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Additional Information

On species distribution modelling, spatial scales and environmental flow assessment with Multi-Layer Perceptron Ensembles: a case study on the redfin barbel (*Barbus haasi*; Mertens, 1925)

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Abstract

Inconsistent performance of Species Distribution Models (SDMs), which may depend on several factors such as the initial conditions or the applied modelling technique, is one of the greatest challenges in ecological modelling. To overcome this problem, ensemble modelling combines the forecasts of several individual models. A commonly applied ensemble modelling technique is the Multi-Layer Perceptron (MLP) Ensemble, which was envisaged in the 1990s. However, despite its potential for ecological modelling, it has received little attention in the development of SDMs for freshwater fish. Although this approach originally included all the developed MLPs, Genetic Algorithms (GA) now allow selection of the optimal subset of MLPs and thus substantial improvement of model performance. In this study, MLP Ensembles were used to develop SDMs for the redfin barbel (*Barbus haasi*; Mertens, 1925) at two different spatial scales: the micro-scale and the meso-scale. Finally, the potential of the MLP Ensembles for environmental flow (e-flow) assessment was tested by linking model results to a hydraulic model. MLP Ensembles with a candidate selection based on GA outperformed the optimal single MLP or the ensemble of the whole set of MLPs. The micro-scale model complemented previous studies, showing high suitability of relatively deep areas with coarse substrate and corroborating the need for cover and the rheophilic nature of the redfin barbel. The meso-scale model highlighted the advantages of using cross-scale variables, since elevation (a macro-scale variable) was selected in the optimal model. Although the

meso-scale model also demonstrated that redfin barbel selects deep areas, it partially contradicted the micro-scale model because velocity had a clearer positive effect on habitat suitability and redfin barbel showed a preference for fine substrate in the meso-scale model. Although the meso-scale model suggested an overall higher habitat suitability of the test site, this did not result in a notable higher minimum environmental flow. Our results demonstrate that MLP Ensembles are a promising tool in the development of SDMs for freshwater fish species and proficient in e-flow assessment.

Keywords

Artificial neural network, genetic algorithm, Iberian Peninsula, Mediterranean river, meso-scale, micro-scale.

1 INTRODUCTION

Species distribution models (SDMs) play a significant role in understanding habitat requirements of fish species, providing a framework from which spatial and temporal distribution patterns can be predicted (Olden et al., 2008). Thereby SDMs are useful tools to select cost-efficient restoration or management actions (Mouton et al., 2010). To date, a wide range of SDMs is available, encompassing several modelling techniques. Examples include Generalized Additive Models (Fukuda et al., 2013), Fuzzy Rule Base Systems (Mouton et al., 2011), or Artificial Neural Networks (ANNs) – most commonly Multi-Layer Perceptrons (MLPs) – (Olaya-Marín et al., 2012). All these techniques are typically applied to generate a single monolithic SDM, which often has proven to be sufficient for ecological modelling (Olden et al., 2008). The MLP paradigm, for instance, has been widely used due to its high predictive performance and its versatility to cope with different kinds of datasets (Olden et al., 2008; Olaya-Marín et al., 2012; Fukuda et al., 2013). Therefore, there are successful examples of single MLPs modelling fish habitat requirements at different scales, from the micro-scale (Brosse and Lek, 2000; Gevrey et al., 2006; Laffaille et al., 2003) to the macro-scale (Olaya-Marín et al., 2012) while at the meso-scale some studies have demonstrated that a single MLP can outperform other statistical approaches (Baran et al., 1996; Lek et al., 1996). Yet, many real-world problems, like demonstrated for marine ecosystems (Meier et al., 2014), are too large and too complex for a single monolithic model (Yao and Xu, 2006). Moreover, SDMs may not perform consistently and even provide discrepant predictions, depending on several factors such as the initial model conditions or the applied modelling technique (Thuiller et al., 2009; Fukuda et al., 2013).

To deal with these inconsistencies, ensemble modelling is now an emerging field of research in ecological modelling (Araújo and New, 2007). Ensemble modelling is based on the minimization of the error through the integration of several models by combining their different predictions into a single forecast. Despite their promising potential for species distribution modelling, only few applications of ensemble modelling have been reported, including an example combining several different techniques to develop SDMs for fish species (Thuiller et al., 2009). To date, Random Forests is the only ensemble modelling technique that could be considered widespread (Mouton et al., 2011; Fukuda et al., 2013; Mostafavi et al., 2014). Although the ANN ensemble modelling counterpart, the MLP Ensemble, was conceived more than twenty years ago (Hansen and Salamon, 1990) and may have the same potential as Random Forests, it has been

rarely applied in fish SDMs so far (*e.g.* Muñoz-Mas et al., 2014; 2015; 2016). Originally MLP Ensembles included all trained MLPs (Hansen and Salamon, 1990) but it was soon demonstrated that active selection of the considered MLPs improved the final predictions (Wang and Alhamdoosh, 2013), and that Genetic Algorithms (GA) were appropriate for this selection (Soares et al., 2013; Wang and Alhamdoosh, 2013).

Therefore, the present study developed SDMs for the redfin barbel (*Barbus haasi*; Mertens, 1925) with GA-optimised MLP Ensembles. The redfin barbel is a small rheophilic barbel mainly inhabiting middle-to-upper stream reaches of mountainous rivers. Although redfin barbel occurs in the North-East quadrant of the Iberian Peninsula, its distribution area has been halved mainly due to pollution and the presence of invasive species (Aparicio, 2002; Perea et al., 2011). Thus, it is a particularly suitable target species for development and testing for these models since it is considered threatened in the Mediterranean region (Freyhof and Brooks, 2011), but a sustainable extant population is still present in our study area. From the ecological viewpoint, the redfin barbel is considered a cover-orientated fish (Grossman and De Sostoa, 1994) preferring deep and slow-flowing pools with abundant cover (Aparicio and De Sostoa, 1999).

In environmental flows (e-flow) assessment the instream habitat has been typically evaluated at the micro-scale (few m² of the instream area) using data and SDMs concordant with the scale (Conallin et al., 2010). The micro-scale SDMs have demonstrated proficient ability to predict fish location (*e.g.* Muñoz-Mas et al., 2014a) and accordingly, this scale is specified in the Spanish norm for hydrological planning as the legal standard in e-flow assessment (MAGRAMA, 2008). However, the use of the micro-scale has been criticized for being time-consuming (Parasiewicz, 2001) and for emphasizing cross-sectional variation over the longitudinal one (Veza et al., 2012). Consequently, some studies highlighted the benefits of the meso-scale – which typically correspond with Hydro-Morphological Units (HMUs) such as pools, riffles or rapids – among the possible spatial scales that can be used to analyse fish habitat requirements (Costa et al., 2012; Veza et al., 2015). Using the meso-scale it is possible to describe the environmental conditions around an aquatic organism, even using biotic predictors, and not only limiting the analysis to the point where fish were observed (Veza et al., 2015). Therefore, meso-scale models demonstrated great ability to properly relate the habitat-suitability predictions and fish presence (Parasiewicz and Walker, 2007). However, more research is needed to dispel any doubt about the advisability of the meso-scale over the micro-scale one and about significant differences in e-flow assessment.

In this paper, we hypothesized i) that the spatial scale affects the SDMs performance and structure and ii) that these differences may lead to differences in the assessed e-flows. We developed models at two different scales; the micro-scale and the meso-scale. Once models were developed, a graphical sensitivity analysis was performed to compare our results with previous literature. To evaluate the practical applicability of these models, the two SDMs were linked with a hydraulic model to infer e-flows. Finally, the merits and demerits of our models and differences in the e-flow assessment are briefly discussed.

