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# Microhabitat competition between Iberian fish species and the endangered Júcar nase (*Parachondrostoma arrigonis*; Steindachner, 1866)

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Competition with invasive species is recognized as having a major impact on biodiversity conservation. The upper part of the Cabriel River (Eastern Iberian Peninsula) harbours the most important population of the Júcar nase (*Parachondrostoma arrigonis*; Steindachner, 1866), a fish species in imminent danger of extinction. Currently, this species cohabits with several non-native species, such as the Iberian nase (*Pseudochondrostoma polylepis*; Steindachner, 1864) and the bermejuela (*Achondrostoma arcasii*; Steindachner, 1866). The potential habitat competition with these species was studied by analysing the spatial and temporal overlapping of suitable microhabitats. Generalized Additive Mixed Models (GAMMs) were developed to model microhabitat selection and these GAMMs were used to assess the habitat suitability (i.e.,

probability of presence) under several flows simulated with River-2D. The Júcar nase will compete, spatially and temporarily, for the few suitable microhabitats with bermejuela and, to a lesser extent, with small Iberian nase; conversely, large Iberian nase was of minor concern, due to increased differences in habitat preference. This study represents an important assessment of potential competition and, therefore, these results might support the definition of future management practices in the upper part of the Cabriel River.

Keywords: Generalized Additive Mixed Model, habitat duration curve, invasive species, Mediterranean river, physical habitat simulation.

## **1 Introduction**

Despite being apparently inoffensive, the introduction of a foreign species in an ecosystem always poses an ecological risk because it can result in negative impacts on native species and, occasionally, on the functioning of the ecosystem (Gozlan et al., 2010). Numerous non-native fish, from a variety of sources, have been introduced across Mediterranean Europe for various reasons, including the biological control of aquatic plants and mosquitoes, aquaculture, to compensate for the decline in native fish stocks, and to create new and more diverse recreational fisheries (Marr et al., 2013). Accordingly, the impacts of foreign fish species are currently recognized as a major threat to freshwater biodiversity, through a variety of adverse impacts, such as: habitat alteration, predation, hybridisation, vectoring diseases, food web alteration and interspecific competition (Almeida and Grossman 2012). Iberian rivers have also suffered multiple and recurrent introductions during the last century and, although they may have resulted in increased economic benefits (Gozlan et al., 2010), such acclimatization of foreign fish has been confirmed as one of the main negative factors affecting the survival of native, mostly endemic, species (Elvira and Almodóvar 2001). The

introduced species have traditionally been categorized as: non-native, invasive (i.e., those non-native species that harm native populations) and translocated, which corresponds to those species transferred between basins within the same country (Gozlan et al., 2010; Leunda 2010). Translocated species have traditionally been viewed acquiescently, although there is evidence that they can produce negative impacts in the same way as non-natives (Oscoz et al., 2006; Alcaraz et al., 2014). Consequently, it is crucial to improve our ability to forecast the risks resulting from translocations, by developing precise and appropriate management tools and mitigation protocols based on the evidence of possible impacts (Gozlan et al., 2010).

The Iberian Peninsula is considered to be one of the hotspots for freshwater fish biodiversity within Europe (Reyjol et al., 2007) with several species in imminent risk of extinction (Leunda 2010). Among these, some paradigmatic species such as the Valencia toothcarp (*Valencia hispanica*; Valenciennes, 1826) have been the subject of thorough research (Rincón et al., 2002, and therein references), whereas very few studies have focused on the Júcar nase (*Parachondrostoma arrigonis*; Steindachner, 1866) (Elvira and Almodóvar 2008; Costa et al., 2012; Alcaraz et al., 2014), even though it has been deemed to be the Iberian fish species most susceptible to extinction (Doadrio 2002). Formerly, the Júcar nase inhabited the entire Júcar River basin from coastal areas to montane streams (Elvira and Almodóvar 2008; Alcaraz et al., 2014). However, habitat fragmentation and the introduction of non-native and invasive species some of them large predators such as the *Esox lucius* (Linnaeus, 1758) – as well as habitat degradation and pollution have reduced its distribution area by up to 20% (Alcaraz et al., 2014). This confluence of impacts, typical of rivers with increasing demands and limited water resources (Paredes-Arquiola et al., 2014), has marginalized native fish populations to the headwaters of the streams, where the remaining populations are isolated one from another by dams and barriers (Aparicio et al., 2000; Alcaraz et al., 2014).

