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RESEARCH ARTICLE

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Joint species distribution models unveil co-occurrences between freshwater mussels and their fish hosts

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Abstract

Aim: Freshwater mussels are among the most threatened taxa in the world, partially due to the dependence on fish hosts to complete their life cycle. Knowledge about the role of environmental and biotic drivers in determining mussels' distribution is currently lacking. We aimed to assess the role of environmental and biotic drivers in determining the distribution of mussels and their fish hosts and to test if co-occurrence patterns were able to identify mussel-host interactions.

Location: Douro River basin (Iberian Peninsula).

Taxon: Four freshwater mussels and ten fish hosts.

Methods: Joint species distribution models (JSDMs) were fitted to presence-absence records for mussel and fish assemblages. Variance partitioning among environmental variables and latent variables was conducted to determine the environmental versus biotic drivers of species distributions. Resulting matrices of pairwise species co-occurrences were used to identify co-occurrence patterns.

Results: The distribution of host generalist mussel species was mainly explained by environmental variables related to climate and topography. The distribution of the host specialist *Margaritifera margaritifera* was mainly explained by land use. Strong positive correlations between mussels and the most relevant fish hosts were consistently captured by JSDMs. Co-occurrence patterns were mainly explained by residual factors, indicating the potential role of biotic interactions.

Main Conclusions: Biotic interactions were expected to play an important role in explaining mussels' distribution, but the contribution of this factor was only meaningful for the host specialist *M. margaritifera*. Correlations between mussels and suitable hosts allowed to infer important fish hosts for freshwater mussels in the Douro River basin from distributional data alone. By finding similarities between the ecological requirements of co-occurring species, conservation measures can be oriented towards several species, which brings a more holistic perspective to the protection of biodiversity.

KEYWORDS
biotic interactions, Douro River basin, ecological niche, environmental drivers, residual factors, species correlation

1 | INTRODUCTION

One of the main goals of ecology is to identify the factors that determine species distributions. Environmental factors play a key role, affecting species according to their physiological limits, as do biotic interactions with the surrounding species pool (Elton, 1927; Grinnell, 1917; Hutchinson, 1957). Species' dispersal capacity, their evolutionary and biogeographical history, and stochastic events further shape the observed distributions (Soberón, 2007; Zurell et al., 2020).

Recently, joint species distribution models (JSDMs) were developed as multivariate extensions of SDMs, allowing to model several species simultaneously and estimating the residual correlation between species co-occurrences not explained by environmental variables (Clark et al., 2014; D'Amen et al., 2018; Kissling et al., 2012; Ovaskainen & Abrego, 2020; Pollock et al., 2014; Warton et al., 2015). JSDMs are therefore useful to disentangle the relative effects of the environmental and biotic filters, and stochastic events (D'Amen et al., 2018; Pollock et al., 2014). In a nutshell, JSDMs are able to isolate the component of species' occurrences that is not explained by the environmental predictors included in the model. This unexplained component can be related to the effects of biotic interactions or environmental variables that were not considered. However, how to disentangle the effects of biotic interactions from unmeasured environmental variables remains unclear and requires empirical tests using species with known interactions (Zurell et al., 2018). Furthermore, JSDMs have rarely been applied to freshwater communities (e.g., Burgazzi et al., 2020; Perrin et al., 2022; Wagner et al., 2019), and, to the authors' best knowledge, only once on freshwater mussels (Inoue et al., 2017).

Often described as ecosystem engineers, freshwater mussels of the Order Unionida Grey 1854 contribute to the maintenance of several ecosystem functions and services that include bioturbation of the sediments, nutrient cycling, water purification, and provision of food and habitat for other organisms, among others (Haag, 2012; Ilarri et al., 2018; Lopes-Lima et al., 2017; Strayer, 1999; Zieritz et al., 2022). Freshwater mussels have a particular life cycle, in which parasitic larvae (glochidia) need to attach to fish hosts to metamorphose into juveniles (Haag, 2012; Modesto et al., 2018). Therefore, recruitment success is dependent on the presence of suitable fish hosts. This strong dependence can lead to the extirpation of entire mussel populations due to the loss of fish hosts (Modesto et al., 2018). The so-called host specialist mussels, i.e., those with one or few host species, face a greater threat when compared to host generalists (Modesto et al., 2018). Freshwater mussels are indeed among the most threatened faunal groups worldwide, with 47% of species currently classified as Near Threatened or Threatened in the IUCN Red List of Threatened Species. Their complex life cycles with obligatory biotic interactions require special conservation attention (Lopes-Lima et al., 2021), and provide the perfect opportunity for testing and applying the potentials of JSDMs in identifying biotic interactions through residual correlations.

In this study, we focused on the four native mussel species occurring in the Douro River basin (Iberian Peninsula, Europe), *Margaritifera margaritifera* (Linnaeus, 1758), *Anodonta anatina* (Linnaeus, 1758), *Potomida littoralis* (Cuvier, 1798) and *Unio delphinus* Spengler, 1793, and the associated native fish assemblages. These mussel species present distinct ranges, habitat requirements, and conservation statuses. *Margaritifera margaritifera* is a habitat specialist widely distributed across Europe (from Portugal to Russia) colonizing oligotrophic streams with coarse substrates and well-oxygenated waters, and currently listed by the IUCN as Critically Endangered in this continent (Geist, 2010; Lopes-Lima et al., 2017; Moorkens et al., 2018). With a particularly narrow host specialization in some European river basins (e.g. Douro River basin), *M. margaritifera* is exclusively dependent on the brown trout *Salmo trutta* (Linnaeus, 1758) to complete its life cycle (Sousa et al., 2015). The Endangered *P. littoralis*, with a disjunct distribution in Europe and Northwest Africa, mainly occurs in middle and lower stretches of rivers (Froufe et al., 2016). *Anodonta anatina*, a habitat generalist with a higher tolerance to environmental conditions, is widely distributed in Europe, North Africa, and part of Asia (Froufe et al., 2014; Gomes-dos-Santos et al., 2019; Hinzmann et al., 2013; Lopes-Lima et al., 2017). Even though it has been assessed as Least Concern, this species has shown a pattern of decline in some European countries (Lopes-Lima et al., 2014, 2017). *Unio delphinus* is restricted to the Iberian Peninsula, and listed as Near Threatened, occurring from small streams to large rivers (Araujo, 2011; Lopes-Lima et al., 2017, 2020). These three mussel species present a much broader range of effective fish host species in comparison to *M. margaritifera*, including *Squalius* spp., *Pseudochondrostoma duriense* (Coelho, 1985), *Luciobarbus bocagei* (Steindachner, 1864), *S. trutta*, *Achondrostoma* spp. and *Cobitis* spp. (Dias et al., 2020; Douda et al., 2013; Lopes-Lima et al., 2020; Ramos, 2011; details on the fish hosts of each mussel species are summarized in Table 1).

