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Environmental filtering and environmental stress shape regional patterns of riparian community assembly and functional diversity

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Abstract

1. Riparian plant communities are key to ecosystem functioning and important providers of ecosystem services on which wildlife and people depend. Ecosystem functioning and stability depend on functional diversity and redundancy. Therefore, understanding which and how different drivers shape community assembly processes and functional patterns is crucial. However, there is limited knowledge of these processes at larger scales for the entire riparian vascular plant community.

2. Two community assembly processes dominate: *environmental filtering*, where species living in similar environments have similar traits leading to trait convergence; and *limiting similarity*, where similar traits cause species to compete more strongly leading to trait divergence. We assessed functional diversity patterns of riparian vascular plant communities across an Atlantic–Mediterranean biogeographical gradient in north Portugal.

3. We used functional diversity indices and null models to detect community assembly processes and whether these processes change along environmental gradients. We hypothesised that environmental filtering associated with precipitation and aridity would be the prevailing assembly process at a regional scale. We also expected a shift from environmental filtering to limiting similarity as precipitation-related stress declined.

4. As hypothesised, patterns of functional diversity were consistent with environmental filtering of species occurrences at the regional scale. Functional patterns were also consistent with a shift between environmental filtering and limiting similarity as cold and aridity stress declined. Under stressful environmental conditions, communities showed lower functional divergence and richness than expected by chance. Environmental filtering was more strongly associated with minimum temperatures than precipitation and aridity.

5. Underlining the need for hierarchical approaches and the analysis of multiple climatic stressors, our results highlighted the relevance of large-scale environmental stress gradients and the potential role of community assembly in influencing

riparian functional diversity. Alterations in stress filters due to climate change will affect assembly processes and functional patterns, probably affecting ecosystem functioning and stability.

KEYWORDS
aridity, functional divergence, functional richness, limiting similarity, minimum temperature

1 | INTRODUCTION

Riparian ecosystems have a range of ecosystem functions and are widely recognised as important ecosystem service providers, especially considering their small surface area (Riis et al., 2020). Riparian vegetation shapes both terrestrial and aquatic community structure and functioning, and influences surface and groundwater hydrology, organic matter availability for aquatic communities; and the composition of animal communities (Kominoski et al., 2013). Anthropogenic activities and stressors have altered riparian plant communities causing shifts in community composition and abundance, functional diversity and structure, and consequently ecosystem functioning and services (Kominoski et al., 2013). Climate change is expected to have additional and possibly synergistic impacts on riparian functional diversity and ecosystem functioning (Capon et al., 2013; Stromberg et al., 2012).

The ability of riparian ecosystems to maintain structure and function relative to reference conditions (i.e. stability, de Bello, Lavorel, et al., 2021), will depend on their functional diversity and redundancy (Kominoski et al., 2013) (Figure 1). Functional diversity supports more ecosystem processes and greater temporal stability as a wider range of functional traits can buffer against abiotic variation (Cadotte et al., 2011; de Bello, Lavorel, et al., 2021; Perkins et al., 2018). Functional redundancy buffers against species loss as functionally redundant species ensure ecosystem functions (Biggs et al., 2020; de Bello, Lavorel, et al., 2021).

Understanding how community assembly processes and environmental variables influence functional diversity and redundancy is key information for predicting the trajectory of communities under environmental change (Götzenberger et al., 2012). Community assembly is generally considered to be dominated by two processes: environmental filtering and competition-based biotic interactions, acting hierarchically at increasingly finer scales (de Bello et al., 2013; Götzenberger et al., 2012). Under *environmental filtering*, it is expected that species living in similar environments have similar traits leading to trait convergence (de Bello et al., 2013; Götzenberger et al., 2012). Under *limiting similarity*, it is expected that similar traits cause species to compete more strongly leading to trait divergence (de Bello et al., 2013; Götzenberger et al., 2012). Additional mechanisms, such as environmental heterogeneity, facilitation, and disturbance, may interfere with these patterns (de Bello et al., 2013; Götzenberger et al., 2012). Community assembly processes change along gradients of environmental stress often representing shifts between belowground competition for resources such as water, to competition for light with declining stress (Mason et al., 2013).
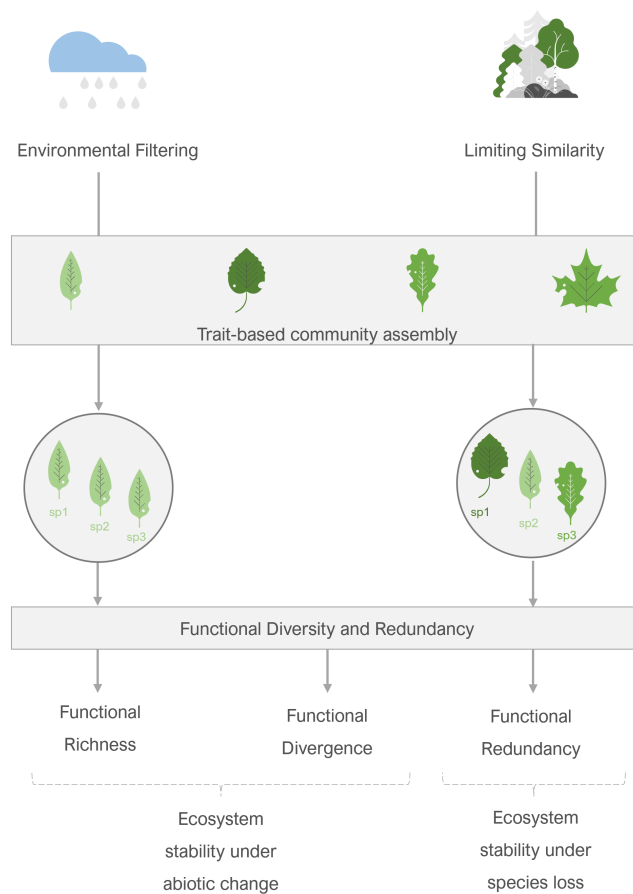

FIGURE 1 Schematic representation of the theoretical framework of this work based mainly on de Bello, Lavorel, et al. (2021). The first part of the figure (from the top of the figure to functional diversity and redundancy) illustrates how community assembly processes lead to trait convergence or divergence and represents the main focus of this study. The second part (from functional diversity and redundancy to the bottom of the figure) illustrates the contribution of functional diversity and redundancy to ecosystem stability. The dashed brackets symbolise implications of the functional diversity and redundancy patterns for ecosystem stability that are not directly tested in this study.