Currently, the Cabriel River (the main tributary of the Júcar River) harbours the most important populations, in terms of presence and fish density, of the Júcar nase (Alcaraz et al., 2014). However, this is not an unspoilt stream, it is split into two stretches of similar length (i.e., upper and lower Cabriel) by a sequence of weirs and dams; the most noteworthy being the Contreras dam. Both segments harbour non-native and invasive species, although invasive piscivorous species are absent in the upper part of the Cabriel River (Olaya-Marín et al., 2012). The non-native species in the upper Cabriel are principally present in the lower part, due to the presence of the Cristinas weir, which also splits the upper part into two unconnected segments, whereas the uppermost river stretch remains largely unspoilt. Thus, the non-native species in the upper Cabriel are the Iberian nase (*Pseudochondrostoma polylepis*; Steindachner, 1864), the Iberian gudgeon (*Gobio lozanoi*; Doadrio & Madeira, 2004) and the bermejuela (*Achondrostoma arcasii*; Steindachner, 1866); the latter has been reported, in 2016, as occurring in several segments of the upper Cabriel, and was sampled in very small numbers during the study made by Olaya-Marín et al. (2012) in the lower part of this river segment. Such fish species were probably translocated through the “Tajo-Segura” inter-basin water transfer canal (Alcaraz et al., 2014) and perhaps, to a lesser extent and distance, by anglers (Leunda 2010). The Iberian nase has demonstrated itself to be a superior competitor and, over time, it has displaced the Júcar nase from a broad expanse of its historical distribution area (Alcaraz et al. 2014). This mechanism of exclusion, typical of competing species (Almeida and Grossman 2012), has been corroborated by a strong spatial segregation between the occurrence of the Júcar nase and the occurrence of the Iberian nase (Alcaraz et al., 2014). Therefore, the study of the mechanisms of competition between both species has been highlighted by several authors as a priority field of research (Leunda 2010; Alcaraz et al., 2014).

To date, several approaches have been followed to study the current or the potential competition of non-native species, from broad-scale approaches (i.e., basin scale) aimed at encouraging ecologically-friendly policies (e.g., alternative water release or management protocols) (Ribeiro et al., 2008; Clavero 2011), to site- and/or species-specific studies in natural river segments (Almeida et al., 2014) or in aquaria, artificial streams or other mesocosms (Rincón et al., 2002; Almeida and Grossman 2012). Although the benefits of direct underwater observation have been highlighted, because the competition mechanism can only be understood at a local scale, interspecific competition is commonly measured via indirect methods, such as descriptive comparisons of habitat use/selection, dietary overlap or stable isotope analysis (Almeida and Grossman 2012). Aquaria and mesocosm studies can provide evidence of impact mechanisms on native fish and ecosystems (Ribeiro and Leunda 2012), but they differ vastly from natural conditions. Furthermore, the ability to distinguish between fish species or the dimensions of the target stream can be a key factor determining the choice of the surveying methodology. The Cabriel River presents deep pools that discourage the use of electrofishing equipment (Veza et al., 2015); in addition the Júcar nase, the juvenile Iberian nase and, to a lesser extent, the bermejuela are hardly distinguishable by direct observation (snorkelling) when they occur concurrently. Consequently, in this research we considered an indirect method based on habitat selection to be necessary.

The potential microhabitat competition between these non-native species, formerly included within the genus *Chondrostoma* (Robalo et al. 2007), and the Júcar nase was studied by analysing the degree of overlapping of suitable microhabitats, named as the Suitable Area (SA), in a river stretch of the upper part of the Cabriel River. The specific objectives of this research were: i) the development of presence/absence Generalized Additive Mixed Models (GAMMs) describing the microhabitat selection by the Júcar nase, bermejuela and Iberian nase (large and small); ii) the assessment of the habitat suitability in a set of simulated river

flows; iii) the analysis of the potential competition of the different fish species by comparing the spatial and temporal overlapping between the suitable microhabitats (i.e., the aforementioned Suitable Areas or SAs).

## **2 Methods**

### ***2.1 Ecology of the target fish species and data collection***

The habitat requirements of the Júcar nase have been poorly documented, thus, there is no consensus about its habitat preferences. Consequently, it has been suggested to be a rheophilic species, occurring more often in riffles with a relatively high velocity, coarse substrate and aquatic vegetation (Alcaraz et al., 2014). Conversely, other studies have suggested a positive correlation between density of the Júcar nase and depth (up to 4 m), and with the presence of backwaters, which suggests a more limnophilic nature (Costa et al., 2012). Nevertheless, as far as we know, in the existing scientific literature, this species has never been the subject of habitat suitability modelling at the microhabitat scale through any multivariate approach, and this is the first article to present such information. The habitat requirements of the bermejuela are even less well documented, but it has been observed that juveniles occur in shallow areas with slow currents and move to deeper and faster waters in late July (Kottelat and Freyhof 2007). This pattern was partially corroborated by Muñoz-Mas et al. (2014a), who used part of the dataset employed in this study. Finally, the Iberian nase is a rheophilic species with large specimens inhabiting deep habitats with a relatively high velocity (Martínez-Capel et al., 2009), therefore, they demonstrate greater swimming capacity than other Iberian cyprinid species of similar size (Romão et al., 2012), whereas small specimens inhabit shallower areas (Martínez-Capel et al., 2009).

