

Interacting effects of latitudinal and elevational gradients on the distribution of Iberian inland fish

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ABSTRACT

Interacting effects of latitudinal and elevational gradients on the distribution of Iberian inland fish

Unraveling the effects of latitudinal and elevational gradients on species distribution has been a central topic in biogeography for decades. However, few studies have evaluated the effects of the interaction between both gradients on species distributions. The main goal of this study was to evaluate the interaction of latitude and elevation in a freshwater context using a regional dataset of Iberian inland fish species. For this purpose, we compiled occurrence data for the 15 most widespread (i.e., present in multiple basins) Iberian fishes. We used generalized linear models including elevation, latitude, their quadratic terms, the interaction between the two gradients, and the basin as sources of variation. Results revealed contrasting species-specific distribution patterns with differing importance of the elevation and latitudinal gradients. Latitude was particularly important in explaining the distribution patterns of *Salmo trutta*, while the distribution of diadromous species and invasive *Gambusia holbrooki* or *Lepomis gibbosus* was mainly mediated by elevation. We detected significant interaction between elevation and latitude for 11 out of the 15 studied species. Consequently, Iberian fish species occupy different elevational niche positions depending on latitude. For example, *Salmo trutta* and *Oncorhynchus mykiss* occupy intermediate and even lower reaches in the northernmost areas. However, their occurrence probability decreases at lower latitudes, despite they can occur in elevated areas in these regions (e.g., Baetic Mountains). Finally, we discuss the potential effects of climate change on distribution patterns of the Iberian fish species studied.

Key words: altitude, Iberian rivers, invasive alien species, niche position, spatial gradient

RESUMEN

Efectos de la interacción entre los gradientes latitudinal y altitudinal sobre la distribución de los peces ibéricos de aguas continentales

Entender los efectos de los gradientes latitudinal y altitudinal en la distribución de las especies ha sido un tema central en biogeografía durante décadas. Sin embargo, pocos estudios han analizado el efecto de la interacción entre ambos gradientes sobre la distribución de especies. Por lo tanto, el objetivo principal de este estudio fue analizar dicha interacción utilizando una base de datos de peces continentales de la Península Ibérica. Para ello, recopilamos datos de presencia de las 15 especies de peces ibéricos continentales más extendidos (es decir, presentes en múltiples cuencas). Utilizamos modelos lineales generalizados que incluyen elevación, latitud, sus términos cuadráticos, la interacción entre ambos predictores y la cuenca como fuentes de variación. Los resultados revelaron patrones de distribución diferenciados para las distintas especies, así como una importancia variable de los gradientes altitudinal y latitudinal. La latitud fue particularmente importante para explicar la distribución de *Salmo trutta*, mientras que la distribución de las especies diádromas y de las invasoras *Gambusia holbrooki* o *Lepomis gibbosus* estuvo condicionada principalmente por la elevación. Además, detectamos una interacción significativa entre la elevación y la latitud para 11 de las 15 especies estudiadas. En consecuencia, los peces ibéricos ocupan diferentes nichos altitudinales dependiendo de la latitud. Por ejemplo, *Salmo trutta* y *Oncorhynchus mykiss* pueden ocupar tramos intermedios

e incluso bajos en el extremo norte de la Península. Por el contrario, la probabilidad de ocurrencia de ambas especies disminuye en latitudes más bajas, a pesar de que pueden ocurrir en áreas elevadas en estas regiones (por ejemplo, las Montañas Béticas). Finalmente, discutimos los posibles efectos del cambio climático en los patrones de distribución de las especies de peces ibéricas estudiadas.

Palabras clave: *elevación, especies exóticas invasoras, gradiente espacial, posición del nicho, ríos ibéricos*

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INTRODUCTION

Understanding the effects of climatic and topographic variables on species' distribution patterns has motivated ecology and biogeography for decades. More specifically, latitude and elevation are two widely studied spatial gradients that are known to shape patterns of species diversity worldwide (Bogoni *et al.*, 2021). The best documented pattern in biogeography is the latitudinal gradient of diversity in which species richness increases from polar to tropical regions for most taxa (Buckley *et al.*, 2010; Sanders & Rahbek, 2012; Bogoni *et al.*, 2021). Similarly, elevation is considered a good proxy capable of representing multiple environmental variables relevant to species distributions (Rahel & Hubert, 1991; Comte *et al.*, 2014; Cano-Barbacil *et al.*, 2022b). Elevation induces relevant changes in abiotic factors (e.g., temperature and precipitation regimes, habitat structure, etc.), resulting in diversity patterns similar to those observed along the latitudinal gradient by applying an additional local filter to the regional species pool (Stevens, 1992; Bogoni *et al.*, 2021). Thus, for most taxa, the species richness of high-elevation areas is generally lower than that of lowland areas (Stevens, 1992).

