

Dispersal and extrapolation on the accuracy of temporal predictions from distribution models for the Darwin's frog

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Abstract. Climate change is a major threat to biodiversity; the development of models that reliably predict its effects on species distributions is a priority for conservation biogeography. Two of the main issues for accurate temporal predictions from Species Distribution Models (SDM) are model extrapolation and unrealistic dispersal scenarios. We assessed the consequences of these issues on the accuracy of climate-driven SDM predictions for the dispersal-limited Darwin's frog *Rhinoderma darwinii* in South America. We calibrated models using historical data (1950–1975) and projected them across 40 yr to predict distribution under current climatic conditions, assessing predictive accuracy through the area under the ROC curve (AUC) and True Skill Statistics (TSS), contrasting binary model predictions against temporal-independent validation data set (i.e., current presences/absences). To assess the effects of incorporating dispersal processes we compared the predictive accuracy of dispersal constrained models with no dispersal limited SDMs; and to assess the effects of model extrapolation on the predictive accuracy of SDMs, we compared this between extrapolated and no extrapolated areas. The incorporation of dispersal processes enhanced predictive accuracy, mainly due to a decrease in the false presence rate of model predictions, which is consistent with discrimination of suitable but inaccessible habitat. This also had consequences on range size changes over time, which is the most used proxy for extinction risk from climate change. The area of current climatic conditions that was absent in the baseline conditions (i.e., extrapolated areas) represents 39% of the study area, leading to a significant decrease in predictive accuracy of model predictions for those areas. Our results highlight (1) incorporating dispersal processes can improve predictive accuracy of temporal transference of SDMs and reduce uncertainties of extinction risk assessments from global change; (2) as geographical areas subjected to novel climates are expected to arise, they must be reported as they show less accurate predictions under future climate scenarios. Consequently, environmental extrapolation and dispersal processes should be explicitly incorporated to report and reduce uncertainties in temporal predictions of SDMs, respectively. Doing so, we expect to improve the reliability of the information we provide for conservation decision makers under future climate change scenarios.

Key words: climate change; ecological niche modeling; extinction risk; model transferability; no-analogue climates; range dynamics.

INTRODUCTION

Anthropogenic climate change is a major threat to biodiversity; the prediction of its effects on species distributions is a priority for conservation biology (Botkin 2007). Predicting changes in species distributions and their extent is a key factor in extinction risk assessment (Rowland et al. 2011), and therefore fundamental to support conservation management (Guisan 2013). The most

commonly used tools to forecast climate-driven changes of species distribution are SDMs, which associate occurrences and environmental conditions at a given time to estimate the probability of occurrence in space (Guisan and Zimmermann 2000). By updating environmental variables, these models can be used to forecast shifts in species distributions over time (Fitzpatrick and Hargrove 2009). Recently, growing evidence is questioning their temporal predictability (i.e., capacity to predict potential distributions accurately over time; e.g., Araújo and Rahbek 2006, Rapacciuolo et al. 2012, Brun et al. 2016), and therefore their utility to decide how limited funds should be allocated in biodiversity conservation efforts (Sinclair et al. 2010, Guisan 2013, Guillera-Arroita et al. 2015).

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There are many methodological and biological shortcomings regarding the temporal predictability of correlative SDMs. Model transference in time should have good performance when modeling a stationary process, when the models are not extrapolated to unsampled environmental conditions, and when the relationship between environmental predictors and occurrence probability is not confounded with unmodeled environmental gradients (Elith and Leathwick 2009). Biological issues are mostly related to the omission of relevant biotic mechanisms and processes, such as demography, dispersal, physiology, evolution, and species interactions (Singer 2016, Urban 2016).