JSDMs offer the possibility of unravelling environmental versus biotic drivers of species occurrences. Given the obligatory interaction between mussels and fish hosts, we applied JSDMs to both assemblages to test the potential of these models for distinguishing the relative effects of environmental conditions and biotic interactions on species occurrence. In this study, JSDMs were built with presence-absence data, and no prior information on mussel-fish host relationships was included in the models. Knowledge of these interactions was then used to assess if these models were able to identify otherwise unknown host–parasite interactions through patterns of species occurrence and co-occurrence. We expect that JSDMs will show higher correlations between mussels and suitable fish hosts, although some factors might influence these results, namely the responses to environmental conditions and the strength of host-preference. Specifically, we used freshwater fish and mussel occurrence records collected in the Douro River basin and aimed at: (i) investigating the drivers of mussels' distribution and association with fish hosts; (ii) analysing co-occurrence patterns between mussels and fish hosts; and (iii) testing whether JSDMs are able to capture signals of biotic interactions between mussels and suitable fish hosts.

2 | MATERIALS AND METHODS

2.1 | Study area

This study took place in the Douro River basin, which is located in the north-western region of the Iberian Peninsula (40.3°–43.2° N 1.7°–8.7° W) (Figure 1). This transboundary river basin is the largest in the Iberian Peninsula (i.e., approximately 97,500 km^2) and harbours several mussel and fish species with high conservation value (Teixeira et al., 2017). The Douro River flows 927 km westward, from the headwaters located in Spain (Urbión Mountains, Cordillera Ibérica) at 1260 m altitude up to the Atlantic Ocean (Porto, Portugal). The climate is predominantly temperate, with a warm to hot summer, but also includes a considerable area of cold arid steppe on the east side of the basin (Beck et al., 2018). Mean annual temperatures are close to 11°C and average rainfall approaches 820 mm (from 381 mm to 1529 mm according to topography and distance to the Atlantic Ocean). The Douro area in Spain lies in an extensive plateau where a substantial part of the watershed was channelized and is currently overexploited for irrigation of extensive agricultural areas, then the river crosses the border to Portugal through gorges, where tributaries become steeper. The basin is heavily impacted by thousands of physical barriers (dams and weirs, Terêncio et al., 2021), and water management is shared

TABLE 1 Fish hosts of the freshwater mussel species occurring in the Douro River basin, divided into primary (good hosts), marginal (poor hosts) and unsuitable hosts according to glochidia transformation rates (proportion of viable juveniles produced).

Fish host	*Margaritifera margaritifera*	*Anodonta anatina*	*Potomida littoralis*	*Unio delphinus*
Achondrostoma arcasii		Marginal	Marginal	Marginal
Achondrostoma sp.[a]				
Achondrostoma oligolepis				
Cobitis calderoni		Marginal		
Cobitis paludica				
Luciobarbus bocagei		Marginal	Marginal	Primary
Pseudochondrostoma duriense		Primary	Primary	Marginal
Squalius alburnoides		Primary	Primary	Primary
Squalius carolitertii				
Salmo trutta	Primary	Primary	Marginal	Marginal

Note: Transformation rates above 40% were the threshold for defining primary hosts, and the remaining suitable host species were defined as marginal. Within primary and marginal hosts, fish hosts' suitability is ranked from the most suitable (darker grey) to the less suitable/unsuitable (white). Based on information available in Ramos (2011), Douda et al. (2013), Lopes-Lima et al. (2017, 2020).

[a] The species has been listed as *Achondrostoma arcasii* (e.g., Ferreira et al., 2016) but probably belongs to an undescribed species according with Collares-Pereira et al. (2021) and Robalo et al. (2006).

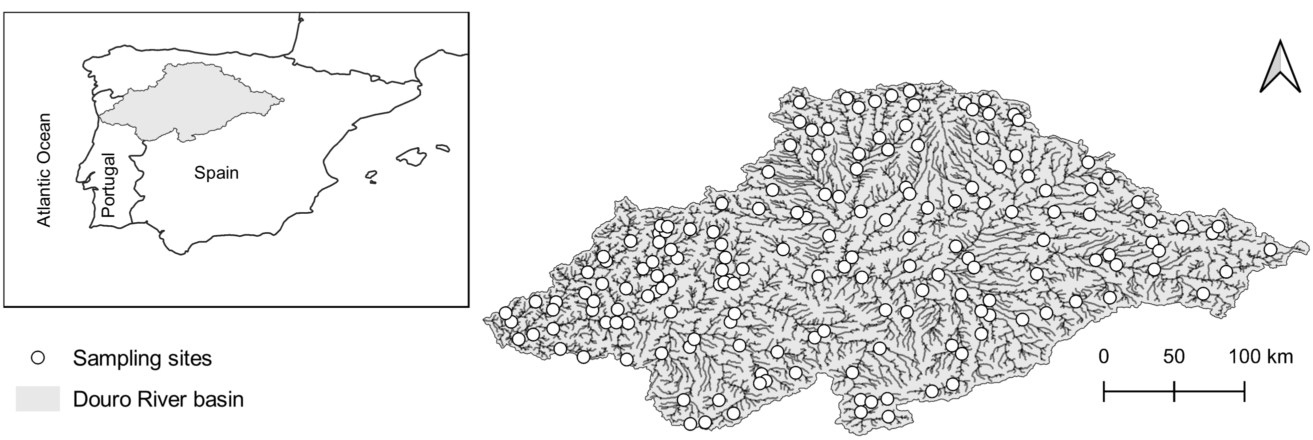

FIGURE 1 Map of the Douro River basin in the Iberian Peninsula, indicating sites where both freshwater mussels and fish assemblages were sampled (white dots). Projection: World geodetic system 1984.

between Portugal and Spain, through an international agreement, for irrigation and development (e.g., energy production) purposes. The catchment is affected by intensive agriculture. In Spain, the Douro valley is one of the main cereal-growing regions of the Iberian Peninsula. Other cultures, such as corn, sunflowers and vineyards are also prevalent across the basin, being the latter the dominant harvest in Portugal.

