BIODIVERSITY OF LARGE RIVERS

The effect of riparian forest on landscape connectivity for the EPT community across European regions

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Abstract Ephemeroptera, Plecoptera and Trichoptera are three orders of freshwater macroinvertebrates with a short terrestrial adult life-stage that they use to disperse by flying upstream. This aerial dispersal can be assisted by native riparian forest, but regional variation has not yet been empirically tested. In this study we compared the EPT community of 153 sampling sites located in freshwater streams in four European regions (Central Plains, Central Highlands, Alps, Iberia). In each site, we assessed the EPT community dispersal ability using the Species Flying Propensity index. We also calculated the native deciduous forest cover in the riparian buffer and several environmental stressors such as saprobic pollution or catchment anthropization. Finally, we tested which of these parameters have a significant effect on the EPT community. In the Central Highlands and in Iberia, the share of weak dispersers increased with native deciduous forest cover, indicating a positive effect on dispersal of EPTs. In the Central Plains and the Alps, no such effect was found. We conclude that the effect of native deciduous forest depends on regional landscape characteristics and the regional species pool, but considering the dispersal of the regional EPT communities is needed to create effective river management policies.

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Introduction

Community composition of macroinvertebrates in rivers is, in general, shaped by two main factors: habitat availability and landscape connectivity. The first one is dependent on the environmental habitat conditions and the ecological niche of the species in the regional species pool, while the second depends on the characteristics of the landscape features and the dispersal of the species in the regional species pool (Downes et al., 2017; He et al., 2022). In other words, the environmental habitat conditions at a site have to fit the ecological niche of a species and it has to be able to reach the site. Ephemeroptera, Plecoptera and Trichoptera (EPT) are three orders of sensitive aquatic macroinvertebrates often used as indicators for local habitat conditions. In the particular case of European EPTs, there are 2367 species described (Schmidt-Kloiber & Hering, 2015) and the pool of species greatly varies across regions (Dos Santos et al., 2011; Vadas et al., 2022). Moreover, some widespread species occupy different ecological niches in different regions as a result of regional adaptations (Bonada & Dolédec, 2018). This diversity of the European regional pools of species means that the environmental habitat conditions of a site often translate into different EPT communities in different geographical areas.

In addition, EPTs can be a good indicator group for landscape connectivity given their merolimnic life cycle (Bauernfeind & Moog, 2000), their relatively similar dispersal range (Peredo Arce et al., 2021) and their shared sensitivity to stressors as pollution or changes in land use (Bauernfield & Moog, 2000; Cruz et al., 2022). As larvae they are aquatic but emerge from the water, reproduce and disperse in their terrestrial adult life stage. Aerial dispersal is a key in the life cycle of EPTs as most of the species have winged terrestrial adult life stages, allowing them to disperse long distances and to compensate for the downstream drift during the aquatic life stage (Elder & Coombs, 2015; Tanvir Rahman et al., 2021). The dispersal ability of different EPT species depends on a series of particular traits, like wing length or adult lifespan (Sarremejane et al., 2017). This translates into a high variability in the dispersal abilities, and dispersal distances greatly differ between EPT species, ranging from a few meters to tens of kilometers (Bauernfeind & Soldán, 2013; Peredo Arce et al., 2021).

Different strategies have been developed to measure this variability on dispersal abilities. On the one hand, experimental studies have been run for decades, using mark and recapture experiments (MacNeale et al., 2005), genetic studies (Geismar et al., 2015) or other techniques to infer flying distances (Gíslason et al., 2015). Nevertheless, these experiments produced limited results (Peredo Arce et al., 2021), leading to scientists to use functional traits related with flight, particularly female wing length (Malmqvist, 2000), but also adult size, number of generations per year or others (Sarremejane et al., 2020). Finally, some researchers have combined several of these traits into complex indices (Li et al., 2016; Sarremejane et al., 2017) that can give a more precise inference of the flight capacity of merolimnic macroinvertebrates (Peredo Arce et al., 2021). However, dispersal not only depends on the dispersal abilities of a species but also on how landscape features influence the landscape connectivity (Fonseca et al., 2021).

Riparian forests likely have a positive effect on landscape connectivity for EPTs by increasing the adults' chances to disperse long distances (Valle et al., 2013). In general, this effect of the forest is attributed to (i) improved habitat conditions and life expectancy for the adults (Nebeker, 1971; Cox & Rutherford, 2000; Parkyn et al., 2003), increasing the time to disperse, (ii) better conditions for dispersal resulting from less harsh weather conditions, especially wind (Briers et al., 2003), and (iii) the provision of visual cues resulting from e.g. light polarization for spatial orientation (Farkas et al., 2016). Furthermore, the effect of riparian forests on EPT dispersal can vary depending on forest characteristics.

Open vegetation and riparian forests can hold different EPT communities in terms of composition and abundance (Collier et al., 1997; Gomes et al., 2022), and can also have a direct effect on the EPT dispersal process. Natural forests can also have different EPT communities in comparison with restored forests (Parkyn et al., 2003) or non-native forests as coniferous plantations (Collier

et al., 1997) or invasive woody species (Little et al., 2021). This can be partly caused by the different microclimatic condition different forests create, as native riparian forests tend to be relatively scarce (Huylenbroeck et al., 2021) providing less shading than a coniferous plantation, and therefore having a milder effect on air temperature reduction (Dugdale et al., 2018). Nevertheless, coniferous species become naturally more common in riparian areas with elevation (Pielech, 2021), whereas at lower elevations (< 1500 m a.s.l.), mixed forests with more complex strata of tall trees and deciduous shrub species of different heights are more common. At lower elevations, these transition to pure deciduous forests, unless conifer species are afforested (Assal et al., 2021) and these afforestations can become dispersal barriers for EPT dispersal (Hering et al., 1993). In sum, changes in the characteristics of the riparian forest, from species composition to tree density can have an impact in the EPT community assemblage and structure, but those effects will be dependent on the particular characteristics of the region (Mc Conigley et al., 2017).

