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## Assessing the effect of fish size on species distribution model performance in southern Chilean rivers

 $\textbf{Daniel Zamorano}^{\ 1,2} \ , \ \textbf{Fabio Labra}^{\ 1,3} \ , \ \textbf{Marcelo Villarroel}^{\ 2} \ , \ \textbf{Luca Mao}^{\ 4} \ , \ \textbf{Shaw Lucy}^{\ 4} \ , \ \textbf{Marcelo Olivares}^{\ 5,6} \ , \ \textbf{Matias Peredo-Parada}^{\ Corresp. \ 2}$ 

Corresponding Author: Matias Peredo-Parada Email address: matias.peredo@ecohyd.com

Despite its theoretical relationship, the effect of body size on the performance of species distribution models (SDM) has only been assessed in a few studies of terrestrial taxa. We aim to assess the effect of body size on the performance of SDM in river fish. We study seven Chilean freshwater fish, using models trained with three different sets of predictor variables: ecological (Eco), anthropogenic (Antr) and both (*Eco+Antr*). Our results indicate that the performance of the *Eco+Antr* models improves with fish size. These results highlight the importance of two novel predictive layers: the source of river flow and the overproduction of biotopes by anthropogenic activities. We compare our work with previous studies that modeled river fish, and observe a similar relationship in most cases. We discuss the current challenges of the modeling of riverine species, and how our work helps suggest possible solutions.

<sup>&</sup>lt;sup>1</sup> Centro de Investigación e innovación en Cambio Climático, Universidad Santo Tomás, Santiago, Chile

<sup>&</sup>lt;sup>2</sup> Area de Ecohidráulica, Plataforma de Investigación en Ecohidrología y Ecohidráulica Itda, Santiago, Chile

<sup>&</sup>lt;sup>3</sup> Programa de Doctorado en Conservación y Gestión de la Biodiversidad, Facultad de Ciencias, Universidad Santo Tomás, Santiago, Chile

<sup>4</sup> Departamento de Ecosistemas y Medio Ambiente, Facultad de Agronomia, Pontificia Universidad Católica de Chile, Santiago, Chile

Departamento de Ingeniería Civil, Universidad de Chile, Santiago, Chile

<sup>&</sup>lt;sup>6</sup> Centro de Energía, Universidad de Chile, Santiago, Chile



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- 5 D. Zamorano<sup>1,2</sup>, F.A. Labra<sup>1,3</sup>, M. Villarroel<sup>2</sup>, L. Mao<sup>4</sup>, S.N. Lacy<sup>4</sup>, M. Olivares<sup>5,6</sup> & M. Peredo-Parada<sup>\*2</sup>
- 6 1.- Centro de Investigación e innovación para el Cambio Climático, Universidad de Santo Tomás
- 7 2.- Plataforma de Investigación en Ecohidrología y Ecohidráulica limitada, Santiago, Chile.
- 8 3.- Programa de Doctorado en Conservación y Gestión de la Biodiversidad, Facultad de Ciencas,
- 9 Universidad Santo Tomás, Santiago, Chile.
- 10 4.-Departamento de Ecosistemas y Medio Ambiente, Facultad de Agronomía e Ingeniería Forestal,
- 11 Facultad de Agronomía, Pontificia Universidad Católica de Chile, Santiago, Chile
- 12 5.- Departamento de Ingeniería Civil, Universidad de Chile, Santiago, Chile.
- 13 6.- Centro de Energía, Universidad de Chile, Santiago, Chile.
- \* Corresponding Author (matias.peredo@ecohyd.com)

#### 15 KEYWORDS

- 16 Chilean fishes, Random Forest, Neural Networks, General Lineal Model, Species Distribution Model,
- 17 Anthropogenic variables.



#### 18 ABSTRACT

19 Despite its theoretical relationship, the effect of body size on the performance of species distribution 20 models (SDM) has only been assessed in a few studies of terrestrial taxa. We aim to assess the effect of 21 body size on the performance of SDM in river fish. We study seven Chilean freshwater fish, using models 22 trained with three different sets of predictor variables: ecological (Eco), anthropogenic (Antr) and both 23 (Eco+Antr). Our results indicate that the performance of the Eco+Antr models improves with fish size. 24 These results highlight the importance of two novel predictive layers: the source of river flow and the 25 overproduction of biotopes by anthropogenic activities. We compare our work with previous studies that 26 modeled river fish, and observe a similar relationship in most cases. We discuss the current challenges of 27 the modeling of riverine species, and how our work helps suggest possible solutions.

#### INTRODUCTION

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29 Species distribution models (SDM) provide an important management tool to support conservation 30 planning. SDMs generate species distribution maps that allow for more efficient and effective field 31 inventories, suggest sites of high potential occurrence of rare species for survey planning, and permit 32 testing biogeographical, ecological and evolutionary hypotheses (Guisan & Thuiller, 2005). Given these advantages, different international organizations (e.g., UNEP, Conservation International, IUCN, WWF) 33 have employed SDM to address key policy objectives at a global scale (Cayuela et al., 2009). 34 35 Different species traits have been shown to influence model performance (Brotons et al., 2004; Segurado 36 & Araújo, 2004; McPherson & Jetz, 2007; França & Cabral, 2016). One important trait is body size 37 (Radinger et al., 2017). Larger species detect less food but can tolerate lower resource concentrations 38 within their food, while smaller species detect more food, but require higher resource concentrations 39 within it (Ritchie, 1998; Ritchie & Olff, 1999). As a result, larger species have larger home ranges than 40 smaller species (Calder & A, 2001; Woolnough, Downing & Newton, 2009).