Under the *environmental harshness hypothesis*, in highly stressed environments, we expect lower species richness and the presence of only highly adapted organisms or generalists leading to lower functional diversity (Mason et al., 2008). Functional diversity indices associated with null models are instrumental in identifying potential community assembly processes and changes along environmental gradients (Götzenberger et al., 2016; Mason et al., 2013).

Functional diversity patterns and community assembly have been widely explored from a theoretical perspective with most developments arising from grassland studies (Götzenberger et al., 2012). There are several studies examining the effects of environmental factors on riparian vegetation functional diversity or functional group diversity (Lozanovska et al., 2020; Lozanovska, Ferreira, Segurado, & Aguiar, 2018); however, few test for the effects of community assembly processes. Existing efforts include a review of the traits involved in riparian community assembly (Catford & Jansson, 2014), a test of the effects of assembly processes on species diversity at local scales (Fraaije et al., 2015), and a test of the effect of environmental filters on functional diversity and redundancy at basin scale (Bruno et al., 2016). Most studies have focused on the influence of the hydrological regime, its alteration, and local water availability on riparian functional diversity patterns (Lozanovska, Ferreira, & Aguiar, 2018). These studies generally report declines in functional diversity and redundancy of riparian vegetation with lower local water availability (Bruno et al., 2016) and precipitation (Lozanovska, Ferreira, Segurado, & Aguiar, 2018). Overall, the effects of community assembly on the functional diversity of riparian vegetation remain poorly explored, and the focus has been on woody vascular plants and on variables related to hydrology (Lozanovska, Ferreira, & Aguiar, 2018; Palmquist et al., 2018). Functional diversity patterns are mostly examined using a priori classification of functional or taxonomic groups and multivariate approaches (Catford & Jansson, 2014; Lozanovska, Ferreira, Segurado, & Aguiar, 2018).

The novelty of this work lies in using functional patterns of the entire riparian vascular plant community to identify potential effects of two competing community assembly processes—environmental filtering and limiting similarity. Additionally, this work identifies potential changes in prevailing assembly processes along environmental stress gradients using null models, at a regional scale in a Temperate–Mediterranean climate transition.

In this work, we investigate community assembly, functional diversity and redundancy patterns using null models in riparian vascular plant communities across the regional climatic and biogeographical transition between Temperate–Atlantic and Mediterranean in north Portugal. We hypothesised that functional patterns would be consistent with a prevailing effect of environmental filtering at the regional scale, and that filtering would be most strongly associated with precipitation and aridity. Nevertheless, we expected the patterns to reflect a shift between environmental filtering and limiting similarity with increasing annual precipitation and decreasing precipitation seasonality and aridity. We expected lower functional richness and divergence in more arid sites, indicating environmental filtering, and higher values in more humid sites, indicating limiting similarity. We compared functional diversity indices with null models to identify potential effects of community assembly processes on species occurrences and abundances and examined changes with climatic, geomorphic, and anthropogenic filters. We discuss the implications of shifts in functional diversity and community assembly under climate change scenarios.

2 | METHODS

2.1 | Study area

This study included 99 sites located across the North Portugal hydrographic region sampled in the scope of the Water Framework Directive monitoring (Figure 2). The study area encompasses a sharp west–east climatic and biogeographical gradient spanning the transition between Temperate–Atlantic and Mediterranean climates due to the influence of the Atlantic Ocean and the barrier effect of mountain ranges located approximately along the centre of the region (Figure 2) (European Environment Agency, 2016a). In the northwest, annual average temperatures are relatively low (12–13°C), especially in mountain areas (11°C), and annual average precipitation is high, over 1900 mm in the mountains and around 1200 mm in the lowlands (INAG, 2008). In the north-east, annual average temperatures are higher (13°C) and annual average precipitation is substantially lower and more seasonal, with an average of 670 mm at medium-high elevations and 600 mm in lowlands (INAG, 2008). The study area is suitable to test our hypothesis, as it encompasses a gradient of environmental stress associated with annual and seasonal precipitation, and an aridity gradient which covers dry sub-humid to humid climate areas (Trabucco & Zomer, 2019), as well as diverse geomorphic and land cover conditions. The patterns observed over this climatic and biogeographical transition are also relevant to anticipate future vegetation trajectories as the Mediterranean-type climate is predicted to expand in the study area and northward into Atlantic areas under climate change (e.g., north Spain, north-west France) (Barredo et al., 2018; Catford et al., 2012; Tramblay et al., 2020).

2.2 | Species data

Species data were obtained from the North Regional Water Administration and correspond to fieldwork undertaken in the scope of the Water Framework Directive surveillance and monitoring for the north Portugal hydrographic region in the first cycle of the River Basin Management Plans (2010–2015). Macrophyte sampling was carried out between April and June 2010 and followed EU standardised methods (Comité Européen de Normalisation, 2014; INAG, 2008a). For each site, a 100-m longitudinal transect was surveyed for macrophytes and the percentage cover was recorded as a measure of abundance (INAG, 2008a). All the species from the channel and the margins up to the line corresponding to the average annual flooding were recorded (INAG, 2008a). To study riparian vegetation, species recorded in the river channel, hydrophytes, and helophytes were excluded from our dataset. Species taxonomy was matched to accepted names using the taxonomic database The Plant List (2013) and synonyms were combined.