However, there are few empirical studies on the effect of riparian forests on EPT dispersal. Peredo Arce et al. (2023) recently investigated the effect of riparian forests on EPT community composition in temperate Central European streams. In low mountain streams (200 to 1000 m a.s.l.), deciduous riparian forest cover indeed increased the proportion of weak dispersers, which the authors considered an indication for a positive effect of riparian forests on landscape connectivity and dispersal. This effect was non-linear and only significant up to a medium riparian forest cover. No such effect was found in lowlands (0 to 200 m a.s.l.), possibly because the effect was masked by other anthropogenic stressors in the heavily degraded lowland streams. Furthermore, coniferous forest did not contribute to the effect of deciduous forest on the EPT community in this study, indicating that this type of forest does not increase landscape connectivity in this region. Moreover, other studies showed that coniferous and non-native riparian forests impact the EPT community composition (Collier & Smith, 1995; Collier et al., 1997; Miserendino & Pizzolon, 2004; Little et al., 2021) even act as a barrier for EPT dispersal (Hering et al., 1993).

Most probably there are regional differences in the effect of riparian forests on EPT dispersal and community composition but there are no empirical studies comparing different ecoregions. In arid landscapes, like the Mediterranean region, riparian forests are potentially more important for EPT dispersal compared to the temperate Central European streams investigated by Peredo Arce et al. (2023), given their important role in providing refugia for EPTs. It is known that high humidity refugia like pools or caves in arid landscapes (Salavert et al., 2008) can act as stepping stones for EPT dispersal (Cañedo-Argüelles et al., 2015) and aerial dispersal routes can be of particular relevance for EPTs in intermittent streams (Graham et al., 2017). Native riparian forests can maintain higher air humidity, infiltration and reduced surface runoff and sediment transport (Hernández-Santana et al., 2011) so it is reasonable to expect that native riparian forests can also be stepping stones. Nevertheless, non-native riparian forests, which are particularly common in the Mediterranean basin (Ferreira & Aguiar, 2006), could have a negative impact on the macroinvertebrate community (Miserendino & Pizzolon, 2004; Little et al., 2021) as they can fail to provide essential ecosystem services for their life cycle.

In cold landscapes, like boreal or alpine regions, riparian forests potentially are less important for EPT dispersal. In these regions, riparian forests are less dense or even missing (Mac Nally et al., 2008) and wide braiding rivers are common (Muhar & Schwarz, 2000). EPT communities probably have adapted to these conditions, which is reflected by the fact that they are generally composed of weaker dispersers (Brittain, 1990; Engelhardt et al., 2011) which rely on wind to fly greater distances (Zwick, 2009). Furthermore, as native riparian forests above the subalpine region are missing (Körner & Körner, 2012), vegetation is not of relevance for dispersal for the Diptera-dominated macroinvertebrate communities found there (Oertli et al., 2010), being dispersal mainly driven by the topography and the channelled winds (Bertin et al., 2015; Ptatscheck et al., 2020). These differences between milder, warmer and colder regions have yet to be addressed.

Given this lack of knowledge, the aim of this study was to test if the effect of riparian forests on the EPT community dispersal ability differs across four European regions: Central Plains, Central

Highlands, Iberia and the Alps. More specifically, we tested the following three hypotheses: first, we expected that native riparian forest cover increases the share of weak dispersers in the EPT community, indicating a positive effect on EPT dispersal, but that this effect differs across regions. Compared to the temperate Central European regions, riparian forest cover was expected to have a stronger effect in the arid Iberia region and a weaker effect in the colder Alpine region. Second, we expected riparian forest composition being relevant and non-native riparian forests to decrease the proportion of weak dispersers in the temperate and arid regions, indicating that it acts as a dispersal barrier. Third, we expected the effect of native riparian forest cover being non-linear,

and the share of weak dispersers to increase only up to a medium cover typical for native riparian forests.

Methods

Study regions and sampling sites

This study was based on 153 sampling sites across four different European regions (Fig. 1): "Central Plains", "Central Highlands", "Iberia" and "Alps". The Central Plains and Central Highlands regions are located in the German Federal State of North Rhine-Westphalia. Environmental conditions at the sampling locations were similar given the relatively small spatial extent (34,112 km^2) and homogenous

Fig. 1 Location of the four study regions, including every sampling site (●), river network (blue lines) and major subcatchments (gray lines)
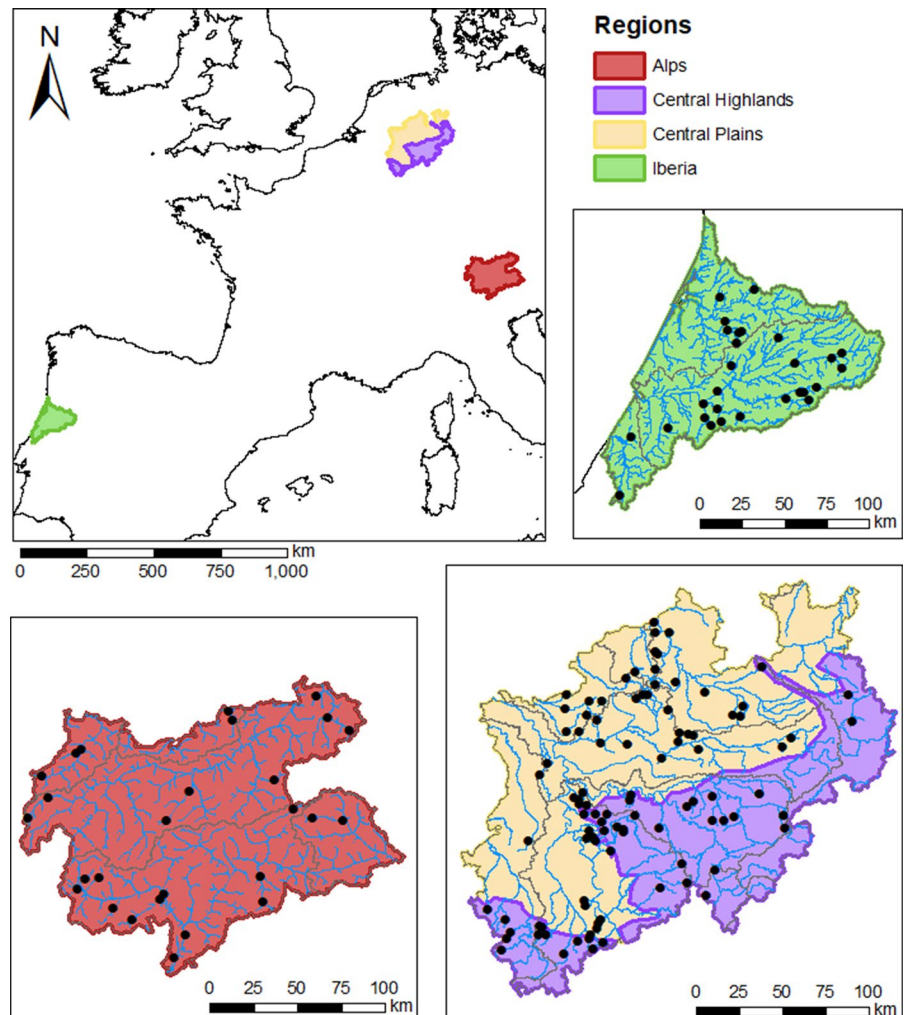
climate (Oceanic and Humid Continental, according to Köppen) of that area. The sites in the Central Plains ($n = 53$) were located at 0 to 200 m a.s.l., and the sites in the Central Highlands ($n = 45$) at 200 to 1000 m a.s.l.. The Iberia region comprised 28 sampling sites located across the Mondego, Lis and Vouga catchments in the center of Portugal. The three catchments cover 11,215 km^2, and the sites were located at 40 to 1000 m a.s.l. across two different climatic zones (cold and warm summer Mediterranean). From the Alps region 27 sampling sites from the northern to the southern face of the Alpine ridge in the federal state of Tyrol (Austria) and the Autonomous Province of Bolzano—South Tyrol (Italy) were included in this study. It covered 20,036 km^2 and the sampling sites were at 200 to 2000 m a.s.l., in the Humid Continental (lower elevation) and Tundra and Subarctic climatic zone (higher elevation). All sampling sites were located in streams of Strahler order ≤ 4. The sites were characterized by region (Fig. 2) on river size using Strahler order and upstream catchment size (in km^2), on Elevation (m a.s.l.), on the geological characteristics ("Calcareous", "Siliceous" or "Mixed" geology) and on the size of the substrate ("Coarse"

