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RESEARCH ARTICLE

Macroclimatic niche similarity and species relatedness shift their influence on species co-occurrence in bryophyte forest communities across scales

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Abstract

1. The processes driving species co-occurrence across scales are poorly understood. Bryophytes are especially interesting in this respect because, while they disperse over long distances and have broad distributions, they are particularly affected by local conditions due to their small size.
2. We investigated the relationship between pairwise species associations within epiphytic bryophytes and their macroclimatic niche similarities and taxonomic relatedness at four scales (global, regional, habitat and microhabitat). We used community data for 2000 trees from 107 forests in the northwest Iberian Peninsula, and global occurrences for the 33 species with broad distributions, to calculate pairwise co-occurrence at each scale and bioclimatic niche similarity. We also obtained taxonomic distance matrices from the bibliography as a proxy for pairwise phylogenetic relatedness between species.
3. Co-occurrence relates to macroclimatic niche similarity at all scales, but this relationship decreases towards smaller scales. Taxonomic affinity was also a good indicator of the pairwise co-occurrence not explained by macroclimatic niche similarity at the finest scales. Interestingly, at all scales, most pairwise relationships are positive or neutral rather than negative, although the direction of approximately 7% of these relationships shifts from positive at the microhabitat scale to negative at the regional scale. Macroclimatic requirements are progressively less important for species coexistence as scale diminishes,

probably due to the effect of unmeasured local interactions, community-level processes, and microclimatic variations.

4. *Synthesis*. Our results highlight that positive interactions may be at least as important as negative ones, if not more, for the coexistence of bryophyte species across scales. They also underscore that co-occurrence patterns may shift across scales, and the critical role of both macro- and microenvironmental conditions in shaping the life strategies and persistence of local populations of a plant group with population dynamics characterized by extensive geographic distributions. The implications of these findings go beyond their relevance for bryophyte ecology, challenging the prevailing assumption that limiting similarity processes primarily shape ecological communities.

KEYWORDS

bioclimatic niche similarity, biodiversity scaling, coexistence, community dynamics, epiphytic mosses, species interactions, species relatedness

1 | INTRODUCTION

Species coexistence is a central element of community ecology, albeit its determinants are under constant debate. The joint appearance or apparent avoidance of species' populations in space (i.e. attraction and repulsion sensu Keil et al., 2021) has been attributed to species interactions and niche similarity—following the classical views of Clements (1916) and Gleason (1926) (Hortal et al., 2012), as well as to neutral processes (Hubbell, 2001). These intertwined mechanisms can lead to either co-occurrence—species sharing the same space and time, or coexistence—which implies that these species also interact (Blanchet et al., 2020). According to Hutchinson's (1957) niche concept, co-occurring species must share part of their niche space (Colwell & Rangel, 2009), potentially leading to competition and displacement if niche overlap involves limiting resources (Gause, 1934; Letten et al., 2017). But co-occurring species may or may not interact (Calatayud et al., 2020; Leibold & McPeek, 2006). In the absence of competition, facilitation or other interactions, or under neutral dynamics, co-occurrence depends on species' responses to abiotic conditions. These contrasting perspectives indicate that the spatial associations between species result from complex, non-exclusive processes operating across multiple scales (Chesson, 2000; Hubbell, 2001; Keil et al., 2021).

Understanding community pattern and process requires explicitly accounting for scale (Chase, 2014; Wu et al., 2006). Scale influences the mechanisms and factors determining species distributions (Hortal et al., 2010), community diversity (Willis & Whittaker, 2002) and species coexistence (Chesson, 2000; Germain et al., 2021; Leibold et al., 2019). However, the scale dependence of these processes varies across systems (see e.g. Zhang et al., 2014), and some processes can have opposing effects at different scales (e.g. environmental heterogeneity may promote species richness at coarse resolutions but reduce it at finer grains; Stein et al., 2014). Indeed, biotic interactions and metapopulation dynamics typically gain importance at smaller scales (Hortal et al., 2010; Pearson & Dawson, 2003), although their effects can also be appreciable at larger scales (Aragón & Sánchez-Fernández, 2013; Cornell & Harrison, 2014; Leibold et al., 1997; Medina et al., 2018).

Species' responses to abiotic factors can be studied through their bioclimatic niches, which describe their multivariate environmental preferences in the geographical space (Soberón, 2007; Soberón & Peterson, 2005). For clarity, in this paper, *macroclimatic niche* refers to species' responses to large-scale climatic conditions affecting metacommunities, while *microclimatic niche* refers to conditions experienced by individuals. In the absence of other influences, the probability that two species co-occur in the same location would depend on the similarity and/or the proximity between their macroclimatic niches (Broennimann et al., 2012). Deviations from these co-occurrence patterns may arise from neutral processes, microclimatic factors, or non-climatic niche dimensions, which can vary across taxonomic levels (Siepielski & McPeek, 2013). Taxonomically (and thus phylogenetically) close species may co-occur less than expected due to competition—following the exclusion principle; or more than expected due to environmental filtering—according to the coexistence principle (den Boer, 1986), depending on whether their niche and functional traits are phylogenetically conserved or not (Pavoine & Bonsall, 2011; Silvertown et al., 2006). Species sharing environmental constraints (beta niche) tend to coexist, while those sharing resources often compete, reducing coexistence (Wilson et al., 2019). Thus, phylogenetic convergence in resource use leads to exclusion (Violle et al., 2011), whereas environmental filtering promotes the coexistence of related species when environmental responses and functional traits converge (Cadotte & Tucker, 2017; Pavoine & Bonsall, 2011).

Bryophytes have particular characteristics that make them especially interesting for studying co-occurrence across scales (see also Ma et al., 2020). They are small, sessile, show high dispersal ability, and enter into physiological inactivity after desiccation due to their poikilohydry (i.e., inability to actively regulate their water status) (Proctor et al., 2007). Also, most of them can reproduce vegetatively (and many of them sexually) (Glime, 2021). These characteristics have a diverse impact at different spatial scales. Species with smaller diaspores tend to produce more spores and potentially have greater dispersal capacity, so the small size of their diaspores favours long-distance dispersal by wind, and thus many bryophyte species have widespread distributions (Tan & Pócs, 2000)—albeit cosmopolitan bryophytes may be less than 1% of species (Medina et al., 2011). On the other hand, their vegetative reproduction and physiological inactivity during unfavourable conditions enhance their prevalence during long periods (Callaghan et al., 2022; Stark & dos Santos, 2024) on the propagule bank and facilitate sustaining their local populations (Glime, 2020, 2021; Schuster, 1983). Consequently, bryophytes may respond to both macro- and microclimatic conditions with different degrees of intensity (Monteiro et al., 2023).