Due to high species richness across sites (420 species) and many low-frequency species only species with 5% frequency or more across sites were retained for functional diversity analysis. The final dataset included 171 vascular plant species reflecting the most
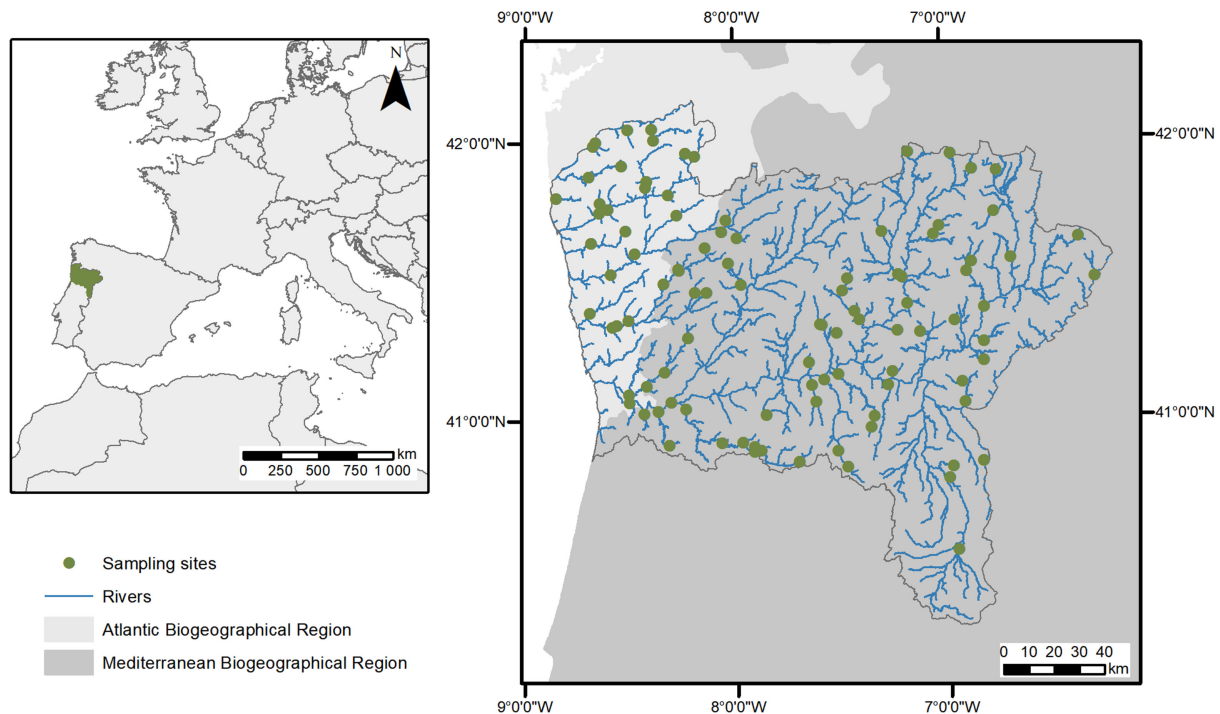
FIGURE 2 Geographical location of the study area (green) in Europe (left) and distribution of sampling sites and European biogeographical regions in the study area (right).

frequent and representative species of riparian plant communities in the study area, as well as more than 80% of the total regional pooled abundance calculated with the R traitor package (Májeková et al., 2016; R Core Team, 2018).

2.3 | Trait data

We used five traits reflecting the Leaf-Height-Seed scheme, life form, and dispersal ability to calculate functional diversity indices (Table S1). Leaf-Height-Seed traits aim to reflect adaptations to disturbance, competition or stress conditions (Westoby, 1998). Specific leaf area is positively correlated with photosynthetic capacity, and leaf nitrogen, and negatively with leaf lifespan, separating species with resource acquisition and conservation strategies (Westoby, 1998). Plant height reflects differences in light competitive ability and resulting differences in canopy dominance (Westoby, 1998). Seed mass reflects a variation in the probability of successful establishment and is an indicator of the ability of seedlings to survive under stress conditions (Westoby, 1998). Life form reflects strategies to deal with the unfavourable season and correlates with plant longevity (Laughlin & Wilson, 2014). Dispersal syndrome is linked to dispersal distance and success (Catford & Jansson, 2014).

Trait data were obtained mainly from online databases, including the TRY Plant Trait Database (Kattge et al., 2020), FLOWBASE—A Riparian Plant Traitbase (Aguiar et al., 2013), BROT 2.0 Functional Trait Database for Mediterranean Basin Plants (Tavşanoğlu & Pausas, 2018), LEDA Traitbase (Kleyer et al., 2008), and Seed Information Database—SID (Royal Botanic Gardens

Kew, 2020), and complemented with information from the literature and floras (Bejarano et al., 2016; Castroviejo, 1986–2012; Cerabolini et al., 2010; Mediavilla & Escudero, 2003; Rodríguez-Gallego et al., 2015). Trait data from regional databases and studies (Mediterranean or European) were privileged in trait search when possible. Duplicate entries were removed when it was possible to identify overlap between databases. Continuous and categorical trait values were harmonised into standard units (Cornelissen et al., 2003) and common categories. Final species traits were obtained from the mean of trait values for continuous traits and from the most frequent category for categorical variables considering the phenotype of species in the study area. The completeness of the species traits dataset was assessed using the traitor package in the R environment (Májeková et al., 2016; R Core Team, 2018). All the selected traits met the threshold of more than 80% of the regional pooled abundance (Májeková et al., 2016). Size-related traits (specific leaf area, height, and seed mass) presented a skewed distribution and were log-transformed to improve normality.

2.4 | Environmental data

We compiled a range of climatic, topographic, geomorphic, soil, and land cover variables to describe environmental gradients of the study area. We selected annual mean temperature, minimum temperature of the coldest month, annual precipitation and precipitation seasonality, potential evapotranspiration, and an aridity index to describe the climatic and water availability gradients of the study area. The variables also reflect key climatic parameters

predicted to shift with climate change with significant impacts on ecosystems (Tramblay et al., 2020). The climatic variables were obtained from WORLDCLIM 2.0 (Fick & Hijmans, 2017) and potential evapotranspiration and aridity were obtained from Trabucco and Zomer (2019). The aridity index is expressed as a ratio between precipitation and vegetation water demand, representing water surplus. Therefore, aridity values are higher in humid conditions and lower in arid conditions. We used elevation, terrain wetness index, Strahler's order, and soil texture to describe the topographical and geomorphic context of sites. Elevation was obtained from the EU Digital Elevation Model (European Environment Agency, 2016b) and used to calculate Terrain Wetness Index in SAGA GIS (Conrad et al., 2015) and Strahler's order in ArcMap (ESRI, 2012). Soil textural classes were obtained from the European Soil Data Centre topsoil physical properties for Europe (Ballabio et al., 2016). We used the amount of agricultural and urban land cover to describe anthropogenic impacts associated with land cover and use intensity (Bruno et al., 2016). The percentage of agriculture and urban land cover in the site (100-m buffer), the vicinity (200-m buffer), and in the catchment was calculated in ArcMap using the national land cover classification for 2010 (DGT, 2010). It was not possible to include flow regime variables due to the spatial mismatch between gauging stations and study sites and extensive gaps in hydrological time series.

2.5 | Functional diversity indices

We characterised the three primary components of functional diversity—functional richness (FRic), functional evenness (FEve), functional divergence (FDiv)—and functional redundancy (FRed). These components are known to shape ecosystem functioning and stability and are useful in identifying potential community assembly processes acting on species occurrences and abundances (de Bello, Carmona, et al., 2021; Mason et al., 2013).