for mean particle size > 6.3 cm, "Medium" for size $= 2$ to 6.3 cm, and "Fine" for size < 2 cm).

Biological data

The multi-habitat macroinvertebrate sampling was done and the taxa lists provided by regional authorities in the Central regions and by the authors of this study for the Alps and the Iberia regions. In the Central Plains and the Central Highlands regions, the macroinvertebrate sampling was carried out in early spring (March, April) between 2005 and 2012 by state authorities in accordance with the Water Framework Directive (Meier et al., 2006). In the Iberia region, the macroinvertebrates were sampled in February and March 2007 according to the WFD protocol for Portuguese rivers (INAG I.P., 2008). Identification was done to genus level. In the Alps region, sampling was carried out in early spring 2018 and 2019. In regards to the treatment and sorting of the samples, the national standard specifications of Austria (Ofenböck et al., 2010) were used in the ALFFA project for the Italian and the

Fig. 2 Characteristics of the sampling sites per region in regard to Strahler order, Catchment size (km^2), Elevation (masl), Geology of the site and Substrate particle size (no data was available for the Iberia region). The y-axis on the "Catchment" plot was broken on the 200 km^2 upper limit, although it cuts the upper whisker (defined as the maximum value of the data that is within 1.5 times the interquartile range over the 75th percentile) of the Iberia region which falls on the 400 km^2, to facilitate the comparison between regions
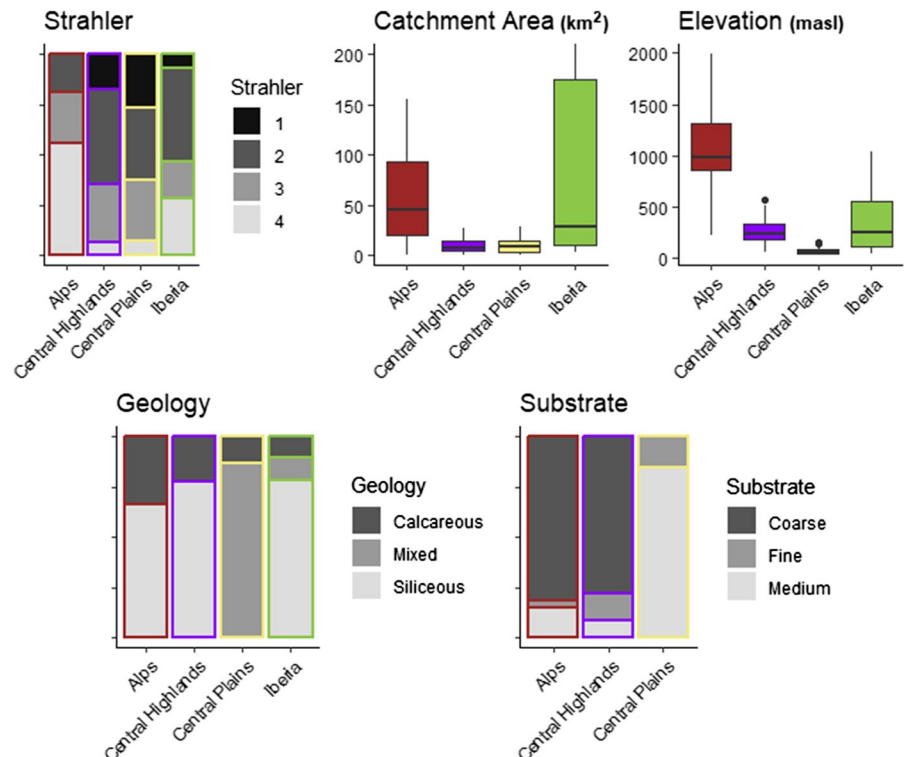
Austrian samples to guarantee comparability and representativeness (Schmölz et al., 2022). The organisms were identified at species level. As a result of these multi-habitat macroinvertebrate sampling campaigns, we generated a list of relative abundances of every taxa present for every site across the four study regions. The sampling effort per site was lower in the Iberia region, but all the macroinvertebrate variables included in this study are weighted using the relative abundance (individuals per square meter).