There are relatively few studies that assess the predictive accuracy of SDM projections over time (Morán-Ordóñez et al. 2017). Here we explore the impacts of two of the above described issues on the accuracy of temporal predictions from SDMs: (1) the lack of species–environment equilibrium due to dispersal limitations and (2) the emergence of novel environments outside the range of conditions used to calibrate the models (i.e., model extrapolation to no-analogue environmental conditions). The consequences of these issues on model predictions are not well understood, because they have not been tested using independent temporal records to validate model predictions through time, despite the recent calls to assess its effects on predictive performance of SDMs over time (Eskildsen et al. 2013, Miller and Holloway 2015, Evans et al. 2016).

Dispersal is a key process in range dynamics (Davis et al. 1998, Estrada et al. 2015, García-Valdés et al. 2015, Urban 2016), but its consequences on the accuracy of SDM predictions over time have received little attention. Furthermore, most SDM studies have ignored dispersal or dealt with it in overly simplistic ways (e.g., no dispersal vs. unlimited dispersal). Incorporating dispersal processes could allow distinguishing the suitable area that is accessible from which that is not, a critical issue to obtain more accurate projections of range shifts (Soberon and Peterson 2005, Barve et al. 2011, Miller and Holloway 2015).

While the inclusion of dispersal processes in mechanistic models usually requires information that is lacking for most species (Dormann 2012, Evans et al. 2016, Singer 2016, Urban 2016), alternative semi-mechanistic SDMs that need little species information and that couple habitat suitability with dispersal rates have been proposed to improve the prediction of range shifts under climate change (Engler and Guisan 2009, Franklin 2010, Bateman et al. 2013, Urban 2016). Species with limited dispersal capacity can be expected to be more vulnerable to climate change, since those species will not be able to track climatic changes at current or future rates (Schloss et al. 2012, Zhu et al. 2012), generating non-equilibrium conditions that challenge range shift predictions (Schurr 2012). Despite the growing number of studies showing geographical differences in model predictions between

unconstrained and dispersal constrained approaches (e.g., Fordham 2012, Martínez et al. 2012, Krause et al. 2015), the consequences of explicitly incorporating dispersal processes on the accuracy of temporal predictions of SDMs remain untested, mainly because they make temporal predictions under future environmental scenarios, rather than assessing the consequences of incorporating dispersal processes on predictive performance of SDMs used to reconstruct observed distributional changes (i.e., past to present SDM transference).

Model extrapolation into environments dissimilar to those characterizing the conditions for which the model was originally calibrated is another factor that could undermine temporal predictability of SDMs (Fitzpatrick and Hargrove 2009). However, this has received scarce attention (Radeloff 2015). In fact, environmental factors that limit distributions may change substantially under a new climatic regime, and observed trends may not be valid beyond the range of initial environmental conditions (Dormann 2007). The emergence of non-analogue climates challenges the capacity to forecast the effects of climate change, because little information exists to predict how species will respond in novel environments (Fitzpatrick and Hargrove 2009). Using an independent temporal data set to assess the accuracy of model predictions over time, Dobrowski et al. (2011) found that model predictions for no-analogue areas had similar accuracy to those of analogue ones but significantly greater variance, indicating a higher uncertainty in model predictions in no-analogue areas.

Within this framework, we assessed the consequences of incorporating dispersal constraints and model extrapolation on the predictability in time of climate-based SDMs, measured as the accuracy of predictions over time. We addressed two questions. First, can the incorporation of dispersal constraints in SDMs improve the accuracy of temporal predictions from SDMs, and if so, by how much?, and second, are environmental extrapolations of SDMs to no-analogue climates leading to decreased temporal predictability? Thus, we hypothesize that (1) incorporating dispersal processes to SDMs transferred in time will restrict range shifts to suitable climates that are accessible, with the consequence that predictions of SDMs transferred in time that explicitly incorporate dispersal processes will outperform those of SDMs that do not, and (2) geographic areas where no-analogue climates have arisen will experience lower temporal predictability than climate analogue areas. We tested our hypotheses using observed distributional data of Darwin's frog (*Rhinoderma darwinii*), a species with high site fidelity and thus, apparently low dispersal capacity (Valenzuela-Sánchez et al. 2014), which could highlight consequences of dispersal processes in the accuracy of SDMs when transferred in time. This species is also endemic to temperate rainforests of South America, a region where climate is changing at unprecedented rates (Jacques-Coper and Garreaud 2015).

