RESEARCH ARTICLE

Bryophyte assembly rules across scales

Juliana Monteiro[1] | Cristiana Vieira[2] | Cristina Branquinho[1]

[1]cE3c-Centre for Ecology, Evolution and Environmental Changes & CHANGE-Global Change and Sustainability Institute, Faculdade de Ciências, Universidade de Lisboa, Lisbon, Portugal

[2]Museu de História Natural e da Ciência da Universidade do Porto (MHNC-UP/UPorto/PRISC), Porto, Portugal

Correspondence
Cristina Branquinho
Email: cmbranquinho@fc.ul.pt

Abstract
1. Understanding how species assemble into communities is a central issue in community ecology. So far, most studies have focused on the assembly mechanisms of vascular plant communities, while the role of deterministic (environmental filtering and biotic interactions) and stochastic (e.g. dispersal limitation) processes structuring bryophyte assemblages remains poorly understood.

2. To evaluate how different assembly processes shape bryophyte communities in mountain streams, we examined functional trait patterns across spatial scales and along environmental gradients. To do so, we sampled 754 microhabitat plots ($0.25\,m^2$) nested within 165 sites (100-m long stream segments) and 13 sub-basins, located in the northwest and central-west of Portugal. At each spatial scale, observed functional diversity indices (Functional Richness and Rao's quadratic entropy) were compared to random expectations derived from null models, followed by the analysis of changes in functional trait patterns along environmental gradients by fitting a series of generalized additive mixed models.

3. At local scales (site and microhabitat plot), coexisting species tended to be more functionally similar than expected, suggesting the prevalence of environmental filtering effects. In contrast, no significant deviations from random expectations were detected at the broadest spatial scale (sub-basin), indicating the prevalence of stochastic processes. We found contrasting assembly processes along environmental gradients: environmental filtering prevailed in stressful environments, while competitive interactions were more important in favourable conditions.

4. *Synthesis*. Our results highlight the role of environmental filtering in bryophyte community assembly at fine spatial scales, emphasizing the importance of measuring environmental conditions at the same spatial scales where biotic interactions take place. In line with the stress-dominance hypothesis, the relative importance of environmental filtering increased with abiotic stress. Thus, analysing functional trait patterns across different spatial scales and environmental gradients may contribute to a better understanding of the mechanisms underlying community assembly.

KEYWORDS
environmental filtering, environmental gradients, limiting similarity, spatial scale, stress-dominance hypothesis, trait convergence, trait divergence

1 | INTRODUCTION

There has been a long-term debate about whether deterministic or stochastic processes determine the assembly of biological communities (Diamond, 1975; Keddy, 1992; Weiher & Keddy, 1995). Previous studies have generally assumed that communities are shaped by either deterministic, niche-based processes (Chase & Leibold, 2003) or by random assembly (Hubbell, 2001). Recent findings suggest that community assembly results from a combination of deterministic (abiotic conditions and biotic interactions) and stochastic (e.g. dispersal limitation) processes that vary in importance depending on the spatial scale of observation (Chase, 2014; Weiher et al., 2011).

Dispersal mechanisms, environmental factors and biotic interactions act as a series of hierarchical filters, selecting species from a regional species pool into local communities based on their functional traits (Bernard-Verdier et al., 2012; Diaz et al., 1998). Focusing on traits rather than species identities has contributed to a better understanding of the mechanisms underlying community assembly across spatial scales and has increased the potential for general principles to emerge (Götzenberger et al., 2012; Messier et al., 2010). Indeed, as functional traits reveal ecological differentiation between species, the distribution of trait values within communities is assumed to reflect the strength of different filtering processes on community assembly (Carmona et al., 2016).

When investigating the mechanisms underlying plant community assembly at fine spatial scales (where neighbouring individuals interact with each other for the same resources), previous studies have shown that competition and other biotic interactions tend to limit the functional similarity of co-occurring species, thereby reducing interspecific competition through niche differentiation (Kraft & Ackerly, 2010; Stubbs & Wilson, 2004). Therefore, under limiting similarity (Macarthur & Levins, 1967), coexisting species are more functionally dissimilar than expected by chance, leading to trait divergence. The opposite pattern, trait convergence, is usually attributed to the effects of environmental filtering and reflects the assemblage of species with shared ecological tolerances (Cornwell et al., 2006). Nevertheless, competition can also increase similarity among coexisting species by excluding species bearing traits associated with low competitive ability (weaker competitor exclusion; Mayfield & Levine, 2010). Ecological processes associated with limiting similarity and weaker competitor exclusion prevail at finer spatial scales, while environmental filtering is expected to operate at coarser scales (de Bello et al., 2013; Weiher & Keddy, 1995). However, recent studies suggest that community assembly at fine spatial scales may also be driven by environmental filtering (i.e. microenvironmental filtering). Indeed, even at fine scales, environmental conditions can be highly heterogeneous, creating distinct microhabitats (Conti et al., 2017; Price et al., 2017). In response to this fine-scale heterogeneity, functionally similar species may occupy microhabitats with similar environmental conditions, leading to spatial aggregation and trait convergence (Mudrák et al., 2016). Random assembly patterns (coexisting species are no more similar or different than expected by chance), on the other hand, are usually interpreted as a result of stochastic processes such as dispersal limitation and colonization/extinction dynamics (Chase & Myers, 2011). Due to increased dispersal limitation, stochastic processes may become more relevant at broader scales (e.g. at the landscape level; de Bello et al., 2013).

Besides spatial scale, the relative importance of different assembly mechanisms is expected to change along environmental gradients (Bernard-Verdier et al., 2012; Lhotsky et al., 2016). The stress-dominance hypothesis, for instance, predicts that environmental filtering will be more important in stressful environments, leading to functional convergence, while competitive interactions prevail in more favourable conditions (Coyle et al., 2014; Swenson & Enquist, 2007), leading to functional divergence. However, facilitation has also been shown to increase functional divergence in stressful environments, by promoting the coexistence of species with contrasting traits (Butterfield & Callaway, 2013), particularly at finer spatial scales (Chalmandrier et al., 2017). Thus, disentangling the role of different assembly processes across spatial scales and environmental gradients is essential for developing a mechanistic understanding of how communities assemble.

While a great number of studies have focused on the assembly mechanisms of woody and herbaceous plant communities (e.g. Spasojevic & Suding, 2012; Swenson et al., 2020), only a few have examined the relative importance of deterministic and stochastic processes in structuring bryophyte communities (but see Fenton & Bergeron, 2013; Tiselius et al., 2019), despite their ubiquitous presence and important functional roles in terrestrial and aquatic ecosystems (Deane-Coe & Stanton, 2017). This lack of research is particularly striking in mountain stream ecosystems, where bryophytes are an important component of freshwater diversity, enhancing habitat heterogeneity and mediating important ecosystem functions (Stream Bryophyte Group, 1999; Suren, 1996).

Mountain streams are excellent model systems for studying how assembly processes vary across spatial scales. Indeed, as hierarchically organized systems, many potential controls on species interactions and trait–environment relationships operate across a range of scales (Lowe et al., 2006). Furthermore, mountain streams exhibit considerable environmental variation over small scales (Harrington et al., 2016), providing an ideal environment to test predictions about changes in the relative importance of environmental filtering and biotic interactions along environmental gradients.

In this study, we disentangled the relative importance of deterministic and stochastic processes structuring bryophyte communities at three nested spatial scales (sub-basin, site and microhabitat plot). We used a null model approach to determine whether observed trait patterns differ from those expected by chance. We hypothesize that at increasing spatial scales (sub-basin scale), dispersal constraints may limit species distributions and result in random patterns of community assembly. We also predict the prevalence of environmental filtering at the intermediate spatial scale (site scale, 100-m long stream segments), where abiotic constraints enable the co-occurrence of functionally similar species. On the other hand, the strength of biotic effects is expected to increase with decreasing spatial scales (microhabitat plot scale, $0.25\,m^2$), resulting in the co-occurrence of species with distinct

trait values. In addition to spatial scale, the role of different assembly mechanisms is expected to vary along environmental gradients. We hypothesize that under harsh conditions, abiotic constraints will limit the range of functional trait values, resulting in communities composed of functionally similar species.