The Species Flying Propensity index ("SFP", Sarremejane et al., 2017) was used to assess the dispersal ability of the EPT community for each sampling site. This index was initially developed to assess the dispersal ability of any European species of freshwater macroinvertebrate, but it was found adequate to use to identify differences in dispersal across EPT species (Peredo Arce et al., 2021) with scores varying between 8 and 16 for the European EPTs. First, the SFP index was calculated for each taxon present at any of the sampling sites. The traits used for calculating the SFP index are functionally related with the dispersal ability of macroinvertebrates and include adult lifespan, aerial dispersal capacity (active and passive), wing size and number of generations in one year (voltinism) and maximum body length (the complete formula of the SFP index can be found in Online Annex I). Trait scores for each sampled taxon were extracted from the DISPERSE database (Sarremejane et al., 2020) at the lowest taxonomic level possible (genus in most cases). In case of taxa with missing information for one or more of the traits, the scores for those traits were taken for the closest relative taxon or it was calculated as the mean score between two equally close taxa. For example, the genus *Ernodes* lacks the value for the voltinism trait in the DISPERSE database. To calculate its final score, the mean value of that trait for the other genera in the family *Beraeidae* was used. Second, the mean SFP index of all the individuals in the community was calculated for each sampling site, weighted by the abundance of the taxa at the sampling site. This parameter will be referred to as "EPT community dispersal ability" or "SFP" in the following.

Riparian forest cover

Riparian forest cover was quantified for every sampling site in a 30 m wide buffer along each side of the stream. The buffer reached up to 5 km upstream and 5 km downstream from the sampling site and exclusively covered the main stem without any tributaries (Fig. 3). The buffer size was chosen based on the results of a previous study (Peredo Arce et al., 2023). The sites were far enough from each other so their riparian buffers did not overlap. Moreover, the riparian buffers did not include large reservoirs or impoundments.

Riparian forest cover in the buffers was given in percentage cover and quantified using a combination of land cover datasets and remote-sensing images. The images were used to delineate and classify small-scale woody features in the riparian buffers, which were not yet included in the land cover datasets using an object-based image analysis (OBIA). The delineation of woody features was done by dividing the images into objects of homogeneous pixel patches using the multiresolution segmentation algorithm in Trimble's eCognition software (Version 9.3.0). These objects were then classified as being woody vegetation or no woody vegetation. In the Central Plains and Central Highlands regions, the ATKIS land cover dataset was used, being part of the official German Topographic-Cartographic Information System. For the remote-sensing image analysis, a mix of mostly color-infrared (CIR) and RGB images was provided by the German Federal Agency for Cartography and Geodesy. After the segmentation process, object classification was done automatically using a customized Support Vector Machine classifier (SVM). In the Iberia region, land cover was assessed using the land use and land cover map for continental Portugal for 2007 (COS2007—Caetano et al., 2009). For the remote-sensing image analysis, satellite images from the year 2011 were used. After segmentation of the images, classification of the objects was done manually. In the Alps region, land cover was quantified using data with a spatial resolution of 1.10.000 (raster file: 5 m), which was used to distinguish 34 natural, near-natural and artificial habitats found in the Central and Southern Alps (Tasser et al., 2009; Schmölz et al., 2022). For the

Fig. 3 Example of an orthophoto overimposed to a land cover dataset. In dark blue, the river line. The dark green line defines the buffer area 30 m at each side of the river. In purple, the areas identified as riparian woody features

remote-sensing analysis, orthophotos were provided by the Autonomous Province of Bolzano and TIRIS (Tyrolean Geographic Information System). After segmentation of the images, the classification of the objects was done manually.

The woody vegetation objects identified in the remote-sensing image analysis were then used to replace non-forested areas in the land cover datasets. Visual inspection revealed that coniferous and non-native trees in the buffers almost always occurred as large planted patches, which were then already included in the land cover datasets. Therefore, the riparian woody features from the OBIA added to the land use datasets were virtually all native riparian forest patches. The modified land cover datasets were then used to calculate the percentage cover of the following types of riparian forest: deciduous forest (as the sum of deciduous, shrubs and mixed woody vegetation cover types), coniferous forest and non-native forest. Deciduous and coniferous forest were considered for the Alps, Central lowlands and Central Highlands regions, while deciduous, coniferous and non-native forest were considered in the Iberia region.

Confounding environmental stressors

In order to disentangle the effect of riparian forest on EPT communities dispersal ability from other confounding environmental stressors, the most important stressors for EPTs and macroinvertebrates in general were included as predictors in the statistical analyses (Peredo Arce et al., 2023). *Saprobic Pollution* was assessed, in the Alps as the Saprobic Index following Zelinka & Marvan (1961), in the Central Plains and Central Highlands as the German Saprobic Index (Hering et al., 2004) and in Iberia as the Saprobic Index of the Iberian Bio-monitoring Working Party (Alba-Tercedor et al., 2002). *Site Naturalness* was assessed in the Central Plains and Central Highlands using the German multimetric index (Böhmer et al., 2004) but not in the other two regions as that index is developed specifically for Central European river habitats and

may not be applicable in other regions. *Catchment Anthropization* was quantified and used as a proxy for catchment-scale stressors by calculating the percentage cover of urban areas in the upstream catchment of the sampling sites. *Elevation* was quantified as the elevation of the sampling sites for the Alps and Iberia regions given the large differences in elevation within those datasets.

Statistical analysis

To ease interpretation of the results, the gradients of the SFP as the response and the main two predictors (percentage cover of deciduous and coniferous riparian forest) were shown using simple boxplots and means as well as the coefficients of variation compared between regions using one-way ANOVAs and modified signed-likelihood ratio tests for equality of CVs, respectively. Tukey's HSD post-hoc tests were performed to find which region mean values were different when needed.

The EPT community composition present across the four regions was described using abundance (number of individuals per square meter), diversity (richness, Simpson diversity index) and dispersal (mean SFP) metrics. For the diversity metrics, genus is used as taxonomic unit and individuals identified at higher taxonomic level are ignored. The Simpson diversity index (D) was calculated using the following formula, where n is the total number of organisms of a particular genus and N is the total number of organisms of all genera:

$$D = 1 - \left(\frac{\sum n(n-1)}{N(N-1)} \right)$$

This index was calculated for every single site (α-or local diversity), for the whole regions (γ-or regional diversity) and as the ratio between both (β-diversity or genus turnover). A detailed list of the taxa present in every region, including the regional density (in individuals per square meter) and SFP scores is supplemented as Online Annex II.