2.2 | Fish and mussels data

Occurrence records for mussel and fish species in the Douro River basin were obtained in three annual campaigns in June 2017, 2018, and 2019 and complemented with data from primary literature and technical reports (e.g., Dias et al., 2020; Modesto et al., 2021). During the field surveys, fish and mussel assemblages were sampled at the same sites and simultaneously. However, due to differences in sampling effort across complementary data sources, occurrence records were converted into presence-absence data per site. Site data was converted to river reach level data, as defined by HydroRIVERS (Lehner & Grill, 2013). Data merged included standardized sampling procedures, namely snorkelling observations for mussels and electrofishing for fish in 50-m long stream reaches (Cummings et al., 2016; Reynolds, 1996). When multiple sampling points were available within the same sub-basin, as defined by the level 12 resolution of HydroBASINS v1.0. (Lehner & Grill, 2013), only one was kept for analyses. We considered a single assemblage per stream reach to reduce spatial autocorrelation (Inoue et al., 2017), drawing up a total of 170 stream reaches with sampled assemblages to be used in the analyses. From the five mussels and 28 fish species recorded in the study area (Table S1), three fish species were removed due to the low number of occurrences (<10 presences). Non-native species were also removed, as considering these species was beyond the scope of the present study. In addition, the non-native Asian clam *Corbicula fluminea* does not need a fish host to complete its life cycle (Ilarri & Sousa, 2012; Sousa et al., 2008) and non-native fish species are usually poor hosts for Iberian mussels (Douda et al., 2013; Lopes-Lima et al., 2020). Consequently, four mussel and ten fish species were included in the analyses (Table 1).

2.3 | Environmental data

A candidate predictor set of environmental variables were downloaded from public databases (Table S2) and depicted to the 12th level of the river network delineation defined in HydroRIVERS by Lehner and Grill (2013). For further details on river network delineation, we refer the reader to HydroRIVERS Technical Documentation Version 1.0 (Lehner & Grill, 2013). Line layers that comprise the dendritic hierarchical structure of river networks are considered more adequate than the point-to-grid mapping commonly used in marine and terrestrial ecosystems (e.g., Domisch et al., 2015; Schmidt et al., 2020). Sampling units were labelled with the corresponding unique identifier for each river reach according to the HydroRIVERS line layers (Lehner & Grill, 2013).

The selected variables include distinct environmental conditions that have been shown to influence the distribution of both mussels and fish hosts, namely the variability in climate (Filipe et al., 2013; Hastie et al., 2003), topography and hydrology (Friedrichs-Manthey et al., 2020), geology and soil (Mcrae et al., 2004), and landcover and anthropogenic impacts (Amoatey & Baawain, 2019; Gillis et al., 2017; Maceda-Veiga et al., 2017). Information describing in-stream conditions (e.g., current velocity, water temperature, sediment size) is sparse and only available for a few sites at a local scale. Due to this limitation, we used correlates of in-stream conditions, namely topography, and climate, that have been widely used to model the distribution of several freshwater species (e.g., Filipe et al., 2002; Low et al., 2020; Yiwen et al., 2016). Climate predictors describe gradients of temperature and precipitation for the 1970–2000 time period. Calcium carbonate content in the soil attempted to account for dissolved calcium carbonate that is essential for mussel shell growth (Prié et al., 2013). For that, the mean value of calcium carbonate content was extracted to each stream reach and then used to calculate the average percentage of the total watershed upstream of each reach, using the River Network Toolkit RivTool v. 2.1 (Duarte et al., 2019). Human footprint was used as a surrogate for cumulative human pressures (Lines et al., 2022), and land use variables to describe the impacts of sediment erosion and diffuse pollution on aquatic organisms. A final predictor set of six weekly correlated variables was used to build the models (Spearman's correlation < 0.75 and variance inflation factor < 10–Figure S3, Table S3): annual mean temperature, annual mean precipitation, elevation, river order, cropland extent, and calcium carbonate content in the soil. Details on the variables' resolution and sources can be consulted in Table S2.

2.4 | Joint species distribution modelling

A joint species distribution modelling approach (JSDM; Pollock et al., 2014; Warton et al., 2015) based on the hierarchical modelling of species communities (HMSC; Ovaskainen et al., 2017) framework was used to address the drivers of the pairwise co-occurrences of mussel and fish hosts in the Douro River basin. JSDMs allow to model multiple species simultaneously and to estimate species-to-species relationships from residual correlation after accounting for the effect of environmental variables (König et al., 2021; Ovaskainen & Abrego, 2020; Pollock et al., 2014). We fitted two models as follows: (i) "Full model"—including environmental variables, that is fixed effects, and a spatial random effect; and (ii) "Environmental model"—including only environmental variables as fixed effects. The spatial random effect in the full model uses latent variables to model both the spatial structure of the occurrence data and species-to-species associations (Ovaskainen & Abrego, 2020). Attributing a spatial structure to the latent variable was intended to account for the spatially explicit nature of the species occurrence data. Specifically, we followed the works of Ovaskainen et al. (2016) and Ovaskainen and Abrego (2020), and used a spatial exponential correlation function to characterize the correlation between sampling units in the latent variables. An Euclidean distance metric was employed in the exponential correlation function, where distances are constructed based on the coordinates of the centroid of each sampled river reach. It should be noted that a spatial correlation instead of covariance function was used, that is the spatial variance is set to one, to ensure the latent variable model is identifiable; see Ovaskainen et al. (2016) for more details on this setup. Here, fixed effects model environmental filtering, i.e., the variation in the environmental conditions and the species niches (Ovaskainen & Abrego, 2020). Thus, matrices of pairwise species co-occurrences resulting from each model were used to identify mussels and fish hosts co-occurring more or less than expected by chance (positive or negative correlation, respectively). The Environmental model yields correlations between species that are due to responses to the environmental variables included in the model, while the full model captures residual correlations after removing the effects of the measured environmental variables. Due to the obligatory character of the interaction between mussel and fish hosts, residual correlations from the full model are expected to represent mainly non-random co-occurrence patterns resulting from biotic interactions between mussels and fish hosts. To disentangle the role of environmental filtering from residual factors in the co-occurrence patterns, the two models were compared (see Table S4 to further interpret all possible combinations of co-occurrence results). Correlations between mussels and fish hosts were considered strong if the estimated correlation value $\rho > 0.6$, and very strong if $\rho > 0.8$ (Evans, 1996). They were also deemed to be statistically significant if the posterior probability that the correlation was not equal to zero exceeded 0.95 (Ovaskainen & Abrego, 2020).

