Patterns of species richness, abundance and individual-size distributions in native stream-fish assemblages invaded by exotic and translocated fishes

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HIGHLIGHTS

- Individual species distribution (ISD) models are used to explore impacts of exotic and translocated fishes on native fishes
- Environmental covariates outweigh the effects of introduced species
- Translocated fishes were more influential predictors than exotic fishes for ISDs and abundance, but not for native fish richness
- ISD models perform better than abundance and species richness-based models
- Discrepancies in ISD patterns among native fishes suggest limitations to the use of ISDs as species-blind indicators of river health

GRAPHICAL ABSTRACT
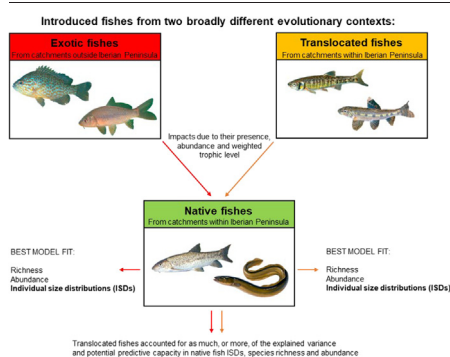
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ABSTRACT

Predicting the impacts of species introductions long has attracted the attention of ecologists yet there still is limited insight into how impacts on native assemblages vary with the degree of shared evolutionary context. Here, we used data from 535 stream-fish surveys from 15 catchments in north-eastern Spain (99,700 km^2) to explore whether the relative effects on native fishes differ between fish introductions from two different ecoregions (i.e., evolutionary contexts), namely, catchments within Iberian Peninsula (i.e., 'translocated species') and catchments beyond Iberian Peninsula (i.e., 'exotic fishes'). We used hierarchical Bayesian models to relate taxon richness, abundance, and the individual-size distributions (ISDs) of native fishes to the presence, abundance, and weighted trophic level (TL) of translocated and exotic fishes, conditional on geographic and habitat covariates. Environmental covariates dominated the percentage of explained variance ($\geq 65\%$) for all responses. Translocated fishes accounted for more of the explained variance than did exotic fishes for ISDs and abundance, but not for native fish species richness. The presence of translocated fishes was associated with lower abundance and richness of native fishes, with individuals being smaller in the presence of translocated fishes of higher TL. The presence of exotic fishes was associated with a greater abundance and richness of native fishes, with individuals generally being larger in the presence of exotic fishes. Our study suggests that translocated fishes could be as problematic as exotic fishes when angling and water transfers among catchments to deal with climate change may increase the establishment of translocated fishes. We also discuss the difficulties of using fish body size as species-blind, transferable assemblage-level trait in fish monitoring.

1. Introduction

The human-assisted movement of species beyond their native range can result in biological invasions, which are one of the major drivers of the global biodiversity crisis (Valéry et al., 2008). Many factors contribute to the severity of the impacts of introduced species on the native biota, including concurrent habitat alterations and the lack of coevolution between introduced and native species (Ricciardi and Mottiar, 2006; Ricciardi et al., 2013; Paolucci et al., 2013; Rejmánek and Simberloff, 2017). Isolated ecosystems, such as islands, appear to be worst affected by introduced species (Bellard et al., 2016). Adverse effects include declines in the abundance and richness of native species and changes in the food-web structure of invaded assemblages (Toussaint et al., 2018; Blackburn et al., 2019). However, the impacts of introducing organisms with more similar biological adaptations to the local assemblage are less well studied, apart from changes in intraspecific diversity in native assemblages (Buoro et al., 2016; Weigel et al., 2019). These translocations (native invasions sensu Simberloff, 2011) are an important environmental concern having societal and management implications, such as having to protect and eradicate the same species in a country (Carey et al., 2012).

Changes induced by introduced species typically have been assessed using scalar measures (e.g., richness, abundance, Light and Marchetti, 2007; Simao et al., 2010). Although these sometimes may be useful for biodiversity management (Margules and Usher, 1981), inferences may not be transferable to other geographical regions because different geographic areas may hold different species (Tedesco et al., 2012; Yen et al., 2017). Trait-based ecology is increasingly used to overcome this limitation (Maire et al., 2015), but needs a relatively good biological knowledge of native species, including taxonomy (Sutton and Jones, 2020). One potentially transferable assemblage-level trait is the individual size distribution (ISD), which is a continuous function where the value at any given size is the abundance irrespective of species (Yen et al., 2018). Body size is correlated with many metabolic and life-history traits (Peters and Peters, 1986), and influences predator-prey relationships, especially in systems where predators are gape limited (Brose et al., 2006). ISDs have proved to be useful for assessing the impacts of environmental perturbations (e.g., Zhao et al., 2015; Yen et al., 2017), but there is little known about their usefulness for understanding the impacts of introduced species (Fritschie and Olden, 2016).

Stream fishes are potentially informative subjects with which to explore how introduced species that have evolved in different evolutionary context (e.g., climate, hydrology) compared to the native biota might affect native species richness, abundance and ISDs. First, streams are spatially restricted spaces for strictly aquatic species, so that inter-basin colonization typically is rare (Reyjol et al., 2007). Moreover, 80% of freshwater fishes are unable to disperse through marine waters, and so, movements between basins only were naturally possible during marine regressions, orogenesis or extensive floods in lowland regions (Winemiller and Jepsen, 1998; Reyjol et al., 2007). Second, freshwater fishes are vulnerable to species introductions from human actions (e.g., angling; Leprieur et al., 2008), which can occur between relatively homogeneous or heterogeneous ecoregions (e.g., Economidis et al., 2000; Matsuzaki et al., 2013). A relatively homogeneous ecoregion is a group of basins in a spatially restricted space limited by large climatic, geographical barriers, which often define a biogeographical sub-unit, whereas heterogeneous aquatic ecoregions typically are from distant parts of continents (see ecoregions in Reyjol et al., 2007). Last, the size structure of fish populations is a key measure in fisheries (Andersen, 2019), yet it is still unclear how to effectively use fish assemblage size structures for appraising river health (Sutton and Jones, 2020; Arranz et al., 2021) and comply with international legislation, such as the European Water Framework Directive (2000/607EC).

Our work was done in an extensive area of north-eastern Spain (99,700 km², 15 catchments), which is a relatively homogeneous aquatic ecoregion (Ferreira et al., 2007). The hydrological cycle of Mediterranean-climate rivers, such as most part of the study area, is a major natural factor governing the life history of fishes (Magalhães et al., 2002). These streams typify how

native-species introductions (hereafter 'translocated fishes') occur within a region due to angling, although these translocations also may arise incidentally from bulk-water transfers (e.g. Maceda-Veiga et al., 2010). The study region also has introduced species from ecoregions with more different evolutionary context to the native fish fauna (hereafter 'exotic fishes'). These fishes were mostly introduced for recreational angling from wide and deep permanent rivers in central Europe and North America (e.g., Ribeiro et al., 2008), and so, they may be less biologically pre-adapted to the conditions of Mediterranean-climate streams than translocated fishes.

