



Effects of the invasive riparian plant *Arundo donax* on riverine fish: a call for action?

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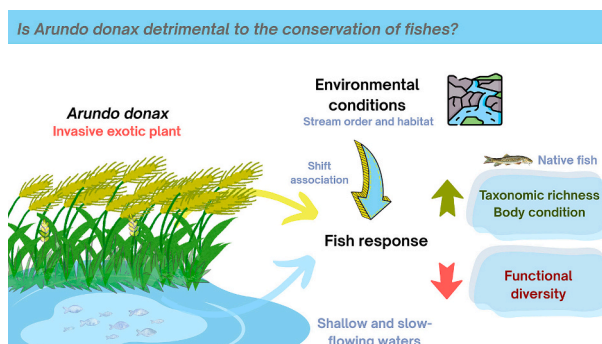
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HIGHLIGHTS

- *Arundo donax* typically occurs in low land, shallow, slow-flowing waters.
- There was correlative evidence for positive effects on native fish richness and individual body condition.
- There was correlative evidence for negative effects on overall functional diversity of fish assemblages.
- Stream order and local habitat conditions may shift these fish-*A. donax* associations.
- *A. donax* should not be regarded as always detrimental to fish conservation.

GRAPHICAL ABSTRACT



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ABSTRACT

Studies that investigate the effects of a given invasive exotic species within real-world contexts are essential for informing effective management decisions. Here, we used extensive surveys of stream reaches in north-eastern Spain to test whether the presence of the widely distributed invasive exotic riparian plant *Arundo donax* is detrimental to the conservation of riverine fishes. To explore potential impacts of *A. donax* at different temporal scales, we examined fish responses using indicators of relatively recent effects (body-condition index) and longer lasting effects (functional diversity indices, taxonomic richness, and the relative abundance of 12 fish species). We found correlative evidence for net positive effects of the presence of *A. donax* on native fish richness and body condition but negative effects on the overall functional diversity of fish assemblages, including invasive exotic and translocated native fish species. Our analyses also revealed significant interactions between *A. donax* and local stream conditions, suggesting that these net effects of the plant on fish might shift in direction in some circumstances. In particular, several indicators at the fish community scale support that the presence of *A. donax* may be beneficial to fishes in streams with high Strahler order values, in-stream habitat diversity and lack of

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channelization. The plant may provide shelter and refugia to fish in these medium, low-land Mediterranean streams with typically poor cover of high riparian vegetation. Therefore, without overlooking the serious threats caused by biological invasions, this study illustrates that, at least under specific environmental conditions, the local removal of *A. donax* alone may not achieve the desired ecological outcomes if pre-existing fish-habitat relationships are not taken into account.

1. Introduction

Invasive exotic plants pose a significant threat to global biodiversity (Vilà et al., 2024), alongside climate change, habitat degradation, chemical pollution, and overharvesting (Pyšek and Richardson, 2010; Reid et al., 2019). Global and regional policies such as the Convention on Biological Diversity (Dobson, 2005), the Decade on Ecosystem Restoration (EC, 2022) or the Invasive Exotic Species of Union Concern Act (EU 1143/2014) urge states to address these global impacts and reverse the current biodiversity crisis. However, management actions are constrained by limited budgets, the need to prioritize human impacts, and the often context-dependent invasive exotic species impacts (Gallardo et al., 2016; García-Díaz et al., 2022; Lopez et al., 2022). Preventive measures and early eradication are arguably the most effective management strategies against biological invasions (Lopez et al., 2022; Vilà et al., 2024). Nevertheless, when these fail, studies demonstrating the effects of a given invasive exotic species within real ecological contexts become essential to promote targeted management interventions.

Long-term field studies, coupled with pertinent experiments, are crucial for detecting the ecological impacts of invasive exotic plants and for understanding the underlying mechanisms involved (Strayer et al., 2006; Jeschke et al., 2014; García-Díaz et al., 2022). However, many invasive exotic species do not have associated long-term studies, and the experiments required for understanding the ecological responses are difficult to implement at relevant ecological scales for large-bodied, long-lived species, such as many vertebrates (e.g. Carpenter, 1996; Kreyling et al., 2018). To address these limitations, one approach is to examine animal responses in the field at various levels of biological organization (Colin et al., 2016). Each level provides insights into potentially lethal and sublethal effects at different temporal scales, ranging from weeks (body-condition responses) to months and years (community-level responses) (Stevenson and Woods Jr, 2006; Friberg et al., 2011). Community-level studies also can reveal habitat avoidance if a species is absent from a community in which it is expected to be present (Adams, 2004; Hammill et al., 2015). Despite the complementarity of these responses demonstrated in other research fields (Colin et al., 2016; Caquet and Lagadic, 2021), no previous study to our knowledge has simultaneously used them to investigate the effects of an invasive exotic plant species on vertebrates.

The giant reed (*Arundo donax* L.) (F. Poaceae) is an important candidate species for applying this research framework. Originating in southern Asia and the oriental Mediterranean, the reed has been introduced into Africa, Europe, Oceania, and the Americas, predominantly for erosion control (Jiménez-Ruiz et al., 2021). *Arundo donax* forms dense, cane-like stands that outcompete native plant species through a combination of shading, phytotoxins, fast growth, and the accumulation of leaf litter and rhizomes (Jiménez-Ruiz et al., 2021). The habitat-induced alterations, a low nutritional value and toxicity to native herbivores and decomposers have the potential to disrupt entire food-webs (Herrera and Dudley, 2003; Maceda-Veiga et al., 2016). However, these cascading effects have been little studied in vertebrates (Kisner, 2004; Bruno et al., 2019; Hardesty-Moore et al., 2020), hindering our ability to predict the multitrophic impacts of invasion by *A. donax*.

Riverine fish assemblages are promising sentinels for investigating the effects of invasion by *A. donax* on higher-order consumers. Fishes are apex consumers within many riverine food webs, are prey for birds and mammals, and are ecologically diverse (Winfield and Nelson, 2012;

Colin et al., 2016). The latter characteristic allows the calculation of functional diversity (FD) indices for local assemblages (Villéger et al., 2008; Mouchet et al., 2010). FD indices capture the variation in ecological traits among species within an assemblage, potentially summarizing the species' functional roles in the ecosystem (Villéger et al., 2008). FD indices have proven to be effective tools for detecting the effects of human impacts, including altered hydro-morphology and water quality, on fish assemblages (e.g. Colin et al., 2018; Stefani et al., 2020; Takács et al., 2021). Moreover, the loss of sensitive species is a well-documented response to various impacts (Kolkwitz and Marsson, 1909; Villéger et al., 2010), so that changes in the taxonomic and functional structure of fish assemblages may be complementary indicators of the impact of invasion by *A. donax* on riverine fishes at the community level.

Body-condition indices based on mass-length relationships, such as the Scaled Mass Index (SMI), provide a non-lethal measure to detect potential sub-lethal human-impact effects on animals (Peig and Green, 2009). The diagnostic value of SMI arises from its standardization of body mass for a fixed body length, effectively accounting for factors affecting an animal's weight or shape (Peig and Green, 2009). SMI has been shown to be a proxy for an animal's fitness (Peig and Green, 2009) and proved to be effective for detecting the effects of various forms of water and habitat degradation on fishes (e.g. Maceda-Veiga et al., 2014; Cano-Rocabayera et al., 2020; Ahnich et al., 2025) but still not the invasion by *A. donax*. A study examining changes in FD measures, taxonomic richness, relative abundances, and SMI values in fishes, as higher-order consumers, should help to detect and provide valuable insights into the ecological consequences of *A. donax* invasion in rivers.