High connectivity, long dispersal ability and good maintenance of local populations represent a solid skillset for bryophytes to extend over broad distributions (Medina et al., 2011). Mosses exhibit distinct physiological adaptations, such as lower optimum growth temperatures (Furness & Grime, 1982), which result in mosses showing species richness peaks in temperate regions, further north than vascular plants (Mateo et al., 2016; Ronquillo et al., 2023). This is most likely the result of moss responses to water availability and temperature. On the one hand, since mosses lack cuticles, they absorb water directly from air, making them highly dependent on humidity, fog and mist, so the diversity of their communities can be affected by factors such as precipitation, particular orographic conditions that retain humidity, or continentality (Möls et al., 2013). On the other hand, moss diversity does respond to geographical variations in mean annual temperatures, and temperatures during the coldest season (Chen et al., 2015), a response that has been recently attributed to niche-related mechanisms in the extreme conditions of Antarctica (Anderson et al., 2025).

At smaller scales, moss densities may largely depend on local mass effects (During, 2006; Medina et al., 2018), which can promote competitive exclusion processes, as their small size ties them to particular microenvironmental conditions such as adequate temperature, shadow, and presence of water—which may be scattered within a given locality. In this respect, environmental fluctuations, small-scale disturbances (e.g. damages caused by animal activity), and the storage effect (a coexistence mechanism based on the positive outcomes of the previous offspring) are important stabilizing mechanisms (Wilson, 2011) that can facilitate the local coexistence of bryophytes, granting other local-scale processes a significant role in explaining and shaping species composition at finer scales (Kimmerer & Driscoll, 2000).

In this study, we assess the relative importance of species' macroclimatic niches and taxonomic relatedness for their co-occurrence across scales. Specifically, we analyse the pairwise species co-occurrence patterns of epiphytic bryophyte species in the north-western Iberian Peninsula across four spatial scales (global, regional, habitat and microhabitat) and compare them with (i) the similarity and proximity of their realized bioclimatic niches (based on macroclimatic factors), and (ii) their taxonomic affinity, as a proxy of their phylogenetic relatedness. We expect the correlation between the bioclimatic niche similarity and proximity of species pairs and their pairwise co-occurrence to decrease from the global to the local scale, following the hypothesis that macroclimate is the primary determinant of species' spatial associations at a large scale. However, unmeasured local factors such as small-scale environmental conditions and biotic interactions occurring at the microhabitat scale of tree trunks can be more important than macroclimate at finer scales. We also assessed this particular aspect by evaluating the scale dependency of the residual variation in the co-occurrence events that is not explained by macroclimatic niche similarity. Besides that, we also expect that the contribution of taxonomic affinity will differ across scales, with related species co-occurring more often at large scales due to the prevalence of processes related to beta niche dimensions (Silvertown et al., 2006) than they do at small scales due to the preponderance of limiting similarity processes (Violle et al., 2011).

2 | MATERIALS AND METHODS

2.1 | Species datasets

We used data at four different scales: microhabitat (tree), habitat (forest), regional, and global. Microhabitat and habitat datasets comprise presence-absence observations, and regional and global datasets comprise presence-only observations (i.e., species occurrences). The tree and forest datasets were obtained from Medina, Lara, et al. (2015), who sampled *Quercus* forests in a topographically complex area of c. 150,000 km^2 in North and Centre Inland Spain, characterized by a central plateau surrounded by several mountain ranges. This region covers different macroclimatic regimes with large variations in precipitation and temperature, from the Atlantic climate in the north—characterized by humid summers and relatively mild temperatures—to several types of Mediterranean climates ranging from mild continental regimes of rainy winters and limited temperature variations to Mediterranean continental conditions with cold winters (up to 170 frost days in the east), precipitations below 500 mm/year, and prolonged summer droughts (see Medina, Lara, et al., 2015 for a detailed description).

Surveys were conducted in several campaigns between August 2009 and March 2013 (Medina, Lara, et al., 2015; Medina, Mazimpaka, et al., 2015). In total, 107 forests were sampled (Figure 1), dominated by *Quercus ilex* L., *Quercus pyrenaica* Willd. and *Quercus faginea* Lam. In each forest, three different stands were sampled, with six or seven trees per stand, with a total of twenty trees per forest. In each tree, epiphytic mosses were surveyed using a single quadrat of 20 × 20 cm placed at a height between 1.20 and 2.00 m above the ground on the side of the tree with the highest bryophyte cover. All mosses present in that quadrat were collected, stored in dry conditions in paper bags, to be later identified in the lab. This design seeks to minimize as much as possible variations in

