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ORIGINAL RESEARCH

# Anthropogenic disturbance and alien plant invasion drive the phylogenetic impoverishment in riparian vegetation

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## Abstract

Anthropization worldwide is increasingly homogenizing biodiversity, i.e., impoverishment of phylogenetic and functional diversity. This study aimed to assess plant phylogenetic relationships of riparian communities in anthropogenically disturbed and undisturbed sites across Continental Portugal. For the analyses, we used 947 species distributed in 205 undisturbed sites and 180 disturbed sites sampled in 100 m plots distributed throughout the country. Then, we assessed the phylogenetic diversity and structure, evolutionary distinctiveness (ED), and conservation of functional traits (life forms) and geographic origin (alien or native) in each site. Our findings. Indicated a higher phylogenetic diversity (higher scores for PD, MPD, MNTD and their standardized effect size) and ED in the undisturbed sites compared to the disturbed ones. The lower phylogenetic diversity in the disturbed sites also relates to the phylogenetic conservatism we found for the lineages of alien and hydrophyte species, which increases the diversity homogenization in those sites. On the other hand, we also recorded higher aliens' ED for the undisturbed sites. Based on the results, we conclude that although the undisturbed sites still harbor higher phylogenetic diversity, they also require monitoring to track the spread of alien species from phylogenetic distant lineages (i.e., high ED) that might thrive in the native communities.

**Keywords** Biodiversity homogenization · Evolutionary distinctiveness · Phylogenetic conservatism · Life forms · Alien species

## Introduction

Anthropization causes changes in the composition and structure of biological communities in distinct ecosystems, thus enhancing biodiversity loss and homogenization (Rogan and Lacher Jr 2018; Wilkinson et al. 2018). Consequently, homogenized biological communities typically harbor a low diversity of species adapted to harsher environmental and

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Extended author information available on the last page of the article anthropized conditions (Elton 1958; Gerhold et al. 2011; Rogan and Lacher Jr 2018). Such a reduced diversity affects the resilience and functioning of ecosystems (e.g., depauperate maintenance of key services like soil nitrogen fixing and water flow) (Rogan and Lacher Jr 2018) and prompt biological invasion of native communities by invasive alien species (IAS) (McKinney and Lockwood 1999; Cui et al. 2019; Cubino et al. 2020; Daru et al. 2021). Then, the assembly of communities in response to anthropized and harsher abiotic conditions will also depend on the phylogenetic relatedness between species and their shared functional traits (i.e., morphology, life form) (Cavender-Bares et al. 2009). The urgency for investigating such influence of anthropization on biodiversity at a broad scale in ecosystems worldwide is warned by several scientists (Le Bagousse-Pinguet et al. 2019).

Combining phylogenetic relatedness and functional trait data is promissory to investigate and monitor plant diversity under distinct environmental conditions (e.g., disturbed or undisturbed) (Winter et al. 2009; Gerhold et al. 2015b; Tucker et al. 2017). Amongst the most efficient and easily applicable approaches, tests of phylogenetic signals allow one to evaluate whether a trait (e.g., life and growth forms) is evolutionarily conserved in the species' lineages and affects the community phylogenetic diversity (Losos 2008; Münkemüller et al. 2012; Diniz et al. 2021). For instance, tests of phylogenetic signal can derive information on the phylogenetic conservation of lineages of set of species (e.g., alien plants), which can be used as indicators of the set of species with a higher potential of leaving their phylogenetic signature in the community structure (i.e., clustering - low phylogenetic diversity or overdispersion - high phylogenetic diversity) (Fritz and Purvis 2010; Münkemüller et al. 2012; Diniz et al. 2021). In addition, by measuring the individual contribution of species in for community evolutionary distinctiveness (i.e., level of endemism or singularity), we can assess the phylogenetic signature of each species across varied environmental conditions (Cadotte and Davies 2010; Cadotte et al. 2010; Edwards et al. 2017). These combined approaches allow one to draw a prognosis on the effects of land use in plant communities in regions under high threat by biodiversity homogenization (Winter et al. 2009).

Plant communities under a strong disturbance and abiotic pressure usually retain a lower phylogenetic diversity, since they shelter a selected group of species that may has conserved their functional adaptations in their evolutionary lineages (Ackerly 2004; Ding et al. 2012; Coyle et al. 2014; Smith et al. 2022). This happen because species sharing recent ancestors may resemble more in functional traits adapted to a condition than distant relatives (Losos 2008). Thus, species without conserved functional traits adapted to specific environmental filters (e.g., anthropogenic disturbance) might be outperformed competitively by others and excluded from the community (Emerson and Gillespie 2008; Lv et al. 2024). On the other hand, undisturbed communities may present higher phylogenetic diversity due to their more suitable environmental conditions that allows harboring functionally and phylogenetically distant (e.g., convergent) species with conserved traits (Grime 2006; Chun and Lee 2019). Consequently, undisturbed sites may have higher functional and phylogenetic endemism (i.e., evolutionary distinctiveness) than the disturbed ones (Kessler 2006; Thorn et al. 2020; Marshall et al. 2022).