This study was conducted in 14 streams in north-eastern Spain (99,700 km²). The study area has species with broad distributions, such as brown trout (*Salmo trutta*), many invasive exotic species, including common carp (*Cyprinus carpio*) and bleak (*Alburnus alburnus*), and many endemic species as it occurs in other fish faunas from Mediterranean-climate regions (Reyjol et al., 2007; Marr et al., 2010). We had three aims: (1) to identify the environmental characteristics of stream reaches invaded by *A. donax*; (2) to explore the potential direct impacts of *A. donax* presence at both the fish community scale (FD measures, taxonomic richness, and relative abundances) and the individual-fish scale (SMI body-condition index) along spatial gradients of stream environmental conditions; and (3) to determine whether variation in stream conditions has potential to modulate the associations between *A. donax* and fish responses. Our hypothesis was that *A. donax* would primarily occur in medium and low-land reaches due to its thermophilus nature (Jiménez-Ruiz et al., 2021) and that the associations with fish responses would be predominantly negative due to food deprivation, habitat alterations, or by the release of deleterious chemicals (Hardesty-Moore et al., 2020; Jiménez-Ruiz et al., 2021). Effects, if sub-lethal, should be detected by SMI values and, if these are more severe, should be detected by changes in fish community responses (Adams, 2004; Colin et al., 2016).

2. Materials and methods

2.1. Study area

The study area was the entire Ebro River catchment, which drains the Cantabrian and Pyrenean Mountains into the Mediterranean Sea, and 13 other catchments of smaller size, originating from high- and medium-

altitude mountain ranges in Catalonia and also discharging into the Mediterranean Sea (Fig. 1). The river network drains both well-preserved forested areas and areas very modified by human activities, including industries, urban developments, and agricultural lands. These modified areas induced a range of human impacts, including inputs of poorly treated wastewater and the presence of irrigation weirs and invasive exotic plant species (Sabater et al., 2009). The catchments mostly have montane and meso-Mediterranean climates (Rivas-Martínez and Rivas-Saenz, 2012), with summer droughts and a high likelihood of floods during autumn and winter (Gasith and Resh, 1999). Our data set reflected the diverse topography of the region, with elevations between 0 and 1814 m.a.s.l. However, large rivers, such as the main Ebro channel, were excluded because they require boats for sampling. In this case, we surveyed a lateral meander of the main river to render sampling methods comparable among sampling sites (see the section below). Thus, the studied reaches primarily represented the typical small- and medium-sized streams found in Mediterranean-climate regions, as they should be shallow enough (depth < 1.5 m) to be sampled by wading (CEN EN 14962 and EN 14011).

2.2. Fish surveys

We used fish data ($N = 535$ sampling sites) from several monitoring projects developed from 2003 to 2010 to assess the ecological status of streams in north-eastern Spain (Maceda-Veiga et al., 2014; Colin et al., 2018; Maceda-Veiga et al., 2018), as required by the European Water Framework Directive (Directive 2000/60/EC). Consequently, sampling sites ensured adequate spatial representation of the environmental and biological conditions within the studied river network. Fish sampling also adhered to an internationally standardized procedure (CEN EN 14962 and EN 14011) and was approved by relevant regional authorities, including the Catalan Water Agency, Confederación Hidrográfica del Ebro, and all participating Autonomous Governments. Each fish sampling consisted of a single-pass electrofishing method (Electracatch WFC4 gear, Wolverhampton, UK) during low-flow conditions in mid-

late summer. This period coincides with greatest fish-population stability and also avoids the effect of spawning events on fish mass (Aparicio et al., 2016; Meador et al., 1993). Each sampling site was a transect with a length 20 times the mean river width traversed in an upstream direction (CEN EN 14962 and EN 14011). The entire wetted width of the river was surveyed, with adjustments to electric power based on water electrical conductivity to ensure effective sampling while minimizing fish mortality (Meador et al., 1993). All stream reaches were sampled only once given the extensive area covered, and we estimated relative fish abundance based on catches per unit effort (CPUE; Meador et al., 1993).

All captured fish in each site were kept on shore in large buckets with battery-powered aerators until the end of the electrofishing survey. Then, specimens were identified to species and counted. For species with <40 individuals, all specimens were measured (± 1 mm) and weighed for wet mass (± 0.01 g). For species with ≥ 40 individuals, a representative subsample of 40 individuals was selected, ensuring that the subsample reflected the body-size distribution of the entire catch. Prior to measurements, fish were anesthetized using buffered MS-222 (0.02 %, Sigma-Aldrich St. Louis, MO, USA). After inspection, all fish were allowed to recover and were released alive at their capture location.

2.3. Fish responses at the community and individual scales

The fish-community response variables were functional diversity (FD) indices, the relative abundance of each fish species, and taxonomic richness. The response at the fish-individual scale was the Scaled Mass index.

To characterize the functional diversity of fish assemblages at each sampling site, we used three Functional Diversity (FD) indices proposed by Colin et al. (2018) for our study area, namely functional entropy (FEnt), functional specialization (FSpe), and functional originality (FOri). These indices effectively address the frequent occurrence of a single fish species per site in Mediterranean rivers, which can lead to computational issues with other FD indices (Maire et al., 2015; Colin



Fig. 1. Locations of the stream surveys conducted in north-eastern Spain to identify the characteristics of stream reaches invaded by the riparian plant *Arundo donax* ($N = 535$ sampling sites). Red dots indicate the location of the pair of stream reaches with and without *A. donax* with comparable environmental conditions for the paired-site approach ($N = 102$ sites in total, see methods) in which we explored the associations between *A. donax* and fish responses at the individual scale (body-mass index) and community scale (functional diversity, taxonomic richness and relative density of 12 fish species).

et al., 2018). As detailed in Colin et al. (2018), FD indices were calculated using various measures of dissimilarity among the nine traits of a given species relative to the trait composition of the entire dataset ($N = 535$ sampling sites). The nine traits were: (1) reproductive strategy (e.g., parental care, ovoviviparous); (2) fecundity (egg number); (3) trophic guild (e.g., herbivore, piscivore, invertivore); (4) swimming position (e.g., benthic, pelagic); (5) river-velocity preference (e.g., fast, low); (6) body-shape ratio (total length/maximal body depth); (7) swimming factor (minimum caudal peduncle depth/maximal caudal fin depth); (8) average body mass (g); and (9) maximum reported age. The limited ecological knowledge about some fish species prevented the inclusion of more traits. Our inferences are based on adult stages, as assumed in other studies at large spatial scales (Colin et al., 2018; Stefani et al., 2020). All FD indices were biomass-weighted because mass is more closely related to the functional impact of a species in the ecosystem than density (Friberg et al., 2011). We calculated FD indices considering the traits of both native and invasive exotic species jointly because all species together were regarded as playing the overall ecological role in the ecosystem at the time of the sampling.

Given the specific management actions prescribed for native and invasive exotic species under legislation (e.g. EU 1143/2014), we also used the number of native, translocated, and exotic fish species at each sampling site as other fish community response variables. This distinction was important because invasive exotic and translocated native species have demonstrably different responses to environmental impacts in our study area, probably due to their different evolutionary histories but both can act as invasive species (Maceda-Veiga et al., 2022). Invasive exotic fish species (hereafter 'exotic fish') were the species that were not present historically within the Iberian Peninsula ecoregion (Maceda-Veiga et al., 2022), while invasive translocated native species (hereafter 'translocated native fish') were species introduced from another basin within the studied ecoregion where they were native. Last, considering the significance of species abundance in fish-population assessments (Meador et al., 1993; Adams, 2004), we used a species composition matrix with CPUE of each fish species as another fish community response.