To evaluate the species' response to the variables included in the models, we plotted heat maps of the parameter estimates of species niches, including only those whose posterior probability of not being equal to zero exceeded 0.95. To determine the factors that contribute to explaining the occurrences of the mussel species, we performed a variance partitioning analysis (Ovaskainen et al., 2017). The relative importance of environmental variables and latent variables in explaining the mussels and fish hosts assemblages was found by comparing variance partitioning's results between the fixed effects and latent variables of the Full model with the fixed effects of the Environmental model.

We modelled presence-absences using a probit-link function and assuming HMSC default priors (Ovaskainen & Abrego, 2020). We ran three parallel Bayesian Markov chain Monte Carlo (MCMC) chains per model with 15,000 iterations, out of which 5000 were discarded as transient, and the remaining 10,000 were evenly thinned by 10 to yield 1000 samples, summing up to a total of 3000 samples per model. Convergence was assessed by calculating the potential reduction factor for the beta (response of the species to the included covariates) and omega (species to species associations) parameters of the HMSC model, as well as by visual inspection of the MCMC trace plots. When the potential scale reduction factors are close to one, we assume a satisfactory MCMC convergence (following Ovaskainen et al., 2017). The models' explanatory power was evaluated using the area under the curve (AUC) and the coefficient of discrimination (Tjur R^2). Additionally, models were compared based on the Widely Applicable Information Criterion (WAIC; Watanabe, 2010). All models were fitted in R 4.1.1., using the package "hmsc" v3.0 (Tikhonov et al., 2020). Correlation plots were built with the "corrplot" v0.92 package (Wei & Simko, 2021), and variance partitioning plots with the "ggplot2" v3.3.3 (Wickham et al., 2016).

TABLE 2 Explanatory power of the full and environmental models built for freshwater mussels and fish hosts assemblages measured by calculating the area under the curve (AUC), the coefficient of discrimination (Tjur R^2), and the widely applicable information criterion (WAIC) between the predicted and observed occurrences, average across species.

	AUC	Tjur R^2	WAIC
Full model	0.91	0.36	4.07
Environmental model	0.87	0.27	4.53

3 | RESULTS

3.1 | Assemblages characterization

Exploratory analyses showed that the prevalence of the species in the sampled catchments of the Douro River basin ranged from 0.06 to 0.45 (Figure S2), and species richness from 0 to 8, with assemblages with lower species richness (<3) being more common (Figure S1). *Unio delphinus* was the most prevalent mussel species, followed by *A. anatina*, while *P. littoralis* was the rarest, closely followed by *M. margaritifera* (Figure S1). *Salmo trutta* was largely the most prevalent fish host, followed by *Squalius* spp., *P. duriense* and *L. bocagei*. Species of *Achondrostoma* spp. showed a clear lower prevalence when compared to the remaining fish hosts (Figure S1).

3.2 | Models evaluation

The three MCMC chains built for each model gave consistent results, as shown by the model convergence diagnostics (potential scale reduction factors of β and Ω parameters very close to the ideal value of 1; Figures S4 and S5), and suggested by visual inspection of trace plots.

The explanatory power of both the Full and the Environmental models was very good, as shown by the AUC (Full model: 0.91; Environmental model: 0.87) and Tjur R2 (Full model: 0.36; Environmental model: 0.27) values (Table 2). Complementarily, based on the WAIC ranking, the Full model was more parsimonious than the Environmental model (Table 2).

3.3 | Drivers of freshwater mussels' distribution

Variance partitioning of the fixed effects and latent variables from the Full model showed that included environmental variables explained a large component of the distribution of freshwater mussels (Figure 2). As such, the results of variance partitioning were very similar among the Full and the Environmental models (Figure 2). For most of the fish hosts, latent variables also played a small part in explaining the variance, with two obvious exceptions being *A. arcasii* and *S. carolitertii* where latent variables represented most of the variation (Figure 2). Notably, every species showed a negative response to cropland extent (Figure 3).

Environmental variables accounted for 85.03% of the explained variance for *M. margaritifera* in the Full model, while the latent variables contributed the remaining 14.97%. Specifically, the distribution of *M. margaritifera* was largely explained by a significant, negative response to cropland extent (43.51%; Figures 2 and 3). For this species, annual average precipitation (11.58%) and calcium carbonate content in the soil (10.40%) were also relevant variables in explaining the variance (Figure 3). Results also showed a negative response to the spatial latent variable and calcium carbonate content, and a positive response to annual average precipitation, although none were statistically significant (Figure 3).