2 METHODS

2.1 Micro-scale data collection

The presence of adult redfin barbel (body length > 5 cm) (Aparicio, 2002) 'feeding' or 'holding a feeding position' (*i.e.* active specimens) was observed by snorkelling in the Mijares River (Jucar River Basin District, east of the Iberian Peninsula) during the early summer of 2012 (Fig. 1). The survey included the area covered by the hydraulic model (Fig. 1) and we surveyed complete HMUs classified as: pools, glides, riffles, and rapids, by selecting a similar area of slow (pools and glides) and fast (riffles and rapids) HMUs (Alcaraz-Hernández et al., 2011). Four abiotic variables were measured in cross-sections randomly distributed over each HMU: mean water velocity (velocity), water depth (depth), the substrate composition (substrate) and the presence of several types of cover (cover) because these variables have been reported to be the most relevant for fish distribution at the micro-scale (Gibson, 1993). Velocity and depth were measured with an electromagnetic flow velocity meter (Valeport®, UK) and a wading rod, respectively. Both substrate and cover were visually estimated. The substrate was classified in bedrock, boulders, cobbles, gravel, fine gravel, sand, silt and macrophytes (Muñoz-Mas et al., 2012), and the percentages of the different substrate types were summarized in a single substrate index (Mouton et al., 2011). The considered types of cover were large boulders, undercut banks, woody debris, roots, shade (intense) and vegetation, and the number of different cover types present at each location was summed to calculate the cover index (e.g. no cover = 0, boulders + undercut banks = 2, etc.) (Table 1). The initial dataset included 92 presences, and 341 instances where redfin barbel was absent, resulting in a data prevalence (proportion of presence data in the entire dataset) of 0.21.

Table 1. Code, summary, description and units of the variables included in the micro-scale MLP Ensemble.

Code	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.	Variable & units
Velocity	0.00	0.29	0.60	0.59	0.86	2.13	Mean water velocity [m/s]
Depth	0.09	0.38	0.54	0.60	0.75	2.75	Water depth [m]
Substrate	1.00	5.00	5.00	5.12	5.56	8.00	Substrate index [-]
Cover	0.00	0.00	0.00	0.36	1.00	3.00	Cover index [-]

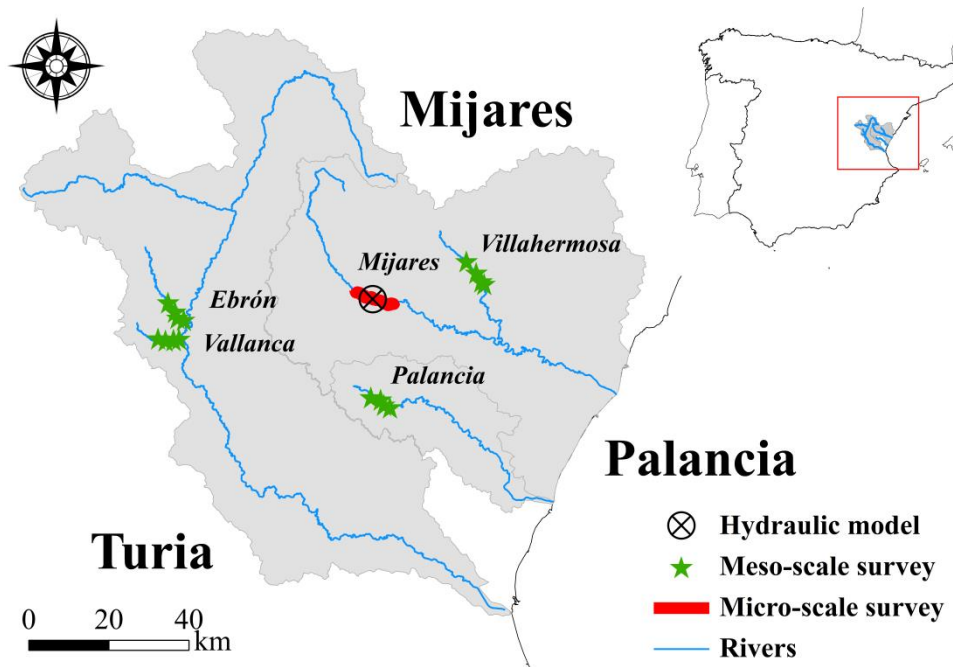


Fig. 1. Location of the target river basins in the Iberian Peninsula (upper–right corner) and study sites in the Mijares, Palancia and Turia River basins.

2.2 Meso–scale data collection

Electrofishing surveys for adult redfin barbel were conducted every summer between 2003 and 2006 in the headwaters of four rivers in the Jucar River Basin District: the Ebrón River and the Vallanca River (both tributaries of the Turia River), the Villahermosa River (a Mijares River tributary) and the Palancia River (Fig. 1). Note that the micro–scale study site was not included in the four meso–scale study sites, although it encompassed the segment of the hydraulic model. Four study sites per river were surveyed following an adaptation of the Basinwide Visual Estimation Technique (BVET, Dolloff et al., 1993); for additional details, see Alcaraz–Hernández et al. (2011) and Mouton et al. (2011). Two HMUs per reach, one slow HMU (pool or glide) and one fast HMU (riffle or rapid), were sampled and, in addition to the HMU type, 13 abiotic habitat variables were assessed in each HMU: length, mean width, mean depth, maximum depth, the percentage of shading, the percentage of embeddedness, the density of woody debris, the substrate index (following the aforementioned classification), the cover index, mean flow velocity, the elevation and slope of the reach and the habitat variability. Length and mean width were measured with tape. Width was measured three times at cross–sections located at $\frac{1}{4}$, $\frac{1}{2}$, and $\frac{3}{4}$ of the total HMU length whereas depth was measured with a wading rod in three uniformly distributed locations per cross–section. For each HMU, depth measurements were then averaged to obtain mean depth and the maximum depth was measured in the corresponding location. The percentage of shading, the percentage of embeddedness (*i.e.* the percentage of the HMU area covered by silt), the number of woody debris particles and the substrate classification were visually estimated. The number of woody debris particles was divided by the HMU area to obtain the density of woody debris. The cover index was calculated as a weighted aggregation of scores assigned to the

presence of undercut banks, shade, large substrate, submerged vegetation and the mean depth (García de Jalón and Schmidt, 1995). The river flow at the time of the survey was gauged with an electromagnetic flow velocity meter (Valeport®, UK) and the mean flow velocity was calculated by dividing the gauged flow by the mean cross-section area. Finally, elevation and slope were derived from digital elevation models (National Centre for Geographic Information, CNIG) and the habitat variability was estimated by the Shannon–Weaver diversity index, considering the number of different HMUs in a 300-m-length stretch surrounding each study site (Table 2). The initial dataset included 39 presences, and 54 HMUs where redfin barbel was absent, resulting in a prevalence of 0.42.

Table 2. Code, summary, description and units of the variables included in the meso-scale MLP Ensemble.

Code	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.	Variable & units
HMU type	1.00	2.00	3.00	2.95	4.00	4.00	HMU type [#]
Depth	0.04	0.22	0.32	0.35	0.46	0.79	Mean depth [m]
M.Depth	0.15	0.43	0.63	0.64	0.83	1.23	Maximum depth [m]
Length	8.60	19.10	24.36	26.92	31.50	54.70	Length [m]
Width	1.26	3.43	4.79	4.66	5.83	8.80	Mean width [m]
Substrate	2.65	4.90	5.20	5.22	5.70	8.00	Substrate index [–]
W.Debris	0.00	0.00	0.00	0.01	0.00	0.16	Woody debris [pieces/m ²]
Elevation	605.00	655.00	743.00	745.80	792.00	968.00	Elevation a.s.l. [m]
Slope	0.01	0.01	0.01	0.02	0.02	0.04	Slope [m/m]
Embeddedness	0.00	0.00	15.00	29.35	50.00	100.00	Percentage of embeddedness [%]
Shade	0.00	20.00	60.00	54.95	85.00	100.00	Percentage of shade [%]
Cover	1.00	2.75	3.50	3.68	4.25	7.50	Cover index [–]
Diversity	0.20	0.62	0.70	0.68	0.76	0.99	HMU diversity [–]
Velocity	0.01	0.09	0.24	0.30	0.42	1.06	Mean flow velocity [m/s]

2.3 Variable selection

Due to the limited number of variables included in the micro-scale sampling and the assumed relevance of these variables for fish distribution (Gibson, 1993), all four variables were included in the micro-scale model. Nevertheless, none of these variables appeared significantly correlated (*spearman* $r^2 < 0.5$) or collinear (variable inflation factor; *vif* < 5).