To test the actual hypotheses, four Generalised Linear Models (GLMs) were set up: one for the Central Plains region ($n = 53$), one for the Central Highlands region ($n = 45$), one for the Iberia region ($n = 28$) and one for the Alps region ($n = 27$). In each of the four GLMs, the SFP was used as the response

variable and the environmental parameters as fixed effects (Deciduous forest, Coniferous forest, Non-native forest, Saprobic Pollution, Site Naturalness, Catchment Anthropization and Elevation). To take into account that native riparian forest in the Alps region can be deciduous or coniferous, one additional GLM was run for that region, combining Deciduous and Coniferous forest cover as one unique fixed effect. The fixed effects were dropped at a time and the resulting nested model always compared to the full model using the likelihood ratio test (ANOVA) to test for significance of the dropped fixed effects. The least significant fixed effect was dropped from the full model and the backward selection repeated until all remaining effects were significant with $\alpha < 0.05$ (Zuur et al., 2009). The GLMs were tested for normality of residuals (Shapiro–Wilk test) and homoscedasticity (Breuch–Pagan test) and spatial autocorrelation (analysing the semivariance using a variogram). In case of a GLM not meeting normality of residuals and homoscedasticity, the initial model was instead fitted using the Generalised Least Squares method (GLS) using a power of the covariate variance structure (Zuur et al., 2009). In case of a GLM showing spatial autocorrelation, the model was fitted using a GLS including a spatial autocorrelation structure (Zuur et al., 2009). Then, the fixed effects were dropped at a time following the same procedure described for the GLMs. Additionally, the environmental stressors (Saprobic Pollution, Site Naturalness, Catchment Anthropization and Elevation) were tested for co-correlation (Pearson's r) separately for each region.

To investigate the first and main hypothesis on differences between regions, the four GLMs with native riparian forest as response were compared. First, GLMs where native riparian forest had a significant negative effect on the SFP were selected (higher share of weak dispersers indicating higher landscape connectivity). Second, regression coefficients were extracted from the significant GLMs to compare the magnitude of the effect between regions.

To investigate the second hypothesis, coniferous riparian forest was used as a fixed effect in the four GLMs and also non-native riparian forest in the Iberia GLM. GLMs where coniferous riparian forest had a significant positive effect on the SFP were selected. The lower share of weak dispersers

indicated that coniferous riparian forests had a negative effect and acted as a dispersal barrier.

To investigate the third hypothesis on the effect of native riparian forest being non-linear, for each GLM where deciduous forest was significant, a comparison between a Linear Model (LM) and its respective non-linear Generalized Additive Model (GAM) using a chi-squared test. The LM and the GAM included the SFP as a response and deciduous forest cover as the only fixed factor, and the GAM used a cubic regression spline as the smoother to build the non-linear trend line. Finally, the slope of the fitted non-linear trend line of the GAM was computed at 200 equally spaced points to identify parts where the 90% confidence interval of its local slope did not include zero, and hence, the SFP values can be considered to decrease significantly (Simpson, 2011). In case such a non-linear effect was found, the dataset was limited to the part of the trend line significantly decreasing, a new GLM set up and the new regression coefficient extracted to assess the magnitude of the effect at the required values of deciduous riparian forest cover.

All statistical analyses were performed in R (R Core Team, 2020), using the cvequality package to test for differences between coefficients of variation, the generic glm function to create the GLMs, the drop1 function to perform the backward selection of predictors, the mgcv function to create the GAM, as well as the R-scripts derivFun and tsDiagGamm described in Simpson (2011) to identify and visualize a significant decrease in the trend lines (downloaded from the github repository at https://github.com/gavinsimpson/random_code).

Results

The four regions did significantly differ in respect to the response variable, the EPT community dispersal ability (Fig. 4). The mean value was significantly different ($F(3) = 7.716$, $P < 0.001$) as it was substantially lower in the Alps compared to the Central Highlands ($P = 0.019$, 95% CI 0.619 to 0.959) and to the Central Plains ($P < 0.001$, 95% CI 0.357 to 1.228), indicating that strong dispersers were less common in the regional species pool in the Alps. Moreover, the coefficient of variation was significantly different between regions ($\chi^2 = 17.734$, $P < 0.001$) and lower in the Iberia region, indicating that sampling sites were rather similar in respect to the dispersal abilities of the EPTs in that region. The forest cover of the riparian buffer was also significantly different between regions. The mean ($F(3) = 13.19$, $P < 0.001$) and the coefficient of variation ($\chi^2 = 26.868$, $P < 0.001$) of the deciduous forest cover were significantly different between regions, being lower in the Alps (Central Highlands: $P = 0.002$, 95% CI 0.041 to 0.244; Central Plains: $P < 0.001$, 95% CI 0.051 to 0.249) and Iberia (Central Highlands: $P < 0.001$, 95% CI $- 0.286$ to $- 0.085$; Central Plains: $P < 0.001$, 95% CI $- 0.290$ to $- 0.095$) and less variable in Iberia. This indicates a high homogeneity in deciduous cover in Iberia and an overall higher cover of deciduous riparian forest in the

