






Effects of disturbance and alien plants on the phylogenetic structure of riverine communities

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Abstract

Questions: Phylogenetic analyses provide important insights in the study of biological invasions. Previous studies have shown contrasting effects of alien species on the phylogenetic structure of recipient communities. In this study, we focus on two riparian plant communities with contrasting natural disturbance regimes: riparian forests and river bar communities. We ask whether these communities differ in alpha diversity and degree of plant invasion. Further, are the phylogenetic diversity (PD) and structure of these habitats related to the level of plant invasion?

Location: Northern Spain.

Methods: We determined level of plant invasion in forest and river bar vegetation plots, and calculated PD using mean pairwise distance (MPD) and mean nearest taxon distance (MNTD). We applied null models to analyse the phylogenetic structure of plots, and we tested whether inclusion of alien plant species was associated with differences in observed phylogenetic structure.

Results: River bar plots experienced more invasion than forest plots, but the level of invasion was only related to the PD of native species in forests. Most plots had random phylogenetic structure, with a minority of plots tending to phylogenetic overdispersion in forests and to phylogenetic clustering in river bars. MPD increased with the inclusion of alien plant species in forest plots, suggesting phylogenetic overdispersion, while no such pattern was detected with MNTD. MPD increased slightly with increasing invasion in river bar plots, suggesting reduced clustering, while MNTD values decreased with increasing invasion, suggesting the opposite trend.

Conclusions: Invasion by alien plants is differentially associated with phylogenetic structure in riparian habitats with different disturbance levels. Our results contrast with those of previous studies of plant invasion of riparian communities, which suggests geographic and ecological variation in the relationship between invasion and phylogenetic community structure in riparian systems. Research is needed to identify the causal factors underlying this variation.

KEYWORDS

alien effect, alien plants, disturbance, MNTD, MPD, northern Iberian Peninsula, phylogenetic diversity, riparian forests, river bar communities, vegetation plots

1 | INTRODUCTION

Biodiversity research on plant communities often focuses on diversity at the level of species, generally by quantifying species richness and indices that incorporate species relative abundances (Peet, 1974). Nevertheless, the biodiversity concept includes additional components besides species richness (Carmona et al., 2012; Dainese et al., 2015). Among these, phylogenetic diversity (PD, i.e., the extent of evolutionary history represented by species within plant assemblages) is a key descriptor of plant community diversity and is now widely used (Procheş et al., 2008; Bennett et al., 2014; Brunbjerg et al., 2014; Kusuma et al., 2018). In particular, PD can provide insights into ecological processes that affect the assembly of plant communities (Cavender-Bares et al., 2009; Cadotte et al., 2010; Purschke et al., 2013). According to this approach, co-occurring species in plant communities can express random, overdispersed or clustered phylogenetic patterns, depending on whether communities are randomly assembled, or contain more or fewer distant relatives than expected under random assembly. Clustered phylogenetic patterns are interpreted to indicate that environmental filtering selects species that share similar traits and ecological requirements (Brunbjerg et al., 2014; Lososová et al., 2015a), while overdispersed patterns suggest the existence of competitive exclusion that limits the coexistence of closely related species (Webb et al., 2002).

Phylogenetic analysis provides important insights in the study of biological invasion, which is a principle anthropogenic cause of biodiversity loss globally (Vitousek et al., 1997; Vilà et al., 2006). Specifically, understanding the degree to which invading species represent novel evolutionary origins is key to inferring the mechanisms of plant invasion (Bezeng et al., 2013; Li et al., 2015; Vilà et al., 2015). Empirical studies at a wide range of spatial scales provide mixed evidence for phylogenetic consequences of plant invasion, with studies supporting the association of species invasion with phylogenetic clustering (Winter et al., 2009; Lososová et al., 2015a; Loiola et al., 2018), phylogenetic overdispersion (Gerhold et al., 2011; Bezeng et al., 2013), or no apparent association (Carvalho and Castro, 2017). These contrasting results indicate the need for research on the association of alien plants with the PD and structure of native communities, and on how ongoing anthropogenic and natural disturbance may alter these relationships (Liendo et al., 2015; Lososová et al., 2015a).

Riparian habitats broadly experience high levels of invasion (Richardson et al., 2007; Pyšek et al., 2010), with riparian plant communities (forests, gravel bars, tall-herb communities, riverine marshes, etc.) differing in frequency and cover of alien species (Campos et al., 2013; Liendo et al., 2015). Riparian communities differ in a number of ways that may influence both the degree of invasion and community PD. Communities on river bars are flooded regularly, intensely and over long periods as a result of their proximal position on the riverbed (Kálníková et al., 2018). In contrast, riparian forests are higher than river bars in elevation relative to the channel centre and, consequently, are flooded

during shorter periods, and experience lower flow and physical disturbance.