Since the meso-scale surveys resulted in a high number of explanatory variables, for the final meso-scale model, a parsimonious suite of variables were selected following the step-forward procedure (May et al., 2011); this procedure consists of adding iteratively one variable at a time while the performance is being improved, and stops adding as soon as performance decreases. This approach has proved computationally efficient and tends to result in relatively small input variable sets (May et al., 2011). During the step-forward procedure, neither correlated (*spearman* r^2) nor collinear (*vif*) combinations of input variables were allowed.

2.4 Multi-Layer Perceptron (MLP) Ensemble development

2.4.1 MLP Candidates training

The overproduce-and-choose approach (Partridge and Yates, 1996) generates the optimal MLP Ensemble by first initiating a large number of MLP Candidate classifiers and then selecting the best performing subset of classifiers (Soares et al., 2013). Diversity among the selected MLP Candidates is a key factor of a MLP Ensemble (Wang and Alhamdoosh, 2013) because the diversity among classifiers generally compensates for the increase in error rate of any individual classifier (Opitz, 1999). In diverse ensembles, each candidate complements the others, and thus improves the aggregated forecast (Akhand et al., 2009). There are several methods to construct a diverse MLP Ensemble (Wang and Alhamdoosh, 2013). However, bagging has proven better than several of the more sophisticated methods (Akhand et al., 2009) and can be easily implemented. Bagging splits the initial dataset in training and a test dataset. First, k training (*bag*) datasets of size m are generated by sampling, with replacement, the initial dataset of size n , with $m < n$. For each training dataset, the test dataset (or the *out-of-bag* dataset) then consists of the non-sampled instances from the initial dataset. MLP Candidates are developed based on these k training datasets and the aggregated forecast is finally obtained by averaging the predictions of the individual MLP Candidates. Since the prevalence of the training dataset may affect the result of SDMs (Mouton et al., 2009; Fukuda, 2013), m was chosen in accordance to the prevalence of the initial dataset.

The micro-scale dataset contained a number of absences that exceeded by far the number of presences and therefore, 66 % of the presences (*i.e.* 61 instances), and the same number of absences were randomly selected ($m=122$). The micro-scale dataset did not allow training all possible combinations with a prevalence of 0.5. Therefore an arbitrary but large number of MLP Candidates ($k=2000$) were trained in order to ensure that every ‘presence’ instance was linked to every ‘absence’ instance several times.

To reduce the number of input variables, the optimisation of the MLP Ensemble at the meso-scale was inserted in the step-forward variable selection procedure (May et al., 2011). The meso-scale dataset had a more balanced prevalence (0.42), therefore instead of the bagging approach the *k-fold* approach was performed. This approach can be seen as a systematic *bagging* without replacement. Thus, the training datasets consisted of all possible combinations of 66 % of the observed cases with varying prevalence ($m=61$). Thus, sixty three MLP Candidates ($k=63$) were trained, with each combination of input variables in the step-forward procedure.

MLP Candidates were trained with the *R* (R Core Team, 2015) package *monmlp* (Cannon, 2012) which optimizes the MLP weights using the non-linear minimization (*nlm*) routine (R Core Team, 2015). The number of neurons corresponded to the integer of half the number of variables included in the MLP Ensemble. Hyperbolic tangent and logistic transformation functions were used in the hidden and the output layers, respectively. In line with the Habitat Suitability Index (Bovee et al., 1998), the model output will hereafter be referred to as suitability index. To assess the degree of overfitting of the model results, we compared the performance, quantified by the True Skill Statistic (TSS) [-1, 1] (see Mouton et al., 2010 for additional details about performance criteria), of each selected MLP Candidate on both the *bag* and the *out-of-bag* datasets.

2.4.2 Selection of candidates – Genetic algorithms

GAs are search and optimization algorithms based on the process of natural selection (Olden et al., 2008). From the wide range of GA approaches to select the optimal subset of MLP Candidates (Wang and Alhamdoosh, 2013; Soares et al., 2013; Muñoz–Mas et al., 2014), we followed Wang and Alhamdoosh (2013) since satisfactory results were obtained with small–sized ensembles. This approach iteratively increases the ensemble size by the stepwise addition of MLPs while in every step the GA searches for the best combination of MLPs. That is to say, the GA first finds the best ensemble of two MLPs, subsequently it finds the best ensemble of three MLPs and so on.

We applied the *rgenoud* package (Mebane Jr and Sekhon, 2011), including nine operators driving the optimization which correspond to cloning, uniform mutation, boundary mutation, non–uniform mutation, polytope crossover, simple crossover, whole non–uniform mutation, heuristic crossover and local–minimum crossover (Mebane Jr and Sekhon, 2011). The phenomenon whereby GAs get stuck on local optima is known as premature convergence (Fogel, 1994). To avoid this, the population diversity and the selection pressure should be balanced (Pandey et al., 2014). Therefore, the cloning operator was restricted (0.25) whereas the operators that increase diversity (i.e. uniform mutation, simple crossover and heuristic crossover) were set relatively high (0.6, 0.6 and 0.4). In summary, the whole set of operators were set to 0.25, 0.6, 0.05, 0.05, 0.05, 0.6, 0.05, 0.4 and 0 respectively. On the other hand, the population size as well as the number of generations varied in accordance with the ensemble size (Ens_{size}). The population size followed $\log_{1.5} \cdot (Ens_{size}) \cdot 4000$ and $\log_{1.5} \cdot (Ens_{size}) \cdot 2000$ in the micro–scale and the meso–scale models respectively whereas the number of generations was set to $\cdot (Ens_{size}) \cdot 10$ in both models. The models were optimised based on a multi–objective function. Specifically, the GA maximized the TSS while stimulating overprediction (sensitivity > specificity) (Mouton et al., 2010) and forcing model outputs to span the whole output range (from 0 to 1) following equation 1,

$$Objective = TSS + \min\{0, Sensitivity - Specificity\} - \min\{MLP Ensemble(Database)\} - [1 - \max\{MLP Ensemble(Database)\}](1)$$

where MLP Ensemble corresponds to the aggregated forecast based on the different predictions performed by each MLP component (i.e. $\sim f(x)$) and Database to the training dataset (i.e. $\sim x$).

To assess the quality of the MLP Ensembles obtained with the Wang and Alhamdoosh approach (Wang and Alhamdoosh, 2013), the performance of three different ensembles was compared: the ensemble containing only the best single MLP Candidate (Best MLP Candidate), the ensemble aggregating all MLPs (Complete MLP Ensemble) and the GA optimised MLP Ensemble (Optimal MLP Ensemble).

2.5 Graphical sensitivity analysis

The applied sensitivity analysis uses modified scatter plots to assess the effects of the model inputs on the output – for a detailed explanation see Cannon and McKendry (2002) or Appendix A. For each variable V_i , the variation of the model output due to variation of V_i (Δ_i) is calculated and plotted as segments, with the slope of these segments equalling the partial derivative of the model output related to V_i . The visualization of the partial derivatives as segments allows the

identification of trends and non-linear relationships between each input variable and the output but also provides other advantages:

- i. The general trend provides information about the overall impact of V_i on the response variable;
- ii. The variable importance is quantified by the overall vertical range of all the segments;
- iii. The interaction with other variables is described by the spread along the y-axis and thus variables with no interaction appear as single lines.

To avoid that the sensitivity analysis would focus only on the conditions sampled during the data collection, two artificial datasets with 1000 instances were generated with the function *runif* (R Core Team, 2015) and both the training and the artificial datasets, were used to perform the sensitivity analysis.

