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

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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.

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

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## KEYWORDS

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

## ABSTRACT

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.

## INTRODUCTION

Species distribution models (SDM) provide an important management tool to support conservation planning. SDMs generate species distribution maps that allow for more efficient and effective field inventories, suggest sites of high potential occurrence of rare species for survey planning, and permit testing biogeographical, ecological and evolutionary hypotheses (Guisan \& Thuiller, 2005). Given these advantages, different international organizations (e.g., UNEP, Conservation International, IUCN, WWF) have employed SDM to address key policy objectives at a global scale (Cayuela et al., 2009).

Different species traits have been shown to influence model performance (Brotons et al., 2004; Segurado \& Araújo, 2004; McPherson \& Jetz, 2007; França \& Cabral, 2016). One important trait is body size (Radinger et al., 2017). Larger species detect less food but can tolerate lower resource concentrations within their food, while smaller species detect more food, but require higher resource concentrations within it (Ritchie, 1998; Ritchie \& Olff, 1999). As a result, larger species have larger home ranges than 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). First, species with larger home ranges may perceive the environment at coarser scales, improving the 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 balance between presences and absences (McPherson, Jetz \& Rogers, 2004). In addition, species with local adaptations in habitat preferences may generate models that overestimate their ecological niches (Stockwell \& Peterson, 2002). To date, the effect of body size on distribution models has been tested in different taxa with unclear results (e.g. M. McPherson \& Jetz, 2007; França \& Cabral, 2016; MoránOrdóñez et al., 2017; Radinger et al., 2017).

In the case of fish, Radinger et. al. (2017) indicate that smaller-body fishes are less sensitive to anthropogenic intervention in the river network, due to their smaller home ranges. However, their study did not explicitly test variation in model performance in response to fish size. Recent research on fish species distribution models has shown that species with different body sizes are impacted differently by the same sets of environmental features derived from anthropogenic activities (Perry et al., 2005; Radinger et al., 2017). A relevant research question is whether SDM performance or accuracy for different body-sized fishes vary in the same manner when considering different predictor variable sets, such as i) ecological predictors, ii) anthropogenic predictors, and iii) ecological and anthropogenic predictors.

The ichthyofauna in Chile comprises a total of 44 species, including two lampreys (Habit, Dyer \& Vila, 2006), and is characterized as being highly endemic, adapted to high slope rivers, and with small body sizes (Vila, Fuentes \& Contreras, 1999; Vila et al., 2006; Habit, Dyer \& Vila, 2006). Despite its high biogeographic value, the Chilean ichthyofauna is broadly endangered, with only two species (Cheirodon australe y Mugil cephalus) classified as non-endangered. In Chile, anthropogenic variables represent the main group of threats to river fishes (Habit et al., 2002, 2006). Therefore, understanding the potential
impact of body size on SDM performance is highly relevant for conservation and management planning 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 species studied; and (3) to compare our results with model performances in previous studies.

## METHODS

## Study area and modeled species

The study area covers the Valdivia and the Bueno river basins, located in the central-southern zone of Chile, between the parallels $39.33^{\circ}$ and $41.08^{\circ} \mathrm{S}$ (Figure 1). The Valdivia River basin has a pluvial 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 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 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, 2009), and Arc GIS version 9.2 (ESRI, 2010).

Our study included seven freshwater fish species (Table 1): Aplochiton taeniatus (Jenyns, 1842), Aplochiton zebra (Jenyns, 1842), Brachygalaxias bullocki (Regan, 1908), Cheirodon australe (Eigenmann, 1928), Odontesthes mauleanum (Steindachner, 1896), Percilia gillissi (Girard, 1855), and Trichomycterus areolatus (Valenciennes, 1846). Statistical analysis of the effect of body size was carried out using theoretical species maximum length, which is available for all these species. Most maximum length estimates were obtained from official species descriptions provided in each species conservation assessment developed by the Chilean Ministry of the Environment (Table 1). The only exception was B. bullocki, which had not been assessed by the Ministry of Environment, and whose maximum length was obtained from Fishbase (Froese \& Pauly, 2017) (Table S1).