Recent studies have shown that inland fish ranges are markedly shaped and maintained by basin boundaries and their historical connections, especially for strictly freshwater species (i.e., primary fish) (Filipe *et al.*, 2009; Cano-Barbacil *et al.*, 2022a). However, latitudinal and elevational gradients are also well-known to shape fish distribution patterns (e.g., Carmona-Catot *et al.*, 2011; Murphy *et al.*, 2015). For example, elevation, temperature, and accumulated flow are highly influential variables for many limnophilic species such as mosquitofish (*Gambusia holbrooki*

Girard, 1859), pumpkinseed (*Lepomis gibbosus* (Linnaeus, 1758)) or black-bass (*Micropterus salmoides* (Lacepède, 1802)), which tend to occur in downstream, warmer waters (Murphy *et al.*, 2015; Bae *et al.*, 2018; Cano-Barbacil *et al.*, 2022a, 2023). Moreover, variation in latitude and elevation causes changes in fish abundance, species richness and taxonomic and functional community composition, which is likely to be attributable to climate and habitat constraints on survival, growth and reproduction (Cook *et al.*, 2004; Kirk *et al.*, 2022). River longitudinal variation, as well as the latitudinal gradient, can explain interspecific variation in life history traits of freshwater organisms (Vannote *et al.*, 1980; Carmona-Catot *et al.*, 2011; Cano-Barbacil *et al.*, 2020a). Thus, fish populations at higher latitudes often show lower growth rates but greater age at maturity, longevity and maximum length, and allocate more energy to reproduction (Blanck & Lamouroux, 2007).

Previous attempts to understand the niche characteristics of Iberian inland fishes indicated a significant correlation between climatic and longitudinal niche positions (i.e., species inhabiting warm regions with high precipitation seasonality were present in large lowland rivers, whereas species occurring in areas with rainy summers, were present in mountain rivers with steep slopes at high elevations; see Cano-Barbacil *et al.*, 2023). However, some species such as the brown trout (*Salmo trutta* Linnaeus, 1758), which are generally found in regions with cold and humid climates, can also occur in areas with warmer climates (e.g., Mediterranean climate with a cool, wet season followed by a warm, dry season) but at higher elevations (Doadrio, 2001; Larios-López *et al.*, 2015b; Cano-Barbacil *et al.*, 2022a).

Although several studies indicate an eleva-

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tional–latitudinal gradient of inland fish distribution, there is a significant lack of knowledge on the interaction between both gradients. Thus, the main objective of this study was to evaluate this interaction between the latitudinal and elevational niche positions using a regional dataset of Iberian inland fish species. We predicted that species would show changes in their elevational niche position along the latitudinal gradient evaluated, i.e., that species present in the north of the Iberian Peninsula in lower reaches would appear in areas of higher elevation in the south. We also discuss the implications of this study for a deeper understanding of the effects of the ongoing climate change on the Iberian freshwater species evaluated.

METHODS

Study area and target species

The study area was the Iberian Peninsula, which is well suited to study the interaction between spatial gradients on species' distributions because of its complex orography and diverse climate (Cano-Barbacid et al., 2022a). This region

is characterized by a broad elevation range (Fig. 1), from sea level to mountainous areas exceeding 3000 m in height, and by a large spatial and temporal climate variability (Sabater et al., 2009). According to the Köppen-Geiger's climate classification, the mountain ranges and the northernmost Peninsula are dominated by oceanic climate (Cfa and Cfb), while the rest of the northern half has a Mediterranean oceanic climate with warm summers (Csb). By contrast, the southern half is dominated by a Mediterranean climate with dry and hot summers (Csa), and southeastern Spain has a semiarid climate (BSk) (Kottek et al., 2006; AEMET, 2011).

Iberian inland waters are inhabited by 100 different fish species, of which 32 are non-native to the region (Cano-Barbacid et al., 2020b), which represent a broad set of species of different global origin. For this study, we evaluated the distribution for the six native and nine alien most widespread (i.e., present in more basins) inland Iberian fishes (see Table 1). Alien fishes included in this study have been introduced more than 50 years ago (with the exception of the bleak, *Alburnus alburnus* (Linnaeus, 1758); see e.g.,

