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Research

Macroclimatic structuring of spatial phylogenetic turnover in liverworts

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Phylogenetic turnover has emerged as a powerful tool to identify the mechanisms by which biological communities assemble. When significantly structured along environmental gradients, phylogenetic turnover evidences phylogenetic niche conservatism, a critical principle explaining patterns of species distributions at different spatio-temporal scales. Here, we quantify the contribution of geographic and macroclimatic drivers to explain patterns of phylogenetic turnover in an entire phylum of land plants, namely liverworts. We further determine whether climatic niche conservatism has constrained the distribution of liverworts in the course of their evolutionary history. Two datasets, one insular, focused on 60 archipelagos and including 2346 species, and the second global, including 6334 species in 451 oceanic and continental operational geographic units (OGUs) worldwide, were assembled. Phylogenetic turnover among OGUs was quantified through π_{st} statistics. π_{st} -through-time profiles were generated at 1 Myr intervals along the phylogenetic time-scale and used to compute the correlation between π_{st} , current geographic distance and macroclimatic variation with Mantel tests based on Moran spectral randomization to control for spatial autocorrelation. The contribution of macroclimatic variation to phylogenetic turnover was about four-times higher than that of geographic distance, a pattern that was consistently observed in island and global geographic settings, and with datasets including or excluding species-poor OGUs. The correlation between phylogenetic turnover and geographic distance rapidly decayed at increasing phylogenetic depth, whereas the relationship with macroclimatic variation remained constant until 100 Mya. Our analyses reveal that changes in the phylogenetic composition among liverwort floras across the globe are primarily shaped by macroclimatic variation. They demonstrate the relevance of macroclimatic niche conservatism for the assembly of liverwort floras over very large spatial and evolutionary time scales, which may explain why such a pervasive biodiversity pattern as the increase of species richness towards the tropics also applies to organisms with high dispersal capacities.



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Introduction

Disentangling the contribution of ecological factors and geographic isolation on the spatio-temporal assembly of biological communities has long been a major focus in ecology and evolutionary biology (Segovia et al. 2020). The definition of the world's biogeographic regions, which dates back to Wallace's (1876) seminal work entitled 'The geographical distribution of animals', reflects the isolation of lineages as a result of historical factors, such as plate tectonics and dispersal limitations, and their subsequent diversification across major environmental gradients (Holt et al. 2013). In organisms with higher dispersal capacities, and plants in particular, plate tectonics has conversely played a very limited role for diversification (Sanmartín and Ronquist 2004), which has primarily taken place following long-distance dispersal within the same macro-environmental niche (Crisp et al. 2009, Gagnon et al. 2019).

Phylogenetic turnover, which quantifies the phylogenetic distance among species within and among communities (Graham and Fine 2008), is precisely affected by two main macroecological and evolutionary processes. On the one hand, trans-oceanic disjunct communities are expected to display higher average interspecific phylogenetic divergence between, versus within, continents, if speciation occurs at a faster rate than inter-continental migration (Hardy et al. 2012). On the other hand, the niche conservatism hypothesis posits that species sharing the same niche should, on average, be more phylogenetically related to each other than pairs of species from different niches, creating significantly higher phylogenetic turnover between than within habitats (Graham and Fine 2008, Segovia et al. 2020). Therefore, phylogenetic niche conservatism can be detected when the distribution of ecological traits matches both species distributions and evolutionary relationships (Losos 2008), i.e. when phylogenetic turnover and environmental variation are significantly correlated (Jin et al. 2015).

While contemporary geographic and environmental filtering may hence have left an imprint on patterns of taxonomic and phylogenetic turnover (Eiserhardt et al. 2013), its effect may, however, be perceived only at certain depths along the phylogenetic time-scale (Duarte et al. 2014, Mazel et al. 2017). For example, two regions may not share any species, but if their species all belong to the same higher taxonomic units due to, for instance, strong phylogenetic niche conservatism, then the phylogenetic turnover between these two regions will be 0 at that taxonomic level. The phylogenetic scale used to define the structure of ecological assemblages may therefore also influence the relationships between phylogenetic patterns and environmental gradients depending on the degree of phylogenetic niche conservatism (Wiens and Graham 2005).

Here, we analyse phylogenetic turnover and its geographic and environmental drivers at different phylogenetic levels within an entire phylum of land plants, the Marchantiophyta or liverworts, which include about 7500 species (Söderström et al. 2016). Following sexual reproduction, they disperse via spores, which are smaller than those of ferns and smaller than angiosperm seeds. Liverworts, and bryophytes in general, thus exhibit high long-distance dispersal capacities that erode any signal caused by geographic isolation, as evidenced by their strikingly low rates of endemism (Söderström 1996, Patiño and Vanderpoorten 2018), skewed presence-per-k-island curves (Söderström 1996), the high frequency of trans-oceanic disjunct distributions (Patiño and Vanderpoorten 2018) and flatter species–area relationships compared to angiosperms (Patiño et al. 2014). As a result, similar levels of bryophyte species richness have been reported in island and continental settings (Patiño et al. 2015a). On oceanic islands, models reflecting environmental heterogeneity therefore explain species richness patterns better than more complex models integrating time and connectivity (Patiño et al. 2013a). Altogether, these observations raise the hypothesis that phylogenetic turnover is better explained by environmental filters than by geographic isolation. Recent studies in specific lineages of mosses, the sister group to liverworts (Wickett et al. 2014), revealed significant niche conservatism (Johnson et al. 2015, Piatkowski and Shaw 2019), but the relevance of this mechanism in shaping species distribution patterns at broad spatial and phylogenetic scales, and in different geological settings, has not been assessed yet. More specifically, we address the following questions:

- Is spatial phylogenetic clustering among liverwort floras significant, i.e. is the observed phylogenetic turnover higher than that expected following randomization of the phylogenetic relationships among species? If so, to what extent is it explained by geographic distance and/or macroclimatic variation, pointing to large-scale macroclimatic niche conservatism? Given the high long-distance dispersal capacities of the group, we hypothesize that macroclimatic variation is a better predictor of phylogenetic turnover than geographic distance, evidencing macroclimatic niche conservatism (H1).
- How did the correlation between phylogenetic turnover, geographic distance and macroclimatic variation evolve through time? Due to the high long-distance dispersal capacities of liverworts, the number of range disjunctions should quickly increase with taxonomic rank, decoupling phylogenetic and geographic distances. We therefore hypothesize that any signal of a correlation between phylogenetic turnover and geographic distance should rapidly erode with increasing evolutionary time (H2). By

contrast, if liverwort diversification has been constrained by macroclimatic conservatism during their evolutionary history, the explanatory power of contemporary macroclimatic variation on phylogenetic turnover is expected to persist over large evolutionary time-scales (H3).