Body size may affect the performance or accuracy of SDM in different ways (McPherson & Jetz, 2007). 41 42 First, species with larger home ranges may perceive the environment at coarser scales, improving the 43 performance of distribution models based on coarse-grained predictors (Suarez-Seoane, Osborne & Alonso, 2002). Second, home-range extent may influence the amount of data available, as well as the 44 45 balance between presences and absences (McPherson, Jetz & Rogers, 2004). In addition, species with 46 local adaptations in habitat preferences may generate models that overestimate their ecological niches 47 (Stockwell & Peterson, 2002). To date, the effect of body size on distribution models has been tested in 48 different taxa with unclear results (e.g. M. McPherson & Jetz, 2007; França & Cabral, 2016; Morán-49 Ordóñez et al., 2017; Radinger et al., 2017). 50 In the case of fish, Radinger et. al. (2017) indicate that smaller-body fishes are less sensitive to 51 anthropogenic intervention in the river network, due to their smaller home ranges. However, their study 52 did not explicitly test variation in model performance in response to fish size. Recent research on fish 53 species distribution models has shown that species with different body sizes are impacted differently by 54 the same sets of environmental features derived from anthropogenic activities (Perry et al., 2005; 55 Radinger et al., 2017). A relevant research question is whether SDM performance or accuracy for 56 different body-sized fishes vary in the same manner when considering different predictor variable sets, 57 such as i) ecological predictors, ii) anthropogenic predictors, and iii) ecological and anthropogenic 58 predictors. 59 The ichthyofauna in Chile comprises a total of 44 species, including two lampreys (Habit, Dyer & Vila, 60 2006), and is characterized as being highly endemic, adapted to high slope rivers, and with small body 61 sizes (Vila, Fuentes & Contreras, 1999; Vila et al., 2006; Habit, Dyer & Vila, 2006). Despite its high 62 biogeographic value, the Chilean ichthyofauna is broadly endangered, with only two species (Cheirodon 63 australe y Mugil cephalus) classified as non-endangered. In Chile, anthropogenic variables represent the 64 main group of threats to river fishes (Habit et al., 2002, 2006). Therefore, understanding the potential



65 impact of body size on SDM performance is highly relevant for conservation and management planning

66 efforts.

In this study, we quantify anthropogenic variables (*Antr*) and ecological variables (*Eco*) at the scale of the river segment, and we generate SDMs for seven native freshwater species. We focus on two well studied southern Chilean basins: Bueno and Valdivia. Our specific objectives are: (1) to assess the effect of fish size on species distribution model performance and variable participation by model, fitted using three sets of environmental features: i) models trained with ecological predictors (*Eco*), ii) models trained models with anthropogenic predictors (*Antr*), and iii) models trained with ecological and anthropogenic predictors (*Eco+Antr*); (2) to examine the predicted biotopes generated by each model for different

#### 75 **METHODS**

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#### 76 Study area and modeled species

77 The study area covers the Valdivia and the Bueno river basins, located in the central-southern zone of

Chile, between the parallels 39.33° and 41.08° S (Figure 1). The Valdivia River basin has a pluvial

species studied; and (3) to compare our results with model performances in previous studies.

79 hydrological regime, and it is characterized by having a chain of interconnected lakes at higher altitudes.

The upper section of the Bueno River basin has a pluvial-nival regime, while the middle and lower part of

81 the basin is governed by a pluvial regime (Errázuriz K. et al., 1998).

To characterize a set of hydrological variables for the study area, we used the national official drainage

83 network generated by the Military Geographic Institute (Instituto Geográfico Militar, Government of

Chile). This drainage network was divided in segments to build the SDM. We considered river segment

between 2 and 10 km of length, having homogeneous hydromorphological conditions with no significant

confluences. This definition was generated using cartographic information, Google Earth (Google inc,

87 2009), and Arc GIS version 9.2 (ESRI, 2010).



Our study included seven freshwater fish species (Table 1): Aplochiton taeniatus (Jenyns, 1842), 88 89 Aplochiton zebra (Jenyns, 1842), Brachygalaxias bullocki (Regan, 1908), Cheirodon australe (Eigenmann, 1928), Odontesthes mauleanum (Steindachner, 1896), Percilia gillissi (Girard, 1855), and Trichomycterus 90 areolatus (Valenciennes, 1846). Statistical analysis of the effect of body size was carried out using 91 92 theoretical species maximum length, which is available for all these species. Most maximum length 93 estimates were obtained from official species descriptions provided in each species conservation 94 assessment developed by the Chilean Ministry of the Environment (Table 1). The only exception was B. 95 bullocki, which had not been assessed by the Ministry of Environment, and whose maximum length was 96 obtained from Fishbase (Froese & Pauly, 2017) (Table S1). 97 This species was selected because represent a good size gradient (between 5.5 cm and 30 cm) (Table 1) 98 to Chilean species case, and particularly all this species encompasses completely the latitudinal range of 99 both basins (Table 1), situation that allow comparing model performance without the distribution range 100 by specie affect in the predicted distribution. **Modeling methods** 101 Species occurrence data 102 103 Historical records of the presences of the study species were obtained from the Ministry of the 104 Environment's (Ministerio del Medio Ambiente, Government of Chile) database on freshwater organisms. 105 This database was generated by collecting published databases of scientific samples in the study area 106 (Ministerio de Energía - División de Desarrollo Sustentable, 2016). 107 In addition, a field sampling campaign was conducted in the study area to complement existing 108 information in the government database. The sampling was done between December 2015 and January 109 2016, using electrofishing equipment (SAMUS, model 745G). We collected all fish along a 100-meter 110 transect, with sampling times of 45 to 60 min, depending of the hydromorphological features of the site.