2.6 Experimental application of the SDMs

Although 2D hydraulic models can be considered the general standard in micro-scale e-flow assessment (*e.g.* Muñoz-Mas et al., 2016) it has been demonstrated that the adequate implementation of 1D model can perform similarly, even over complex river morphologies such as braided river channels (Jowett and Duncan, 2012). The meso-scale model was based on one single value of each input variables per surveyed HMU thus the use of 2D models would have required the oversimplification of hydraulics and thus worthless modelling effort. Therefore, to balance the modelling effort and the requirements of each scale (the micro-scale and the meso-scale) and following previous studies (Costa et al., 2012), the hydraulics were simulated with RHYHABSIM (Clausen et al., 2004) in a Mijares River segment that overlapped only with the area surveyed for the micro-scale model (Elevation = 659 m a.s.l) (Fig. 2). RHYHABSIM is a one-dimensional hydraulic model based on cross-sections and the water surface elevation. The habitat simulation encompassed a river segment of 383.94 m length where 20 cross-sections were placed covering all the significant elements in the river channel (mean distance = 20.2 m). The cross-sections were marked so that they could be located for subsequent measurements. Detailed topography (mean distance between measurements = 0.58 m) was surveyed over the study site and both water surface elevation and water velocity along the cross-section were surveyed twice at two different flow rates (0.372 and 1.525 m³/s). Substrate composition and the presence of cover were assessed and an additional survey was carried out at a flow rate of 4.21 m³/s to ascertain the stability of the limits of the HMU. We simulated 50 evenly distributed flows and for each flow the habitat suitability was simulated using the optimal MLP Ensembles. In addition the Weighted Usable Area (WUA) (Bovee et al., 1998) was calculated and to assess the practical applicability of our models in e-flow assessment, a minimum e-flow was derived from the WUA-flow curves based on Spanish legislation. Specifically, the Spanish norm for hydrologic planning (MAGRAMA, 2008) establishes that the minimum e-flow should correspond with 50 % to 80 % of the maximum WUA. If no maximum could be observed in the WUA-Flow curve, the inflection point should determine the minimum e-flow.

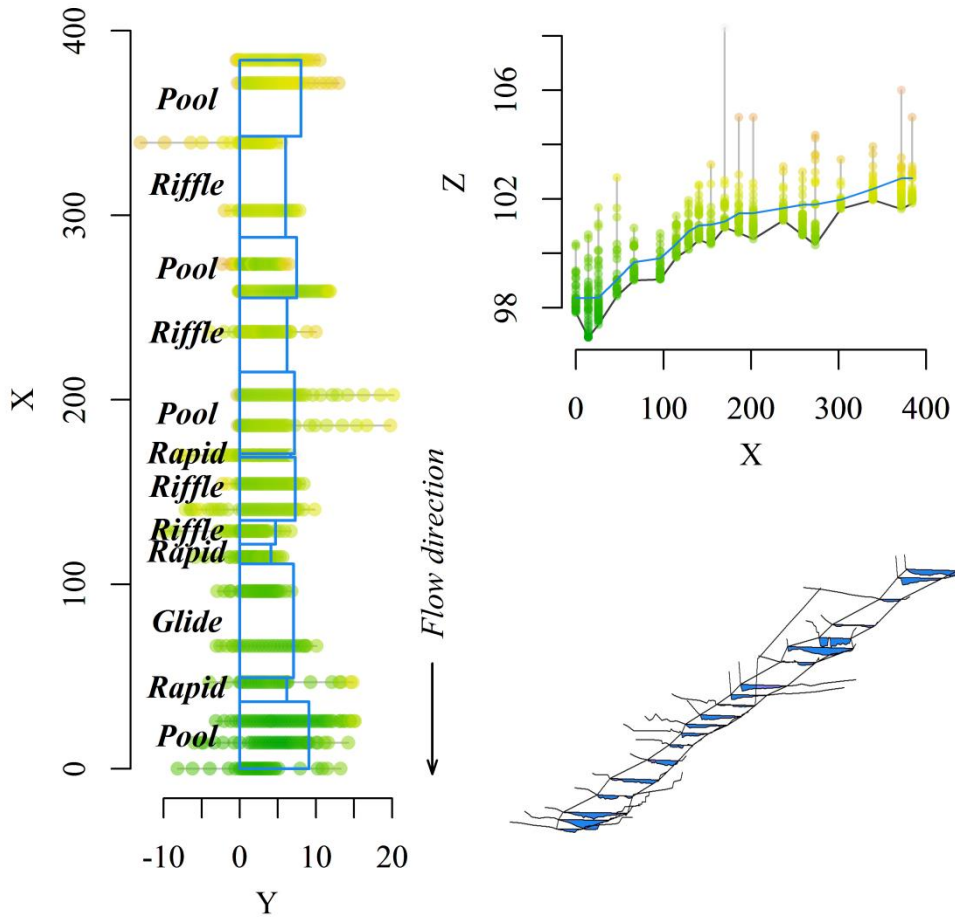


Fig. 2. General view of the model, located in the Mijares River (Elevation = 659 m a.s.l), used to simulate hydraulics at the working scales (micro-scale and meso-scale). The figure depicts the plain, lateral and isometric views of the topographic data (coloured dots), the wetted perimeter and the water surface elevation for one of the calibration flows ($0.372 \text{ m}^3/\text{s}$). The data are depicted in meters and local coordinates.

3 RESULTS

3.1 Training results

Following the step-forward algorithm, the meso-scale model with the highest performance (Optimal MLP Ensemble) contained four variables: elevation, velocity, maximum depth and substrate (in order of selection) (Table 3). For both the micro-scale and the meso-scale model, the complexity of the MLPs involved in the Ensemble was low since only two nodes were considered for each MLP.

The GA-optimised MLP Ensemble (Optimal MLP Ensemble) outperformed the Best MLP Candidate and the ensemble aggregating the prediction of all candidates (Complete MLP Ensemble) (Table 3). For the micro-scale model, the predictions of the absent and present instances strongly overlapped, which revealed lower discriminant (classificatory)

capability (Fig. 3 – Top). Nevertheless, the TSS was high (0.62) and the number and values predicted for the present instances were higher than the absent instances (*i.e.* sensitivity > specificity). The meso-scale model showed a stronger distinction between the predictions of absent and present instances and consequently it presented higher, almost perfect (TSS=0.92), discriminant capability (Fig. 3 – Bottom).

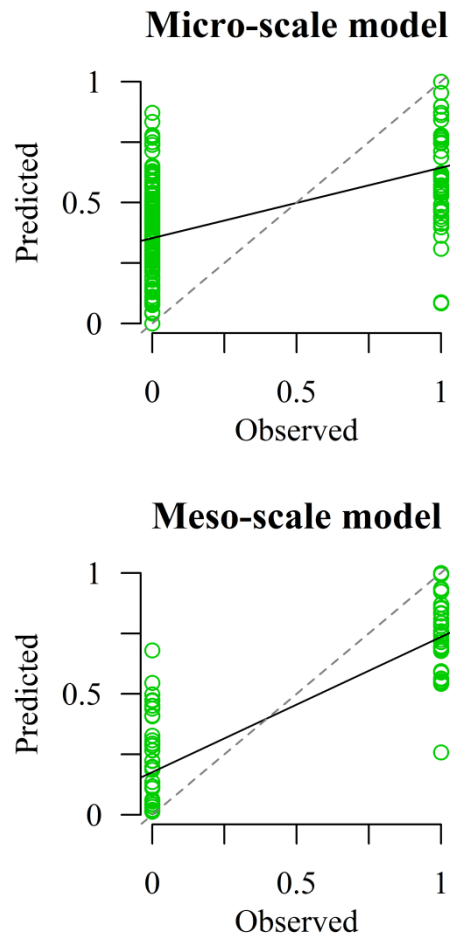


Fig. 3. Observations versus predictions for the micro-scale and the meso-scale models. Solid line depicts the regression line whereas the dashed line corresponds to the perfect discrimination.