The dedicated, or retrieved, fish data (converted into presence/absence data) was collected in several river basins and sites where these species naturally occur and the competitor fish species were absent (Figure 1). All of the sampled rivers run under a continental Mediterranean climate and the study sites were placed in river segments of similar stream order, with good underwater visibility and minimal influence from human activity (Martínez-Capel et al., 2009). In order to improve the transferability of the models (Thomas and Bovee 1993; Vilizzi et al., 2004), the study sites tried to encompass the largest microhabitat variability by surveying different types of hydro-morphological units (i.e., pool, glides, runs, riffles and rapids (Martínez-Capel et al., 2009) (Table 1).

The data for the Júcar nase were purposefully collected in three sites of the Cabriel River both downstream and upstream of the Traqueiro fall; a natural barrier in the vicinity of the municipality of Boniches (Cuenca, Spain), which isolates the upper population from the lower one. During these surveys 2091 individuals were observed spread over 123 different microhabitats. Conversely, the bermejuela and Iberian nase data were collected in previous studies carried out in the Palancia River and several streams and tributaries of the Tagus River (Martínez-Capel et al., 2009; Muñoz-Mas et al., 2014a).

[Figure 1 here]

[Table 1 here]

Although the surveys for data collection were distant in time, they were performed following similar approaches. In each case they were carried out in late-spring and summer (warm period), during low flow conditions and considering complete hydro-morphological units in the data stratification prior to surveying, by direct observation (snorkelling).



Snorkelling was selected as the sampling approach because it proved to be superior to direct observation from the shoreline and the electrofishing sampling approach (Heggenes et al., 1990).

The diver moved carefully from downstream to upstream and placed a marker in each occupied microhabitat, but skipped those microhabitats occupied by fish that had evidently been disturbed. Regarding fish size, the Iberian nase was divided into two different classes ( $< 7$  or  $> 7$  cm) in accordance with its ecology and maximum body length (see Martínez-Capel et al., 2009) whereas one single-size class was considered for the other fish species (Table 1).

The hydraulic conditions for the presence data were measured in the occupied microhabitats, whereas the absence data (unoccupied microhabitats) was measured at several points through cross-sections distributed over each hydro-morphological unit. Three of the measured abiotic variables coincided among datasets: mean flow velocity of the water column (velocity), water depth (depth), and substrate composition (substrate). Velocity was measured with a current meter [m/s]; depth was measured with a wading rod to the nearest centimetre [m] and substrate was visually estimated by size classes, i.e., bedrock, boulders, cobbles, gravel, fine gravel, sand, silt and macrophytes (Martínez-Capel et al., 2009; Muñoz-Mas et al., 2014a). Subsequently, the percentages of the different substrate types were summarized in a single substrate index [-] (Mouton et al., 2011), which may range from 0 (vegetated silt) to 8 (bedrock) (Figure 2).

[Figure 2 here]

Microhabitat studies are undertaken using high resolution, which typically leads to low data prevalence (i.e., ratio of presence cases over the entire dataset) (Guisan et al., 2007).

It is assumed that there are not enough individuals to occupy each suitable microhabitat, thus,

in such a situation, model optimization usually takes place by selecting loss functions irrespective of data prevalence (e.g., True Skill Statistic – TSS) (Mouton et al., 2010), and stimulating over-prediction by favouring a larger proportion of presence predictions (e.g., Fukuda et al., 2013). To deal with low prevalence contributing to over-prediction, the Neighbourhood Cleaning Rule algorithm (Laurikkala 2001) implemented in the *R* (R Core Team 2015) package *unbalanced* (Dal Pozzolo et al., 2015) was applied to each dataset prior to model training. This algorithm first removes those absence data misclassified by their three nearest neighbours and, then, the neighbour of each presence data is found and those belonging to the absence class are removed.

## **2.2 *Habitat suitability modelling – Generalized Additive Mixed Models (GAMMs)***

Traditionally the habitat suitability at the microhabitat scale has been modelled by means of univariate – unimodal or monotonic – Habitat Suitability Curves (HSCs) (e.g., Jowett and Davey 2007; Muñoz-Mas et al., 2012). However, HSCs treat the input variables (e.g., velocity or depth) independently and the method employed to aggregate their individual predictions affects the ultimate prediction, finally compromising the reliability of the habitat assessment (Jowett and Davey 2007). For the foregoing, the HSCs have been demonstrated to be less transferable than other multivariate approaches  $y$  (Guay et al., 2000), thus, the scientific community currently advocates multivariate approaches (e.g., Jowett and Davey 2007; Fukuda et al., 2013; Muñoz-Mas et al., 2016b). Generalized Additive Models (GAMs) (Hastie and Tibshirani 1990) are a semi-parametric extension of generalized linear models especially suitable for ecological modelling, since they do not presuppose any type of statistical distribution of the input variables (Jowett and Davey 2007). GAMs are characterized by the use of regression splines that resemble the HSCs (i.e. the  $f_i$  in equation

1) to model the effects of the inputs over the desired output (Jowett and Davey 2007).