Functional richness represents the amount of functional space occupied by the community estimated here as the multivariate trait volume (Villeger et al., 2008). FEve measures the regularity of species abundances in the functional space and was estimated using distance to the nearest neighbour species (Villeger et al., 2008). FDiv measures the degree to which species abundances are distributed toward the extremes of functional space, and was estimated using Rao quadratic entropy (Rao) (Botta-Dukát, 2005), mean pairwise dissimilarity (MPD) (Weiher & Keddy, 1995), FDiv (Villeger et al., 2008), and functional dispersion (FDis) (Laliberté & Legendre, 2010). Rao measures mean dissimilarity between individuals while MPD measures mean dissimilarity between species (de Bello et al., 2016). Therefore, MPD can be considered an estimate of species' functional uniqueness (de Bello et al., 2016). FDis and FDiv measure the distance of species to the centroid of the functional space using the mean and deviance from the mean. We also calculated Rao and MPD unweighted by species abundances (RaoPres and MPDPres) to include a FDiv metric comparable to FRic (Mason et al., 2013). FRed reflects how much a community is *saturated* with species with similar traits (de Bello et al., 2007) and was estimated following Ricotta et al. (2016) ([Simpson-Rao]/Simpson) which considers that if all species are functionally unique Simpson diversity reflects the maximum dissimilarity.

We calculated FRic, FEve, FDiv, and FDis with R package *FD* (Laliberté & Legendre, 2010) and Rao, MPD, RaoPres, MPDPres, and FRed using the function *melodic* (de Bello et al., 2016). We used species cover as a measure of species abundance in abundance-weighted indices.

2.6 | Null models

We used null models to control for the dependence of functional diversity indices on species richness and to detect the presence and changes of community assembly rules along the environmental gradients (Mason et al., 2013). We tested for patterns consistent with the effect of environmental filtering and limiting similarity assembly rules on species occurrences and abundances.

We simulated 1000 null communities for each site and calculated the functional indices. For each site, the deviation from the null expectation was calculated with the standardised effect size (SES = observed value – mean simulated values / *SD* of simulated values) (Gotelli & McCabe, 2002). Positive SES values indicate that the observed functional indices are greater than expected by chance, while negative values indicate the opposite (Gotelli & McCabe, 2002).

Presence-only indices, FRic, MPDPres, and RaoPres were compared to null expectation under a matrix-swap null model which preserves species richness of communities and species relative frequency (de Bello, Carmona, et al., 2021; Mason et al., 2013). Abundance-weighted indices FDis, FDiv, Rao, and MPD were compared to null expectation under two null models: (1) randomisation of abundances within species across sites to detect the effects of environmental filtering, hereafter frequency null model (Götzenberger et al., 2016); and (2) randomisation of abundances across species within sites to detect the effects of limiting similarity, hereafter abundance null model (Mason et al., 2013). Observed values for FEve were not compared with any null model as it is not clear how abundance randomisations should be interpreted (Mason et al., 2013).

Positive SES values were considered indicative of overdispersion and negative SES as under-dispersion, and the magnitude of the SES indicated the strength of association with the assembly processes (de Bello, Carmona, et al., 2021; Montaño-Centellas et al., 2019; Swenson, 2014). To understand whether SES values across communities were different from the null expectation, we tested whether SES were significantly different from zero using a two-tailed Wilcoxon signed rank test (Bernard-Verdier et al., 2012). This approach, together with a boxplot representation of SES values, allowed us to understand which was the general functional pattern for all the communities in the study area and indicated which was the associated assembly process (Bernard-Verdier et al., 2012; de Bello, Carmona, et al., 2021). Additionally, to depict an alternative, more conservative

approach to the significance of each community SES deviance from null expectation we added two lines to the boxplots (1.96 and −1.96). The lines correspond to the thresholds above or below which a community is considered to significantly deviate from null expectation under this approach (de Bello, Carmona, et al., 2021).

Null models were constructed in R environment using the function *randomizeMatrix* available in package *picante* (Kembel et al., 2010) and code adapted from Götzenberger et al. (2021).

2.7 | Relating functional diversity to environmental gradients

We used regression to understand how each functional diversity component changed along environmental gradients observed in the study area. For all the indices subjected to null model comparison, SES values were used in regression instead of observed values. We fitted linear, linear quadratic and generalised least squares models including variance structures (varExp) and spatial correlation structures (corSpher, corLin, corGaus, corExp) for each combination of functional diversity SES and environmental variable. The different model fits were then compared using the Akaike information criteria to rank the models. The model with the lowest Akaike information criteria value was considered the best fit (Zuur et al., 2009). The selected models were then filtered by significance ($p < 0.05$). The residual and quantile plots of the significant models were assessed to ensure the models met statistical assumptions of homoscedasticity. The model ranking was conducted using R package *MuMIn* (Barton, 2020). For generalised least squares models the pseudo-R^2 and p values were estimated using R package *rcompanion* and the Nagelkerke measure (Mangiafico, 2022).

As many of the key environmental variables in the study area were correlated, we conducted a principal components analysis to synthesise the main axis of environmental stress in the study area (Bernard-Verdier et al., 2012; Spasojevic & Suding, 2012). We used axis scores for the first principal component as a measure of the environmental stress gradient and conducted regression of SES scores on those values.

3 | RESULTS

3.1 | Influence of assembly processes on species occurrences

We found unweighted diversity indices FRic (Wilcoxon test $p < 0.01$) and MPDPres (Wilcoxon test $p = 0.05$) were significantly lower than expected by chance (Figure 3). SESMPDPres and SESRaoPres showed similar significant positive trends for annual mean temperature and minimum temperature of the coldest month gradient ($R^2 = 0.24$ and $R^2 = 0.23$) and an opposing significant negative trend for elevation ($R^2 = 0.23$; Figure 4; Figure S2). In addition, SESMPDPres and SESRaoPres values shifted from lower to higher

than expected by chance as temperature increased and elevation decreased (Figure 4). SESMPDPres and SESRaoPres values also showed a significant quadratic trend with precipitation ($R^2 = 0.09$ and $R^2 = 0.09$) and precipitation seasonality ($R^2 = 0.06$ and $R^2 = 0.07$), although with lower explained variance (Figure S2). SESFRic showed a significant positive trend along the precipitation and aridity gradients, but with low explained variance ($R^2 = 0.05$, pseudo $R^2 = 0.08$; Figure 4). SESFRic was generally lower than expected by chance, however, at the high precipitation end of the gradient it started to show some values higher than expected (Figure 4).