When assessing the levels of phylogenetic diversity and endemism for both the species pools of alien and native species in disturbed versus undisturbed sites, it is important to verify whether the species are conserved in their evolutionary lineages. Disturbed sites tend to favor the dominance of alien native species with conserved traits that are competitively superior to the native ones (Kulmatiski 2006; Strauss 2006). However, undisturbed sites might offer favorable conditions (e.g., moderate temperature ranges) for sheltering alien and native species with similar traits (Tecco et al. 2010). In this case, the species (alien or native) with conserved traits reflecting the best competitive capabilities and lacking natural enemies thrive in the community (Elton 1958). Further, at undisturbed sites the aliens from lineages representing a high degree of evolutionary endemism might succeed in enhancing their phylogenetic diversity over the natives (Gerhold et al. 2011; Bezeng et al. 2015). Overall, it is still very poorly understood the levels of phylogenetic endemism of alien and native species assessed in both disturbed and undisturbed communities.

Despite the global concerns about functional and phylogenetic diversity loss, it remains poorly understood for several types of ecosystems how anthropogenic disturbances (e.g., urbanization, agriculture, hydro-morphological changes, water waste, climate change) drive this diversity across large regions and determine levels of biotic homogenization (Abadie et al. 2011; Fulton et al. 2019; Saladin et al. 2020; Cordier et al. 2021; Tretyakova et al. 2021; Ge et al. 2022). For riparian and riverine plant communities, this knowledge gap is more pronounced regarding the effects of anthropogenic-induced hydro-morphological disturbance (e.g., discontinuity in streamflow regime) on their functional and phylogenetic diversity (Vukov et al. 2022) (Lozanovska et al. 2020). Enhancing the understanding of this relationship between anthropogenic disturbances and phylogenetic diversity is crucial for anticipating its effects on future species distributions and controlling biodiversity homogenization (Saladin et al. 2020; Kalusová et al. 2021).

The impact of anthropogenic disturbance on biodiversity in riparian ecosystems in the region of the large Mediterranean basin recorded massive alien plant invasion over the last decades (Ferreira and Aguiar 2006; Stella et al. 2013; Aguiar et al. 2018; Lozanovska et al. 2020). Although the Mediterranean area relative to the Iberian Peninsula (IF) shelters the most persistent plant diversity in Europe and represents a refugium of high beta phylogenetic and functional diversity, it also holds a favorable niche for several invasive alien species (Morais et al. 2017; Saladin et al. 2020). For instance, continental Portugal has recorded intense alien plant invasion in disturbed sites of both terrestrial and aquatic communities (Vicente et al. 2010; Morais et al. 2017; Pabst et al. 2022; Plantas invasoras em Portugal 2022). However, we emphasize a lack of studies assessing the plant phylogenetic relationships and functional traits (e.g. growth forms, dispersal types) in anthropogenically disturbed (e.g., discontinued streamflow regime, enhanced soil erosion) versus undisturbed riparian plant communities in Mediterranean ecosystems (e.g., Continental Portugal) and the whole Europe (Lambdon 2008; Lososová et al. 2015; Funk et al. 2016; Liendo et al. 2016a, 2021). Particularly, in Continental Portugal, such studies remain unexplored.

In this study, we aimed to investigate the phylogenetic relationships (i.e., diversity, distinctiveness, and trait and lineage conservation) of species in riparian plant communities in two types of sites, anthropogenically disturbed and undisturbed, across Continental Portugal. Specifically, we analyzed their phylogenetic diversity and structure, evolutionary distinctiveness, and conservation of functional traits and geographic origin (alien or native). We hypothesized opposite phylogenetic patterns between disturbed and undisturbed sites: (a) disturbed sites hold lower phylogenetic diversity (i.e., clustered communities) and trait conservation, while (b) undisturbed sites present higher phylogenetic diversity (i.e., overdispersed communities) and trait conservation; (c) alien and native species present phylogenetically conserved lineages and traits (i.e., life forms) in both sites; (d) undisturbed sites harbor higher evolutionary distinctiveness, i.e., endemism, than the disturbed sites.

# Materials and methods

## Study area and sampling

The study sites are distributed over Continental Portugal, Iberian Peninsula (Fig. 1), between 37 and 42º N and 6–9º W. The climate in Portugal encompasses a marked latitudinal gradient but is predominantly Mediterranean, with mild winters and dry summers, except for some mountainous areas and its occidental northwestern part. Among the main environmental impacts, agriculture, industry, and cities predominate in the coastal areas, and agricultural crops are widespread in the South and Eastern regions. Further, anthropogenic disturbances in fluvial areas are mostly related to hydromorphological alterations such as water diversion, water regulation, forestry (e.g., monocultures), and urban land use in adjacent areas. Thus, following the requirements of the Water Framework Directive (WFD, EU/2000/60) (European Council 2000), a sampling network was established that included classifying them as reference (least disturbed sites) and non-reference (impacted by anthropogenic activities) (Instituto da Água 2012). The criteria we adopted to classify the reference sites follow the methodological procedure accounting for human disturbance proposed by Pont et al. (2006a). In short, this procedure considered sites as references those reflecting totally or nearly undisturbed conditions for the following features: morphological conditions and