Therefore, although different in nature, the structure of the GAMs could be considered the natural succession of the HSCs because the effect of the set of inputs is simultaneously optimized to maximize the predictive capability of the model (Jowett and Davey 2007).

However, environmental data may present temporal and spatial auto-correlation, violating the data independence assumed for the development of GAMs (Girard et al., 2014). For instance, in our specific situation, data collected in one river is likely to be more correlated to each other than to the data collected in any of the remaining rivers (Zuur et al., 2009). To overcome such limitations, Generalized Additive Mixed Models (GAMMs) have been proposed (Lin and Zhang 1999). GAMMs maintain the flexibility of GAMs by using nonparametric regression, while accounting for correlation between observations by using random effects (Lin and Zhang 1999). The GAMMs structure follows equation 1:

$$g(\mu_i^b) = \beta_0 + f_1(x_{i1}) + \dots + f_p(x_{ip}) + \theta_i^T b \text{ (Equation 1)}$$

where  $g(\cdot)$  is a monotonic differentiable link function,  $\mu_i^b$  are the expected values,  $\beta_0$  is the intercept,  $f_j$  is a centred twice-differentiable smooth function (e.g., Nadaraya-Watson Kernel Smoothing or the smoothing spline),  $x_j$  are the environmental variables, the random effects  $b$  are assumed to be distributed as  $N\{0, D(\theta)\}$  and  $\theta$  is a  $c \times 1$  vector of variance components.

The GAMMs were developed in *R* (R Core Team 2015) with the *mgcv* package (Wood 2004). As recommended in a number of publications (e.g., Arlot and Celisse 2010), a stratified (considering river and class) fivefold cross-validation was performed to search for the most generalizing model, including each microhabitat variable once (i.e., velocity, depth

and substrate), either independently or in two- and three-way interactions and the random effects (i.e., random intercepts) were the sampled rivers (Table 1). The selected link function ( $g$ ) was the *binomial* (outputs between 0 and 1), to accommodate the dichotomous nature of the output data, and the smooth functions were cubic regression splines when variables were considered independently and tensor product smooths when they were considered within interactions. The latter type were selected because they are especially indicated for representing functions of covariates measured in different units (Wood 2006). Compared to previous studies (i.e., Girard et al., 2014), we relaxed the imposed constraints by increasing the maximum number of allowed knots (i.e., the number of bends of the smooth function) up to 4, and the selected mathematical structure among the different model alternatives was the one producing the largest mean TSS on the test datasets. TSS relies on the aggregation of the ratio of presences correctly classified (Sensitivity –  $S_n$ ) and the ratio of absences correctly classified (Specificity –  $S_p$ ) (see Mouton et al., 2010 for additional information about performance criteria) as follows:

$$TSS = S_n + S_p - 1 \text{ (Equation 2)}$$

Data prevalence has been proven to significantly impact the classificatory capability of GAMs (e.g., Beakes et al., 2014), similarly, it should affect GAMMs. Therefore, in order to reduce the number of erroneously predicted absences (stimulating over-prediction) and keeping the discriminant threshold at 0.5, the presence data in the training dataset were randomly replicated to obtain 0.5 prevalence datasets. This resampling was carried out employing the function *UBOver* implemented in the *R* (R Core Team 2015) package *unbalanced* (Dal Pozzolo et al., 2015). Following previous studies (e.g., Fukuda et al., 2013; Muñoz-Mas et al., 2016a), once the optimal mathematical structure had been determined, one

single GAMM per group of fish was trained with the aforementioned settings, the complete dataset (i.e., without cross-validation), and the optimal mathematical structure for the corresponding group.

### **2.3 Study area and hydraulic modelling**

The upper part of the Cabriel River Basin, where the study site is located, has an average riverbed gradient of 1.1% and the land cover – from the CORINE Land Cover classification – mainly consists of forested areas (86%) and crops (12%) (Bossard et al., 2000). This river basin has been affected by a marked human depopulation (Instituto Nacional de Estadística 2013), allowing us to consider any anthropogenic impact as negligible (e.g., measurable water abstraction or pollution) as well as the corresponding synergistic effects with the presence of these non-native species. The study area has a typical Mesomediterranean climate with a mean annual precipitation of ca. 500 mm, resulting in low flows and high evapotranspiration in summer and high flows in spring and autumn (Veza et al., 2015). Therefore, summertime would represent the period of highest potential competition, due to the smaller wetted area (Figure 3).