This species was selected because represent a good size gradient (between 5.5 cm and 30 cm ) (Table 1) to Chilean species case, and particularly all this species encompasses completely the latitudinal range of both basins (Table 1), situation that allow comparing model performance without the distribution range by specie affect in the predicted distribution.

## Modeling methods

## Species occurrence data

Historical records of the presences of the study species were obtained from the Ministry of the Environment's (Ministerio del Medio Ambiente, Government of Chile) database on freshwater organisms. This database was generated by collecting published databases of scientific samples in the study area (Ministerio de Energía - División de Desarrollo Sustentable, 2016).

In addition, a field sampling campaign was conducted in the study area to complement existing information in the government database. The sampling was done between December 2015 and January 2016, using electrofishing equipment (SAMUS, model 745G). We collected all fish along a 100-meter 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 electrofishing was approved by National Fisheries Service permit number 630.

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 (Fig. 1). The number of presences modeled for each species ranged between 9 and 39 (Table 1). We considered other records ( $118-\mathrm{n}$ ) as true absences in each generated model.

## Predictor variables

The predictor variables or features considered were: accumulated rainfall, catchment area, source-offlow, altitude, slope, channel width, riparian vegetation percent, land-use, cross-channel construction, and within-channel construction. All variables were grouped according to their origin (ecological variables and anthropogenic variables) and their spatial scale (inter-basin, basin or segment) (Table 2).

Accumulated rainfall was obtained by relating the isolines of annual rainfall published by the Water General Directorate (Dirección General de Aguas, Government of Chile), accumulated over the basin. Catchment area was calculated with a DEM image of $1 \mathrm{~km} \times 1 \mathrm{~km}$ (Landsat 7 images from 2015, https://landsat.usgs.gov/) using the Hydrology package in of ArcGIS. Source-of-flow was obtained from the published REC-Chile classification (Peredo-Parada et al., 2011). Altitude and slope were estimated using the altitudes of the ends of each river segment, based on the DEM. Channel width, riparian vegetation coverage, land-use, cross-channel construction, and within-channel construction were estimated by visual analysis of Google Earth imagery. Channel width was calculated as the mean of three points along the section. Riparian vegetation coverage was considered up to 50 m distant from the stream, with sections and land use percent considered up to 200m. Within-channel constructions includes road parallel to the river, bank reinforcement, maintenance river channel, channelization, among others. Cross-channel cnstructions include bridges, dams and intake structure.

## 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 0 . 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-
independent measure for model performance obtained from ROC curves. These curves are constructed using all possible thresholds to classify the scores into confusion matrices (Allouche, Tsoar \& Kadmon, 2006).

For RF and NNET, the Caret R package was used to fitting and tuning. Many predictive and machine learning models have structural or hyperparameters that cannot be directly estimated from the data. For example, in the case of RF models, the classification trees may be built using a given number of randomly selected predictors, which are named " $m$ try" (Kuhn \& Johnson, 2013a). A hyperparameter such as mtry is 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 algorithm to find the best value of mtry to obtain the best model performance (given a set of calibration and validation data points). In our implementation of RF models, the search for an optimal mtry value spanned the space between 2 and 10 variables. Thus, the tuning process allowed us to explore a range of values for the RF hyperparameter, further improving model performance. This generated a final model with the best hyperparameter value for a given search grid (Kuhn \& Johnson, 2013b). For NNET models, two tuning hyperparameters were used. These were the weight decay for successive neural layers ("decay") and the number of hidden units ("size"). The grid search procedure examined weight decay values ranging between 4 and 6 , while the number of hidden units was allowed to vary between 0.05 and 0.9. Both hyperparameter range are calibrated by trial and error process, optimizing the model 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).

Occurrence probabilities were categorized to presence/absence for all models. Thresholds were determined so as to maximize the sum of sensitivity and specificity (MaxSens+Spec; PresenceAbsence package in R v 2.3.3) ( R Core Team, 2017). This criterion is independent of the theoretical prevalence (Manel, Dias \& Ormerod, 1999; Allouche, Tsoar \& Kadmon, 2006), causing the distribution of rare species to be overpredicted. In our particular case, the theoretical prevalence in the study area for all the species
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, $\log _{10}$-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 \& Legendre, 1998).