Material and methods

Data sampling

The world checklist of liverworts (Söderström et al. 2016) served as a taxonomic basis to standardize species names and higher taxonomic ranks across reference sources and filter out all species with ‘serious doubts’ (915 species). We scored species distributions in operational geographic units (OGUs) from the most comprehensive database of liverwort species distributions available to date, which combines existing data on nomenclature, taxonomy and distribution, and has been built in the context of the Early Land Plants Today project (Söderström et al. 2020). The checklist and distribution data are derived from a working database centralizing nomenclature, taxonomy and geography on a global scale. As of January 2019, the database included about 39 000 names of about 8600 ‘accepted’ taxa, a bibliography of more than 11 000 references and more than 1 000 000 distribution records. Since, unlike in higher plants, introductions of bryophytes species are very rare (Mateo et al. 2015), complete species lists were employed. We ensured that the checklists were sufficiently complete, i.e. that the number of reported species fell into a reasonable range for the given biome and area. In arid areas such as the Sahel for instance, many OGUs include a very low liverwort species richness, primarily comprised of

complex thalloid liverworts (Wigginton 2018). Nevertheless, problems associated with limitations in our knowledge of species identities (the Linnean shortfall) and distributions (the Wallacean shortfall) are particularly severe in taxa with reduced morphologies like bryophytes (Norhazrina et al. 2017), potentially affecting beta diversity analyses and in particular, the richness component of beta diversity. We therefore employed diversity metrics that are reasonably robust to differences in species richness, and tested the impact of species richness on the results (below).

Our sampling primarily focused on oceanic archipelagos for two main reasons. First, they represent naturally circumscribed OGUs. Second, having never been connected to any landmass, they offer an ideal context for addressing the question of geographic isolation, as they are surrounded by an unsuitable matrix for potential colonisers, rendering long-distance dispersal mandatory (Whittaker and Fernández-Palacios 2007). Since the islands of a same archipelago share the same geological history, they cannot be considered as independent sampling units (Bunnefeld and Phillimore 2012). As recommended by Santos et al. (2010) for large-scale macroecological studies, entire archipelagos instead of single islands were therefore employed as OGUs to avoid pseudo-replication issues. Altogether, the distributions of 2346 liverwort species were reported from 60 archipelagos world-wide (hereafter, the ‘archipelago’ dataset (Fig. 1)). Species richness per archipelago ranged between 2 and 400 species (Supporting information).

Because oceanic islands are geographically isolated, the distance separating them from continental sources acts as a filter for potential migrants (Whittaker and Fernández-Palacios 2007), and consequently island biota typically differ from continental ones. This phenomenon, termed island

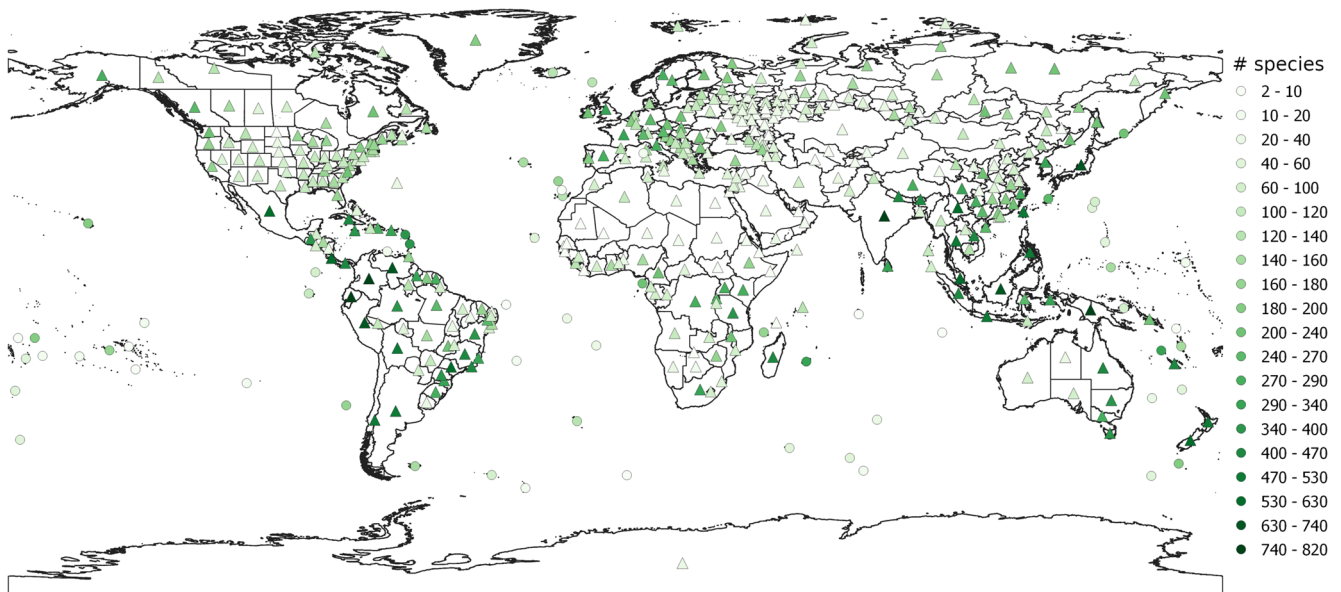


Figure 1. Location and species richness of the 451 operational geographic units (OGUs), including 60 oceanic archipelagos, used to measure phylogenetic turnover among liverwort floras. The centroids of oceanic archipelagos are represented by a circle and those of the remaining OGUs by a triangle.

disharmony (König et al. 2021), affects the patterns of beta diversity between island and continental biota (Stuart et al. 2012, König et al. 2017). We therefore analysed a second dataset (hereafter, the ‘global’ dataset) composed of 6334 liverwort species from 451 OGU world-wide (Fig. 1). For practical reasons, these OGUs were mostly defined based on political limits. Species richness per OGU ranged between 2 and 820 species (Supporting information).