[Figure 3 here]

The hydraulic simulation was retrieved from Muñoz-Mas et al. (2012; 2014b; 2016a) and is located approximately 7.5 km downstream of the Júcar nase sampling points (Figure 1). It encompassed an approximately 300 m long reach of the Cabriel River that met various requirements, such as habitat heterogeneity and representativeness, and had been proven to have a stable channel for more than a decade (Muñoz-Mas et al., 2014b), which will extend

the validity of the predictions. Data collection and model development followed common procedures (Jowett and Duncan 2012) whereby the topographic data of the river channel and banks were collected using a Leica© Total Station with an average area of ca. 2 m<sup>2</sup> per topographic measurement, collecting concomitantly the substrate composition as described above. The hydrometry was performed in 11 cross-sections, with depth and velocity measured along these sections and the resulting information was used to gauge the flow rate.

Measurements were performed at three different flow rates (0.54, 1.04 and 2.75 m<sup>3</sup>/s) and these were used to calibrate the model. The 2D hydraulic simulation was performed with River2D© (University of Alberta, 2002) modifying the bed roughness ( $k_s$ ) to adjust the outcomes to the measurements performed during the hydrometric campaigns. Once the model rendered acceptable results (mean error in water surface elevation around 5 cm and similar velocity distribution patterns), thirty-four different flows were simulated, ranging from 0.05 to 6.5 m<sup>3</sup>/s; in all cases the water level was below the bankfull stage of the river channel.

#### **2.4 Comparison of the modelled microhabitat suitability**

The relationship between the input variables and the probability of presence was graphically characterized with partial dependence plots (Friedman 2001) adapting the code implemented in the package *randomForests* (Liaw and Wiener 2002). Partial dependence plots depict the average of the response variable (i.e., the output rendered by the *binomial* link function) versus each input variable and account for the effects of the other variables within the model by averaging their effect (Friedman 2001). Consequently, partial dependence plots are a useful way to visualize the marginal effect of the target variable on the predicted probability of presence when multivariate models present interacting variables (VeZZa et al., 2015;

Shiroyama and Yoshimura 2016; Muñoz-Mas et al., 2016a). The function being plotted is defined as:

$$\tilde{f}(x) = \frac{1}{n} \sum_{i=1}^n f(x, x_{iC}) \text{ (Equation 3)}$$

where  $n$  corresponds to the amount of points in which the function is being plotted,  $x$  is the variable for which partial dependence is sought, and  $x_{iC}$  are the remaining variables in the dataset, whereas  $f$  corresponded to the predictions exerted by the GAMMs. The partial dependence was computed for each of 50 equally spaced points over the range of each examined variable.

## ***2.5 Assessment of potential microhabitat competition***

The four GAMMs were used to assess the set of 34 simulated flows in a multivariate manner by considering the varying velocity and depth obtained from the hydraulic model and the underlying substrate, rendering the suitability (from 0 to 1) for every pixel (1 m × 1 m) on the hydraulic model. Then, the general suitability of the study site (i.e., the habitat quantity and quality for the simulated flows and species) was assessed with a modification of the Weighted Usable Area (WUA) versus flow curves (Bovee et al., 1998). The WUA consists of the sum of the area of every pixel multiplied by the corresponding suitability; however, in this specific study, only the classificatory nature of the GAMMs was taken into account, thus the Suitable Area (SA; i.e., the one with suitability > 0.5, corresponding to fish presence) was aggregated to develop the SA versus flow curves. The Overlapping Area (OA) counterparts were likewise calculated as the aggregation of the area, considering those pixels

concomitantly assessed as presence (i.e., suitability > 0.5) for the Júcar nase and the

competitor analysed.

However, the information provided by both types of curves (SA and OA) is restricted to the general suitability of the spatial competition at a given flow and neglects the frequency of occurrence. Therefore, the time series analysis was performed by developing and comparing the duration curves of SA and OA, inspired by the work carried out by Milhous et al. (1990). For this task, after calculating the SA and OA versus flow curves, the time series were implemented by interpolating the different summer mean monthly flows (Figure 4) upon the corresponding curves; 2% of the data were extrapolated because the mean monthly flow exceeded the largest simulated flow.

[Figure 4 here]

Accounting for uncertainty in a model has been highlighted in a number of publications (e.g., Elith and Leathwick, 2009) and the package *mgcv* allows predictions to be made by taking into account the uncertainty of the estimation of parameters. Therefore, the aforementioned indicators, including the partial dependence plots, were also calculated for the 95% confidence interval in order to estimate the reliability of the potential microhabitat competition.