Only SESRaoPres and SESMPDPres showed a significant negative relationship with environmental stress ($R^2 = 0.14$ and $R^2 = 0.13$; Figure 5). The principal components analysis first principal component used to derive the environmental stress gradient explained 63% of variation and was associated with minimum temperature, precipitation, and aridity (Figure 5; Figure S3). The first component showed a gradient from higher temperatures and precipitation and low aridity to lower temperatures and precipitation and high aridity.

3.2 | Influence of assembly processes on species abundances

Abundance-weighted functional diversity indices—FDis, FDiv, FRed, MPD, Rao—did not show a significant difference from null expectation under the frequency null model (Wilcoxon test $p > 0.05$; Figure 3). Nevertheless, we found significant trends for the frequency null model SES along the gradients of some environmental variables. SESFDiv and SESFDis showed similar significant positive trends with temperature ($R^2 = 0.08$ and $R^2 = 0.13$) and minimum temperature gradients ($R^2 = 0.1$ and $R^2 = 0.12$) and a negative trend with the elevation gradient ($R^2 = 0.07$ and $R^2 = 0.14$; Figure 4; Figure S2). Like the results for species occurrences, SESFDiv and SESFDis values shifted from lower to higher than expected by chance as temperature increased and elevation decreased. SESFDiv also showed a quadratic trend for evapotranspiration ($R^2 = 0.08$; Figure 4).

Under the abundance null model, MPD and Rao showed average values significantly higher than expected by chance (Wilcoxon test $p < 0.01$), while FRed showed values significantly lower than expected (Wilcox test $p < 0.01$, Figure 3). However, we did not find significant trends along the gradients of any of the environmental variables.

The main results were summarised in a schematic representation based on Bernard-Verdier et al. (2012) to facilitate the interpretation and discussion (Figure 6).

4 | DISCUSSION

Our results support the hypothesis that functional patterns are consistent with a prevailing effect of environmental filtering at the regional scale, declining as environmental stress diminishes. Minimum temperature gradients were most strongly associated with patterns
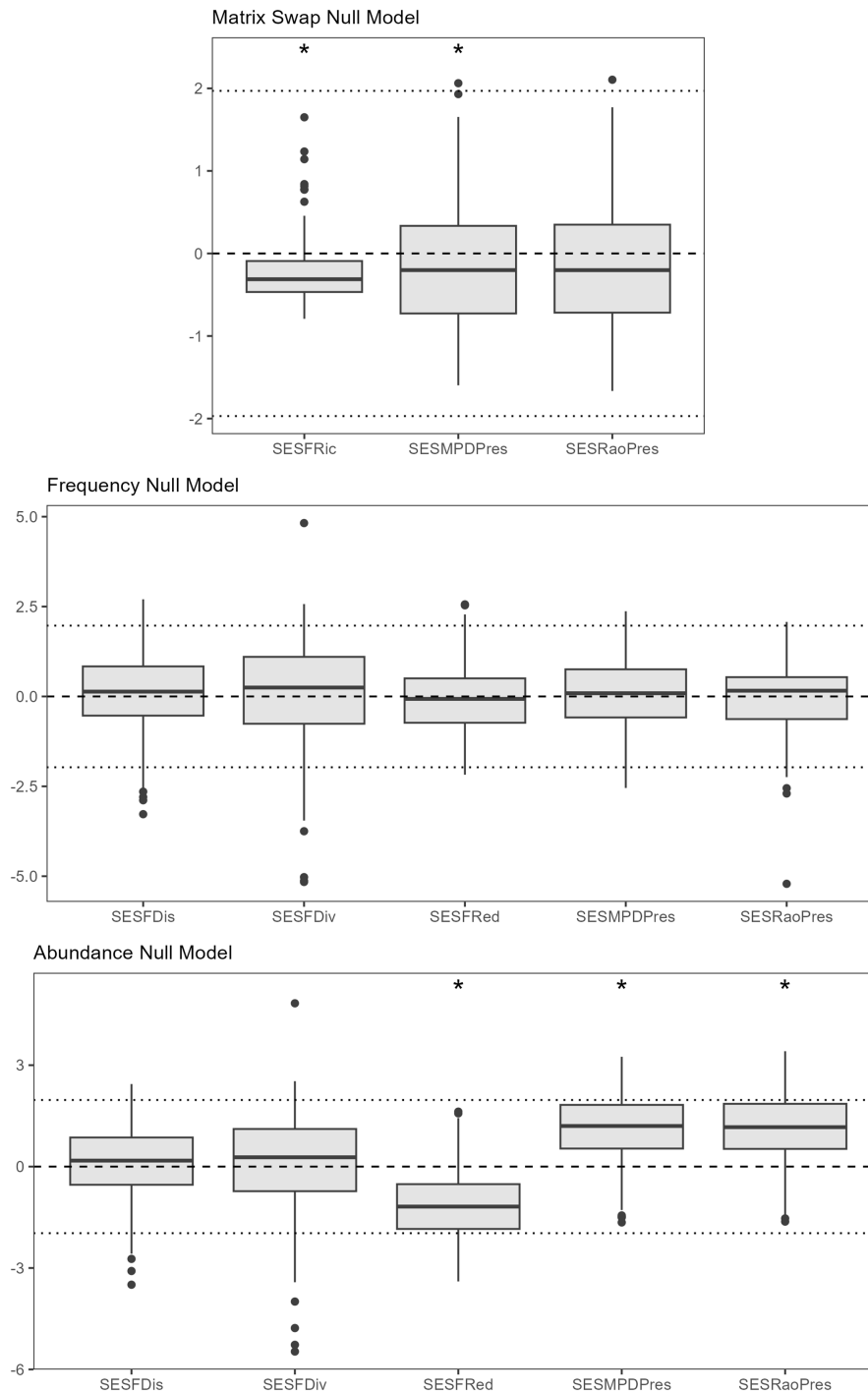
FIGURE 3 Boxplots for standardised effect sizes of the functional diversity metrics under the three null models (matrix swap, frequency, and abundance null model). The asterisks above boxplots signal values significantly different from null expectation as assessed with the Wilcoxon test. The dashed line corresponds to null expectation in the null model comparison. The dotted lines correspond to a more conservative threshold for assessing the significance of the deviation of individual standardised effect sizes from null expectation.

consistent with environmental filtering than were precipitation and aridity. The functional patterns are also consistent with the hypothesis of a shift in assembly processes acting on species occurrences between environmental filtering and limiting similarity with declining minimum temperature and aridity stress. Under more stressful environmental conditions, namely lower temperatures, lower precipitation, and higher aridity, communities showed lower unweighted FDiv and FRic than expected by chance.