We investigated the impact of the inclusion of species-poor OGUs and repeated the analyses twice, first with all OGUs included (‘full’ dataset), second with only OGUs harboring > 10 species (‘reduced’ dataset). The reduced archipelago and global datasets included 2344 species × 51 OGUs and 6333 × 415 OGUs, respectively.

Finally, we investigated variation among the four major lineages of liverworts: 1) the Marchantiopsida (or complex thalloids); the Jungermanniopsida (or leafy liverworts), further divided into 2) Porellales and 3) Jungermanniales; and 4) the simple thalloids (Metzgeriidae + Pelliidae) (Söderström et al. 2016). Globally, complex thalloids tend to be ground-dwelling. They include genera that rarely produce specialized asexual diaspores, but fairly large spores. For instance, the spores of *Riccia*, the most speciose genus of complex thalloids, typically range between 50 and 100 µm, and are produced within a capsule that is embedded within the thallus, thereby limiting dispersal capacities, but enabling the species to thrive in harsh environments, such as soil crusts (Rosentreter and Root 2019). By contrast, leafy liverworts tend to be much more sensitive to drought, and can sometimes produce both specialized asexual diaspores and comparatively smaller spores. Leafy liverworts can further be divided into two main groups, namely the Porellales, which include the vast majority of epiphytic lineages, and the Jungermanniales, which tend to be primarily terricolous.

The centroid of each OGU was determined in QGIS ver. 3.14.1 (QGIS Development Team 2020) with shapefiles from GADM ver. 3.6 (gdam.org). A geographic distance among the centroids of each pair of OGU was computed in R ver. 4.0.2 (<www.r-project.org>) with the package raster (Hijmans 2020). To characterize each OGU macroclimatically, 19 bioclimatic variables at a resolution of 30 arcseconds were downloaded from Chelsa ver. 2.1 (Karger et al. 2017, 2018). Although the investigated OGUs, and archipelagos in particular, may experience substantial climatic variation across their range, we summarized this variation by the average value across pixels, assuming that, given the worldwide scale of the geographic framework, this average would sufficiently characterize the differences in macroclimatic conditions among OGUs. Subsequent analyses were performed at the level of each macroclimatic variable individually. We also generated a compound, synthetic macroclimatic variable by standardizing each variable and implementing them in a principal component analysis (PCA) with the package ade4 (Bougeard and Dray 2018). The two first principal components, accounting for 77% of the total variance, were kept to generate a matrix of Euclidian climatic distance between each pair of OGUs. Wind connectivity, which has been shown to account for

present distribution patterns in spore-producing plants on islands (Muñoz et al. 2004), was not investigated here. In fact, the underlying hypothesis that we test is that phylogenetically closely related species are more likely to occur 1) under similar climatic conditions due to niche conservatism and 2) in geographically close areas due to dispersal limitations. Since wind patterns substantially vary over short periods of thousands of years, i.e. much less than the timeframe of speciation processes, we assume that present-day wind conditions are unlikely to affect the phylogenetic structure of liverwort floras.

Phylogenetic information was derived from the chronogram of the Liverwort Tree of Life, which is based on the analysis of eight genes from all genomic compartments, includes 303 genera representing 84% of the total extant generic diversity, and is to date the taxonomically and molecularly most densely sampled phylogeny of liverworts (Laenen et al. 2014). Since the phylogeny includes a single species per genus, all congeneric species included in the distribution database 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. Species that belong to an unsampled genus (162 species) were deleted from the analyses. 100 trees with randomly resolved relationships among congeneric species were then generated and analyzed as described below to take phylogenetic uncertainty into account.

Data analysis

Phylogenetic turnover in relatedness of species (or higher taxa) among sites (hereafter, phylogenetic turnover, Miller et al. 2017) was quantified through the π_{st} statistics (Hardy 2008, Hardy et al. 2012) as implemented by Spacodi (Hardy 2010). π_{st} is defined as $1 - MPDw/MPDa$. MPDw and MPDa represent the mean divergence time between distinct species sampled within and between OGU, respectively:

$$MPDw = 1 / N \sum_k \left(\sum_i \sum_{j \neq i} \delta_{ij} P_{ik} P_{jk} / \sum_i \sum_{j \neq i} P_{ik} P_{jk} \right)$$

$$MPDa = 1 / N(N-1) \sum_k \sum_{l \neq k} \frac{\sum_i \sum_{j \neq i} \delta_{ij} P_{ik} P_{jl}}{\sum_i \sum_{j \neq i} P_{ik} P_{jl}}$$

N is the total number of OGUs. Since we only considered pairwise measures, $N=2$ here. δ_{ij} is the divergence time between species i and j , $P_{ik}=1$ if species i occurs in OGU k , otherwise $P_{ik}=0$ and similarly for P_{jl} for species j in OGU l .

A positive π_{st} indicates that species co-occurring in the same OGU are, on average, more related than species sampled among OGUs, reflecting a spatial phylogenetic turnover between OGUs. π_{st} is negative when species are less related within, than between, OGUs, which may result from biotic interactions. To test the hypothesis that $\pi_{st} > 0$, 100 π_{st} values

were generated from each of the 100 phylogenies (thus for a total of 10 000 π_{st} values) whose species were randomized among the tips to build the distribution of the null hypothesis, and then compared to the observed π_{st} values.