All collected fish were identified in situ, using a field identification manual (Habit et al. 2006). The 111 112 electrofishing was approved by National Fisheries Service permit number 630. 113 Each presence record was associated with the closest river segment in the GIS, thus building a presence database for species distribution modeling. Overall, 118 river segments had at least one presence record 114 115 (Fig. 1). The number of presences modeled for each species ranged between 9 and 39 (Table 1). We 116 considered other records (118 - n) as true absences in each generated model. Predictor variables 117 118 The predictor variables or features considered were: accumulated rainfall, catchment area, source-of-119 flow, altitude, slope, channel width, riparian vegetation percent, land-use, cross-channel construction, 120 and within-channel construction. All variables were grouped according to their origin (ecological variables 121 and anthropogenic variables) and their spatial scale (inter-basin, basin or segment) (Table 2). 122 Accumulated rainfall was obtained by relating the isolines of annual rainfall published by the Water 123 General Directorate (Dirección General de Aguas, Government of Chile), accumulated over the basin. 124 Catchment area was calculated with a DEM image of 1km × 1km (Landsat 7 images from 2015, 125 https://landsat.usgs.gov/) using the Hydrology package in of ArcGIS. Source-of-flow was obtained from 126 the published REC-Chile classification (Peredo-Parada et al., 2011). Altitude and slope were estimated 127 using the altitudes of the ends of each river segment, based on the DEM. Channel width, riparian 128 vegetation coverage, land-use, cross-channel construction, and within-channel construction were 129 estimated by visual analysis of Google Earth imagery. Channel width was calculated as the mean of three 130 points along the section. Riparian vegetation coverage was considered up to 50m distant from the 131 stream, with sections and land use percent considered up to 200m. Within-channel constructions 132 includes road parallel to the river, bank reinforcement, maintenance river channel, channelization, among 133 others. Cross-channel costructions include bridges, dams and intake structure.



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Model training and evaluation

We used three algorithms to estimate SDM for all seven species: random forest (RF) (Breiman, 2001), neural network (NNET) (Stern, 1996), and general lineal model (GLM) (McCullagh, 1984). These methods were chosen based on their good performance with presence and absence or pseudoabsences for species-distribution data (Mastrorillo et al., 1997; Cutler et al., 2007; Elith & Leathwick, 2009). RF uses a learning strategy, based on the generation of many classification trees, then aggregating their results in the final output (Breiman, 2001). NNET is derived from a simple model that mimics of the structure and function of the brain, and maximizes the prediction during the model-training phase by comparing actual outputs with desired outputs (Manel, Dias & Ormerod, 1999). GLM is a statistical model that predict values determined by discrete and continuous predictor variables and by the link function (e.g. logistic regression, Poisson regression) (Bolker et al., 2009). Using these different models allowed us to compare the performance of anthropogenic predictors in algorithms with different interpretation methods. Analysis was performed in R (v 2.3.3), using the Caret package (Kuhn, 2008). For all the algorithms and species, we first trained the models using 70% of the dataset randomly selected, and evaluated SDM final performance with the remaining 30%. Each model was trained using a 5-fold cross-validation scheme, except for the O. mauleanum (9 presences), where we used bootstrapping, due its low presences. During the training, imbalanced classes were corrected selecting a random sample (with replacement) of the minority class to be the same size as the majority class. For each specie, we trained 10 models with presences/absences resample of 70% of the original dataset. The final model was designated as the consensus of these 10 models based on the area under the curve (AUC) of the receiver operator characteristic (ROC). In order to assess model performance for each algorithm and species, we calculated the mean and confidence intervals of AUC (Fielding & Bell, 1997) and true skill statistic (TSS) (Allouche, Tsoar & Kadmon, 2006) using the 30% of observations separated at the beginning. TSS compares the number of correct forecasts, minus those attributable to random guessing, to that of a hypothetical set of perfect forecasts. In comparison, AUC is a single threshold-



160 using all possible thresholds to classify the scores into confusion matrices (Allouche, Tsoar & Kadmon, 161 2006). 162 For RF and NNET, the Caret R package was used to fitting and tuning. Many predictive and machine 163 learning models have structural or hyperparameters that cannot be directly estimated from the data. For 164 example, in the case of RF models, the classification trees may be built using a given number of randomly 165 selected predictors, which are named "mtry" (Kuhn & Johnson, 2013a). A hyperparameter such as mtry is 166 usually fixed at a given value when training and calibrating an RF model, which is an iterative optimization process itself. Hyperparameter tuning of an RF model refers to the grid search procedure that allows the 167 168 algorithm to find the best value of mtry to obtain the best model performance (given a set of calibration 169 and validation data points). In our implementation of RF models, the search for an optimal mtry value 170 spanned the space between 2 and 10 variables. Thus, the tuning process allowed us to explore a range of 171 values for the RF hyperparameter, further improving model performance. This generated a final model 172 with the best hyperparameter value for a given search grid (Kuhn & Johnson, 2013b). For NNET models, 173 two tuning hyperparameters were used. These were the weight decay for successive neural layers 174 ("decay") and the number of hidden units ("size"). The grid search procedure examined weight decay 175 values ranging between 4 and 6, while the number of hidden units was allowed to vary between 0.05 and 176 0.9. Both hyperparameter range are calibrated by trial and error process, optimizing the model 177 performance. GLM algorithms were optimized using a stepwise procedure for variable selection (Zhang, 2016), implemented with the "stepAIC" function (R MASS package in R v 2.3.3) (R Core Team, 2017). 178 179 Occurrence probabilities were categorized to presence/absence for all models. Thresholds were 180 determined so as to maximize the sum of sensitivity and specificity (MaxSens+Spec; PresenceAbsence 181 package in R v 2.3.3) (R Core Team, 2017). This criterion is independent of the theoretical prevalence 182 (Manel, Dias & Ormerod, 1999; Allouche, Tsoar & Kadmon, 2006), causing the distribution of rare species 183 to be overpredicted. In our particular case, the theoretical prevalence in the study area for all the species

independent measure for model performance obtained from ROC curves. These curves are constructed



is close to 0.5, but presences of our species are low, requiring a relaxation of this criterion when defining the threshold that allows for the definition of each of the species distribution across the studied watersheds.

In order to examine the predicted distribution for each species across the study area, each river segment was categorized into eight classes, according of the presence/absence results of each model: 1) no model selection as presence, presence determined by 2) only *Eco*, 3) only *Antr*, 4) *Eco+Antr*, 5) *Eco* and *Antr*, 6) *Eco* and *Eco+Antr*, 7) *Antr* and *Eco+Antr*, and 8) all models.