The goal of this study was to explore whether native fishes are affected differently by the establishment of introduced fishes with moderately ('translocated fishes') or widely divergent ('exotic fishes') biological adaptations from the native fish assemblages (Lee and Gelembiuk, 2008). First, we used series of models to look for general patterns of taxon richness, abundance and ISD in native fishes. Second, we built separate models for the four most common native species to examine whether shifts in individual sizes were due to changes within species or species turnover. If native fishes are better adapted to deal with species that have evolved under similar environmental and biological contexts (i.e., translocated fishes), we expected that exotic fishes would be associated with more severe impacts on native assemblages. These expectations would lead to:

1. Better model fits with exotic fish predictors than with those of translocated fish species, after having accounted for the effects of covariates, such as differences in elevation or water chemistry (Maceda-Veiga et al., 2014; Sutton and Jones, 2020; Arranz et al., 2021).
2. Associations of exotic fishes with well-established indicators of 'unhealthy' fish assemblages, such as reduced abundances, reduced species richness and shifts in fish-assemblage size structure towards small body sizes (Andersen, 2019).
3. Impacts of exotic fishes modulated by the trophic level of exotic fishes given the role of trophic interactions in regulating the food-web structure (Andersen, 2019).

2. Methods

2.1. Study system

We surveyed 535 sites in 15 catchments from 2002 to 2009 to collect fish and environmental data as part of several projects to assess the ecological status of rivers in north-eastern Spain (European Water Framework Directive; EU Directive 2000/60/EC) (Fig. 1). The catchments had mountainous and meso-Mediterranean climates (Rivas-Martínez and Rivas-Sáenz, 2016), with high chances of floods in autumn and summer droughts. The study sites reflect the diverse orography of the region with elevations ranging from 0 to 1814 m.a.s.l. and represent relatively large spatial gradients of variation in habitat conditions (e.g., pH range from 7 to 9.5; conductivity range from 20 to 5220 μS/cm). Each study site was surveyed once in low-flow conditions from middle summer to middle autumn because this is when fish populations are most stable and can be sampled most effectively by using electrofishing methods. Low-flow conditions are the most stressful conditions so we could better account for the magnitude of perturbations other than fish introductions on native fish assemblages. The studied rivers typify the small and medium-size streams of the Mediterranean-climate regions (Gasith and Resh, 1999). Our data set does not include the large rivers (e.g., main Ebro River channel) because this sampling requires the use of boats, and so, the survey methods would not have been comparable among sampling sites.

2.2. Fish surveys

We sampled fish following the guidelines of CEN standards EN 14962 and EN 14011, using single-pass electrofishing with a portable power unit that generated up to 200 V and 3 A pulsed direct current; the whole wetted width of ≥100-m reaches (mean ± standard error = 140 ± 30 m) was surveyed at each site moving upstream. Stream-water conductivity was
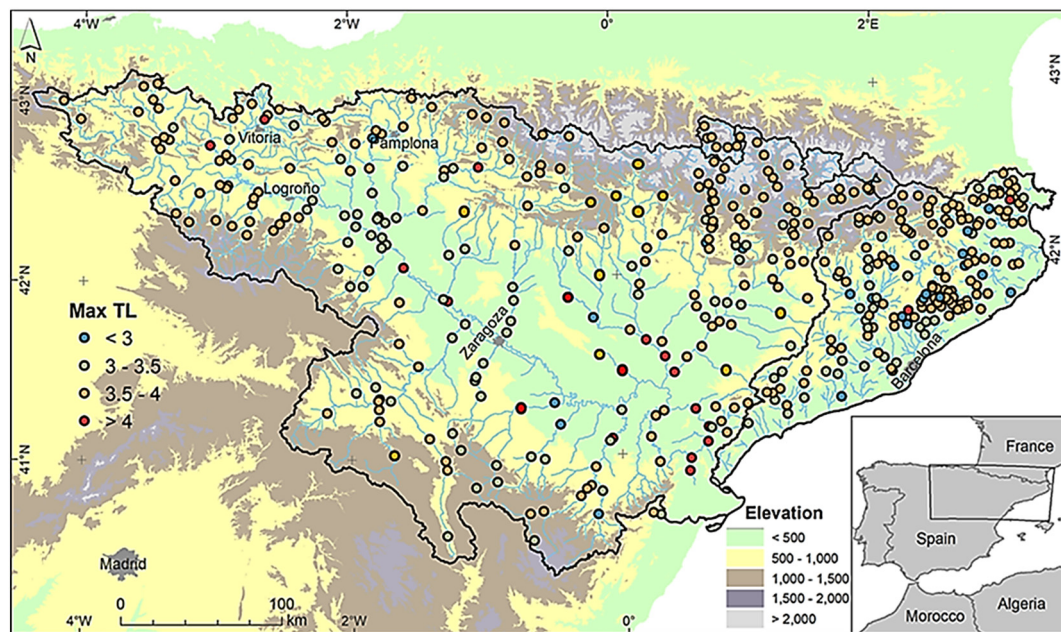
Fig. 1. Location of the 466 sampling sites with fish out of the 535 surveyed in streams of north-eastern Spain with indication of elevation and of the variation in the maximum trophic level of fish assemblages.

measured prior to electrofishing to determine the appropriate power levels for effective sampling but minimizing fish mortality (Arranz et al., 2021). Each site was sampled once, usually with an area ≥ 100 m^2 (560 $\pm$ 50 m^2) and included one riffle-run-pool sequence (e.g., Maceda-Veiga et al., 2018). This sampling strategy detects $\geq 80\%$ of the species and 60–90% of the individuals compared with estimates from four-pass electrofishing (A.S., unpublished data). Fish captures were expressed as captures per unit of effort (CPUE, individuals min^{-1} m^{-2} = number of individuals caught/ [fishing time (minutes) X area surveyed (m^2)]. The fish-survey methods were management authorized (AP/003), and the electrofishing sampling method is regarded as being adequate for exploring associations between stream-habitat quality and the community-size structure of fishes (e.g., Figuerola et al., 2012; Arranz et al., 2021).

All individuals were identified to species and counted. When there were <40 individuals of a given species, all individuals were weighed (wet mass, $\pm$ 0.01 g). Otherwise, a sample of 40 individuals was selected so that the samples represented the body-size proportions of all individuals captured for a given species. Fishes were anaesthetized with buffered MS-222 (0.02%, Sigma-Aldrich, St. Louis, MO, USA) before mass measurements. Fishes were allowed to recover and returned live to the sites of capture. The introduced fishes were defined as: (1) exotic fish, if the species did not occur historically in the ecoregion Iberian Peninsula; or (2) translocated fish, if introduced from another basin within the studied ecoregion in which the species is native (Appendix S1a; Matsuzaki et al., 2013). We refer to exotic and translocated fishes collectively as 'introduced' when inferences apply to both. The community body-size structure was based on the measured individuals regardless of the total number captured and abundance and richness data reflected all captures.