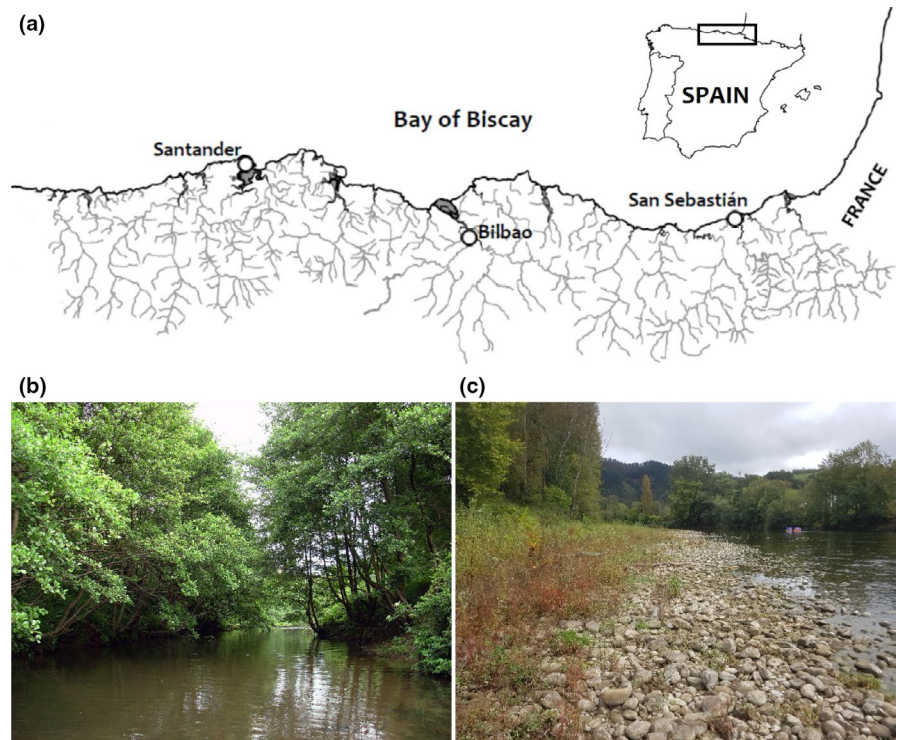
In this study, we address how plant invasion and natural disturbance covary with PD and species composition in plant communities in two physically close riparian habitats, riparian forest and nitrified river bar. These two habitat types experience natural flooding of differing intensities and durations due to their distinct topographic locations and proximity to channel centre. We examine the relationships among habitat type, alien invasion and PD using plot data on plant community composition. We ask: (a) do riparian forests and river bar plant communities, with their contrasting natural disturbance regimes, differ in alpha diversity patterns and degree of plant invasion? and (b) are the PD and structure of these habitats related to the level of plant invasion? We expect that the more frequent and intense flooding experienced by river bars leads communities in this habitat to exhibit greater phylogenetic clustering than riparian forests as a result of environmental filtering, favouring closely related species that are adapted to the disturbance regime (Helmus et al., 2010). As a result of this, we expect that the alien plants colonising river bars will be closely related to the resident community, thus increasing average phylogenetic clustering (Lososová et al., 2015a). In contrast, environmental filtering due to disturbance may be less intense in riparian forests and, thus, competition may be more important for species assembly in this habitat. Here, we expect that alien species will also include distantly related species. Increasing invasion in riparian forest should either have no association with observed PD or accompany increased overdispersion.

2 | METHODS

2.1 | Study area and data collection

This study was conducted in the riparian forests and therophyte communities of nitrified river bars in several Cantabrian rivers of northern Spain (Figure 1a). These rivers are short and steep, with fast running waters and moderate flow reduction in summer when river bars emerge (Liendo et al., 2015; Liendo et al., 2016). Riparian forests include alder (*Alnus glutinosa*) and ash (*Fraxinus excelsior*) forests of the associations *Hyperico androsaemi-Alnetum glutinosae* and *Stegnogrammo pozoi-Alnetum glutinosae* (Biurrun et al., 2016; Figure 1b). River bar communities include nitrophilous macroterophyte communities of the association *Bidenti frondosi-Polygonetum lapathifolii* (Campos, 2010; Figure 1c). We constructed the data set by considering data on vegetation plots that were previously sampled following the phytosociological method (Braun-Blanquet, 1951) and stored in the Vegetation-Plot Database of the University of the Basque Country (BIOVEG; GIVD code EU-00-011; Biurrun et al., 2012). When more than one plot of either habitat was available in the same Universal Transverse Mercator grid cell of 1 km × 1 km, we selected one of them randomly. Plot size ranged from 100 to 200 m² for riparian forests and 10–50 m² for river bars (Appendix S1). Plots

FIGURE 1 Study area showing the fluvial network and the main cities (a) and examples of a riparian forest (b) and a river bar (c)



without alien species were excluded from the analyses. The final dataset included 60 forest plots and 38 river bar plots from the period 1985–2015 (Appendix S1), with a total of 421 species. Species nomenclature follows Euro+Med (2019).

2.2 | Diversity patterns and level of invasion of forests and river bars

We calculated the total number of native and alien taxa at different taxonomic levels in each habitat and the mean number and cover of native and alien taxa at plot level. We quantified the level of plant invasion with three indices: the number of alien species in each plot (absolute alien species richness, AR), the proportion of alien species in a plot (relative alien richness, RAR) and the proportion of alien species cover in relation to the total plant cover in a plot (relative alien cover, RAC; Catford et al., 2012; Liendo et al., 2016). All alien plant species, irrespective of their invasion status, were included in the analyses. We determined the statistical significance of differences in diversity measures and levels of plant invasion between riparian forests and river bar communities with Student's *t* tests.

2.3 | Spatial patterns

We tested for spatial structure in the datasets for forest and river bar plots separately by generating matrices of Jaccard distances using the “vegan” R package. We then conducted Mantel tests of these matrices against the matrix of straight-line geographic distances with the “ade4” R package (Dray and Dufour, 2007). In no case was

spatial structure detected (randomisation $p > 0.05$, $n = 60$ in riparian forests; randomisation $p > 0.05$, $n = 38$ in river bars). Additionally, spatial autocorrelation (SAC) in regression residuals was evaluated with Moran's *I* using the `correlog()` function of the package “ncf”. To remove effects of SAC prior to decisions on statistical significance, spatial eigenvectors were generated with the `dnearneigh()` and `SpatialFiltering()` functions of package “spdep” (Bivand and Wong, 2018). These vectors were added to ordinary least-squares regressions, resulting in adjusted *F*-statistics and error degrees of freedom for the effects of interest.