2 | MATERIALS AND METHODS

2.1 | Study areas and sampling design

The study was carried out in streams distributed throughout 13 sub-basins, located in the northwest and central-west of Portugal (Figure 1). North-western territories are characterized by a warm-summer Mediterranean climate, with considerable intra- and interannual variability of precipitation. However, due to the moderating effect of the Atlantic Ocean, most watercourses maintain a minimum water flow in the driest period. Average annual precipitation ranges from 910 to 1790 mm/year and temperature from 8.9 to 15.2°C. In this region, base-poor streams flow over schist and granite bedrocks, surrounded by *Alnus glutinosa* (L.)

Gaertn., *Fraxinus angustifolia* Vahl and *Salix atrocinerea* Brot riparian formations. Central-western Portugal is characterized by limestone riverbeds with neutral water (pH ~7), and a hot-summer Mediterranean climate. Lower levels of annual precipitation (from 665 to 1330 mm/year) and higher temperatures (from 12.3 to 16.5°C) result in drier watercourses with high seasonal flow variation. Typical riparian vegetation includes *Populus alba* L., *Populus nigra* L. and *Salix alba* Goerz formations.

Sampling sites, defined here as 100-m long stream segments and their margins, were located in upland sections of the studied sub-basins, with elevations ranging from approximately 40 to 1440 m a.s.l. Streambeds are dominated by bedrock and boulders, and watercourses show typical features of steep mountain streams, with shifting currents and riffle-pool sequences.

Fieldwork was conducted from May 2003 to October 2008 in 165 sites, selected according to the spatial distribution and density of river networks within each sub-basin. Sites were also chosen to span the range of hydromorphological conditions. We did not need permission for fieldwork. In each site, bryophyte species abundance was registered as percentage cover using sampling plots of 0.25 m^2 (0.5×0.5 m), placed in distinct microhabitats recognized in
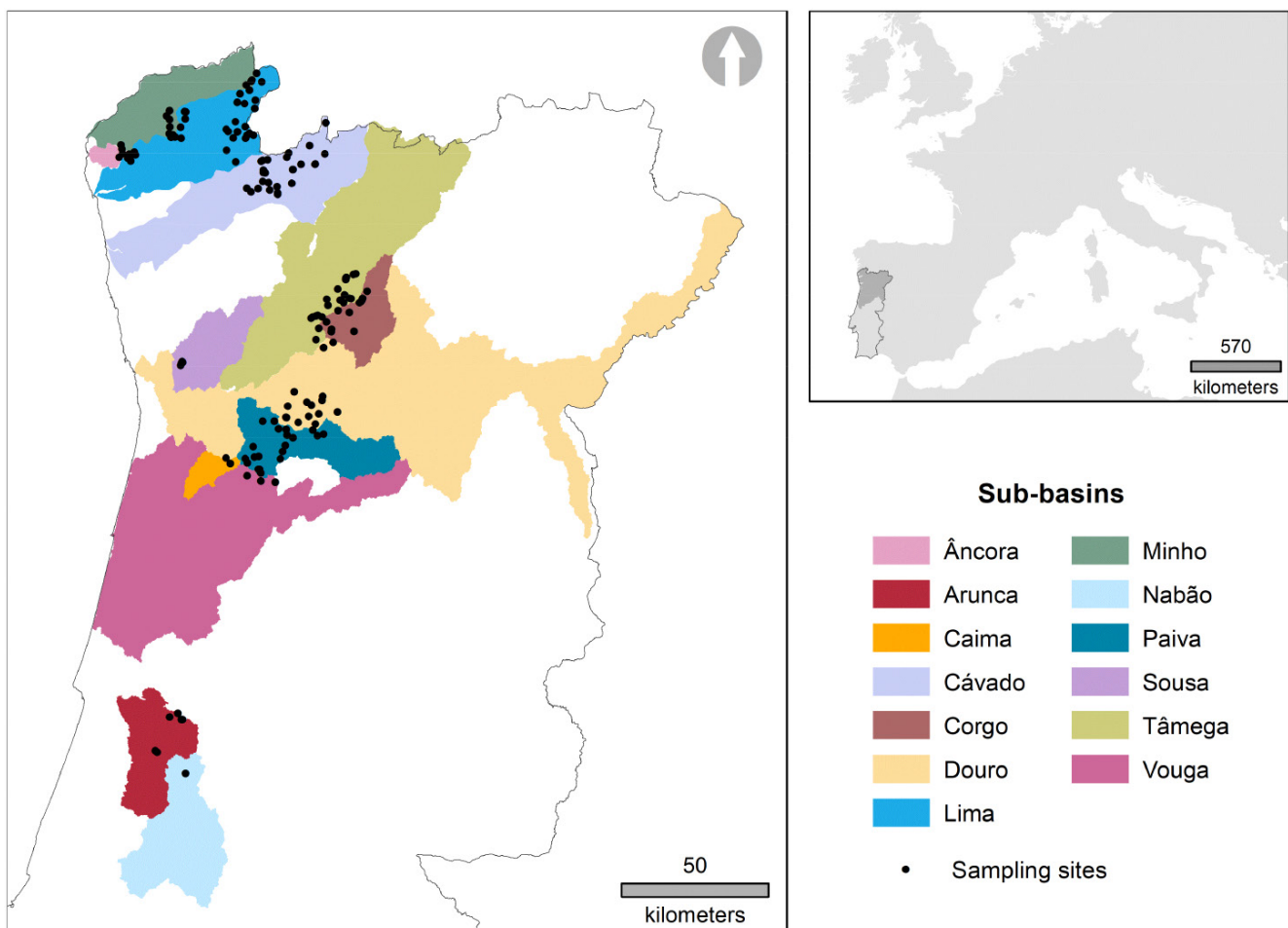

FIGURE 1 Map of the study area the showing the 165 sampling sites (100-m long stream segments) distributed throughout 13 sub-basins located in the northwest and central-west of Portugal.

the streambed structure, with different levels of submersion and substrate stability. Thus, within each site, each microhabitat plot represents a distinct micro-hydromorphological unit. The number of microhabitat plots in each of the 165 sites was proportional to the diversity of micro-hydromorphological conditions (1–18 plots per site). In total, this survey resulted in 754 microhabitat plots. At the site scale, species abundance was estimated as the mean value of species abundances across microhabitat plots within each 100-m stream segment. Likewise, species abundance at the sub-basin scale was calculated as the mean value of species abundances across microhabitat plots within each sub-basin.

2.2 | Trait data and functional diversity indices

We recorded a total of 156 bryophyte taxa (74% mosses, 25% liverworts and one hornwort species, see Table S1.1 in Appendix S1). Rare taxa, that is, those cumulatively representing <1% of the total abundance, were excluded from the analysis. As a result, 89 bryophyte taxa were classified according to nine morphological, reproductive and autecological traits, reflecting bryophyte strategies related to establishment, persistence and dispersal (Table 1). Autecological traits correspond to Ellenberg indicator values (Ellenberg et al., 1991), used as a numerical system to classify species' habitat niches and their peak occurrence along environmental gradients. Given that functional diversity indices are sensitive to missing trait data, we discarded from the

analysis eight of the 754 microhabitat plots where trait-assigned species accounted for <80% of the accumulated cover (Pakeman, 2014). Functional traits were assigned using multiple sources, including the BRYOATT (Hill et al., 2007) and BRYOTRAIT-AZO (Henriques et al., 2017) databases, regional floras, field observations and personal knowledge (Tables S1.2 and S1.3).

Functional diversity indices, measuring either functional richness (FRic) or functional divergence, have the potential to detect community assembly processes (Botta-Dukát & Czúcz, 2016; Mason et al., 2013). Thus, for each spatial scale, we calculated two multitrait functional diversity indices: FRic and Rao's quadratic entropy (RaoQ). FRic represents the amount of functional space filled by the community (Villeger et al., 2008). When multiple traits are evaluated, FRic is measured as the volume of the minimum convex hull that includes all the species considered (Cornwell et al., 2006). RaoQ combines two components of functional diversity: functional richness and functional divergence (Laliberté & Legendre, 2010). RaoQ was calculated as the sum of the pairwise distances between species in multidimensional trait space weighted by their relative abundance (Botta-Dukát, 2005). Environmental filtering is expected to restrict the range and divergence of trait values within a community, and thus decrease functional richness and divergence, while limiting similarity is expected to generate higher values for both components (Mouchet et al., 2010). Functional diversity indices were computed using the *dbFD* function in the 'FD' R package (Laliberté et al., 2014).