For a subset of our dataset containing the most frequently caught and most abundant fish species, we calculated the Scaled Mass Index (SMI) for each species following the methodology outlined by Peig and Green (2009). The SMI formula is $SMI = W_i[L_0/L_i]^{b_{SMA}}$, where: W_i and L_i are the weight and length of each specimen, respectively; L_0 is the arithmetic mean of the analysed data set for each fish species; and b_{SMA} is the scaling exponent, corresponding to the slope of a standardized major axis (SMA) regression of the mass-length relationship. We used b_{SMA} values derived from a previous study conducted in our study area (Maceda-Veiga et al. (2014)).

2.4. Invasion by *A. donax* and environmental covariates

Within each sampled stream reach, we recorded the dominant riparian plant species based on percentage cover. Due to the original purpose of the data set, which was not specifically designed to study the effects of *A. donax* (see the Study Area section), we used presence/absence (P/A) data rather than cover values. We note that when present, *A. donax* tends to be a monoculture that covered >70 % of the entire riparian area, so P/A data are reasonable. Despite this limitation, the data set is valuable for our study because it allowed us to provide correlative evidence for the impact of *A. donax* presence on fish responses along spatial gradients of variation in stream environmental conditions. This approach allows an ecological realism that is difficult to achieve in manipulative experiments or more localized field studies (Friberg et al., 2011; Kreyling et al., 2018).

To facilitate the study of potential effects of invasion of *A. donax* on fishes within relatively comparable environments, we identified nearby pairs of sites with and without *A. donax* ($N = 102$ sites). While detailed

movement studies are not available for most of the studied fish species, we assumed that pairs of sites spaced ≥ 2 km apart would have a high probability of having multiple relatively resident fish species. Our assumption was based on the observation that medium-sized benthic barbels have been observed to move <20 m throughout the year (Aparicio and De Sostoa, 1999), and that pelagic chubs have a median home range of 2000 m (Capra et al., 2018). The only long-distance migratory fish species in our study was *A. anguilla*. However, other large-bodied species, such as *Salmo trutta* and *Luciobarbus graellsii*, undertake shorter reproductive migrations (Aparicio et al., 2016), which further emphasizes the importance of examining responses species-by-species, as we outlined above for CPUE and SMI. Therefore, we are confident that our results will reflect any potential impact of *A. donax* on fishes as a result of trophic interactions or habitat avoidance.

We used 11 covariates to characterize environmental conditions at each sampling site to account statistically for their effects when determining the associations between the presence of *A. donax* and fish responses. Prior to fish sampling, we measured in-situ temperature, pH, and electrical conductivity using a digital multiparametric YSI®. We used the colorimetric test kit VISOCOLOR® (Germany) to determine concentrations of ammonia (mg L^{-1}), nitrite (mg L^{-1}), nitrate (mg L^{-1}), and phosphate (mg L^{-1}). To reduce the number of covariates in subsequent modelling, ammonia and nitrite were grouped as $[\text{NH}_3 + \text{NO}_2]$ due to their high toxicity to aquatic fauna, while nitrate and phosphate were grouped as $[\text{NO}_3 + \text{PO}_4]$ due to their relatively lower toxicity (Noga, 2010). Following fish sampling, we traversed the entire sampled area to calculate mean water depth and water velocity at 20-m intervals, using three measurements along perpendicular transects to the water flow.

To further characterize habitat characteristics, we assessed habitat diversity and channel conservation using the U.S. Rapid BioAssessment Protocol adapted for Mediterranean streams (see in Maceda-Veiga and De Sostoa, 2011). This habitat-diversity measure, scored on a 1–10 scale, considers various forms of in stream fish refuge, including the presence of deep pools, which are crucial for fish survival during Mediterranean droughts (Gasith and Resh, 1999; Aparicio and De Sostoa, 1999). The channel conservation score (0–25 scale) decreases with stream channelization, that is the presence of weirs and concrete walls on stream banks (Munné et al., 2003; Maceda-Veiga et al., 2018). We recorded the geographical factors basin name, elevation, and Strahler stream order number of each sampling site to account for its spatial location along the river network. The Strahler stream-order number characterizes the hierarchical structure of streams within a drainage basin according to the branching pattern of tributaries, with first-order streams being the smallest unbranched headwater streams that increase in order only at the confluence of two streams of the same order downstream (Strahler, 1952).

2.5. Statistical analyses

First, we calculated Pearson's pairwise correlations coefficients among the 11 environmental covariates to assess potential issues of collinearity. Second, we used hierarchical Bayesian models to: (1) establish associations between *A. donax* and the environmental covariates to identify the characteristics of the stream reaches in which *A. donax* was present (Model 1); and (2) establish associations of the presence of *A. donax* with responses at the fish community scale (FD measures, variation in multiple species CPUEs, and taxonomic richness) (Models 2–4) and at the fish individual scale (SMI) (Model 5), while accounting for the effects of environmental covariates. Model 1 used the entire data set ($N = 526$) and the paired-site approach in Models 2–5 used a subset ($N = 102$ sites for Models 2–4; 1830 individual fish records for Model 5). Details on model structures are stated in Table 1, with further details provided in Table S1 and <https://github.com/jdyen/adonax>. Briefly, all continuous covariates were standardized to a comparable scale by subtracting their mean and dividing by the

Table 1

Description of statistical models. The linear predictor column is a simplified representation of the model structure on the link scale, intended to convey the main predictor variables and any group-level terms. Full model descriptions are included in Table S1. *Environment* and *Fish species* refer to multiple predictor variables (described in main text). The notation ($x \times y$ | *Species*) denotes species-specific effects of variables x and y and their interaction, and implicitly includes species-specific model intercepts. Origin, Basin, Pair, Site, Order, Family, and Genus were included as grouping variables (i.e., random effects). Model 2 was fitted as three separate models (one for each FD measure), all with the same model structure.

Model	Model type	Response variable	Linear predictor
Model 1	Logistic regression	Presence/absence of <i>A. donax</i>	Environment + Basin
Model 2	FD measures	Biomass-weighted FEnt, FS _{pe} , and FOr of all detected species	Environment $\times$ <i>A. donax</i> + Basin + Pair + Site
Model 3	Negative Binomial regression model	Species richness of native, translocated, and exotic species	(Environment $\times$ <i>A. donax</i> Origin) + (<i>A. donax</i> Origin) + Basin + Pair + Site
Model 4	Negative Binomial regression model	CPUE of fish species with less than 90 % zero values (12 species)	(Environment $\times$ <i>A. donax</i> Species) + Origin + Basin + Pair + Site
Model 5	Lognormal linear model	Scaled mass index (individual size standardized within species)	(Environment $\times$ <i>A. donax</i> Species) + (<i>A. donax</i> Species) + Origin + Basin + Pair + Site + Order + Family + Genus

standard deviation. Models were built to include the presence of *A. donax* and environmental covariates as main effects along with the corresponding pair of interactions between the covariates and the presence of *A. donax*. The latter explored whether the effects of the presence of *A. donax* on fish responses had potential to be modulated by local stream environmental conditions (i.e. the interaction term *A. donax* $\times$ environmental covariates was deemed important).