Relationship between fish size and models

In order to examine statistical effect of body size, log<sub>10</sub>-transformations of maximum length (*max. length*) were calculated for each species. *Max. length* was related with TSS and AUC. Also, *max. length* and the predictors variables for all (Eco, Antr and Eco+Antr) models was related by correlating its participation For

each models (Eco, Antr and Eco + Antr) the level of participation of their predictor variables was

correlated to the max. length. This relationship was corrected by the permutation procedure (Legendre &

#### **Biotope comparisons**

Legendre, 1998).

We compared *Eco*, *Antr*, and *Eco+Antr* biotopes generated for each species by using Venn diagrams.

Overlap of the ellipses in the Venn diagrams let us determine whether these models predicted the same observed river sections as shown by presence records. Non-overlapping of *Antr*, *Eco*, and *Eco+Antr* ellipses meant that at least one model predicted a different pattern of river segment occupation.

Geographic information was processed in QGIS software v 2.18.10 (QGIS, 2015). Models were executed and evaluated in R v 3.3.2 (R Core Team, 2017).



#### Comparison with prior research

206 We conducted a bibliographic review of research that used SDMs for assessing riverine fish, considering 207 three characteristics: 1) modeled groups of fish (n > 5); 2) used ecological and anthropogenic predictor 208 variables; and 3) had a river-segment-scale model grain. To compare results, we obtain the maximum 209 length of each modeled fish from Fishbase (Froese & Pauly, 2017). 210 Filipe, Cowx & Collares-Pereira (2002) indicated that percent of total correctly classified; percent of 211 presences correctly classified; and percent of absences correctly classified functioned as measurements 212 of fit. These were transformed to TSS for results comparisons. 213 In order to compare our results with previous studies, it was necessary to perform two statistical analyzes. The first analysis was compared result with TSS, while the second was compared result with 214 215 AUC. In both, we use an ANCOVA (Heiberger & Holland, 2013) with log<sub>10</sub>-transformed maximum length 216 for each species as covariable and the fit metric as the response variable. In the AUC test, the response 217 variable used a Box-Cox transformation (Box & Cox, 1964) to obtain normal residuals. Finally, for 218 comparing the number of records used per species, we used a Kruskall-Wallis test (Hollander & Wolfe, 219 1999) to compare all the papers at the same time. All analyses were done using R (R Core Team, 2017).

#### **RESULTS**

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#### TSS relates positively with size fishes

Results show that only in four species (*A. zebra*, *A. teniatus*, *P. Gillisi*, and *C. australe*) have good model

performances with AUC values greater than 0.75 (Table 1).

The TSS of the *Eco+Antr* models are related positively and marginally significant with fish sizes (R = 0.73, p

value = 0.06, p perm = 0.07). For *Antr* and *Eco* models, the relationships with fish size were not

significant, but there was a negative relationship between fish size, TSS and AUC values in the *Eco* 

models, and a positive relationship between fish size, TSS and AUC values in the Antr models.



Only "altitude" (*Eco+Antr* model: R = -0.72, p value = 0.06, p perm = 0.08; and *Eco* model: R = -0.71, p

value = 0.07, p perm = 0.09) and "slope" (*Eco* model: R = -0.74, p value = 0.06, p perm = 0.09) showed a

marginally significant and negative relationship with fish size (Table S3).

#### Variable scale determining its participation

Regarding variable participation, in the *Eco+Antr* and *Eco* models, the "accumulated rain" (regional scale) had the biggest average percent participation (82% and 77%, respectively), followed by "source-of-flow" (64% and 65%, respectively) and "catchment" (60% in both models). Source-of-flow and catchment were considered at the basin scale. Anthropogenic variables (segment scale) did not show important participation, except in the *Eco+Antr* models of *O. mauleanum*, *B. bullocki*, and *P. gillisi*. In these cases, land-use was the most important variable. In the other species, *Eco* and *Eco+Antr* models held the same important predictor variables (Figure 3). In *Antr* models, mean variable participation was: 77% to "cross-channel construction", 75% to "land-use" and 62% to "within-channel construction;" all variables at the segment scale.

In all models, except in *B. bullocki*, the *Antr* models represented over the 40% of the all biotopes predicted by all the models. In these cases, *Eco* and *Eco+Antr* models coincided in the most segments predicted in common by both models. All species models predicted presences over more than 50% of total river-distance (Figure 4).

#### Similar results to prior research

Our main results were compared with three previous pieces of research: Filipe, Cowx & Collares-Pereira (2002) (Sample unit = river lineal segment, Fit metric = TSS); Markovic, Freyhof & Wolter (2012) (Sample unit = pixel; Fit metric = AUC); and Radinger et al. (2017) (Sample unit = pixel; Fit metric = AUC).

In the TSS test, only the fish size covariate shows a significant relation, interacting positively (Appendix S1). In the AUC test, there is a significant difference in AUC values between both studies. In Radinger et al. (2017), the relationship between AUC and fish size is negative, opposite to what was shown by



Markovic, Freyhof & Wolter (2012) (Appendix S2). When we compared species presence numbers
between papers, the Kruskal-Wallis test reported significant differences (chi-squared = 54.52, df = 3, pvalue < 0.001). Markovic, Freyhof & Wolter (2012) worked with a greater number of presences (Markovic,
Freyhof & Wolter (2012), ☐ = 932.32 presences per species; the others papers, ☐ = 43.05 presences per
species) (Appendix S3).