The correlation between π_{st} , geographic distance (and its log-transformation) and macroclimatic variation was computed through partial Mantel tests. Significance was tested by 999 permutations with the package *vegan* (Oksanen et al. 2019). Because standard permutation procedures of regular Partial Mantel tests largely fail to actually control for spatial autocorrelation (Guillot and Rousset 2013), we implemented the procedure described by Crabot et al. (2019) with the packages *ade4* (Bougeard and Dray 2018), *adespatial* (Dray et al. 2020) and *spdep* (Bivand and Wong 2018). This procedure is based on Moran spectral randomization, preserving the spatial structures of the original variables so that spatial autocorrelation is taken into account, avoiding the issue of inflated correlations and type I error rates associated with regular Partial Mantel tests.

To investigate the variation of π_{st} through time, we generated π_{st} -through-time profiles, analogous to the β -diversity through time framework (Groussin et al. 2017) at 1 Myr intervals along the phylogenetic time-scale. To this end, the phylogenetic tree was pruned to the desired depth by collapsing all descendent leaves of each of the branches encountered at 1 Myr periods, so that the branch lengths leading to these new terminal nodes progressively shortened. The geographic distribution of these branches was calculated as the union of the distributions of their descending leaves. Importantly, as Mazel et al. (2017) highlighted, this approach does not intend to estimate the ancestral geographic range of these branches, but simply the current extent of their geographic distribution at that phylogenetic level. Furthermore, while our π_{st} through-time analyses thus incorporates phylogenetic information, they also have limitations inherent to phylogenies themselves. In particular, they do not explicitly account for extinctions (Mazel et al. 2017). Since species with narrow climatic niches and/or low dispersal capacities could potentially be more prone to extinctions, failure to incorporate extinctions could bias the correlation analysis between π_{st} and climatic and geographic drivers among communities that progressively become dominated by species characterized by high dispersal capacities and wide climatic ranges. The fact, that we observed significant correlations between π_{st} and climatic variation through time, and also, in some lineages, with geographic distance, suggests, however, that extinctions did not completely erode the relationships between π_{st} , geographic and environmental drivers.

To help visualizing whether broad climatic niche preferences are conserved at high taxonomic levels, we calculated for each species of the global dataset a 'tropicality index' (Supporting information) as the proportion of its latitudinal range that falls within the tropics, circumscribed by the 23.5° latitude parallels (Economo et al. 2018, Rabosky et al. 2018), minus the proportion of the latitudinal range that falls within extratropical areas. This produces a continuous measure from -1 (extratropical only) to 0 (one-half extratropical,

one-half tropical) to 1 (tropical only) (Kerkhoff et al. 2014). We derived the most likely sets of ancestral states under a Brownian motion model as implemented by the *fastAnc* function in the R package *phytools* (Revell 2012). The analysis was performed on one of the 100 randomly resolved trees at the species level as we focused on the evolution of the tropicality index at the level of the earliest branches.

Finally, we explored whether other metrics of phylogenetic turnover than π_{st} would return similar results. Among these metrics, the *PhyloSor* index (Swenson 2011) has been widely used in recent analyses of phylogenetic community structure (Qian et al. 2013, Jin et al. 2015, Segovia et al. 2020). *PhyloSor* sums the total branch length of shared clades between sites relative to the sum of branch lengths of both sites. *PhyloSor* can be further split, like taxonomic beta diversity, into two separate components accounting for 'true' phylogenetic turnover (*PhyloSor_{turn}*) and phylogenetic diversity gradients (*PhyloSor_{PD}*), respectively (Leprieur et al. 2012). *PhyloSor* and its components, generated with the R package *betapart* (Baselga et al. 2020), were correlated to geographic distance and macroclimatic variation using the full 'archipelago' dataset.

Results

Phylogenetic turnover among liverwort floras, as expressed by pairwise π_{st} among OGUs, was significantly higher than 0 ($p < 0.001$ in all pairwise comparisons across the 100 phylogenetic trees) for both the global and archipelago datasets. Partial Mantel tests revealed low ($r = 0.08$ on average across trees), but significant correlations between phylogenetic turnover and geographic distance for the archipelago dataset (Supporting information), but not for the global dataset (Table 1). Phylogenetic turnover was also significantly correlated with macroclimatic variation, as expressed by the first two axes of a PCA of 19 bioclimatic variables. After correction for spatial autocorrelation using Moran spectral randomization, average r values reached 0.35 and 0.36, i.e. more than four times higher than with geographic distance, with the archipelago and global dataset, respectively (Table 1). These correlations increased to an average of $r = 0.55$ and 0.41 for the archipelago and global dataset, respectively, in analyses based on 'reduced' datasets including OGUs with > 10 species (Table 1). Similar results were obtained with analyses based on phylogenetic beta diversity (*PhyloSor*), with significant correlation between the turnover component of the latter (*PhyloSor_{turn}*) and geographic distance and macroclimatic variation, but not with its nestedness component (*PhyloSor_{PD}*) (Supporting information).

Analyses at the level of each of the 19 investigated bioclimatic variables showed the same trends (Supporting information). Temperature-related variables were more frequently significantly correlated (seven out of 11 variables), and exhibited higher correlation coefficients ($r = 0.24$ on average, up to 0.36 for annual mean temperature, minimum temperature of coldest month, mean temperature of wettest quarter, and mean temperature of coldest quarter) than precipitation-related variables ($r = 0.08$ on

Table 1. Average (\pm SD across 100 trees, for which species relationships within each genus were randomized) correlation coefficients r and associated p -values between the phylogenetic turnover π_{st} of liverwort floras among oceanic archipelagos ($n=60$) and among OGU's of a global dataset of both oceanic and continental OGU's ($n=451$) and 1) the logarithmic geographic distance and 2) macroclimatic variation (as expressed by the first two axes of a PCA of 19 bioclimatic variables, Supporting information for correlations with each variable independently) using partial Mantel tests implementing Moran spectral randomization to control for spatial autocorrelation. 'Full' and 'reduced' correspond to datasets with all OGU's included and only OGU's with > 10 species, respectively.