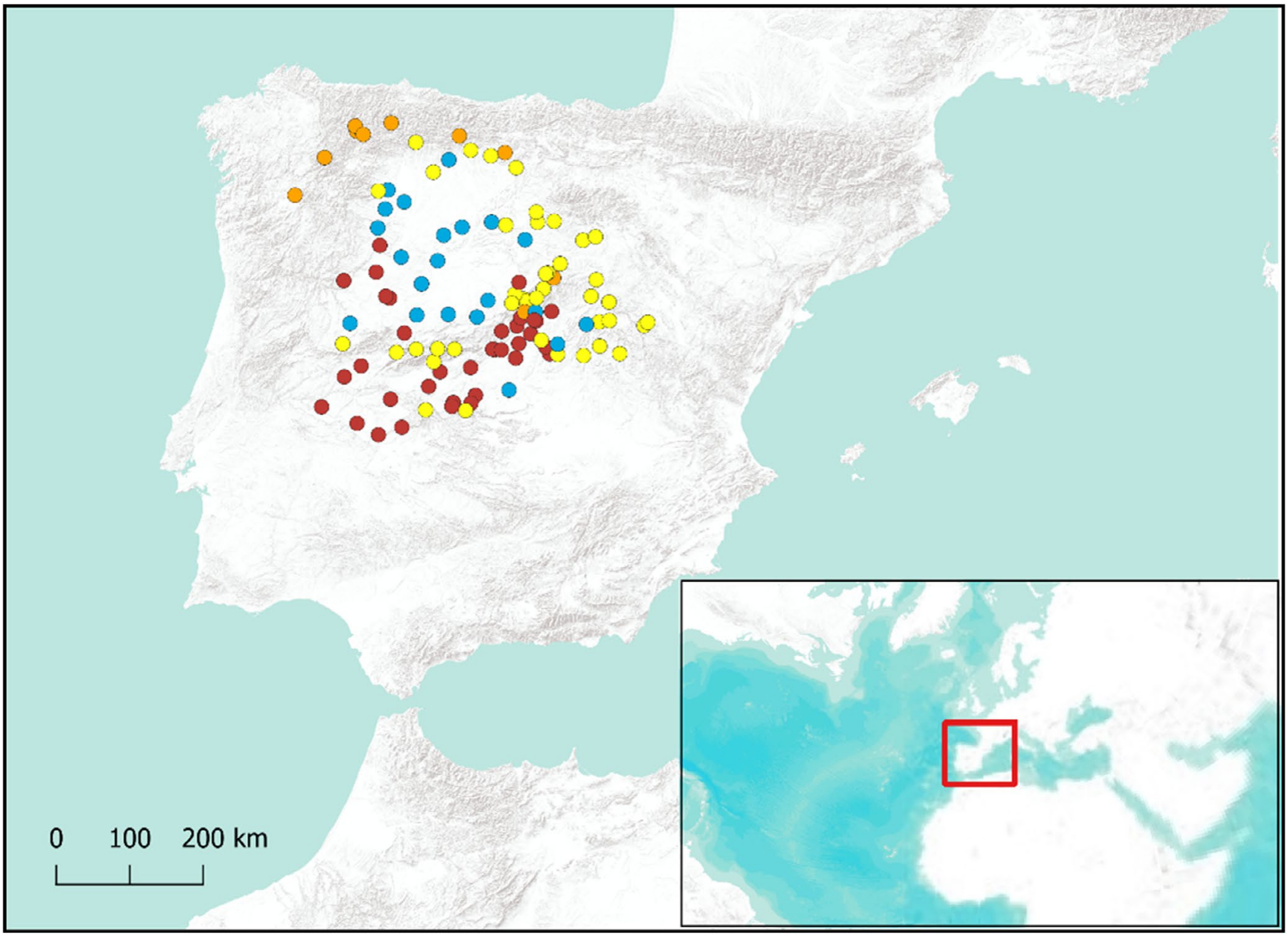

FIGURE 1 Location of the 107 sampled forests in the northwestern Iberian Peninsula. Colours correspond to the four biogeographic modules: Groups of forests with different floristic compositions identified through modularity analyses by Medina et al. (2021), referred to as module 1 (yellow), module 2 (blue), module 3 (red), and module 4 (orange) herein.

moss cover due to microclimatic conditions, and often resulted in sampling either a single pad of mosses or several contiguous ones within each quadrat.

For this study, we selected those bryophyte species present in more than 15 of the 107 *Quercus* forests, totalling more than 2000 trees sampled (Medina, Lara, et al., 2015; Medina, Mazimpaka, et al., 2015). Rare species (those present in less than 15 forests) were discarded as their low degree of occupancy would not allow fair comparisons of species co-occurrence between scales (Figures S1.1 and S1.2). In total, we selected 33 species (32 mosses and one liverwort) from a total of 88 bryophyte species in the dataset (Table S1). Also, we assigned all forests to one of four intertwined regions across the northwestern Iberian Peninsula, based on the four biogeographic modules composed of forests with distinct epiphytic bryophyte floras classified through network analyses by Medina et al. (2021) (Figure 1).

To create the global dataset, we downloaded the records separately for the 33 selected species from GBIF (https://www.gbif.org/) (see Appendix S1 for references of each species' dataset). Albeit sparse and subject to some temporal biases, data on the occurrence of these species from GBIF provides a relatively fair picture of the geographical distribution and responses to macroclimate of the most common bryophyte species, both in the Iberian Peninsula and the whole of Europe (Ronquillo et al., 2020, 2023). To ensure that estimates of macroclimatic niche and co-occurrence are based on reliable data, we conducted a thorough record cleaning and filtering procedure following some of the steps detailed in Ronquillo et al. (2024), as follows. In the first step, we filtered by species name and status 'PRESENT', collecting ca. 650,000 occurrences. Then, we conducted a taxonomical harmonization of species names using specialized checklists (Hill et al., 2006; Ros et al., 2013), The Plant List (which served as the taxonomic backbone for current World Flora Online, https://www.worldfloraonline.org/) and TROPICOS (https://tropicos.org/home), updated with Aleffi et al. (2020) and Hodgetts et al. (2020)—which resulted in some taxonomical modifications but yielding no variation in the bryophyte species distinctness or number. We kept only those records in which the 'scientific_name' field contained the accepted species name or their corresponding synonyms and excluded varieties and subspecies. We then filtered the dataset to keep records with 'year of collection' information in a temporal range between 1950 and 2021 to match as much as possible the climatic information used to estimate the realized macroclimatic niches (see below). We validated each occurrence geographically, discarding records without values for coordinates and also those with coordinates rounded to 0 decimal digits, or the same value for latitude and longitude. To reduce sample bias, we discarded records placed in a 1 km buffer near scientific institutions, records whose country location did not match the country assigned by recorders, and those that did not fall on terrestrial land. Finally, we selected occurrences with a unique combination of species name, collection year, and latitude-longitude values. The final dataset for the global scale has a total of 527,191 records (Figures S1.1 and S1.2).

2.2 | Calculation of species co-occurrence matrices

We checked every presence/absence observation at microhabitat and habitat scales; that is, in the 2000 trees for the tree scale and the 107 forests at the forest scale. We also retrieved species presences in the four regions, transforming and filtering each scale dataset into a matrix using R (version 4.1.2; R Core Team, 2021). Then, pairwise species associations for each scale were calculated as a co-occurrence distance matrix using Jaccard distance in the 'vegan' R package (Oksanen et al., 2020) (Figures S1.1 and S1.2). Finally, to create a matrix denoting pairwise species co-occurrence at the global scale, we employed an equal-area hexagon gridding system available from R package dggridR (Barnes & Sahr, 2022). This equal-area grid system avoids distortions caused by rectangular grids with geographic coordinate systems, preventing biased comparisons with unequal sample/cell sizes. Since multiple nested resolutions exist for this grid, based on our previous knowledge of the distribution and geographical coverage of bryophyte occurrence data in the Iberian Peninsula (Ronquillo et al., 2020), we selected resolutions of hexagonal cells of around 23 and 8 km^2. We then created a matrix of species co-occurrence based on the presence coordinates (from the global dataset) intersecting at each grid cell. If a species pair is found in the same hexagon cell, the matrix value equals one, and zero otherwise. This analysis was employed for each species pair and grid size. In a preliminary evaluation, both resolutions performed similarly in the rest of the analyses (not shown). Therefore, adopting a conservative approach, we discarded the resolution of 23 km^2, as it provided potentially more spurious co-occurrences of species present in distant forest fragments but not actually co-occurring in the same ones. We thus used a resolution of 8 km^2 for the global scale co-occurrence matrix (Figures S1.1 and S1.2).