#### **DISCUSSION**

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#### Fish size and model fit

The relationship between fish sizes and model performance can be summarized as follows. First, Eco+Antr models showed the best performance in larger fish species, while Antr models show a marginally significant trend. Secondly, SDM fitted for smaller fish species did not achieve good fits, regardless of hyperparameter grid search procedure used to optimize the machine learning algorithms or the stepwise procedure used for GLM. A third emerging pattern is that performance to smaller fish species in Eco models improves slightly, without achieving good fit. As mentioned earlier, these body-size effects on SDM performance have been demonstrated in a few previous studies, despite the expected theoretical relationship (McPherson & Jetz, 2007). For example, Morán-Ordóñez et al. (2017) found no relationship between body size and model performance for trees and birds. França & Cabral (2016) successfully related model performance to species feeding mode and estuarine functional groups, with little involvement of body size in the relationship. In studies aimed at river fish, both Radinger et al. (2017) and Filipe, Cowx & Collares-Pereira (2002) found that fish size increased model performance, which coincides with our main results. However, Markovic, Freyhof & Wolter (2012) did not find this pattern. The main difference between those studies is the number of presences used in each model. The observed correlation between fish size and the model fits might be explained by this difference. Identifying pattern distributions for small fishes is more difficult due to small homes range and other considerations (McPherson & Jetz, 2007), but we could get better model results for small fishes when we



increased the number of presences for model calibration and validation, as suggested by Stockwell & 276 277 Peterson (2002) and done by Markovic, Freyhof & Wolter (2012). 278 Our results are even more relevant in regions where the entire fish community is particularly small, like in 279 Chile (Vila et al., 2006). Moreover, in Chile there are no SDM reports for fish implemented with more 280 than 100 presences as in Markovic, Freyhof & Wolter (2012). In that case, one option is to obtain 281 predictor variables at a lower spatial resolution. In general, Radlinger et al. (2017) achieved good 282 performances with a pixel resolution of 250m, using secondary variables as predictors in a 1,094 km long 283 basin. So, methodology of Radlinger et al. (2017) could apply in Chile. Since Chilean rivers are 150 km 284 long aprox, selection of predictor variables of Radlinger et al. (2017) should be adjust to small basins, as 285 our case. 286 To develop models that perform well in small basins, besides incorporating predictor variables at 287 different spatial scales, as we did, in further research we recommend incorporating different 288 hydromorphological features to our variable set at the reach scale, such as sediment type or 289 morphological classification and anthropogenic variables related to industrial development, like pollution 290 or water extraction, that would play significant roles in riverine ecology according to the literature 291 (Torgersen et al., 1999; Lange et al., 2014; Ramezani et al., 2016). For example, T. areolatus shows 292 preferences for river bedrock, so we would expect that the incorporation of the "sediment type" variable 293 would improve the model performance. 294 We found two important results, but non-significant tendencies: Smaller fishes have better fit in Eco 295 models, and larger fishes have better fit in Antr models. This pattern can be explained by fish home 296 ranges. Larger fishes are expected to be substantially restricted by movement barriers, given an ability to 297 disperse farther than small fishes (Radinger & Wolter, 2015; Radinger et al., 2017), and so they respond 298 better to Antr variables. Conversely, the lower dispersal ability of smaller fishes implies a slower response 299 to anthropogenic drivers (Radinger & Wolter, 2015; Radinger et al., 2017), so it is better modeled with



Eco variables, since these variables project a potential distribution without anthropogenic interventions. 300 301 These results are coherent with current literature and shows the differential relationship between anthropogenic pressure and fish size (Radinger et al., 2017). 302 303 Altitude (in Eco+Antr and Eco models) and slope (in Eco+Antr models) were the predictor variables 304 associated to body size: for large fishes, altitude and slope weren't important for model fit. This 305 relationship between altitude and body size was also reported by Markovic, Freyhof & Wolter (2012) (r =306 -0.48, p value = 0.03). We associate this result to river turbulence, since large fishes better resist 307 turbulence (Lupandin, 2005), which is often greater at higher altitudes and higher slopes (Elliott, 2010). 308 This resistance would indicate that altitude and slope are not relevant environmental filters in habitat 309 selection among larger fishes, decreasing its participation in these SDMs. Participation by predictor variable 310 311 On the Eco+Antr and Eco models, regardless fish size, the relevance by predictor variable for all models 312 responded to the hierarchical framework of stream habitat proposed in literature (Frissell et al., 1986; 313 Snelder & Biggs, 2002; Creque, Rutherford & Zorn, 2005; Steen et al., 2008; Peredo-Parada et al., 2011), and while predictor variables (or landscape filters) at bigger scales have more participation in the models, 314 315 as the geographical scale of the variables decreases, so does its participation in the model, and their 316 importance is resolved species by species. 317 While accumulated rain structures the landscape from east to west (from mountain to ocean), and from 318 north to south (greater precipitation to the South), source-of-flow represents territorial particularities, 319 like glaciers, lakes, and valleys. In this way, both variables summarize much of the spatial variability of 320 both basins, having more participation in the majority of Eco+Antr and Eco models. 321 We want to highlight the use in our study of source-of-flow as a predictor variable, which is not found in 322 any research of river species modelling (Filipe, Cowx & Collares-Pereira, 2002; Chu, Mandrak & Minns, 323 2005; Steen et al., 2008; Markovic, Freyhof & Wolter, 2012; Jähnig et al., 2012; Domisch et al., 2013;