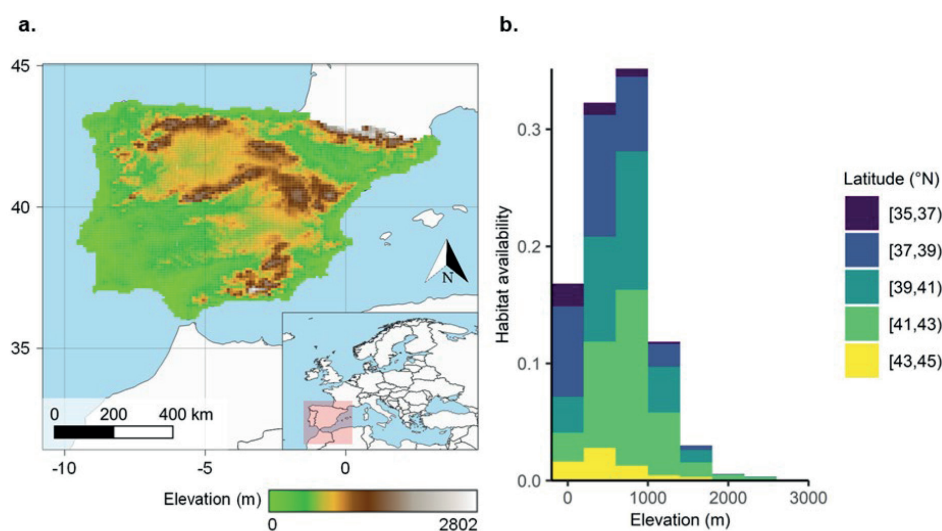


Figure 1. (a) Mean elevation of the Iberian Peninsula (grid resolution of 10×10 km Universal Transverse Mercator, $n = 6142$ total cells). Source: Spanish National Center for Geographic Information (<http://centrodedescargas.cnig.es>). (b) Available proportion of elevational habitats in the Iberian Peninsula by latitude. (a) *Elevación media de la península ibérica (resolución de las celdas de 10×10 km Universal Transverse Mercator, $n = 6142$ celdas totales).* Fuente: Centro Nacional de Información Geográfica (<http://centrodedescargas.cnig.es>). (b) *Disponibilidad de hábitat altitudinal en la península a diferentes latitudes.*

Latorre *et al.*, 2023), and they have most likely experienced multiple introduction events (Clavero & Villero, 2014). As a consequence, they are currently present in the majority of Iberian basins, reflecting a wide regional niche breadth (Cano-Barbacil *et al.*, 2023).

We obtained distribution data for these 15 species between 2000 and 2020 from Instituto da Conservação da Natureza e das Florestas and GBIF (see specific references in Cano-Barbacil *et al.* 2022a) (Fig. 2). Occurrence records ranged from 148 points (sea lamprey, *Petromyzon mari-*

Table 1. Distribution summary of the 15 most widespread inland fish present in the Iberian Peninsula. Introduction date of alien species in the Iberian Peninsula, elevation range and the rheophilic (Rh) or limnophilic (Lim) character of the species according to Cano-Barbacil *et al.* (2020b, 2022b, 2023) is shown. Critical thermal maximum (CT_{max}), as indicator of the thermal tolerance and habitat selection of the species, was obtained from Comte & Olden (2017). *Resumen de la distribución de las 15 especies de peces de aguas continentales con una distribución más amplia en la península ibérica. Se muestra la fecha de introducción en la península ibérica de las especies exóticas, el rango de distribución altitudinal y el carácter reofilico (Rh) o limnofílico (Lim) de las especies según Cano-Barbacil et al. (2020b, 2022b, 2023). CT_{max} , un indicador de la tolerancia térmica de las especies y de la selección de hábitat, se obtuvo de Comte y Olden (2017).*

Species	Intro. date	Distribution description	Rh	Lim	CT_{max} (°C)
Sea lamprey <i>Petromyzon marinus</i> (n = 148)	-	Present in the Cantabric and Atlantic rivers. There are some references in the Ebro basin. Elevation range: 0 – 868 m	+		NA
European eel <i>Anguilla anguilla</i> (n = 898)	-	Distributed in almost all basins. Elevation range: 0 – 1439 m			35.1
Goldfish <i>Carassius auratus</i> (Linnaeus, 1758) (n = 639)	ca. 1650	Distributed in almost all basins. Elevation range: 0 – 1494 m		+	38.5
Common carp <i>Cyprinus carpio</i> Linnaeus, 1758 (n = 1166)	ca. 1650	Abundant in all basins with the exception of the NW rivers. Elevation range: 0 – 1644 m			36.4
Gudgeon <i>Gobio lozanoi</i> Doadrio & Madeira, 2004 (n = 826)	-	Present in the Bidasoa, Duero, Oria and some other rivers of the Basque Country, Mondego, Ebro, Guadalete, Guadiana, Guadalquivir, Júcar, Llobregat, Mijares, Nalón, Nansa, Miño, Segura, Tagus and Turia, but it constantly appears in new basins, where it behaves like an invasive species. Elevation range: 0 – 2001 m			NA
Bleak <i>Alburnus alburnus</i> (n = 402)	1990	Present in almost all basins, lacking in some rivers in northern Spain. Elevation range: 0 – 1699 m			34.5
Bermejuela <i>Achondrostoma arcasii</i> (n = 1240)	-	Present in the Miño, Ulla, Umia, Marín, Duero, Ebro, Tajo, Francolí, Júcar, Turia, Palancia and Mijares. Elevation range: 33 – 2001 m			35.5
Tench <i>Tinca tinca</i> (Linnaeus, 1758) (n = 177)	1560	Distributed in almost all basins. Elevation range: 11 – 1423 m		+	34.3
Southern Iberian spined loach <i>Cobitis paludica</i> (n = 1093)	-	Present in almost all basins, lacking in some rivers in northern Spain. Elevation range: 0 – 1581 m		+	36.7
Rainbow trout <i>Oncorhynchus mykiss</i> (Walbaum, 1792) (n = 318)	1898	Present in all basins, especially in those with fish stocking. Elevation range: 57 – 2423 m	+		29.8
Brown trout <i>Salmo trutta</i> Linnaeus, 1758 (n = 1665)	-	Present in almost all basins, lacking in some rivers in eastern and southern Spain, and in the Guadiana basin. Elevation range: 36 – 2575 m	+		29.5
Northern pike <i>Esox lucius</i> Linnaeus, 1758 (n = 303)	1949	Distributed in almost all basins. Elevation range: 0 – 1335 m			29.0
Pumpkinseed <i>Lepomis gibbosus</i> (Linnaeus, 1758) (n = 849)	1910	Present in all basins with the exception of the NW rivers. Elevation range: 0 – 1193 m		+	35.9
Black-bass <i>Micropterus salmoides</i> (Lacepède, 1802) (n = 841)	1955	Present in all basins with the exception of the NW rivers. Elevation range: 0 – 1374 m		+	35.7
Mosquitofish <i>Gambusia holbrooki</i> Girard, 1859 (n = 1106)	1921	Present in almost the entire Peninsula, it is only absent in most of the Miño basin and in the rivers that flow into the Cantabrian Sea. Elevation range: 0 – 1142 m		+	39.8