TABLE 1 Description of functional traits and main implications in population dynamics in aquatic systems. Full references to trait information sources and categories are given in Table S1.3.

Trait	Description	Main implications in population dynamics
Morphological		
Growth form	Morphological term, expressing the structural architecture of the individual moss plant	*Species persistence*: related to light conditions and water availability
Life form	Life forms encompass the overall organization of growth form, branching pattern, the general assemblage of individuals and modification of a population by the environment	
Reproductive		
Life strategy	The general life-strategy system consists of several components, including life span, breeding system, main reproductive effort, spore size and dispersal strategy	*Species persistence*: related to habitat stability and disturbance regime
Specialized vegetative propagules	Occurrence and frequency of vegetative propagules (tubers, gemmae, bulbils, deciduous branches and leaves)	*Dispersal and establishment*: contribute to local dispersal and population growth after colonization; long-distance dispersal may also occur
Sporophytes	Frequency of sporophytes	*Dispersal and establishment*: related to long-distance dispersal
Ecological		
Light preference	Ellenberg indicator values for light	*Species persistence*: indicates species' peak occurrence along an environmental gradient
Moisture preference	Ellenberg indicator values for moisture	
pH preference	Ellenberg indicator values for pH	
Nitrogen preference	Ellenberg indicator values for nitrogen	

2.3 | Null models

To investigate the main processes driving community assembly across spatial scales and discriminate between limiting similarity and environmental filtering, observed functional diversity indices were compared to random expectations derived from null models. At each spatial scale, random communities were generated using the independent-swap algorithm (Gotelli, 2000), implemented in the 'PICANTE' R package (Kembel et al., 2010). This constrained randomization approach maintains species occurrence frequency and sample species richness while shuffling species occurrences across sampling units.

To control for the effects of species richness on functional diversity indices, for each spatial scale we compared our estimates of FRic and RaoQ to those estimated from random communities (Mason et al., 2013) using the standardized effect size (SES) of Gotelli and McCabe (2002):

$$SES = \frac{FD_{obs} - \text{mean of } FD_{null}}{\text{Standard deviation of } FD_{null}}$$

where FD_{obs} represents the observed functional diversity value (FRic or RaoQ); the mean and standard deviation of FD_{null} were calculated from 9999 randomly generated communities. SES values (termed SESFRic and SESRao hereafter), instead of the observed FRic and RaoQ values, were used in subsequent analyses. Positive SES values indicate that the observed index is higher than expected by chance (trait divergence, coexisting species are more functionally dissimilar than expected), whereas negative SES values indicate that the observed index is lower than expected by chance (trait convergence, coexisting species are more functionally similar than expected). To determine whether mean SES values were significantly different from zero, we performed one-sample t-tests for each spatial scale.

2.4 | Environmental data

Each sampling site was characterized by four sets of environmental variables known to influence the distribution of stream bryophyte communities (Suren, 1996; Tremp et al., 2012): (i) climate and topography, (ii) land-use and riparian vegetation structure, (iii) water chemistry and temperature and (iv) hydromorphology (Table S2.1 in Appendix S2). Climatic variables were extracted from the WorldClim 2 database (Fick & Hijmans, 2017), and elevation data were obtained from the CGIAR Consortium for Spatial Information (https://srtm.csi.cgiar.org). Hydromorphological and land-use and riparian vegetation structure variables were assessed during fieldwork using predefined classes adapted from existing protocols (e.g. River Habitat Survey, Raven et al., 1998). Water temperature, pH and conductivity were measured in situ using a Multi 340i multimeter (WTW GmbH). In each microhabitat plot we also gathered information on micro-hydromorphological conditions, which were included in the micro-hydromorphology

set (Table S2.2). Environmental variables were classified according to the spatial scales—regional, local or microhabitat—at which they are expected to operate.

2.5 | Statistical analysis

To reduce variable dimensionality, while preserving as much statistical information as possible, we conducted a principal component analysis (PCA) for each set of environmental variables (Table S2.3 and Figure S2.1 in Appendix S2). Principal component (PC) axes with eigenvalues greater than one were retained and the respective scores were used as independent variables in subsequent analyses. Variables with loadings above |0.30| (considered significant, McGarigal et al., 2000) were used to interpret the retained PC axes (Table 2).

We performed generalized additive mixed models (GAMMs) to explore potential changes in the relative importance of environmental filtering and biotic interactions along environmental gradients. GAMMs are a nonparametric form of regression modelling that use smooth functions to model nonlinear relationships. Since we had no a priori assumptions about the shape of the relationship between predictors and response variables, GAMMs were an appropriate modelling technique. The choice of using GAMMs was also motivated by the hierarchical structure of our data set (Zuur et al., 2009). Indeed, mixed-effects models reduce the potentially confounding problems of spatial autocorrelation by adding random effects to the additive predictors.

We conducted a series of GAMMs considering functional diversity indices (SESFRic and SESRao) measured at the (i) site and (ii) microhabitat plot scales as response variables, since nonrandom patterns of community assembly were only detected at these levels ($p < 0.05$, one-sample t-tests). GAMMs were fitted with a Gaussian error distribution and identity link function using PC axis scores as predictors. At the site scale, models were built using PC axis scores computed for regional- and local-scale variables as predictors. Random effects included sites nested within sub-basins. At the microhabitat plot scale, models also included PC axis scores computed for microhabitat-scale variables as predictors. Random effects included microhabitat plots nested within sites and sites nested within sub-basins. Predictors were included as smooth terms (thin plate regression splines).

For each of the four response variables, we built a set of candidate models considering all possible combinations of predictor variables, setting the maximum number of variables up to five to avoid overfitting. We then used a multimodel inference approach to determine the best-approximating model in a given candidate set (Burnham & Anderson, 2002). Akaike's information criterion corrected for small sample sizes (AICc) was used as a measure of information loss of each candidate model, with the best fitting model having the lowest AICc and consequently the highest Akaike weight (w_i). Models were considered to be equally supported if the difference in AICc was less than two units. When models were equally supported, we selected the most parsimonious one (i.e. with the lowest number of

PC axes	Environmental variables	Gradient
clim1	(+) BIO10, BIO9	Summer temperature
clim2	(−) BIO13 (+) BIO7, BIO4	Temperature seasonality
clim3	(+) BIO15, BIO19, BIO16, BIO13	Precipitation seasonality
clim4	(−) BIO7, BIO2, BIO5	Temperature range (annual and mean diurnal)
rip1	(−) dry woodlands, CMAR, continuous or semicontinuous riparian vegetation (+) rock outcrops, tree cover, LUMI	Light incidence and riparian fragmentation
rip2	(−) nonfertilized agricultural fields, fertilized agricultural fields (+) FONV	Conservation status of natural riparian formations
rip3	(−) shrub cover, tree cover (+) herbaceous cover	Herbaceous cover
rip4	(−) plantations (+) meadows, scrublands	The presence of tree plantations and/or exotic species
rip5	(−) scrublands, CMAR (+) peatlands, LUMI, shrub cover	Peatland cover
hydro1	(−) CAUD, TURB, PROF, PERM, LARG, ORDE	Stream flow and turbulence
hydro2	(−) ESTA, INSU, SUBM	Substrate size and stability
hydro3	(−) HETC, HETS (+) EROS, LARG	Erosion
water1	(−) ph, COND, TEMP	pH and conductivity
micro1	(−) VELO (+) POSI, LOCI, SEDI	Water velocity and depth
micro2	(−) SUBS, SITU, LOCI	Substrate size

TABLE 2 Retained principal component (PC) axes for each set of environmental variables (climate and topography, *clim*; land-use and riparian vegetation structure, *rip*; hydromorphology, *hydro*; water chemistry and temperature, *water*; micro-hydromorphology, *micro*) and respective gradients. Only variables with loadings above |0.30| are shown; loading signs are given between brackets. For details on environmental variables and PCA results, see Appendix S2.

predictors). The relative importance of each predictor variable was calculated by summing the Akaike weights of all models in which that predictor variable was included.

GAMMs were built using the 'mgcv' (gamm function, Wood, 2021) and 'MuMIn' (uGamm and dredge functions, Barton, 2020) R packages.

3 | RESULTS

3.1 | Bryophyte community assembly across spatial scales

At the microhabitat plot and site scales, mean SESFRic and SESRao values were significantly lower than expected by random assembly (Table 3; $p < 0.05$), indicating the prevalence of trait convergence. On the contrary, at the sub-basin scale, mean SESFRic and SESRao values were not significantly different from random expectations (Table 3; $p > 0.05$).

