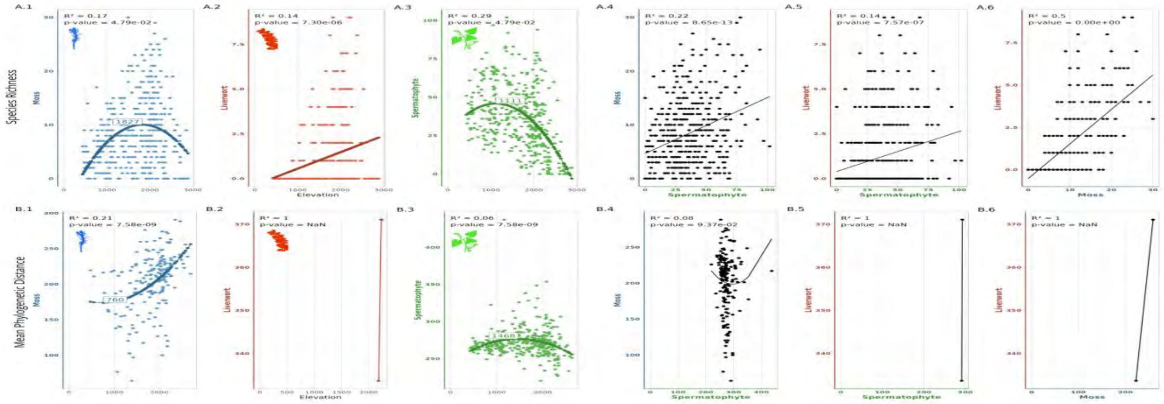

Figure 2. Variation and co-variation of species richness (A) and Mean Phylogenetic Distance (B) among land plant lineages along an elevation gradient based on 4m² plots containing at least eight species (number of plots depending on taxa and metrics, see Table 1) in the western Alps. 1-3: variation depending on elevation, with optimum values indicated. 4-6: cross-taxon correlations (4: mosses vs spermatophytes; 5: liverworts vs spermatophytes; 6: liverworts vs mosses).