Elliott et al., 2015; Pletterbauer, Graf & Schmutz, 2016; Radinger et al., 2017; Taylor, Papeş & Long, 2017), 324 325 especially in torrential basins like those found in Chile, which have short runs, with relatively large lakes, 326 glaciers, or salt pans that significantly affect hydrological and hydraulic conditions. Source-of-flow variable is implement in river of New Zealand (Snelder & Biggs, 2002) and Chile (Peredo-Parada et al., 327 328 2011) what would facilitate its use in SDMs. 329 In Antr models, that within-channel construction generating a direct impact in the reach, Land-Use and 330 cross-channel construction were the anthropogenic variables with the most participation in the Antr and 331 Eco+Antr models. We relate this result to impact scale of within-channel construction. This variable 332 frequently represents a proxy of intervention at reach scale, and since the model grain was the segment 333 scale, the model resolution probably was unable to completely capture the impacts to reach scale. 334 In the current context of river species modeling, there is no broad agreement on predictor variables for 335 modeling, unlike terrestrial species modeling, where Bioclim is the most used spatially database for 336 predictor variables (Booth et al., 2014). In case of river species models, consideration of hierarchical, 337 longitudinal, lateral and vertical river links to select predictors (Domisch et al., 2015) is necessary, and the 338 most of riverine predictor variables are correlated theoretical and statistically (Leopold, 1969; Elliott, 339 2010). This makes the number of potential predictors of a riverine freshwater SDM very high, and allow 340 that many of these variables can be change by proxies, diversifying hugely the predictor selected 341 between papers. For example, many authors have used common proxies for river temperature, discharge 342 and turbulence, like altitude, flow accumulation, slope, catchment, among others (Filipe, Cowx & 343 Collares-Pereira, 2002; Markovic, Freyhof & Wolter, 2012; Elliott et al., 2015; Pletterbauer, Graf & 344 Schmutz, 2016; Radinger et al., 2017; Taylor, Papeş & Long, 2017), but there is no general agreement in 345 the literature as to which proxy to use. This ecological context hindering to systematic use of any variable 346 as predictor, and the lack of an agreement between researchers difficult to compare results between 347 them. This problem should be resolve in a future, increasing consensus in terms of predictor variables selection. 348



#### Spatial patterns of distribution

350 We interpret the biotope overprediction of Antr models for six from seven species models as a 351 consequence of statistic structure of the Antr variable predictors. Land-use is categorical variable, and the 352 others are discrete variable with low variability (maximum number of within-channel construction: 8, 353 maximum number of cross-channel construction: 10), and the segment percent without interventions 354 (exclusively natural land use, and without any intervention that cross the river or within the river) is 51%. 355 Thus, when the models relate the presence of any species with little disturbed segment, the number of 356 river segment matching this condition is very high, increasing the biotope in comparison to the Eco+Antr 357 and Eco models. Regrettably, we do not find other research where modeled only with anthropogenic 358 variables, so we cannot compare our results with current literature. 359 The great coincidence between the biotopes generated by the Eco+Antr and Eco models was unexpected, 360 since Eco biotopes were expected to be bigger than Eco+Antr biotopes, as reported in Taylor, Papeş & 361 Long (2017), since the Eco models estimate potential niche, while Eco+Antr models estimate realized 362 niche, with the former always larger than the latter (Jackson & Overpeck, 2009). While, the Bueno and 363 Valdivia River basins have significant levels of anthropogenic pressures, these are apparently insufficient 364 for to change the projected biotopes in under the Eco+Antr models. This result provides an optimistic 365 view of the environmental conditions for the presence of threatened fishes in the Valdivia and Bueno 366 River basins.

#### **CONCLUSIONS**

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SDM performance for small fish was found to be less accurate due to modelling grain of variable predictors, but would this effect can be alleviated by increasing the number of presences. When ecological and anthropogenic variables were considered together, ecological variables at the higher spatial scale were more relevant than predictor variables at the lower spatial scale, adjusting them to the hierarchical stream framework of Frissell et. al. (1986). Source-of-flow was found as a novel predictor



variable at the basin scale, with an important participation in the models of different sized fishes. High

coincidence between the biotopes generated by *Eco+Antr* and *Eco* models, suggest that Bueno and

Valdivia River basins have low anthropogenic interventions. We found evidence of how physiological

characteristics determine SDM performance. This research serves as a base for future studies of river fish

modelling in a particular ecological context, with relatively small fishes in moderately intervened,

relatively short, torrential river basins.

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#### FIGURE LEGENDS

**Figura 1.** Study area.

**Figure 2.** Relationship between model fit and size fishes (Log<sub>10</sub> of maximum length). Fit index is area under the curve (AUC) of the receiver operating characteristic (ROC) and the true skill statistic (TSS). *Eco* (model with only ecological predictors), *Antr* (only anthropogenic predictors), *Eco+Antr* (both sets of predictors). Solid line represents the significant relationships.

**Figure 3.** Participation of predictor variables in each model by species. From left to right, the first five anthropogenic variables that only participate in *Antr* models and *Eco+Antr* models, the second ten ecological variables that only participate in *Eco* models, and *Eco+Antr* models. Categories with suffix "use" belong to the land-use predictor, and categories with suffix F.S. belong to source-of-flow predictor.

**Figure 4.** Maps of potential distribution by species and model. Each map represents the distribution of one species. Each color represents which model or sets of models determined a species present in each river section.

**Figure 5**. Venn diagrams representing the river sections defined as having species presence by the different models that coincided in the same river segments for each species. For example, if the *Antr*, *Eco*, and *Eco+Antr* circles completely overlap, the three models selected exactly the same river segments as having species presence. The percentages of river kilometers determined as having species presence by each the model is noted for each species.

#### TABLE LEGENDS

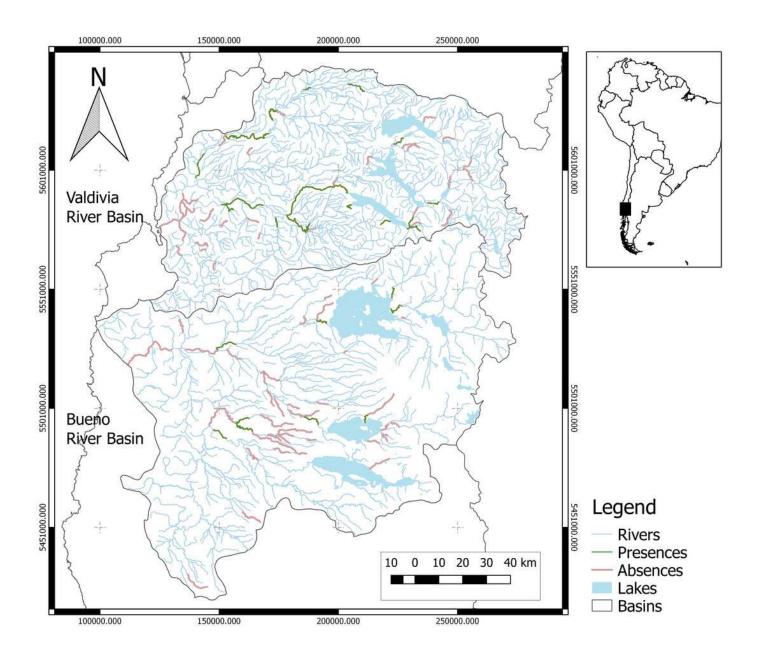
Table 1. Modeled species, modeled presences, and TSS and AUC values for each model with different setpredictors.