2.3. Environmental covariates

There were ten covariates to describe the environmental conditions of each sampling site. We recorded basin name and elevation (m.a.s.l.) using Google Earth® for geographical variables. Water properties were measured in situ using the colorimetric test kit VISOCOLOR® for nutrient concentrations (ammonium, nitrite, nitrate and phosphate-P; mg/l) and a digital multiparametric YSI® probe for temperature (°C), conductivity (µS/cm) and pH. Many pollutants in sewage discharges (e.g., chlorides, sodium, heavy metals, pesticides, and drugs) alter nutrients, pH and conductivity

in rivers (e.g., textile industry in Colin et al., 2016a, 2016b), which explains why these parameters are among the most frequently used indicators of water quality in streams. We calculated mean water depth and water velocity 20-m intervals from three values measured along perpendicular transects to water flow. We used the U.S. Rapid BioAssessment Protocol (RBA) adapted for Mediterranean rivers as an integrated measure of the stream's physical habitat quality (Maceda-Veiga and De Sostoa, 2011). The protocol ranks ten features of stream hydromorphology and riparian quality (e.g., stream bank stability, water flow, riparian vegetation) on 1–10 scales. We estimated the percentage of deadwood accumulated in each site because this indicator of stream-habitat complexity (Antón et al., 2011) is not specifically included in the RBA protocol.

2.4. Data analyses

2.4.1. Response and predictor variables

We used three response variables to explore the effects of exotic and translocated fishes on native assemblages. We compiled the species richness and abundance of native fishes from survey data. We used body-size measurements of individuals to estimate the individual size distribution (ISD) at each sampling site (Yen et al., 2017). Analyses of ISDs commonly focus on the exponent of the power-law size spectrum, often estimated by log-transforming size bins and abundances and standardizing abundances by bin widths (White et al., 2008). We present an alternative, semi-parametric approach that does not assume a power-law size spectrum, and so, is less sensitive to data standardizations and transformations (Yen et al., 2017). Avoiding the assumption of a power-law relationship removes the need to estimate an exponent (or log-log linear slope), which can be highly sensitive to sampling error or data transformations. This approach has been shown to be highly effective in identifying non-linearities in ISDs (Yen et al., 2017), which would be missed with these other relatively simpler, parametric methods.

Changes in the ISD were assessed at both the *interspecific* and the *intraspecific* levels. The interspecific analysis used the ISD as a species-blind measure to detect potentially transferable patterns among native species, while the intraspecific analysis explored patterns in the ISDs of the most frequently captured native fish species (Appendix S1). We allocated individual sizes into 20 bins of equal width on a logarithmic scale and used counts in each bin as a discrete approximation of a continuous distribution (Yen

et al., 2017). The midpoint (on a log scale) was used as the reference size for each bin. We used the minimum (0.01 g) and maximum (2370 g) of observed individual sizes as the upper and lower bounds for the size-bin array. We used a logarithmic scale so that observations were not concentrated in the smallest few bins (Yen et al., 2017). All bins contained individuals apart from one size bin (0.02–0.03 g).

The characteristics of exotic and translocated fishes were compiled into three potential predictors: (1) presence; (2) abundance; and (3) the weighted FishBase trophic level (TL) of the introduced fish assemblage calculated separately for exotic and translocated species. TLs were defined as the weighted average of species FishBase TL estimates (Froese and Pauly, 2010; Maceda-Veiga et al., 2018), with weights based on relative species abundance at a site. Fish TL in FishBase is calculated by using the TROPH routine (Pauly et al., 2000) and estimates correlate closely with those based on stable isotope ratios (Kline and Pauly, 1998). More than 800 studies were used to support the diet information in FishBase, which reports the mean TL for a given species (e.g., Romanuk et al., 2011). Despite this, we acknowledge that Fishbase TL estimates are imprecise compared to the use of trophic tracers at a site. However, Fishbase TL estimates probably are a better cost-efficient way to describe the 'basic building blocks' of fish food-webs than the use of coarser trophic categories (e.g., predators, herbivores) (Hargreaves et al., 2017).

Models with presence or abundance as predictor variables used all sampling sites with fish ($N = 435$) (Tables 1, 2). Models with weighted TL as a predictor variable used subsets because TLs were defined only at sites where exotic ($N = 109$) or translocated fishes ($N = 56$) were caught (Table 2). River basin and sampling year were included as random effects in all analyses to account for potential systematic differences among years and basins. These terms were defined as random rather than fixed effects to account for repeated sampling of sites *within* years or basins without attempting to resolve the processes driving broad variation among years or river basins.

All predictor variables were standardized prior to analyses (zero mean and unit standard deviation). We calculated pairwise correlation coefficients (based on Pearson's *r*) and Variance Inflation Factors (VIF) and found no pairs of covariates and predictors with $|r| > 0.7$ or individual covariates with VIF > 1.7, so that (multi)collinearity among predictors is unlikely to be an estimation problem (Fig. S1). A more detailed description of all models, computational details, and links to code to reproduce all analyses are in Appendix S1b.

2.4.2. Models for native-species richness and abundance

We used hierarchical Bayesian models to relate the species richness and abundance of native fish species to exotic and translocated fish predictors

Table 1
Summary of fitted models. A full model was fitted to data from all locations, with subset models used to include weighted trophic level as a predictor variable. Subset models were required because weighted trophic level was not calculable for locations where the relevant species group was not detected.

Model name	Primary predictor variables	Other predictor variables
Full model ($N = 435$)	Presence and abundance of exotic species and presence and abundance of translocated species	Elevation, water temperature, water depth, water velocity, conductivity, pH, nutrient levels, % cover of deadwood, Rapid Bioassessment Index
Subset model: exotic species ($N = 109$)	Presence, abundance, and weighted trophic level of exotic species	Elevation, water temperature, water depth, water velocity, conductivity, pH, nutrient levels, % cover of deadwood, Rapid Bioassessment Index
Subset model: translocated species ($N = 56$)	Presence, abundance, and weighted trophic level of translocated species	Elevation, water temperature, water depth, water velocity, conductivity, pH, nutrient levels, % cover of deadwood, Rapid Bioassessment Index

Table 2
McFadden pseudo-r^2 values from fitted models of native species richness, abundance, and individual size distributions (ISDs). Pseudo-r^2 values were calculated directly from modelled data (in-sample model fit) and from predictions generated through ten-fold cross validation (predictive model fit). Pseudo-r^2 values can be less than zero; negative values were set to 0.00. The full model included as predictor variables the presence and abundance of all exotic and translocated species. The subset models (†) included as predictor variables the presence, abundance, *and* the weighted FishBase trophic level of each species group (exotic or translocated species), restricted to those sites where each species group was present.