Model 1, for the presence of *A. donax*, was a logistic regression, blocked for basin (i.e., random effect) to account for the potential non-independence of stream reaches sampled within a basin. Model 2, for FD measures, was a lognormal regression, blocked for basins and pairs of sites to study the effects of invasion by *A. donax* within the most comparable sampling sites. Models were fitted separately for each FD measure, but all three models had the same structure so are grouped under Model 2 here. Model 3, for fish taxonomic richness, was similar to Model 2 but used a Negative Binomial response distribution and included grouping terms to account for species origin (native, exotic, and translocated). Model 4, for all fish species CPUEs, was a Bayesian version of a generalized linear mixed model for a species composition matrix and allowed intercepts and associations of covariates or the presence of *A. donax* with fish CPUEs to differ among fish species. All CPUE values were multiplied by a factor of 10 and rounded to the nearest integer, enabling use of a Negative Binomial model. Although a continuous, non-negative distribution (e.g., Lognormal-hurdle model) might have been used to model CPUEs directly, such approaches introduce less-interpretable parameters than the Poisson or Negative Binomial models. Last, Model 5, for SMI values, used a log-normal structure and included blockings to account for non-independence of measurements on individuals of the same genus, family, and order and of individuals captured in the same sampling site.

We used Normal (0, 5) priors for all fixed terms in the linear predictor, and used exchangeable Normal (0, σ) priors for the grouping terms (random effects). The standard deviations of these priors were assigned half-Normal (0,2) distributions, restricted to positive values. We used a Student-t (3,0,1) prior for the Negative Binomial dispersion parameter, which was specified independently for each species. We fitted all Bayesian models using Stan 2.32.2 (Stan Development Team,

2024a), called from R 4.4.1 (R Core Team, 2024) with the *rstan* 2.32.6 package (Stan Development Team, 2024b). We based inferences on 4 chains of 10,000 iterations each, discarding the first 5000 iterations (warmup) and retaining every fourth iteration thereafter, which resulted in 5000 posterior samples. We assessed sampler performance with Gelman-Rubin statistics (Rhat) and the effective number of samples (Neff), with Rhat values near 1 indicative of well-mixed chains and Neff values near or exceeding 1000 indicating sufficient independent samples. We also calculated model fit based on the area under the receiver operating curve (AUC) for Model 1 and correlations (based on Pearson's r) between fitted and observed values for Model 2–5. We used posterior predictive checks to assess whether model structures were suitable for our data.

The effects of *A. donax* on fish responses in isolation or in interaction with the environmental covariates were judged based on the strength and direction of standardized regression coefficients of the models (i.e. effect sizes). Notwithstanding causation cannot be definitely established by correlative studies, effect sizes are measures of the direct effects of *A. donax* on fish responses after statistically accounting for the effects of environmental covariates. Effects were deemed strong when the error bars of the median fitted values of the models, representing the 95 % credible intervals (CIs), did not cross zero. Effects were considered moderate when the median fitted values differed clearly from 0 despite CIs crossing 0. Effects were deemed weak or nearly absent in all other situations. The presence of *A. donax* was considered to have a modulatory effect on fish-environment associations if the slopes of fish responses along environmental gradients differed depending on whether the plant was present or absent.

3. Results

3.1. Characteristics of the stream reaches invaded by *A. donax*

The likelihood that *A. donax* was present strongly decreased with elevation and with river water depth (Fig. 2). The presence of *A. donax* was moderately associated with reduced habitat diversity, modified river channel morphology, lower pH, or slow-flowing waters (Fig. 2). The associations between the presence of *A. donax* and values of

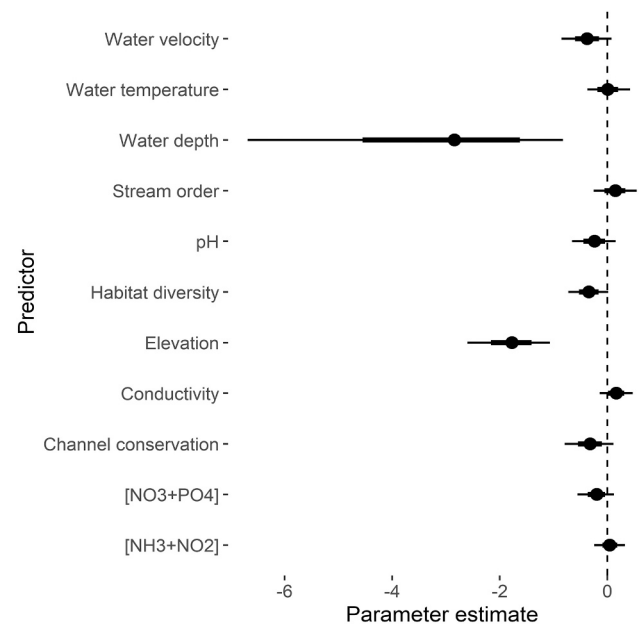


Fig. 2. Characteristics of the stream reaches successfully invaded by the plant *A. donax* based on the 11 environmental descriptors. Points are median fitted values, thick bars span 66 % credible intervals, and thin bars span 95 % credible intervals. Estimates are shown on a logit scale.

nitrogen and phosphorous, conductivity, Strahler stream order or water temperature were very weak or nearly absent (Fig. 2).

3.2. Potential direct effects of *A. donax* on fish responses

Models for responses at the fish community and individual scales revealed moderate to weak associations with the presence of *A. donax* after accounting for the effects of the 11 environmental covariates (Table 1 and Table 2). All three FD indices (FEnt, FSpe, and FOr) showed moderate negative associations with the presence of *A. donax* (Fig. 3). For taxonomic richness, native fish species richness was moderately positively related to presence of *A. donax*, while translocated native fish richness had a negative association (Fig. 3). There were no clear association for exotic fish species richness (Fig. 3). For the species composition approach, the presence of *A. donax* did not substantially affect CPUE values of most of the 23 fish species (i.e. fitted value on the zero line) (Fig. 3). However, there was moderate evidence for CPUE values of *A. alburnus* (ALAL), *L. graellsii* (LUGR), *C. carpio* (CYCA) increasing with presence of *A. donax*, while *B. haasi* (BAHA) CPUE vales decreased (Fig. 3). For the fish-individual approach (SMI), there was moderate evidence for 11 out of the 12 species having a positive association with presence of *A. donax* (Fig. 3). The fitted value of *Parachondrostoma miegii* (PAMY) was on the zero line (Fig. 3).

3.3. Potential interactive effects of *A. donax* and the environment on fish responses

Besides direct associations between *A. donax* and fish-response variables, there was some evidence that environmental covariates may modulate the effects of the presence of *A. donax* on fish responses. To facilitate the visualization of these interactive effects, only the covariates whose associations with fish responses were most substantially altered by the presence of *A. donax* are shown. These covariates were the geographical factor stream order, the physical habitat descriptors channel morphology, habitat diversity, and water velocity, and the water-quality variables concentrations of ammonia and nitrite (NH3 + NO2) and conductivity (Figs. 4–7; see the rest of covariates in Fig. S1–S4). For the geographical factor, all three FD measures had positive associations with stream order, particularly at sites with *A. donax* (Fig. 4). Similarly, the taxonomic richness of exotic, native, and translocated native fish species increased substantially with stream order, again more prominently at sites with *A. donax* (Fig. 5). The presence of *A. donax* had an overall weak impact on the associations between stream order and CPUE values for all 23 fish species although associations between stream order and CPUE tended to be more positive at sites with *A. donax* (Fig. 6). The presence of *A. donax* weakly affected the associations between stream order and SMI values of the 12 selected fish species *A. donax* (Fig. 7).

For the physical habitat descriptors, high channel conservation scores (i.e. non-channelized stream reaches) were associated with greater FD measures when *A. donax* was present (Fig. 4). For taxonomic richness, the presence of *A. donax* was associated with greater native taxonomic fish richness across all channel types but patterns for exotic and translocated native fish were more variable (Fig. 5). Furthermore,

Table 2

Estimates of model fits based on area-under-curve (AUC) for logistic regressions and r^2 based on Pearson's r for the three models of count or continuous data.