- 577 Table 2. Predictor variables used in SDMs, indicating variable type (ecological or anthropogenic), spatial
- 578 categories, statistical description, and mean participation by models with different set predictor
- 579 variables.



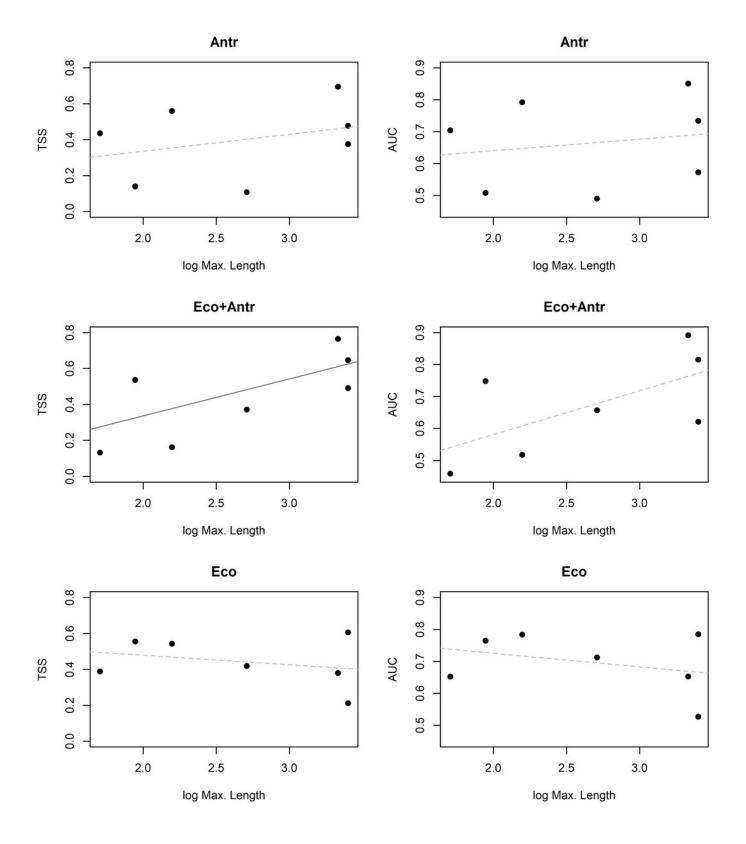
Study area





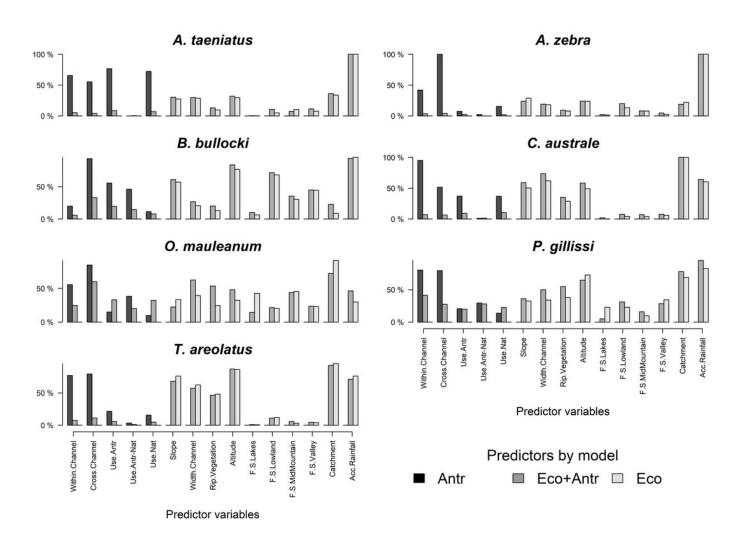
Relationship between model fit and size fishes ( $Log_{10}$  of maximum length). Fit index is area under the curve (AUC) of the receiver operating characteristic (ROC) and the true skill statistic (TSS). *Eco* (model with only ecological predictors





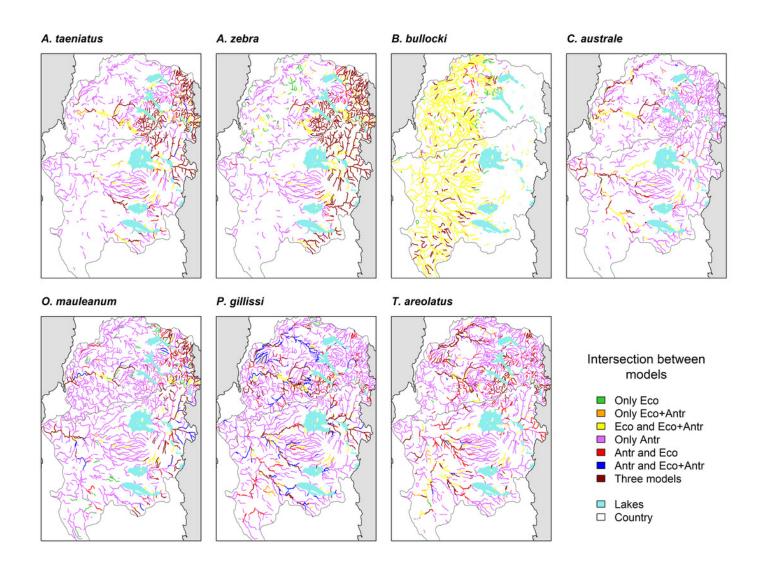


Participation of predictor variables in each model by species. From left to right, the first five anthropogenic variables that only participate in *Antr* models and *Eco+Antr* models, the second ten ecological variables that only participate in [i