## Biotope comparisons

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

We conducted a bibliographic review of research that used SDMs for assessing riverine fish, considering three characteristics: 1) modeled groups of fish ( $n>5$ ); 2) used ecological and anthropogenic predictor variables; and 3) had a river-segment-scale model grain. To compare results, we obtain the maximum length of each modeled fish from Fishbase (Froese \& Pauly, 2017).

Filipe, Cowx \& Collares-Pereira (2002) indicated that percent of total correctly classified; percent of presences correctly classified; and percent of absences correctly classified functioned as measurements of fit. These were transformed to TSS for results comparisons.

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 AUC. In both, we use an ANCOVA (Heiberger \& Holland, 2013) with $\log _{10}$-transformed maximum length for each species as covariable and the fit metric as the response variable. In the AUC test, the response variable used a Box-Cox transformation (Box \& Cox, 1964) to obtain normal residuals. Finally, for comparing the number of records used per species, we used a Kruskall-Wallis test (Hollander \& Wolfe, 1999) to compare all the papers at the same time. All analyses were done using $R$ ( $R$ Core Team, 2017).

## RESULTS

## 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: $\mathrm{R}=-0.72$, p value $=0.06$, p perm $=0.08$; and $E$ co model: $\mathrm{R}=-0.71$, p value $=0.07$, p perm $=0.09$ ) and "slope" (Eco model: $\mathrm{R}=-0.74, \mathrm{p}$ value $=0.06, \mathrm{p}$ 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 "crosschannel 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 $=54.52, \mathrm{df}=3, \mathrm{p}$ value < 0.001). Markovic, Freyhof \& Wolter (2012) worked with a greater number of presences (Markovic, Freyhof \& Wolter (2012), $\square=932.32$ presences per species; the others papers, $\square=43.05$ presences per species) (Appendix S3).

## DISCUSSION

## 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 \& Peterson (2002) and done by Markovic, Freyhof \& Wolter (2012) .

Our results are even more relevant in regions where the entire fish community is particularly small, like in Chile (Vila et al., 2006). Moreover, in Chile there are no SDM reports for fish implemented with more than 100 presences as in Markovic, Freyhof \& Wolter (2012). In that case, one option is to obtain predictor variables at a lower spatial resolution. In general, Radlinger et al. (2017) achieved good performances with a pixel resolution of 250 m , using secondary variables as predictors in a 1,094 km long basin. So, methodology of Radlinger et al. (2017) could apply in Chile. Since Chilean rivers are 150 km long aprox, selection of predictor variables of Radlinger et al. (2017) should be adjust to small basins, as our case.

To develop models that perform well in small basins, besides incorporating predictor variables at different spatial scales, as we did, in further research we recommend incorporating different hydromorphological features to our variable set at the reach scale, such as sediment type or morphological classification and anthropogenic variables related to industrial development, like pollution or water extraction, that would play significant roles in riverine ecology according to the literature (Torgersen et al., 1999; Lange et al., 2014; Ramezani et al., 2016). For example, T. areolatus shows preferences for river bedrock, so we would expect that the incorporation of the "sediment type" variable would improve the model performance.

We found two important results, but non-significant tendencies: Smaller fishes have better fit in Eco models, and larger fishes have better fit in Antr models. This pattern can be explained by fish home ranges. Larger fishes are expected to be substantially restricted by movement barriers, given an ability to disperse farther than small fishes (Radinger \& Wolter, 2015; Radinger et al., 2017), and so they respond better to Antr variables. Conversely, the lower dispersal ability of smaller fishes implies a slower response 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. These results are coherent with current literature and shows the differential relationship between anthropogenic pressure and fish size (Radinger et al., 2017).