2.4 | Phylogenetic diversity and data analyses

A phylogenetic tree was assembled to include native and alien species in both habitats. Some previous studies have excluded pteridophytes because of their early divergence and resulting long branch lengths, which may strongly influence observed PD (Van Meerbeek et al., 2014; Čeplová et al., 2015). However, pteridophytes are an important natural component of Cantabrian riparian forests (Biurrun et al., 2016) and, consequently, were included in the phylogeny (Table 1). Nonetheless, phylogenetic indices were also calculated excluding pteridophytes to assess the effect of their inclusion given the potential influence of being distantly related with respect to the dominant angiosperm flora, their minor contribution in river bars and the absence of alien pteridophytes in the dataset. The complete phylogeny including pteridophytes contained 413 species and was constructed with the “`phyloomatic`” function of the R package “`branching`”, using the time-calibrated `zanne2014` tree (Zanne et al., 2014) as the reference to which species names were matched. Ten



TABLE 1 Mean plot values and standard deviation of plant groups at different taxonomic levels in riparian forests ($n = 60$) and river bar communities ($n = 38$) of the northern Iberian Peninsula

	Forests		River bars	
	Mean	SD	Mean	SD
Angiosperm species	41.2	12.2	25.8	16.4
Gymnosperm species	0.1	0.2	0	0
Pteridophyte species	4.2	2	0.5	0.6
Plant families	30.8	6.3	14.4	7.5
Plant genera	41.7	10.7	22.8	13.9
Exclusively alien families	0.8	1	0.3	0.5
Exclusively alien genera	1.9	1.5	3.2	2.5

pteridophyte species were missing from this time-calibrated tree, so they were included as other congeneric or confamilial species. Additionally, we randomly resolved 26 polytomies using the “multi2di” function of the R package “ape” to obtain a fully resolved tree (Paradis and Schliep, 2019).

Indices of PD were calculated separately for forests and river bar plots for the native species component alone, and again including both native and alien species (four community classes in total). Two complementary PD indices were calculated: mean pairwise distance (MPD) and mean nearest taxon distance (MNTD). The first of these, MPD, is the average pairwise distance between species in a plot or community and is a measure of the overall PD (Swenson, 2014). In contrast, MNTD is the mean distance between a species and its closest relative in a plot (Swenson, 2014). This measure focuses on diversity at the tips of the community phylogeny, since closely related species may be ecologically similar and likely experience stronger interactions than distant relatives. Small MNTD values indicate the co-occurrence of closely related species. These indices can be affected by differences in species richness (Vellend et al., 2011). For this reason, we calculated the standardised effect sizes of MPD and MNTD, MPD_{SES} and $MNTD_{SES}$, which are equivalent to the negative of the net relatedness index and nearest taxon index (Webb et al., 2002), respectively, and independent of species richness (Pavoine and Bonsall, 2011). Standardisation was done by comparing the observed MPD and MNTD values with the values of 999 random communities using the “taxa.labels” null model in the “picante” package, which shuffles labels of all taxa in the phylogenetic distance matrix (Kembel et al., 2010), thus holding constant species richness of plots and the species turnover among them. The indices MPD_{SES} and $MNTD_{SES}$ were calculated as $(MPD_{OBS} - MPD_{RAND.MEAN}) / SD MPD_{RAND.MEAN}$, where MPD_{OBS} is the observed MPD, and $MPD_{RAND.MEAN}$ and $SD MPD_{RAND.MEAN}$ are the mean and standard deviation of expected MPD from the randomised communities, respectively. We used the standardised indices to test for non-random phylogenetic structure of communities. Near-zero values indicate random phylogenetic structure, while values below -1.96 or above $+1.96$ indicate significant clustering and overdispersion, respectively, with a 5%

Type-I error rate (Lososová et al., 2015a). We used species presence/absence in calculating the raw and standardised indices in order to consider the entire phylogeny and avoid bias caused by species dominance (Loiola et al., 2018).

The standardised effect sizes of MPD and MNTD were used to create boxplots to visualise the overall phylogenetic structure at the habitat level with and without inclusion of aliens, with these overall differences tested by means of t tests. These standardised effect sizes were also used in the linear regressions assessing the relationship between the PD of the native communities and the level of plant invasion (AR, RAR and RAC). The level of plant invasion was log-transformed (natural logarithm) to improve normality of residuals. Finally, at the plot level the effect of the inclusion of alien species on phylogenetic structure (i.e., “alien effect”) was estimated for each plot separately as the difference between the standardised index calculated with native and alien species and the index calculated with native species alone (Winter et al., 2009; Qian and Sandel, 2017). This alien effect was regressed against the standardised MPD and MNTD of the native component of riparian forest and river bar plots. The assumptions of normality of residuals and homoscedasticity were tested with the Shapiro-Wilks statistic and plots of residuals. All analyses were performed using R version 3.5.2 (R Core Team, R Foundation for Statistical Computing, Vienna), and R code is included in Appendix S2.