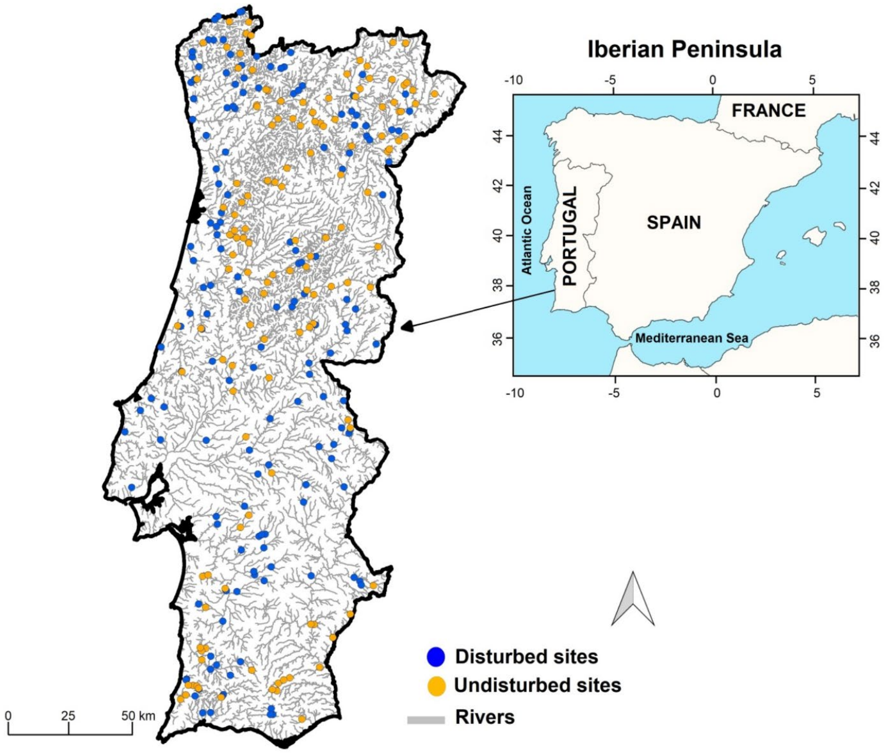

**Fig. 1** Location of Portugal in the Iberian Peninsula and distribution of the study sites (disturbed and undisturbed)

regime of the hydrology of the river streams, organic contamination, nutrient enrichment, sediment load, acidification, and toxicity, riparian zone integrity, minimal land-use (including urban areas) in the water catchments area. Then, these features are ranked from 1 (no obvious deviation from the reference condition, minimally disturbed) to 5 (highly impacted) (Pont et al. 2006). Hereafter, we refer to the term "disturbed" for describing conditions related to the study sites under the effects of anthropogenic disturbances determined according to the classification criteria (Pont et al. 2006).

We included samples of all plant species surveyed to each site category (disturbed and undisturbed). In each site, the plant surveys were made by wading upstream in a zig-zag manner across the channel or by walking in banks along a 100 m length of the river (Aguiar et al. 2000). We used 205 reference (non-disturbed) and 180 non-reference sites (disturbed) with the composition of plant communities sampled in the whole fluvial corridor (banks and river channels) and encompassing aquatic macrophytes, i.e., all higher aquatic plants and plants associated with the fluvial system, including vascular plants, bryophytes, and macroalgae. Each plant species also had their percentage cover estimated. The most dominant trees were alder *Alnus glutinosa* (L.) Gaertner), ash (*Fraxinus angustifolia* Vahl. ssp. *angustifolia*), willows (mostly the *Salix atrocinerea* Brot., *S. alba* L., *S. salviifolia* Brot.), and black poplar (*Populus nigra* L.). The most frequent riparian shrubs were hawthorn (*Crataegus monogyna* Jacq.), black elder (*Sambucus nigra* L.), dyer's buckthorn (*Frangula alnus* Mill.), and tree heath (*Erica arborea* L.). For further details on the sampling procedures (e.g., ecological quality, season, plant species coverage) and species dominance, please see Aguiar et al. (2009).

## Climatic data

Since the sampled sites are widely spread across the Continental Portugal, which encompass great environmental variability, we added climatic variables in our statistical models (see Section Statistical Analysis) to account for possible influence of environmental differences between disturbed and undisturbed sites when comparing their phylogenetic indices (see next section). For that, we acquired data on the 19 bioclimatic variables from the WorldClim database version 2 at a very high spatial resolution (approximately 1 km2) (Fick and Hijmans 2017). We extracted these bioclimatic variables for our sites using the worldclim_country function from the geodata R package (Hijmans et al. 2024). From the 19 variables, we selected and used in the models only the ones with acceptable level of correlation, i.e., Pearson coefficients $<0.70$ (Dormann et al. 2013). This aimed to avoid biased models due to multicollinearity. Therefore, our final set of climatic variables was composed of mean diurnal range, isothermality, temperature seasonality, minimum temperature of coldest month, and precipitation seasonality.

## Phylogenetic reconstruction, diversity, and structure

First, we pruned the megatree GBOTB.extended (Jin and Qian 2019) to all the 947 taxa distributed in the disturbed and undisturbed sites using the phylo.maker function from the V. PhyloMaker package (Jin and Qian 2019) in R version 4.2.2 (R Development Core Team 2022). Then, we created the data frame of this mega-tree using the function build.nodes.1, which extracts the largest cluster's root and basal node information at the genus or family level (Jin and Qian 2019). With this data frame, we generated a phylogenetic tree under phylogenetic scenario 3 (Qian and Jin 2016) by binding the tip for a new genus between the family root node and basal node to the midway point of the family branch. Scenario 3 may favor higher phylogenetic resolution by producing phylogenies with most species fully phylogenetically resolved (Qian and Jin 2016).

In order to analyze phylogenetic dissimilarity across the disturbed and undisturbed sites, we used the aforementioned generated phylogeny to calculate an evolutionary PCA (Principal component analysis) using the function evoPCAHellinger of the package adiv (Pavoine 2020) based on Hellinger distance (Rao 1995; Pavoine 2016). The Hellinger distance normalizes data by centering the data of the community matrix based on either the abundance or presence or absence of the species in the sites (Rao 1995). Thus, the output of evoPCAHellinger enables the investigation of phylogenetic patterns along distinct gradients, e.g., environmental conditions and levels of disturbance (Pavoine 2016). Then, we accounted for the individual contribution of the study sites and species to the variance in the evoPCA by decomposing the inertia for its axes using the function inertia.dudi of the package ade4 (Dray and Dufour 2007).

