



# Subtle ecological effects of the invasive signal crayfish (*Pacifastacus leniusculus*) on Iberian fish communities

Bruno Oliveira · António B. Nogueira ·  
Amílcar Teixeira · Ronaldo Sousa

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**Abstract** The introduction of non-native species can disrupt the structure of communities and affect the functioning of freshwater ecosystems, disturbing various taxonomic groups, including fish. This study aimed to assess the ecological effects of the recent introduction of the signal crayfish *Pacifastacus leniusculus* in the fish communities in the Rabaçal and Tuela River basins (Montesinho Natural Park and adjacent areas; NE of Portugal), an area with very low human disturbance. A total of 34 sites (18 invaded and 16 non-invaded) were sampled in the summer of 2022 and comparisons were made between invaded and non-invaded sites concerning abundance, biomass, richness and diversity of fish communities. In addition, we compared the physiological condition of the sampled species. A total of 2307 fishes belonging to six different species were collected and results

indicated almost no negative (except diversity) effects at the community level. However, species-specific analysis revealed a decrease in the abundance of the Iberian chub *Squalius carolitertii* in invaded sites. We also observed a lower physiological condition of the brown trout *Salmo trutta*. Although the ecological effects appear to be subtle, ongoing monitoring of signal crayfish populations and their effects on fish communities is essential, using this study as a baseline for future comparisons. Additionally, urgent management measures—such as controlling and containing signal crayfish populations and raising local awareness—should be considered, given the conservation significance of the study area and the potential negative ecological effects of this non-native species.

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B. Oliveira (✉) · A. B. Nogueira · R. Sousa  
Department of Biology, CBMA – Centre for Molecular and Environmental Biology/ARNET-Aquatic Research Network/IB-S, Institute of Science and Innovation for Bio-Sustainability, University of Minho, Campus Gualtar, 4710-057 Braga, Portugal  
e-mail: bruno.mso97@gmail.com

A. Teixeira  
Centro de Investigação de Montanha (CIMO), Instituto Politécnico de Bragança, Campus de Santa Apolónia, 5300-253 Bragança, Portugal

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## Introduction

One of the greatest challenges facing humanity today is the loss of biodiversity (McCauley et al. 2015; Ceballos et al. 2017; Rosenberg et al. 2019; Tickner et al. 2020). With the decrease in the number of species, or reductions in their abundance, ecosystems become more fragile and less resilient, calling into question their stability and, consequently, affecting the services generated by them (Srivastava and

Vellend 2005; Tilman 1999). Freshwater ecosystems such as rivers, lakes, ponds, among others, have played a key role in human societies throughout history (Wantzen et al. 2016). These diverse ecosystems support a wide range of species, which collectively provide essential ecosystem services, including provision of water, climate regulation, food, energy, and recreational opportunities that benefit society (Hanna et al. 2018). These ecosystem services, more than having a high economic value, are essential to maintain the quality of life we know today.

Despite their ecological role and economic importance, freshwater ecosystems are among the most vulnerable ecosystems on Earth (Dudgeon et al. 2006; Balian et al. 2008; Dudgeon 2019; Sayer et al. 2025). Over the past decades, there has been a significant decline in the area covered by these ecosystems, with Europe alone witnessing a 50% decrease between 1970 and 2008 (Gozlan et al. 2019). This decline is mainly due to direct habitat loss. However, other anthropogenic disturbances, such as the construction of dams that alter and fragment river habitats; the introduction of non-native species, which destabilize the balance of ecosystems through predation, competition, and the introduction of parasites and diseases; intensive fishing; excessive use of water for agriculture and other activities; and climate change may be responsible for great declines in freshwater biodiversity and even extinctions (Dudgeon 2019; Lopes-Lima et al. 2023; Sayer et al. 2025).

From the many taxonomic groups that colonize freshwater ecosystems, fish are without a doubt one of the most charismatic (Mammola et al. 2023) and have been used by humans since immemorial times. Freshwater fish are a diverse group, with approximately 15,000 described species, most of which are affected by the human disturbances described above (Closs et al. 2015). In freshwater ecosystems, fish play crucial roles in maintaining ecological health and biodiversity (Closs et al. 2015). Fish serve as vital links in the food chain, preying on smaller organisms while being preyed upon by larger predators. Nonetheless, these organisms are highly susceptible to population declines. In the Iberian Peninsula the decline of endemic fish species is due to a number of factors acting synergistically, which may include the introduction of non-native species (Hermoso and Clavero. 2011). Non-native species are known to impact negatively freshwater fish due

to increase competition, predation and introduction of parasites and diseases (Aloo et al. 2017; Parvez et al. 2023) or changing environmental conditions (Weber and Brown 2009; Sousa et al. 2009). These impacts have been also described in protected areas, being freshwater fish particularly affected by non-native species (Carneiro et al. 2025).

The signal crayfish *Pacifastacus leniusculus* is a freshwater decapod that is native to the west coast of North America and was introduced in Spain around the 1970s for commercial and recreational purposes (Vedia and Miranda 2013). The introduction of this species in Iberia, negatively affected macrophytes, macroinvertebrates, reptiles, benthic fish and amphibians (Alves et al. 2025; Carvalho et al. 2022a). It is known that the presence of this and others non-native crayfish species can alter the aquatic biodiversity directly and indirectly through complex interactions (Jackson et al. 2014; Strayer 2010). Some studies also point out that signal crayfish is an effective predator of freshwater mussels (Meira et al. 2019; Sousa et al. 2019) and other macroinvertebrates (Carvalho et al. 2022a), being also responsible for changes in ecosystem functioning, including leaf litter decomposition and nutrient cycling (Alves et al. 2025; Carvalho et al. 2022b). Regarding its effects on fish fauna, there are studies showing that signal crayfish can outcompete benthic fishes in relation to micro-habitat use, resulting in increased mortality (Guan and Wiles 1997). However, the number of studies assessing the possible ecological effects of signal crayfish on fish communities are low (Galib et al. 2021).

Considering the lack of information about the topic, this research aimed to assess the potential ecological effects of the recent introduction of the invasive signal crayfish into the Montesinho Natural Park and adjacent areas, Portugal. It should be noted that the first detection of the signal crayfish in the Montesinho Natural Park was in 2013 (Sousa et al. 2015). To achieve this, and using multiple sampling sites within the Tuela and Rabaçal River basins, we compared the fish communities in terms of abundance, biomass, richness and diversity in invaded and non-invaded sites. At the individual level we also assess possible differences in the physiological condition between invaded and non-invaded sites. This study also aimed to enhance understanding of the fish communities in these almost pristine mountain rivers. The obtained

results may inform future management actions and may help to better protect these delicate ecosystems from further degradation caused by the introduction of non-native species.