3.2 | Environmental drivers of stream bryophyte functional diversity

Site-scale models of SESFRic and SESRao showed an overall better fit (adjusted $R^2 = 0.40$ and 0.33 respectively) than microhabitat-scale models (adjusted $R^2 = 0.11$ and 0.10, respectively; Table 4).

TABLE 3 Standardized effect sizes (SES; mean ± SD) of functional richness (FRic) and Rao's quadratic entropy (RaoQ) at the microhabitat plot (0.25 m²), site (100-m long stream segments), and sub-basin scales. Significant departure of SES values from a null expectation of zero indicated in bold ($p < 0.05$, one-sample t-test).

Spatial scale	Functional index	SES	p
Microhabitat plot	FRic	−0.130 ± 1.270	**0.020**
	RaoQ	−0.192 ± 0.951	**<0.001**
Site	FRic	−0.204 ± 1.014	**0.012**
	RaoQ	−0.302 ± 1.063	**<0.001**
Sub-basin	FRic	−0.116 ± 1.178	0.739
	RaoQ	−0.420 ± 1.410	0.322

At the site scale, we observed a shift from trait divergence to convergence (i.e. from positive to negative SESFRic and SESRao values) along the light incidence and riparian fragmentation gradient (Figure 2a,e). Regarding hydromorphological conditions, SESFRic values decreased along the stream flow and turbulence gradient (Figure 2c), while SESRao values decreased along the substrate size and stability gradient (Figure 2g). Trait convergence became weaker (i.e. SESFRic values were less negative) with decreasing water pH and conductivity (Figure 2d). Functional divergence/convergence patterns were also shaped by large-scale climatic filters. We found a shift from trait convergence to divergence (i.e. from negative to positive SESFRic values) along the temperature seasonality gradient

TABLE 4 Summary of GAMMs relating standardized effect sizes of functional richness (SESFRic) and Rao's quadratic entropy (SESRao), measured at the site and microhabitat plot scales, to climate and topography (clim), land-use and riparian vegetation structure (rip), water chemistry and temperature (water), hydromorphology (hydro) and micro-hydromorphology (micro). Predictors were summarized by the respective retained principal component (PC) axes, derived from separate PCA (see Table 2 and Appendix S2 for details). Δ AICc, change in Akaike's information criterion corrected for small sample sizes (AICc) value; w_i, Akaike weight; Adj. R^2, Adjusted R^2. Significant smoothing terms are shown in bold ($p < 0.05$).

Scale	Response	Predictors	Δ AICc	p	w_i	Adj. R^2
Site	SESFRic	rip1	1.727	**<0.001**	0.999	0.40
		water1		**0.001**	0.763	
		clim2		**0.023**	0.606	
		hydro1		**0.030**	0.417	
	SESRao	rip1	1.898	**<0.001**	0.973	0.33
		hydro2		**0.003**	0.765	
		clim1		**0.021**	0.638	
Microhabitat plot	SESFRic	rip1	1.831	**<0.001**	0.984	0.11
		micro1		0.127	0.581	
		clim2		**0.005**	0.534	
		hydro3		0.083	0.458	
	SESRao	micro1	0.314	**<0.001**	0.999	0.10
		rip1		**<0.001**	0.731	
		water1		**0.003**	0.728	
		rip2		**0.003**	0.528	

(Figure 2b). SESRao values, on the other hand, showed a nonlinear decrease along the summer temperature gradient (Figure 2f).

At the microhabitat plot scale, we also observed a shift from convergence to divergence (i.e. from negative to positive SESRao values) along the water velocity and depth gradient (Figure 3f).

4 | DISCUSSION

4.1 | Assembly patterns across spatial scales

Our study revealed that both deterministic and stochastic processes play an important role in bryophyte community assembly, with varying strengths depending on the spatial scale considered.

Contrary to our expectations, environmental filtering, as indicated by trait convergence, was the main driver of bryophyte community assembly at the microhabitat plot scale. The detection of environmental filtering is in contrast with the general expectation that competitive interactions determine the assembly of plant communities at fine spatial scales, leading to trait divergence due to limiting similarity (de Bello et al., 2013; Laliberté et al., 2013; Weiher et al., 2011). However, environmental heterogeneity may affect species coexistence at the same spatial scales where competition and other biotic interactions take place (Pescador et al., 2020). Indeed,

even at fine scales, environmental conditions in mountain streams can be substantially heterogeneous, which might explain the prevalence of environmental filtering in bryophyte community assembly, as reported for vascular plants (Conti et al., 2017; Mudrák et al., 2016; Price et al., 2017). In our case, micro-hydromorphological heterogeneity, and the resulting fine-scale patchiness, may have promoted the coexistence of functionally similar species within stream sites, as species with similar trait values occupy patches (i.e. microhabitat plots) with similar hydromorphological conditions. Besides micro-environmental filtering, weaker competitor exclusion can also lead to trait convergence at fine scales, by favouring the coexistence of species with similar competitive abilities (Mayfield & Levine, 2010). However, it was not possible to determine if competitive exclusion was an important driver of community assembly at the microhabitat plot scale, as selected traits only partially capture differences in species' competitive abilities (Götzenberger et al., 2016).

Indeed, the main limitation of our study concerns the origin of trait data—obtained from databases and literature sources—and the consequent lack of intraspecific variation. Recent studies have shown that accounting for intraspecific trait variation, that is, considering trait values at the individual level, may influence the detection of assembly processes at fine spatial scales (Chalmandrier et al., 2017; Siefert et al., 2015). In our case, intraspecific shifts in trait values could have revealed a stronger role of competitive hierarchies in community assembly, rather than the prevalence of micro-environmental filtering.

As predicted, environmental filtering determined the assembly of stream bryophyte communities at the intermediate spatial scale (site scale), leading to trait convergence. Our results are consistent with the view that environmental filtering plays an important role at relatively coarse spatial scales (i.e. hundreds of metres), where abiotic constraints filter out species that do not have the proper traits or trait combinations to cope with the prevailing conditions, as observed in vascular plants (de Bello et al., 2013; Pescador et al., 2021). Indeed, larger spatial scales tend to encompass greater environmental variation (e.g. higher substrate heterogeneity), providing opportunities for species to sort according to their functional traits (Willis et al., 2010).