2.3 | Calculation of bioclimatic niche metrics

To account for the macroclimatic conditions in the period of study, we selected five bioclimatic variables from CHELSA climate dataset version 2.1 (derived from data on the climatology between 1979 and 2013; Brun et al., 2022; Karger et al., 2017). Note that we include species records from before and after the period used to create this database, assuming that it provides a fair reference to the macroclimatic conditions experienced during the establishment of forest bryophyte species before and (to a lesser extent) immediately after such period. Annual mean temperature (BIO1) and annual precipitation (BIO12) provide a broad definition of the macroclimatic range; Temperature and precipitation seasonality (BIO4 and BIO15) summarize macroclimatic variability; and the mean temperature of the wettest quarter (BIO8) does so for the large-scale relationship between water availability and temperature in evapotranspiration and photosynthesis, which is key for bryophyte growth, reproduction and life cycles (Oliver et al., 2005; Proctor et al., 2007) (Figures S1.1 and S1.2). All macroclimatic variables were centred and scaled previously to hypervolume analyses. Niche hypervolumes were calculated using the R package 'hypervolume' (Blonder et al., 2018, 2022) through the Support Vector Machine (SVM) method (with default parameters to facilitate comparisons among species and studies). Using this technique, hypervolumes are built through a one-class SVM that classifies data points as 'inside' and other locations as 'outside'. The algorithm proceeds by: (i) transforming the input data into a high-dimensional nonlinear space where data points can be optimally separated from the background by a single hyperplane; (ii) back-transforming the hyperplane into the original space; (iii) delineating an adaptive grid of random points near the original data points; and (iv) using the calibrated SVM to predict if points are inside or outside the cloud of occurrences of the species, thus defining the limits of its niche hypervolume.

To obtain niche similarity, we calculated the total volume of each species' hypervolume as well as the intersection between the hypervolumes for each species pair. From these two values, we then calculated Jaccard similarity (J_S, Equation 1), and its complement, i.e. the Jaccard Dissimilarity (J_D) as:

$$J_S(i,j) = \frac{V(H_i \cap H_j)}{V(H_i \cup H_j)}, \tag{1}$$

$$J_D = 1 - Js,$$

where V is the estimated volume of niche hypervolumes (H), for species i, and j, with $i \neq j$, and $i, j = \{1, .., N\}$ with N equal to the total number of species. A total of 1×10^6 random points were used for intersection calculations. In addition, we measured niche proximity between species pairs by calculating the Euclidean distance (see Shirkhorshidi et al., 2015) between hypervolume centroids (Mammola, 2019). All computations were done with the R package 'hypervolume' (Blonder et al., 2018, 2022) (Figures S1.1 and S1.2).

2.4 | Calculation of taxonomic distance matrices

We retrieved two taxonomic classifications: a conservative synthetic version based on Casas et al. (2006) and Guerra and

Cros (2007–2018) and an updated analytical version (following Aleffi et al., 2020; Hodgetts et al., 2020) including the latest changes in the families Orthotrichaceae, Brachytheciaceae and Bryaceae. The only liverwort species selected, *Frullania dilatata*, has not undergone any nomenclatural changes. We created two taxonomic trees based on these taxonomic classifications (Figures S2.1 and S2.2) with all the species selected for the study using 'networkD3' and 'data.tree' (Allaire et al., 2017; Glur, 2020). We then selected two different penalties (distances) for the paths between each species pair, one that starts at the genus level for synthetic and analytical versions and one at the family level for the analytical version (Table S2), due to the subtle differences at the family level between both taxonomic trees. The resulting distances for each pair of species were compiled in three taxonomic distance matrices: TD1 (conservative, genus level), TD2 (analytical, genus level) and TD3 (analytical, family level) (Table S2; Figures S1.1 and S1.2).

2.5 | Statistical analyses

To estimate the effects of environmental filtering on pairwise co-occurrences, Mantel tests with 1000 permutations were conducted using the 'vegan' R package (Oksanen et al., 2020). These analyses characterize the overall correlation between the pairwise co-occurrence of epiphytic bryophyte species and the similarity in their niches at each scale of analysis. That is, the Jaccard distance matrix of species co-occurrences, and two different matrices depicting, respectively, bioclimatic niche similarity (i.e., the Jaccard distance between the hypervolumes of both species) or bioclimatic niche proximity (i.e. the distance between niche centroids) (Figures S1.1 and S1.2). After accounting for shared responses to the environment, we obtained the residuals from the relationship between niche similarity metrics and pairwise co-occurrence to analyse the remaining patterns of co-occurrence in the data. We used the R package 'daee' (Debastiani, 2021), and package 'ggplot2' for visualization (Wickham, 2016). The residuals of these Mantel tests, hereafter called macroclimate residual associations, account for the variation not explained by the previous correlation that can be due to other factors different from macroclimate. We, therefore, examined their patterns and assessed the scale dependency in the relationship between these macroclimate residual associations and taxonomic affinity (Figures S1.1 and S1.2).

3 | RESULTS

The 33 selected species were widely distributed in the study area (Table S1). Values of species richness per tree ranged between 0 and 14 (average = 3.86), and between 3 and 25 per forest (average = 12.4 species per forest) (Figure S3). Three of the regional modules depicted in Figure 1 hosted most of these species (32, 30 and 31 species in modules 1, 2 and 3, respectively); however, module 4 only had 20 out of the 33 species included in this study. These widespread distributions resulted in a high number of co-occurrences; on average, each species co-occurred 4357 times with other species in the same 8 km hexagon of the grid used for the global analyses, ranging between the 263 co-occurrences of *Orthotrichum comosum* to the 9792 of *Syntrichia ruralis*. Coexistence at the tree scale was also high; on average, each species co-occurred 1217.4 times with other species in the same quadrat. Strikingly, patterns of co-occurrence per species were widely different between scales, as *Syntrichia ruralis* showed the minimum number of co-occurrences in single trees, with 154 in total, compared to the maximum of 3985 co-occurrences shown by *Orthotrichum affine*, or the 603 of *O. comosum* (Table 1). Indeed, the number of co-occurrences per species at these two scales was not related (Pearson correlation = 0.078, $p = 0.436$).