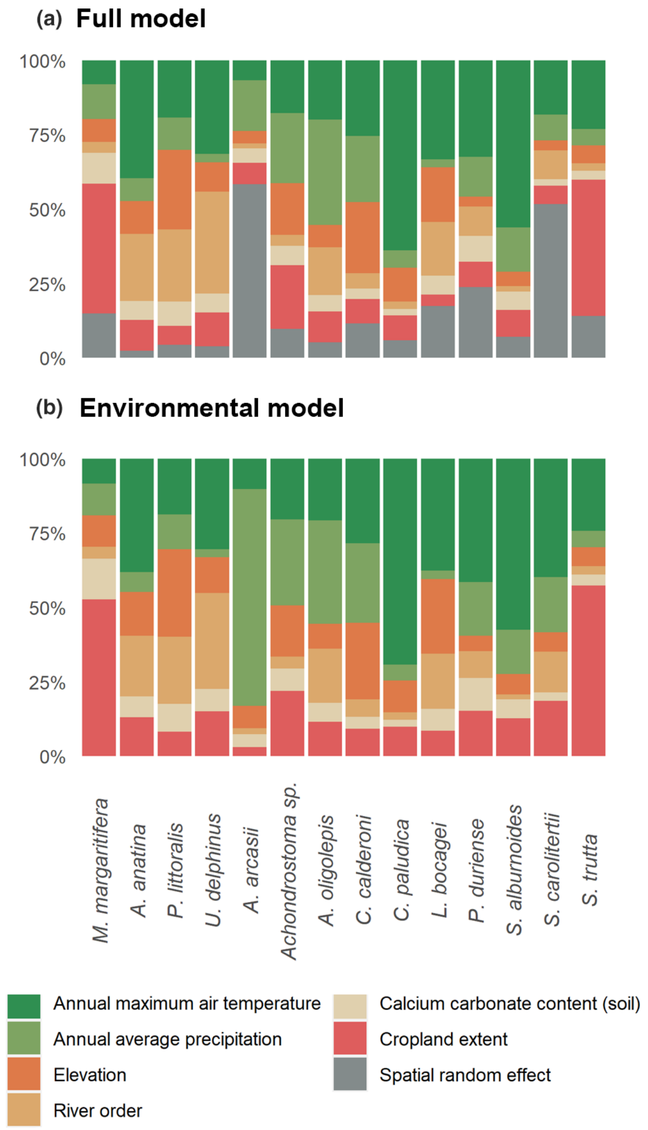

FIGURE 2 Variance partitioning among the environmental variables (fixed effects) and the spatial latent variable (random effect) included in the full model (a), and among the fixed effects of the environmental model (b) used for modelling freshwater mussels and their fish hosts in the Douro River basin.

A consistent pattern in variance partitioning results of the Full model was found for the remaining mussel species, as their distribution was mainly attributed to climatic and topographic variables (Figure 2). For *A. anatina* and *U. delphinus*, environmental variables accounted for 97.55% and 96.16%, respectively. Among these, annual maximum temperature (*A. anatina*: 39.70%, *U. delphinus*: 31.55%), river order (*A. anatina*: 22.57%, *U. delphinus*: 34.24%), cropland extent (*A. anatina*: 10.35%, *U. delphinus*: 11.34%) and elevation (*A. anatina*: 11.03%, *U. delphinus*: 9.75%) were the most important variables in explaining their occurrences (Figure 2). These mussel species showed a statistically significant positive response to annual maximum temperature and river order, and a statistically significant negative response to cropland extent (Figure 3). The negative response to elevation was not statistically significant for either of these mussel species (Figure 3). For these species, the contribution of the latent variable was slight (*A. anatina*: 2.45%, *U. delphinus*: 3.84%—Figure 2).

Environmental variables explained about 95.65% of the variance for *P. littoralis*, with topographic variables showing greater contributions (Figure 2). The Full model similarly attributed them to elevation (26.78—Figure 2) and river order (24.22%—Figure 2). Climatic variables (annual maximum temperature: 19.31%; annual average precipitation 10.75%—Figure 2) also played a relevant role for this species. The response of *P. littoralis* to elevation was negative, and the response to river order was positive, with both effects found to be statistically significant (Figure 3). For this species, the role of latent variables was also negligible (2.95%—Figure 2).

3.4 | Associations between freshwater mussels and fish hosts

Native mussel and fish hosts associations in the Douro River basin were highly dominated by positive correlations in both models (Figure 4). Accordingly, in the Full model, where latent variables account for the co-occurrences that remain after removing the effects of environmental variables, residual correlations between mussels and fish hosts were generally very strong (Figure 4). From a total of 27 mussel-fish hosts pairs in the Douro River basin (Table 1), this model showed a very strong correlation for 11 pairs and a strong correlation for 5 pairs (Figure 4), although only 4 of these correlations were statistically significant. In the environmental model, whose co-occurrences are due to the species' shared responses to environmental conditions, mussel-fish host pairs were mostly positively and highly correlated, but a few correlations between mussel and fish hosts highly differed from the Full model (Figure 4). In this model, only 9 mussel-fish host pairs showed a very strong correlation, which were all statistically significant (Figure 4). A further consistent