Model	Fit statistic	Value
Model 1	AUC	0.88
Model 2 (FEnt)	r^2	0.93
Model 2 (FSpe)	r^2	0.90
Model 2 (FOri)	r^2	0.91
Model 3	r^2	0.97
Model 4	r^2	0.81
Model 5	r^2	0.84

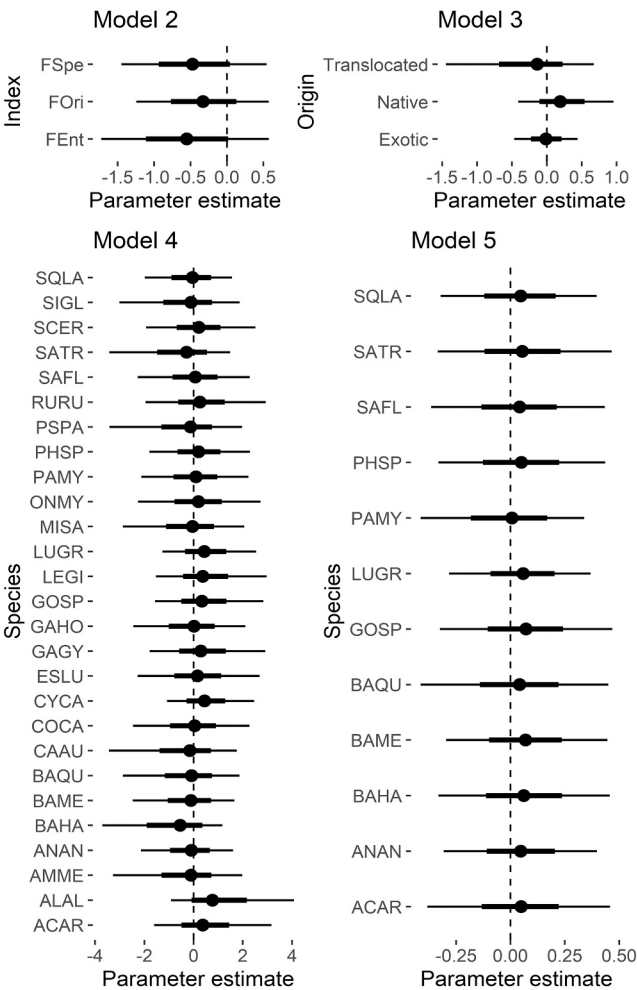


Fig. 3. Correlative evidence for the direct effects of the presence of *A. donax* at both the fish-community scale (Functional diversity indices, Model 2; Taxonomic richness, Model 3; Species composition CPUEs, Model 4) and fish individual scale (SMI, Model 5). Points are median fitted values, thick bars span 66 % credible intervals, and thin bars span 95 % credible intervals of model coefficients on a log scale accounting the effects of the environmental covariates. See species acronyms in Table S2.

the association between channel conservation and CPUE values for fish species was negative when *A. donax* was absent but positive when *A. donax* was present (Fig. 6). This association with channel conservation was consistently negative for SMI values (Fig. 7). Concerning habitat diversity, its positive effect on FD measures was more marked at sites with *A. donax* (Fig. 4). A similar trend was observed for the taxonomic richness of native, exotic, and translocated native fish species (Fig. 5). The presence of *A. donax* weakly affected the associations between habitat diversity and fish CPUE values, which were positive in all cases (Fig. 6). However, there was weak evidence that the association between habitat diversity and SMI values was more negative at sites with *A. donax* (Fig. 7). The absence of *A. donax* also tended to promote FD measures of fish assemblages and the taxonomic richness of native fish species at high stream water velocities (Figs. 4–5). However, the associations between water velocity and fish CPUEs or SMI values became more negative at sites with *A. donax* (Figs. 6–7).

The effect of *A. donax* on the impacts of all water-quality variables on fish responses were generally weaker than geographical and physical habitat factors (Figs. 4–7). Despite this, the presence of *A. donax* tended to be associated with lower FD measures at low ammonia and nitrite levels, and lower taxonomic fish richness measures at high ammonia and nitrite levels (Figs. 4–5). The presence of *A. donax* weakly influenced the

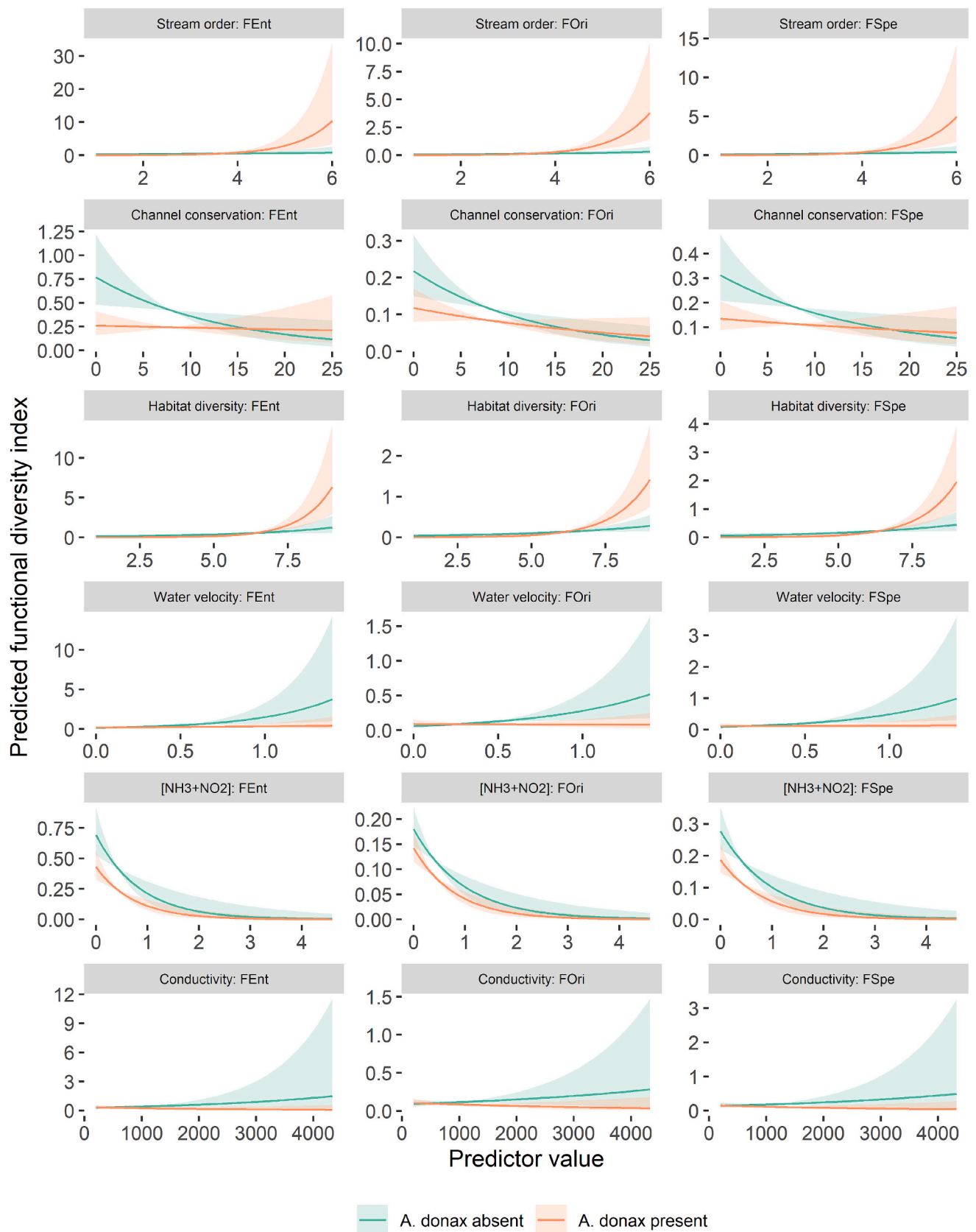


Fig. 4. Correlative evidence for the interactive effects between the presence or absence of *A. donax* and the most relevant environmental covariates on the three functional diversity indices of fish assemblages, namely Functional Entropy (FEnt), Functional Originality (FOri); and Functional Specialization (FSpe). Shaded lines indicate 66 % credible intervals.