3.1 | Effect of environmental filtering on pairwise species co-occurrences across scales

The co-occurrence distance matrices present species pairwise differences ranging between 1.00 and 0.57 (mean = 0.95) for the microhabitat (tree) scale, between 1.00 and 0.25 (mean = 0.76) for the habitat (forest) scale, and between 0.75 and 0 (mean = 0.21) for the regional scale. Pairwise bioclimatic niche distance metrics ranged between 1.00 and 0.28 (mean = 0.85) for similarity and between 5.53 and 0.22 (mean = 2.24) for proximity. These co-occurrence patterns were largely similar at different levels of coverage of mosses within each tree quadrat sampled, and among the *Quercus* species sampled. On the one hand, the co-occurrence distance matrices obtained by dividing the trees and with different thresholds of moss cover were highly correlated with each other (0.81 and 0.88 for thresholds of 80% and 50% moss cover, respectively; both Mantel correlations showed $p < 0.0001$). On the other hand, although not all bryophyte species are present in the tree-trunk samples of all *Quercus* species studied, in all cases, these absent species are relatively rare in our dataset (Table S1). Further, the pairwise co-occurrence distance matrices derived from the data of individual *Quercus* species were correlated between them in all cases (Table S3). Given that most differences in the bark roughness of the trees sampled were due to tree age rather than to tree species (N.G. Medina, unpublished field observations), for the purpose of our analyses we conclude that it is safe to assume that all trees sampled share a common bryophyte species pool. We note, however, that some of the unexplained variability in our analyses may come from the

TABLE 1 Values of Mantel *r* statistic between distance matrices of pairwise species co-occurrence between different scales.

Scales	Global	Regional	Forest
Regional	0.24 [$p = 0.01$]		
Forest	0.32 [$p = 9.99 \times 10^{-5}$]	0.48 [$p = 9.99 \times 10^{-5}$]	
Tree	0.25 [$p = 4.99 \times 10^{-4}$]	0.30 [$p = 9.99 \times 10^{-5}$]	0.83 [$p = 9.99 \times 10^{-5}$]

impact of potential host differences in the co-occurrence patterns of some of these rare species.

The co-occurrence of bryophyte species pairs was more similar between the tree and forest scales than either of them with the regional or global scale (Table 1). Also, bioclimatic niche metrics and co-occurrence are correlated at all scales studied (Table S4; Figure 2). This result means that pairs of species with similar niches and closer niche centroids tend to co-occur more at all scales studied. Mantel scores were generally higher for niche proximity than niche similarity, except for the global scale. Coexistence at the global scale presents high correlations with niche similarity and proximity. Mantel scores decrease steeply at the regional scale and then continue to diminish with decreasing scale for both metrics, except for niche proximity at the forest scale (Figure 2).

3.2 | Variation in co-occurrence not explained by bioclimatic niche differences across scales

The average values of the residuals of the Mantel tests between pairwise bioclimatic niche similarity or proximity and co-occurrence are similar to zero regardless of the scale (Figures S4.1 and S4.2), despite the large differences in the relationships between these metrics and co-occurrence. This result indicates no consistent bias in the results of the Mantel tests. However, the patterns of pairwise macroclimate residual associations are inconsistent across scales (Figure 3; Figure S5; Table S4). Although the sign of most species pairs remains similar across scales, some pairwise residuals are negative at one scale but positive at other scales, and vice versa (Table 2). These shifts in sign are more numerous between forest and regional scales (7% of all species pairs for niche proximity and 6% for niche similarity) and between regional and global scales (6.4% of all species pairs in niche proximity). Niche similarity metrics and co-occurrence relationships change across scales, and the distribution of residual values switches gradually from negative at the smallest scales to positive at larger ones. This is valid for all comparisons between scales, except between forest and tree scales, which are relatively more similar. Strikingly, the patterns of pairwise macroclimate residual associations found at the smaller scales are disrupted at the regional and global scales (Figure 3; Figure S4; Tables S5.1–S5.6), so species pairs with positive residuals at fine scales show negative residuals at larger ones, and vice versa (Table 2).

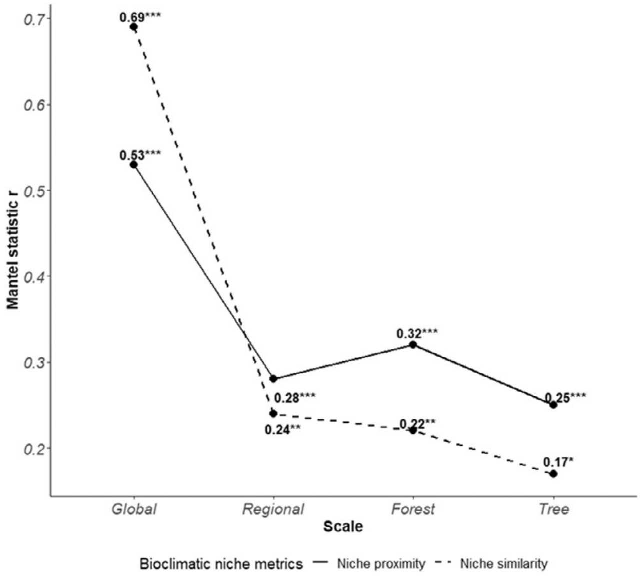

FIGURE 2 Mantel test scores of the correlations between the pairwise co-occurrence of bryophyte species and the similarity and the proximity of their bioclimatic niches at each scale. The dashed line stands for niche similarity (i.e. Jaccard distance between hypervolumes), and the solid line for niche proximity (i.e., the distance between centroids). All tests were statistically significant: $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.005$ (Table S4).

Importantly, we also found a higher proportion of positive associations at the two finer scales (Figure 3; Figure S4), indicating that many species co-occur in the same tree trunks and forests more than expected according to their bioclimatic niche similarity. However, when using a threshold to classify residuals close to zero, most are neutral at the microhabitat scale (Table 2). Also, negative residuals present larger maximum values at the microhabitat and habitat scales (Figures S4.1 and S4.2), indicating that at these small scales, pairs of species co-occur much less than expected by their macroclimatic requirements. In contrast, the regional scale shows the opposite pattern, with less positive residuals but of higher magnitude (Table 2; Figures S4.1 and S4.2), indicating lower pairwise co-occurrence than expected by bioclimatic niche similarity within each biogeographical module and positive residuals more distant from what is expected by these niche metrics (Figure 3; Figure S4).

3.3 | Effect of taxonomic affinity on macroclimate residual associations

The taxonomic distance between species pairs is significantly and positively related to macroclimate residual associations at the forest and tree scales (Table 3). This pattern is similar for both the conservative and analytical classifications (Figures S2.1 and S2.2) when considering distances from the genus level (TD1 and TD2) at the tree scale, probably due to the signal being consistent also at the family level (TD3). The explanatory power of the relationships between taxonomic affinity and macroclimate residual associations obtained from bioclimatic niche similarity and proximity is similar at forest and tree scales (Table 3).