3 | RESULTS

3.1 | Diversity patterns and level of invasion

A total of 338 taxa (including subspecies and taxa identified at genus level) are represented in the 60 forest plots. Of these taxa, 285 are native and 53 are alien. As many as 112 taxa (33.1%) occur in only one plot, including 85 native and 27 alien taxa. The most frequent native species (occurring in more than 50 plots) are *A. glutinosa* (57), *Hedera hibernica* (56), *Brachypodium sylvaticum* (55), *Hypericum androsaemum* (54), *Carex pendula* (53) and *F. excelsior* (52). The most frequent alien species (occurring in more than 20 plots) are *Crocsmia × crocosmiiflora* (22), *Platanus hispanica* (22) and *Robinia pseudoacacia* (22). A total of 238 taxa (including subspecies and those identified at the generic level) occur in the 38 river bar plots, including 176 native and 62 alien taxa. As many as 78 taxa (32.8%) appear in only one plot, including 58 native and 20 alien taxa. The most frequent native species (occurring in more than 19 plots) are *Lythrum salicaria* (25), *Persicaria lapathifolia* (25), *P. maculosa* (25), *Calystegia sepium* (21), *Urtica dioica* (20) and *Rumex obtusifolius* (20). The most frequent alien species (occurring in more than nine plots) are *Paspalum distichum* (25), *Cyperus eragrostis* (23), *Echinochloa crus-galli* (15), *Bidens frondosus* (12), *Cyperus longus* (10), *Digitaria sanguinalis* (10) and *Erigeron floribundus* (10). A total of 131 species are found at least once in both habitats, which represent 57% of the river bar dataset and 40% of the forest dataset. Of these 131 shared species, 59 of them occur in <5% of forest plots, including a

number of annual and/or nitrophilous species more typical of river bars that can occasionally be found in riparian forests (Appendix S1). On the other hand, 61 of the shared species occur in <5% of river bar plots, many of them being herbaceous or woody species characteristic of riparian forests that are occasionally present in river bars (Appendix S1). No significant relationship between numbers of native and alien species exists in riparian forests ($r_p = 0.023$; $df = 36$; $p = 0.86$), whilst there is a positive and significant relationship between the number of native and alien species in river bars ($r_p = 0.35$; $df = 58$; $p = 0.028$).

The mean number of angiosperm and pteridophyte species, plant families, and plant genera is higher in forest plots (Table 1). The mean number of alien families is also slightly higher in forest plots representing, on average, 2.6% of plant families compared to 2.1% of families in river bar plots. On the other hand, the mean number of exclusively alien genera is higher in river bar plots representing, on average, 14.0% of plant genera compared to 4.6% in forest plots. When data are pooled within habitats, forests and river bars show a similar percentage of alien families (12.5% and 13.6%, respectively), whilst at the genus level river bars harbour substantially more alien genera than forests (23.4% and 16.2%, respectively). Exclusively alien families in riparian forests include Commelinaceae, Myrtaceae, Moraceae, Balsaminaceae, Hydrangeaceae, Juglandaceae (with two genera, *Juglans* and *Pterocarya*), Platanaceae, Garryaceae, Cannaceae and Bignoniaceae. Exclusively alien families in river bars include Actinidiaceae, Moraceae, Platanaceae and Juglandaceae.

River bar communities have significantly higher alien richness, as RAC and RAR, than do riparian forests, but they do not differ significantly in alien cover (Table 2). Forest plots show positive mean MPD_{SES} and $MNTD_{SES}$ values, indicative of a tendency towards phylogenetic overdispersion, while river bar plots exhibit negative mean values for both indices, indicative of a tendency to phylogenetic clustering (Figure 2). However, these standardised indices at the plot level reveal that the majority of plots show no evidence of either clustering or overdispersion (Appendix S3). Nonetheless, some differences exist between these habitats. Both MPD_{SES} and $MNTD_{SES}$ indicate that the native component of forest plots is significantly more overdispersed than that of river bar plots (Table 3, Figure 2). In fact, 30% of forest plots show MPD_{SES} values that indicate significant phylogenetic overdispersion, with a slightly lower percentage for $MNTD_{SES}$ (Appendix S3). No forest plot is phylogenetically clustered. On the other hand, 8% of river bar plots present MPD_{SES} values that indicate significant clustering and this percentage increases to 29% for $MNTD_{SES}$ (Appendix S3). Neither index indicates phylogenetic overdispersion for any river bar plot. When pteridophytes are excluded from the analyses, no forest plot is significantly overdispersed with respect to MPD_{SES} , whilst the percentage of overdispersed plots regarding $MNTD_{SES}$ decreases to 15% (Appendix S3). As for river bar plots, there is an increase in the percentage of significantly clustered plots for both MPD_{SES} (from 8% to 36%) and $MNTD_{SES}$ (from 29% to 52%).

TABLE 2 Mean plot values and SD of the level of plant invasion and the floristic diversity indices in riparian forests and river bar communities of the northern Iberian Peninsula

	Forests		River bars		Forests vs. river bars (t test)
	Mean	SD	Mean	SD	
Alien cover (%)	20.64	28.02	30.33	28.10	-1.66 (n.s.)
Native cover (%)	245.16	77.15	103.7	46.63	11.32*
Total cover (%)	265.80	72.05	134.03	54.91	10.23*
RAC (%)	8.21	11.05	21.34	17.42	-4.15*
Alien richness (AR)	2.97	2.15	6.55	5.25	-3.99*
Native richness	43.10	12.36	19.79	13.98	8.41*
Total richness	46.07	12.59	26.34	16.59	6.27*
RAR (%)	6.84	5.11	26.97	14.23	-8.38*

Bonferroni correction for multiple comparisons was applied, ($\alpha_{Bon} = 0.00625$).