Altitude (in Eco+Antr and Eco models) and slope (in Eco+Antr models) were the predictor variables associated to body size: for large fishes, altitude and slope weren't important for model fit. This relationship between altitude and body size was also reported by Markovic, Freyhof \& Wolter (2012) (r = $-0.48, p$ value $=0.03)$. We associate this result to river turbulence, since large fishes better resist turbulence (Lupandin, 2005), which is often greater at higher altitudes and higher slopes (Elliott, 2010). This resistance would indicate that altitude and slope are not relevant environmental filters in habitat selection among larger fishes, decreasing its participation in these SDMs.

## Participation by predictor variable

On the Eco+Antr and Eco models, regardless fish size, the relevance by predictor variable for all models responded to the hierarchical framework of stream habitat proposed in literature (Frissell et al., 1986; 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, as the geographical scale of the variables decreases, so does its participation in the model, and their importance is resolved species by species.

While accumulated rain structures the landscape from east to west (from mountain to ocean), and from north to south (greater precipitation to the South), source-of-flow represents territorial particularities, like glaciers, lakes, and valleys. In this way, both variables summarize much of the spatial variability of both basins, having more participation in the majority of Eco+Antr and Eco models.

We want to highlight the use in our study of source-of-flow as a predictor variable, which is not found in any research of river species modelling (Filipe, Cowx \& Collares-Pereira, 2002; Chu, Mandrak \& Minns, 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), especially in torrential basins like those found in Chile, which have short runs, with relatively large lakes, 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., 2011) what would facilitate its use in SDMs.

In Antr models, that within-channel construction generating a direct impact in the reach, Land-Use and cross-channel construction were the anthropogenic variables with the most participation in the Antr and Eco+Antr models. We relate this result to impact scale of within-channel construction. This variable frequently represents a proxy of intervention at reach scale, and since the model grain was the segment scale, the model resolution probably was unable to completely capture the impacts to reach scale.

In the current context of river species modeling, there is no broad agreement on predictor variables for modeling, unlike terrestrial species modeling, where Bioclim is the most used spatially database for predictor variables (Booth et al., 2014). In case of river species models, consideration of hierarchical, longitudinal, lateral and vertical river links to select predictors (Domisch et al., 2015) is necessary, and the most of riverine predictor variables are correlated theoretical and statistically (Leopold, 1969; Elliott, 2010). This makes the number of potential predictors of a riverine freshwater SDM very high, and allow that many of these variables can be change by proxies, diversifying hugely the predictor selected between papers. For example, many authors have used common proxies for river temperature, discharge and turbulence, like altitude, flow accumulation, slope, catchment, among others (Filipe, Cowx \& Collares-Pereira, 2002; Markovic, Freyhof \& Wolter, 2012; Elliott et al., 2015; Pletterbauer, Graf \& Schmutz, 2016; Radinger et al., 2017; Taylor, Papeş \& Long, 2017), but there is no general agreement in the literature as to which proxy to use. This ecological context hindering to systematic use of any variable as predictor, and the lack of an agreement between researchers difficult to compare results between them. This problem should be resolve in a future, increasing consensus in terms of predictor variables selection.

## Spatial patterns of distribution

We interpret the biotope overprediction of Antr models for six from seven species models as a consequence of statistic structure of the Antr variable predictors. Land-use is categorical variable, and the others are discrete variable with low variability (maximum number of within-channel construction: 8, maximum number of cross-channel construction: 10), and the segment percent without interventions (exclusively natural land use, and without any intervention that cross the river or within the river) is $51 \%$. Thus, when the models relate the presence of any species with little disturbed segment, the number of river segment matching this condition is very high, increasing the biotope in comparison to the Eco+Antr and Eco models. Regrettably, we do not find other research where modeled only with anthropogenic variables, so we cannot compare our results with current literature.

The great coincidence between the biotopes generated by the Eco+Antr and Eco models was unexpected, since Eco biotopes were expected to be bigger than Eco+Antr biotopes, as reported in Taylor, Papeş \& Long (2017), since the Eco models estimate potential niche, while Eco+Antr models estimate realized niche, with the former always larger than the latter (Jackson \& Overpeck, 2009). While, the Bueno and Valdivia River basins have significant levels of anthropogenic pressures, these are apparently insufficient for to change the projected biotopes in under the Eco+Antr models. This result provides an optimistic view of the environmental conditions for the presence of threatened fishes in the Valdivia and Bueno River basins.