The fact that we found no significant evidence of trait convergence or divergence at the sub-basin scale is consistent with the hypothesis that dispersal limitation constrains species' distributions at broader spatial scales (Tiselius et al., 2019), resulting in random assembly patterns. Although bryophytes are typically seen as extremely efficient dispersers (Barbé et al., 2016), previous studies have reported both high dispersal capacity (Astorga et al., 2012) and dispersal limitation (Hutsemékers et al., 2013) in different bryophyte groups. For instance, Heino and Virtanen (2006) found that 'truly aquatic' species (i.e. growing in submerged conditions) were limited by dispersal and metapopulation processes, while semiaquatic species (i.e. growing temporarily submerged or just above the air–water interface) were more likely to be limited by habitat availability. Indeed, stream bryophytes, particularly 'truly aquatic' species, rely almost exclusively on vegetative diaspores (asexual propagules
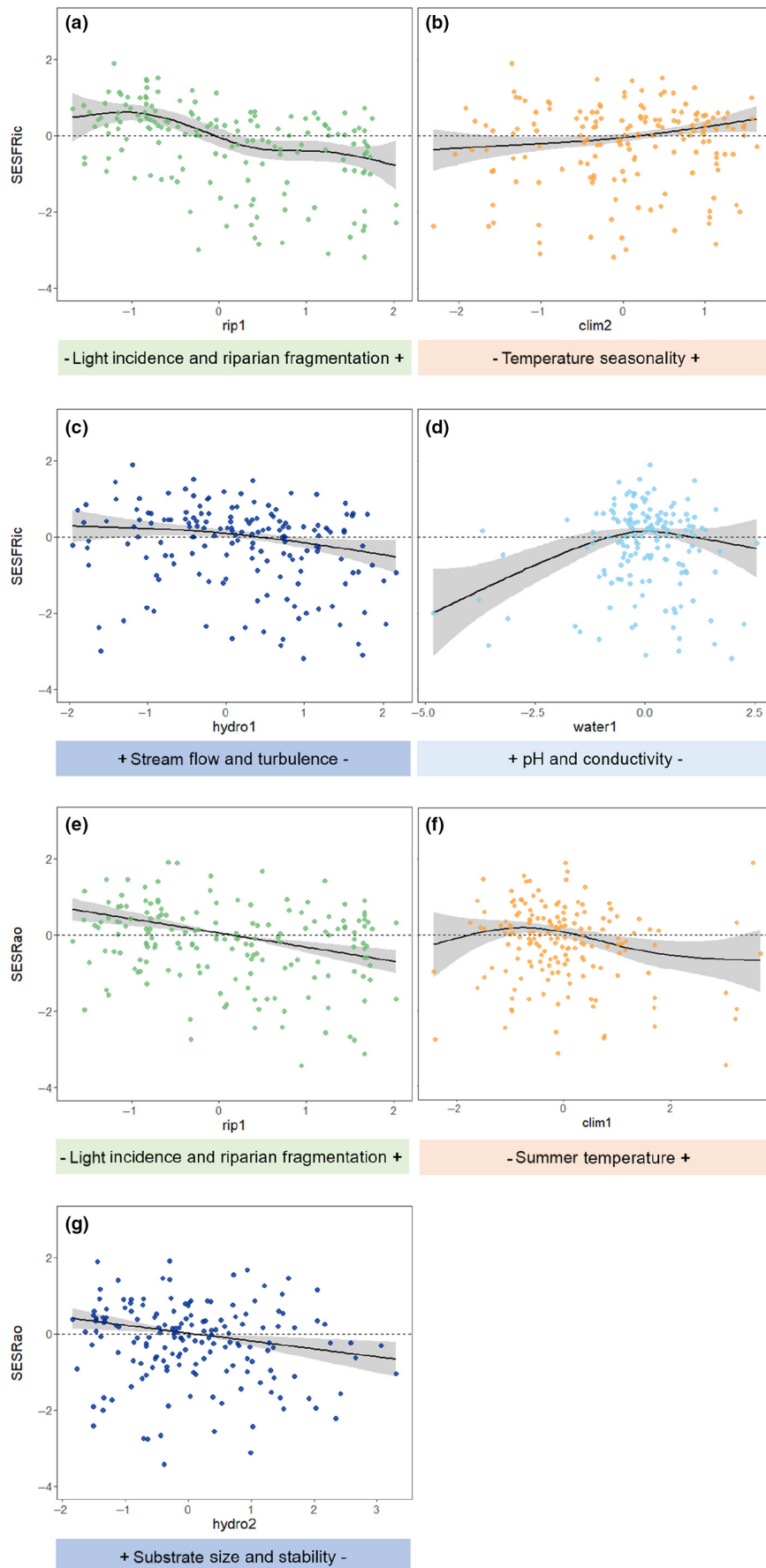
FIGURE 2 GAMM results for standardized effect sizes (SES) of functional richness (SESFRic) and Rao's quadratic entropy (SESRao) in relation to climate and topography (clim; (b) and (f)), land-use and riparian vegetation structure (rip; (a) and (e)), water chemistry and temperature (water; (d)) and hydromorphology (hydro; (c) and (g)). Predictors were summarized by the respective retained principal component (PC) axes, derived from separate PCA (see Table 2 and Appendix S2 for details). Models were built using functional diversity indices measured at the site scale. Positive SES values indicate that functional diversity indices are greater than expected by chance and negative SES values indicate the opposite. Shaded areas represent 95% confidence intervals.
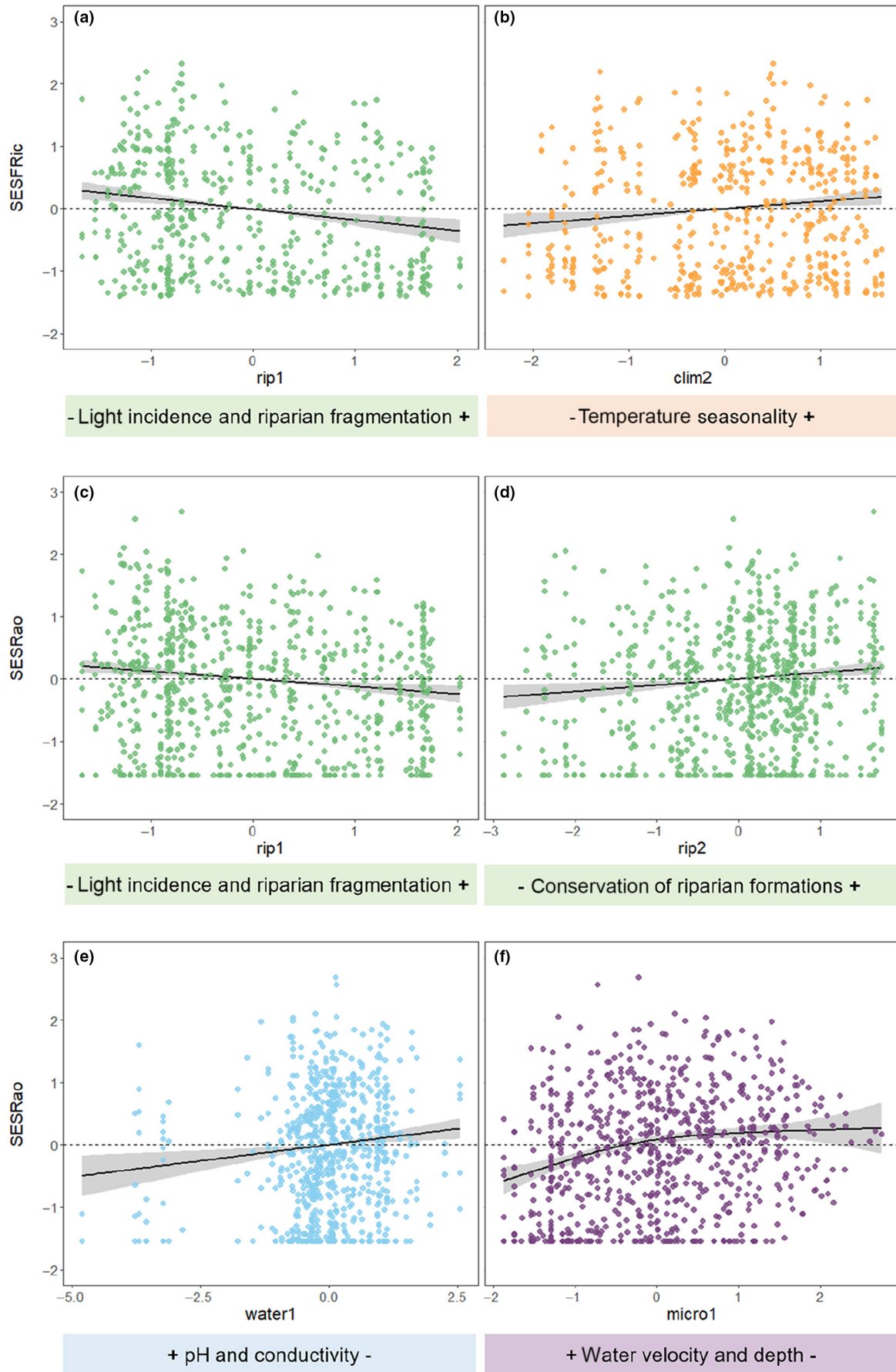
FIGURE 3 GAMM results for standardized effect sizes (SES) of functional richness (SESFRic) and Rao's quadratic entropy (SESRao) in relation to climate and topography (clim; (b)), land-use and riparian vegetation structure (rip; (a), (c) and (d)), water chemistry and temperature (water; (e)), and micro-hydromorphology (micro; (f)). Predictors were summarized by the respective retained principal component (PC) axes, derived from separate PCA (see Table 2 and Appendix S2 for details). Models were built using functional diversity indices measured at the microhabitat plot scale. Positive SES values indicate that functional diversity indices are greater than expected by chance and negative SES values indicate the opposite. Shaded areas represent 95% confidence intervals.

and shoot fragments), which mainly contribute to local dispersal (Boedeltje et al., 2019).

4.2 | Community assembly along environmental gradients

Our findings were consistent with the stress-dominance hypothesis (Coyle et al., 2014; Swenson & Enquist, 2007): environmental filtering had a stronger effect under harsh conditions, while competitive interactions were more important in favourable conditions. Thus, our results indicate that contrasting patterns of community assembly along environmental gradients may reflect shifts in the relative importance of abiotic filtering and biotic interactions.