## Methods

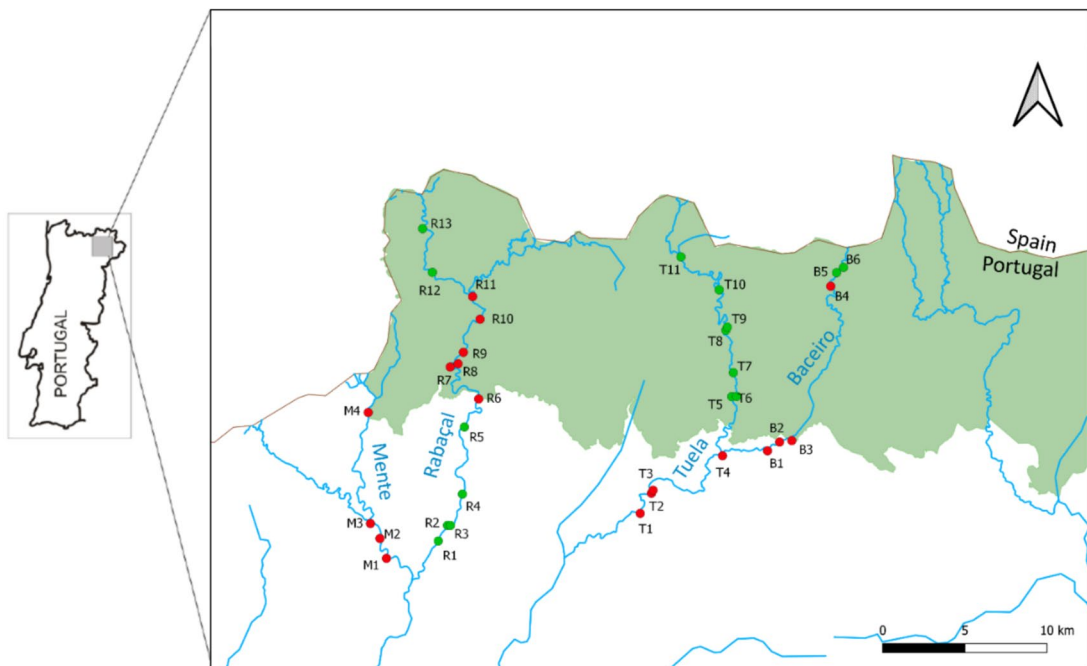
### Study area

This study was conducted in the Montesinho Natural Park and adjacent areas, located in the northeast region of Portugal. This protected area, created in 1979, is located from 41°43'47" to 41°59'24" N and 6°30'53" to 7°12'9" W. The landscape is characterized by gentle reliefs with rounded peaks, separated by river valleys, and there is a predominance of schist, limestone (in plateau areas), and granite. The climate is Mediterranean with influence from the Atlantic Ocean, with medium annual temperatures of 12.5 °C. In terms of precipitation, the study area has an annual average of 1000–1600 mm. The Montesinho Natural Park covers a total area of around 75 thousand

hectares and was mainly created to protect birds, terrestrial vertebrates and plants. The studied region is traversed by multiple rivers and streams, providing essential habitats for a diverse range of aquatic species, including aquatic invertebrates, mammals, birds, reptiles, amphibians, and fish. Among the fish species, the brown trout (*Salmo trutta*), the Douro nase (*Pseudochondrostoma duriense*), the Iberian barbel (*Luciobarbus bocagei*), the Iberian chub (*Squalius carolitertii*), the Iberian roach (*Squalius alburnoides*), and the Northern Iberian spined loach (*Cobitis calderoni*) are present in the study area (Nogueira et al. 2021c).

### Sampling strategy

The fish and crayfish sampling was performed during the summer of 2022. Thirty-four sites were sampled (18 invaded and 16 non-invaded) in the Mente (4 invaded sites), Rabaçal (6 invaded and 7 non-invaded sites), Tuela (4 invaded and 7 non-invaded sites) and Baceiro (4 invaded and 2 non-invaded sites) Rivers (Fig. 1). The selection of these sites was based on



**Fig. 1** Map of the surveyed area showing the location of the 34 sampling sites (18 invaded—red; 16 non-invaded—green) in Mente, Rabaçal, Tuela and Baceiro Rivers. The marked green area represents the Montesinho Natural Park.

earlier information available about the signal crayfish distribution (Carvalho et al. 2025). For environmental characterization, temperature (°C), oxygen (mg/L), conductivity ( $\mu\text{S}/\text{cm}$ ), total dissolved solids (TDS) (mg/L) and pH were measured in situ in the middle of the river and near the bottom at all sites using a HACH HQ 40d multi-parameter probe.

To assess the degree of naturalness and/or disturbance and to obtain the current hydromorphological status of the analysed invaded and non-invaded sites, a River Habitat Survey (RHS) was performed (Raven et al. 1998, 2000). A river stretch with a total length of 500 m at each site was sampled to obtain the Habitat Modification Score (HMS) and Habitat Quality Assessment (HQA) indexes (following Raven et al. 1998). The HMS index made it possible to measure the degree of artificialisation of the channel by observing the presence and impact of artificial structures present in each site (Raven et al. 1998), by using a group of sub-indices (Table S1). The HQA index measured the rarity, richness and diversity of river habitats and is also made up of several sub-indices (Table S2) based on the relevance of certain habitat characteristics for biological communities. In addition to these two indices, the Riparian Quality Index (RQI) was also assessed. The RQI represents the naturalness, complexity and continuity of the riparian zone (Table S3). The final RQI score is classified into 5 equal classes that represent an increasing value of riparian quality, ranging from “Very low” (1st quintile) to “Very high” (last quintile).

The fish community was sampled using a portable electrofishing equipment (Hans Grassl) with a pulsed DC-300-600 V generator. The electrofishing passes were always performed for 20 min in a river stretch with a total length of 100 m, where the fish were stunned and collected in order to measure their weight (measured with a precision digital scale), length (measured with a ruler) and to identify their species. Therefore, abundance and biomass of fish species per site was expressed as the total number and weight of individuals per catch per unit of effort (CPUE/20 min). After collecting this information, the fish were released without any harm. To assess the fish condition, the Fulton’s condition factor was used, calculated with the equation  $K_c = 100 * W/L$ , where  $W$  is the total weight of the fish and  $L$  is the total length.

The abundance of the signal crayfish was assessed in the same 34 sites sampled to characterize the fish communities (Fig. 1). Crayfishes were captured by placing 8 funnel traps, five rectangular ( $50 \times 30 \times 20$  cm; 0.5 cm mesh) and three cylindrical (43 cm diameter; 22 cm height; 1.5 cm mesh), per site for 24 h, along a river stretch with a total length of 100 m. Therefore, abundance of crayfish per site was expressed as the total number of individuals per catch per unit of effort (ind. CPUE/24 h). All traps were baited with dead fish (*Trachurus trachurus*).

#### Data analyses

For the environmental characterization, eight variables were used: temperature, dissolved oxygen, water conductivity, total dissolved solids (TDS), pH, altitude, HMS and HQA results. The data was fourth rooted transformed to perform a Principal Component Analysis (PCA), in order to sort the different sites according to the environmental variables measured. This analysis was performed on Primer 6 (version 1.0.3, Primer-E Ltd, Plymouth).

To analyze the fish communities a non-metric Multi-Dimensional Scaling (nMDS) was performed, using the abundance data previously square root transformed, to create a matrix of similarity using Bray–Curtis distance. A two-way PERMANOVA test (9999 permutations), was performed to evaluate the influence of the basin (Rabaçal and Tuela) and the presence of the signal crayfish (Yes and No) in the fish communities. If the number of permutations was lower than 150 the Monte Carlo test  $P$  value was considered. In order to appraise the species most contributing for the dissimilarity between basins and between invaded and non-invaded sites a SIMPER analysis was conducted. We also calculated the Richness ( $S$ ), abundance ( $N$ ), Shannon–Wiener diversity index ( $H'$ ) and the Pielou’s evenness ( $J'$ ) on Primer 6 using the Diversity option (version 1.0.3, Primer-E Ltd, Plymouth). To test possible differences in abundance, biomass, richness, Shannon–Wiener and Pielou’s evenness, and Fulton’s condition between basins and between invaded and non-invaded sites nonparametric Kruskal–Wallis multiple comparison tests were performed, since normality or homogeneity of variance were not met, even using several transformations.