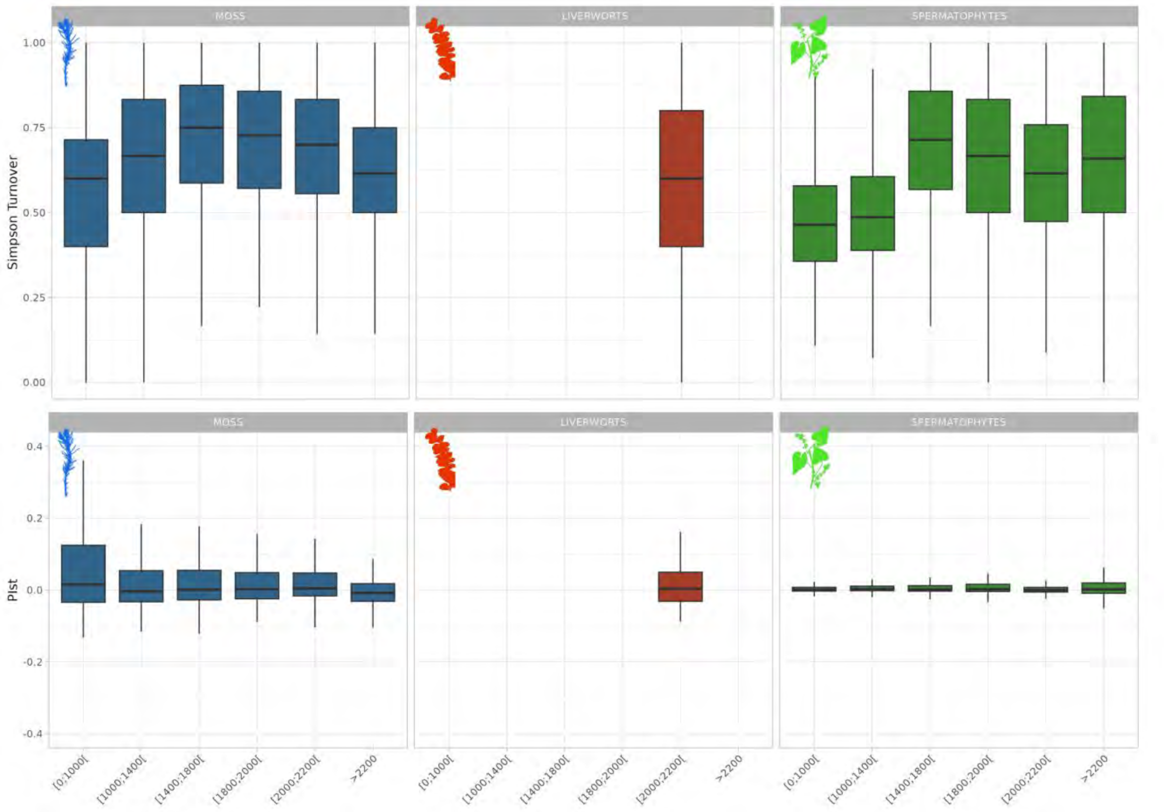

Figure 3. Variation of βsim and PIst among 4m² plots containing at least five species (number of plots depending on the taxa and the metric, see Table 1) in mosses, liverworts and spermatophytes per elevation belt along an elevation gradient in the western Alps. Box-plots (showing the 1st and 3rd quartiles (upper and lower bounds), 2nd quartile (centre), 1.5* interquartile range (whiskers) and minima-maxima beyond the whiskers) represent the range of variation among pairs of 4m² plots within each of six elevation belts.