Response variables (native fishes)	Validation type	Full model (435 sites)	Subset: exotic species (109 sites)	Subset: translocated species (56 sites)
Size distribution (ISDs)	In-sample	0.43	0.50†	0.71†
	Predictive	0.26	0.05	0.22
Species richness	In-sample	0.34	0.39†	0.52†
	Predictive	0.07	0.02	0.07
Abundance	In-sample	0.25	0.36†	0.50†
	Predictive	0.00	0.02	0.00

and environmental covariates. We used a Poisson likelihood with logarithmic link and the general structure of our models was:

$$\text{Log(response)} \sim \text{exotic fishes} + \text{translocated fishes} + \text{environmental covariates} + (1 \mid \text{basin}) + (1 \mid \text{year}), \quad (1)$$

where: *response* is the species richness or abundance of native fish species in a given site, *exotic fishes* is the set of predictor variables used to describe the exotic fish species impacts at a site (presence, abundance, weighted trophic level), *translocated fishes* is the set of predictor variables used to describe the translocated fishes impacts at a site, *environmental covariates* is the set of physical, chemical, and other biological variables at a site; and $(1 \mid basin)$ and $(1 \mid year)$ specifies a random intercept for *basin* and *year*.

We fitted three models: a full model with data from all sampling sites with the presence and abundance of exotic and translocated fish species as predictor variables, and two subset models with data restricted to sites where exotic or translocated fishes were present (Table 1). The latter two models were necessary because the calculation of TL requires that there is at least one species from the exotic or translocated species groups (see above).

2.4.3. Models for the interspecific distributions of individual fish body sizes

We used Bayesian function regression to relate distributions of individual sizes (ISDs) of native fishes to predictor variables following Yen et al. (2015). The general structure of these analyses is the same as Eq. (1), but the response variables were functions rather than scalar values. The model parameters (intercepts and slopes) in analyses of function-valued response variables are continuous functions rather than scalar values (Yen et al., 2015). This form of analysis can be viewed as a generalized additive model of size-class abundances with a smooth spline fitted to individual size and linear interactions between this spline and all other predictor variables (Yen et al., 2015). This model structure yields parameter estimates that are interpretable as size-specific regression coefficients for each predictor (Yen et al., 2015).

2.4.4. Models for four individual fish species

Shifts in ISDs can be due to changes in size distributions within species or changes in species composition (Petchey and Belgrano, 2010), which often occurs in our stream fish assemblages (Maceda-Veiga et al., 2017). Therefore, we analysed intraspecific size distributions of four native fish species with different ecological characteristics and distributional ranges to examine whether observed changes in ISDs were apparent within species, which would be indicative of intraspecific changes in size distributions in response to introduced fishes. The four native fishes (*Salmo trutta* Linnaeus, 1758; *Barbus meridionalis* Risso, 1827; *Parachondrostoma miegii*

Steindachner, 1866; and *Luciobarbus graellsii* Staindachner, 1866) included head- and mid-river reach (*S. trutta* and *B. meridionalis*) and mid- and downstream reach species (*P. miegii* and *L. graellsii*) (Sostoa et al., 1990). The trophic guilds included an invertivore-piscivore (*S. trutta*), a mostly algivore (*P. miegii*) and mostly invertivores (*B. meridionalis* and *L. graellsii*) (Sostoa et al., 1990; Colin et al., 2016b). There were endemic (and almost endemic) Iberian cyprinids (*B. meridionalis*, *P.miegii* and *L. graellsii*) and a widely distributed salmonid in Europe and in other continents (*S. trutta*) (Sostoa et al., 1990; McIntosh et al., 2012). We fitted intraspecific models to data from the subset of sites containing exotic or translocated fishes, respectively. There were two sets of models for each of the four species, one with the presence, abundance, and weighted TL of exotic fishes and the other with these predictor variables but for translocated fishes.

2.4.5. Model validation

We used McFadden's pseudo-r^2 (one minus the model deviance divided by the deviance of an intercept-only model) to assess fit. This is the improvement in model fit with and without predictor variables in models. We calculated pseudo-r^2 values from observed and modelled values (in-sample model fit) and undertook ten-fold cross validation to calculate pseudo-r^2 values from observed and predicted values (cross-validated model fit). Cross validation estimates the potential predictive capacity of a model by withholding subsets of the data (folds) when fitting models and using fitted models to predict the observations in the withheld data (Roberts et al., 2017). We note McFadden's pseudo-r^2 differs slightly from the classical definition of r^2 based on Pearson's r or proportion of variation explained. These procedures often return r^2 values higher than McFadden's pseudo-r^2 but, coupled with cross validation, ours is a more effective method to detect over-fitted models.

2.4.6. Variance decomposition

We used hierarchical partitioning (HP) of the pseudo-r^2 values to estimate the amount of variation in native-fish responses (ISDs, species richness, and abundance) attributable to exotic fishes, translocated fishes, and environmental covariates. HP uses incremental improvements in fit as predictors are added to a model to calculate the independent contribution of each variable (or set of variables). HP then required a comparison of eight model structures for models of *all species* (all possible combinations of the three sets of variables, including a null model) and four model structures for subset models restricted to exotic fishes or translocated fishes (all combinations of two sets of variables, including a null model). We used the *partition* function in the hier.part R package (Mac and Walsh, 2004).

3. Results

3.1. General results

Fish were caught in 435 of the 530 stream reaches. There were 16 native species (50% cyprinids and 12% cobitids), 18 exotic species (50% cyprinids and 11% centrarchids), and six translocated species (66% cyprinids), mostly native from the Ebro basin, which had been translocated into other catchments (Appendix S1a). Exotic species had higher average FishBase trophic levels (TL) than native species and translocated species (Appendix S1a).

There were low pairwise correlations ($r < |0.3|$) between exotic and translocated fish measures and indicators of environmental degradation (e.g. the habitat-quality index, RBA, water conductivity, nutrient concentrations, Fig. S1).