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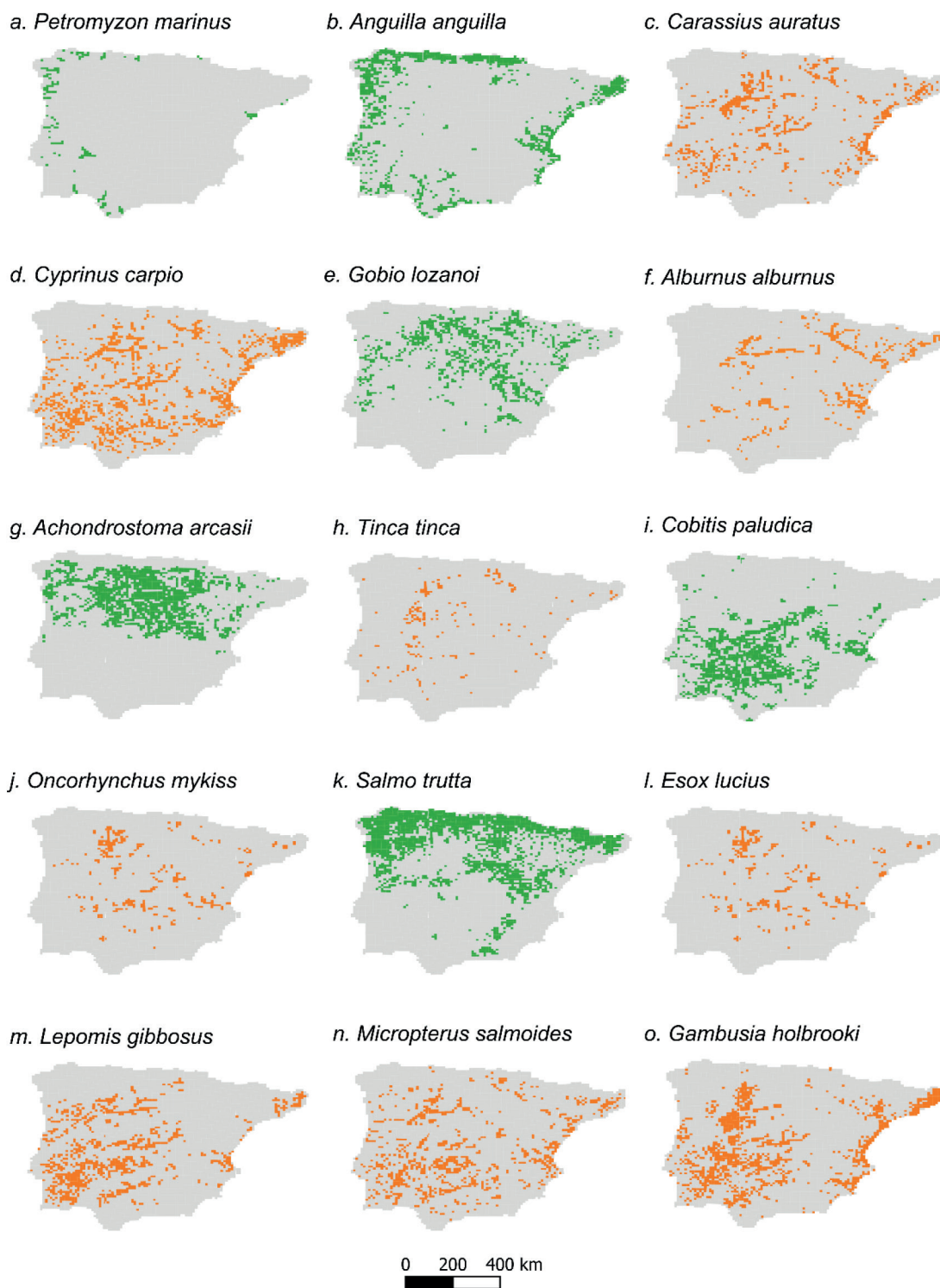