Abbreviations: n.s.: non-significant differences; RAC, relative alien cover; RAR, relative alien richness.

* $p < 0.001$.

3.2 | Level of invasion and community phylogenetic diversity

Phylogenetic diversity of the native component of river bar plots, in terms of both the MPD_{SES} and $MNTD_{SES}$ indices, is not significantly related to the level of plant invasion (Appendix S4). To the contrary, a weakly negative but significant relationship emerges in forest plots between $MNTD_{SES}$ and the level of plant invasion, either measured as AR, RAR or RAC (Appendix S4), indicating decreasing levels of plant invasion in forest plots with higher $MNTD_{SES}$ values. In river bars, despite some regressions yielding significant statistical effects of some of the spatial eigenvectors, neither MPD_{SES} nor $MNTD_{SES}$ were significantly related to any variable representing the level of plant invasion (all $p > 0.05$; Appendix S4).

3.3 | Effect of alien species on phylogenetic relatedness

There is a significant overall increase in phylogenetic overdispersion in forest plots as indicated by MPD_{SES} when alien species are included in the analysis (Figure 2, Table 3). This translates into an additional 10% increase (from 30% to 40%) in the forest plots exhibiting significant overdispersion (Appendix S3). On the contrary, no such significant change is observed in the analysis of $MNTD_{SES}$. Similar

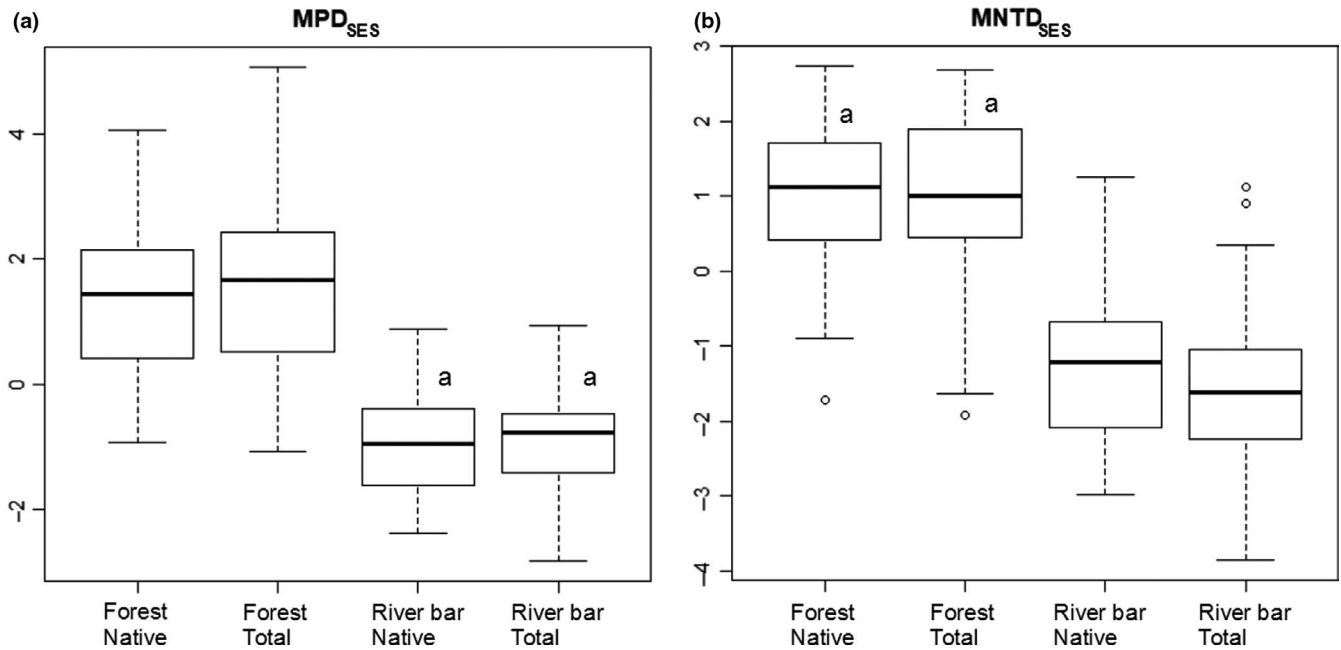


FIGURE 2 Box plots showing the median and the dispersion of the standardised mean phylogenetic distance (MPD_{SES} , left) and the standardised mean nearest taxon distance ($MNTD_{SES}$, right) in riparian forests and river bar communities. N: native component; T: whole community (native + alien species). Letters indicate lack of significant differences after applying the Bonferroni correction for multiple comparisons ($\alpha_{Bon} = 0.00625$; see Table 3)

TABLE 3 *T* tests between the native and total (native + alien) components of riparian forests and river bars with respect to the standardised mean phylogenetic distance (MPD_{SES}) and the standardised mean nearest taxon distance ($MNTD_{SES}$)

	MPD_{SES}	$MNTD_{SES}$
Forest		
Total vs. native	6.46*	-0.03 (n.s.)
River bar		
Total vs. native	2.37 (n.s.)	-4.45*
Total		
Forest vs. river bar	11.60*	12.10*
Native		
Forest vs. river bar	11.78*	9.88*

Bonferroni correction for multiple comparisons was applied ($\alpha_{Bon} = 0.00625$).

Abbreviation: n.s., non-significant differences.