	$r \pm SD$	
	Full dataset	Reduced dataset
Archipelago dataset		
Geographic distance	0.08 ± 0.001 $p < 0.01$	0.12 ± 0.001 $p < 0.01$
Macroclimatic variation	0.35 ± 0.004 $p < 0.01$	0.55 ± 0.003 $p < 0.01$
Global dataset		
Geographic distance	$-0.02 \pm 4 \times 10^{-4}$ $p > 0.05$	-0.02 ± 10^{-4} $p > 0.05$
Macroclimatic variation	$0.36 \pm 2 \times 10^{-3}$ $p < 0.001$	0.41 ± 0.001 $p < 0.01$

average, up to 0.21 for precipitation seasonality, the only one of the seven precipitation-related variables significantly correlated with phylogenetic turnover). These correlations varied substantially among the main lineages of liverworts (Table 2), as phylogenetic turnover was significantly correlated with geographic distance for the Jungermanniales, but not for the other lineages. Regarding macroclimatic variation, the correlation was highest in leafy liverworts and absent in simple thalloids.

The relative effect of geographic distance and macroclimatic variation on phylogenetic turnover through a phylogenetic time-scale is shown in Fig. 2 and the Supporting information for the archipelago and global datasets, respectively. The correlation between phylogenetic turnover and geographic distance rapidly reaches non-significance (Fig. 2a, Supporting information). In turn, the contribution of macroclimatic variation to phylogenetic turnover remains fairly constant and significant until about 100 Mya (Fig. 2b, Supporting information). In fact, reconstructions of the 'tropicality index' (Fig. 3) graphically illustrated that tropical and extra-tropical lineages tend to be phylogenetically clustered.

Discussion

Phylogenetic turnover of liverwort communities revealed significant correlations with macroclimatic conditions,

independently from geographic distance, adding to emerging evidence for the role of environmental filtering on community assembly through time (Saladin et al. 2019, Segovia et al. 2020). These correlations were observed with two different metrics of phylogenetic turnover, π_{st} and PhyloSor. The fact that the turnover of PhyloSor, and not its nestedness component, is correlated with macroclimatic variation, suggests that the patterns observed are not caused by phylogenetic diversity gradients, but by a true phylogenetic turnover among communities. The correlation between phylogenetic turnover and macroclimatic variation is evidence for niche conservatism shaping macroclimatic niche preferences at a world scale, reinforcing the idea that biome conservatism is a primary driver of present-day distribution patterns of plant biodiversity (Crisp et al. 2009, Segovia et al. 2020). Evidence for phylogenetic conservatism of microhabitat conditions is mounting in bryophytes (Johnson et al. 2015, Piatkowski and Shaw 2019), and we demonstrate here the significance of this mechanism for also shaping large-scale patterns of liverwort assemblage distributions. Phylogenetic niche conservatism of macroclimatic factors is further illustrated by the phylogenetic clustering of the 'tropicality index'. Although further analyses based on actual measures of the phylogenetic signal present in climatic niche traits would be necessary, these results suggest that the evolution of macroclimatic niches is evolutionary constrained, as if they were heritable.

Despite the fact that oceanic island biota have been pre-filtered upon colonization depending on their dispersal capacities, causing differences of beta diversity patterns of angiosperms and vertebrates in island and continental settings (Stuart et al. 2012, König et al. 2017), phylogenetic turnover was also correlated with geographic distance with the oceanic archipelago dataset, but not the global one. This result is, at first sight, surprising because island species must have had, at least upon colonization, high dispersal capacities, potentially erasing any signal of geographic isolation in patterns of phylogenetic turnover. Congruently with the idea that island species have been filtered depending on their dispersal capacities, a bias towards bisexuality was reported in island bryophytes and interpreted as a result of the higher capacity of bisexual species than unisexual ones to produce spores, which are supposedly more prone to long-distance dispersal,

Table 2. Average (\pm SD across 100 trees, for which species relationships within each genus were randomized) correlation coefficients r and associated p -values between the phylogenetic turnover π_{st} between the floras of the four major liverwort clades (Porellales and Jungermanniales composing the leafy liverworts) among oceanic archipelagos ($n=60$) and 1) the logarithmic geographic distance and 2) macroclimatic variation (as expressed by the first two axes of a PCA of 19 bioclimatic variables using partial Mantel tests implementing Moran spectral randomization to control for spatial autocorrelation).

Clade	Geographic distance	Macroclimatic variation
Complex thalloids	0.020 ± 0.005 $p > 0.05$	0.27 ± 0.02 $p < 0.05$
Simple thalloids	0.050 ± 0.010 $p > 0.05$	-0.02 ± 0.02 $p > 0.05$
Leafy liverworts	0.01 ± 0.001 $p > 0.05$	0.51 ± 0.003 $p < 0.01$
Porellales	-0.024 ± 0.004 $p > 0.05$	0.31 ± 0.10 $p < 0.01$
Jungermanniales	0.25 ± 0.004 $p < 0.01$	0.29 ± 0.003 $p < 0.01$