Figure 2. Distribution maps of the 15 studied species. Occurrences of native and alien species are indicated in green and orange, respectively. *Mapas de distribución de las 15 especies estudiadas. Las presencias de las especies autóctonas e introducidas se muestran con colores verde y naranja, respectivamente.*

Table 2. Results of the generalized linear models. The McFadden’s pseudo- R^2 of the model, the deviance explained by each predictor and their significance (ns: $P > 0.05$; *: $P \leq 0.05$; **: $P \leq 0.01$; ***: $P \leq 0.001$) are shown. *Resultados de los modelos lineales generalizados. Se muestra la pseudo- R^2 de McFadden del modelo, la devianza explicada por cada predictor y su significación (ns: $P > 0.05$; *: $P \leq 0.05$; **: $P \leq 0.01$; ***: $P \leq 0.001$).*

Species	R^2	Elevation	Latitude	Elevation ²	Latitude ²	Elevation × Latitude	Basin
<i>Petromyzon marinus</i>	0.311	274.8 ***	44.9 ***	0.7 ns	9.1 **	23.5 ***	80.5 ***
<i>Anguilla anguilla</i>	0.323	653.2 ***	374.8 ***	8.5 **	115.5 ***	18.7 ***	480.9 ***
<i>Carassius auratus</i>	0.128	102.0 ***	33.7 ***	32.8 ***	149.3 ***	11.0 ***	197.4 ***
<i>Cyprinus carpio</i>	0.126	268.1 ***	14.1 ***	35.2 ***	147.5 ***	0.0 ns	289.8 ***
<i>Gobio lozanoi</i>	0.184	81.9 ***	211.9 ***	48.5 ***	142.6 ***	7.1 **	399.9 ***
<i>Alburnus alburnus</i>	0.187	41.6 ***	44.4 ***	43.2 ***	80.5 ***	3.4 ns	343.6 ***
<i>Achondrostoma arcasii</i>	0.378	374.6 ***	647.9 ***	385.0 ***	446.0 ***	33.7 ***	451.0 ***
<i>Tinca tinca</i>	0.080	1.0 ns	11.8 ***	29.6 ***	19.8 ***	0.9 ns	64.4 ***
<i>Cobitis paludica</i>	0.268	198.9 ***	345.3 ***	149.4 ***	480.2 ***	12.3 ***	352.8 ***
<i>Oncorhynchus mykiss</i>	0.126	68.5 ***	26.3 ***	25.8 ***	6.1 *	17.7 ***	172.0 ***
<i>Salmo trutta</i>	0.379	668.1 ***	1495.1 ***	0.0 ns	107.1 ***	37.1 ***	411.5 ***
<i>Esox lucius</i>	0.142	0.1 ns	13.0 ***	126.4 ***	48.7 ***	1.9 ns	153.3 ***
<i>Lepomis gibbosus</i>	0.227	304.4 ***	15.5 ***	104.6 ***	257.6 ***	30.4 ***	407.5 ***
<i>Micropterus salmoides</i>	0.134	191.3 ***	14.6 ***	121.1 ***	133.4 ***	8.7 **	188.8 ***
<i>Gambusia holbrooki</i>	0.221	518.3 ***	3.4 ns	58.6 ***	362.6 ***	12.1 ***	330.3 ***

nus Linnaeus, 1758) to 1665 (brown trout), with a mean value of 778 occurrences per species. The spatial resolution for subsequent analyses was set to 10×10 km UTM (Universal Transverse Mercator, i.e., 100 km^2 , $n = 6142$ total cells), which reflected the most common resolution in the species’ occurrence records (see e.g., Doadrio, 2001).

Statistical analyses

We used generalized linear models (GLMs) with binomial errors (i.e., logistic regression) to evaluate the interaction of latitudinal and elevation gradients on the distribution (presence/absence) of each of the selected Iberian inland fish species. We included quadratic terms for latitude and elevation since the responses of species along broad-scale spatial gradients (e.g., latitude or elevation) are generally unimodal (Anderson et al., 2022). We also added the water district (hereafter, “basin”) to account for the evolutionary history of native species and the invasion dynamics (e.g., introduction date) of alien species (see Cano-Bar-