MATERIALS AND METHODS

Based on historical occurrence records (1950–1975) and data on observed climatic change over the last 40 yr, we constructed SDMs including and not including dispersal processes, and projected them to the current climate to predict potential range shifts of *R. darwinii*. In order to assess model accuracies, we contrasted model predictions with time-independent present-day presence-absences for 2000–2014. We then compared model accuracy between SDMs that incorporated dispersal limitations and those that did not. Finally, to assess the effects of environmental extrapolation of SDMs on temporal predictability, we stratified model projections to no-analogue climates and climatic analogue areas.

Study case

Rhinoderma darwinii was chosen as subject of study because of its (1) low mobility, small home range, and high site fidelity (Crump 2002, Valenzuela-Sánchez et al. 2014); (2) well-studied distribution, with a number of known present and past georeferenced occurrences, from which updated distribution range maps have been produced (Soto-Azat et al. 2013a); and (3) endangered condition, undergoing rapid population declines in recent years due mainly to habitat loss, while climate change and infectious diseases are cited as potential drivers of extinction (Soto-Azat et al. 2013a, b). Despite the clear influence of habitat disturbance on the distribution of *R. darwinii*, we were unable to incorporate land use change as driver of range shifts in SDMs, because of the lack of data documenting them for the baseline period (1965–1969).

The study area covers central and southern Chile and adjacent areas of Argentina (35°46' S, 71°75' W; Fig. 1). It spans about 37,000 km² and is characterized by a highly irregular topography, including the Pacific Coast, Coastal Range, longitudinal valley, Andes Range, and fjords of northern Patagonia. Its territory includes the Chilean Winter Rainfall-Valdivian Forests, a well-recognized global biodiversity hotspot (Mittermeier et al. 2005). An increase in mean temperature and decrease in annual precipitation is expected, identifying high vulnerability and exposure to climate change within this area (Santibañez et al. 2013).

Historical and current georeferenced records

Both historical and current occurrences were obtained from the most recently published review of Darwin's frog's distribution (Soto-Azat et al. 2013a) and incorporate additional non-published records. Historical occurrence records for the species correspond to scientific literature and archived specimens found in all museums worldwide with *R. darwinii* specimens collected between 1950 and 1975 (Soto-Azat et al. 2013a), while current presences and absences (i.e., sites

prospected but no individual found) included georeferenced records from individuals captured between 2000 and 2014 from 36 comprehensive field campaigns across the entire historical distribution of *R. darwinii*. The historical data set included 97 records, corresponding to 28 unique occurrences (i.e., information regarding a single cell in a grid-based georeferenced data with ~1 × 1 km resolution); the present-day data set included 1,422 records, corresponding to 83 unique occurrences plus 54 unique absences. It was assumed that the absence of a record from a sampled grid cell corresponds to a true absence of the species. For details on georeferenced records, see Appendix S1 in Supporting Information.

Past and present climatic layers

As there are not available high resolution climatic surfaces for past periods for our study area, we used point data of meteorological stations between 34°48' S and 70°75' W, to generate new climatic surfaces for three recent past periods (1970; 1990; 2010). Meteorological data encompassed 293 weather stations (see Appendix S2 in Supporting Information), and were extracted from three databases: Dirección Meteorológica de Chile (DMC); Dirección General de Aguas de Chile (DGA); and the FAOclim-NET Agroclimatic database management system (FAO 2001), recording monthly records of mean daily minimum temperature, mean daily maximum temperature, and total rainfall for 5-yr periods (1965–1969 for 1970 climatic conditions, 1985–1989 for 1990 climatic conditions, and 2005–2009 for 2010 climatic conditions). For each period, monthly mean values of each climatic variable were interpolated to generate surfaces using Anusplin v.4.4 (Hutchinson and Xu 2013), which applies the same algorithm used to derive the WorldClim bioclimatic surfaces (Hijmans et al. 2005). Interpolations were fitted following Plischoff et al. (2014) at a ~1 × 1 km resolution, with elevation as an independent variable using the GTOPO30 global digital elevation model (USGS 1996). Because some weather stations do not have information for every month, we used the non-data option of Anusplin. The quality of interpolations of climatic data was assessed calculating the Pearson correlation coefficient at the cell level between the monthly climatic values from the CRU-TS v3.10.01 Historic Climate Database for GIS (Climatic Research Unit Time-Series 2012), and the monthly climatic values from the new climatic layers. Finally, surfaces of 19 bioclimatic variables were generated using the dismo package in R (Hijmans et al. 2014). To investigate the observed change in the last 40 yr, we assessed differences on the selected bioclimatic variables between baseline climatic conditions (1965–1969) and current climatic conditions (2005–2009) for a random subset of 10,000 grid cells using nonparametric Friedman analysis of variance on ranks for repeated measures.