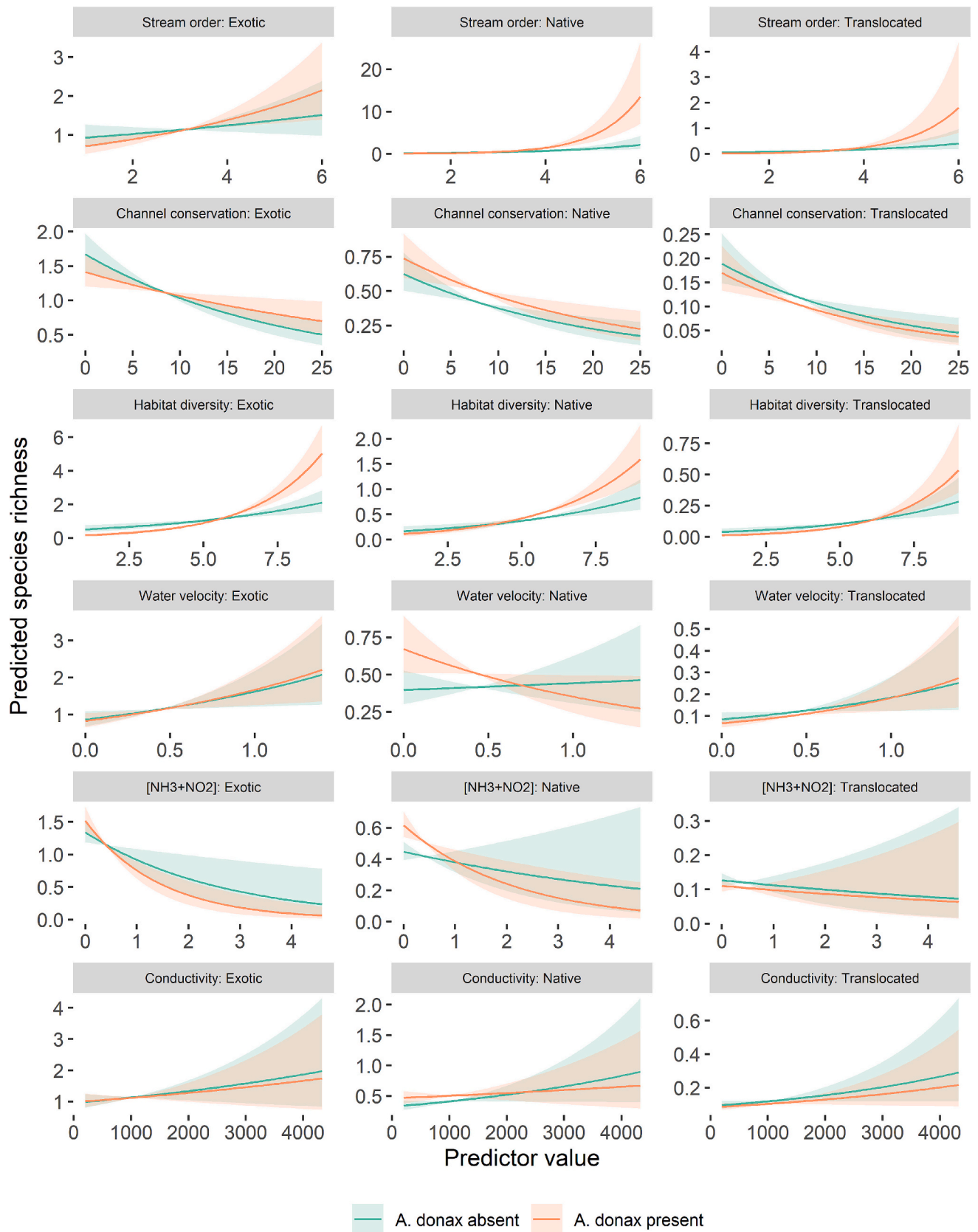


Fig. 5. Correlative evidence for the interactive effects between the presence or absence of *A. donax* and the most relevant environmental covariates on the taxonomic richness of exotic, native, and translocated native fish species. Shaded lines indicate 66 % credible intervals.

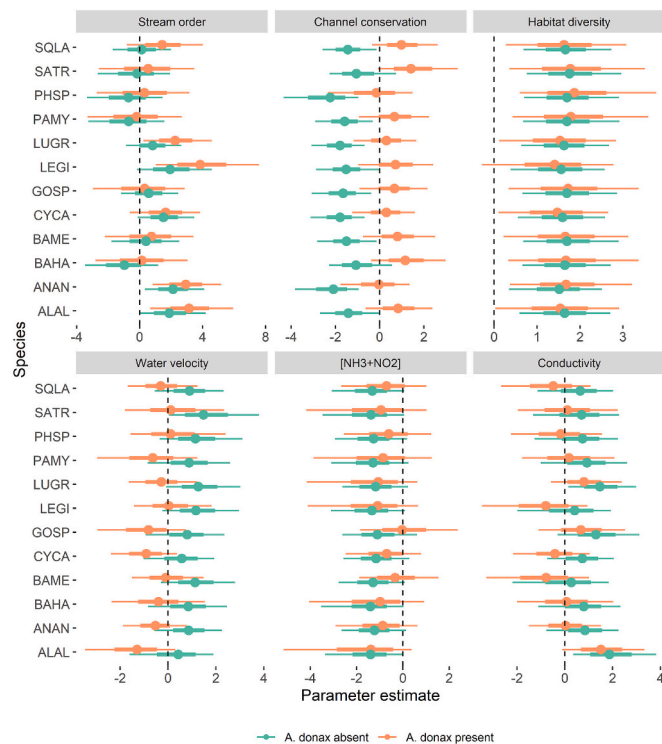


Fig. 6. Correlative evidence for the interactive effects between the presence or absence of *A. donax* and the environmental covariates highlighted in previous analyses on individual CPUE of fish species present in >10 % of sampling sites. Points are median fitted values, thick bars span 66 % credible intervals, and thin bars span 95 % credible intervals of model coefficients on a log scale. See species acronyms in Table S2.

associations between concentrations of ammonia and nitrite and fish CPUEs or SMI values (Fig. 6–7). Regarding conductivity, it showed more negative associations with FD measures and fish taxon richness at sites with *A. donax* (Figs. 4–5). Furthermore, the presence of *A. donax* shifted the association between conductivity and fish CPUEs to more negative values (Fig. 6). The same trend was observed for SMI values (Fig. 7).

4. Discussion

Our surveys in north-eastern Spain provide correlative evidence that the presence of *A. donax* has positive direct effects on native fish taxon richness and the SMI body condition values of many native fishes after controlling for the effects of environmental covariates. However, the presence of *A. donax* was also associated with a decrease in overall fish functional diversity (FD), including invasive exotic and invasive translocated native fish species (hereafter exotic and translocated native fish species, respectively). Examining interactions between *A. donax* presence and environmental covariates revealed complex patterns, but our results indicated that the effects of *A. donax* on responses at both the fish community scale and fish individual scale have potential to be modulated by stream order and local environmental conditions. These findings partially align with this plant being listed as one of the 100 world's worst invasive species (Jiménez-Ruiz et al., 2021) but also emphasize the context-dependent nature of invasive plant impacts (Tasker et al., 2022; Vilà et al., 2024). We discuss potential mechanisms behind these contrasting outcomes and the management implications.