Fig. 4 Distribution of the values for the EPT community dispersal ability and percentage of riparian forest cover (Deciduous and Coniferous) across the four study regions
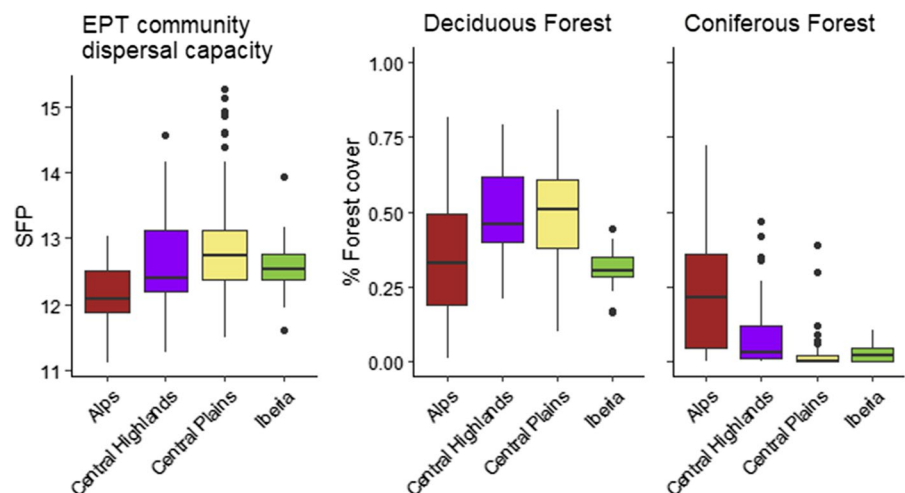
Central regions. The mean ($F(3) = 21.57$, $P < 0.001$) and the coefficient of variation ($\chi^2 = 9.91$, $P = 0.019$) of the coniferous forest cover were significantly different between regions, being higher in the Alps than in the other regions (Central Highlands: $P < 0.001$, 95% CI -0.221 to -0.074; Central Plains: $P < 0.001$, 95% CI -0.283 to -0.139; Iberia: $P < 0.001$, 95% CI -0.285 to -0.122) as well as more variable and higher in the Central region compared to the Central Plains ($P\,0.040$, 95% CI -0.125 to -0.002). This
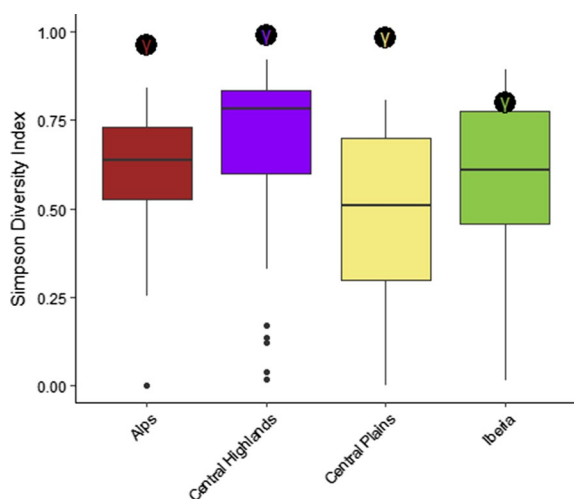
Fig. 5 Genus diversity (Simpson diversity index) in each region. The boxplots show the α-diversity (local diversity) while the black circles show the γ-diversity (regional diversity)

indicates a consistently low cover of coniferous forest in all the regions but in the Alps.

Regarding the EPT community structure across the four regions (Fig. 5), there was no clear relationship between diversity at any scale and SFP. Regional or γ-diversity was high in every region, but slightly lower in Iberia (Alps = 0.96; Central Highlands = 0.99; Central Plains = 0.98; Iberia = 0.80). Local diversity or α-diversity was more variable, being lower in the Central Plains (Alps = 0.58; Central Highlands = 0.67; Central Plains = 0.47; Iberia = 0.59). Hence, genus turnover or β-diversity was higher in the Central Plains (Alps = 1.66; Central Highlands = 1.48; Central Plains = 2.10; Iberia = 1.66) indicating a higher variability of the EPT community across the region. These values show no direct relationship with the mean regional SFP (Alps = 12.2; Central Highlands = 12.7; Central Plains = 13.0; Iberia = 12.6), indicating that the SFP captures the differences on dispersal abilities regardless of the particularities of each EPT community.

The main hypothesis on the regional differences of the negative effect of deciduous forest on the EPT community dispersion ability was supported by the results as this effect appeared just in two of the regions: Central Highlands and Iberia (Table 1, Fig. 6). Furthermore, in those two regions, the deciduous forest cover was not correlated with any of the other significant predictors in these two GLMs, indicating that the SFP index is unambiguously reacting to changes in the deciduous forest cover. In the

Table 1 Resulting models after the backward selection of predictors (GLS for the Central Plains and GLMs for the other regions)

	Estimate	Std. Error	z value	P value
Central Plains				
Intercept	6.449	0.859	7.510	<0.001
Saprobic pollution	2.710	0.442	6.135	<0.001
Site naturalness	2.523	0.466	5.416	<0.001
Catchment anthropization	−1.517	0.566	−2.679	0.010
Central Highlands				
Intercept	18.586	1.573	11.816	<0.001
Deciduous vegetation cover	−2.167	0.612	−3.541	0.001
Saprobic pollution	−1.818	0.722	−2.519	0.016
Site naturalness	−2.932	0.746	−3.930	<0.001
Iberia				
Intercept	13.149	0.326	40.321	<0.001
Coniferous vegetation cover	6.522	2.134	3.056	0.005
Deciduous vegetation cover	−2.542	1.026	−2.477	0.020

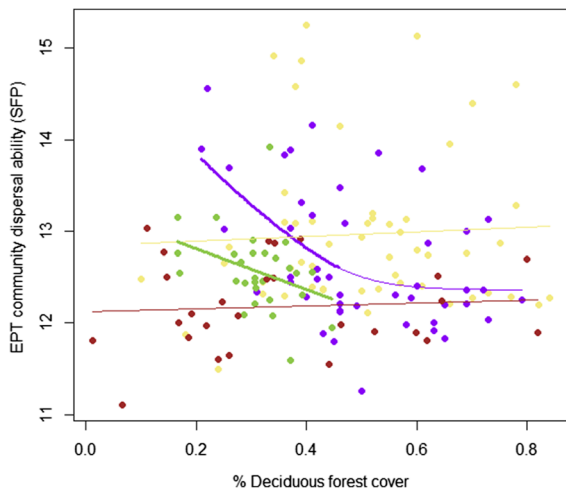There are no values for the Alps as no predictor was found significant

Fig. 6 Relationship between EPT community dispersal ability and deciduous riparian forest cover by region. The lines show linear regression models (LM) for Alps, Central Plains and Iberia regions and an additive model (GAM) for Central Highlands. The bold lines indicate a significant relation between both parameters

Central Highlands GLM deciduous forest was not correlated either with Saprobic pollution (Pearson's $r(43) = 0.24$, $P = 0.107$) or with Naturalness (Pearson's $r(43) = -0.14$, $P = 0.372$). In the Iberia GLM deciduous forest was not correlated with coniferous forest (Pearson's $r(26) = 0.53$, $P = 0.600$). The Central Plains model did not meet the required assumptions so a GLS including a rational quadratic structure to reduce the spatial autocorrelation was run instead. No effect was found significant in the deciduous forests of the Central Plains and Alps regions, nor in the combined deciduous and coniferous forests of the Alps. As predicted, the effect of the riparian forest

was weaker in the Alps region and stronger in the Iberia region. Several environmental stressors were co-correlated in some of the regions (Table 2): As expected, Saprobic Pollution and Site Naturalness were negatively correlated (except Iberia, where there was no statistically detectable correlation); Saprobic Pollution and Catchment Anthropization were also correlated in 3 of 4 regions (except Central Plains); Site Naturalness and Catchment Anthropization were negatively correlated only in the Alps.