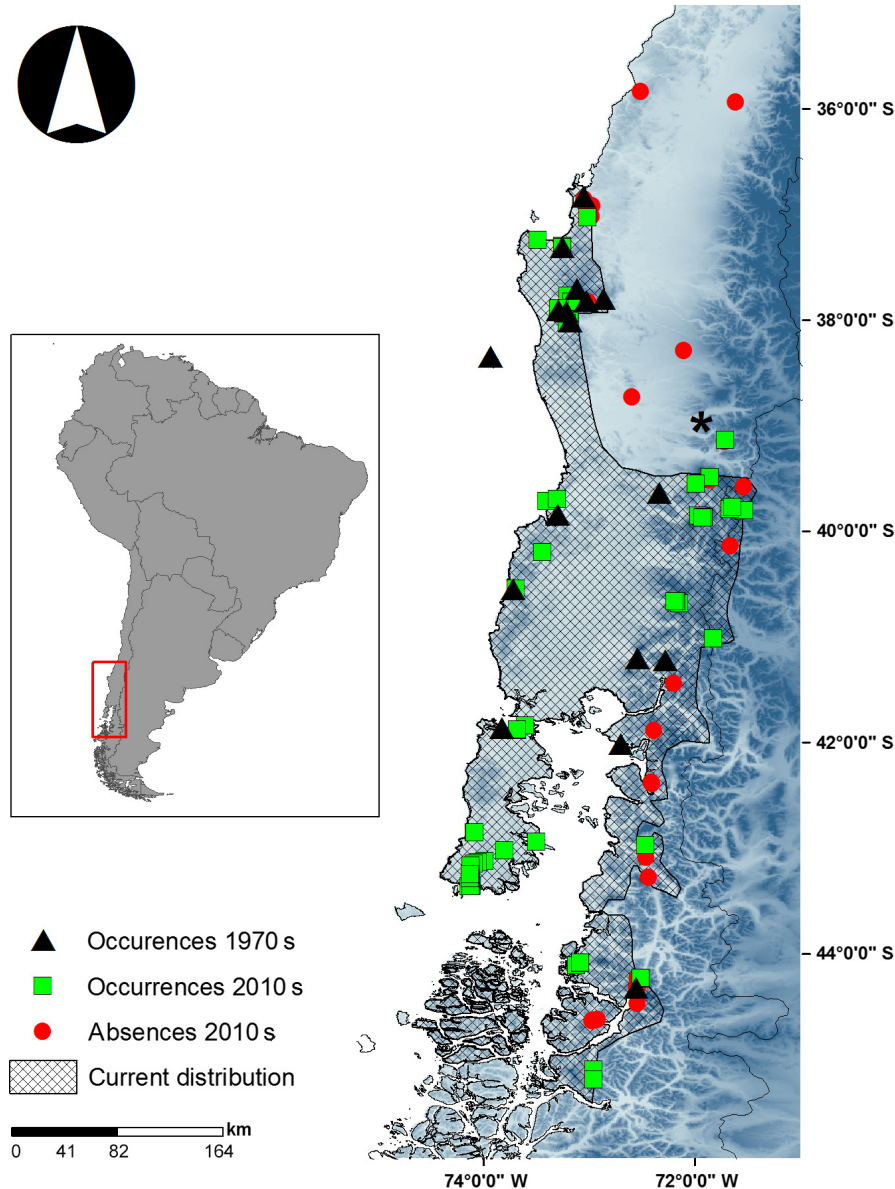


FIG. 1. Study area, geographic distribution (available from IUCN Red List Website, visited on 6 January 2017) and location of historical and current presence–absence data sets for *Rhinoderma darwini*. The star shows a new record from Huerquehue National Park, reported in Soto-Azat et al. (2013a), but still not updated in the IUCN Red List Website. [Color figure can be viewed at wileyonlinelibrary.com]

Species distribution models

Habitat suitability models were fitted using the maximum entropy algorithms implemented in the Maxent software (Phillips et al. 2006), which shows a good performance with limited presence data (Elith et al. 2010) and a combination of high spatial and temporal predictability (Heikkinen et al. 2012, Rapacciuolo et al. 2012). Habitat suitability models were fitted using historical occurrences, which exceeded both the theoretical minimum sample size (i.e., 13 for an ideal, balanced, and

orthogonal world) and the practical minimum sample size (i.e., 25) required to reach good model performance (i.e., $AUC > 0.9$; van Proosdij et al. 2016). As spatial variation in local population densities reflect the niche requirements of a species (Brown et al. 1995), climate variables that were closely related to local abundance of *R. darwini* were prioritized, selecting a subset of 5 of the 19 bioclimatic variables by their degree of correlation with the population density of 15 populations across the entire distribution of *R. darwini* but avoiding the incorporation of pairs of collinear bioclimatic variables (i.e.,

Pearson's $r \geq 0.7$). Using this selection procedure, temperature seasonality (standard deviation \times 100), mean temperature of the wettest quarter, annual precipitation, precipitation seasonality (coefficient of variation) and precipitation in the coldest quarter were selected. To characterize the effects of model extrapolation to no-analogue climates, the default setting "do clamping," which constrains the upper and lower bounds of future values of environmental variables to the range in which the model is calibrated (Phillips et al. 2006), was toggled off. We only allowed linear, quadratic, and product features in the models to control model complexity, producing better predictions when transferred in time or space (Merow et al. 2014). Default values were used for other MaxEnt setting.