bacil et al., 2022a). The basin factor consisted of single river catchment in the case of large rivers (e.g., Duero, Tajo or Ebro), or sets of small rivers with similar environmental characteristics and faunas (e.g., Eastern Pyrenees basins, see Fig. S1, available at <https://www.limnetica.net/en/limnetica>). After model fitting, we analyzed the residuals for broad spatial autocorrelation by using the Moran’s I statistic and corresponding P values. This statistic varies from -1 to 1 , with values more different from 0 indicating spatial autocorrelation (Moran, 1948). As Moran’s I statistics were not significant in all model residuals, we decided to maintain non-spatial GLM models (see e.g., Oberdorff et al., 2019). We also calculated the McFadden’s pseudo- R^2 for each GLM model as a measure of model fit by using null and residual deviances (see e.g., Cano-Barbacil et al., 2020). Note that McFadden’s is one of the simplest and most widely used pseudo- R^2 measures, although it tends to give lower values than other measures (Smith & Mckenna, 2013). All statistical and modelling tasks were performed with the software R, version 4.2.2 (R Core Team, 2023).

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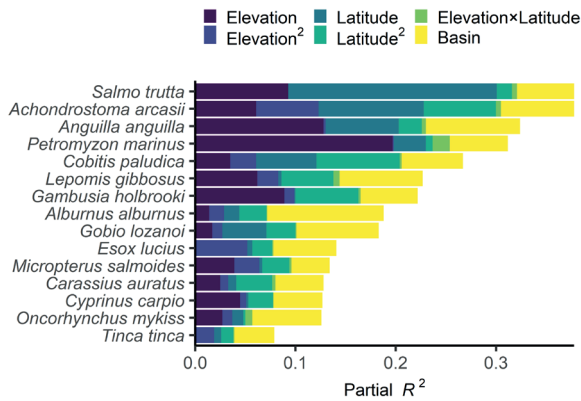


Figure 3. Variation in fish distribution explained (partial R^2 obtained with generalized linear models) by elevation, latitude, their quadratic terms, the interaction and the basin for the 15 most widespread inland fish present in the Iberian Peninsula. *Variación en la distribución de los peces explicada (R^2 parcial obtenida usando modelos lineales generalizados) por la elevación, la latitud, sus términos cuadráticos, su interacción y la cuenca para las 15 especies de peces de aguas continentales con una distribución más amplia en la península ibérica.*

RESULTS

Models explained between 8.0 and 37.9 % of the total variation in species' distribution (Table 2 and Fig. 3). The species with greatest explained variation were brown trout (37.9 %) and bermejuela (*Achondrostoma arcasii* (Steindachner, 1866)) (37.8 %), while little variation in distribution patterns could be explained in rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)) (12.6 %) and tench (*Tinca tinca* (Linnaeus, 1758)) (8.0 %). Generally, the effect of each gradient differed across species. Elevation and its quadratic term constituted a significant predictor of fish distribution in 13 out of the 15 species studied. The linear effect of latitude was not significant for mosquitofish, although the quadratic term of latitude was significant for all species. Partial R^2 values (Fig. 3) indicated that elevation (and its quadratic term) explained between 1.9 and 19.8 % of the variation, while latitude (and its quadratic