3.2. Native fish assemblages and environmental covariates

Species richness of native fish species was negatively associated with elevation and nutrient concentrations and was positively associated with mean water temperature, water depth, and water velocity (Fig. 2a). The summed abundance of native species was negatively associated with elevation, water conductivity, mean water depth or nutrient concentrations, but
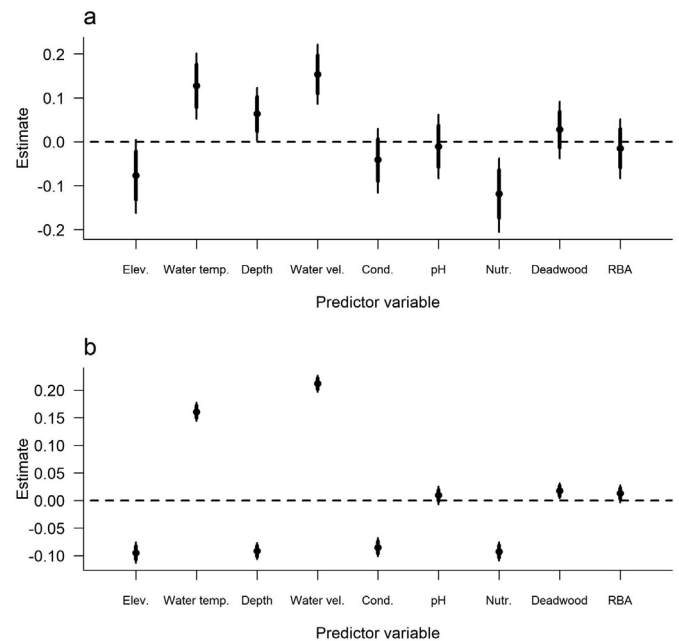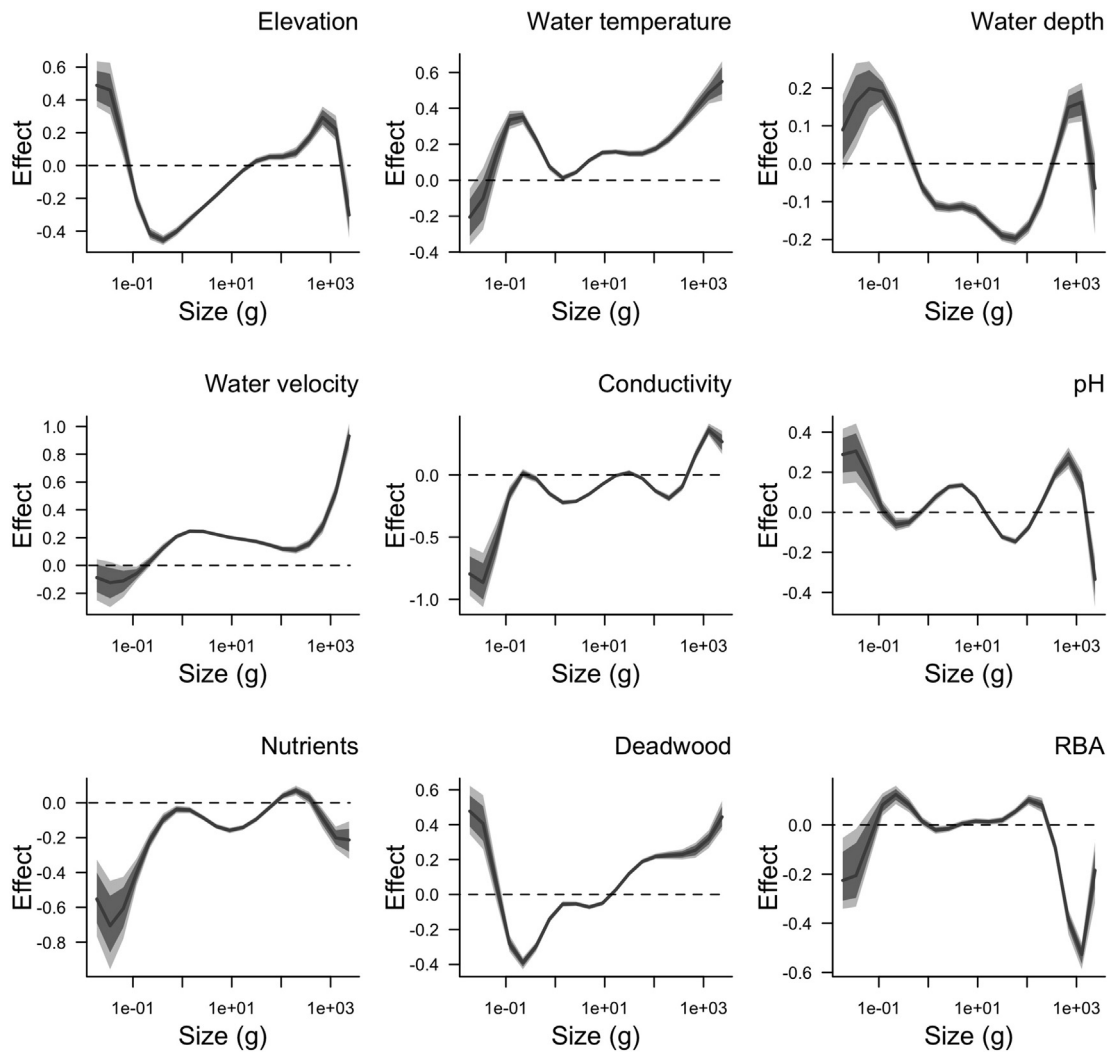

Fig. 2. Associations between environmental predictor variables and native fish species richness (a) and abundance (b). Points are mean parameter estimates from the fitted model, thick bars bound 80% credible intervals, and narrow bars bound 95% credible intervals. Key: elev. – elevation; water temp. – average water temperature; depth – average water depth; water vel. – average water velocity; cond. – water conductivity; pH – pH; nutr. – nutrient concentrations; deadwood – percentage cover of deadwood; RBA – Rapid Bioassessment Index.

was positively related to mean water velocity and water temperature (Fig. 2b). Native fishes tended to be bigger in stream reaches with warmer waters, high water conductivities or rapid-flow waters (Fig. 3). Estimated associations between native fish ISDs and nutrient concentrations or mean water depth indicated that native fish assemblages had fewer intermediate-sized individuals in deeper rivers, and lower abundances with fewer small individuals at greater nutrient concentrations (Fig. 3). Native fish assemblages tended to have fewer intermediate-sized individuals in stream reaches with more deadwood, although this relationship did not hold for other indicators of habitat complexity, such as the RBA habitat-quality index (Fig. 3).

3.3. Associations between native fish responses and exotic and translocated fish predictors

3.3.1. Native ISDs

Models of native fish individual size distributions (ISDs) explained 43–71% of variation in ISDs (Table 2). The inclusion of abundance-weighted FishBase TL of translocated fish species produced a better fit (71% of variation explained) than did the model that included weighted TL of exotic species (50%) (Table 2). Cross-validated pseudo-r^2 values indicated that fitted models had low-to-moderate predictive capacity for ISDs (5–26%). The presence and abundance of exotic species accounted for 10.9% of the explained variance in native fish ISDs, with translocated species accounting for a further 15.8%, while environmental covariates accounted for the other 73.3% (based on hierarchical partitioning results, Table 3). Inclusion of abundance-weighted FishBase TL of exotic or translocated species, alongside presence and abundance, accounted for c. 35% of the explained variance in native fish ISDs (Table 3). Although not directly comparable, these values suggest that weighted FishBase TL of introduced species may explain at least as much variation in native fish ISDs than do presence or abundance of introduced species (Table 3).

Fig. 3. Associations of the individual size distributions of native species (i.e. species-blind changes in the ISD) with environmental variables. Effects are log-transformed, size-specific associations between ISDs and a given predictor variable. Effects at a given size are equivalent to slope parameters in a linear model. For example, the top-left panel indicates that increasing elevation has a positive association with the abundance of small (< 0.1 g) and larger (50–1000 g) fish and a negative association with intermediate-sized fish (0.1–50 g). Solid lines are mean parameter estimates from the fitted model, dark shaded regions bound 80% credible intervals, and light shaded regions bound 95% credible intervals. Key: deadwood – percentage cover of deadwood; RBA – Rapid Bioassessment Index.