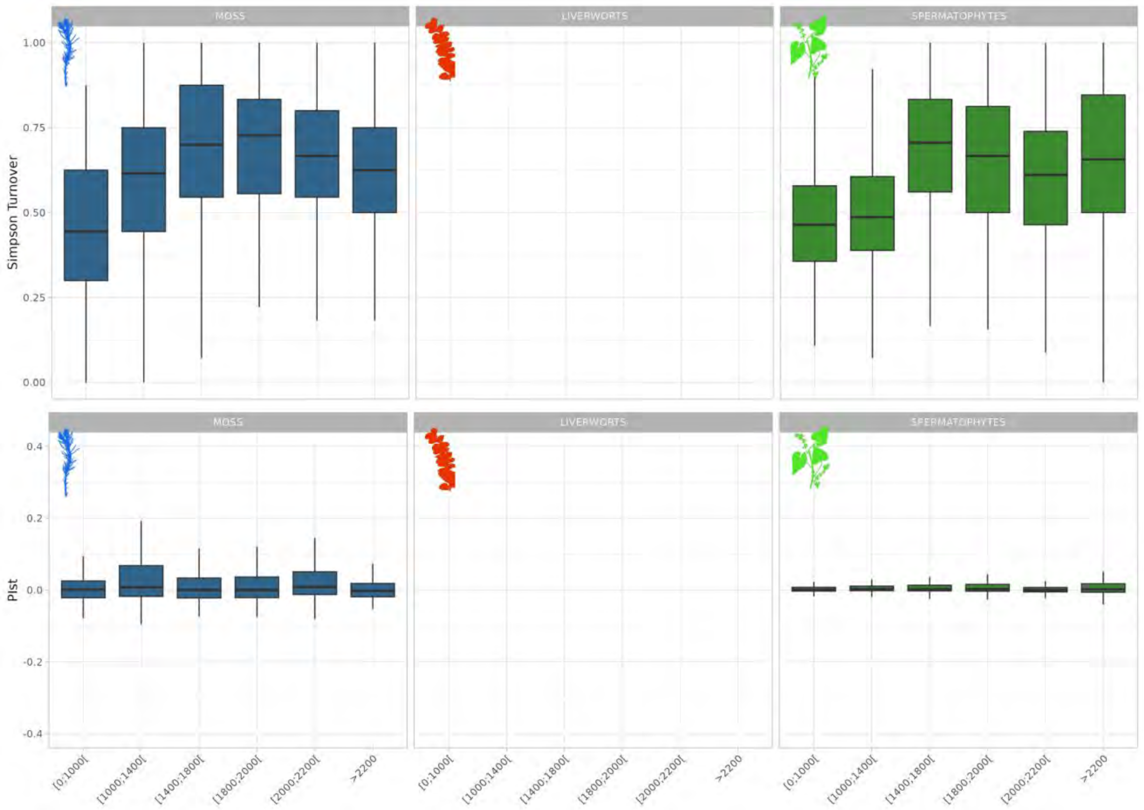

Figure 4. Variation of βsim and PIst among $4m^2$ plots containing at least five species (number of plots depending on the taxa and the metric, see Table 1) in mosses, liverworts and spermatophytes per elevation belt along an elevation gradient in the western Alps. Box-plots (showing the 1st and 3rd quartiles (upper and lower bounds), 2nd quartile (centre), 1.5* interquartile range (whiskers) and minima-maxima beyond the whiskers) represent the range of variation among pairs of $4m^2$ plots within each of six elevation belts.

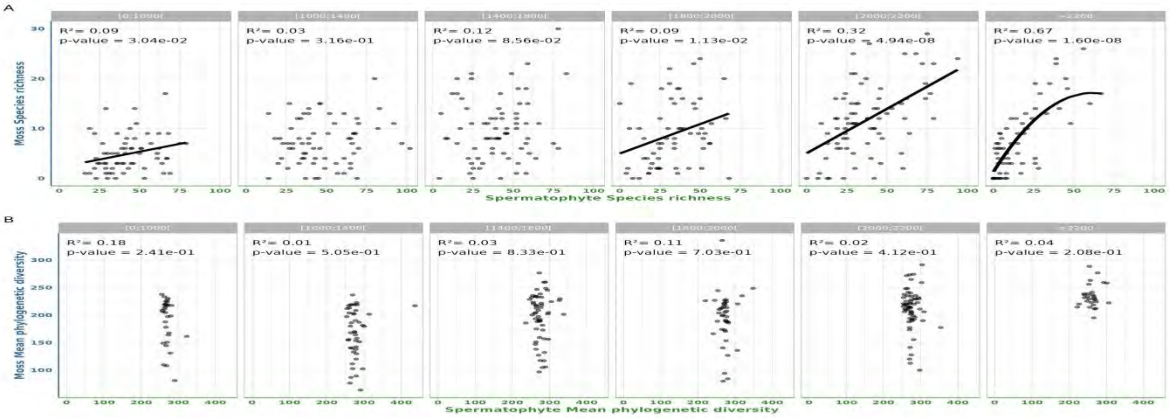

Figure 5. Cross-taxon variation of species richness and Mean Phylogenetic Distance in spermatophytes and mosses per 4m² plots containing at least five species (number of plots depending on the taxa and the metric, see Table 1) within each of six elevation belts in the western Alps. Trend lines shown for significant relationships.