These statistical tests were carried out on R studio (Version 2023.06.1-524).

## Results

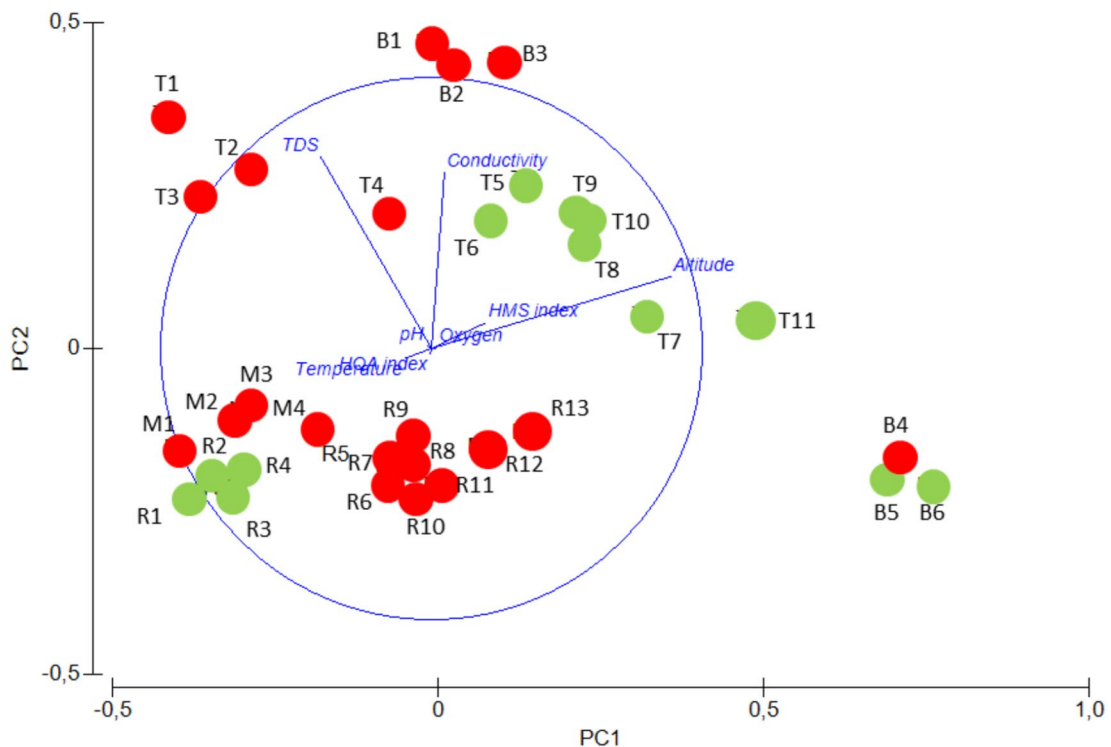
### Environmental characterization

Temperature varied between 16.1 (site B5) and 23 °C (site R7); dissolved oxygen between 7.98 (site B1) and 9.47 mg/L (site T8); water conductivity between 24.5 (site R11) and 62.4  $\mu$ S/cm (site T1); total dissolved solids between 5.0 (site B6) and 28.9 mg/L (site B1); pH between 6.45 (site B4) and 7.10 (site R6) and altitude between 385 (sites M1 and R1) and 843 m (site B6) (Table S4).

The RHS showed that in general, in the Rabaçal River basin, HQA scores were quite high (Table S5). All sites, except Rab 6 (Class 2—"Good"), achieved the "Excellent" class (95% of sites). Regarding the Tuela River basin (Table S6), all sites exhibited

"Excellent" quality. Regarding the HMS index, the scores obtained ranged from 0 (Class 1 in both studied basins) to 955 in the Rabaçal River basin (Class 4–Rab 6) and 1635 in the Baceiro River basin (Class 5–Bac 3). Regarding hydromorphological quality, the Rabaçal River basin stands out for generally having better quality compared to the Tuela River basin (Table S7). The Rabaçal River basin has a higher number of sites with "Excellent" quality (6), whereas the Tuela River basin only four sites reached this quality level. In fact, in the Tuela River basin one site was classified with the worst quality ("Bad quality") and 4 sites had "Mediocre quality".

The PCA performed using the collected environmental data mainly separated the sampling sites into two large groups (Fig. 2): The Rabaçal group, that consisted in the sites from the Rabaçal and Mente Rivers and the Tuela group, that aggregated the sites from the Tuela and Baceiro Rivers. PC1 explained 53.4% of all the variation and PC2 explained 28.4% (Table S8). Of all the environmental variables, the



**Fig. 2** Principal Components Analysis (PCA) showing the 34 sampling sites disposition based on the environmental factors measured. PC1 explains 53.4% of all variance and PC2 28.4%.

Green dots indicate absence of the signal crayfish while red dots indicate presence

ones that explained most of the differences in PC1 were altitude, HMS index (positive values) and TDS (negative values), while for PC2 the variables were conductivity, TDS and altitude (positive values) and temperature and the HQA index (negative values).