Table 3
Percentage of explained variance in native species richness, abundance, and ISDs that is attributable to exotic species, translocated species, and environmental variables. The full model included as predictor variables the presence and abundance of all exotic and translocated species. The subset models included as predictor variables the presence, abundance, and weighted FishBase trophic level of each species group (exotic or native invaders), restricted to those sites where each species group was present. Values were calculated using hierarchical partitioning of pseudo-r^2 values calculated for all combinations of variables.

Response variables (native fishes)	Models	Exotic species (4 predictors – full model; 3 predictors – subset models)	Translocated species (4 predictors – full model; 3 predictors – subset models)	Environmental variables (10 predictors)
Individual size distribution	Full model	10.9	15.8	73.3
	Subset: exotic species	34.5	Not modelled	65.5
	Subset: translocated species	Not modelled	34.9	65.1
Species richness	Full model	13.4	8.6	78.0
	Subset: exotic species	39.3	Not modelled	60.7
	Subset: translocated species	Not modelled	12.3	87.7
Abundance	Full model	1.9	15.9	82.2
	Subset: exotic species	30.7	Not modelled	69.3
	Subset: translocated species	Not modelled	31.4	68.6

The presence of exotic species was associated with larger native fishes (Fig. 4a) and the presence of translocated species was associated with fewer total fishes and many fewer larger fishes (Fig. 4b). More exotic or translocated species favour native fish individuals from intermediate size classes relative to the extreme size classes (Figs. 4c,d). Greater abundance-weighted FishBase TL of exotic species appeared to shift native fish ISDs towards larger sizes (Fig. 5a), whereas the reverse held for greater weighted FishBase TL of translocated species (Fig. 5b).
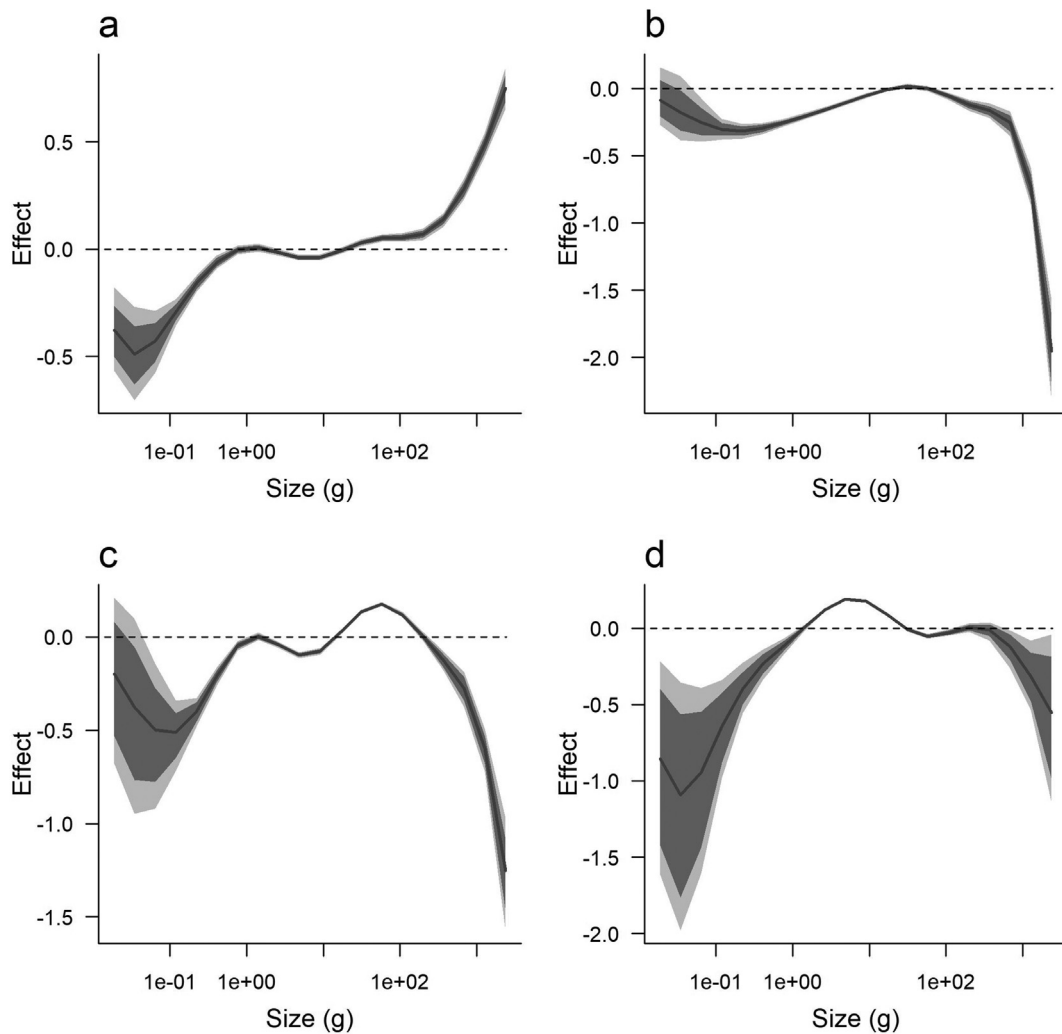
Fig. 4. Associations of individual size distributions of native species (i.e. species-blind changes in the ISD) with the presence of exotic (a) and translocated species (b) and the abundance of exotic (c) and translocated species (d). Solid lines are mean parameter estimates from the fitted model, dark shaded regions bound 80% credible intervals, and light shaded regions bound 95% credible intervals.

3.3.2. Native species richness and abundance

Models explained 25–52% of variation in native fish species richness or abundance (in-sample values in Table 2). The inclusion of abundance-weighted FishBase TL of translocated species produced better fits (52%, 50% of variation explained) than did models that included weighted FishBase TL of exotic species (39%, 36%) (Table 2). However, cross-validated pseudo-r^2 values indicated that fitted models had relatively little predictive capacity for native fish species richness (2–7%) or abundance (0–2%) (Table 2). Environmental covariates accounted for most of the explained variance (HP, 78–82.2%), and there was evidence that weighted FishBase TLs may explain as much or more variation than do the presence and abundance of exotic or translocated species per se (HP, Table 3). Translocated species appeared to account for more of the explained variation in abundance than did exotic species, while the reverse may hold in models of native species richness (Table 3).

Native fish species richness appeared to be positively associated with the presence of exotic species, negatively associated with the presence of translocated species, and negatively associated with the abundance-weighted FishBase TL of exotic species (Fig. 6a). Native fish abundance was positively associated with abundances of exotic and translocated species (Fig. 6b). However, native fishes were less abundant at sites with greater abundance-weighted FishBase TLs of exotic and translocated species (Fig. 6b).