* $p < 0.001$.

results were obtained when pteridophytes are excluded (Appendix S3). The percentage of river bar plots with significant clustering in MPD_{SES} decreases by six percent with the inclusion of alien species (Appendix S3) although this is not significant (Figure 2, Table 3). There is a significant overall increase in phylogenetic clustering, as indicated by $MNTD_{SES}$, when alien species are included (Figure 2, Table 3), which translates into an increase in the incidence of clustering in river bar plots by 5% (Appendix S3). When pteridophytes are excluded, the percentage of plots with significant clustering in MPD_{SES} decreases by 25% with the inclusion of alien species, whilst

for $MNTD_{SES}$ there is a decrease in the incidence of clustering by 2% (Appendix S3).

Similarly, plotting the incremental effect of inclusion of aliens against the MPD_{SES} and $MNTD_{SES}$ of the native component illustrates the effect of alien inclusion on PD ("alien effect"; Figure 3). In forest plots, positive alien effects increase with increasing MPD_{SES} of the native component (i.e., with increasing overdispersion); more-overdispersed plots are even more overdispersed with the addition of aliens (Figure 3a). Additionally, the MPD_{SES} is significantly related to the alien effect ($\beta_1 = 0.148$; $F_{1,58} = 17.57$; $p < 0.001$; Appendix S4). The analogous effect of alien inclusion for river bar data, in which MPD_{SES} values are predominantly negative, is non-significant. When pteridophytes are excluded from the phylogenetic tree the effect of alien inclusion in forests becomes non-significant, but a strong increase of the alien effect with decreasing MPD_{SES} is detected in river bars, i.e., the more clustered the native community is, the stronger the positive effect of alien species is in the phylogenetic structure (Appendix S5). On the other hand, the effect of the inclusion of aliens in forest and river bar plots leads to little change in $MNTD_{SES}$ when this index for native species is negative (i.e., in phylogenetically clustered native communities). In river bar plots, however, it becomes increasingly negative when $MNTD_{SES}$ of native communities increases towards zero (i.e., in less-strongly clustered communities; Figure 3b). Additionally, the $MNTD_{SES}$ is significantly related to the alien effect ($\beta_1 = -0.192$; $F_{1,36} = 6.24$; $p = 0.018$; Appendix S4). When pteridophytes are excluded from the analyses, the regression of alien effect on $MNTD_{SES}$ is also significant in river bar plots (Appendix S5).

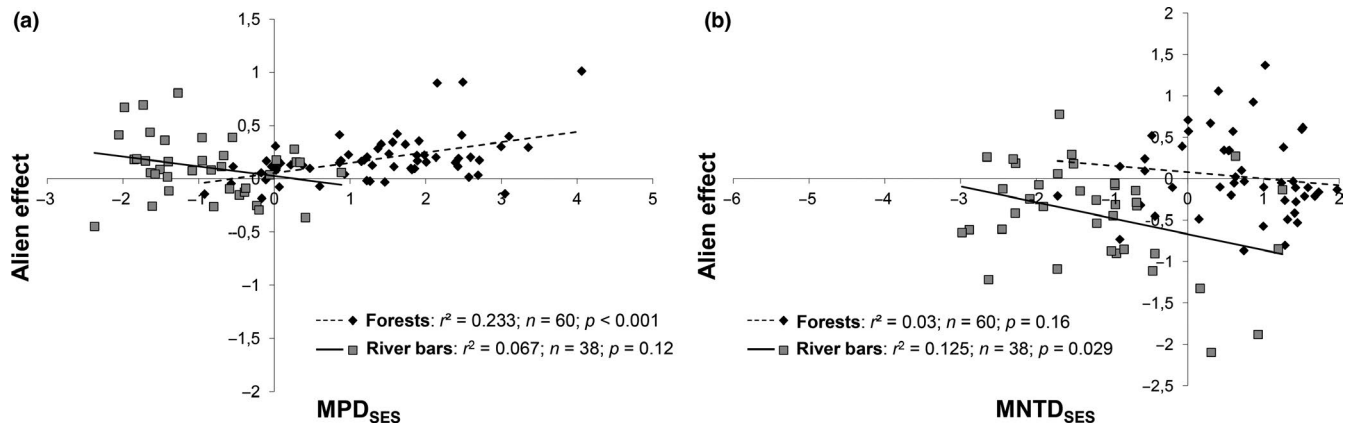


FIGURE 3 Relationship between the alien effect ($SEStot - SES_{nat}$) and the SES values of the mean phylogenetic distance (MPD; a) and mean nearest taxon distance (MNTD; b) calculated for the native component in riparian forests and river bar communities. SES, standardised effect sizes. For parameters of the significant regressions, see Appendix S4

4 | DISCUSSION

Our results are consistent with previous research showing that river bar communities are notably more invaded than riparian forests, with values of invasion level similar to those obtained for both habitats along Atlantic rivers (Tabacchi and Planty-Tabacchi, 2005; Campos et al., 2013). The higher level of invasion observed in river bar communities is probably the result of the stronger hydrological disturbance they experience relative to riparian forest (Davis et al., 2000). River bars emerge seasonally in late spring and are colonised primarily by annual species through seed dispersal (Assini, 2001). By late autumn to early winter, this vegetation is almost totally removed by water flow and, consequently, a variety of species may colonise in a low-competition environment (Hobbs and Huenneke, 1992). Additionally, river bars in the study area are concentrated at low elevations near human settlements (Liendo et al., 2016). As a result, they receive plentiful nutrients, especially nitrogen, allowing for the establishment of opportunistic nitrophilous alien therophytes, such as *Amaranthus* spp., *Xanthium strumarium* and *B. frondosus* (Campos et al., 2013; Bolpagni and Piotti, 2015).