## Biotic characterization

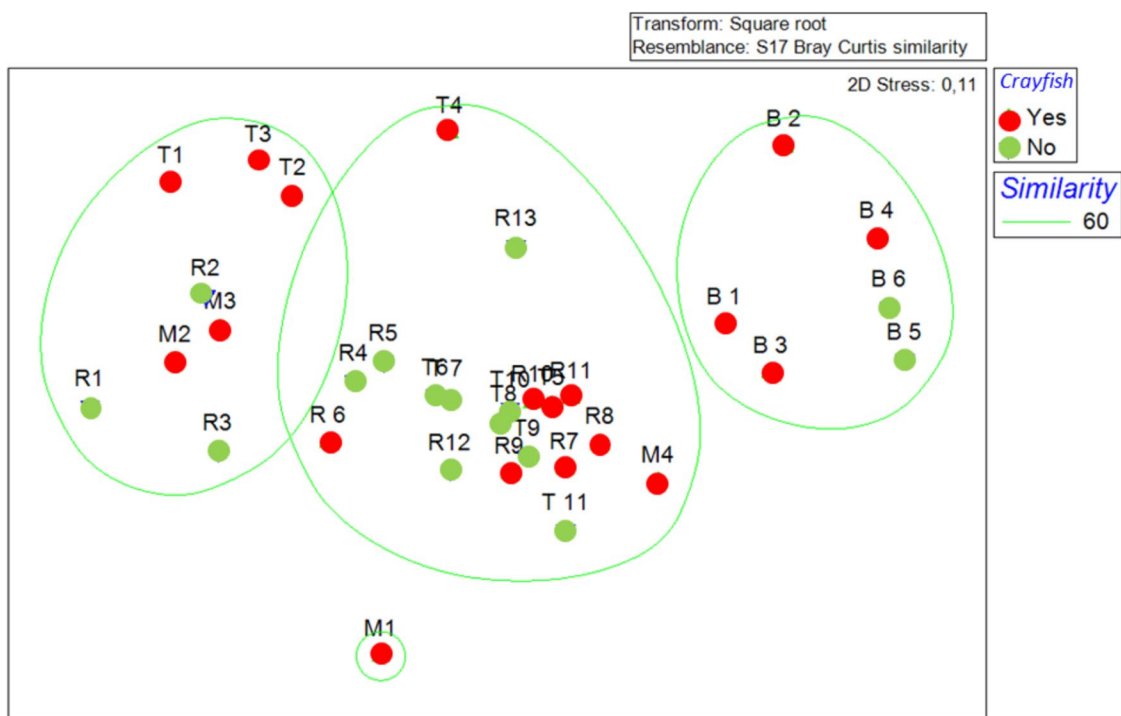
### Fish communities

A total of 2307 fishes belonging to six different species were collected: brown trout *Salmo trutta*, Douro nase *Pseudochondrostoma duriense*, Iberian barbel *Luciobarbus bocagei*, Iberian roach *Squalius alburnoides*, Iberian chub *Squalius carolitertii* and Northern Iberian spined loach *Cobitis calderoni*. The nMDS of the fish communities is shown in Fig. 3 with four groups retrieved using a similarity of 60%, with the largest one showing most of the non-invaded sites. The PERMANOVA results revealed no significant differences between basins (Pseudo F=2.13);

$p=0.10$ ) or invaded and non-invaded sites (Pseudo F=1.41;  $p(\text{MC})=0.39$ ).

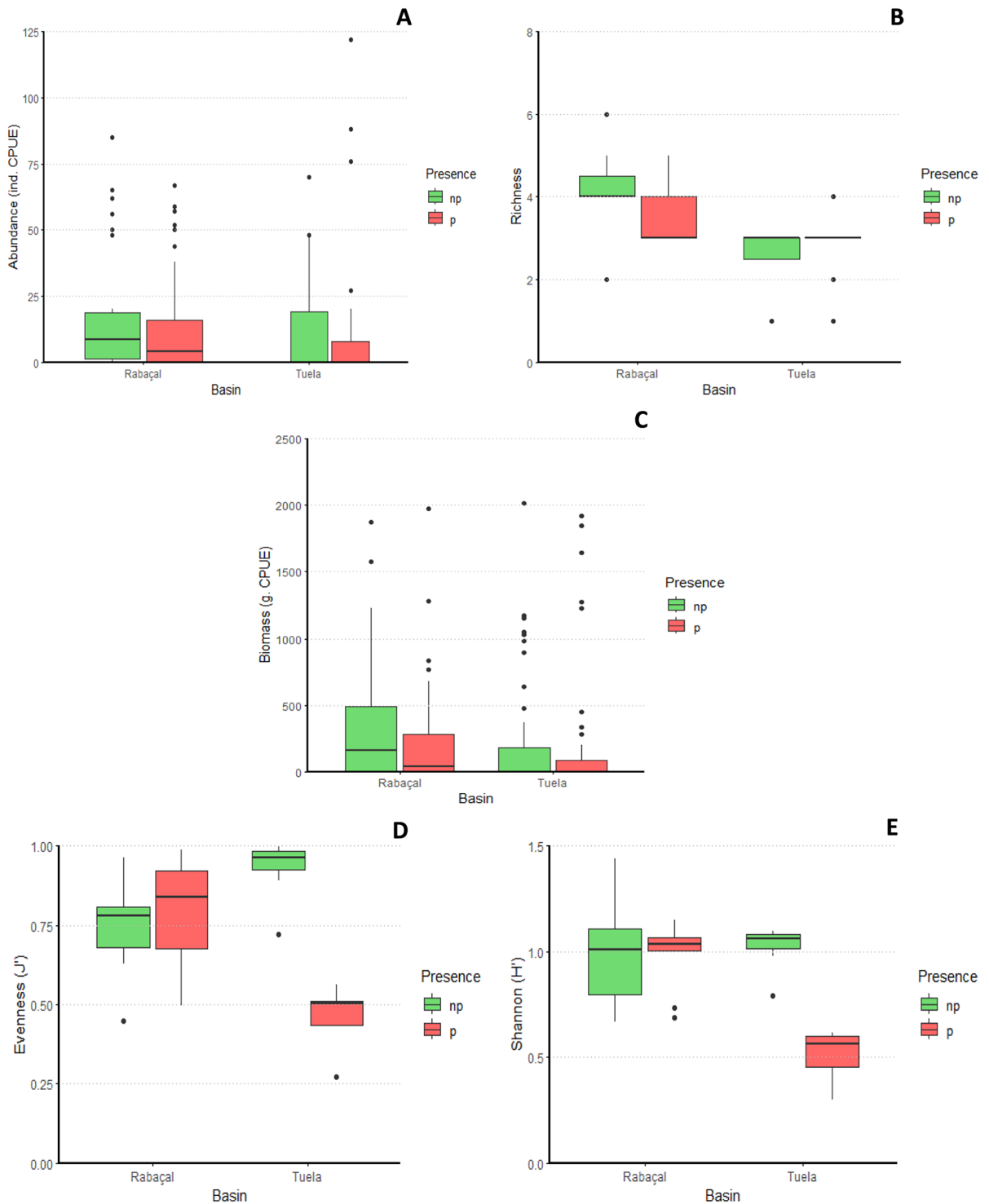
According to the SIMPER analysis the three species contributing the most to the dissimilarity between the Rabaçal and Tuela River basins were Douro nase (15.30%), brown trout (10.95%), and Iberian chub (7.37%). The three species contributing the most to the dissimilarity between invaded and non-invaded sites were Douro nase (34.58%), Iberian chub (21.93%), and brown trout (19.19%).

Concerning abundance, the Rabaçal River basin had an average abundance value of 11.2 (ind. CPUE) at invaded sites and 17.4 (ind. CPUE) at non-invaded sites, while at Tuela River basin the average value was 9.21 (ind. CPUE) at invaded sites and 10.0 (ind. CPUE) at non-invaded sites (Fig. 4A). Significant differences in abundance were found between basins ( $p<0.05$ ), with the Rabaçal River basin showing higher abundance at both invaded and non-invaded sites than the Tuela River basin. No significant differences were found between invaded and non-invaded sites within each basin ( $p=0.29$ ).



**Fig. 3** Non-metric Multi-Dimensional Scaling (nMDS) of the fish community showing the sampling sites and the presence or absence of the signal crayfish. Sampled sites grouped by 60%

similarity. Green dots indicate absence of the signal crayfish while red dots indicate presence



**Fig. 4** Abundance (A), Richness (B), Biomass (C), Evenness (D) and Shannon index (E) of the fish community on Rabaçal and Tuela River basins. Boxplots show median values (central line), the range from the 25th to 75th percentile (box) and the

largest and lowest value within 1.5 times interquartile range below and above the 25th and 75th percentile (whiskers) and dots represent extreme values. Np—signal crayfish not present; p—signal crayfish present

Regarding species richness, the Rabaçal River basin had an average richness value of 3.6 at invaded sites and 4.14 at non-invaded sites, while at Tuela River basin the average value was 2.88 at invaded sites and 2.56 at non-invaded sites (Fig. 4B). Significant differences in species richness between basins were found ( $p < 0.005$ ), with the Rabaçal River basin having a higher richness at both invaded and non-invaded sites than the Tuela River basin sites. No significant differences were found between invaded and non-invaded sites within each basin ( $p = 0.9$ ).