### **3 Results**

#### ***3.1 Comparison of the modelled microhabitat suitability***

The optimal model structure varied for each groups of fish, although in any case the considered terms were always significant ( $p$ -value  $< 0.05$ ) (Figure 5). Therefore, the optimal model for the Júcar nase was that where the three variables interacted fully, whereas the one



for the bermejuela did not present interactions. The models for the Iberian nase, both large and small, each presented one two-way interaction.

The performance of the models did not vary significantly between species although the model for the Júcar nase outperformed any other, presenting the highest TSS, whereas the GAMM for large Iberian nase presented the lowest value (Table 2).

[Figure 5 here]

[Table 2 here]

The Júcar nase selected low flow velocity, high depth and fine substrate (Figure 6). The bermejuela also selected microhabitats with low flow velocity and fine substrate but appeared more often in microhabitats of medium depth, and large Iberian nase preferred medium flow velocity, the greatest depth, and coarse substrate. Conversely, small Iberian nase were inclined to appear nearer the river banks, thus selecting low flow velocity, but medium-to-low depth and finer substrate.

[Figure 6 here]

### **3.2 Assessment of potential microhabitat competition**

The hydraulic model mainly encompassed a run-type river segment – which is characterized by medium depth and relatively high velocity – also including areas of riffle, rapid and pool. In accordance, the river reach presented a low overall suitability for the Júcar nase with a slight increment of SA below 1 m<sup>3</sup>/s. Nevertheless, the maximum SA, achieved

for 0.1 m<sup>3</sup>/s, barely represented 10% of the wetted area (Figure 7 – Upper sequence). The bermejuela presented the largest SA around 0.5 m<sup>3</sup>/s decreasing for larger flows. Beyond 2.5 m<sup>3</sup>/s it stabilized slightly above ca. 20% of the wetted area. The bermejuela SA versus flow curve showed a constant overlap with the curve of the Júcar nase, based on the 95% confidence interval. The SA versus flow curve for large Iberian nase presented a parabolic increment showing the maximum at 2 m<sup>3</sup>/s; at that point it achieved the largest SA among all the species (ca. 60% of the wetted area for that flow). Above this flow, the curve decreased almost linearly, approximating the Júcar nase curve for the largest simulated flow. The curve for small Iberian nase presented the maximum at 1 m<sup>3</sup>/s (ca. 60% of the wetted area) and decreased rapidly for the larger flows due to the increment in water velocity and depth. This SA versus flow approximated the curve of the Júcar nase for the larger simulated flows, considering only the 95% confidence interval.

[Figure 7 here]

In absolute terms (m<sup>2</sup>) the potential microhabitat competition was low in all cases in comparison with the maximum wetted area (ca. 4000 m<sup>2</sup>) (Figure 7 – Central sequence). However, in accordance with the SA and the OA versus flow curves, the Júcar nase will spatially compete for every suitable microhabitat with the bermejuela and, to a lesser extent, with small Iberian nase, which presented lower values but some overlap considering the 95% confidence interval. Finally, large Iberian nase represent a minor concern due to the increased differences in habitat preferences.

The match of the SA duration curve for the Júcar nase and the OA duration curve for bermejuela corroborated that both species would compete spatially and temporarily for the same microhabitats (Figure 7 – Lower sequence), even taking into account the uncertainty of

the predictions (95% confidence interval). Conversely, large Iberian nase represent a minor competitor, because the OA duration curve was appreciably displaced below the SA duration curve for the Júcar nase. Finally, small Iberian nase presented a similar pattern to their larger counterpart. Nevertheless, considering the uncertainty of the predictions, the competition could be greater than that exerted by their larger counterpart, as the 95% confidence interval presented greater overlapping.

#### **4 Discussion**

The GAMMs developed presented satisfactory results because they achieved values of performance criteria analogous to those of previous studies that modelled the microhabitat suitability with several techniques and similar prevalence (e.g., Fukuda et al., 2013; Muñoz-Mas et al., 2014b). Furthermore, as depicted in the partial dependence plots, they fitted the ecological gradient theory well (Austin 2007), by modelling the effects of the input variables with straight (almost linear) or unimodal (curved) smooth functions.

Following previous studies that employed GAMs (e.g., Jowett and Davey 2007; Fukuda et al. 2013; Muñoz-Mas et al. 2016b), we assumed the relevance of the three input variables: velocity, depth and substrate. In accordance, neither variable selection nor significance inspection was carried out and only the structure of each model was optimised (Anderson et al. 2000; Platts et al. 2008). This optimization of each model was performed through cross-validation on the basis of a global measure of model performance (i.e., TSS) and with each test fold of similar prevalence and proportion of data from each site than the original dataset. To the best of our knowledge, three main approaches have been described in the literature to maximize the performance of GAMs trained with low prevalence datasets: (i) down- and

over-sampling (as followed here) (Barbet-Massin et al. 2012), case weighting (Maggini et al. 2006; Muñoz-Mas et al. 2016c) and the modification of the classification threshold (Liu et al. 2005). However, each may present limitations either with regards of the terms significance or models transferability. For instance, the modification of the classification threshold (e.g., based on the prevalence) may present poor transferability to other sites of different frequency of occurrence (Fukuda et al. 2013) whereas the use of case weighting may lead to unreliable p-values (Simon Wood personal communication), a phenomenon perhaps extensible to down- and over-sampling, which will require dedicated analyses. Therefore, our approach could be unsuitable when model terms are selected scrutinizing the calculated p-values.