4.1. Associations of *A. donax* presence with stream environmental factors

The negative effects of *A. donax* on fish were observed primarily in low-elevation and shallow streams within our study area. This distribution is concordant with the thermophilus nature of *A. donax* and with

shallow streams potentially providing the plant with more stable substrate for its establishment and growth (Jiménez-Ruiz et al., 2021). Our results also revealed that *A. donax* often occurs in stream reaches affected by other human impacts; its presence correlated positively with reduced in-stream habitat diversity, or a highly modified morphology of the stream channel. These alterations are common in low-land Mediterranean streams, where water abstractions and inputs from urban and agricultural activities often concentrate (Sabater et al., 2009). Despite the inevitable collinearity among any set of environmental variables (Graham, 2003), our sampling design and statistical approach reduced its influence on our findings. We used a paired-site sampling design to explore the effects of *A. donax* within the most comparable stream reach conditions and accounting for variation in these local stream conditions including in models a set of 11 environmental covariates related to geography, physical habitat descriptors and water-quality variables. Pairwise correlations among these covariates were low (mean absolute Pearson's correlation = 0.18; maximum value = 0.48) and our modelling visualized the marginal effects of the presence of *A. donax* on fish responses, that is statistically accounting for the fact that there are not true sampling replicates in real-world conditions. Therefore, although our correlative study cannot establish cause-effect relationships, it offers a more ecologically realistic assessment than spatially restricted experiments by examining impacts across a broader spatial scale and under more naturally variable environmental conditions (Friberg et al., 2011; Kreyling et al., 2018).

4.2. Potential direct effects of *A. donax* on fish responses

While our analyses identified some potential direct effects of *A. donax* on fish, these associations ranged from weak to moderate in strength. This aligns with previous research highlighting that the primary factors governing the structure of stream fish assemblages are geographical factors, hydro-morphological alterations, and water-quality deterioration, alongside the introduction of invasive exotic species (Moyle, 1995). Although riparian vegetation is often considered a hydro-morphological factor (Pusey and Arthington, 2003), its impact on the fish assemblage structure in our study likely was less pronounced than that of other hydro-morphological alterations, such as the presence of concrete stream banks and bridges (Kawaguchi et al., 2006; Liu et al., 2022). These habitat alterations reduced the scores of two covariates, namely natural stream channel morphology and in-stream habitat diversity (Maceda-Veiga et al., 2018). These two variables were not evidently affected by the presence of *A. donax* as occurs with total scores of habitat indices widely used by regional managers such as the QBR index, which decreases with the presence of invasive exotic plants (Munné et al., 2003).

Our analysis suggested that *A. donax* had some direct effects on both fish assemblage structure and fish individuals, as indicated by the Scaled body Mass condition Index (SMI) (Peig and Green, 2009). Three FD indices consistently showed that fish assemblages in streams with *A. donax* had less trait diversity. This reduction in functional originality and specialization of fish assemblages is often associated with environmental degradation, which lead to the replacement of unique species with functionally redundant ones (Villéger et al., 2010; Colin et al., 2018). In our study, this appeared to occur alongside an increase in native fish species richness and a decrease in translocated native fish species. The net reduction in FD suggests that often translocated native fish species in the study area, such as *S. trutta* and *P. miegii*, have unique trait combinations; indeed, the former is the unique salmoniform in the assemblage and *P. miegii* mostly feeds on biofilm (Aparicio et al., 2016). At the same time, patterns for FD indices and taxonomic richness indicate certain functional redundancy among the extant native species, as has been suggested for other European fish faunas dominated by cyprinids (Buisson et al., 2013; Toussaint et al., 2018). However, the effects of *A. donax* presence on fish FD warrants further investigation because using a single value per trait and species probably offers a coarser

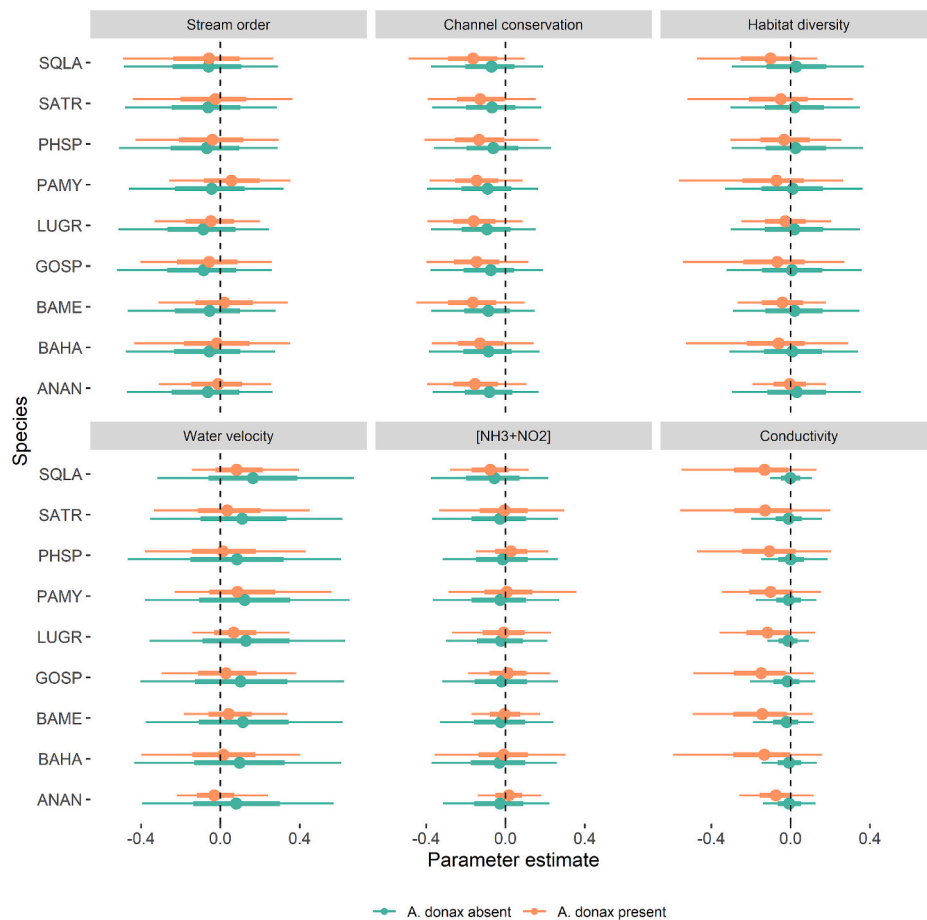


Fig. 7. Correlative evidence for the interactive effects between the presence or absence of *A. donax* and the environmental covariates highlighted in previous analyses on individual Scaled Mass Index values (as proxy for fish body condition) of fish species present in >10 % of sampling sites. Points are median fitted values, thick bars span 66 % credible intervals, and thin bars span 95 % credible intervals of model coefficients on a log scale. Points are median fitted values, thick bars span 66 % credible intervals, and thin bars span 95 % credible intervals of model coefficients on a log scale. See species acronyms in Table S2.

picture of the impacts than more detailed studies, such as the use of stable isotopes to detect changes in the trophic niche of species (Gutmann Roberts and Britton, 2018).