With the mentioned generated phylogeny, we also computed the metrics of phylogenetic diversity and structure for all sites (disturbed and undisturbed). For that, we calculated all pairwise phylogenetic distances between all species co-occurring within those sites as observed MPD (mean pairwise phylogenetic distance) and MNTD (mean nearest taxon distance), and their ses (standardized size effect) (sesMPD and sesMNTD) using the functions ses.mpd and ses.mntd in picante package, respectively (Kembel et al. 2010). We calculated sesMPD and sesMNTD using 10,000 randomizations under the null model phylogeny pool (i.e., unconstrained null model; (Kembel and Hubbell 2006), which randomizes the community data matrix by drawing species from the entire species pool with equal probability of being included in the random community. Therefore, using this null model to calculate the metrics allows for obtaining more consistent inferences on the drivers of community assembly (Swenson 2014). The two types of metrics provide complementary phylogenetic information. MPD is a metric more sensitive to phylogeny-wide (i.e., entire phylogeny including older clades and nodes) patterns of phylogenetic clustering and overdispersion. MNTD is more efficient in detecting the patterns closer to the tips of the phylogeny (i.e., shallower clades from more recent evolutionary history) (Webb et al. 2002). The larger the value for MNTD and MPD, the larger the phylogenetic distance between a pair of taxa co-occurring in a site. We considered outputs of ses (standardized size effect) of these metrics to draw interpretations on community (i.e., site level in our case) phylogenetic structure. Significant positive values for sesMPD and sesMNTD indicate phylogenetic overdispersion, while negative values indicate higher phylogenetic clustering than expected by chance.

We calculated the phylogenetic diversity for the sites using the function ses.pd in the picante package, which returns the observed PD, i.e., the sum of the branch lengths in a phylogenetic tree, and its standardized size effect (ses). Significant positive values for sesPD indicate higher phylogenetic diversity, while negative values indicate lower phylogenetic diversity than expected by chance. To calculate sesPD, we also ran 10,000 randomizations under the null model phylogeny pool, which provides an unbiased measure of PD by diluting its correlation with species richness when comparing the observed values with the randomized ones (Swenson 2014).

## Phylogenetic signal

We applied the D statistics of Fritz and Purvis (2010) as a measure for phylogenetic signal (i.e., evolutionary conservation) strength based on the sum of sister-clade differences in our phylogeny. The D statistics allowed us to test for the phylogenetic conservatism of the species life forms (Hygrophyte, Terrestrial, Helophyte, and Hydrophyte) and their geographical origin (alien or native species). For that, we assigned the number 1 in our dataset for species having a life form or being alien and the number 0 for species not having these attributes. The D statistics measures the level of phylogenetic clumping under a given binary trait or condition (e.g., extinction risk), i.e., the lower sum of sister-clade differences leads to stronger phylogenetic clumping (i.e., signal) of traits or conditions (e.g., disturbed site). Conversely, higher differences in traits or conditions indicate a strong phylogenetic overdispersion, i.e., weak or absent phylogenetic signal (Fritz and Purvis 2010). In short, this measure tests whether the estimated D value shows a significant departure from random and clumped phylogenetic association under a Brownian evolution model (BM). We calculated D for species life form and geographic origin by using the function phyo.d from the caper package (Orme et al. 2018), which returns results based on two models: (a) phylogenetic randomness: trait values randomly shuffled relative to the tips of the phylogenetic tree and D; (b) Brownian threshold model: uses an estimated threshold to determine the relative prevalence of the observed trait. Values of D smaller than 0 indicate a highly conserved trait or condition (i.e., stronger phylogenetic signal), while greater than 1 represent high overdispersion (Fritz and Purvis 2010).

## Evolutionary distinctiveness

To evaluate species uniqueness (i.e., phylogenetic endemism) in the disturbed and undisturbed sites, we extracted evolutionary distinctiveness (ED) scores from our phylogenetic tree. ED is a metric that indicates how much unique evolutionary history a species contributes to a phylogenetic tree, i.e., combined evolutionary and spatial features for investigations on the distribution patterns of biodiversity and identification of hotspots (Rosauer et al. 2009; Cadotte and Davies 2010; Cadotte et al. 2010). Species with high values of ED indicate that they have no extant close relatives, whereas the ones with low values of ED have close extant species (Isaac et al. 2007; Edwards et al. 2017). Thus, one can assume that species with high ED scores are potentially more functionally and genetically distinct than the others with moderate- or low-ranked scores (Cadotte et al. 2008; Redding et al. 2010).

## Phylogenetic resolution

Our phylogeny, generated as aforementioned, contained 947 tips and 809 internal nodes, corresponding to 85.54% of resolved taxa and 14.46% of unresolved taxa. This presence of unresolved taxa in a phylogeny, i.e., more than two taxa per node (polytomy), may result in the underestimation or overestimation of the phylogenetic diversity and dispersion (clustering and overdispersion patterns) due, respectively, to the loss of terminal resolution or by the increase in the total phylogenetic tree length (Swenson 2009). This 14.46% of the unresolved taxa in the originally reconstructed phylogeny could still eventually influence the outcomes of the phylogenetic diversity and dispersion measures of phylogenetic structure metrics (Swenson 2009). Considering this possible limitation of the resolution, we extracted a resolved phylogeny by randomly generating 10,000 fully bifurcated phylogenies into a series of dichotomies using the algorithm bifurcatr of the package PDcalc (Nipperess and Wilson 2020). The backbone of the ifurcatr comprehends a modification of the approach of Rangel et al. (2015), which resolves polytomies into rooted (ultrametric phylogenies) by randomizing both polytomies and branch lengths in order to adjust the length of the descendent edges and preserve ultrametricity.