4.1 | Influence of environmental filtering

The hypothesis that functional patterns would be consistent with a prevailing effect of environmental filtering at the regional scale was supported by the average FRic and unweighted FDiv being lower than expected from null expectation. This finding is consistent with the general expectation that environmental filtering is the dominant assembly process at larger spatial scales (de Bello et al., 2013) and it leads
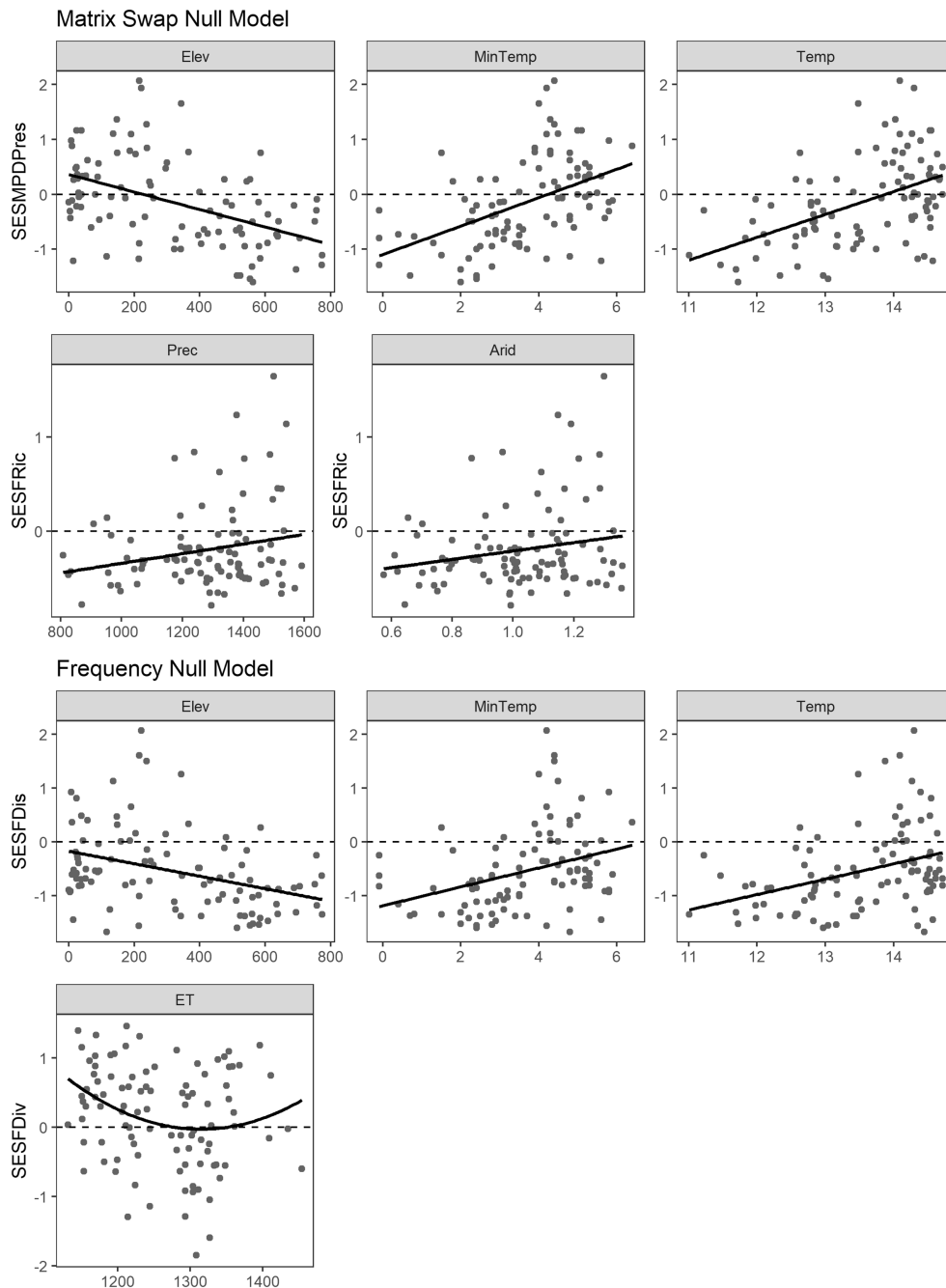
FIGURE 4 Main significant regressions of standardised effect sizes on to environmental variables (Elev, elevation; MinTemp, minimum temperature of the coldest month; Temp, annual mean temperature; Prec, annual precipitation; Arid, aridity; ET, potential evapotranspiration). Note that aridity values represent water surplus, therefore values are higher in humid conditions and lower in arid conditions.

to trait convergence by selecting species with similar traits from the regional species pool (Mason et al., 2008; Mason et al., 2013). Other riparian vegetation studies have also identified prevailing effects of environmental filtering on species richness at a local scale (Fraaije et al., 2015) and on functional composition at the landscape level (Brice et al., 2016), as well as significant effects of environmental filters on riparian functional diversity at basin-scale (Bruno et al., 2016).

The results were also consistent with the environmental harshness hypothesis. Unweighted FDiv and FRic showed lower values than expected by chance in more stressful environmental conditions, particularly lower minimum and annual temperatures and

higher elevations, and to a smaller extent higher aridity and lower annual precipitation. This trend was also confirmed in the regressions using the combined environmental stress gradient. The results are consistent with the general expectation that under stressful conditions fitness is enhanced by traits that maximise the acquisition and retention of the limited resources available (Mason et al., 2008; Mason et al., 2013). This finding is consistent with other studies on riparian functional diversity that found declines in the FRic of functional groups along environmental stress gradients, despite not testing explicitly for the environmental harshness hypothesis (Bruno et al., 2016; Lozanovska, Ferreira, Segurado, & Aguiar, 2018).