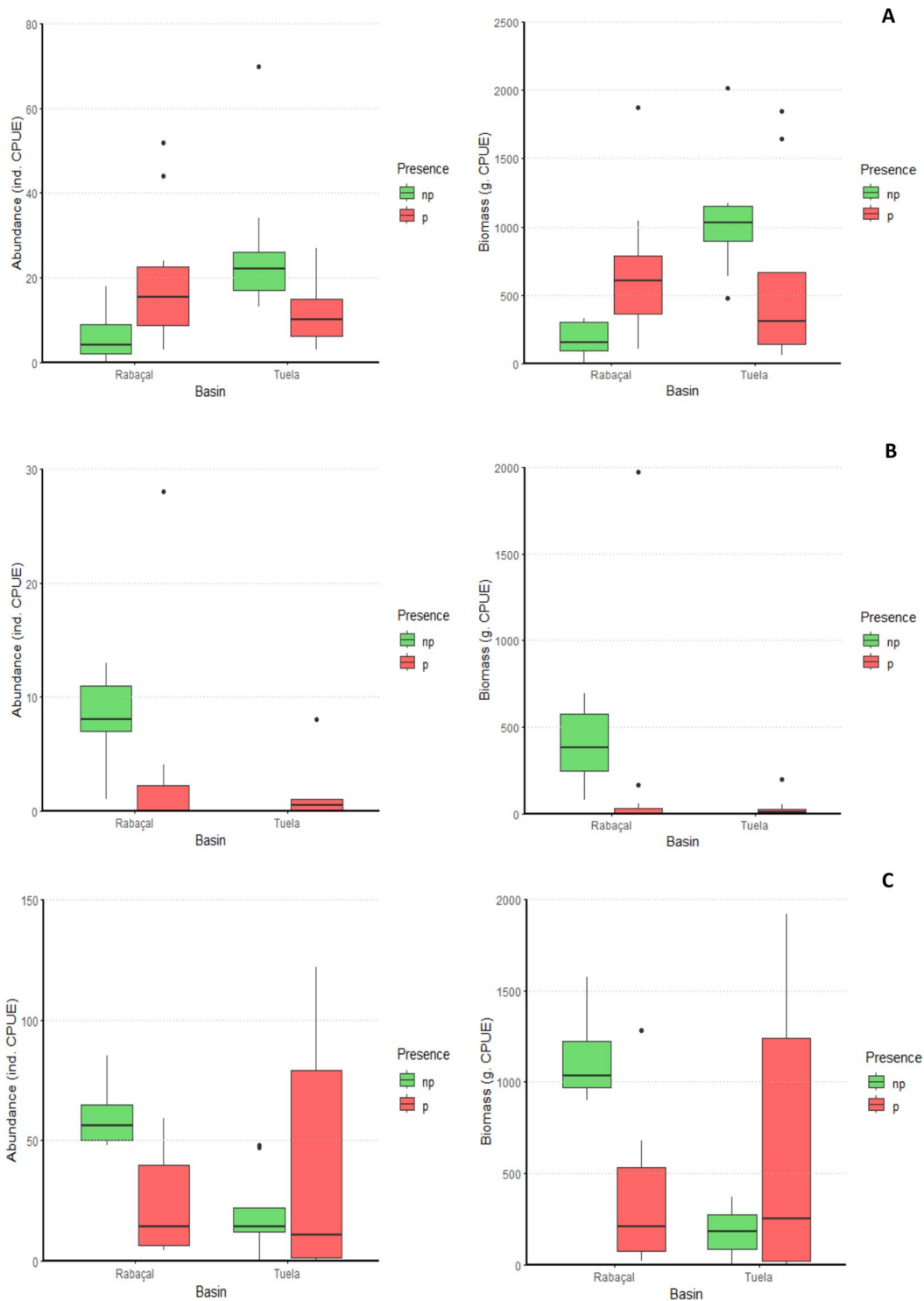
Biomass in the Rabaçal River basin had an average value of 206 (g. CPUE) at invaded sites and 343 (g. CPUE) at non-invaded sites, while at Tuela River basin the average was 212 (g. CPUE) at invaded sites and 223 (g. CPUE) at non-invaded sites (Fig. 4C). Significant differences in biomass were found between basins ( $p < 0.05$ ), with the Rabaçal River basin showing significantly higher biomass at non-invaded sites. However, no significant differences were found between invaded and non-invaded sites within each basin ( $p = 0.29$ ).

The Evenness index at Rabaçal River basin had an average value of 0.80 at invaded sites and 0.74 at non-invaded sites, while at Tuela River basin the average value was 0.40 at invaded sites and 0.72 at non-invaded sites (Fig. 4D). Significant differences were found between invaded and non-invaded sites ( $p < 0.05$ ), with significantly lower Evenness at invaded sites in the Tuela River basin. No significant differences were found between basins ( $p = 0.16$ ). The Shannon–Wiener diversity index at Rabaçal River basin had an average value of 0.99 both on invaded and non-invaded sites, while at Tuela River basin the average value was 0.45 at invaded sites and 0.80 at non-invaded sites (Fig. 4E). Significant differences were found between basins ( $p < 0.05$ ), with the Rabaçal River basin exhibiting higher diversity at both invaded and non-invaded sites when compared with the Tuela River basin, and between invaded and non-invaded sites ( $p < 0.05$ ), with the diversity being higher at non-invaded sites in the Tuela River basin.

Analyzing species by species, no significant differences were found for brown trout abundance between basins ( $p = 0.1$ ) or invaded and non-invaded sites ( $p = 0.8$ ). Similarly, for brown trout biomass, no significant differences were found between basins ( $p = 0.09$ ) or invaded and non-invaded sites ( $p = 0.6$ ) (Fig. 5A). For the Iberian barbel, significant