The second hypothesis on the positive effect of coniferous forest on EPT community dispersion ability was only partly supported by the results. Coniferous forest was a significant predictor for the SFP in the Iberia region (Table 1) but not in any of the other three regions. Also, non-native forest did not show any significant effect on the EPT community in the Iberia region.

The third secondary hypothesis on the non-linearity of the effect of deciduous forest cover on EPT community dispersal ability was backed up for the Central Highlands region. Although the comparison between the GLM and the GAM does not show significant differences ($P = 0.124$), upon visual inspection it seems clear that the relationship between both parameters is not linear. The slope of the trend line was negative and significantly different from zero up to a medium deciduous forest cover of 46%. A backward selection of predictors was performed over a GLM using the data subset covering the sampling points from the Central Highlands region with a Deciduous forest cover value lower than 46% ($n = 19$). The Deciduous vegetation cover (Estimate $= -3.995$, Std. Error $= 1.726$, $z = -2.315$, $P = 0.034$) and the Site naturalness (Estimate $= -2.206$, Std. Error $= 0.611$,

Table 2 Co-correlation tests ($r =$ Pearson's r, $P =$ significance level; df $=$ degrees of freedom) between the environmental stressors (Saprobic pollution, catchment anthropization, site naturalness, elevation) for each region

	Central Plains		Central Highlands		Alps		Iberia	
	(df = 51)		(df = 43)		(df = 25)		(df = 26)	
	r	P	r	P	r	P	r	P
Saprobic pollution × Site naturalness	**−0.78**	**<0.001**	**−0.85**	**<0.001**	–	–	–	–
Site naturalness × Catchment anthropization	0.11	0.432	−0.28	0.151	–	–	–	–
Saprobic pollution × Catchment anthropization	−0.02	0.879	**0.35**	0.019	**0.44**	0.023	**−0.39**	0.040
Saprobic pollution × Elevation	–	–	–	–	**−0.58**	0.002	0.27	0.167
Elevation × Catchment anthropization	–	–	–	–	**−0.40**	0.037	−0.28	0.155

Statistically significant differences are in bold

$z = -3.608$, $P = 0.002$) were determined to be significant predictors of the SFP. In the Iberia region, there were no significant differences between the GLM and the GAM ($P = 0.999$) and the relation between parameters remained linear.

Finally, it could not be confirmed that the magnitude of the effect of deciduous forest on the SFP community dispersal ability is different between the Central Highlands and the Iberia regions. Although the regression coefficient for the deciduous forest cover as a predictor of the SFP indicated a stronger effect in the Central Highlands (Central Highlands = −3.995, Iberia = −2.542), the difference is very small.

Discussion

The results of this study support the principal hypothesis: the effect of riparian forest on the EPT community differs across regions. First of all, a riparian buffer covered by native woody vegetation can lead to an increased proportion of weak dispersers in the EPT community. Second, that effect is region dependent, as the riparian forest does not always drive the EPT community structure. Both conclusions were derived, at least partially, in a previous study in Germany (Peredo Arce et al., 2023) and expanding the dataset to other regions confirmed both aspects. Nevertheless, the reasons behind the regional differences are yet to be explored.

On the one hand, no effect of the riparian forest, assessed separately by forest type or combining every type of forest, was detected in the Alps region. This can be explained by the particularities of the Alpine landscape and the regional pool of EPT species. Above the 2000 m a.s.l. woody riparian vegetation is scarce and small (e.g. *Alnus alnobetula* and *A. viridis*) or above the tree line non-existent (Mac Nally et al., 2008; Körner & Körner, 2012). Below that elevation the riparian forest is composed mostly of deciduous species (mainly *Alnus incana*) that are gradually mixed with coniferous trees. This is, the structure of the riparian vegetation is very heterogeneous, being likely that the EPTs are not as dependent on a specific structure (ie. continuous deciduous riparian forest) as they can be in other regions. Moreover, the EPT species pool is different to what is found in the other study regions, dispersion-wise: in the

Alps region most of the EPTs present are weak dispersers (Brittain, 1990; Engelhardt et al., 2011). This indicates that EPT dispersal is different in the Alps, as the EPT species do not have an apparent need for functional traits typically associated with strong dispersal abilities. Hence, it is to be expected that the main drivers of the EPT dispersal are others, namely wind (Zwick, 2009; Epele et al., 2021) and topography (Hoppeler et al., 2016; Schröder et al., 2022) instead of riparian forest.

On the other hand, native riparian forest increased the proportion of weak dispersers in the EPT community in the Iberia region, even as native riparian forest cover was generally scarce (Ferreira & Aguiar, 2006). This is likely to be caused by the riparian forest increasing local humidity and decreasing air temperature (Kail et al., 2021), as both factors are known to increase EPT adult lifespan (Nebeneker, 1971; Collier & Smith, 2000; Briers & Gee, 2004). As the Iberia region is located in the Mediterranean climate zone, characterized for its dry and hot summer, logically the effect of riparian forest on local climatic conditions can be particularly relevant. Moreover, it is known that in intermittent rivers in dry regions merolimnic macroinvertebrates use humid landscape features as pools (Cañedo-Argüelles et al., 2015) or caves (Salavert et al., 2008) as stepping stones to disperse and survive periods of drought. Finally, non-native vegetation did not contribute to the increase of weak dispersers and the coniferous cover had the opposite effect, potentially acting as a dispersal barrier (Hering et al., 1993; Peredo Arce et al., 2023). Given that these forests also decrease air temperature and increase air humidity, it is likely that coniferous and non-native forests do not provide another key service for EPT dispersion, as provision of suitable microhabitats for the adults (Rupprecht, 1982; Smith & Collier, 2000; Tierno de Figueroa et al., 2019).