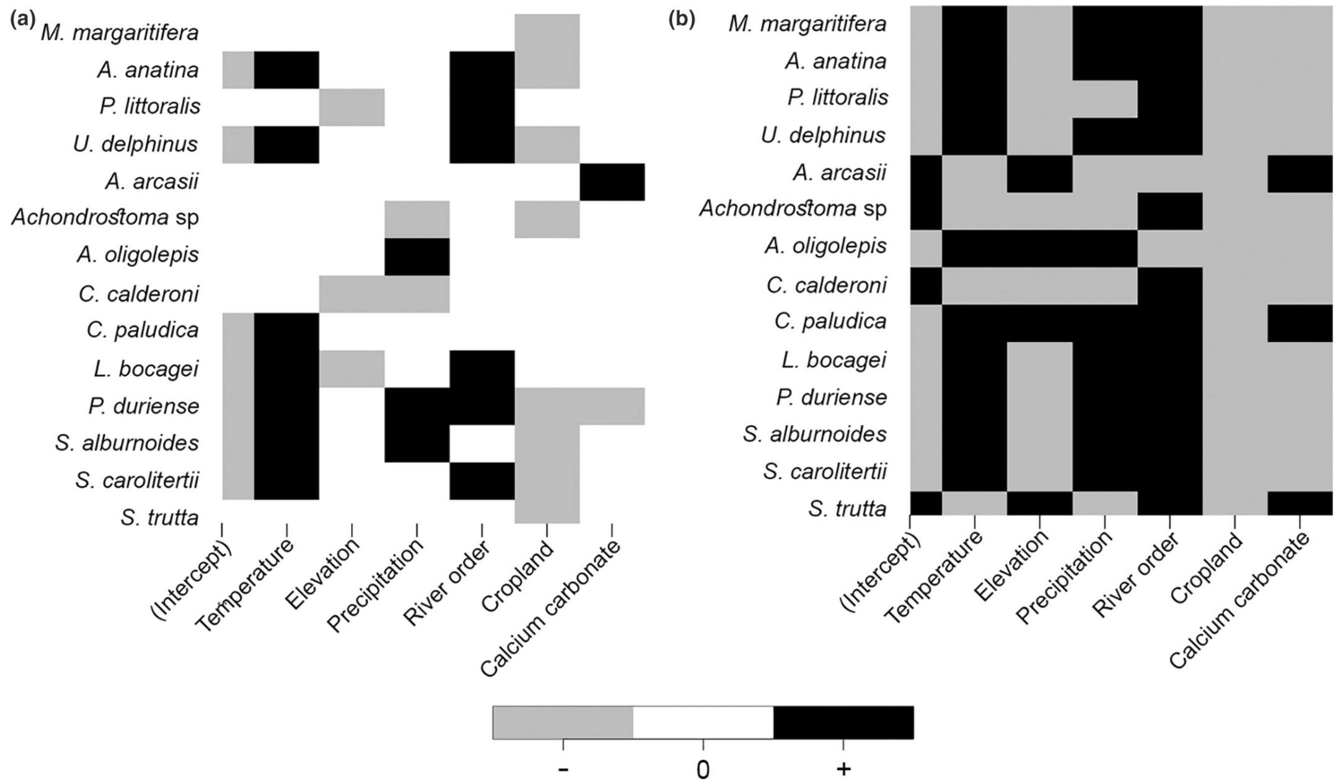

FIGURE 3 Heatmap of estimated freshwater mussels and fish hosts niches in the Douro River basin, with positive (black) and negative (grey) responses to environmental variables resulting from the full model. (a) Shows only the estimated parameters whose corresponding posterior probability of not being equal to zero exceeded 0.95, and (b) shows all estimated parameters regardless of support level.

pattern in both models was a clear tendency for higher correlations between mussels and primary fish hosts when compared to correlations with marginal hosts (Figure 4 and Table 1).

Specifically, *M. margaritifera*'s residual correlation with its unique fish host, *Salmo trutta*, was strong and positive in the Full model, and negative and weak in the Environmental model, both below the defined threshold of statistical significance (Figure 4).

The full model showed a very strong correlation between *A. anatina* and its primary hosts *P. duriense*, *S. alburnoides* and *S. carolitertii*, although none of these correlations were statistically significant (Figure 4, Table 1). The environmental model also showed a very strong correlation with the primary hosts *P. duriense* and *S. carolitertii* and a strong correlation with *S. alburnoides*, among which the correlation *A. anatina*–*S. alburnoides* was the only one that was not statistically significant (Figure 4, Table 1). *Anodonta anatina* was also strongly correlated with the marginal host *L. bocagei* in both models, but this relationship was only statistically significant in the Environmental model (Figure 4). Correlations between this mussel and the remaining, marginal hosts were weaker and not statistically significant in both models (Figure 4, Table 1).

Potomida littoralis showed a very strong residual correlation with its primary hosts *P. duriense* and *S. carolitertii*, and a strong correlation with *S. alburnoides*, although none was statistically significant (Figure 4). On the contrary, the pairs *P. littoralis*–*P. duriense* and *P. littoralis*–*S. carolitertii* were very strongly correlated in the Environmental model (Figure 4). For this mussel species, correlations with marginal hosts were very strong for the *P. littoralis*–*L. bocagei* pair and strong for *P. littoralis*–*S. trutta* pair in the Full model, but both sets were not statistically significant (Figure 4). In the Environmental model, *P. littoralis* and *L. bocagei* exhibited a strong statistically significant correlation (Figure 4).

The residual correlation between *U. delphinus* and all its primary hosts was very strong and statistically significant in the Full model (Figure 4). A similar pattern was found in the Environmental model, but the *U. delphinus*–*S. alburnoides* pairwise correlation was only strong and not statistically significant (Figure 4). *Unio delphinus* showed a further very strong correlation with the marginal host *P. duriense* and a strong correlation with *S. trutta* in the Full model, in addition to a statistically significant correlation with *P. duriense* in the Environmental model (Figure 4).

Despite *Achondrostoma oligolepis* being recognized as a suitable marginal host for *A. anatina*, *P. littoralis* and *U. delphinus*, these mussel-fish host pairs showed a strong negative association (Figure 4). High residual correlations between *M. margaritifera* and unsuitable hosts were also registered by the Full model (Figure 4).

4 | DISCUSSION

This study provided important knowledge about the drivers of freshwater mussels' distribution and association with fish hosts across the largest Iberian river basin. Overall, our results revealed