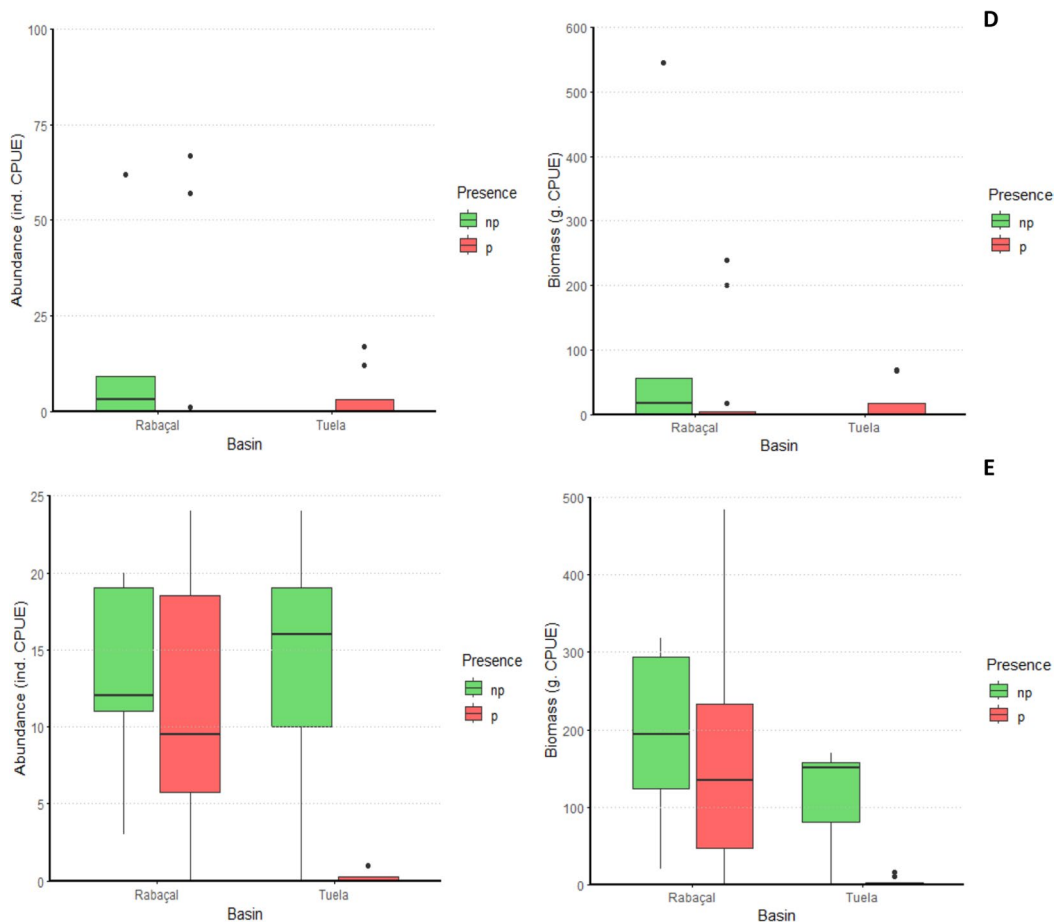
differences in abundance were found between basins ( $p < 0.05$ ), with higher abundance in the Rabaçal River basin, but not between invaded and non-invaded sites ( $p = 0.9$ ). For biomass significant differences were found between basins ( $p < 0.05$ ), with higher biomass in the Rabaçal River basin, but not between invaded and non-invaded sites ( $p = 0.7$ ) (Fig. 5B). For the Douro nase, no significant differences in abundance were found between basins ( $p = 0.2$ ) or invaded and non-invaded sites ( $p = 0.4$ ). For biomass no significant differences were found between basins ( $p = 0.09$ ) or invaded and non-invaded sites ( $p = 0.7$ ) (Fig. 5C). For the Iberian roach, no significant differences in abundance were found between basins ( $p = 0.1$ ) or invaded and non-invaded sites ( $p = 0.7$ ) and for biomass, no significant differences were found between basins ( $p = 0.1$ ) or invaded and non-invaded sites ( $p = 0.7$ ) (Fig. 5D). For the Iberian chub, significant differences in abundance were found between invaded and non-invaded sites ( $p < 0.05$ ), with higher abundance at non-invaded, but not between basins ( $p = 0.053$ ). For biomass significant differences were found between basins ( $p < 0.05$ ), but not between invaded and non-invaded sites ( $p = 0.09$ ) (Fig. 5E).

Analyzing the physiological condition through Fulton's condition factor, significant differences in brown trout were observed between invaded and non-invaded sites ( $p < 0.05$ ), with better condition at non-invaded sites, but not between basins ( $p = 0.18$ ) (Fig. 6A). For the Iberian barbel, no significant differences were found between basins ( $p = 0.2$ ) or invaded and non-invaded sites ( $p = 0.3$ ) (Fig. 6B). For the Douro nase, significant differences were found between basins ( $p < 0.005$ ), with better condition in the Tuela River basin, and between invaded and non-invaded sites ( $p < 0.005$ ) with better condition at invaded sites (Fig. 6C). For the Iberian roach, no significant differences were found between basins ( $p = 0.1$ ) or invaded and non-invaded sites ( $p = 0.97$ ) (Fig. 6D). For the Iberian chub, significant differences were found between invaded and non-invaded sites ( $p < 0.05$ ), with better condition at invaded sites, while no differences were found between basins ( $p = 0.14$ ) (Fig. 6E).



**Fig. 5** Abundance and biomass of the *Salmo trutta* (A), *Luciobarbus bocagei* (B) *Pseudochondrostoma durienae* (C), *Squalius alburnoides* (D) and *Squalius carolitertii* (E). Boxplots show median values (central line), the range from the 25th to

75th percentile (box) and the largest and lowest value within 1.5 times interquartile range below and above the 25th and 75th percentile (whiskers) and dots represent extreme values. Np—signal crayfish not present; p—signal crayfish present



**Fig. 5** (continued)

### *Crayfish abundance*

A total of 3157 signal crayfish were sampled in 18 (out of 34) sites. There were significant differences between the two basins ( $p < 0.005$ ), with the Tuella River basin showing higher abundance compared to Rabaçal River Basin (Fig. 7A and B).

### Discussion

We hypothesized that the presence of the invasive signal crayfish would lead to a significant negative effect on abundance, biomass, richness and diversity of fish communities. That was not the

case, since we only found significant differences in the diversity of fish communities when comparing invaded and non-invaded sites. However, at the species level, both brown trout and Iberian chub seem to be negatively affected by the presence of the signal crayfish.

### Environmental characterization

Rabaçal and Tuella River basins were environmentally similar. The only sampling sites that stand out are the ones from the Baceiro River, where lower values of water temperature, conductivity and TDS were measured, especially at sites B4, B5 and B6 that are located at higher altitudes. Almost all sites in both

basins obtained the "Excellent class" in the HQA. Those scores are attributed to the nearly natural character of the channel habitats and adjacent riparian areas, resulting in good longitudinal and lateral connectivity within the river corridor (Raven et al. 1998, 2002). The HMS was not so high compared to the HQA, with the "Pristine" and "Predominantly unmodified" classes being achieved in 63.2% of all the sampling sites. Earlier studies, using the same or similar methodologies support the high-quality status of both basins (Oliveira et al. 2012; Sousa et al. 2015; Nogueira et al. 2021a). Although this high-quality status, recently these basins have been subjected to extreme droughts (summers of 2017 and 2022) that left some parts of the Mente and Baceiro Rivers without water and ended up severely affecting several species, including the endangered pearl mussel *Margaritifera margaritifera* (Sousa et al. 2018; Nogueira et al. 2021a).

Overall, the results from the environmental characterization reflect the very low human disturbance of all studied rivers. These results enhance our confidence when assessing the possible effects of the invasive signal crayfish on fish communities, as the environmental conditions were very similar along all the surveyed sites and so possible differences between invaded and non-invaded sites will not be masked by these biases.