The micro-scale model encompassed four MLPs whereas the meso-scale model involved seven MLPs. Consequently, four *bag* and four *out-of-bag* datasets were involved in the micro-scale MLP Ensemble, and seven by seven in the meso-scale counterpart. Cross-evaluation (*i.e.* the evaluation of every *bag* and *out-of-bag* dataset with every selected MLP Candidate) rendered similar distributions (*i.e.* they presented evident overlapping) of the TSS, thus it revealed low overfitting to the data. As a consequence both models were considered suitable for further analysis (Fig. 4).

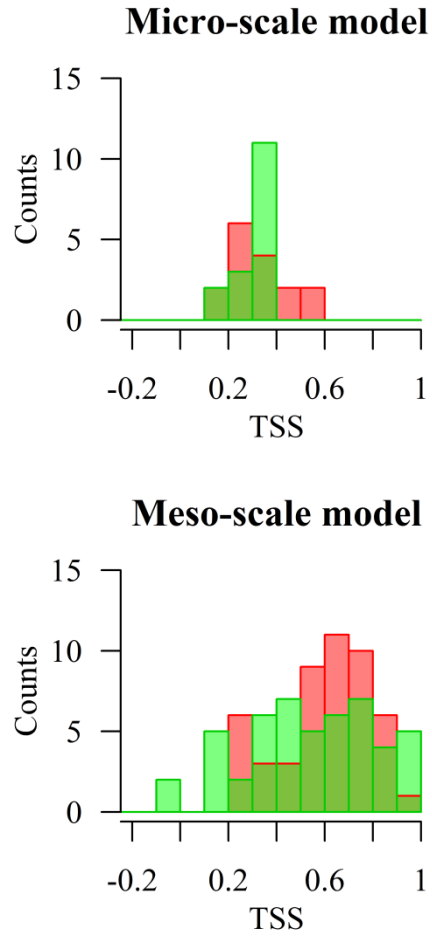


Fig. 4. Distribution of the TSS (True Skill Statistic) rendered by each MLP over each *bag* (dark colour or red in the digital version) and *out-of-bag* (light colour or green in the digital version) datasets involved in the Optimal MLP Ensembles (4×4 for the micro-scale model and 7×7 for the meso-scale). The distributions for both models, with 16 and 79 data respectively, presented significant overlapping revealing low overfitting to the data.

Table 3. Summary of the performance TSS (True Skill Statistic) of developed MLP Ensembles at the micro-scale and the meso-scale (Optimal MLP Ensemble) and the counterparts without MLP selection (Complete MLP Ensemble) and considering no MLP aggregation (Best MLP Candidate).

		# MLPs	TSS
Micro-scale	Best MLP Candidate	1	0.49
	Optimal MLP Ensemble	4	0.62
	Complete MLP Ensemble	2000	0.52
Meso-scale	Best MLP Candidate	1	0.71
	Optimal MLP Ensemble	7	0.93
	Complete MLP Ensemble	63	0.69

3.2 Sensitivity analysis – Micro-scale model

All the input variables presented interactions, as demonstrated by the spread over the ordinate axis (Fig. 5). Although differences in variable importance appeared small, depth was the most important variable. Depth demonstrated a quadratic relationship with a parabolic trend inflecting around 0.85 m, while velocity appeared negatively linearly related to redfin barbel presence. Cover had an asymptotic relationship with a remarkable increment from absence of cover (0) to presence of cover (1). Substrate was the least important variable and showed a positive trend. The sensitivity analysis of the artificial dataset showed a similar response than the one based on the original dataset.

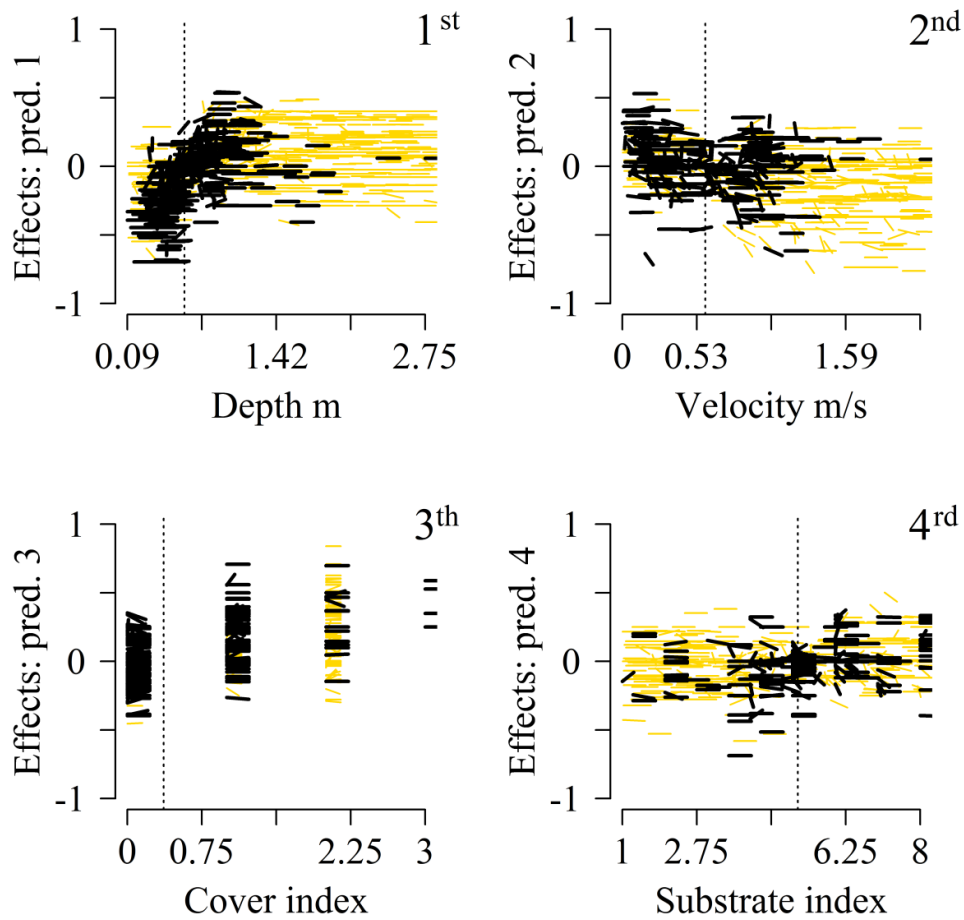


Fig. 5. Micro-scale sensitivity analysis of the original dataset and the artificial dataset; black segments correspond to the original dataset and yellow ones to the artificial dataset. The variable importance is indicated in the upper right corner.

3.3 Sensitivity analysis – Meso-scale model

In the meso-scale model, also all included variables showed interactions (Fig. 6). Elevation showed a clear linear negative effect on fish presence and was the most important variable. Velocity showed an asymptotic trend with positive effects beyond 0.25 m/s. Substrate presented a small negative trend, in contrast to the micro-scale model. Maximum depth was the least important variable and only showed a slightly positive trend. Sensitivity analysis of the artificial dataset also matched the one based on the training dataset.