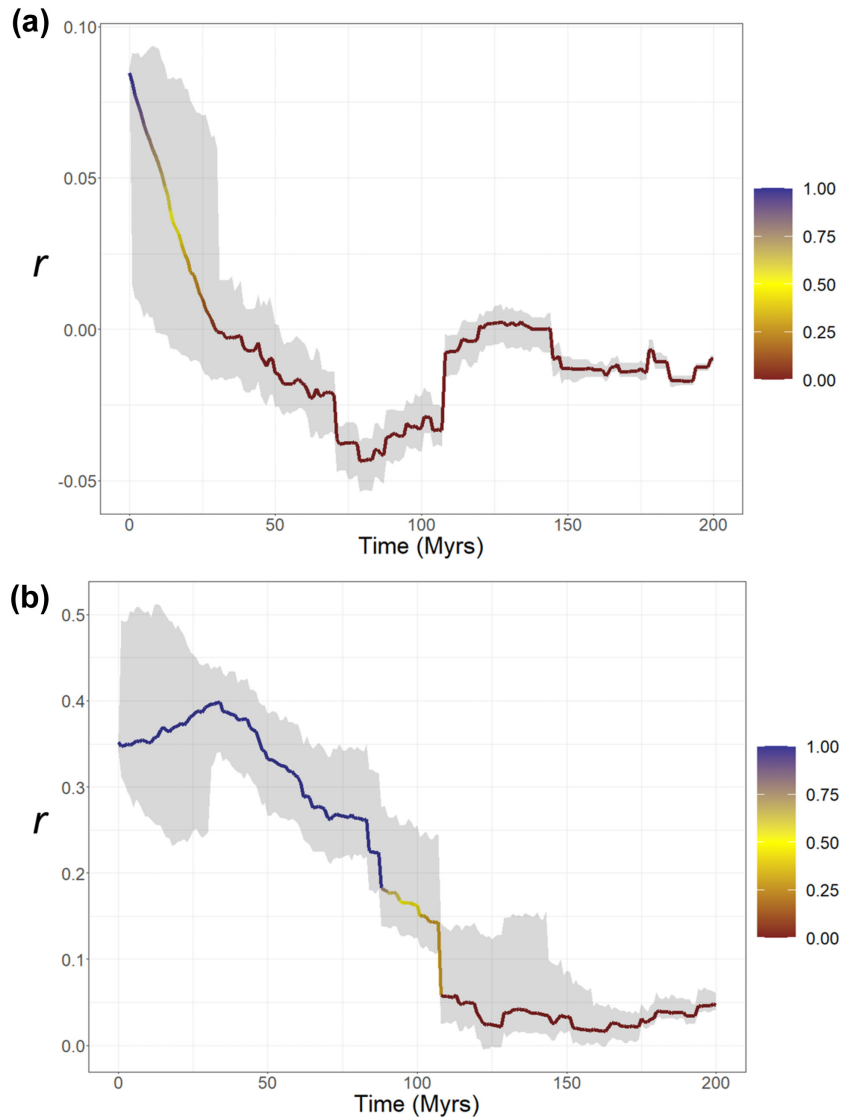


Figure 2. Relative effect, as expressed by the correlation coefficient r of a partial Mantel test, of (a) geographic distance and (b) macroclimatic variation, as expressed by the first two axes of a PCA of 19 bioclimatic variables, following Moran spectral randomization to control for spatial autocorrelation on phylogenetic turnover in oceanic archipelago liverwort floras through a phylogenetic time-scale. Lines and grey ribbons represent, at 1 Myr intervals, the mean correlation coefficient and its minimum–maximum range, respectively, across 100 trees, for which species relationships within each genus were randomized. The color gradient shows the percentage of significant correlations at the 0.05 level and ranges between 0 (red) and 100% (blue) of significant correlations across 100 trees.

and hence, to reach remote islands (Patiño et al. 2013b). The idea, that bisexual species exhibit larger ranges than unisexual ones has, however, been challenged (Laenen et al. 2016) and in fact, the low, but significant signal of geographic isolation observed among oceanic archipelago floras in liverworts vanished in the analyses of the global dataset. Although oceans are not a major impediment for diaspore dispersal, as evidenced by overlapping slopes of isolation-by-distance curves in populations separated by an identical distance above continents and oceans (Hutsemekers et al. 2011, Kyrkjeeide et al. 2016), we interpret the presence of a geographic signal on patterns of phylogenetic turnover in oceanic archipelagos

in terms of the true geographic isolation from any potential source of the latter.

The observed correlations between phylogenetic turnover and climatic drivers lay in the range of the few previous studies addressing similar questions in vascular plants (e.g. correlation coefficients of 0.4 and 0.2 were reported between climatic variation and phylogenetic turnover in angiosperm floras across China (Qian et al. 2020) and in tropical rainforests (Hardy et al. 2012), respectively). Although higher correlations, up to 0.5, were observed in the present study between phylogenetic turnover and climatic and geographic distance when species-poor OGU were removed, the analysis of the