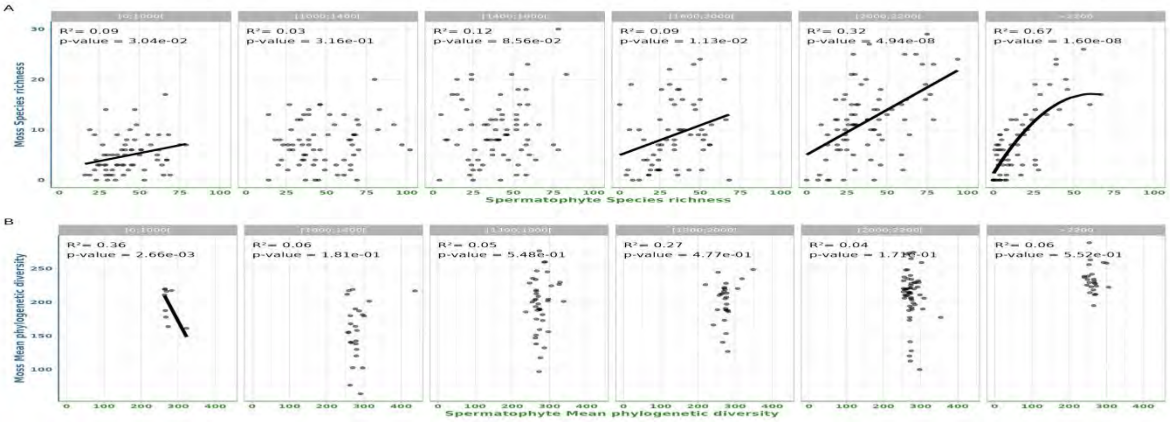

Figure 6. Cross-taxon variation of species richness and Mean Phylogenetic Distance in spermatophytes and mosses per 4m² plots containing at least eight species (number of plots depending on the taxa and the metric, see Table 1) within each of six elevation belts in the western Alps. Trend lines shown for significant relationships.

Journal name: Ecological Monographs

Manuscript title: Strong elevation-dependence of cross-taxon diversity patterns in plants.

Authors:

Antonia Salces-Castellano[1], Thibault Kasprzyk[2], Bernard Goffinet[3], T. Kiebacher[4], Nikisha Patel[3], Yang Liu[5], Shanshan Dong[5], Matt Johnson[6], Antoine Guisan[7,8,9], Flavien Collart[2], Alain Vanderpoorten[2]

Appendix 2. Protocols for targeted sequencing of nuclear protein-coding genes in mosses and liverworts and data processing

Target-capture sequencing for mosses

DNA was extracted from dried gametophytic or sporophytic tissue using a modified version of the CTAB method (Doyle and Doyle, 1987), as follows:

CTAB extraction buffer: 1 M Tris-HCl pH 8, 5 M NaCl, 0.5 M EDTA pH 8, 3% (w/v) CTAB (cetyl trimethylammonium bromide), 3% (w/v) PVP-40 (polyvinylpyrrolidone, average molecular weight 40,000), 2% (v/v) 2-mercaptoethanol.

TE buffer: 10 mM Tris pH 8, 1 mM EDTA pH 8.

1. Pulverize plant sample using liquid nitrogen.
2. Add 500 µl of CTAB plant extraction buffer. Mix and thoroughly vortex.
3. Place the tube into a 60 degree water bath for 30 min.
4. Centrifuge the homogenate at 10,000 x g for 10 min.
5. Transfer supernatant to a new tube.
6. Add 5 µl of RNAse (10mg/ml in water) and incubate at room temperature for 15 min.
7. Add an equal volume of chloroform: isoamyl alcohol (24:1).
8. Vortex for 5 sec and then centrifuge at 10,000 x g for 1 min.
9. Transfer the upper phase to a new tube (repeat until upper phase is clear).
10. Add 0.7 volume of isopropanol, mix and incubate at -20ºC for 15 min.

11. Centrifuge at 10,000 x g for 10 min.
12. Decant the supernatant and wash with 500 µl of 70% ethanol.
13. Decant the ethanol.
14. Dry the pellet in a SpeedVac to remove alcohol, but not overdry the DNA.
15. Dissolve the DNA pellet in 50 µl of TE buffer. This may need to be warmed.