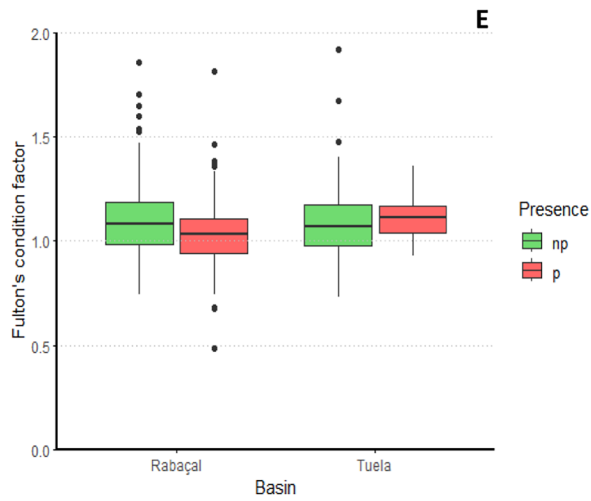
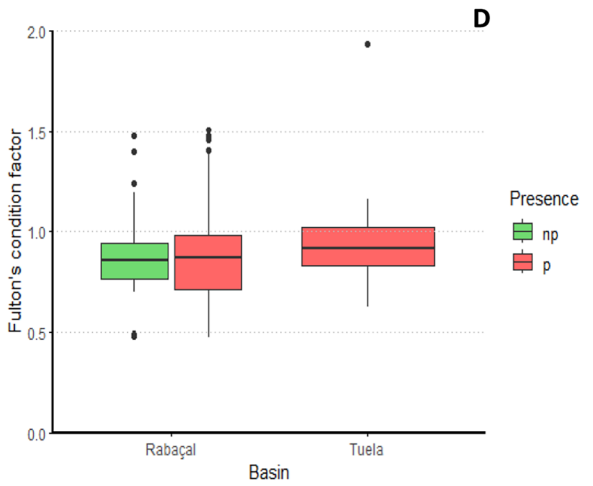
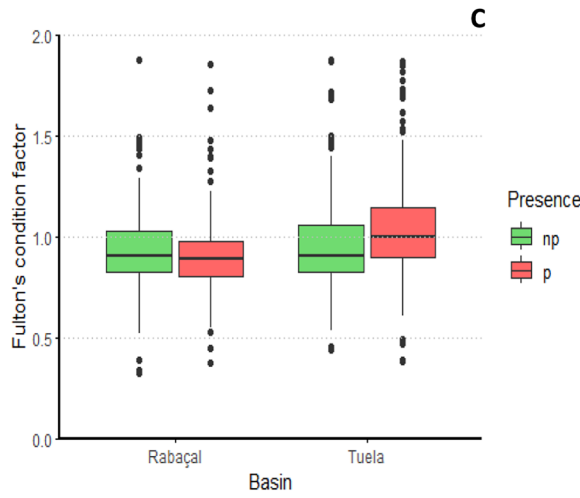
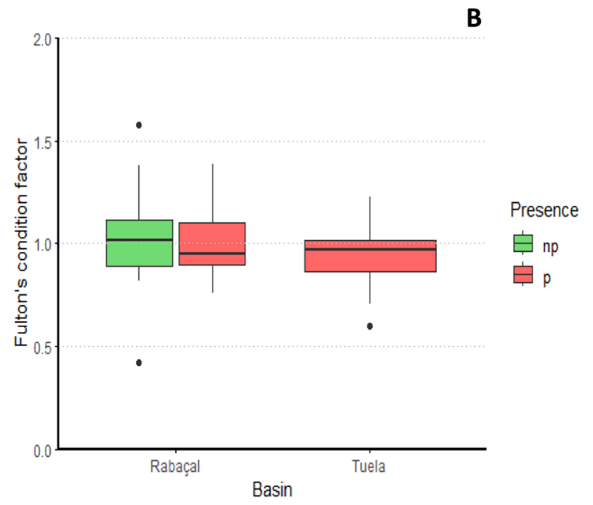
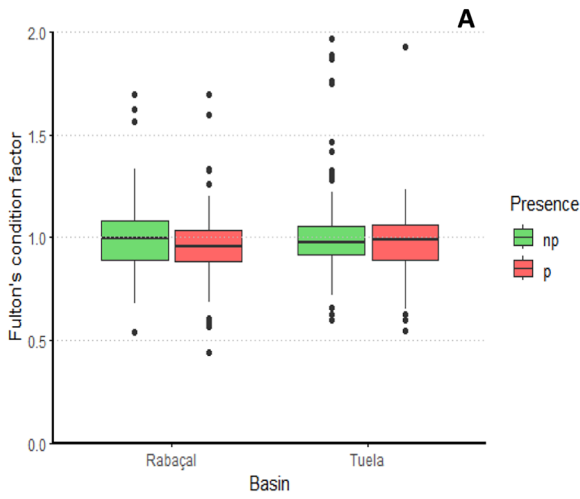
### Biotic characterisation

At the community level, and contrary to our expectations, we only observed a negative effect of the presence of the signal crayfish on the fish diversity. Abundance, biomass and species richness did not show any significant difference between invaded and non-invaded sites. These results are supported by some studies that showed no effects of the signal crayfish on fish populations (Stenroth and Nyström. 2003; Degerman et al. 2007). However, other studies found negative effects due to the presence of the signal crayfish (Guan and Wiles. 1997; Peay et al. 2009; Galib et al. 2021), but those are mainly associated with benthic fish species. In our studied area most fish are pelagic, being the only exception the Northern Iberian spined loach.

When analyzing fish species abundance and biomass independently, brown trout, Iberian barbel, Douro nase and Iberian roach were not affected by

the presence of the invasive species signal crayfish, only showing significant differences between basins. However, the Iberian chub exhibits lower abundance in the presence of the signal crayfish. This result may suggest some interaction between the signal crayfish and the Iberian chub, since crayfish species are known to compete with some fish for shelter putting them at higher risk of predation (Vaeßen and Hollert 2015). Therefore, and from all the six fish species, only the Iberian chub abundance seems to be negatively affected by the signal crayfish. Anyway, it should be noted that before the introduction of the signal crayfish, and mainly in the Rabaçal River, Northern Iberian spined loach was much more widespread and abundant (Amílcar Teixeira, personal communication). Being Northern Iberian spined loach a true benthic fish species and since the recent decline in distribution and abundance occurred at the same time that the invasion of the signal crayfish was progressing in the Rabaçal River we may speculate that this non-native species is negatively affecting *C. calderoni*. Similar results were reported, for example in the United Kingdom, for the bullhead *Cottus perifretum*, also a benthic fish species (Galib et al. 2021). Although our study cannot give a definitive answer about the recent decline in the Northern Iberian spined loach, since this species was only found in one sampling site, future studies should address this topic given their high conservation status (listed as Endangered in the IUCN Red list).

At the individual level we predicted that the presence of the signal crayfish would likely decrease fish physiological condition, as has been documented in other studies (Light 2005; Vaeßen and Hollert 2015). However, in our study, only brown trout exhibited a poorer condition in the presence of signal crayfish, while Douro nase and Iberian chub showed a better condition at the invaded sites. The poorer physiological condition of brown trout could be the result of lesser availability of food, since signal crayfish are known to prey on aquatic invertebrates (Crawford et al. 2006; Galib et al. 2021; Twardochleb et al. 2013), including in the studied rivers (António Nogueira, personal observation). The costs induced by competition for shelter and food can also alter the behavior of brown trout, while it is also important to not discard the importance of environmental factors (e.g., physical habitat, water chemistry) that can be changed at a smaller scale by the signal crayfish