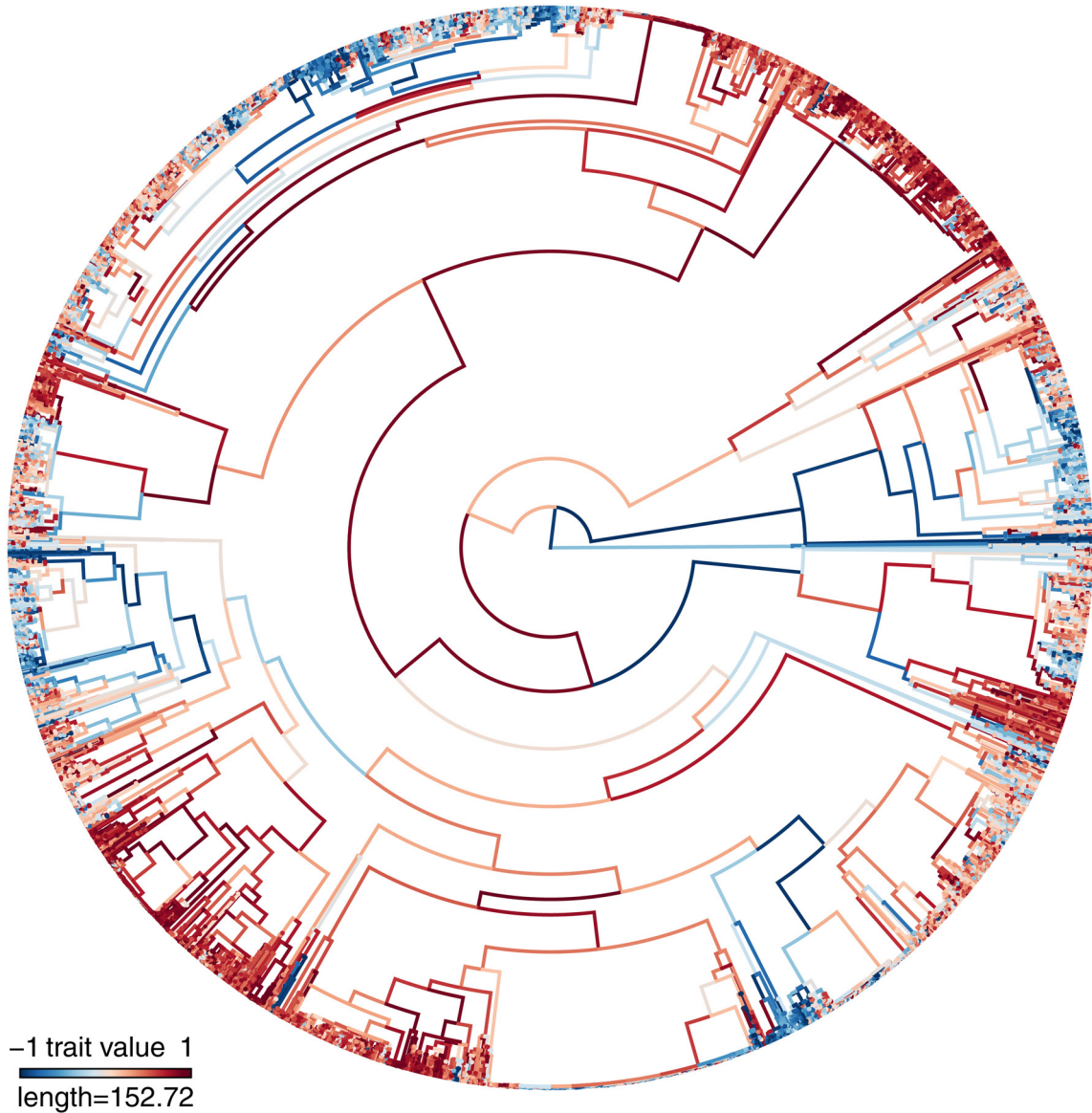


Figure 3. One of the 100 trees of the liverwort phylogeny randomly resolved at the species level, with branches colored according to the estimated tropicity TI value ranging from red (TI = 1) to blue (TI = -1).

full and reduced datasets, using two very different datasets in terms of numbers of OGUs and geographic context, revealed identical patterns. This strengthens the robustness of our conclusions and reinforces the idea that π_{st} , as a measure of the ratio between the average phylogenetic distance among species within versus among OGUs, is reasonably robust to differences in species richness among OGUs (Hardy et al. 2012). We suggest that the large fluctuations of the π_{st} statistic reported by Ives and Helmus (2010) in small communities were caused, at least in part, by their redefinition of this statistic, so that the mean inter community phylogenetic distance includes pairwise comparisons between pairs of identical species, which departs from the original definition by Hardy and Senterre (2007). The robustness of π_{st} to differences in species richness among OGUs makes it unnecessary

to define an arbitrary threshold for selecting OGUs included in the analysis. By contrast, other metrics such as PhyloSor, which includes a phylogenetic species richness component (PhyloSor_{PD}), should be sensitive to variations of species richness among OGUs, and hence, of the completeness of the species inventory of the OGUs.

Most importantly, phylogenetic turnover is four times less strongly correlated with geographic distance than with climatic variation. These results contrast with those reported for birds and mammals (Mazel et al. 2017), wherein contemporary geographic distances explain beta diversity better than climate, suggesting that dispersal limitations in these lineages have a greater influence on phylogenetic turnover than climatic filtering, which is in line with the idea that, at the global scale, faunas of different continents exhibit striking

differences due to ancient geographic isolation associated with plate tectonics. Within continents, recent analyses in angiosperms suggest that tree lineages tend to retain their ancestral environmental relationships and that phylogenetic niche conservatism is the primary force structuring their distributions (Qian et al. 2020, Segovia et al. 2020). In line with the fact that contemporary ecological factors prevail over factors associated with dispersal limitations, such as island age and geographic isolation, to explain patterns of species richness in island bryophytes (Sundberg et al. 2006, Patiño et al. 2013a, Aranda et al. 2014, Tiseliu et al. 2019, Torre et al. 2019), the present results also suggest that macroclimatic filters play a much more important role than dispersal limitations in the assembly of liverwort floras, emphasizing the prevalence of macroclimatic variation over geographic distance for shaping pattern of phylogenetic turnover in plants in general (Qian et al. 2020) across large geographic scales.

Major lineages of liverworts substantially differ, however, in their response to macroclimatic and geographic variation. The absence of correlation between phylogenetic turnover and geographic distance was expected in the Porellales, which include the bulk of the diversity of epiphytic liverworts, a condition that substantially impacts on spore height release, and thus dispersal capacities (Zanatta et al. 2020). By contrast, geographic distance significantly accounted for phylogenetic turnover in Jungermanniales, but not in the complex thalloids, despite a series of life-history traits in the latter that, at first sight, do not promote dispersal. In fact, although molecular work would be needed to control for potential cryptic diversification, some complex thalloids exhibit striking amphitropical ranges, potentially achieved by bird-mediated dispersal of their mostly bisexual spores (Gradstein 2017). Finally, in line with the globally higher ability of thaloid liverworts to thrive in harsh environments, phylogenetic turnover of thaloid lineages did not or only weakly correlate with macroclimatic variation, whereas the highest correlations between phylogenetic turnover and macroclimatic variation were observed in the more drought-sensitive leafy liverworts.