With the fully bifurcated and resolved (without polytomies) phylogeny, we additionally calculated all metrics (PD, MPD, MNTD, and their ses - standardized size effects) again. Then, we performed regression analysis to obtain slopes and coefficients between the metrics from the unresolved phylogeny (containing polytomies) and the resolved phylogeny. These slopes and coefficients provide a statistical overview of how much the unresolved taxa in the originally unresolved phylogeny could influence phylogenetic dispersion (i.e., clustering or overdispersion) (Swenson 2009). Values equal to 1 for the coefficients and slopes indicate a perfect correlation between the metrics from resolved and unresolved phylogeny, i.e., lack of phylogenetic resolution does not bias the outcomes of phylogenetic metrics. Conversely, slopes different from 1 represent over- or underestimation of phylogenetic dispersion, while correlation coefficients smaller than 1 indicate that lack of phylogenetic resolution does influence the outcomes of phylogenetic dispersion (Swenson 2009).

## Statistical analysis

Within each of the sites within disturbed and undisturbed conditions we tested whether the means of sesMPD and sesMNTD were significantly different from zero using the One Sample T Test, i.e., test of significance for the found phylogenetic pattern (clustering or overdispersion) demonstrated by the mean. We then compared the average of observed MPD and MNTD between different sites within each of these conditions (disturbed and undisturbed) using the Welch Two Sample T-test. This comparison of observed MPD and MNTD aimed to test if their averages were significantly higher (high phylogenetic overdispersion) or lower (high phylogenetic clustering) between these two types of sites and within them. Additionally, we conducted linear models (LM) with the observed and ses versions of PD, MPD and MNTD as dependent variables and including as predictors the site type (disturbed and undisturbed) and the previously selected climate variables (mean diurnal range, isothermality, temperature seasonality, minimum temperature of coldest month, and precipitation seasonality). The use of these additional models aimed to compare the trends of the phylogenetic metrics between site types while accounting for the effects of their climatic variables. We assessed the reliability of the models through the residual plots, evaluating parameters such as normality adjustment (Q.Q. Plot) and frequency of distribution of residuals. All models were well adjusted, demonstrating independence of the residuals. The overall significance of the effects of predictor variables on phylogenetic metrics was assessed using the Anova function of the car package (Fox and Weisberg 2019). Finally, we compared the average ED between the disturbed and undisturbed using a Wilcoxon rank sum test with continuity correction (W). We conducted all these tests in R 4.2.2.

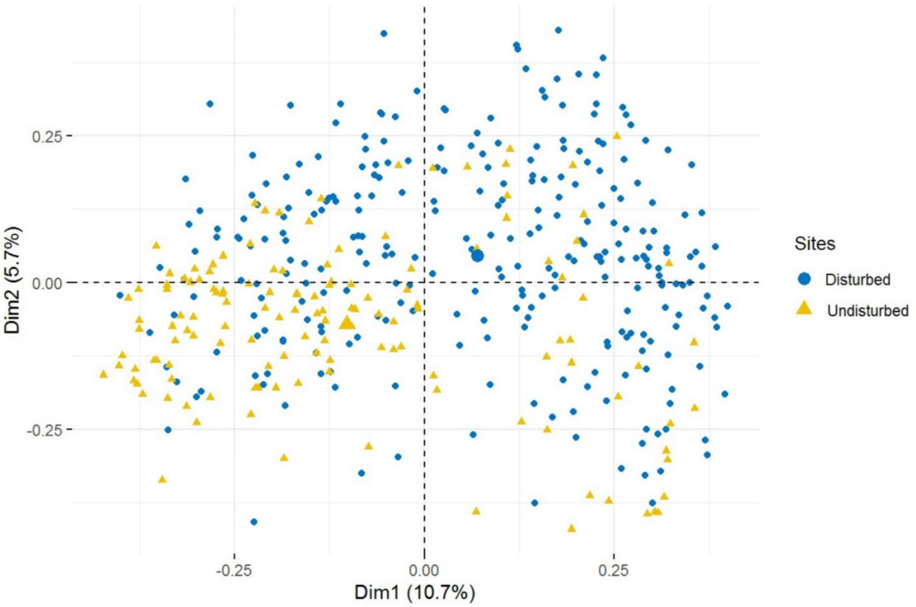

**Fig. 2** Phylogenetic diversity dissimilarity across the disturbed and undisturbed sites demonstrated by evolutionary principal component analysis (evoPCA)

**Table 1** Percentage of contributions of the study sites (disturbed and undisturbed) for the variations in all of the two main axes of the evolutionary principal component analysis (evoPCA)

| Sites | Axis1 | Axis2 |
|---|---|---|
| Disturbed | 0.22 | 0.25 |
| Undisturbed | 0.30 | 0.24 |

## Results

Among the 947 species sampled, 548 are terrestrial, 283 are hygrophytes, 75 are helophytes, and 41 are hydrophytes. Furthermore, 103 of the totals are alien species. The counts of the species for the disturbed sites were 85 alien species, 402 terrestrial species, 212 hygrophytes, 57 helophytes, and 30 hydrophytes. We counted 18 aliens, 146 terrestrial species, 71 hygrophytes, 18 helophytes, and 11 hydrophytes in the undisturbed sites.