3.3.3. Single native-species models

The intraspecific ISD models for the four most abundant native species provided some support for changes in ISDs arising from exotic or translocated species irrespective of changes in species composition (Figs. S2–S9). Single-species and interspecific models mostly were consistent in the directions of associations with the abundance of exotic species. At sites with more exotic species, there were fewer small and fewer large individuals of *B. meridionalis*, *L. graellsii* and *S. trutta* (Figs. S2, S4, S8). However, *P. miegii* shifted from greater numbers of small to more large individuals with more exotic species (Fig. S6). There were weaker associations between abundances of translocated species and the ISDs of the four native species (Figs. S3, S5, S7, S9). There was not a clear overall pattern in responses of native species to increased FishBase TL of exotic or translocated species. For example, while the TL of exotic species was related negatively to the abundance of all size classes in *B. meridionalis* (Fig. S2), there was an increase in the abundance of large *L. graellsii* but little change for *S. trutta* (Figs. S4, S8).

4. Discussion

We found some evidence that translocated species (i.e., introduced fishes originating from the same ecoregion) accounted for as much, or more, of the explained variance and potential predictive capacity in native fish ISDs, species richness and abundance than did exotic species
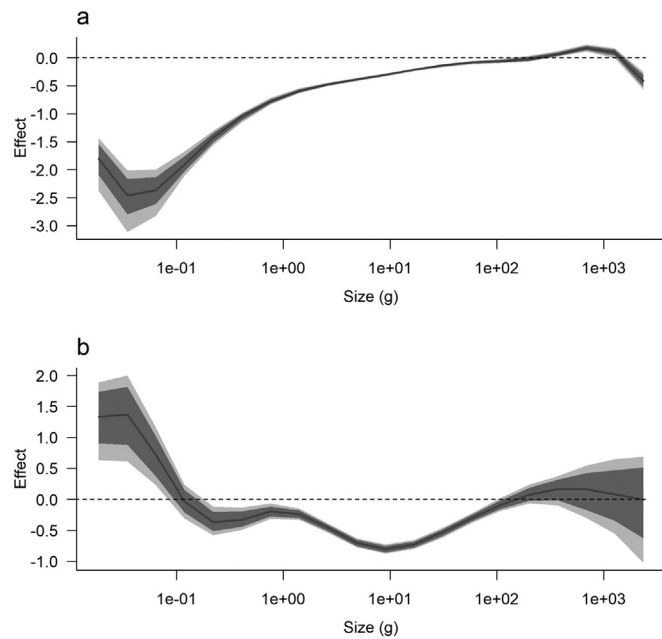
Fig. 5. Associations of individual size distributions of native species (i.e. species-blind changes in the ISD) with the abundance-weighted FishBase trophic level of exotic (a) and translocated (b) fish species at sites where each species group was present. Solid lines are mean parameter estimates from the fitted model, dark shaded regions bound 80% credible intervals, and light shaded regions bound 95% credible intervals.

(i.e., introduced fishes from different ecoregions). Our findings are consistent with prior work on riverine salmonids suggesting that species with more similar evolutionary contexts interact more strongly (Buoro et al., 2016). Variation in the species abundance, species richness, and individual size distributions (ISDs) of native fishes in north-eastern Spain appeared to be attributable primarily to environmental factors and, to a lesser extent, to

Fig. 6. Changes in native fish species richness (a) and abundance (b) as a function of the presence, abundance, and weighted FishBase trophic level of exotic and translocated (Transl.) fish species. Trophic level coefficients were estimated from models fitted to subsets of the data where exotic or native invaders were present. Points are mean parameter estimates from the fitted model, thick bars bound 80% credible intervals, and narrow bars bound 95% credible intervals.
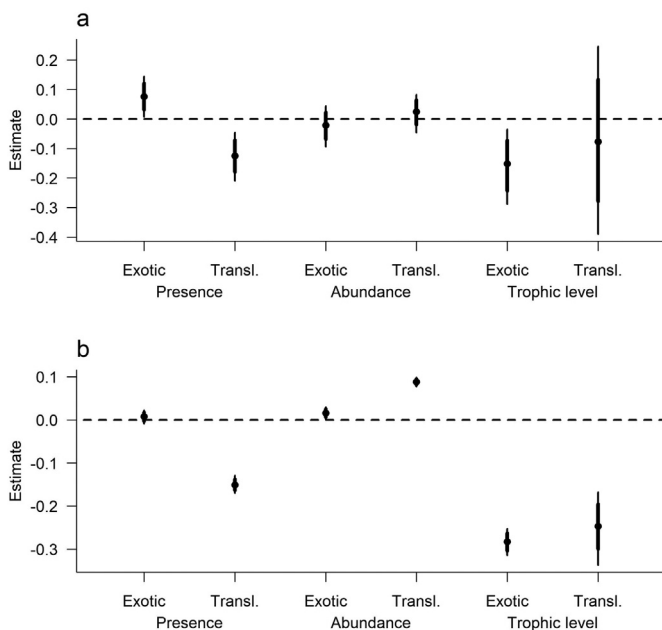
introduced fishes, which is consistent with work elsewhere using other analytical approaches (e.g., Godinho and Ferreira, 1998; Maceda-Veiga et al., 2014, although see Light and Marchetti, 2007; Hermoso et al., 2011). While levels of explained variation are reasonable by ecological standards ($\geq 25\%$, Table 3) and typical of highly dynamic stream assemblages at broad scales such as ours (15 catchments; 99,700 km^2) (Heino et al., 2015; Maceda-Veiga et al., 2017; Arranz et al., 2021), the predictive capacity of non-ISD models was limited (Table 3), and so, the discussion is mostly focused on ISD model outcomes.

4.1. Environmental impacts appear to outweigh introduced-species effects

Variation in the species richness, abundance and ISDs of native fishes mostly was due to environmental covariates. We note that, while there are more environmental covariates (ten) than predictors for exotic species (three) or translocated species (three), the predominance of environmental covariates for explaining variation in all three response variables was $\geq 73\%$ even when the maximum number of introduced-species predictors was included (4 predictors in the full model). Therefore, introduced-species predictors were not as important as environmental covariates when predictor numbers were most similar (four vs ten). Our findings should not be interpreted as to which factor was the driver of the native fish change because the study sites were sampled only once. Biological interactions may intensify as the drought season in the study area progresses because fishes often remain in isolated pools as a result of stream-flow discontinuities (Gasith and Resh, 1999; Magalhães et al., 2007). However, pairwise correlations among the modelled variables were low (see results), and our data set spanned broad ranges of environmental (e.g., conductivity was from 20 to 5220 μS/cm) and biological conditions (e.g. trophic levels were from 2.86 to 4.40).Therefore, our inferences may be sufficiently broad to apply, at least, to native fishes with similar life histories to ours (e.g., California, Central Chile, the Mediterranean Basin, the Cape Region of South Africa, and south-western and south-eastern Australia) (Gasith and Resh, 1999; Economidis et al., 2000; Reyjol et al., 2007). We provide some commentary on relationships between environmental covariates and native fish measures in Appendix S1c because this information may be useful for natural resource managers. For example, ISD models showed that native fishes were larger in more rapidly flowing waters. Given that fast flowing waters often typify streams with an unimpacted, natural hydrology (Light and Marchetti, 2007; Maceda-Veiga, 2013), our results may inform the effects that reduced water flows due to climate change or water abstractions might have on native fishes.