Interestingly, analyses performed at the level of individual climatic variables revealed that liverwort phylogenetic turnover was better correlated with temperature than precipitation, a pattern that was at first sight unexpected in liverworts due to the reliance of the latter on rainfall for water uptake, making them prime indicators of climate change (He et al. 2016). Given the very large scale of the present study, this result should, however, be interpreted with caution, because the relative contribution of climatic drivers to beta diversity may differ between latitudinal and altitudinal gradients, and among biogeographic regions (Tang et al. 2012).

Congruent with our second hypothesis, the correlation between phylogenetic turnover and geographic distance rapidly decays with increasing phylogenetic depth. By contrast, the explanatory power of contemporary macroclimatic variation on phylogenetic turnover only slightly decreases towards deep branches and becomes insignificant only beyond 100 Myrs, pointing to the crucial role of climatic

niche conservatism for the assembly of liverwort assemblages over very large evolutionary time scales. Such a persistence of the importance of macroclimatic factors for explaining large-scale distributions of high-level taxa, recently evidenced in angiosperms (Kusumoto et al. 2021), is, at first sight, more striking in liverworts, whose genera and higher-level taxa tend to be broadly distributed worldwide. Nevertheless, even widely distributed taxa are not necessarily equally distributed across regions. For example, *Lejeunea* and Lejeuneaceae are sub-cosmopolitan, but originated in tropical areas, where they are still much more widely distributed today (Lee et al. 2020). In fact, reconstructions of the ‘tropicality index’ show that broad climatic niche preferences of liverworts are largely conserved over large evolutionary time-scales, accounting for the persistence of the correlation between phylogenetic turnover of higher taxa and climatic variation reported here.

Our results thus lend support to the idea that contemporary geographic and climatic distances do not impact beta diversity patterns at the same phylogenetic time-scale (Mazel et al. 2017, Roy et al. 2019). They contrast, however, with previous reports in mammals and birds, wherein contemporary geographic distances explain the β -diversity of deep branches better than the β -diversity of shallow branches, whereas climatic distances explain the β -diversity of species better than that of deep branches (Mazel et al. 2017). Such a discrepancy suggests that, while mammals and birds first diversified in geographic isolation due to either plate tectonics or rare long-distance dispersal events and then across climatic gradients within large continental areas, liverworts diversified primarily through time along macroclimatic gradients. A signature of geographic isolation can only be found at the level of the shallowest branches, as species may not have had the time yet to disperse across long distances. In turn, the sharp decrease of the correlation between macroclimatic variation and phylogenetic turnover 100 Mya can be interpreted in terms of a burst of diversification (Laenen et al. 2014), especially obvious at the level of epiphytic lineages (Feldberg et al. 2014), triggered by the development of large, humid megathermal angiosperm forests, after which lineage diversification would have been constrained macroclimatically.

Our results have several consequences. First, evidence for macroclimatic niche conservatism at shallow phylogenetic depths lends support to the application of species distribution models, which are among the most widely used tools in ecology (Araújo et al. 2019), but rely on the assumption of niche conservatism for model projection at different spatial and temporal scales (Wiens et al. 2009).

Second, the very weak contribution of geographic distance on phylogenetic turnover may explain why so few bryophyte species are invasive, because virtually all species would have already colonized their climatically suitable range. In turn, the relationship between phylogenetic turnover and macroclimatic variation suggests that bryophyte invasions are constrained by the availability of suitable climates in the invaded range. The observed signal for climatic niche conservatism in fact suggests that alien species may not have the ability to shift niche, as further evidenced by the absence of any signal

of niche expansion upon invasion in invasive mosses and liverworts (Mateo et al. 2015).

Third, macroclimatic niche conservatism in liverworts may explain why, even in organisms with high dispersal capacities, such a pervasive biodiversity pattern as the increase of species richness towards the tropics also applies (Wang et al. 2017), in line with the hypothesis that plant biodiversity is evolutionarily structured globally following a tropical–extratropical pattern (Segovia et al. 2020). While tropical niche conservatism may hence globally limit opportunities for tropical lineages to establish into extratropical regions, this macroclimatic filter is not impermeable, and many tropical lineages have successfully colonized extratropical regions, as illustrated by the reconstruction of the ‘tropicality index’. Such ‘irradiations’ of tropical lineages into extratropical regions can still be found today, as exemplified by the colonization of the western fringe of Europe by lineages of tropical origin (Patiño et al. 2015b), and this recurrent pattern explains the high uncertainty in ancestral area reconstructions in liverworts at and above the genus level (Laenen et al. 2018).

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Author contributions

Flavien Collart, Jian Wang, Jairo Patiño, Olivier J. Hardy and Alain Vanderpoorten contributed equally to this publication. **Flavien Collart**: Formal analysis (lead); Investigation (lead); Methodology (lead); Writing – original draft (supporting); Writing – review and editing (supporting). **Jian Wang**: Data curation (lead); Investigation (equal); Methodology (equal); Project administration (equal); Writing – original draft (equal); Writing – review and editing (equal). **Jairo Patiño**: Conceptualization (lead); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Anders Hagborg**: Data curation (lead); Resources (lead); Writing – original draft (supporting); Writing – review and editing (supporting). **Lars Söderström**: Data curation (lead); Resources (lead); Writing – original draft (supporting); Writing – review and editing (supporting). **Bernard Goffinet**: Investigation (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Nicolas Magain**: Formal analysis (supporting). **Olivier J. Hardy**: Formal analysis (supporting); Investigation (equal); Methodology (lead); Software (lead); Writing – original draft (supporting); Writing – review and editing (supporting). **A. Vanderpoorten**: Conceptualization (lead); Investigation (lead); Methodology (supporting); Supervision (lead); Writing – original draft (lead); Writing – review and editing (lead).

Data availability statement

The molecular data sets and phylogenetic trees can be obtained from <http://purl.org/phylo/treebase/phyloids/study/TB2:S15950?x-access-code=98d94511d8c016de8eae6f21c851826e&format=html>. Species distribution data are available from www.catalogueoflife.org/data/dataset/1074.

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