In the Central regions we found dissimilar results for the Plains and the Highlands. This is not surprising as the same data was previously analyzed with similar results in Peredo Arce et al. (2023). As expected, deciduous riparian forests increased the proportion of weak dispersers in the Central Highlands but not in the Plains, where the EPT community did not show any response to vegetation cover (Fig. 6). EPTs are particularly sensitive to environmental stressors (Schletterer et al., 2010), meaning that in highly

degraded areas the effect of riparian forest could be completely masked by those stressors. That is often the case of lowland areas (Palt et al., 2023), like the Central Plains region in this study, as the mean value for Saprobic pollution was higher than in the Central Highlands and the site naturalness mean value was lower. Hence, even in geographically close regions, it is possible to find differences in the effect of riparian forest over EPTs due anthropogenic disturbance (Schletterer et al., 2010). Finally, the difference in the effect of the forest in the Central Highlands compared to the Iberia region is not strong enough to draw clear conclusions. As the difference is relatively small, we cannot rule out that the magnitude of the effect is the same in both regions and we cannot either dismiss that it is not an artifact caused by the small sample size.

The effect of the forest and the differences found between the four regions are likely connected with the particular characteristics of the regional pool of species and the riparian vegetation. The EPT communities in the Central regions are easy to compare, as both regions are adjacent. Maybe as a consequence of the higher overall degradation, the EPT community in the Plains is less diverse and made up of stronger dispersers (Fig. 4). This can be interpreted as a community dominated by pioneer species, more able to survive and recolonize sub-optimal habitats which do not rely on riparian forest to disperse. Both in the Central Highlands and the Iberia region the characteristics of the forest indicate that non-native non-natural vegetation cannot substitute the native riparian forest, despite the provision of similar services regarding microclimatic conditions (Dugdale et al., 2018). In the Alps region, the EPT pool of species differs greatly from other regions (Fig. 4) indicating that dispersal traits are less relevant, maybe because other factors as wind or topography drive the community structure (Bertin et al., 2015; Ptatscheck et al., 2020) as they do not react to changes in riparian vegetation cover. In sum, depending on the characteristics of the ecosystem, some EPT communities do not rely on forests to disperse, but those that do may heavily rely on native riparian vegetation.

An alternative explanation for the differences found between regions is that they could be caused by differences in the characteristics of the data analyzed (Fig. 2). Given that the index used to measure the dispersal abilities of the EPT community is based on functional traits, differences in the regional pool of species directly caused by the elevation, geology or substrate should not have any effect on the outcome of our analyses. Nevertheless, other local characteristics not considered in this study due a lack of data, such as the strength and direction of dominant winds or the season when the macroinvertebrate were sampled, could impact the EPT community and its dispersal. Stream size is a factor that should be taken into account, although in this study the existing differences on stream size between regions should not significantly impact the outcome for three main reasons: first, the differences in Strahler order are relatively small and can be caused by differences in the resolution of the river network between regions, as the river network of the Alps region has a particularly high resolution (Paillex et al., 2020). Second, as a proxy for stream size, catchment area does not take into account the relative discharge. The discharge depends partially on the climate, so for a catchment of a similar size, a stream will be bigger in a wetter region (as the Central regions; Cornes et al., 2018) and smaller in a drier region (as the Iberia region; Cornes et al., 2018). Third, the effects of riparian vegetation are expected to be stronger on smaller streams, as a closer forest would create stronger effects on the microclimatic conditions and would provide relatively more shelter (see also Allen, 2016). On the one hand, in the Iberia region the streams appear to be bigger than in other regions, but we still found a positive effect of the riparian forest on the EPT community. On the other hand, in the Alps the smaller streams are most commonly found at higher elevations, where riparian vegetation is scarce or non-existent. This fits the hypothesis that the effect of the riparian vegetation would be stronger in arid regions and weaker in high mountains. In sum, the differences on the considered stream characteristics between regions are relatively mild and should not have a strong impact in the results of this study.

Overall, we conclude that regional characteristics of the landscape and regional pool of species has to be considered when assessing the role of the EPT community drivers (He et al., 2022). We should not assume that the same features or conditions are equally important in every region. Hence, every assessment on the provision of services by riparian forest, either to study an ecological process or to

consider conservation and restoration measures, has to be done regionally.

The EPT community is particularly important to measure the quality of riverine ecosystems but the effect of dispersal to explain their community structure has been traditionally neglected (Downes et al., 2017; Tonkin et al., 2018), leading to a lack of results after the restoration of river habitats for no apparent reason (Rupprecht, 2009). Considering the restoration and conservation of riparian forest, prioritizing it in certain scenarios could directly translate into more natural communities of macroinvertebrates and better ecological status for many streams. In this sense, it is key to know where and when to prioritize the conservation and restoration of the riparian forest.

For example, in the Mediterranean and other arid regions, which are particularly vulnerable to the effects of climate change as flow regime is decreasing, intermittency of rivers increasing (De Girolamo et al., 2022), and water temperatures rising (Alba-Tercedor et al., 2017), prioritizing the conservation of the native riparian forests that can act as refugia for EPTs is a sensible conservation strategy, particularly given the need of EPTs for aerial dispersal corridors when streams temporarily dry out (Graham et al., 2017). Furthermore, riparian forests could provide migration pathways for species sensitive to climate change, allowing them to access more favorable climatic conditions (Alba-Tercedor et al., 2017). Despite this, our results indicate that such migrations are unlikely to occur in mountain EPT species that are particularly sensitive to climate change (Brown et al., 2007), as their dispersal is not impacted by riparian forest. Moreover, in regions where the human impact on riverine and riparian ecosystems is particularly strong, other strategies probably need to be prioritized in order to achieve a good ecological status for freshwater ecosystems.

Finally, riparian forest provides an important spawning habitat for some species (e.g. drumming stoneflies—Rupprecht, 1982; Tierno de Figueroa et al., 2019) as well as food resources (Smith & Collier, 2000). Our results show the particular relevance of native riparian forest, which could be explained by the provision of these services. Moreover, they provide additional reasons to prioritize natural riparian forest conservation, particularly in regions where invasive plant species are widespread, such as Iberia (Castro-Díez & Alonso, 2017).

We strongly advise to consider the function of riparian forest as dispersal corridors and to understand such forests as integral elements of the rivers which need to be managed altogether. A more precise knowledge of EPT communities in different regions, understanding their main threats but also their adaptations to local conditions, can assist in identifying the best management strategies to improve the quality of rivers and the preservation of mayflies, stoneflies and caddisflies.

Data availability Data is available from the authors upon reasonable request.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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