The presence of *A. donax* was not associated with a reduction but rather with an increase native fish species richness, suggesting the impact of *A. donax* on the stream biota may be less severe than previously believed (Kisner, 2004; Maceda-Veiga et al., 2016; Bruno et al., 2019). Our hypothesis is that *A. donax* can provide shelter and shading, particularly benefiting native fishes in medium and low-land stream reaches that often have a poor riparian conservation status (Sabater et al., 2009). This idea is supported by the positive associations observed for SMI values in 11 of the 12 species examined, although with high degree of uncertainty. SMI standardizes fish mass to fish length and is a proxy for energetic reserves (Peig and Green, 2009), so that fish individuals, within comparable lengths, had potentially more energy reserves in the presence of *A. donax*. Fish may have saved energy because the intricate underwater *A. donax* patch might reduce predation risk and increase foraging efficiency of the fish. Our field observations support that fish tended to aggregate in the pools excavated by stream flow under the *A. donax* patch (AMV, NC and AS pers. observ.). It is unlikely that *A. donax* could provide more food resources to insectivorous fish, which is the dominant trophic guild in the fish assemblage studied (Aparicio et al., 2016; Colin et al., 2016). Previous studies reported that *A. donax* leaf litter reduces the growth of aquatic insects (Going and Dudley, 2008) and the abundance and richness of various groups of riparian arthropods (Herrera and Dudley, 2003; Maceda-Veiga et al., 2016). In any case, there is trophic plasticity among fish and some native

or exotic and translocated native fish species potentially favoured by the presence of *A. donax* often show high degrees of omnivory (e.g. *Luciobarbus graellsii*, *Cyprinus carpio*), as is common among cyprinids (Winfield and Nelson, 2012; Sánchez-Carmona et al., 2012).

4.3. Potential interactive effects of *A. donax* and environmental conditions on fish responses

Beyond potential direct impacts, our analyses revealed that the effect of *A. donax* presence on fish responses is contingent upon the characteristics of the invaded stream reach and the specific fish responses employed. These intricate relationships underscore the importance of utilizing indicators that evaluate environmental impacts across multiple levels of biological organization of the studied faunistic group, rather than relying on single response variables (Colin et al., 2016; Caquet and Lagadic, 2021). In our study, fish community-level responses, notably FD, taxonomic richness, and, to a lesser extent, fish CPUEs, exhibited the most pronounced associations with *A. donax* along spatial gradients of environmental variation. Therefore, while acknowledging the necessity of incorporating FD measures in biomonitoring studies (Elmqvist et al., 2003; Cadotte et al., 2011), we also emphasize the importance of including commonly used taxonomic measures. These are likely more readily interpretable for managers, given that conservation actions still remain largely focused at the species level (Margules and Usher, 1981; Tidball, 2023). Similarly, assessing individual fish responses, such as the SMI body condition index, is also relevant. The weak but often negative association between *A. donax* and SMI values under specific

environmental conditions may suggest that the positive associations observed at the fish community scale could be transient. If the environmental conditions prevail, they might reduce too much the energetic reserves of individuals—the fundamental unit of all ecological processes and patterns seen (Begon and Townsend, 2020; Caquet and Lagadic, 2021).

Among geographical factors, our analysis revealed a positive correlation between higher stream order values and fish FD indices, especially in the presence of *A. donax*. Given that stream order is a good proxy for stream size (Strahler, 1952), this suggests a general trend of increasing ecosystem resources and, consequently, functional diversity with stream size (Vannote et al., 1980). The presence of *A. donax* may amplify this association by providing riparian resources that are often scarce in downstream reaches. At high stream order numbers, the presence of *A. donax* was also positively associated with native, translocated native and exotic fish richness, implying that a positive effect on FD indices at higher stream order values may indicate a species replacement with others that promote trait diversity within the fish assemblage (Villéger et al., 2010; Maceda-Veiga et al., 2017; Colin et al., 2018).

Evidence further supporting that *A. donax* may benefit fish under certain environmental conditions included the positive correlations observed between functional diversity and native fish richness with habitat diversity at sites where *A. donax* was present. In streams exhibiting relatively high instream habitat diversity, this plant likely enhances shelter and refugia through leaf litter deposition and stream flow modification, a role similar to that of other large riparian vegetation (Pusey and Arthington, 2003; Tasker et al., 2022). Notably, extensive *A. donax* patches may facilitate the formation of larger pools, which are critical for fish survival during the drought periods characteristic of Mediterranean-climate streams (Gasith and Resh, 1999; Aparicio and De Sostoa, 1999). The capacity of this plant to influence stream morphology could explain the greater FD, native fish richness, and fish CPUE values recorded in stream reaches with *A. donax* and high channel conservation scores. These scores mean stream reaches lack concrete stream banks (Munné et al., 2003; Maceda-Veiga et al., 2018), so it was possible a deep contact between the stream bed and adjacent riparian area. However, in these habitat conditions, sites also had a greater richness of exotic and translocated native fish species, suggesting that removal or reduction of *A. donax* patches may have limited impact on the relative abundance of native, exotic or translocated native fish species. Despite this, our analyses also revealed a clear positive association between *A. donax* presence and native fish richness, particularly in slow-flowing waters. This finding might stem from the fact that *A. donax* is easily fragmented and transported by stream water (Coffman, 2020; Jiménez-Ruiz et al., 2021), potentially limiting its ability to create stable refugia and shelter for fish in high stream-water velocity environments.

The lack of positive associations between *A. donax* presence and fish responses at high levels of ammonia, nitrite, and conductivity suggests that this plant may have limited capacity to reduce their effects on fishes. Ammonia and nitrite are two highly toxic compounds to aquatic taxa (Noga, 2010). Similarly, high water conductivity is another indicator of stream water pollution (Kaushal et al., 2018; Reid et al., 2019) and natural water salinity, which can suppress *A. donax* growth (Allinson, 2017). Although our study was not designed to specifically examine *A. donax* as a water-treatment system, these findings align with the limited usage that *A. donax* has in phytoremediation of polluted waters compared to morphologically similar native plants in Europe such as *Phragmites australis* (Vymazal, 2011; Nsanganwimana et al., 2014). Our findings may also suggest that the leaf litter input from *A. donax* could further exacerbate water conductivity and toxic ammonia and nitrite levels in polluted streams compared to other plant species, as indicated by recent experimental evidence (Cano-Rocabayera et al., 2020).

5. Conclusions

This study, employing indicators of multiple levels of fish biological organization, suggests that the effects of *A. donax* presence on stream biota are not always detrimental. By examining fish—*A. donax* associations along varying environmental conditions, we found overall direct positive effects on native fish richness and the body condition of 11 fish species, including both upstream (e.g. *B. haasi* and *B. meridionalis*) and downstream (e.g. *A. anguilla* and *Squalius laietanus*) taxa (Aparicio et al., 2016). Conversely, *A. donax* presence exhibited an overall negative impact on functional diversity, indicating substantial shifts in the biological traits of the target fish assemblages (Villéger et al., 2010; Colin et al., 2018). However, our study also revealed significant heterogeneity in fish responses, particularly influenced by stream order, channelization, in-stream habitat diversity, and water velocity. Further research investigating the effects of *A. donax* on less mobile taxa than fish and ecosystem properties (e.g. flooding and fire risks) (Spencer et al., 2013; Coffman, 2020) is crucial for determining the most appropriate management strategy for *A. donax* patches at sites under these conditions. Nevertheless, our findings suggest that, at least under specific environmental conditions, the removal of *A. donax* alone may not achieve the desired ecological outcomes if pre-existing fish-habitat relationships are not taken into account.

CRedit authorship contribution statement

Alberto Maceda-Veiga: Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Nicole Colin:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization. **Ralph Mac Nally:** Writing – review & editing, Conceptualization. **Humbert Salvadó:** Writing – review & editing, Investigation, Conceptualization. **Adolfo de Sostoa:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Jian D.L. Yen:** Writing – review & editing, Writing – original draft, Visualization, Software, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

Authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2025.180139>.

Data availability

Data will be made available on request.

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