In our case, the Júcar nase achieved the maximum value of the TSS (over the non-replicated data) between the four models because it presented the most specific microhabitat use, selecting microhabitats with slow flow velocity, high depth and fine substrate. This pattern of habitat selection contradicts its classification as a rheophilic species with a preference for riffles of relatively high velocity and coarse substrate (Alcaraz et al., 2014). Conversely, it better fits the preference for deep habitats with low or null velocity (i.e., backwaters) as demonstrated along the Cabriel River in Costa et al. (2012), or its correlation with the presence of other native cyprinids of the Cabriel River, which, in turn, showed a positive correlation with depth (Veza et al., 2015). Therefore, we contend that, in the Cabriel River, this species cannot be classified as rheophilic and that the previous assertion made for this river can only be attributable to the inherent limitations of the electrofishing sampling approach (wadeable river stretches) (Brosse et al., 2001). Certainly, the former distribution area of the Júcar nase encompassed areas from coastal to montane water bodies (Elvira and Almodóvar 2008; Alcaraz et al., 2014), suggesting a wider plasticity in the selection of microhabitat than that depicted here. We also acknowledge that it could be suggested that

such differences may be attributable to seasonal changes in fish behaviour, as has been demonstrated indoors and outdoors for other fish species and assemblages (e.g., Baltz et al., 1991; Vilizzi et al., 2004). However, in addition to the observations performed in this study, the Cabriel River was frequently and extensively surveyed for several years to collect the data for Costa et al. (2012) and Vezza et al. (2015), confirming a strong site fidelity for the Júcar nase. Thus, specimens of the Júcar nase were never observed occupying any riffle or fast flow habitat. Therefore, although we recognize that the Júcar nase may present different preferences in other rivers, it becomes clear that the classification of the Júcar nase within the group of eurytopic species would be more in accordance with current knowledge about the species.

In regard to the predicted potential competition, the use of different modelling techniques can render divergent patterns of habitat selection (Fukuda et al., 2013; Muñoz-Mas et al., 2016b). In this study, the restriction of the models complexity by limiting the number of *knots* (up to four) suggested preferences for the bermejuela (Muñoz-Mas et al., 2014a) and the Iberian nase (Martínez-Capel et al., 2009) similar to those found in the previous studies, which were carried out using a varied set of modelling approaches. The bermejuela presented the largest similarity with the habitat selection of the Júcar nase by selecting microhabitats with slow flow velocity, fine substrate and medium depth, which finally determined our evaluation regarding the threat posed by this species. The match of the SA and the OA versus flow curves, as well as the coincidence of SA and the OA duration curves for the Júcar nase and for the bermejuela predicted that both species shall steadily compete for the same microhabitats. It can be argued that an over-predictive model ( $S_n > S_p$ ) by nature can predict presence and overlap in habitats where there will be no fish, thus overestimating potential competition. However, this over-predictive nature was not observed to be very relevant, either in the model for the Júcar nase or in that for bermejuela ( $S_p \approx 0.7$ ), and we considered it to be

negligible. The flow rate is undoubtedly another factor in the competition. Our direct observations in sites where the Júcar nase is very abundant indicate that this species is gregarious, occupies deep pools and is associated with aquatic vegetation and helophytes (Costa et al., 2012; Vezza et al., 2015). Therefore, in other river stretches with deeper hydro-morphological units, there would be a potential segregation between these two species due to the bermejuela's preference for microhabitats of intermediate depth. Furthermore, very few specimens of bermejuela were found in the Cabriel River (Olaya-Marín et al., 2012), fortunately, suggesting that either the propagule pressure (sensu Gozlan et al., 2010) or the recruitment success were low. However, uncertainty exists, because its presence could be masked due to its hybridization with the Júcar nase or the Iberian nase, since there is previous evidence of hybridization between bermejuela and the Iberian nase (*i.e.* *P. polylepis* × *A. arcasii*) (Collares-Pereira and Coelho 1983).

The preference for deep microhabitats suggests increasing overlap with the microhabitats occupied by large Iberian nase for lowland and for deeper river segments. However, large Iberian nase tended to occupy the centre of the channel, which typically lacks any element of cover (e.g., aquatic vegetation), while the Júcar nase tended to avoid these open waters. Thus, we discarded such possibility. Consequently, large Iberian nase may pose a minor threat for the Júcar nase in terms of competition for the suitable microhabitats.