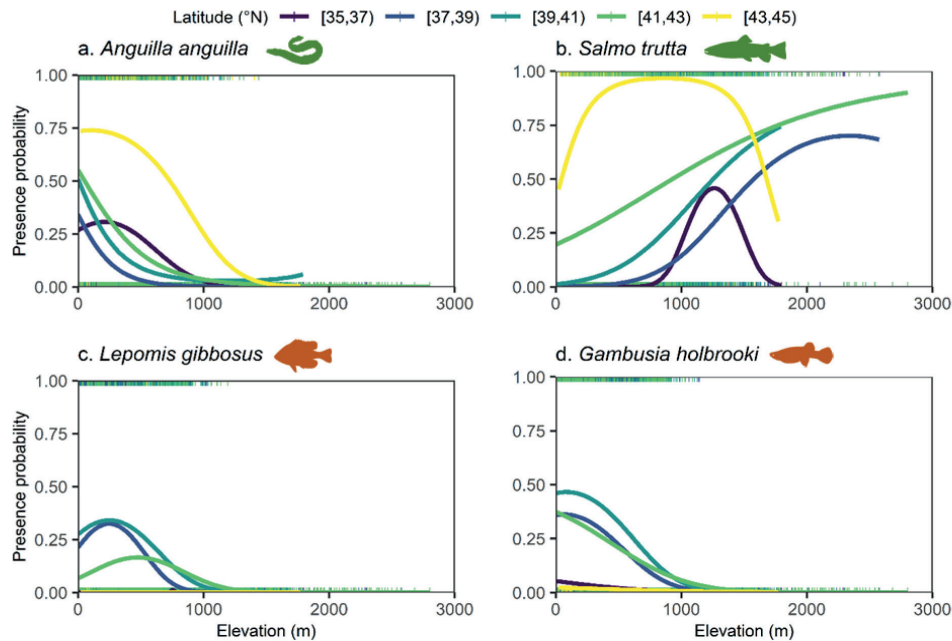


Figure 4. Response curves showing the relationship between the probability of species occurrences and elevation at different latitudinal ranges for (a) European eel (*Anguilla anguilla*); (b) brown trout (*Salmo trutta*); (c) pumpkinseed (*Lepomis gibbosus*); and (d) mosquitofish (*Gambusia holbrooki*). Native and alien species are represented by green and orange silhouettes, respectively. *Curvas respuesta que muestran la relación entre la probabilidad de ocurrencia y la elevación en diferentes rangos latitudinales para (a) anguila europea (Anguilla anguilla); (b) trucha común (Salmo trutta); (c) percasol (Lepomis gibbosus); y (d) gambusia (Gambusia holbrooki). Las especies autóctonas e introducidas se han representado mediante siluetas verdes y naranjas, respectivamente.*

term) explained between 1.3 and 22.3 %. We found significant interaction between elevation and latitude for 11 out of the 15 studied species, which explained between 0.1 and 1.7 % of the total variation. Basin was also a significant predictor of fish distribution for all studied species and explained between 4.0 and 11.6 % of the total variation. This result suggests that the prevalence of the 15 species varies across the different basins within the Iberian Peninsula.

Elevation, and its quadratic term, was the most important variable explaining the distribution of sea lamprey and European eel (*Anguilla anguilla* (Linnaeus, 1758)) (Fig. 3). Both diadromous species are mainly present in the lower reaches of Iberian rivers (see e.g., Fig. 4a). Similarly, the distribution of invasive mosquitofish, pumpkinseed, black-bass or common carp (*Cyprinus carpio* Linnaeus, 1758) was rather determined by elevation (Fig. 3). These species are more prevalent at low/intermediate elevations (see e.g., Fig. 4c and Fig.4d) and are mostly absent in the northern range of the Iberian Peninsula but also in southernmost Iberian Peninsula. By contrast, latitude, and its quadratic term, was the most important variable explaining the distribution of brown trout, bermejuela and southern Iberian spined loach (*Cobitis paludica* (de Buen, 1930)) (Fig. 3). For instance, we found a very high probability of occurrence of brown trout in the northern range of the Iberian Peninsula, especially at intermediate elevations (see e.g., Fig. 4b). However, the probability of occurrence decreased at lower latitudes, where the species is only frequent in higher areas, similarly to the rainbow trout.

DISCUSSION

In this study, we showed that the interaction of latitudinal and elevation gradients is a significant aspect in shaping the distributions of widespread native and alien Iberian inland fish. Good examples of this interaction are found in salmonids (i.e., brown and rainbow trout) and native gudgeon. Correspondingly, the probability of occurrence of these species is high for the entire range of elevations in the northern range of the Iberian Peninsula, and decreases at lower latitudes, where they are only present in areas of higher elevation.

For instance, water temperature, flow energy or substrate sizes are known to be key factors limiting salmonid distributions, which commonly inhabit relatively cold and fast-flowing waters (Magnuson *et al.*, 1979), despite there is some variation in thermal range between different populations (Elliott *et al.*, 1995; Parra *et al.*, 2009). More specifically, water temperature is considered one of the most pervasive environmental variables affecting growth and physiological performance in trouts (Elliott, 1994; Myrick & Cech, 2000; Jiang *et al.*, 2021; and see CT_{max} in Table 1). As a consequence, the Baetic Mountains in southern Spain (36 – 37° N) represent the ecological and geographical limit for the distribution of brown trout in Europe. Within that region, brown trout usually occurs at sites above 1000 m and within a narrow altitudinal range (Larios-López *et al.*, 2015b; Cano-Barbacid *et al.*, 2022b). Overall, southern brown trout populations are primarily delimited by natural boundaries at higher altitudes, including insurmountable natural barriers such as waterfalls. At lower altitudes, however, anthropogenic and climatic factors, such as dams, water abstraction, and summer drought, also contribute to population limitations (Larios-López *et al.*, 2015 a). However, we note that the current distribution of both brown and rainbow trout is conditioned by fish stocking practices carried out throughout the Peninsula. Some brown trout populations are maintained entirely by stocking (see e.g., Alonso *et al.*, 2017), and populations of rainbow trout are basically sustained due to regular releases and escapes from fish farms, as reproduction in Iberian rivers is rare (Doadrio, 2001).

Similarly, to brown and rainbow trout, our results also indicated latitudinal variation in elevational niche position in gudgeon. In the northernmost Peninsula and southern France, gudgeon occur in intermediate reaches with moderate currents, clear waters and sand or gravel bottoms (Doadrio & Madeira, 2004). By contrast, at intermediate latitudes of the Iberian Peninsula, where the species was translocated, it can be found also in the upper part of river basins (e.g., Segura, Mundo and Taibilla rivers) (Martínez-Morales *et al.*, 2010). Gudgeon is practically absent in the south of the Iberian Peninsula, which could be a result of less (or less successful) introduction events oc-

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curing at these latitudes (Doadrio, 2001). For instance, in the Guadalquivir basin, it only appears in the upper reaches of rivers belonging to three sub-catchments (Fernández-Delgado et al., 2014).