FIGURE 5 Results of regression of standardised effect size (SES) along the combined environmental stress gradient obtained through principal components analysis. The first principal component (PC1) reflects the combined minimum temperature and aridity gradient, with lower minimum temperatures and higher aridity in the more stressful end of the gradient.
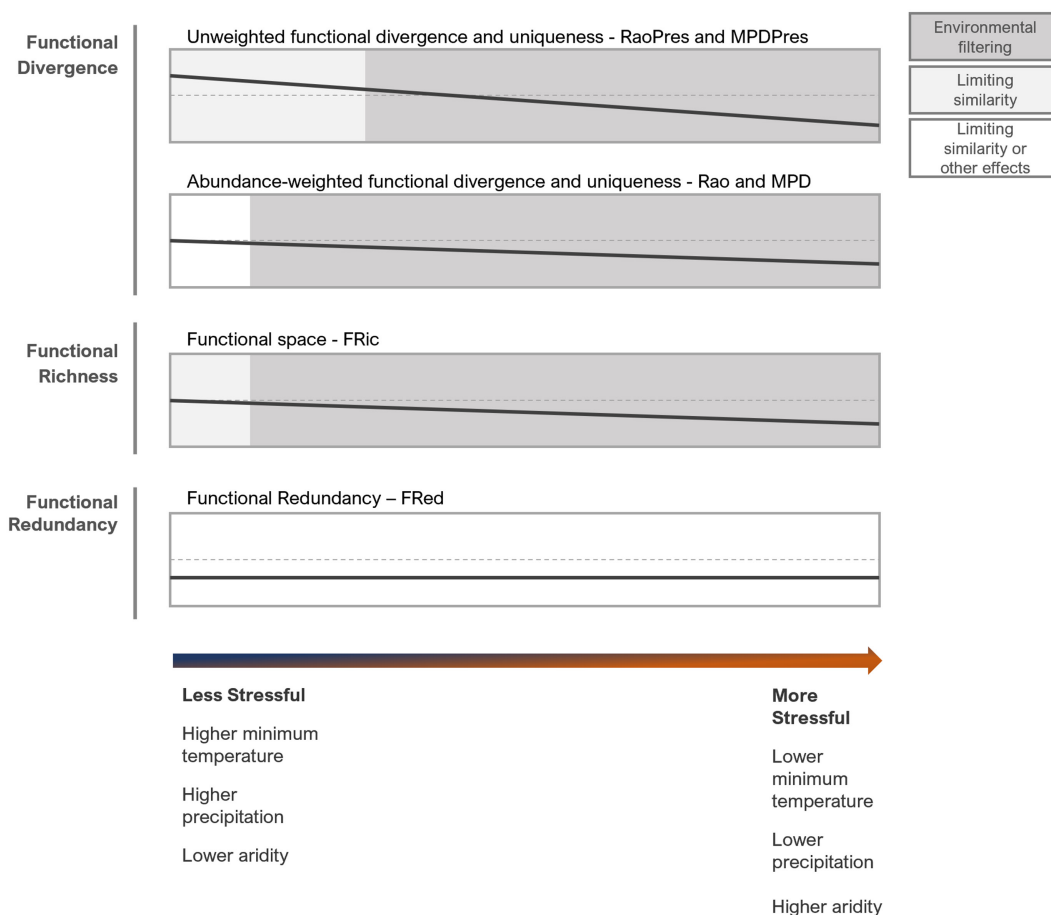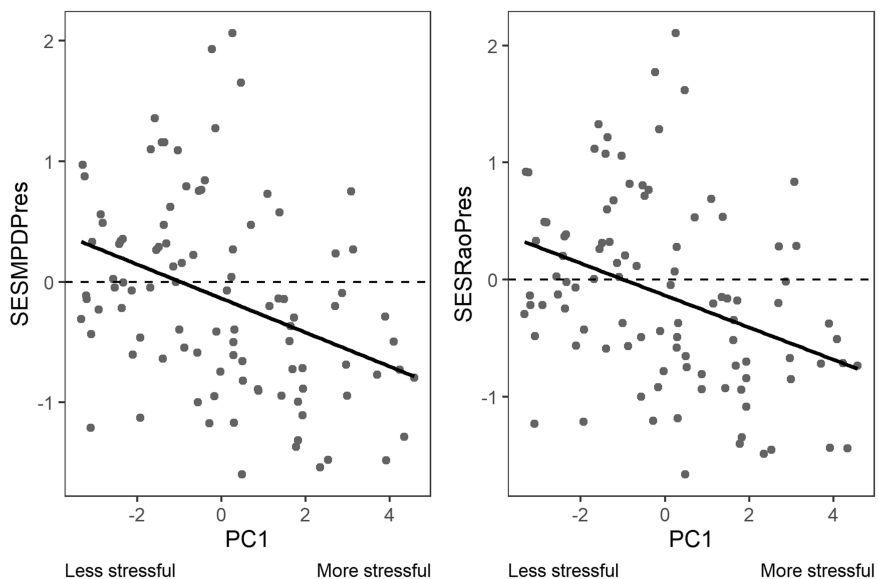

FIGURE 6 Schematic representation of the main results regarding functional diversity patterns and community assembly processes. The dashed line corresponds to null expectation and full lines represent the general trends for individual environmental gradients and the combined stress gradient. The fill colours represent the presumed assembly process.

4.2 | Influence of limiting similarity

The hypothesis that functional patterns would be consistent with a prevailing effect of limiting similarity under less stressful conditions was also supported for species occurrences. Despite average

values lower than expected by chance, unweighted FDiv and FRic showed significant positive trends for individual variables and the combined stress gradient, and a tendency for higher values in less stressful environmental conditions. This is consistent with an increasing influence of limiting similarity on species occurrences as

environmental stress declines (Mason et al., 2013). As previously mentioned, there are studies that report declines in FRic with increasing environmental stress, consistent with these patterns (Bruno et al., 2016; Lozanovska, Ferreira, Segurado, & Aguiar, 2018). However, as the assembly processes are not tested, the effect of limiting similarity under lower environmental stress remains poorly studied. Nevertheless, one study reported that riparian plant functional groups that tended to co-exist within study sites had distinct traits suggesting complementary in resource use, which appears to be consistent with limiting similarity (Hough-Snee et al., 2015).

The results for species abundances are consistent to some extent with limiting similarity; however, it is possible that other assembly processes are involved. Functional divergence was significantly higher than expected by chance; however, we did not find it to be significantly associated with any environmental variable. Therefore, we cannot exclude possible effects of disturbance (e.g., flood disturbance) or environmental heterogeneity (e.g., lateral hydrological gradients) processes that characterise riparian ecosystems (Catford & Jansson, 2014). Both processes are expected to lead to trait divergence, either through biomass removal decreasing the probability of competitive exclusion or through co-existence in different niches (de Bello et al., 2013).