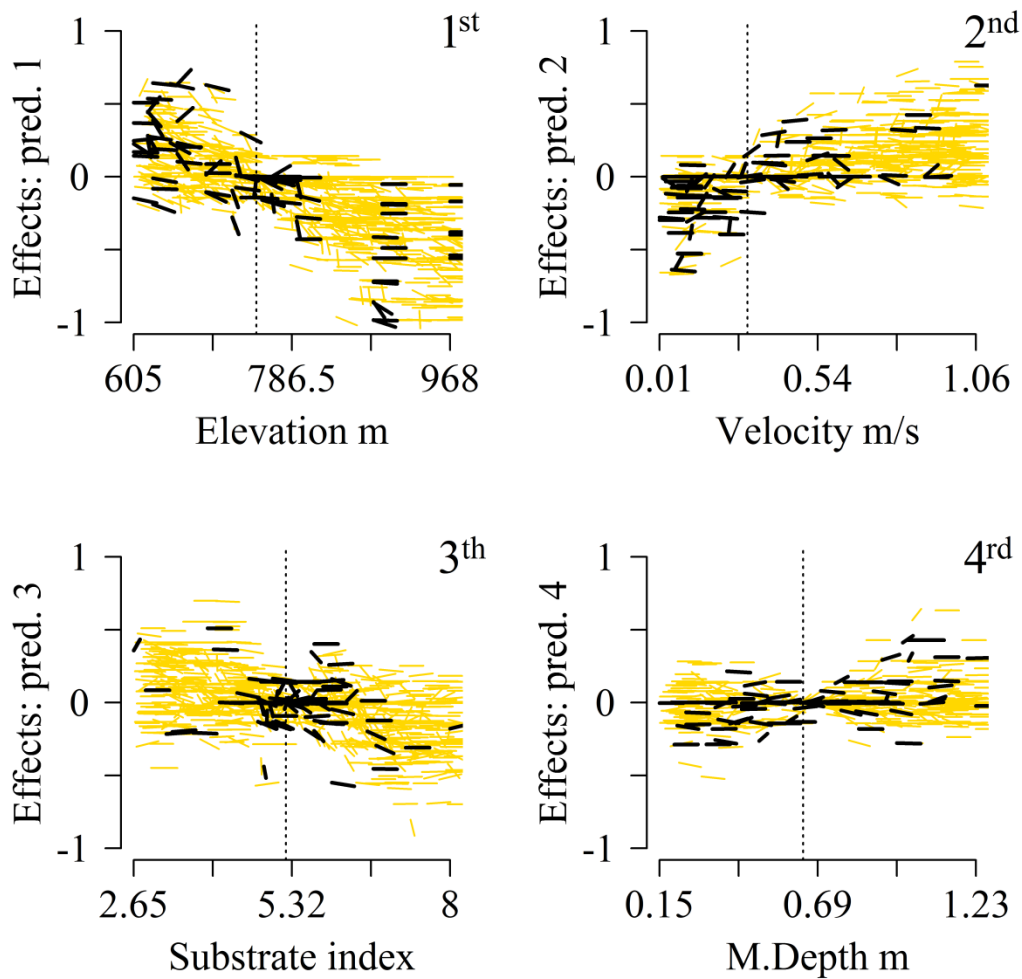


Fig. 6. Meso-scale sensitivity analysis of the original dataset and the artificial dataset, black segments correspond to the original dataset and yellow ones to the artificial dataset. The variable importance is indicated in the upper right corner.

M. Depth = Maximum depth.

3.4 Habitat assessment

The WUA-Flow curves for of the micro-scale and the meso-scale models neither presented an asymptote nor a clear optimum (Fig. 7). The *smooth.spline* function in *R* (R Core Team, 2015) was used to remove curve irregularities and to calculate the inflection points of both curves. The inflection point of the micro-scale WUA-Flow curve appeared at 1.1 m³/s whereas the meso-scale WUA-Flow curve inflection point occurred at 0.7 m³/s.

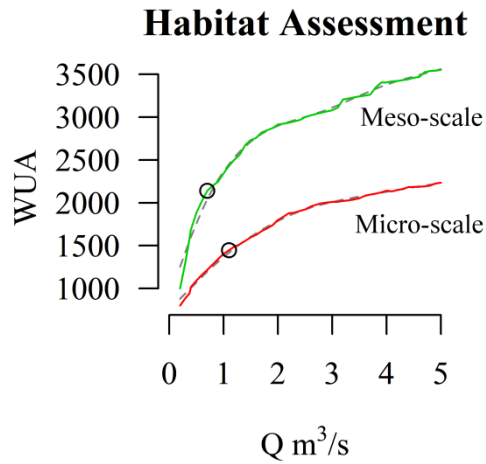


Fig. 7. Weighted Usable Area (WUA) – Flow curves derived from the micro–scale and the meso–scale MLP Ensembles at the test site. Dashed lines show the smoothed curves whereas dots indicate the inflection points.

Habitat conditions at the minimum simulated flow (0.2 m³/s) and at the flows corresponding to the inflection points (1.1 and 0.7 m³/s for the micro–scale and the meso–scale respectively) were then evaluated and visualised for spatially explicit inspection (Fig. 8). The habitat assessment at the micro–scale yielded suitable areas all along the hydraulic model for the minimum simulated flow and the inflection flow, although habitat suitability was significantly higher at the latter flow. Conversely, the meso–scale model assessed most of the low flow with low to middle suitability but a very little narrow rapid whereas practically all of the HMUs at the inflection flow were assessed with high or very high suitability.

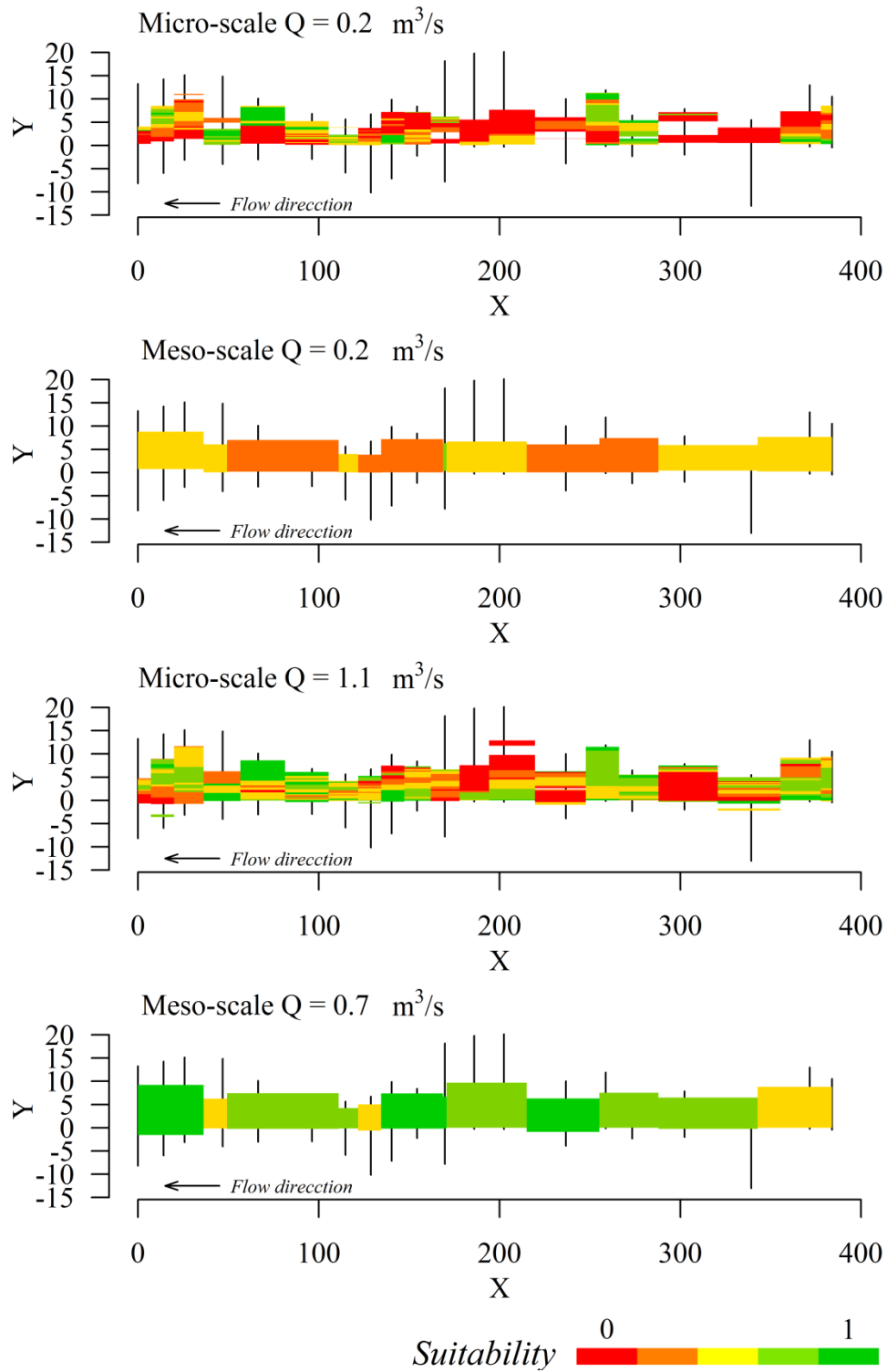


Fig. 8. Assessment of the minimum simulated flow ($0.2 \text{ m}^3/\text{s}$) and of the minimum environmental flow corresponding to $1.1 \text{ m}^3/\text{s}$ for the micro-scale SDM and to $0.7 \text{ m}^3/\text{s}$ for the meso-scale SDM. Black lines indicate the cross-sections.