## CONCLUSIONS

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 ( $\log _{10}$ 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), 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 set predictors.

Table 2. 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.

## Figure 1

Study area


## Figure 2

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


## 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 [i


## 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
A. taeniatus (53.9\%)

O. mauleanum (75.2\%)

A. zebra (56.2\%)

P. gillissi (82.6\%)

B. bullocki (59\%)


## T. areolatus (76.6\%)


C. australe (55\%)


Percent of intersection between modelsOnly Eco
Only Eco+Antr E Eco and Eco+Antr $\square$ Only Antr
$\square$ Antr and Eco
$\square$ Antr and Eco+Antr
$\square$ Three models

## Table $\mathbf{1}_{\text {(on next page) }}$

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 | $\begin{aligned} & \hline \text { Antr } \\ & \text { AUC } \end{aligned}$ | $\begin{aligned} & \hline \text { Antr } \\ & \text { TSS } \end{aligned}$ | $\begin{aligned} & \text { Eco+Antr } \\ & \text { AUC } \end{aligned}$ | $\begin{aligned} & \text { Eco+Antr } \\ & \text { TSS } \end{aligned}$ | $\begin{aligned} & \hline \text { Eco } \\ & \text { AUC } \end{aligned}$ | $\begin{aligned} & \hline \text { Eco } \\ & \text { TSS } \end{aligned}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Aplochiton taeniatus ${ }^{1}$ | $38^{\circ}-55^{\circ}$ Lat. S | 30 | 17 | RF | 0.73 | 0.48 | 0.82 | 0.65 | 0.79 | 0.61 |
| Aplochiton zebra² | $35.88^{\circ}-55^{\circ}$ Lat. S | 28 | 15 | RF | 0.85 | 0.69 | 0.89 | 0.77 | 0.65 | 0.38 |
| Brachygalaxias bullocki ${ }^{3}$ | 35.88 ${ }^{\circ}-43.81^{\circ}$ Lat. S | 5.5 | 27 | GLM | 0.70 | 0.44 | 0.46 | 0.13 | 0.65 | 0.39 |
| Cheirodon australe ${ }^{4}$ | 39.32 ${ }^{\circ}-43.81^{\circ}$ Lat. S | 7 | 21 | RF | 0.51 | 0.14 | 0.75 | 0.54 | 0.76 | 0.56 |
| Odontesthes mauleanum ${ }^{5}$ | $32.25^{\circ}-43.81^{\circ}$ Lat. S | 30 | 9 | NNET | 0.57 | 0.38 | 0.62 | 0.49 | 0.53 | 0.21 |
| Percilia gillissi ${ }^{6}$ | $32.25{ }^{\circ}-43.81^{\circ}$ Lat. S | 9 | 33 | NNET | 0.79 | 0.56 | 0.52 | 0.16 | 0.78 | 0.54 |
| Trichomycterus areolatus ${ }^{7}$ | 29.13 ${ }^{\circ}-43.81^{\circ}$ Lat. S | 15 | 36 | RF | 0.49 | 0.11 | 0.66 | 0.37 | 0.71 | 0.42 |

2 Reference to fish size:
$3{ }^{1}$ Ministerio del Medio Ambiente (2011a)
${ }^{2}$ Ministerio del Medio Ambiente (2011b)
${ }^{3}$ Ministerio del Medio Ambiente (2008d)
${ }^{4}$ Ministerio del Medio Ambiente (2008a)
${ }^{5}$ Ministerio del Medio Ambiente (2008b)
${ }^{6}$ Froese \& Pauly (2017)
${ }^{7}$ Ministerio del Medio Ambiente (2008c)

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


|  |  |  |  | Max: 8 |  |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Within-channel <br> constructions | Anthropic of | Inter- <br> segment | Number <br> Works <br> Median: 0 <br> Max: 10 |  |  |  |