Stream bryophyte communities showed a clear functional response to changes in land-use and riparian vegetation structure, regardless of the spatial scale considered. In particular, we found a significant shift from trait divergence to trait convergence with increasing light incidence and riparian fragmentation. The effects of environmental filtering were, therefore, stronger in streams flowing through fragmented riparian areas, with low levels of canopy shading (i.e. under harsh environmental conditions), as evidenced by the prevalence of trait convergence. These results were not surprising, considering the well-established importance of riparian vegetation for bryophyte communities (Suurkuukka et al., 2014; Turunen et al., 2021). Indeed, despite exhibiting differences in light tolerance, aquatic and semiaquatic bryophytes typically thrive in streams where riparian shading limits algal and vascular plant growth (Bowden et al., 2017).

The relative importance of environmental filtering and biotic interactions also varied along hydromorphological gradients. Bryophyte communities tended to be more functionally convergent in stream sites with lower streambed stability and smaller substrate particles. Thus, disturbance caused by substrate movement may have limited the range of viable ecological strategies, resulting in trait convergence, while competition may have favoured the coexistence of functionally dissimilar species under more stable conditions, resulting in trait divergence. Similar to our study, Suren and Duncan (1999) found that only a few bryophyte species were able to grow in unstable streams. We also observed a shift from trait divergence to convergence with decreasing stream flow and turbulence. Environmental filtering at the low-flow end of this gradient was likely due to a lower concentration of CO_2 for photosynthesis (Fernández-Martínez et al., 2019; Glime, 2014).

The assembly of bryophyte communities was also mediated by macroclimatic factors. However, contrary to our expectations, at the

site and microhabitat plot scales, communities tended to be more functionally divergent with increasing temperature seasonality (i.e. under stressful environmental conditions). One possible explanation for the observed trait pattern could be that the length of the studied gradient (i.e. the difference between the more mesic and drier ends) was not sufficient to capture the effects of environmental filtering, which might occur in areas with more extreme and variable climatic conditions. Facilitative interactions could produce similar patterns, as biotic interactions tend to shift from competition to facilitation with increasing abiotic stress (Butterfield & Callaway, 2013). However, facilitation is expected to occur at fine scales, where individuals are close enough to interact directly (Chalmandrier et al., 2017). Since trait divergence was also detected at the site scale, we could rule out the role of facilitation as a coexistence mechanism in the studied mountain streams.

At the microhabitat plot scale, trait convergence/divergence patterns were also shaped by micro-hydromorphological conditions. Coexisting species tended to be more functionally similar with increasing water velocity and depth, suggesting the prevalence of environmental filtering in stressful environments. Although bryophytes are more common in low-order, fast-flowing streams (Bowden et al., 2017; Suren, 1996), the mechanical stress imposed by drag forces at high velocities (Suren et al., 2000) may have limited the range of possible trait values, resulting in trait convergence. The relative importance of environmental filtering also increased with water depth, possibly due to CO_2 limitation and reduced light (Glime, 2014).

5 | CONCLUSIONS

Our study highlights the role of environmental filtering in bryophyte community assembly at fine spatial scales, where biotic interactions are expected to prevail. Even at fine scales, environmental conditions in mountain streams can be highly heterogeneous, affecting community assembly through changes in the relative importance of abiotic constraints. Thus, our findings support the idea that environmental heterogeneity may promote the coexistence of functionally similar species within communities, leading to trait convergence at fine scales. Besides spatial scale, our results revealed contrasting patterns of community assembly along environmental gradients, in line with the hypothesis that environmental filtering plays a major role in stressful environments, while competitive interactions predominate in more favourable conditions. Analysing functional trait patterns across different spatial scales and along environmental gradients may therefore contribute to a better understanding of the mechanisms underlying community assembly. In addition, our study stresses the importance of measuring environmental conditions at

scales relevant to ecological processes, as abiotic filters may govern community assembly at the same spatial scales where biotic interactions take place.

AUTHOR CONTRIBUTIONS

Juliana Monteiro, Cristiana Vieira and Cristina Branquinho conceived the ideas and designed the methodology; Cristiana Vieira conducted the fieldwork; Juliana Monteiro analysed the data; Juliana Monteiro and Cristina Branquinho led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14117.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5mkkwh7b5 (Monteiro et al., 2023).

ORCID

Cristiana Vieira https://orcid.org/0000-0003-4252-8498
Cristina Branquinho https://orcid.org/0000-0001-8294-7924

REFERENCES

Astorga, A., Oksanen, J., Luoto, M., Soininen, J., Virtanen, R., & Muotka, T. (2012). Distance decay of similarity in freshwater communities: Do macro- and microorganisms follow the same rules? *Global Ecology and Biogeography*, *21*, 365–375. https://doi.org/10.1111/j.1466-8238.2011.00681.x

Barbé, M., Fenton, N. J., & Bergeron, Y. (2016). So close and yet so far away: Long-distance dispersal events govern bryophyte metacommunity reassembly. *Journal of Ecology*, *104*, 1707–1719. https://doi.org/10.1111/1365-2745.12637

Barton, K. (2020). *Multi-model inference*. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn

Bernard-Verdier, M., Navas, M. L., Vellend, M., Violle, C., Fayolle, A., & Garnier, E. (2012). Community assembly along a soil depth gradient: Contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. *Journal of Ecology*, *100*, 1422–1433. https://doi.org/10.1111/1365-2745.12003

Boedeltje, G., Sollman, P., & Lenssen, J. P. M. (2019). Floating ability, shoot length and abundance facilitate hydrochorous dispersal of moss and liverwort fragments. *Journal of Vegetation Science*, *30*, 30–41. https://doi.org/10.1111/jvs.12695

Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, *16*, 533–540. https://doi.org/10.1111/j.1654-1103.2005.tb02393.x

Botta-Dukát, Z., & Czúcz, B. (2016). Testing the ability of functional diversity indices to detect trait convergence and divergence using individual-based simulation. *Methods in Ecology and Evolution*, *7*, 114–126. https://doi.org/10.1111/2041-210X.12450

Bowden, W. B., Glime, J. M., & Riis, T. (2017). Chapter 13—Macrophytes and bryophytes. In F. R. Hauer & G. A. Lamberti (Eds.), *Methods in stream ecology, Volume 1* (3rd ed., pp. 243–271). Academic Press.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multi-model inference: A practical information-theoretic approach* (2nd ed.). Springer. https://doi.org/10.1007/b97636

Butterfield, B. J., & Callaway, R. M. (2013). A functional comparative approach to facilitation and its context dependence. *Functional Ecology*, *27*, 907–917. https://doi.org/10.1111/1365-2435.12019

Carmona, C. P., de Bello, F., Mason, N. W. H., & Lepš, J. (2016). Traits without borders: Integrating functional diversity across scales. *Trends in Ecology & Evolution*, *31*, 382–394. https://doi.org/10.1016/j.tree.2016.02.003

Chalmandrier, L., Münkemüller, T., Colace, M.-P., Renaud, J., Aubert, S., Carlson, B. Z., Clément, J.-C., Legay, N., Pellet, G., Saillard, A., Lavergne, S., & Thuiller, W. (2017). Spatial scale and intraspecific trait variability mediate assembly rules in alpine grasslands. *Journal of Ecology*, *105*, 277–287. https://doi.org/10.1111/1365-2745.12658

Chase, J. M. (2014). Spatial scale resolves the niche versus neutral theory debate. *Journal of Vegetation Science*, *25*, 319–322. https://doi.org/10.1111/jvs.12159

Chase, J. M., & Leibold, M. A. (2003). *Ecological niches: Linking classical and contemporary approaches*. University of Chicago Press.