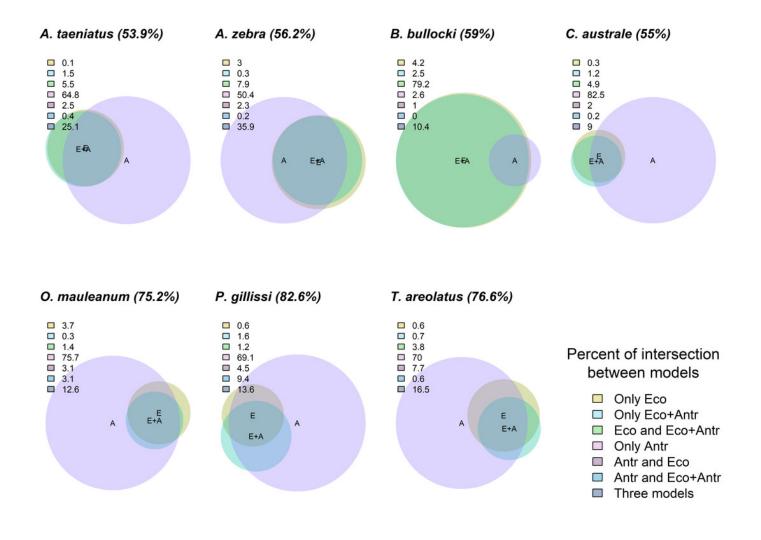
Maps of potential distribution by species and model. Each map represents the distribution of one species. Each color represents which model or sets of models determined a species present in each river section.





Venn diagrams representing the river sections defined as having species presence by the different models that coincided in the same river segments for each species.

For example, if the *Antr*, *Eco*, and *Eco+Antr* circles completely overlap, the three models selected exactly the same river segments as having species presence. The percentages of river kilometers determined as having species presence by each the model is noted for each species





#### Table 1(on next page)

Modeled species, modeled presences, and TSS and AUC values for each model with different set predictors.

1 Table 1. Modeled species, modeled presences, and TSS and AUC values for each model with different set predictors.

Species	Distribution in Chile	Max. Length (cm)	Presences	Algorithms selected	Antr AUC	Antr TSS	Eco+Antr AUC	Eco+Antr TSS	Eco AUC	Eco TSS
Aplochiton taeniatus <sup>1</sup>	38° - 55° Lat. S	30	17	RF	0.73	0.48	0.82	0.65	0.79	0.61
Aplochiton zebra²	35.88° - 55° Lat. S	28	15	RF	0.85	0.69	0.89	0.77	0.65	0.38
Brachygalaxias bullocki <sup>3</sup>	35.88° - 43.81° Lat. S	5.5	27	GLM	0.70	0.44	0.46	0.13	0.65	0.39
Cheirodon australe <sup>4</sup>	39.32° - 43.81° Lat. S	7	21	RF	0.51	0.14	0.75	0.54	0.76	0.56
Odontesthes mauleanum <sup>5</sup>	32.25° - 43.81° Lat. S	30	9	NNET	0.57	0.38	0.62	0.49	0.53	0.21
Percilia gillissi <sup>6</sup>	32.25° - 43.81° Lat. S	9	33	NNET	0.79	0.56	0.52	0.16	0.78	0.54
Trichomycterus areolatus <sup>7</sup>	29.13° - 43.81° Lat. S	15	36	RF	0.49	0.11	0.66	0.37	0.71	0.42

2 Reference to fish size:

3 <sup>1</sup> Ministerio del Medio Ambiente (2011a)

4 <sup>2</sup> Ministerio del Medio Ambiente (2011b)

5 <sup>3</sup> Ministerio del Medio Ambiente (2008d)

<sup>4</sup> Ministerio del Medio Ambiente (2008a)

7 <sup>5</sup> Ministerio del Medio Ambiente (2008b)

8 <sup>6</sup> Froese & Pauly (2017)

9 <sup>7</sup> Ministerio del Medio Ambiente (2008c)

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### Table 2(on next page)

Predictor variables used in SDMs, indicating variable type (ecological or anthropogenic), spatial categories, statistical description, and mean participation by models with different set predictor variables

- 1 Table 2. Predictor variables used in SDMs, indicating variable type (ecological or anthropogenic), spatial categories, statistical description, and
- 2 mean participation by models with different set predictor variables.

Predictive Variable	Туре	Spatial Scale	Unit	Description	Variable participation		
		Jeane			Antr	Eco+Antr	Eco
Accumulated rainfall	Ecological	inter-basin	mm	Min: 954			
				Median: 2302			
				Max: 5099159		81.5	77.8
Catchment	Ecological	intra-basin	km2	Min: 0.11			
				Median: 38.022			
				Max: 15033		60.1	60.0
Source-of-flow	Ecological	intra-basin	Categories: lake,	lake: 163			
			glacier,	Plains: 891			
			mountian,	Foothills: 538			
			foothills, valley,	Valley: 619			
			plains			75.7	35.9
Altitude	Ecological	intra-basin	m.a.s.l.	Min: 2			
				Median: 264			
				Max: 1751		56.8	52.9
Slope	Ecological	Inter-	m/m	Min: 0			
		segment		Median: 0.018			
				Max: 3		43.0	43.7
Channel width	Ecological	Inter-	m	Min: 1			
		segment		Median: 8			
				Max: 1500		45.6	38.0
Percent riparian	Ecological	Inter-	%	Min: 0			
vegetation		segment		Median: 182			
				Max: 200		33.2	24.3
Segment land-use	Anthropic	Inter-	Categories	Antr: 371			
		segment		Antr_Nat: 189			
				Nat: 1252	75.7	35.9	
Cross-channel	Anthropic	Inter-	Number of	Min: 0			
constructions		segment	Works	Median: 0	62.2	13.7	



					Max: 8			
Within-channel	Anthropic	Inter-	Number	of	Min: 0			
constructions		segment	Works		Median: 0			
					Max: 10	77.7	20.9	