4 DISCUSSION

4.1 General prospect

The approach employed by Wang and Alhamdoosh (2013) proved proficient to develop optimal MLP Ensembles since it provided small sized ensembles, and the Optimal MLP Ensembles outperformed the corresponding Best MLP Candidate and the Complete MLP Ensemble. The sensitivity analysis indicated that the effects of the artificial dataset matched the effects derived from the training datasets, emphasizing the reliability of the two SDMs. The outputs of both models also covered the whole feasible range (from 0 to 1), which facilitates the interpretation by inexperienced readers, but especially by stakeholders and managers. Furthermore, the output span allows its treatment as probabilistic-like outputs and its comparison with previous physical habitat modelling studies (Bovee et al., 1998) as being analogous to the outputs rendered by the more traditional univariate Habitat Suitability Curves (HSCs) (Muñoz-Mas et al., 2012). Altogether should encourage the use of MLP Ensembles in e-flow assessment studies (e.g. Muñoz-Mas et al., 2016).

4.2 Micro-scale model

The micro-scale model achieved a TSS similar to previous studies that used ensemble techniques at this scale (*i.e.* Random Forests) (Fukuda et al., 2013) and it showed a good trade-off between specificity and sensitivity, regardless of the prevalence of the original training dataset. However, it achieved the lowest TSS between the two models. Nevertheless, the results were considered satisfactory because it achieved high values of TSS in comparison with previous studies (Fukuda et al., 2013; Muñoz-Mas et al., 2014a). MLP Ensembles are sensitive to prevalence like other techniques (Fukuda, 2013), but training the MLP Candidates with 0.5 prevalence datasets contributed to our objectives, which included maximising TSS, obtaining a sensitivity higher than the specificity and overlapping *bag* and *out-of-bag* TSS distributions. Therefore, we strongly recommend this approach in the development of micro-scale suitability models with MLP Ensembles.

The habitat suitability for the redfin barbel was optimal from 0.5 m to 1 m depth and where cover and medium-to-coarse substrate were present; on the other hand, flow velocity presented a general negative influence on fish presence, although positive effects were found all along the surveyed range even at the maximum surveyed velocity (2.13 m/s). The differences in variable importance were small, although we consider the ranking coherent with the prior knowledge about the species (Grossman and De Sostoa, 1994; Aparicio, 2002). The redfin barbel certainly should be categorized within the group of rheophilic barbels (Aparicio, 2002) because our results modelled high velocity as suitable. Interestingly, this result contrasts with previous HSCs for this species that suggest a more limnophilic nature (Sostoa et al., 2005), although our results on depth agree with those of the aforementioned study. These differences could have been influenced by circumstances at the time when data were collected (Copp, 2008) or the kind of available microhabitats (Ayllón et al., 2009). Unfortunately the reasons for such differences cannot be revealed based on the available information. Literature disagrees on substrate suitability, either suggesting a preference for algae and organic matter (Grossman and De Sostoa, 1994) or the opposite, for coarse substrates (Sostoa et al., 2005). This discrepancy probably originates from the fact that those previous studies have joined some substrate and cover types rather than providing a clear preference for any of them. Yet, substrate appeared to be of lesser importance within our micro-scale model. Finally, the results agreed with

previous studies demonstrating that the redfin barbel is a cover-orientated species (Grossman and De Sostoa, 1994), based on the influence of cover on fish presence. Consequently, the micro-scale model combines novel insights and information from previous studies, and thus it improves the knowledge about redfin barbel's habitat preferences at the micro-scale.

4.3 Meso-scale model

The meso-scale model proved the competence of the GA-optimised MLP Ensembles because it yielded a similar performance to previous studies that modelled the presence-absence of freshwater fish species with Random Forests (Mouton et al., 2011; Vezza et al., 2015). Some studies indicated that models based on multiple spatial scales usually outperform single-scale analyses (Olden et al., 2006) mainly because environmental variables rarely act at a single spatial scale (Boulangeat et al., 2012). The optimal meso-scale model included not only three purely meso-scale variables (velocity, substrate and maximum depth) but elevation as one meso-to-macro scale variable. The selected variables significantly interacted, thus modifying the predicted effects positively or negatively. However, despite the higher performance, the step-forward algorithm for selecting variables may have been conditioned by the first selected variable (elevation), which could lead the algorithm to get stuck in a local minimum (May et al., 2011). There are examples of the use of GAs in variable selection procedures (May et al., 2011; Olden et al., 2008) and in MLP candidates' selection (Soares et al., 2013; Wang and Alhamdoosh, 2013). Therefore, further research should be performed in order to inspect the capabilities of GAs to simultaneously undertake the selection of the variables and the MLP Candidates.

Elevation had a linear and negative effect on redfin barbel presence. This variable is broadly accepted as a proximal predictor of water temperature (Elith and Leathwick, 2009). In the Iberian Peninsula, cyprinids increase their dominance in fish assemblages in the lower river segments (Santos et al., 2004) thus we considered such a pattern reliable. However elevation may also partially explain the effect of slope and the fact that the upper segments had very low flow and thus shallow HMUs. In contrast with the micro-scale model, velocity had purely a positive effect on redfin barbel's presence, which agrees with its rheophilic classification (Aparicio, 2002). Nevertheless, the meso-scale model involved data from several years in contrast to the micro-scale study, which was performed in one single campaign, and thus we cannot discard that such discrepancy is not reflecting differences on the sampled running flows. In a previous study that involved the redfin barbel's meso-scale dataset (Muñoz-Mas et al., 2015) the influence of the study site and sampling year, which can be univocally related to the running flow at the time of the sampling, was ruled out. However, flow significantly varied among years thus some of the uppermost river stretches became completely dried up during two sampling campaigns. The redfin barbel have demonstrated a strong site-fidelity, which is only contravened when the habitat suitability significantly degrades (*e.g.* by noticeable reductions on the available water depth) (Aparicio and De Sostoa, 1999). In such situation the redfin barbel undertakes the largest displacements in search of suitable habitats, typically moving towards extant lowland pools (Aparicio and De Sostoa, 1999). Consequently, the patterns observed for flow velocity could be depicting such type of migrations toward suitable habitats, which in our study area would be associated with higher flows and, given the slope of the study sites, also with higher flow velocity. Maximum depth surprisingly was the least important variable, in contrast to depth being the most important variable in the micro-scale model.