4 | DISCUSSION

Our results show that macroclimate largely determines the co-occurrence of bryophyte species through the convergence in their bioclimatic niches, but also that this is not the only factor modulating their co-occurrence. Although pairs of species with closer niche centroids and higher niche similarity tend to co-occur more at all

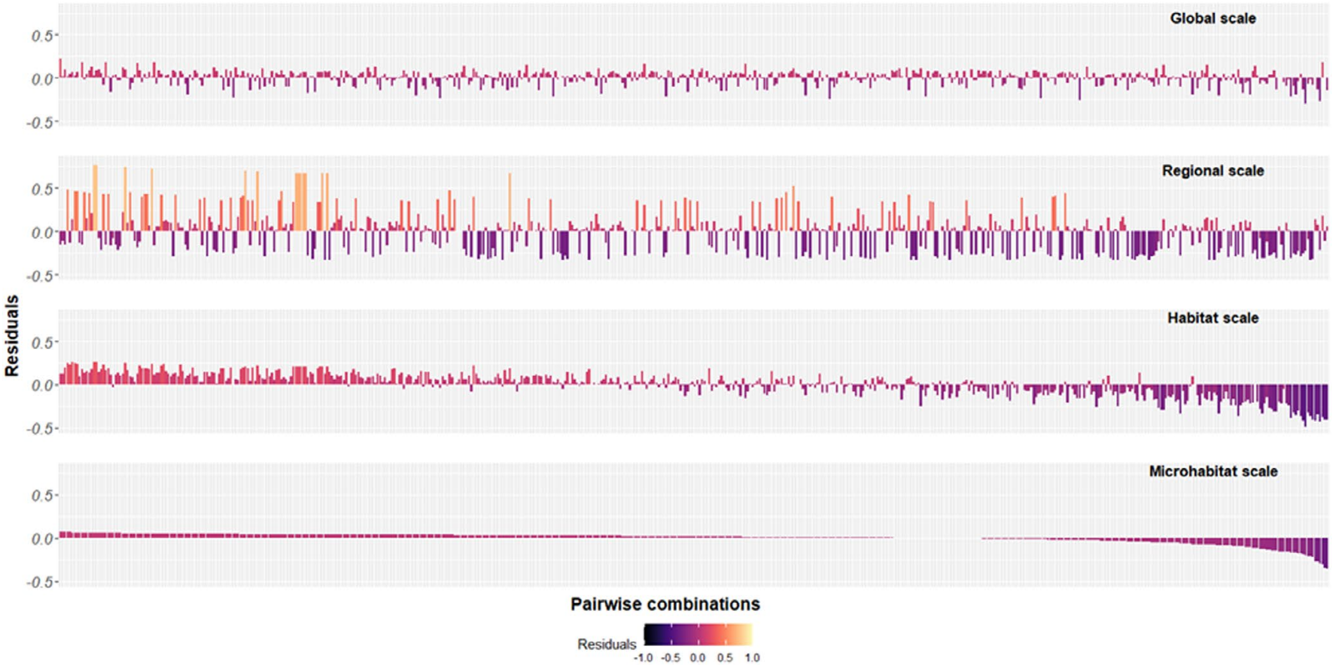

FIGURE 3 Comparison between spatial scales of residuals from Mantel tests performed with niche similarity and co-occurrence distance matrices for each spatial scale. Pairwise combinations are ordered by highest to lowest values from the tree scale as the reference and are kept in the same order at all the scales for comparison purposes.

TABLE 2 Number of positive and negative residuals and percentage of change between them across spatial scales for bioclimatic niche metrics.

Bioclimatic niche metrics	Scales	Number of residuals			Percentage of change from positive to negative residuals				Percentage of change from negative to positive residuals			
		+	−	Neutral	Tree	Forest	Regional	Global	Tree	Forest	Regional	Global
Niche similarity	Tree	0	35	493	0.00	0.00	0.00	0.00	0.00	0.00	0.76	0.38
	Forest	127	111	290	0.00	0.00	6.06	2.08	0.00	0.00	2.84	1.33
	Regional	140	196	192	0.76	2.84	0.00	1.89	0.00	6.06	0.00	2.84
	Global	31	70	427	0.38	1.33	2.84	0.00	0.00	2.08	1.89	0.00
Niche proximity	Tree	0	35	493	0.00	0.00	0.00	0.00	0.00	0.00	0.76	0.76
	Forest	120	108	300	0.00	0.00	7.01	2.27	0.00	0.00	2.46	2.84
	Regional	131	205	192	0.76	2.46	0.00	1.33	0.00	7.01	0.00	6.44
	Global	89	80	359	0.76	2.84	6.44	0.00	0.00	2.27	1.33	0.00

Note: Values were considered positive or negative if they departed from zero at >0.1 and <−0.1 thresholds, respectively. Residual values in between these values are considered neutral for this table.

the spatial scales studied, pairwise spatial associations between species change across scales. Indeed, the number of co-occurrences shown by each species is uncorrelated between the tree and global scales. Further, Mantel correlation values are higher at the global than at the regional, forest, or local scales, so the inverse pattern is found for residuals. Positive residuals are more numerous than negative ones at the forest scale, but this proportion changes with scale; bryophyte species co-occur more than expected at the forest scale and less than expected at the regional scale. Interestingly, the structure of the residuals is quite similar for both tree and forest scales, a potential consistency across small scales that may be interesting to investigate in other taxa and ecosystems. Information about niche optima and taxonomic affinity evidences that species relatedness also affects their co-occurrence; although, contrary to expectations, taxonomically related species tend to co-occur more often than expected due to niche similarity.

Given that the importance of the effect of bioclimatic niche similarity diminishes with scale, it is necessary to study different scales to understand the determinants of coexistence (Germain et al., 2021; Leibold et al., 2019; Willis & Whittaker, 2002). The macroclimatic range limits of the epiphytic bryophytes studied here are akin to the regional, forest and tree scales, as they all inhabit

TABLE 3 Results of the Mantel tests (Mantel statistic *r*) between the matrices of macroclimate residual associations and the taxonomic distance matrices (TD1: conservative synthetic classification, distances accounting for Genus; TD2: up-to-date analytical classification, distances accounting for Genus; and TD3: up-to-date analytical classification, distances accounting for Families).