We found a separation among the disturbed and undisturbed sites in the evolutionary principal component analyses (Fig. 2) that indicates moderate phylogenetic diversity dissimilarity across these sites. Axis 1 (Dim1) explained most of the observed phylogenetic diversity variation between the sites (10.7%), with most of this variation attributed to the undisturbed sites (Table 1). Axis 2 (Dim2) explained the second largest portion (5.7%) of the variation of the phylogenetic diversity, and the individual contributions of the sites for this variation were almost similar between them (Table 1). To access the contribution of the other axes for variance explanation, please see Fig. S1 (Online Resource).

We observed a significant phylogenetic overdispersion by sesMPD for the undisturbed sites, i.e., higher phylogenetic distance accounted for older clades and nodes (Table 2). On

**Table 2** Mean phylogenetic distance (MNTD and MPD) among the co-occurring taxa in the disturbed and undisturbed sites and their averaged phylogenetic diversity (PD). MNTD: mean nearest taxon distance; MPD: mean pairwise distance; ses: standardized size effect of MNTD, MPD, and PD. My = million years

| | Disturbed | Undisturbed | | |
|---|---|---|---|---|
| Metric | Mean | Mean | T | p-value |
| MPD | 274.64 my | 307.72 my | -8.48 | < 0.001 |
| sesMPD | -0.11 | 1.17* | -9.11 | < 0.001 |
| MNTD | 108.47 my | 119.15 my | -5.11 | < 0.001 |
| sesMNTD | -0.49* | 0.25* | -4.67 | < 0.001 |
| PD | 4104.697 | 4420.029 | -3.87 | < 0.001 |
| sesPD | -0.56* | 0.42* | -7.79 | < 0.001 |

* Mean differing significantly (< 0.05) from zero according to One Sample T Test; T = Welch Two Sample t-test for the comparisons between the metrics calculated for disturbed and undisturbed sites; p-value = significance (threshold < 0.005) of T

the other hand, sesMPD was non-significant for the disturbed sites. These results are congruent with the higher observed MPD (i.e., higher overdispersion and phylogenetic diversity) for the undisturbed compared to the disturbed sites (Table 2). Complementarily, when considering shallower clades from more recent evolutionary history in our phylogeny, sesMNTD exhibited significant phylogenetic clustering (i.e., lower phylogenetic diversity) for the disturbed sites and significant overdispersion for the undisturbed ones. This is congruent with the higher phylogenetic overdispersion found for the MNTD of the undisturbed sites in relation to the disturbed sites (Table 2). Regarding sesPD, we found significantly lower phylogenetic diversity for the disturbed sites and higher for the undisturbed sites (Table 2). The undisturbed sites also presented higher observed PD (Table 2). Although three of the selected climatic variables (isothermality, temperature seasonality, and minimum temperature of coldest month) differed significantly ($p < 0.001$) between disturbed and undisturbed sites, only minimum temperature of coldest month had a significant effect on the phylogenetic indices of both types of sites (Fig. S2). That is, the minimum temperature of the coldest month led to significant ($p < 0.001$) phylogenetic clustering (expressed in a reduction of the observed means and ses MPD, and MNTD and sesPD). The increase of this minimum temperature also led to increase of observed PD.

The lineages of alien species represented the highest phylogenetic signal (i.e., conservation/clumping of their species), followed secondly by the lineages of native species and third by the lineages of the Hydrophyte species which showed reasonable phylogenetic signal (Table 3). For all other life forms (Terrestrial, Hygrophyte, species, and Helophyte species), we found only weak phylogenetic signal, i.e., proximity to a random distribution of their species in the phylogeny, especially Helophyte species showed the weakest phylogenetic signal (Table 3).

Our tests regarding phylogenetic resolution confirmed the reliability regarding the patterns we observed in the metrics of phylogenetic diversity (PD and sesPD) and structure (MPD, MTND, and their ses-standardized effect size versions). These metrics derived from the original unresolved phylogeny were highly correlated ($r2 > 0.95$) with those derived from the resolved phylogeny (Table S1, Online Resource), with slope values ranging from 0.99 to 1. Further, MPD from the unresolved and resolved phylogenies presented a perfect correlation (slope and $r2 = 1$; Table S1), i.e., lack of phylogenetic resolution does not affect their outcomes. MPD and PD were also highly accurate (slope = 1 and $r2 = 0.99$; Table S2).

**Table 3** Phylogenetic signal in different categories of life forms and their geographical origin (alien and native species) tested with D statistics

| Category | D | *p* (random) | *p* (BM) |
|---|---|---|---|
| Alien | 0.47 | < 0.0001 | < 0.0001 |
| Native | 0.45 | < 0.0001 | < 0.0001 |
| Hygrophyte | 0.92 | 0.008 | < 0.0001 |
| Terrestrial | 0.86 | < 0.0001 | < 0.0001 |
| Helophyte | 0.96 | 0.266 | < 0.0001 |
| Hydrophyte | 0.62 | < 0.0001 | 0.001 |

P (random) testing if D is significantly different from 1; p (BM) testing whether D is significantly different from 0 under the Brownian Motion model. Further details are in the section Phylogenetic Signal. The average of species' ED was significantly higher for the undisturbed sites (36.56) than the disturbed ones (30.97) (W = 73258, p-value = 0.0004). The undisturbed sites also have a higher average of ED for both native and alien species (table 4). This finding implies that the undisturbed sites harbor most of the evolutionary endemism of species