However, the deepest surveyed HMUs were predicted to be most suitable for redfin barbel, which matches the aforementioned studies that considered the redfin barbel a pool dweller (Aparicio and De Sostoa, 1999). The meso-scale analysis for substrate indicated an inverse pattern compared to the micro-scale model. Such discrepancy in the response across scales has been reported previously (Gosselin et al., 2010). However it is remarkable that the meso-scale results are not necessarily different from the micro-scale model because the substrate index is calculated as the average value of the different types of substrate present. Therefore, the micro-scale model depicts the substrate observed at fish locations and due to the small sampled area around the fish, it is unlikely to encompass a heterogeneous group of substrates. Conversely, the meso-scale model depicts the mean value for the patches appearing at the sampled HMUs and they may encompass multiple types of substrate, as this patchy distribution is common at the meso-habitat scale (e.g. Inoue and Nunokawa, 2002). Substrate heterogeneity has previously been considered in the study of the redfin barbel (Aparicio and De Sostoa, 1999) and it certainly could clarify these apparent discrepancies, although given the accuracy of the developed model it was considered unnecessary. Nevertheless, the values of maximum depth in the meso-scale data corresponded to the median depth in the micro-scale model, and, in contrast to the micro-scale study, the meso-scale survey assessed several rivers. Therefore, comparison between them should be taken cautiously in broad terms; the meso-scale model might be considered a regional model focusing on broader scale aspects and the microscale model was more specific for the Mijares River.

4.4 Habitat assessment and implications of developed SDMs

Previous comparisons of micro- and meso-scale models also yielded differences in the assessed suitability (Parasiewicz and Walker, 2007). The sampling methods have been identified as potential sources of bias in the development of SDMs, since no method can ensure that all fish are detected (Mcmanamay et al., 2014). At the micro-scale, snorkelling has been proved preferable over electrofishing (Brosse et al., 2001); while every HMU was netted off before carrying out any survey at the meso-scale. Moreover, the use of presence/absence data rather than abundance data can be a cost-effective and accurate approach to monitor aquatic species (Joseph et al., 2006). Consequently, we considered the effect of the sampling method negligible and assumed the observed differences mainly occurred due to ecological and mathematical aspects. The micro-scale model could be assumed to represent 'feeding' or 'holding a feeding position' behaviour because it is assumed that such positions are the most energetically profitable (Rincón and Lobón-Cerviá, 1993) and hiding and/or disturbed fish observations were ruled out. However, the redfin barbel was observed several times in multi-species shoals mainly composed by cyprinids (e.g. *Squalius valentinus*; Doadrio y Carmona, 2006), with which the redfin barbel has shown evident affinity (Muñoz-Mas et al., 2015), and these observations were included in the ultimate dataset. These shoals were wandering nearby elements of cover (e.g. logs and woody debris) with some individuals foraging on the debris and substrate. There are no specific studies on the redfin barbel's diet (Verdiell-Cubedo, 2011), although it has been suggested its preference for drifting invertebrates such as *Chironomidae*, *Ephemeroptera* and *Trichoptera* (Miranda et al., 2005). Other akin Iberian species (Gante et al., 2015) (i.e. *Barbus spp.* and *Lucioababus spp.*) typically ingest a great variety of items without any clear preference (omnivory, eurifagy), even presenting significant proportions of the diet composed by vegetation (Collares-Pereira et al., 1996; Magalhães, 1993). In accordance with these generalist feeding behaviour we considered our choice adequate, although based on previous studies about the diel dynamics of habitat use

of the European barbel (*Barbus barbus*; Linnaeus, 1758) (Baras and Nindaba, 1999) our dataset could be including a mixture of activities. Then, despite of a great uncertainty, these data could be depicting the so-called activity centre or the daily activity area, which can be roughly estimated as the HMU encompassing the residence and the feeding area (Baras, 1997).

Conversely, the meso-scale model is based on fish catches in HMUs where the fish develop any of the diel activities such as 'feeding' but, in this case, it surely encompassed also 'hiding' or 'resting' individuals as long as electrofishing does not allow the differentiation of the activity undertaken by fish captures. Therefore, in the meso-scale model, the training data considered all the fish in the HMU without any distinction of activity and assuming that any potential migration occurred in spring, before sampling (Aparicio and De Sostoa, 1999). Significant changes in habitat use have been demonstrated for the European barbel depending on the time of the day and the season (Baras and Nindaba, 1999). Therefore, these two SDMs could represent different habitat needs.

Despite the potential ecological differences between models and the ranges of the sampled input variables, the patterns of the two WUA curves were similar. However, the micro-scale approach assessed the hydraulics in a very detailed way (every cell can be assessed differently) whereas the meso-scale approach presented a coarser resolution, and thus as soon as it considered an HMU suitable it added the entire HMU area to the WUA. Consequently, there is a difference in magnitude between both WUA flow rating curves, which would principally be caused by the discrepant resolution used in the habitat assessment (*i.e.* the mean size of the assessed cells were larger in the meso-scale model). The use of a density-based suitability index could provide more gradual information on species habitat selection in the meso-scale model (Fukuda et al., 2011) and may thus lead to more similar WUA-flow curves, although it should be corroborated by dedicated studies.

Compared to the traditional micro-scale evaluation the meso-scale approach permitted the survey of longer river segments, involving a wider range of habitat variables that could consider diverse fish behaviour at larger spatial scales (Veza et al., 2012). Indeed, by sacrificing some detail it is possible to reveal larger spatial and temporal ecological patterns (Jewitt et al., 2001). Consequently, in this study a hydraulic model developed on a longer river segment may enable a more thorough and varied meso-scale assessment. However, this issue was already partially dealt with by simulating water depth and flow velocity for unmeasured discharge conditions (following RHYHABSIM) in contrast to some other approaches, which are based in a finite number of observations (MesoHABSIM; Veza et al., 2012). Taking into account that no habitat time series analysis has been performed (Milhous et al., 1990), the differences in the magnitude of the WUA-Flow curves did not result in notable differences in the minimum legal e-flow (1.1 m³/s and 0.7 m³/s). Nevertheless, the micro-scale models, which is the scale specified in the Spanish norm for hydrological planning for e-flow assessment (MAGRAMA, 2008), remained on the conservative side because it has determined a slightly higher e-flow.

Previous research already demonstrated that a lower e-flow is derived from a WUA-Flow curve that presented larger values of the WUA (Muñoz-Mas et al., 2012), which suggests that a revision of these legal specifications may be appropriate. The capability to simulate large numbers of flows has risen along the decade and thus the WUA-Flow curves nowadays present smooth transitions from flow to flow. In this case the inflection point is determined by a very little difference and could vary by reducing the number of simulated flows. Further, the Mijares River is subject to severe

droughts, with one of the calibration flows being 0.372 m³/s. The species naturally occurs in this river segment and its adaptation to droughts has been confirmed (Aparicio and De Sostoa, 1998; 1999). Therefore, it can be concluded that the minimum legal e-flow derived from both SDMs would not eventually pose any threat to the species.

4.5 Conclusions

The MLP Ensembles appeared efficient to develop SDMs, and the Wang and Alhamdoosh (2013) approach provided accurate small-sized models. Thereby the meso-scale model presented almost a perfect accuracy (TSS = 0.93) with four variables. The final models confirmed previous studies and complemented existing knowledge on the habitat preferences of redfin barbel (Sostoa et al., 2005; Aparicio and De Sostoa, 1999; Aparicio, 2002; Grossman and De Sostoa, 1994). Since modelling results may strongly depend on the training dataset, future research should compare the MLP Ensembles developed following the Wang and Alhamdoosh (2013) approach with some benchmarking techniques (*e.g.* Random Forests). However, MLP Ensembles should be considered a suitable technique to develop SDMs since they provided competent results at both spatial scales. The habitat assessment demonstrated the value of MLP Ensembles in e-flow assessment because both SDMs suggested a similar minimum legal e-flow based on the methodology for the analysis of the WUA-flow curves described in the Spanish norm for hydrological planning (MAGRAMA, 2008). This legal norm stated that studies on e-flow assessment must be performed at the microscale, which eventually predicted a slightly higher e-flow. Therefore, from the legal viewpoint, this scale can be at least equally adequate as the meso-scale in e-flow assessment studies. Although additional comparison between modelling scales would be advisable it can be concluded that the MLP Ensemble should be taken into consideration in future e-flow assessments.

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