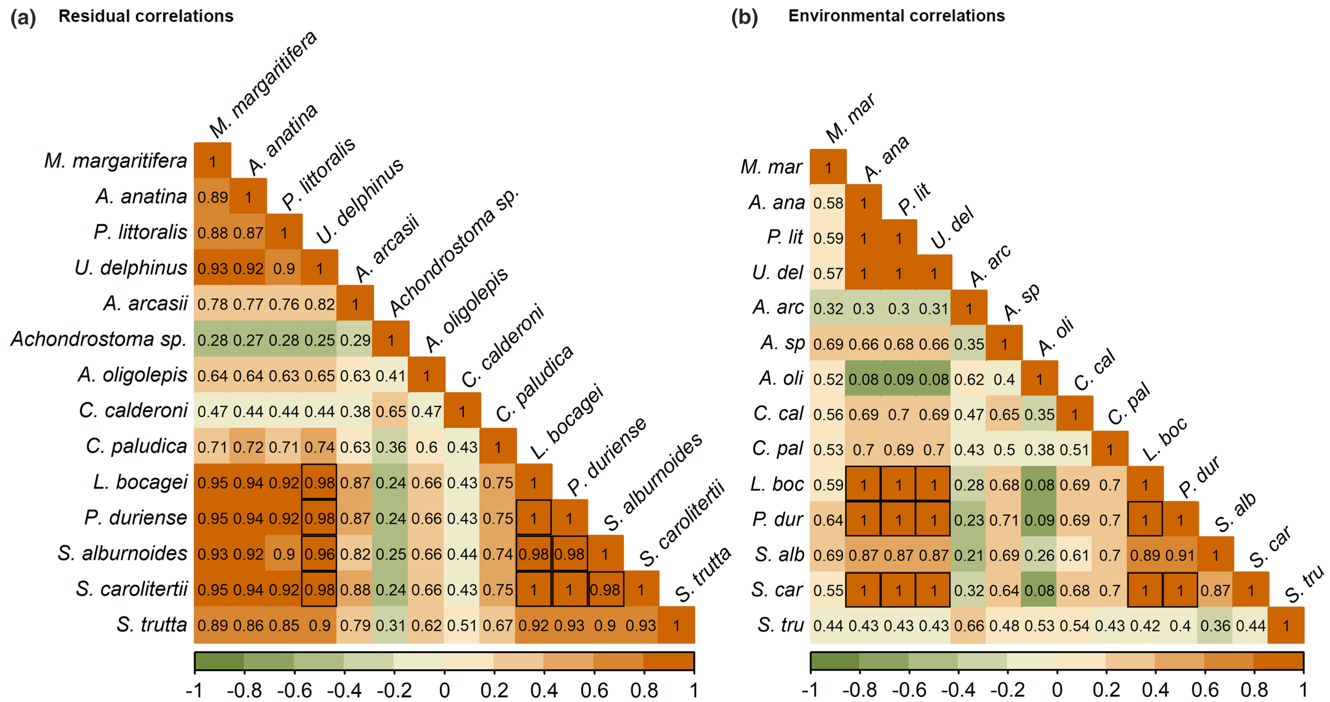

FIGURE 4 Correlations between freshwater mussels and fish hosts in the Douro River basin. Residual correlations show species associations after removing the effects of the environmental variables included in the full model (a). Environmental correlations show associations due to responses to the environmental variables included in the environmental model (b). Orange gradient shows positive correlations, while green gradient shows negative correlations. Numbers indicate the posterior probability that the correlation was not equal to zero. Pairs with posterior probability at least equal to 0.95 are marked with a black square.

that assemblages of freshwater mussels and fish hosts in the Douro River basin could be mostly predicted by climate and topography. Additionally, species' co-occurrences largely showed positive associations between mussels and suitable fish hosts. Here, we specifically attempted to unveil the relative roles of environmental and biotic filters in determining mussels' distribution and co-occurrences with fish hosts, and JSDMs allowed us to, at least partially, uncover the complex intertwining between these factors. Nevertheless, despite past and recent theoretical and methodological advances regarding community assembly processes (Elton, 1927; Grinnell, 1917; Hutchinson, 1957; Pollock et al., 2014; Soberón, 2007), this study suggests that further methodological improvements are needed to disentangle biotic from environmental drivers, and reliably identify species interactions based on occurrence data alone.

The two fitted models contain overlapping information, i.e., both include the same environmental predictors, but the full model further included latent variables. Even though the full model showed higher explanatory power and better model fit, both models showed very good evaluation metrics and proved useful to answer our objectives. The full model informed our attempt to disentangle the effects of environmental versus biotic factors in species distributions, while the comparison between residual and environmental correlations allowed us to infer the drivers of mussels and fish hosts co-occurrences. The spatial latent variables included in the Full model played only a small role in explaining the occurrences of freshwater mussels, evident from the very similar variance partitioning results between both Full and Environmental models. Although the studied mussels mostly shared their positive or negative responses to environmental variables, the relative importance of each variable suggests a separation between habitat generalists, namely *A. anatina*, *P. littoralis*, and *U. delphinus*, and the habitat specialist *M. margaritifera*. Particularly, habitat generalists' distributions were mainly explained by climate (annual maximum temperature and annual average precipitation) and topography (elevation and river order), and *M. margaritifera*'s occurrences were mainly explained by cropland extent.

Generally, mussels were associated with warmer and higher precipitation conditions in the Douro River basin. Suitable climatic conditions have been recognized to be essential for the maintenance of viable mussel populations, as shown by the strong influence of temperature on growth, reproduction, and recruitment success (Lopes-Lima et al., 2017). Water availability is a strong requirement for population persistence, as sharp population declines follow decreases in water availability, for instance, due to water abstraction and climatic events (Lopes-Lima et al., 2017). Habitat generalist species tended to occur in lower sections of larger rivers within the Douro River basin. Accordingly, *A. anatina* and *U. delphinus* can occur in most river systems, while *P. littoralis* occurs in middle to downstream stream sections but only in lotic stretches (Araujo et al., 2009; Lopes-Lima et al., 2014, 2017). On the other hand, *M. margarifera* seemed to only occur far from cropland areas, which follows previous findings that associate this species with pristine streams with a low human disturbance within Europe (da Silva et al., 2022; Inoue et al., 2017; Lopes-Lima et al., 2017). Furthermore, regardless of the different contribution of cropland extent for each one of these species, we found a consistent pattern across all mussels and most of the fish species inhabiting the Douro River basin, that being their negative response to this variable. This basin is highly impacted by intensive agriculture, which could be threatening the persistence of some mussel and fish populations, with emphasis on the critically endangered *M. margaritifera*. Hence, freshwater biodiversity loss, including mussels, has often been associated with land use, urbanization, and human population density (Burlakova et al., 2011; Dudgeon, 2019; Dudgeon et al., 2006; Gillis et al., 2017).

Given the obligatory interaction between freshwater mussels and fish hosts, it is expected that biotic interactions play a determinant role in explaining mussels' distributions (da Silva et al., 2022; Modesto et al., 2018), and JSDMs are arguably able to accommodate this component in the latent variables (Ovaskainen & Abrego, 2020). Here, the contribution of this random effect was meaningful for *M. margaritifera*, but not for the remaining three mussel species. This result was expected for *M. margaritifera*, but for the remaining mussel species, results rebutted our general expectation. In fact, finding a suitable fish host may be more likely for a host generalist mussel than for a host specialist (Modesto et al., 2018). In this vein, the probability of *M. margaritifera* finding *S. trutta* individuals (the only available host in the Douro River basin; Sousa et al., 2015) might be much lower than for any of the remaining mussels, which can use up to 10 fish species occurring in this area (Table 1). Specialist parasite–host relationships are often strongly affected by their interactors, while generalist ones can be influenced by a large range of host species but with weaker effects (Anderson, 2017). Hence, the role of biotic interactions is expected to be more important for a host specialist than a generalist. This could be the case in the relevant contribution of the latent variables for *M. margaritifera*, particularly if we assume that it indeed accounts for biotic interactions. As such, the host generalist versus host specialist character of mussel species possibly influences the extent to which biotic interactions contribute to explaining mussels' distribution, although this hypothesis remains to be clarified. Although the latent variables may be reflecting the importance of biotic interactions, it could also mean that relevant environmental variables were not included in the predictors (Ovaskainen & Abrego, 2020). As such, we cannot rule out that important variables for *M. margaritifera* might have been unaccounted for, thus explaining the increased importance of the latent variables. Another possibility is that we were not able to fully capture the scale at which mussels and fish interact. Models built on spatially explicit data are very sensitive to spatial resolution, which in turn largely influences the relative importance of predictor variables (Friedrichs-Manthey et al., 2020; Zurell et al., 2018). Individuals interact with each other at the local scale, after passing through the abiotic filters and consequently, the importance of species interactions can be diluted at larger scales and coarser resolutions (Araújo & Rozenfeld, 2014; Hutchinson, 1957; Wisz et al., 2013; Zurell et al., 2018).