Fifty replicates were conducted using the cross validation method, but only the 15 replicates that had the best performance (i.e., highest Area Under Curve [AUC] values of the receiver operating characteristic ROC function, measured against independent occurrences excluded at the subsampling step) on training conditions were selected for further analysis. The models were projected from 1970 to 1990 and 2010 climatic conditions for the 15 selected replicates. Finally, projections of those replicates were transformed from logistic output (an estimate of probability of occurrence) to binary maps of presence-absence. To do so, the maximum training sensitivity plus specificity threshold was used, calculated for each SDM, to transform predicted probabilities of occurrence above the selected threshold to presences, and those below to absences. This threshold algorithm has previously been found to perform better than others (Swets 1988, Jiménez-Valverde and Lobo 2007).

Incorporating dispersal processes

To simulate species-specific dispersal constraints we used MigClim (Engler and Guisan 2009), a cellular automaton-based dynamic SDM, which can be used in conjunction with habitat suitability and demographic information to explore the spatial consequences of climate change. In this model, the colonization probability of an unoccupied cell is a function of propagule production and distance from nearby occupied cells, dispersal barriers and habitat "invasibility" (based on habitat suitability at a given time; Engler and Guisan 2009). Using dispersal and demographic parameters, maps of initial distribution (1970), and climatic habitat distributions based on changing climate conditions (i.e., 1990 and 2010) as inputs, it was possible to distinguish suitable climates that were accessible from those which were not. The MigClim model includes two parameters that control the flow of a dispersal simulation: (1) environmental steps, representing the period in which the environment may change, and depicted as an update in the habitat suitability layer, and (2) dispersal steps, which are nested in the environmental steps and will usually be 1 yr. The