4.2. Exotic vs translocated fish species effects

After having accounted for environmental covariates, our work suggested that translocated species had potential stronger impacts on native fishes than did exotic species despite the latter containing some widely recognized exotic species (e.g., *Cyprinus carpio*, *Alburnus alburnus*) (e.g., Ribeiro et al., 2008; Light and Marchetti, 2007). The positive association between abundances of native and exotic fishes may be due to exotic fishes mainly being present in the most productive stream reaches (e.g., downstream) (Angermeier and Winston, 1998; Maceda-Veiga et al., 2017), where there may be sufficient habitat and food for native and exotic fishes, at least at the time of our surveys. The positive association between the abundances of native and translocated fishes suggests that similar stream conditions may promote these two fish groups (see also Angermeier and Winston, 1998; Maceda-Veiga, 2013). However, there may be time-lags in responses in native assemblages after invasion (Parker et al., 1999). Moreover, fewer species or fewer larger individuals of native fishes in the presence of translocated fishes may suggest agonistic biological interactions (see below), changes in species compositions (Petchey and Belgrano, 2010) or altered fish growth due to differences in the spatial location of sampling sites (Arranz et al., 2021). For example, most exotic fishes occur in downstream reaches in north-eastern Spain (Maceda-Veiga et al., 2017), and native fishes with larger adult body sizes

are more frequent in lowlands (e.g., >100 cm *Anguilla anguilla*) than in headwaters (e.g., ≥ 30 cm *Barbus haasi* (Mertens, 1925), *B. meridionalis*; Sostoa et al., 1990). Therefore, these distributional patterns may explain, partly, why bigger native fishes were less common in the presence of translocated species than in the presence of exotic species.

Potential agonistic biological interactions affecting native fish assemblages in north-eastern Spain include trophic interactions, hybridization, behavioural interferences, and parasites (Maceda-Veiga, 2013; Arranz et al., 2021). Regarding trophic competition and predation, most of the studied native and exotic fishes were cyprinids, which do not prey on adult fish and often are regarded as trophic generalists (e.g., Colin et al., 2016a). Differences in mouth position and gape may contribute further to trophic segregation among cyprinid species, as suggested by diets of the invasive, benthic cyprinid *Barbus barbus* Linnaeus, 1758 and three native pelagic cyprinids in a UK stream (Roberts and Britton, 2018). However, the latter may not hold for *L. graellsii* (Steindachner, 1866), a native species from the Ebro River translocated into other studied catchments (Appendix S1), given that this fish has a similar mouth structure to the native *Barbus* spp. (Sostoa et al., 1990). We also found fewer of the smallest native fish size classes when translocated fishes were more abundant. *Phoxinus* spp., which are translocated fish released by anglers as food for trout, are likely to compete for food with trout juveniles potentially decreasing trout stocks (Oscoz et al., 2008).

An alternative explanation is that translocated fishes may be aggressive towards native fishes as this has been seen between the translocated *Gobio* spp. and the native cobitids *Cobitis palludica* and *C. calderoni* (Almeida and Grossman, 2012). Changes in population size structure also may be due to hybridization between fishes with very different adult body sizes and the large, translocated *L. graellsii* can hybridise with the smaller natives *B. meridionalis* or *B. haasi* (Gante et al., 2015). Last, effects of parasitic infections borne by translocated fishes (e.g., *L. graellsii* Maceda-Veiga et al., 2019), or predation by translocated fishes on larvae or eggs of local natives could be related to the presence of fewer of the smallest native fish size classes when translocated fishes co-occur, but there are only aquaria observations for the latter in the studied native fishes (A.M.V. pers. observ.)

Exotic piscivores were rare in the studied stream reaches (Appendix S1), probably because our study sites did not include reservoirs and other >2 m deep main river sections (see methods), where these species are more likely to occur (Sostoa et al., 1990). Therefore, predation of large exotic fishes (e.g., *Micropterus salmoides*, *Sander lucioperca*) on large native fishes probably had little influence on our results. At sites where exotic fish with high trophic positions were abundant, the strength of associations with our native fish measures were greater, which supports the ecological importance of these species as top consumers in food webs (Andersen, 2019). However, based on comparable model fits, the potential effects of translocated fishes seemed to be more, or as important as, those of exotic fishes for explaining variation in ISDs of native fishes, at least in the kind of streams we surveyed, which are common in Mediterranean-climate areas (Gasith and Resh, 1999).

4.3. ISDs as potential complementary measures to inform the health status of stream fish assemblages and global ecological patterns

Our study partly was designed to explore the potential advantages of using ISD models to explore introduced-species impacts. Our ISD models effectively had greater explanatory and predictive power than those based on species richness or abundance, and changes in body-size spectra may contain more information on aspects of organismal or ecosystem function (e.g. production and respiration) than simpler metrics such as species richness (White et al., 2007). However, the lack of clear patterns in ISDs in response to perturbations among native fishes illustrates the difficulties of using fish body size as species-blind indicator of the health status of stream fish assemblages. More informative predictors might have increased the explanatory power of modelling. For example, the use of trophic tracers in each site could inform better the TL of fishes than FishBase TL estimates. Assuming a unique value of TL per species fails to consider within-population

variation in diet and ontogenetic changes in trophic levels, which are common in fishes (Sánchez-Hernández et al., 2019). Moreover, our outcomes might have been influenced by the durations for which native and introduced fishes were interacting at individual sites (Lee and Gelembiuk, 2008) and there is evidence that species may have been repeatedly introduced (e.g., Vidal et al., 2010). However, all these limitations are common in broad-scale studies in which detailed information is not available or disregarded to seek general patterns with practical data (e.g., individual body size can be easier to obtain from an assemblage than species identities per se).

The use of individual-based traits, such as changes in body size or physiological data, is central to appraising the health status of species-poor fish assemblages such as those in Mediterranean streams. Only one or three native species may be present (Sostoa et al., 1990; Maceda-Veiga, 2013) and the diagnostic power of biotic indices based on fish species composition often is poor (Colin et al., 2016a, 2016b). In this regard, we present our modelling as another tool by which to explore patterns of variation in traits of native fishes. Such patterns of variation are likely to have the greatest diagnostic value if they are developed at the species level as occurs for the variables used in human and domestic animal medicine. Despite this, our study suggests that translocated fishes might be causing greater ecological impacts than exotic fishes, at least in some catchments. Native species declining in some basins and expanding as translocated species in other basins in the same country is a serious challenge for the current legislation and management.

CRediT authorship contribution statement

Sampling: ADS, AMV
Conceptualization: AMV, ADS, JY and RM
Analyses: JY
Writing: AMV, JY
Review & editing: AMV, JY, RM, ADS

Declaration of competing interest

Authors declare no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.155953.

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