Co-occurrence patterns from both models generally showed high correlations between mussels and suitable fish hosts, particularly through residual correlations between mussels and primary fish hosts. However, just a few residual correlations were statistically significant. We believe this could be related to the models' increased parameter uncertainty resulting from the low number of occurrence records for some species with low prevalence in the Douro River basin. Accordingly, *U. delphinus* is the most prevalent mussel in our study area and indeed showed many supported correlations with suitable fish hosts. Furthermore, identifying biotic interactions through residual analysis usually requires extensive datasets (Ovaskainen & Abrego, 2020). Nevertheless, in our study, all mussels showed strong residual correlations with primary hosts (all correlations were above 0.7). As correlations were previously considered statistically significant if the corresponding posterior probability that they were not zero exceeded 0.9 (e.g., Abrego et al., 2020), we decided to further examine nonsignificant patterns of species correlations. Many mussel-fish host pairs showed a strong association in the residual but not in the environmental correlations. For some pairs, strong positive residual correlations corresponded to negative environmental correlations. The association between *M. margaritifera* and its only primary host *S. trutta* was a nice example, whereby they show a strong positive residual correlation and a negative environmental correlation, meaning that these species would be segregated due to environmental conditions but still co-occurred due to residual factors. Due to the specificity of their relationship, those residual factors potentially translated the effects of their biotic interaction. This implies that, based on occurrence data alone, the environmental preferences of these species would not be able to identify the mussel-host relationship. Here, JSDMs seem to be able to overcome this, by considering the effects of residual factors included in the latent variables approach. Nevertheless, we acknowledge that these species are likely to share at least some habitat requirements that could be represented by variables not included here, as shown by Inoue et al. (2017). On the other hand, for some mussel-host pairs, residual and environmental correlations showed concordant results. In these cases, mussels and fish hosts likely share their responses to environmental conditions, therefore occurring in similar environments, but they also co-occurred due to factors not explicitly included in these analyses, either biotic or environmental.

We acknowledge that JSDMs showed strong residual correlations between mussels and unsuitable hosts, particularly for the host specialist *M. margaritifera*. Non-random associations such as these may be caused by several factors that do not necessarily imply positive interactions between species, namely shared responses to unaccounted environmental conditions, or even indirect interactions, and should therefore be interpreted with caution (Blanchet et al., 2020). Mussels-fish hosts correlation patterns also show negative associations between mussels and marginal hosts, namely between *Achondrostoma* spp. species and *A. anatina*, *P. littoralis*, and *U. delphinus*. Because this was not true for all marginal hosts, we argue that these fish species may be less important for the reproduction of the mussels in this region. Even host generalists are known to have varying levels of host specificity (Douda et al., 2013; Lopes-Lima et al., 2020; Ramos, 2011; Table 1), and the weaker or even negative correlations indeed corresponded to associations with less effective hosts. On the other hand, it is possible that stronger correlations represented a spatial sign of the most important fish hosts for each mussel, i.e., the species pairs that co-occur more often, regardless of what factors drive their co-occurrences. As such, knowledge regarding the potentially most important fish hosts in a certain area could inform more adequate conservation measures for the joint conservation of specific mussels-hosts pairs. JSDMs could be of great help in this regard, by allowing the identification of the distributional drivers of species pairs that can be used for the conservation of several species at the same time (Ovaskainen & Abrego, 2020). For example, in this study, we showed that *A. anatina*, *P. littoralis* and *U. delphinus* are positively correlated with *L. bocagei*, *P. duriense*, and *S. carolitertii* due to their similar responses to environmental conditions. As these are all suitable mussel-fish host pairs, conservation measures should consider this subset of species simultaneously to maximize its effectiveness while lowering management costs.

In conclusion, this study acknowledged the importance of favourable environments for maintaining viable freshwater mussel populations, while opening the debate about the importance of biotic interactions. While biotic interactions play an important role for mussels to complete their life cycle, we were only able to show this for the host specialist *M. margaritifera*. For this mussel, we found a strong association with its fish host, despite the dissimilarities between the realized niches of these species. Fish hosts' distributions have been recognized as very important dimensions of the mussels' niches (da Silva et al., 2022; Lois et al., 2014; Schwalb et al., 2013), but here JSDMs mainly highlighted the role of environmental conditions on mussels' distribution, particularly for the remaining mussel generalist species. Nonetheless, JSDMs allowed us to empirically infer important fish hosts for freshwater mussels in the Douro River basin from distributional data alone and with a low number of occurrence records. Testing the potentials of JSDMs with larger datasets and finding the best scale to detect this very particular relationship between mussels and fish hosts should be further investigated. Hence, we strongly recommend improving species occurrence records to be comparable among taxa, by maximizing taxa detection (e.g., by using novel techniques as environmental DNA and metabarcoding), and standardizing sampling efforts.

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CONFLICT OF INTEREST

We have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

Data and code used in this study are available at Mendeley Data (doi: https://doi.org/10.17632/3pwckn63m9.3).

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BIOSKETCH

Janine P. da Silva is interested in calling upon a holistic perspective to conservation by considering species interactions in biodiversity modelling. This research article represents a component of her PhD work on the joint conservation of freshwater mussels and their fish hosts from a macroecological perspective resorting to modelling tools.

Author contributions: Janine P. da Silva: conceptualization, methodology, validation, formal analysis, investigation, data curation, writing—original draft, writing—review & editing, visualization. Duarte Vasconcelos Gonçalves: conceptualization, validation, data curation, writing—review & editing. Aina Garcia-Raventós: data curation, validation, writing—review & editing, visualization. Manuel Lopes-Lima: data curation, validation, writing—review & editing, visualization, funding acquisition. Simone Varandas: data curation, validation, writing—review & editing, visualization. Elsa Froufe: data curation, validation, writing—review & editing, visualization. Amílcar Teixeira: data curation, validation, writing—review & editing, visualization, funding acquisition. Francis Hui: methodology, validation, formal analysis, writing—review & editing, visualization. Ana Filipa Filipe: conceptualization, validation, data curation, writing—review & editing, supervision, funding acquisition. Ronaldo Sousa: conceptualization, validation, data curation, writing—review & editing, supervision, project administration, funding acquisition.

SUPPORTING INFORMATION

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

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