	Macroclimate residual associations		
	Bioclimatic niche similarity	Bioclimatic niche proximity	Taxonomic distance matrices
Global	0.005	−0.034	TD1
	−0.014	−0.051	TD2
	−0.035	−0.066	TD3
Regional	0.014	0.004	TD1
	0.013	0.003	TD2
	0.018	0.010	TD3
Forest	**0.219****	**0.217***	TD1
	0.187*	**0.184***	TD2
	0.173*	**0.173***	TD3
Tree	**0.295*****	**0.293*****	TD1
	0.270***	**0.268*****	TD2
	0.25***	**0.252*****	TD3

$^{*}p < 0.05$.
$^{**}p < 0.01$.
$^{***}p < 0.005$.

the studied region. However, those presences are a subset of their global distributions, so the species studied have different macroclimatic niches. If the macroclimatic niches of two species are closely even, it can be expected that local spatial divergence due to limiting similarity and competitive exclusion processes will decrease the probability that they co-occur locally, thus diminishing the relevance of macroclimate for the coexistence of bryophytes at local scales. Also, negative interactions are less prone to scale up from the local scale (Araújo & Rozenfeld, 2014), so species can escape displacement through competitive exclusion by exploiting otherhabitats, a strategy facilitated by the presence of landscape spatial heterogeneity at broader scales. Here, habitat heterogeneity may act as a stabilizing factor at the regional scale, which could explain the co-occurrence of species pairs that do not coexist at the habitat and microhabitat scale (Chase, 2014) by 'alleviating' the regional niche overlap (Letten et al., 2017).

Bryophyte coexistence at small scales has already been related to environmental filtering associated with similar functional traits, particularly under stressful microhabitat conditions (Monteiro et al., 2023). Here note that in this study, the co-occurrence data collected from tree to regional scales is gathered from the same kind of microhabitats, as all species are epiphytic bryophytes recorded at the same part of the tree trunks (Medina et al., 2021; Medina, Lara, et al., 2015), thus reducing the possible increase of co-occurrence through habitat heterogeneity detected by Monteiro et al. (2023) for bryophytes growing on mountain streams (see also Heino & Virtanen, 2006). We should also note that previous studies have shown that microclimatic conditions and other aspects of microhabitat explain a significant part of the small-scale variability in bryophyte distributions that is not explained by macroclimate (e.g., Hespanhol et al., 2010; Kimmerer & Driscoll, 2000; Man et al., 2022). Still, in our study, species with similar niches are more likely to co-occur at local scales, evidencing that macroclimatic conditions play a major role in species coexistence for the studied bryophytes, as they do for their co-occurrence at small scales (Monteiro et al., 2023).

As macroclimate determines the co-occurrence of bryophyte species, and this correlation is higher at the global scale, it can be argued that the processes dominating their coexistence are related to their beta niche dimensions (Silvertown et al., 2006). Thus, the differences in correlation across scales would be explained by the changing differential relevance of the alpha and beta components of the niche (sensu Wilson et al., 2019) across spatial scales. Interestingly, the species that shifts from co-occurring the most with other species at the global scale to the least at the tree scale, *Sytrichia ruralis*, is a generalist soil moss species, which is widespread in biological soil covers in the studied region but that colonizes only rarely tree trunks, at points where the bark accumulates dust or organic matter (N.G. Medina and B. Estébanez, unpublished field observations). This highlights the importance of microenvironmental conditions for the coexistence of species. When recreating the bioclimatic niche, the selected macroclimatic variables embrace both niche components, framing not only the environmental limitations of the species (Beta component) at large scales, but also the resources related to factors like substrate or water availability within the ecosystem (Alpha component) at local scales. Thus, at broader scales, beta niche similarity enhances coexistence, while at local scales alpha-niche similarity favours competition, hampering coexistence.

Residuals provide information on the co-occurrence not explained by the bioclimatic niche metrics, as not all the species were equally fitted to the macroclimatic environmental filtering (Zambrano et al., 2017). Many pairs of species shift from co-occurring more than predicted by their bioclimatic niche similarity at the global scale to less than expected at forest and tree scales, and vice versa. To some extent, this may be related to the findings that bryophyte species occurrences are often uncorrelated between local and regional scales (Virtanen, 2014), which is exemplified by the extreme case of *Syntrichia ruralis* highlighted above. However, this effect may also indicate that the patterns originated from positive interactions permeate from small to larger scales more often than those from negative interactions, which rarely scale up (Araújo & Rozenfeld, 2014). Indeed, at tree and forest scales, it seems that species pairs co-occur more than predicted by their macroclimatic niche, but when two species co-occur less than expected, these negative residuals are of higher magnitude. These differences in co-occurrence concerning the predictions based on macroclimate could be attributed to different factors, such as biotic interactions, neutral processes (Medina et al., 2018), differences in fitness, and other specific differences in establishment success related to diaspore traits (Hurtado et al., 2022; Virtanen, 2014), or taxonomic affinity. In contrast, at the regional scale, the positive residuals are of higher magnitude than their negative counterparts, indicating that the signal of the attractions and repulsions does not scale up in the same way, probably due to the scale dependency of the processes (Chase, 2014). This effect implies that local processes such as positive interactions or stabilizing mechanisms (i.e., seasonality, storage effect) may promote co-occurrence at the local scale, but their effect dissipates at coarser scales. Here, we must note that we did not directly study biotic interactions or neutral processes due to the methodological limitations and limited feasibility of gathering these data at the scales studied, and the limited data available. However, we framed the relevance of taxonomic affinity in the co-occurrence of bryophytes, either independently of bioclimatic niche metrics or controlling for them by analysing the macroclimate residual associations.

According to our results, taxonomically similar species of bryophytes may coexist at local scales by convergence and ecological filtering, as they tend to be also ecologically similar (i.e., coexistence principle, den Boer, 1986). However, the relationship between taxonomic affinity and species co-occurrence does not scale up to broader scales. This is in apparent contradiction with the importance of limiting similarity processes for explaining species co-occurrence at local communities (Violle et al., 2011; but see Zambrano et al., 2017). Taxonomic affinity may reflect phylogenetic and functional similarities, as well as a shared history. Indeed, some of these families, such as Orthotrichaceae, have radiated in epiphytic environments (Draper et al., 2022). Thus, a reasonable explanation may be that the good dispersal abilities, persistence, and maintenance of bryophytes may ease their coexistence in communities. In fact, since facilitation is common in their early stages of development (Malkinson & Tielbörger, 2010), and their local populations are in constant renewal, bryophytes are expected to show more positive than negative interactions at local scales. Spatial mass effects could also enhance the co-occurrence of related species when negative interactions appear, balancing the limiting similarity at local scales by the connectivity and dispersal across scales.