Chase, J. M., & Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 2351–2363. https://doi.org/10.1098/rstb.2011.0063

Conti, L., de Bello, F., Lepš, J., Acosta, A. T. R., & Carboni, M. (2017). Environmental gradients and micro-heterogeneity shape fine-scale plant community assembly on coastal dunes. *Journal of Vegetation Science*, *28*, 762–773. https://doi.org/10.1111/jvs.12533

Cornwell, W. K., Schwilk, D. W., & Ackerly, D. D. (2006). A trait-based test for habitat filtering: Convex hull volume. *Ecology*, *87*, 1465–1471. https://doi.org/10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO;2

Coyle, J. R., Halliday, F. W., Lopez, B. E., Palmquist, K. A., Wilfahrt, P. A., & Hurlbert, A. H. (2014). Using trait and phylogenetic diversity to evaluate the generality of the stress-dominance hypothesis in eastern North American tree communities. *Ecography*, *37*, 814–826. https://doi.org/10.1111/ecog.00473

de Bello, F., Vandewalle, M., Reitalu, T., Lepš, J., Prentice, H. C., Lavorel, S., & Sykes, M. T. (2013). Evidence for scale-and disturbance-dependent trait assembly patterns in dry semi-natural grasslands. *Journal of Ecology*, *101*, 1237–1244. https://doi.org/10.1111/1365-2745.12139

Deane-Coe, K. K., & Stanton, D. (2017). Functional ecology of cryptogams: Scaling from bryophyte, lichen, and soil crust traits to ecosystem processes. *New Phytologist*, *213*, 993–995. https://doi.org/10.1111/nph.14408

Diamond, J. M. (1975). Assembly of species communities. In M. L. Cody & J. M. Diamond (Eds.), *Ecology and evolution of communities* (pp. 342–444). Harvard University Press.

Diaz, S., Cabido, M., & Casanoves, F. (1998). Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science*, *9*, 113–122. https://doi.org/10.2307/3237229

Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W., & Paulissen, D. (1991). Zeigerwerte von pflanzen in Mitteleuropa. *Scripta Geobotanica*, *18*, 1–248.

Fenton, N. J., & Bergeron, Y. (2013). Stochastic processes dominate during boreal bryophyte community assembly. *Ecology*, *94*, 1993–2006. https://doi.org/10.1890/12-1944.1

Fernández-Martínez, M., Berloso, F., Corbera, J., Garcia-Porta, J., Sayol, F., Preece, C., & Sabater, F. (2019). Towards a moss sclerophylly continuum: Evolutionary history, water chemistry and climate control traits of hygrophytic mosses. *Functional Ecology*, 33, 2273–2289. https://doi.org/10.1111/1365-2435.13443

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315. https://doi.org/10.1002/joc.5086

Glime, J. M. (2014). Photosynthesis in aquatic bryophytes. In D. T. Hanson & S. K. Rice (Eds.), *Photosynthesis in bryophytes and early land plants* (pp. 201–231). Springer.

Gotelli, N. J. (2000). Null model analysis of species co-occurrence patterns. *Ecology*, 81, 2606–2621. https://doi.org/10.1890/0012-9658(2000)081[2606:NMAOSC]2.0.CO;2

Gotelli, N. J., & McCabe, D. J. (2002). Species co-occurrence: A meta-analysis of J. M. Diamond's assembly rules model. *Ecology*, 83, 2091–2096. https://doi.org/10.1890/0012-9658(2002)083[2091:SCOAMA]2.0.CO;2

Götzenberger, L., Botta-Dukát, Z., Lepš, J., Pärtel, M., Zobel, M., & de Bello, F. (2016). Which randomizations detect convergence and divergence in trait-based community assembly? A test of commonly used null models. *Journal of Vegetation Science*, 27, 1275–1287. https://doi.org/10.1111/jvs.12452

Götzenberger, L., de Bello, F., Bråthen, K. A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., & Pärtel, M. (2012). Ecological assembly rules in plant communities—Approaches, patterns and prospects. *Biological Reviews*, 87, 111–127. https://doi.org/10.1111/j.1469-185X.2011.00187.x

Harrington, R. A., Poff, N. L., & Kondratieff, B. C. (2016). Aquatic insect β-diversity is not dependent on elevation in Southern Rocky Mountain streams. *Freshwater Biology*, 61, 195–205. https://doi.org/10.1111/fwb.12693

Heino, J., & Virtanen, R. (2006). Relationships between distribution and abundance vary with spatial scale and ecological group in stream bryophytes. *Freshwater Biology*, 51, 1879–1889. https://doi.org/10.1111/j.1365-2427.2006.01624.x

Henriques, D. S. G., Ah-Peng, C., & Gabriel, R. (2017). Structure and applications of BRYOTRAIT-AZO, a trait database for Azorean bryophytes. *Cryptogamie, Bryologie*, 38, 137–152. https://doi.org/10.7872/cryb/v38.iss2.2017.137

Hill, M. O., Preston, C., Bosanquet, S., & Roy, D. (2007). *BRYOATT: Attributes of British and Irish mosses, liverworts and hornworts*. NERC Centre for Ecology and Hydrology.

Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.

Hutsemékers, V., Hardy, O. J., & Vanderpoorten, A. (2013). Does water facilitate gene flow in spore-producing plants? Insights from the fine-scale genetic structure of the aquatic moss *Rhynchostegium riparioides* (Brachytheciaceae). *Aquatic Botany*, 108, 1–6. https://doi.org/10.1016/j.aquabot.2013.02.001

Keddy, P. A. (1992). Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science*, 3, 157–164. https://doi.org/10.2307/3235676

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Kraft, N. J. B., & Ackerly, D. D. (2010). Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecological Monographs*, 80, 401–422. https://doi.org/10.1890/09-1672.1

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299–305. https://doi.org/10.1890/08-2244.1

Laliberté, E., Legendre, P., & Shipley, B. (2014). *FD: Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology*. R package version 1.0-12. https://CRAN.R-project.org/package=FD. https://doi.org/10.1213/XAA.0000000000000074

Laliberté, E., Norton, D. A., & Scott, D. (2013). Contrasting effects of productivity and disturbance on plant functional diversity at local and metacommunity scales. *Journal of Vegetation Science*, 24, 834–842. https://doi.org/10.1111/jvs.12044

Lhotsky, B., Kovács, B., Ónodi, G., Csecserits, A., Rédei, T., Lengyel, A., Kertész, M., & Botta-Dukát, Z. (2016). Changes in assembly rules along a stress gradient from open dry grasslands to wetlands. *Journal of Ecology*, 104, 507–517. https://doi.org/10.1111/1365-2745.12532

Lowe, W. H., Likens, G. E., & Power, M. E. (2006). Linking scales in stream ecology. *Bioscience*, 56, 591–597. https://doi.org/10.1641/0006-3568(2006)56[591:LSISE]2.0.CO;2

Macarthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, 101, 377–385. http://www.jstor.org/stable/2459090. https://doi.org/10.1086/282505

Mason, N. W. H., Bello, F., Mouillot, D., Pavoine, S., & Dray, S. (2013). A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science*, 24, 794–806. https://doi.org/10.1111/jvs.12013

Mayfield, M. M., & Levine, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, 13, 1085–1093. https://doi.org/10.1111/j.1461-0248.2010.01509.x

McGarigal, K., Stafford, S., & Cushman, S. (2000). Ordination: Principal components analysis. In K. McGarigal, S. Stafford, & S. Cushman (Eds.), *Multivariate statistics for wildlife and ecology research* (pp. 19–80). Springer.

Messier, J., McGill, B. J., & Lechowicz, M. J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters*, 13, 838–848. https://doi.org/10.1111/j.1461-0248.2010.01476.x

Monteiro, J., Vieira, C., & Branquinho, C. (2023). Data from: Bryophyte assembly rules across scales. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.5mkkwh7b5

Mouchet, M. A., Villéger, S., Mason, N. W. H., & Mouillot, D. (2010). Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, 24, 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x

Mudrák, O., Janeček, Š., Götzenberger, L., Mason, N. W. H., Horník, J., de Castro, I., Doležal, J., Klimešová, J., & de Bello, F. (2016). Fine-scale coexistence patterns along a productivity gradient in wet meadows: Shifts from trait convergence to divergence. *Ecography*, 39, 338–348. https://doi.org/10.1111/ecog.01723

Pakeman, R. J. (2014). Functional trait metrics are sensitive to the completeness of the species' trait data? *Methods in Ecology and Evolution*, 5, 9–15. https://doi.org/10.1111/2041-210X.12136

Pescador, D. S., de Bello, F., López-Angulo, J., Valladares, F., & Escudero, A. (2021). Spatial scale dependence of ecological factors that regulate functional and phylogenetic assembly in a Mediterranean high mountain grassland. *Frontiers in Ecology and Evolution*, 9, 622148. https://doi.org/10.3389/fevo.2021.622148