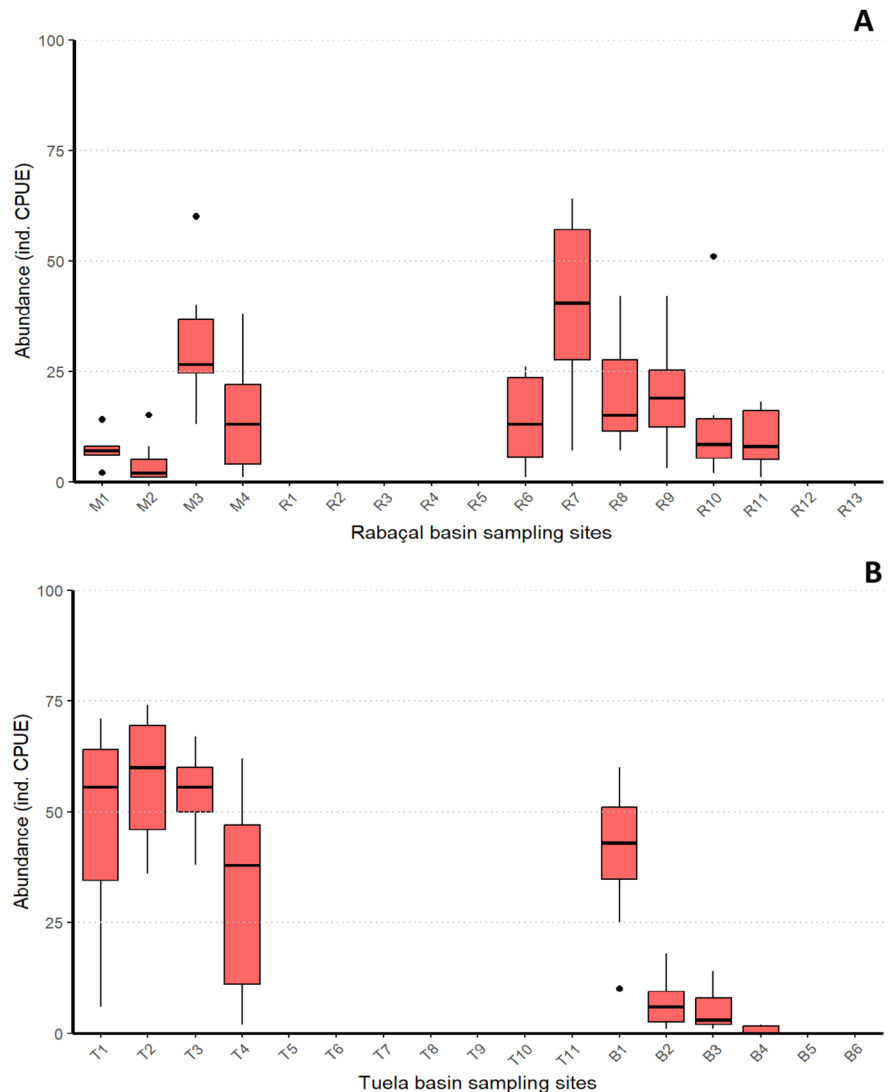
**Fig. 6** Fulton's condition factor of *Salmo trutta* (A), *Luciobarbus bocagei* (B), *Pseudochondrostoma duriense* (C), *Squalius alburnoides* (D) and *Squalius carolitertii* (E) on Rabaçal and Tuela River basins. Boxplots show median values (central line), the range from the 25th to 75th percentile (box) and the largest and lowest value within 1.5 times interquartile range below and above the 25th and 75th percentile (whiskers) and dots represent extreme values. Np—signal crayfish not present; p—signal crayfish present

(Nunn et al. 2007). The positive results for the Douro nase and Iberian chub are concordant with Wood et al. (2017). These authors assessed the effect of the signal crayfish on the growth of the chub (*Squalius cephalus*) and found that older individuals seemed to benefit from the presence of the signal crayfish. The better condition exhibited by Douro nase and Iberian chub might be related to the higher concentration of fine particulate organic matter since the signal crayfish is also known to consume leaf litter and increase the concentration of fine particulate matter (Carvalho et al. 2022a). In this way both fish species may benefit from this higher availability of food resources. In addition, the invaded sites of the Tuela River basin are located downstream where the river is wider and more productive and therefore more suitable for these two species. The results showing an increase in the Iberian chub physiological condition alongside a decrease in abundance may seem contradictory. However, the signal crayfish is known for its ability to alter habitats by burrowing, which reduces shelter availability and disrupts spawning sites for fish. Additionally, the signal crayfish may predate fish eggs, larvae, and juveniles. Therefore, and although the signal crayfish may reduce the recruitment of the Iberian chub, contributing to a lower abundance, those fish that survive may have a higher physiological condition due to lower intra-specific competition and higher food availability as described above (Wood et al. 2017). Anyway, these results concerning the physiological condition of fish must be interpreted with caution since the Fulton's condition factor is affected by the size of the organisms (Blackwell et al. 2000; Froese 2006). In our case, the fish analyzed in the invaded and non-invaded sites have similar ranges in total length and so the bias introduced was probably low. Further studies should be done to assess these possible differences in the physiological condition due to the presence of the signal crayfish also considering the age and sex of the fish species.

Overall, it seems that the results indicate that the invasion of the signal crayfish is already causing sublethal effects in some fish species (i.e. physiological condition) but these effects were subtle enough to not cause major changes at the community level. The lack of observable effects at the community level, with the exception of diversity, could be due to the fact that the invasion is still recent (around 10 years since the first individuals were detected in 2013; Sousa et al. 2015) and progressing. In addition, the low level of anthropogenic disturbance in the study area and the presence of high-quality habitats, provide adequate ecological conditions to maintain a stable and healthy fish community. However, this situation may worsen in the future since the signal crayfish is still spreading and some sites have already a high abundance and biomass (Alves et al. 2025; Carvalho et al. 2025). Therefore, the monitoring of the signal crayfish populations and their possible ecological effects in the fish (and other organisms) communities should be pursued.

All the fish individuals caught in this study were native, with some of them having high conservation status. This is important to emphasize because the current situation of the fish communities in the Douro River basin and in other Iberian basins is quite precarious since many native fish are disappearing and being displaced by non-native species (Nogueira et al. 2021b; Sáez-Gómez and Prenda 2022; Valerio et al. 2022). This fact makes the rivers studied and the surrounding areas of great conservation importance for the fish species (and other organisms). Therefore, this study is highly relevant for future comparisons, as it provides a baseline for determining whether the signal crayfish is affecting fish communities at various ecological levels (from individuals to communities). However, much work remains to be done to fully understand where and how to control the signal crayfish and mitigate its ecological effects. In fact, urgent integrated management actions are needed, including prevention measures in order to avoid possible introductions to other hydrological basins, control measures to reduce signal crayfish abundance (and potentially their impact) and containment measures to prevent their spread in the studied area. Since in the study area, prevention is not an option anymore, management could incorporate mechanical, biological, physical, and chemical approaches (Carvalho et al. 2025) while evaluating their advantages and

**Fig. 7** Crayfish abundance per sampling site in in the Rabaçal basin (A) and Tuella basin (B). Boxplots show median values (central line), the range from the 25th to 75th percentile (box) and the largest and lowest value within 1.5 times interquartile range below and above the 25th and 75th percentile (whiskers) and dots represent extreme values



disadvantages. Trapping and the installation of artificial or natural barriers can be effective in controlling or containing non-native crayfish species. Native predators, including the Eurasian otter *Lutra lutra* and brown trout can also contribute for the control of this non-native crayfish species. Emerging control methods should also be considered, such as the release of sterile males (e.g., Piazza et al. 2015) or the use of biotechnological techniques like biocides and pheromones (Manfrin et al. 2019). Additionally, outreach campaigns to raise local awareness and citizen science initiatives should be implemented. These and other measures are crucial for preserving the high

conservation value of fish communities in Montesinho Natural Park and its surrounding areas.

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## Declarations

**Conflict of interest** The authors have no competing interests to declare.

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