4.1 | Habitat type and phylogenetic structure

We found significant differences in MPD_{SES} and $MNTD_{SES}$ between riparian forests and river bar communities, a pattern that is consistent with previous findings in a variety of habitats of Central Europe and South Africa (Procheş et al., 2015; Lososová et al., 2015a). These differences are expressed in overall negative values for both PD indices in river bar plots and by overall positive values in forest plots (Figure 2). This indicates that, as expected, the native component is predominantly clustered in river bar plots and overdispersed in forest plots. Phylogenetically clustered patterns are also reported from natural habitats, such as coastal dunes (Brunbjerg et al., 2014) and from anthropogenic habitats such as urban plant communities (Čeplová et al., 2015). Phylogenetic clustering is consistent with

environmental filtering driven by disturbance (Brunbjerg et al., 2012; Brunbjerg et al., 2014; Lososová et al., 2015a), which would select closely related species from few lineages that share similar ecological requirements (Čeplová et al., 2015), assuming trait conservatism across the phylogenetic tree (but see Gerhold et al., 2015). In contrast, frequent overdispersed phylogenetic structure in forest plots is consistent with less intense hydrological disturbance and greater habitat stability than found on river bars. In these forests, this may promote coexistence of species from distant lineages via niche differences (Kitagawa et al., 2015; Lososová et al., 2015a). Additionally, habitat age has also been linked with the phylogenetic structure of plant communities (Lososová et al., 2015b). In this regard, overdispersed phylogenetic structure may prevail in historically older communities in which biotic interactions may be stronger than in recently disturbed communities. Further, forests, and especially riparian forests in our study area, harbour several species belonging to phylogenetically old and distinct lineages, such as pteridophytes, which influences phylogenetic patterns of these communities by contributing to PD (Lososová et al., 2015b; Šipoš et al., 2020).

Despite river bar communities being more invaded and phylogenetically less diverse than riparian forests, we find little association of the PD of the native component of either habitat with levels of plant invasion. We had expected a negative relationship between PD and level of species invasion (Lososová et al., 2015a). Only the $MNTD_{SES}$ values of forest plots are weakly, though significantly, negatively related to the level of plant invasion (Appendix S4). This means that, in riparian forests, those plots which are phylogenetically more diverse at the tip of the phylogenetic tree (i.e., with species belonging to different genera) are less colonised by alien plants. Thus, our results are only partly consistent with previous studies in which plant communities with greater phylogenetic clustering experience increased invasion by alien species (Gerhold et al., 2011; Lososová et al., 2015a; Ng et al., 2018). These studies report the relationship between PD and invasion across a variety of spatial extents and resolutions. However, our study was conducted with small vegetation plots at a limited spatial extent and

within just two community types. The scope of habitat variation in a study can influence observed relationships between invasion intensity and phylogenetic community structure (Loiola et al., 2018), and this may be the cause of our mixed results, with an increase in invasion with increasing phylogenetic clustering only detected for $MNTD_{SES}$ of riparian forest plots.

4.2 | Alien invasion, phylogenetic structure and scope of habitat variation

We found that the level of invasion by alien species is associated with phylogenetic structure of riparian forests and river bar communities in contrasting ways.

First, inclusion of alien plants in analysis of forest plot data significantly increased overall overdispersion as indicated by MPD_{SES} , which translated into a ten-percent increase of forest plots exhibiting significant overdispersion, while no significant change was detected in $MNTD_{SES}$ (Figure 2, Appendix S3). This result suggests that alien plants invading northern Iberian riparian forests represent phylogenetically distant families not present in the native flora (Table 1). These families include species such as *Tradescantia fluminensis* (Commelinaceae), *P. hispanica* (Platanaceae) or *Impatiens balfourii* (Balsaminaceae) that increase the mean phylogenetic distance among all species in the forest plots, increasing phylogenetic overdispersion in invaded plots (Figures 2a and 3a). Plots with relatively strong phylogenetic overdispersion of natives may provide environmental or biotic conditions that promote invasion primarily by non-related and functionally distinct taxa, perhaps due to existing levels of competition or niche filling, further increasing the level of overdispersion. Elsewhere in Europe alien species establishment can increase overdispersion in forest communities (Lososová et al., 2015a). Despite this general pattern, Lososová et al. (2015a) also showed that alluvial forests present contrasting patterns, with no significant effect due to the inclusion of alien species on MPD_{SES} , but increased clustering signalled by trends in $MNTD_{SES}$. These contrasting results may indicate that the influence of alien plant invasion on phylogenetic structure is not uniform across scales of vegetation assessment. Studies employing small plots that correspond closely to the scale at which biotic interactions occur (Carboni et al., 2013) and where alien species might affect native species most negatively (Stohlgren et al., 1999; Gerhold et al., 2011) may present different phylogenetic patterns than studies with larger plots that contain substantial environmental heterogeneity. Alternatively, communities may vary in the influence of particular traits that are acted on by environmental filters, and influential traits may present differing levels of phylogenetic conservatism in differing floras and communities. This suggests the need for additional research, including field experiments, to determine key functional traits that influence community composition and the degree to which those traits demonstrate phylogenetic conservatism.