DNA samples (250 ng in 15 µl) were used to prepare libraries with the NEBNext Ultra II FS DNA Library Prep Kit for Illumina and NEBNext Multiplex Oligos for Illumina (96 Unique Dual Index Primer Pairs) #E6440. We followed the manufacturer's protocol for DNA library preparation. For both extractions and libraries, DNA concentration was measured with the Qubit fluorometer system (Invitrogen, Carlsbad, CA, USA). Libraries were enriched for the 809 targeted protein-coding nuclear genes (exons complemented by their flanking regions) by hybridization, using the custom Mybaits kit (MYcroarray, Ann Arbor, MI, USA) designed by Medina et al. (2019) and Liu et al. (2019), and following the manufacturer's protocol.We selected a temperature of 65ºC for the hybridization capture, and used KAPA HiFi HotStart/NEB Ultra II Q5 polymerase for the post-capture amplification of libraries. Finally, the enriched, pooled libraries were paired-end sequenced on an Illumina MiSeq platform using the 600-cycle v3 sequencing kit (Illumina, San Diego, CA, USA) in the Center for Genome Innovation at the University of Connecticut at Storrs.

Target-capture sequencing for liverworts

Genomic DNA was extracted from approximately 1.0 g of dried liverwort tissue using the NucleoSpin Plant Midi DNA Extraction Kit (Macherey-Nagel, Düren, Germany). About 1 µg of genomic DNA was used to construct paired-end sequencing libraries with an insert size of 300–500 bp. High-throughput sequencing was performed on the BGISEQ-500 platform at BGI (Shenzhen, China), generating approximately 100 Gbp of PE150 raw sequence data per sample. Raw reads were quality-checked, trimmed, and filtered to remove adaptor contamination, low-quality reads, short inserts, and duplicates using Trimmomatic (Bolger et al., 2014). Targeted nuclear genes were subsequently retrieved using the HybPiper pipeline (https://github.com/mossmatters/HybPiper).

Data processing

The demultiplexed raw reads were trimmed by Trimmomatic v0.39 (Bolger et al., 2014), removing: (i) Illumina adapters provided in the TruSeq3-PE-2.fa file, allowing maximally 2 mismatches and applying clip thresholds of 30 (about 50 bases) and 10 (about 17 bases) for paired and single ended reads, respectively; (ii) leading and trailing bases with a quality below 10; (iii) bases within a 4-base wide sliding window with an average quality below 20; and (iv) reads with less than 36 bases long. For both raw and trimmed reads, quality was checked by FastQC v0.11.9 (https://www.bioinformatics.babraham.ac.uk/projects/fastqc) and multiQC v1.12 (Ewels et al., 2016). Targeted genes from paired and unpaired forward reads were extracted using HybPiper v2.0 (Johnson et al., 2016), in which (i) the trimmed reads were mapped to the reference genes using BWA (nucleotide sequences), (ii) mapped reads for each gene were separately assembled into contigs using an average nucleotide coverage of 4, (iii) the assembled contigs were aligned to the reference sequence, and (iv) nucleotide coding sequences were extracted from each gene. Individual genes including paralogs were aligned (MAFFT v7.453; Katoh and Standley, 2013) and corresponding trees under the GTR model (FastTree v2.1.11; Price et al., 2010) were built to identify paralog copies, retaining genes with the main copy if all paralogs were Type I (monophyletic within species, possibly recent duplicates or alleles), and removing all Type II paralog copies (result of ancient gene or genome duplications); complete genes were removed if they contained more than five samples with Type II paralogs. Genes with unexpected stop codons and putative chimeric were also deleted. To find a balance between missing data and number of species, only taxa with a minimum recovery of 50 genes were kept. For the outgroup, nuclear genes of the hornwort genera Leiosporoceros and Anthoceros (for the phylogeny of liverworts) and the moss genera Sphagnum and Takakia (for the phylogeny of mosses) were extracted from the 1KP Project (Leebens-Mack et al., 2019).

For each gene, nucleotide coding sequences, including outgroups, were aligned using their amino acid translations by MACSE v2.03 (Ranwez et al., 2018) subprogram alignSequences. Detected frameshift mutations were deleted, and alignments were trimmed with trimAl v1.4.1 (Capella-Gutiérrez et al., 2009), removing sites with more than 50% of missing data. The individual genes were merged into a concatenated alignment with the script fasta_merge.py (https://github.com/mossmatters/HybPiper).

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