**Table 4** Average of Evolutionary distinctiveness (ED) for alien and native species occurring in disturbed and undisturbed sites

| Sites | Species | ED |
|---|---|---|
| Disturbed | Native | 30.01 |
| Undisturbed | Native | 36.35 |
| Disturbed | Alien | 37.98 |
| Undisturbed | Alien | 39.22 |

## Discussion

Our findings demonstrated opposite trends regarding phylogenetic diversity and structure between the anthropogenically disturbed and the undisturbed sites, thus confirming our expectation. We sustain the reliability of our findings on the high phylogenetic resolution observed with the high correlation between the phylogenetic diversity and structure metrics (i.e., PD, MPD, MNTD, and their ses derivations) of the unresolved and resolved phylogenies. The undisturbed sites evidenced the highest phylogenetic dissimilarity, overdispersion, and diversity, congruently with their highest average of evolutionary distinctiveness (ED). Conversely, the disturbed sites had lower phylogenetic diversity and higher clustering. The minimum temperature of the coldest month influenced the increase in phylogenetic clustering at both sites (disturbed and undisturbed). However, the phylogenetic diversity (PD) increased with such a minimum temperature in the undisturbed sites. Altogether, these results suggest better ecological quality of the undisturbed sites encompassing conditions that favor the establishment of distinct lineages of both alien and native species.

The reduced phylogenetic diversity in the disturbed sites is consistent with its highest clustering of close relatives as an outcome of environmental filtering driven by abiotic conditions (e.g., increased temperature) (Santa et al. 2020) and theanthropogenic disturbances commonly determinant in shaping the composition of riverine and riparian communities, e.g., hydromorphological alterations (changes in hydrological regime, water flow, sediment accumulation, and erosion) (Hooke 2006; Pont et al. 2006b; Rivaes et al. 2017; Wiatkowski and Tomczyk 2018; Tomczyk et al. 2021). Hydromorphological alterations (see Aguiar et al. 2009) recorded in our disturbed sites combined to the influence of increasing temperature might promote harsher conditions that sort fewer phylogenetically and functionally close species adapted to them (Helmus et al. 2010; Brunbjerg et al. 2014; Dalle Fratte et al. 2019). Moreover, increased temperature in colder periods can favor germination of alien species that outcompete native species (Trotta et al. 2023). Therefore, probably the worse environmental conditions (i.e., increased temperature and higher anthropogenic pressure) of the disturbed sites explain their lower phylogenetic diversity compared to the undisturbed sites.

The negative effects of pronounced anthropogenic disturbances (e.g., hydrologic regime change) on the phylogenetic diversity of the disturbed sites are associated with a strong phylogenetic signal (i.e., conservatism) we found for the lineages of alien species, which might favor their invasion and establishment (Van Oorschot et al. 2017; Meyer et al. 2021) (Brunbjerg et al. 2012; Gerhold et al. 2015a). Alien species with lineages phylogenetically conserved relative to the same geographical preferences (i.e., geographical niche) of native species can better succeed in their establishment if they also hold conserved and competitively superior traits (Kalusová et al. 2021).

The reasonable phylogenetic signal of the lineages of hydrophytes is another factor that might facilitate conditions for alien invasion. Alien hydrophytes with their lineages phylogenetically conserved might spread over the native community (Chefaoui and Varela-Álvarez 2018). Some stress-tolerant and ruderal hydrophytes (e.g., *Myriophyllum aquaticum* in our sampling), considered indicators of water quality (Rørslett 1989; Willby et al. 2000), are alien species (Hrivnák et al. 2019). Alien invasive hydrophytes might contribute to reinforcing alpha and beta phylogenetic diversity impoverishment, since they may alter hydromorphodynamic processes creating unfavorable conditions that suppress native vegetation (Van Oorschot et al. 2017). The poorer the community phylogenetic diversity, the higher the probability of alien invasion, e.g., alien ruderal hydrophytes (Loiola et al. 2018; de la Riva et al. 2019; Yessoufou et al. 2019). On the other hand, if plant communities hold a higher diversity of native hydrophytes, it might work as phylogenetic buffers against the alien establishment, especially if these native species occur in less productive habitats that provide fewer resources for aliens (Capers et al. 2007).

Liendo et al. (2021) found phylogenetically clustered plant communities with high occurrence of alien species in disturbed river bar sites in the Basque Country. Some regions of Portugal and Spain share similar disturbances at river streams that might prompt plant invasion (Vicente et al. 2010; Lapiedra et al. 2015; Morais et al. 2017). Thus, low phylogenetic diversity triggered by disturbance and followed by the establishment of alien species possibly influenced the lower phylogenetic diversity we found in disturbed sites. Nevertheless, phylogenetic patterns derived from alien invasion are way more complex since they can also arise from other distinct drivers acting concomitantly. Beyond the anthropogenic pressures, we should also consider the influence of environmental constraints distributed along biogeographic gradients (e.g., landscape configuration; temperature range) and how they might affect river stream's structure (e.g., flow direction and continuity) and consequently shape the communities of plants through the relationship between alien and native species (Liendo et al. 2016b; Rivaes et al. 2017; Meyer et al. 2021). Moreover, the phylogenetic, functional (e.g., morphological, physiological), and niche relationships among the aliens and natives vary across distinct environmental and biogeographic gradients (Lambdon 2008; Procheş et al. 2008; Vicente et al. 2010; Liendo et al. 2016; de la Riva et al. 2019) and at different stages of colonization (Omer et al. 2022).