Pescador, D. S., de la Cruz, M., Chacón-Labella, J., Pavón-García, J., & Escudero, A. (2020). Tales from the underground: Soil heterogeneity and not only above-ground plant interactions explain fine-scale species patterns in a Mediterranean dwarf-shrubland. *Journal of Vegetation Science*, 31, 497–508. https://doi.org/10.1111/jvs.12859

Price, J., Tamme, R., Gazol, A., de Bello, F., Takkis, K., Uria-Diez, J., Kasari, L., & Pärtel, M. (2017). Within-community environmental variability drives trait variability in species-rich grasslands. *Journal of Vegetation Science*, 28, 303–312. https://doi.org/10.1111/jvs.12487

Raven, P. J., Holmes, N. T. H., Dawson, F. H., & Everard, M. (1998). Quality assessment using river habitat survey data. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 8, 477–499. https://doi.org/10.1002/(SICI)1099-0755(199807/08)8:4<477::AID-AQC299>3.0.CO;2-K

Ros, R. M., Mazimpaka, V., Abou-Salama, U., Aleffi, M., Blockeel, T. L., Brugués, M., Cano, M. J., Cros, R. M., Dia, M. G., Dirkse, G. M., Saadawi, W. E., Erda, A., Ganeva, A., González-Mancebo, J. M., Herrnstadt, I., Khalil, K., Kürschner, H., Lanfranco, E., Losada-Lima, A., ... Söderström, L. (2007). Hepatics and anthocerotes of the mediterranean, an annotated checklist. *Cryptogamie, Bryologie*, *28*, 351–437.

Ros, R. M., Mazimpaka, V., Abou-Salama, U., Aleffi, M., Blockeel, T.L., Brugués, M., Cros, R.M., Dia, M.G., Dirkse, G.M., Draper, I., El-Saadawi, W., Erdağ, A., Ganeva, A., Gabriel, R., González-Mancebo, J. M., Granger, C., Herrnstadt, I., Hugonnot, V., Khalil, K., Kürschner, H., ... Werner, O. (2013). Mosses of the mediterranean, an annotated checklist. *Cryptogamie, Bryologie*, *34*, 99–283. https://doi.org/10.7872/cryb.v34.iss2.2013.99

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., L. Dantas, V., Bello, F., Duarte, L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., ... Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, *18*, 1406–1419. https://doi.org/10.1111/ele.12508

Spasojevic, M. J., & Suding, K. N. (2012). Inferring community assembly mechanisms from functional diversity patterns: The importance of multiple assembly processes. *Journal of Ecology*, *100*, 652–661. https://doi.org/10.1111/j.1365-2745.2011.01945.x

Stream Bryophyte Group. (1999). Roles of bryophytes in stream ecosystems. *Journal of the North American Benthological Society*, *18*, 151–184. https://doi.org/10.2307/1468459

Stubbs, W. J., & Wilson, J. B. (2004). Evidence for limiting similarity in a sand dune community. *Journal of Ecology*, *92*, 557–567. https://doi.org/10.1111/j.0022-0477.2004.00898.x

Suren, A. M. (1996). Bryophyte distribution patterns in relation to macro-, meso, and micro-scale variables in South Island, New Zealand streams. *New Zealand Journal of Marine and Freshwater Research*, *30*, 501–523. https://doi.org/10.1080/00288330.1996.9516738

Suren, A. M., & Duncan, M. J. (1999). Rolling stones and mosses: Effect of substrate stability on bryophyte communities in streams. *Journal of the North American Benthological Society*, *18*, 457–467. https://doi.org/10.2307/1468378

Suren, A. M., Smart, G. M., Smith, R. A., & Brown, S. L. R. (2000). Drag coefficients of stream bryophytes: Experimental determinations and ecological significance. *Freshwater Biology*, *45*, 309–317. https://doi.org/10.1111/j.1365-2427.2000.00621.x

Suurkuukka, H., Virtanen, R., Suorsa, V., Soininen, J., Paasivirta, L., & Muotka, T. (2014). Woodland key habitats and stream biodiversity: Does small-scale terrestrial conservation enhance the protection of stream biota? *Biological Conservation*, *170*, 10–19. https://doi.org/10.1016/j.biocon.2013.10.009

Swenson, N. G., & Enquist, B. J. (2007). Ecological and evolutionary determinants of a key plant functional trait: Wood density and its community-wide variation across latitude and elevation. *American Journal of Botany*, *94*, 451–459. https://doi.org/10.3732/ajb.94.3.451

Swenson, N. G., Hulshof, C. M., Katabuchi, M., & Enquist, B. J. (2020). Long-term shifts in the functional composition and diversity of a tropical dry forest: A 30-yr study. *Ecological Monographs*, *90*, e01408. https://doi.org/10.1002/ecm.1408

Tiselius, A. K., Lundbäck, S., Lönnell, N., Jansson, R., & Dynesius, M. (2019). Bryophyte community assembly on young land uplift islands—Dispersal and habitat filtering assessed using species traits. *Journal of Biogeography*, *46*, 2188–2202. https://doi.org/10.1111/jbi.13652

Tremp, H., Kampmann, D., & Schulz, R. (2012). Factors shaping submerged bryophyte communities: A conceptual model for small mountain streams in Germany. *Limnologica—Ecology and Management of Inland Waters*, *42*, 242–250. https://doi.org/10.1016/j.limno.2012.01.003

Turunen, J., Elbrecht, V., Steinke, D., & Aroviita, J. (2021). Riparian forests can mitigate warming and ecological degradation of agricultural headwater streams. *Freshwater Biology*, *66*, 785–798. https://doi.org/10.1111/fwb.13678

Villeger, S., Mason, N. W., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, *89*, 2290–2301. https://doi.org/10.1890/07-1206.1

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., & Bentivenga, S. (2011). Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 2403–2413. https://doi.org/10.1098/rstb.2011.0056

Weiher, E., & Keddy, P. A. (1995). Assembly rules, null models, and trait dispersion: New questions from old patterns. *Oikos*, *74*, 159–164. https://doi.org/10.2307/3545686

Willis, C. G., Halina, M., Lehman, C., Reich, P. B., Keen, A., McCarthy, S., & Cavender-Bares, J. (2010). Phylogenetic community structure in Minnesota oak savanna is influenced by spatial extent and environmental variation. *Ecography*, *33*, 565–577. https://doi.org/10.1111/j.1600-0587.2009.05975.x

Wood, S. (2021). *mgcv: Mixed GAM computation vehicle with automatic smoothness estimation*. R package version 1.8-34. https://CRAN.R-project.org/package=mgcv

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media.

SUPPORTING INFORMATION

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

Appendix S1. Bryophytes and functional traits.

Table S1.1. Bryophyte *taxa* recorded in the study area, respective codes, family, genus, and class. H, Hornwort; L, Liverwort; M, Moss. Nomenclature follows Ros et al. (2007) for liverworts and Ros et al. (2013) for mosses.

Table S1.2. List of bryophyte *taxa* and trait values for growth-form, life-form, life-strategy, occurrence and frequency of vegetative propagules, frequency of sporophytes, and Ellenberg indicator values for light, moisture, pH, and nitrogen. Abbreviations in Table S1.3.

Table S1.3. Description of functional traits, categories adopted, and main implications in vegetation processes. GB, Great Britain; IE, Ireland.

Appendix S2. Environmental variables and principal components analysis.

Table S2.1. Environmental variables, respective codes, classes (or units), and data sources. Variables were grouped into four sets: (i) climate and topography, (ii) land-use and riparian vegetation structure, (iii) water chemistry and temperature, and (iv) hydromorphology. Variables were also classified according to the spatial scales (regional or local) at which they are expected to operate.

Table S2.2. Micro-hydromorphological variables assessed at the microhabitat plot scale (0.25 m^2), respective codes, classes (or units), and data sources.

Table S2.3. Summary of principal components analysis (PCA) performed separately for climate and topography (clim), land-use and riparian vegetation structure (rip), hydromorphology (hydro), water chemistry and temperature (water), and micro-hydromorphology (micro). Percentage of explained variance and loading scores for each retained PC axis (eigenvalue >1) are shown. Loading scores above |0.30| are highlighted. See Tables S2.1 and S2.2 for variable details.

Figure S2.1. Principal components analysis (PCA) for each set of environmental variables: (a) climate and topography, (b) land-use and riparian vegetation structure, (c) hydromorphology, (d) water chemistry and temperature, and (e) micro-hydromorphology. See Tables S2.1 and S2.2 for variable details.