A complementary view of the origin of the scale-dependence of pairwise co-occurrence may be related to the key difference between co-occurrence and coexistence (Blanchet et al., 2020). The fact that two species share the same place in space and time does not imply that they interact at multiple scales (Calatayud et al., 2020; Leibold & McPeek, 2006). For instance, presence-absence data and coexistence theory do not delineate well when two species strongly interact negatively (Blanchet et al., 2020). However, when bryophyte species co-occur at the microhabitat scale sharing the same moss pad in the same tree trunk, they are physically in touch and share resources (fundamentally water), so it is extremely likely that they interact and thus effectively coexist. This argument, however, contrasts with the difficulty of detecting interactions at higher spatial scales (e.g., regional, global). Perhaps due to this, the relevance of biotic interactions for species occurrence is thought to decay when scaling up (Hortal et al., 2010; Pearson & Dawson, 2003). However, at least in the case of bryophytes, the empirical studies of their species interactions at large scales present important limitations, and there is a general lack of information about their distribution and interactions. Therefore, the interactions between co-occurring species should neither be assumed nor discarded.

Our study presents some limitations. Some caution is needed when interpreting Mantel tests between distance matrices originated with continuous and discrete data (i.e., taxonomic affinity and co-occurrence). There are limitations in using correlative observational data to the environment instead of abundance or growth traits (Cadotte & Tucker, 2017). In our study, false positives are difficult to assess, as bryophyte species often persist locally due to asexual reproduction and permanence in the diaspore bank (During, 2001). Furthermore, the same happens with false negatives, as absences do not necessarily imply that the environmental conditions for surviving and reproducing are not met at that scale (Cadotte & Tucker, 2017). However, as suggested by Cadotte and Tucker (2017), for this type of data, we use 'environmental filtering' in a non-strict definition, as we cannot separate the biotic interplay of the studied species at any of the scales studied. Also, the sampling effort and detection probabilities vary widely across hexagons on the global scale. However, these large hexagon units allow us to average out the local differences and, since only (co-)occurrence is annotated, this is less prone to uncertainties than, e.g., diversity metrics or abundance. In addition, we should also note that the extensive geographic coverage of the surveys (2000 trees from 107 forests across the Iberian Peninsula) presented significant methodological challenges, such as the impossibility of leaving dataloggers to record seasonal and yearly variations in microclimate or insolation between trees, or the lack of measurements of chemical variations in bark composition, which prevented accounting for data on microenvironmental conditions—except for bark roughness, which had some effect on bryophyte cover in these forests (Medina et al., 2018). Thus, future works delving into the nature of the impacts of local and microhabitat conditions on species coexistence should develop strategies to gather relevant environmental information at the forest stand and tree scales.

5 | CONCLUSIONS

The multi-scale approach of this study allowed us to identify how the importance of different factors affecting species co-occurrence shifts progressively across scales. Our results show that macroclimate is a determinant for the co-occurrence of the bryophytes studied, but also that co-occurrence patterns may shift with scale, as local conditions and taxonomic affinity promote coexistence at the smallest scales. We found that epiphytic bryophytes display positive pairwise co-occurrence more frequently than negative. This effect occurs more often at finer than at coarser scales and is more frequent between closely related species, even after considering the effects of macroclimatic niche similarity. This downweights the importance of limited similarity processes for determining the diversity of epiphytic moss species that, arguably, compete for adequate trunk areas. These results call for a preponderance of positive interactions promoting the coexistence of bryophytes in multispecies moss pads and their co-occurrence in diverse local communities.

Microenvironmental conditions are vital in the life strategies and maintenance of local moss populations, and their population dynamics embrace broad distributions and complex connectivity systems between them. Thus, it is hard to extrapolate whether these results will stand out for bryophyte communities in other types of habitats, such as soil, rock, or streams. However, they seemingly indicate that positive interactions may regulate species coexistence, at least for those growing in multispecies moss pads. This opens an avenue for future research, as understanding the drivers of coexistence in bryophytes requires quantifying it, examining interaction strength, and assessing species responses across different scales. Importantly, the implications of the results presented here go beyond their relevance for bryophyte ecology, as they inform against the common assumption that ecological communities are mainly structured by competitive processes. To determine the generality of this pattern, future research should focus on quantifying coexistence and gathering information on interaction strength and species responses across scales, as well as identifying traits that may be related to these interactions. We suspect that as more high-quality data on species co-occurrence and interactions become available, more examples of taxa showing a higher proportion of species attractions than of repulsions in space and time will be found.

AUTHOR CONTRIBUTIONS

Conceptualization and methodology: Fernando Hurtado, João Gonçalves, Helena Hespanhol, Belén Estébanez, Pedro Aragón, Nagore G. Medina and Joaquín Hortal. Data retrieval and curation: Nagore G. Medina, Cristina Ronquillo, João Gonçalves and Fernando Hurtado. Investigation: João Gonçalves, Helena Hespanhol, Belén Estébanez and Fernando Hurtado. Analyses: Fernando Hurtado, João Gonçalves, Helena Hespanhol and Nagore G. Medina, with Cristina Ronquillo, Belén Estébanez, Pedro Aragón and Joaquín Hortal. Manuscript writing: Fernando Hurtado, João Gonçalves and Joaquín Hortal, with Helena Hespanhol, Cristina Ronquillo, Nagore G. Medina, Belén Estébanez and Pedro Aragón.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The dataset of bryophyte occurrence records for the global co-occurrence matrix and for the hypervolume calculations is available at Digital CSIC repository (https://doi.org/10.20350/digitalCSIC/15317). The specific download references of GBIF are listed in Appendix S1 and at Digital CSIC repository (https://doi.org/10.20350/digitalCSIC/15317).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: List of GBIF references with corresponding DOIs.

Figures S1.1 and S1.2: Flowcharts of the methodology.

Figures S2.1 and S2.2: Taxonomy classification trees followed for the taxonomic distance matrices.

Figure S3: Violin plots showing the distribution of the number of bryophyte species used in this study per tree, forest and 8 km hexagon from the grid cell used for the analyses.

Figures S4.1 and S4.2: Boxplots of Mantel test residuals for the bioclimatic niche metrics and co-occurrence.

Figure S5: Comparison between spatial scales of residuals from Mantel tests performed with niche proximity and co-occurrence distance matrices of each spatial scale.

Table S1: Distribution of the studied bryophyte species in the trees of each *Quercus* species.

Table S2: System used for taxonomic distance (TD) matrices.

Table S3: Similarity between pairwise bryophyte species co-occurrence distance matrices at the tree scale constructed for each host tree species.

Table S4: Results of the Mantel tests (Mantel statistic r) for co-occurrence distance matrices at different scales and bioclimatic niche metrics.

Tables S5.1–S5.6: Mean and median of Mantel tests residuals.

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