Conversely, FRed was significantly lower than expected by chance, but we also did not find it to be significantly associated with any environmental variable. A highly divergent community with high number of low-frequency species, such as those studied here, will necessarily have low redundancy, and therefore is expected to be more vulnerable to species loss (Ricotta et al., 2016). We cannot exclude the possibility that FRed may be underestimated in this study, since we were not able to include low-frequency species in our analyses. Nevertheless, the species included represent 80% of the regional pooled abundance, which provides some confidence in the general trend of low redundancy, even if there is some underestimation of observed values. Additionally, riparian vegetation typically has a high species richness and large numbers of relatively low abundance species (Naiman et al., 2005; Stella et al., 2012) therefore, based on our results, this trend of low FRed may be widespread. These patterns encourage further studies using null models to improve our understanding of how assembly processes interact to shape riparian FDiv and FRed (Catford & Jansson, 2014).

4.3 | Shifts in assembly processes along environmental stress gradients

Overall, our findings supported the hypothesis of a shift in assembly rules acting on species occurrences from environmental filtering to limiting similarity with declining environmental stress (Mason et al., 2013). Functional richness and unweighted FDiv were lower than expected by chance for lower precipitation, as predicted, but also for lower minimum temperatures, and the combined stress gradient. We did not find evidence for a shift in assembly rules acting on species abundances, as previously discussed. This suggests that

large-scale environmental gradients associated with increasing cold and aridity stress govern the selection of species from the regional pool, and that other processes and local factors govern species abundances.

4.4 | Environmental variables associated with community assembly and functional patterns

Minimum temperature, annual temperature, and elevation were unexpectedly more influential environmental filters than aridity or precipitation, presenting the highest explained variance in this study. This finding suggests an important limiting effect of winter minimum temperatures on FDiv in a Mediterranean climate that differs from our initial hypothesis. However, a similar effect was reported in a semi-arid river where both woody and herbaceous riparian vegetation composition responded more strongly to changes in minimum temperature than in maximum temperature or precipitation (Butterfield et al., 2018). A declining trend with elevation has been reported for FRic in Mediterranean riparian plant assemblages; however, the effect of temperature was not tested (Lozanovska, Ferreira, Segurado, & Aguiar, 2018). Similar observations were made for Mediterranean shrublands, drylands, and grasslands (Boonman et al., 2021; Butterfield & Munson, 2016; Pérez-Ramos et al., 2017). Vegetation closely tracks minimum temperature (Woodward & Williams, 1987), since freezing temperatures can cause xylem embolism, reduced leaf conductance, and photochemical efficiency, similarly to drought conditions (Pérez-Ramos et al., 2017). However, minimum temperature is often overlooked as a climatic stressor in Mediterranean climates (Pérez-Ramos et al., 2017). Similarly, in the formulation of our hypothesis, we focused on the effect of precipitation considering because of the findings of previous studies on the effect of water availability on riparian vegetation and the location of the study area is in a Temperate–Mediterranean climate transition zone. However, the study area also has several mountain ranges, characterised by lower temperatures and high river discharge volumes (INAG, 2008b), which explains the importance of temperature and elevation gradients found here.

The aridity–precipitation gradient had a smaller but significant contribution to explaining functional diversity patterns. Riparian vegetation is known to be sensitive to spatio-temporal precipitation patterns as they strongly affect river hydrology (Capon et al., 2013). The results are consistent with experimental and observational studies that reported declines in FRic and FRed due to drought occurrence and duration (Baattrup-Pedersen et al., 2018; Bruno et al., 2016). However, our results show that we should consider water availability together with other climate stressors (Butterfield et al., 2018; Pérez-Ramos et al., 2017). Studies in semi-arid regions have found similar trends of decreasing species richness and functional group diversity driven by combined effects of elevation, temperature, and precipitation seasonality (Palmquist et al., 2018).

4.5 | Implications for riparian ecosystems under climate change

Considering climate change predictions, the first major implication of our findings is that mountain riparian ecosystems may experience a functional shift due to decreasing influence of environmental filtering associated with rising minimum temperatures. Increases in mean annual and winter temperatures and decreases in the number of frost days can allow the colonisation of higher elevations by a wider set of species, including exotic species, increasing FRic and FDiv, at the cost of the existing cold-adapted species and communities (Nilsson et al., 2012). This functional shift may increase ecosystem multifunctionality and temporal stability; however, it raises concerns about the conservation of cold-adapted species and the possible expansion of exotic species.

The second major implication is that lowland riparian ecosystems may experience declines in functional diversity due to an increasing influence of environmental filtering associated with annual and seasonal water availability. In most of the study area, declines in annual and seasonal precipitation are expected to shift communities toward lower FRic and FDiv and increase the presence of drought-adapted species with conservative traits (Baattrup-Pedersen et al., 2018; Bruno et al., 2016). This may lead to a decline in ecosystem functioning and temporal stability compared to the current baseline, particularly in the Temperate–Atlantic areas (Lozanovska, Ferreira, Segurado, & Aguiar, 2018; Rohde et al., 2021).

Management and restoration are increasingly concerned with ecosystem functioning and stability, and adaptive capacity (Capon et al., 2013; Capon & Pettit, 2018). Thus, functionally diverse riparian plant communities should be protected and restored to ensure continued riparian functioning and stability under increasing climatic fluctuations, considering current baselines and conservation concerns (Cadotte et al., 2011).

5 | CONCLUSION

Using functional patterns as indicators of competing assembly processes, we found that riparian community assembly at regional scale is influenced by environmental filtering and environmental stress. Functional patterns indicated that environmental filtering was the prevailing assembly process acting on species occurrences at the regional scale, but its influence declined as cold and aridity stress decreased. Minimum temperature was more strongly associated with environmental filtering patterns than precipitation or aridity. Our results highlighted the relevance of large-scale environmental stress gradients and community assembly in influencing riparian functional diversity, underlining the need for hierarchical approaches and the analysis of multiple climatic stressors. This study improves our understanding of how community assembly and environmental variables jointly influence functional diversity patterns in riparian ecosystems and supports the prediction of climate change impacts on ecosystem functioning

and stability. Trait-based approaches are essential to improve the understanding of how riparian functional diversity interacts with climatic and local factors to shape ecosystem stability, resistance, and resilience.

AUTHOR CONTRIBUTIONS

Conceptualisation: A.P.P., I.D. Developing methods: A.P.P., C.V., J.H. Conducting the research, data analysis, preparation of figures and tables: A.P.P. Data interpretation, writing: A.P.P., C.V., I.D., J.H.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

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SUPPORTING INFORMATION

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