Opposite to the disturbed sites, the most favorable conditions (i.e., lower anthropogenic pressure and positive effect of increased minimum temperature) in the undisturbed sites

(Aguiar et al. 2009) shelter higher levels of phylogenetic diversity, attested by the higher phylogenetic overdispersion and the higher ED (evolutionary distinctiveness). The positive effect of the minimum temperature on PD in the undisturbed sites might be reflecting higher number of taxa functionally well adapted to warmer conditions than in the disturbed sites (Manfrin et al. 2023). Consequently, the undisturbed sites also respond for the large amount of phylogenetic dissimilarity observed among the two types of sites. The higher ED averages for aliens and natives in the undisturbed sites also indicate their biological value regarding the phylogenetic singularity sustained by higher numbers of distinct lineages. Since riparian areas are highly productive ecosystems that encompass a variety of habitats with favorable conditions for harboring large numbers of plant species (e.g., alien species from other landscapes), it might favor the establishment of a high diversity of both aliens and natives (Pollock et al. 1998; Ward et al. 2002; Zelnik et al. 2020).

Protected and undisturbed sites can harbor a high diversity of plants from distinct phylogenetic lineages, which is imperative for minimizing the risk of success of alien invasion in native communities (Kalusová et al. 2021). A higher diversity of lineages (i.e., evolutionary distinctiveness) of aliens and natives decreases competition for resources usually expected in communities with lower phylogenetic diversity (Strauss et al. 2006; Procheş et al. 2008; Gerhold et al. 2011; Lapiedra et al. 2015; Liendo et al. 2021). Thus, conserving the undisturbed riparian zones has a practical implication for their biodiversity conservation (Zelnik et al. 2020), as it implies favoring the maintenance of high phylogenetic distinctiveness. Maintaining native species from distinct evolutionary lineages and with phylogenetically conserved niche in the undisturbed sites can contribute to the maintenance of high phylogenetic diversity in native floras (Mack 2003; Rowe and Speck 2005; Loiola et al. 2018).

## Implications for management and conservation

Despite the higher phylogenetic diversity and distinctiveness in the undisturbed sites that can act as a buffer against alien plants' establishment in their river streams and riparian zones, attention still must be given to the alien species recorded in these sites due to their higher average of ED in comparison to the disturbed sites. It can sound counterintuitive once higher ED and phylogenetic diversity can make it difficult for invasion. However, as mentioned before, phylogenetic patterns from the relationships between aliens and natives are not a straight-line outcome. If we consider, for instance, Darwin's Naturalization Hypothesis - DNH (Darwin 1859; Omer et al. 2022), successful alien invaders might also be phylogenetically distantly related to the taxa in the invaded native community studies (Strauss et al. 2006; Park and Potter 2013; Bezeng et al. 2015). According to the DNH, alien invaders succeed in invading if they hold functional traits' singularity that allows them to exploit empty niches without difficulty imposed by competition with natives and other aliens (Elton 1958).

From the perspective of a possible trait singularity of alien species, we can expect that only the phylogenetic distinctiveness might not be enough to prevent invasion. It is also necessary to consider the level of singularity of functional traits in the pool of alien and native species in the investigated community (Funk et al. 2016). Thus, it is fundamental to monitor natural and undisturbed communities, especially in highly productive ecosystems, such as riparian corridors, to record their changes in species composition and functional traits and groups (Rodríguez-González et al. 2022). Such monitoring can contribute to restoration plans, e.g., by tracking riparian and riverine communities under strong anthropogenic disturbance conditions, where alien species have functional capabilities better adapted to these conditions and are superior competitors compared to the native species (Engels and Jensen 2010; Abbas et al. 2015). With records from periodic monitoring, it is possible to evaluate if an alien invasive species holds any advantage in trait singularity (e.g., a superior competitive morphological trait) that might lead them to succeed in the host communities.

In this study, we demonstrated that phylogenetic diversity, analyzed by different metrics, in riverine communities distributed along the inland territory of Portugal is higher in undisturbed sites. These findings highlight the importance of conserving suitable environmental quality in rivers and streams and their associated riparian zones for sustaining high levels of biodiversity. Considering its known high beta phylogenetic diversity, Portugal, besides Spain and Italy, is a hotspot in assisting the prevention of homogenization of phylogenetic diversity at the European level (Saladin et al. 2020). On the other hand, Mediterranean regions are also historically recognized as prompt to alien plant invasion (Andreu and Vilà 2010; Vicente et al. 2010; Morais et al. 2017; Crosti et al. 2020). Therefore, to predict invasion success in undisturbed sites and control it in disturbed ones, it is vital to conduct research for gathering detailed information on functional traits of the alien species related to invasion success (e.g., root traits, leaf nitrogen production, clonal and sexual reproduction, light availability, hydrological parameters) (Vecchia et al. 2020) and niche preferences (e.g. climate, type, and length of rivers) besides the phylogenetic relationships between alien and natives.

## Conclusions

Our findings allowed us to conclude that disturbed sites are less capable of harboring high phylogenetic diversity and distinctiveness, thus sorting fewer clustered phylogenetic lineages. Furthermore, the lineages of alien and hydrophyte species, more frequently found in the disturbed sites, were evolutionarily conserved. This finding suggests a higher sensitivity of the disturbed sites to alien plant invasion and phylogenetic homogenization in riparian ecosystems. Although the undisturbed sites shelter higher phylogenetic diversity, they require monitoring to track and prevent the spread of alien species from phylogenetic distant lineages (i.e., higher average of phylogenetic endemism) that might thrive in the native communities.

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## Declarations

**Competing interests** The authors declare no competing interests.

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