Results showed that elevation was particularly important in shaping the current distribution of diadromous sea lamprey and European eel. The occurrence of both species is greatly limited by anthropogenic factors such as the presence of large dams (Cano-Barbacil et al. 2022a). Thus, after the construction of most of the reservoirs during the last century, sea lamprey upstream migration was blocked at the lower reaches of major Iberian rivers (Mateus et al., 2012), causing an estimated 80 % loss of accessible habitat particularly into the headwaters of rivers. Similarly, the European eel has disappeared from most of the Ebro, Duero and Tagus basins.

The current distribution of invasive mosquitofish, pumpkinseed, black-bass and common carp in the Iberian Peninsula was also markedly mediated by elevation. These results agree with previous studies that found, for example, that temperature, elevation, and water flow strongly affect survival and reproduction of mosquitofish at local scales (Murphy et al., 2015). Thus, sites of higher elevation, which are typically associated with colder and steeper stream habitats, reduce the competitive capacity, reproductive performance and probability of occurrence of mosquitofish (Carmona-Catot et al., 2013; Murphy et al., 2015). However, we also found a significant effect of latitude and the interaction between both factors on mosquitofish distribution. Hence, this species is barely present in the northern latitudes of the Iberian Peninsula due to the climatic conditions that prevent its successful establishment (Murphy et al., 2015). Mosquitofish is also not present in the southernmost Peninsula, probably because of the absence of adequate habitats with many streams and lagoons being only temporary, which impedes establishment (Gómez et al., 2005). Similarly, water temperature is also a very important variable affecting the distribution pumpkinseed, black-bass and common carp (see CT_{max} values in Table 1), despite they show a wide climatic niche breadth (Bae et al., 2018; Cano-Barbacil et al., 2022a, 2023). Accordingly, these limnophilic species mainly occur in low and intermediate

river reaches with slow-flowing waters of the warmer regions of the Iberian Peninsula, and are often the dominant species in reservoirs (Cano-Barbacil et al., 2022b). Again, with the exception of the Guadiana and Guadalquivir basins, they are not abundant neither in the northern range nor in the southernmost Iberian Peninsula, probably due to the absence of appropriate permanent habitats (Vilizzi, 2012; Bae et al., 2018; Cano-Barbacil et al., 2022a). By contrast, the current distribution of invasive bleak in the Iberian Peninsula is mostly shaped by basin boundaries, and therefore, by their invasion history. Bleak was introduced in 1990 and it is still absent in several Iberian river basins, especially in the northern range (Latorre et al., 2023).

Ongoing climate change is expected to strongly impact the distribution patterns of many organisms (see e.g., Root et al., 2003; Thomas, 2010). Freshwater biodiversity is especially vulnerable to broad-scale global change due to their limited dispersal capacity and because of their dependence to specific thermal and hydrological regimes (e.g., Markovic et al., 2014). Therefore, based on our results and previous studies, cold water species (e.g., salmonids) are most at risk of losing suitable habitats, especially at the most extreme margins (latitudinal or elevational) of their range (Almodóvar et al., 2012). In fact, there has already been a significant reduction in brown trout distribution range in the last 150 years, coinciding with a warming trend (Clavero et al., 2017). It is expected that the range of brown trout in Spain will be reduced by 46 % by 2050 and this species is likely to be extirpated from the majority of headwater streams in the southern half of the Peninsula (Muñoz-Mas et al., 2016; Clavero et al., 2017). By contrast, fish species preferring warmer waters (e.g., cyprinids, centrarchids or cyprinodontiformes) are expected to gain habitats as a result of climate change in northern latitudes (Lappalainen & Lehtonen, 1997; Cano-Barbacil et al., 2022a). For invasive goldfish (*Carassius auratus* (Linnaeus, 1758)), common carp, tench, pumpkinseed or mosquitofish, reduced flows and warmer temperatures will cause new regions in the northernmost Peninsula or at higher elevations to become suitable in the near future (Murphy et al., 2015; Jakubčinová et al., 2018; Jia et al., 2019; Ilarri et al., 2022).

To conclude, our study highlights that latitude and elevation are two important spatial gradients to understand the distribution of Iberian inland fishes. Further, since both gradients strongly interact, the elevation at which a species occur simultaneously depends on latitude. This interaction between latitude and elevation is especially evident in salmonids (i.e., brown and rainbow trout), which tend to occupy intermediate and even lower reaches in the northernmost Peninsula, while they are mainly present in headwater streams of mountainous areas in the southern basins. However, our findings also suggest that additional factors such as evolutionary history, invasion dynamics, or migratory behavior play an important role in shaping the current distribution of Iberian fishes at the regional scale.

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