Regarding small Iberian nase, they were observed near river banks (Martínez-Capel et al., 2009); thus, they selected low flow velocity, low depth and fine substrate. Therefore, they could potentially compete in a distant second tier with the Júcar nase. In accordance with the SA and the OA duration curves such encounters should be rare and restricted to the lower flows. However, they will become recurrent if the predicted climatic changes for the study site finally occur (see Muñoz-Mas et al., 2016a), which will increase the frequency of low flow periods, even resulting in the complete depletion of the Cabriel River. Despite the

differences in the optimal microhabitats and the low overlapping of the suitable areas, as we performed some prior surveys by snorkelling (Costa et al., 2012; Vezza et al., 2015), we observed different escape behaviours in the areas where we would expect to find the Júcar nase. Consequently, we suspected that in the Cabriel River both species would eventually occupy similar microhabitats. These areas of cohabitation were surveyed with electrofishing by Olaya-Marín et al. (2012), who captured individuals of both species. The number of catches and electrofishing sites in the Cabriel River were too low for statistical analysis, although, partially contradicting our results; they provided evidence that both may compete for the same microhabitat in a greater extent than predicted. Nevertheless, it should be the subject of further thorough study in order to be confirmed.

On the basis of the previous knowledge and the habitat suitability models developed, we here provide a reasonable assessment of the threat posed by these potential competitors, but several additional phenomena should also be considered in the near future. For instance, the general threat posed by potential hybridisation with the bermejuela cannot be discarded. Thus, studies on genetic introgression should be performed in order to better analyse the underlying mechanisms operating in the spatial segregation of both species (Alcaraz et al., 2014). Furthermore, one of the main limitations in competition studies is the lack of pre-invasion information and the assumption that different locations with and without non-native species are adequate proxies of pre- and post-invasion scenarios (Ribeiro and Leunda 2012). The bermejuela and Iberian nase were absent in the areas where the Júcar nase microhabitat selection was studied. The Iberian nase is contained by the presence of the Cristinas weir, which we consider should be preserved, despite the negative impact that it exerts on the river continuum. However, in several places the Júcar nase was already cohabiting with another invasive species, the Iberian gudgeon, and recent news (2016) has suggested the presence of the bermejuela upstream of the Traqueiro fall, although 2014 captures did not confirm its

presence. Downstream of this fall, the Júcar nase co-occurred with the Iberian gudgeon; a species that behaves as invasive when translocated (Alcaraz et al., 2014). We have not observed significant differences in the patterns of habitat selection in any of the studies performed, in either the upstream or the downstream river segments (Costa et al., 2012; Olaya-Marín et al., 2012; Vezza et al., 2015). However, the analysis of the contribution of non-native species to the decline of native species is often difficult because it is usually concurrent with habitat degradation in synergistic processes (Brook et al., 2008). Although some studies suggested the introduction of non-native species as the main driver of the decline of the Júcar nase (Maceda-Veiga 2013) another study performed in the Júcar River basin highlighted the hydrological alteration over the non-native species as the fundamental factor (Olaya-Marín et al., 2012). Thus, the apparently neutral coexistence of the Júcar nase with the Iberian gudgeon or, currently, with the bermejuela, can only represent a biased snapshot at the very outset of the negative effects on populations of the Júcar nase. Consequently, it would be necessary to perform additional studies in order to thoroughly analyse the patterns of coexistence of these species.

Although the study site was largely unsuitable for the Júcar nase in comparison with the sites sampled upstream, in accordance with the habitat suitability depicted in the partial dependence plots, we concluded that there is a high potential microhabitat competition with the bermejuela. However, this asseveration is solely valid in terms of competition for suitable microhabitats, as other ecological factors, such as food resources or optimal spawning sites, were not analysed. The Júcar nase could face secondary competition from small Iberian nase and, finally, from large Iberian nase. Nevertheless, further studies encompassing different river geometries and study sites are considered necessary because the Júcar nase is scarce in the river segment partially covered by the hydraulic model (Vezza et al., 2015) and other river segments further upstream are more favourable to the presence of the species. Bearing in



mind the state of conservation of the Júcar nase, this piece of research is considered a necessary pilot study to inspect the potential competition between these cohabiting species.

Finally, we would like to reiterate the need to maintain the Cristinas weir in its current condition, avoiding measures to improve connectivity, as it is the only barrier impeding the colonization of the uppermost part of the Cabriel River. This study should contribute towards evaluating potential risks for the Júcar nase, guiding and triggering urgent management actions for the protection of the species, such as fish catches to control non-native species or informing and educating local fishermen to avoid tentative introductions.

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