Second, inclusion of alien species in analysis of river bar plots did not have a significant effect on the overall values of MPD_{SES} ,

although the percentage of plots with significantly clustered structure decreased by 6% (Figure 2, Appendix S3). On the contrary, inclusion of alien species produced a weak, significant decrease in $MNTD_{SES}$, with a 5% increase in the incidence of clustering at the plot level. The response of MPD_{SES} suggests that only a few alien species colonising river bars come from major lineages with little representation in the native community (Qian and Sandel, 2017), as MPD_{SES} measures the overall PD among all species in the community. In fact, less than one plant family is, on average, exclusively alien at the plot level (Table 1). In contrast, the increase in the degree of phylogenetic clustering registered with $MNTD_{SES}$ suggests that alien plant species establishing in river bar communities have some close (congeneric or confamilial) relatives in the native species assemblages, as this index focuses on the tips of the phylogenetic tree (Swenson, 2014). This is partly confirmed by the fact that in river bars there is a considerable number of exclusively alien plant genera per plot, a pattern not found at family level (Table 1). This variation could mean that alien genera belong to families already present in the native flora (especially Asteraceae and Poaceae), so that the effect of alien species on the phylogenetic structure of river bars is close to the tips of the phylogenetic tree, to which $MNTD_{SES}$ is most sensitive. A similar pattern has been reported for plant communities along climate gradients in California (Qian and Sandel, 2017) and suggests the preadaptation hypothesis, which states that alien species with a close native relative have better chances of establishment (Schlaepfer et al., 2010; Cadotte et al., 2018). In our case, given the intense hydrological disturbance to which river bars are subjected, these alien species would include species with advantageous traits (annual, fast-growing, seed-dispersed species; Campos, 2010) and ecological requirements similar to those of native species, as likely occurs among *Amaranthus* spp., *Eragrostis* spp., *Erigeron* spp. and *Paspalum* spp.

4.3 | Effects of pteridophyte inclusion/exclusion

Finally, we highlight the implications of pteridophyte inclusion on observed patterns. When these plants are excluded from the analyses, PD in forest plots is reduced and alien plants have no significant effect on phylogenetic structure, measured either as MPD_{SES} or $MNTD_{SES}$ (Appendix S5). The significant positive relationship between alien effect and increasing MPD_{SES} (i.e., increasing overdispersion, PD) of forest plots only appears when pteridophytes are included. Aliens do not increase PD when pteridophytes are omitted, which suggests that alien species are distributed on the phylogenetic tree similarly to native non-pteridophytes. The inclusion of pteridophytes allows detection of a significant effect of alien inclusion on MPD_{SES} , perhaps because of the greater PD in the more inclusive data set. Since no aliens are pteridophytes, this effect on MPD_{SES} is fully attributable to alien angiosperms.

In contrast to forest plots, alien plants in river bar plots reduce phylogenetic clustering more in strongly clustered plots (i.e., stronger positive effects of aliens on PD at more-negative



MPD_{SES} values) than in weakly clustered ones. This is reflected in the predominance of river bar points in the upper-left quadrant and the negative slope of the regression (Figure 3a, Appendix S5A). Aliens lead to a more-random phylogenetic structure in plots with clustered species distributions, as measured by MPD_{SES}, but do not substantially affect phylogenetic structure when is already random. In contrast, aliens increase clustering in river bar plots (greater negative alien effect) when MNTD_{SES} values are near zero (i.e., less clustering; Figure 3b), meaning aliens increase clustering at the terminal branches of the phylogenetic tree. When pteridophytes are excluded, this trend remains significant (Appendix S5B). Thus, our results do not vary with the exclusion of pteridophytes, demonstrating consistent support for effects of aliens on PD in the data from river bars. Pteridophytes should be included in analysis of pteridophyte-rich communities in order to understand how alien species may influence patterns of PD and underlying ecological processes.

5 | CONCLUDING REMARKS

This study reports data from vegetation plots in two habitat types, riparian forests and river bar communities, that differ in levels of natural disturbance within the same ecosystem. It offers insight on the potential effects of alien plants on community phylogenetic structure in riparian habitats. These habitats differ markedly in level of plant invasion, which shows a nuanced relationship with the PD of the native component of the vegetation. Alien plants influence indices of phylogenetic structure of both habitats, albeit differently. In addition, our results differ from previous research that was based on data from widely differing community types, especially regarding riparian forests, where MPD_{SES} is the phylogenetic index that significantly changes due to the inclusion of alien plant species. Further research should investigate the relationship between the scope of habitat variation and the effects of alien species on observed indices of diversity, and the role of pteridophytes in alien invasion of pteridophyte-rich plant communities.

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AUTHOR CONTRIBUTIONS

DL, IB, IGM, JAC and PBP conceived and designed the research; DL and PBP conducted the analyses and led the writing; all authors discussed the results and critically commented on the manuscript.

DATA AVAILABILITY STATEMENT

Riparian forest and river bar vegetation plots used in the present work are included in the Vegetation-Plot Database of the University

of the Basque Country, registered in the Global Index of Vegetation Databases (GIVD code: EU-00-011; Biurrún *et al.*, 2012). They are available in Appendix S1. Additionally, R code for the calculation of the PD indices are included in Appendix S2.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Vegetation plots used in the present study.

Appendix S2. R code for the calculation of the phylogenetic indices.

Appendix S3. Proportion of plots with random, clustered or overdispersed phylogenetic structure with and without pteridophytes.

Appendix S4. Statistical descriptors of the linear regressions.

Appendix S5. Alien effect when pteridophytes are excluded from the analyses.

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