initial distribution was the potential climate distribution modeled from habitat suitability models fitted and projected on for 1970 climatic conditions, while the environmental steps were the same climate envelope model projected to 1990 and 2010 climatic conditions, transformed to binomial maps (suitable/unsuitable) using thresholds as described above. Since the dispersal kernel of *R. darwinii* has not been fitted, extreme values from currently published dispersal kernels of amphibians were used, as minimum (*Triturus cristatus*; Kovar et al. 2009) and maximum (*Rana temporaria*; Kovar et al. 2009) potential dispersal scenarios (see Appendix S3 in Supporting Information for all published dispersal kernels fitted for amphibian species). Finally, first reproduction age was estimated from the experience of ex situ conservation, establishing the age of first reproduction and sexual maturity at 3 and 6 yr, respectively (Busse 2002, Bourke 2010). As probability densities of dispersal by distance at annual time periods were incorporated and the environmental steps (1990, 2010) were separated by 20 yr, the cellular automaton model produced had a total of 40 annual steps (or "dispersal steps"). For calibration parameters see Appendix S4 in Supporting Information. All dynamic models were developed using the MigClim package in R (Engler et al. 2012).

Quantifying emergence of no-analogue climates

To measure the emergence of no-analogue climates from 1970 to 2010 climatic conditions (i.e., the degree of extrapolation in SDM projections over last 40 yr) we used the Extrapolation Detection tool (ExDet), based on Mahalanobis distances (Mesgaran et al. 2014). The Exdet tool, implemented in the ExDet software (Climond.org, Australia), measures the similarity between the reference and projection domains by accounting for both the deviation from the mean (novelty type I) and changes in the correlation between variables (novelty type II; Mesgaran et al. 2014). The climatic novelty (i.e., no-analogue climates) was assessed employing the same climatic variables used to calibrate SDMs, by using the 1970 layers as reference and the 2010 layers as projected climates. We finally reclassified the study area into analogue and no-analogue climates, to assess the effects of model extrapolation comparing the accuracy of temporal prediction of SDMs between extrapolated and no-extrapolated areas (i.e., no-analogue climates and analogue climate areas, respectively).

Accuracy of temporal predictions from SDMs

Usually, the accuracy of SDM predictions is assessed using a data split or a resampled set of the distribution records used to build the models. However, this limited approach has been considered as a critical issue for correlative SDM models (Dormann 2012), because it can overestimate the predictive accuracy when transferred in time (Dobrowski et al. 2011). An alternative and more robust

approach to assess the temporal predictability of SDMs is contrasting model predictions across time with presence–absence data from the projected time period (temporal independent validation data sets; e.g., Pearman et al. 2008, Kharouba et al. 2009, Dobrowski et al. 2011, Rapacciuolo et al. 2012, Watling et al. 2013, Morán-Ordóñez et al. 2017). Thus to quantify the temporal predictability of SDMs, we estimated the models' ability to discriminate between occupied and non-occupied sites, comparing model predictions with contemporary (2000–2014) presences and absences (validation temporal-independent data set). This was done for each of the 15 replicates of the three different model parametrizations separately by calculating two alternative measures of prediction accuracy: AUC, the area under the Receiver Operating Characteristic curve (Fielding and Bell 1997); and True Skill Statistics (TSS; Allouche et al. 2006), using the SDMTools package (VanDerWal et al. 2012). We also computed sensitivity (i.e., proportion of correctly predicted presences) and specificity (i.e., proportion of correctly predicted absences) rates. Interpretation of AUC scores followed the guidelines recommended by Swets (1988): excellent $AUC > 0.90$, good $0.80 < AUC < 0.90$, fair $0.70 < AUC < 0.80$, poor $0.60 < AUC < 0.70$, and fail $0.50 < AUC < 0.60$. TSS scores interpretation followed Landis and Koch (1977): excellent $TSS > 0.75$, good $0.40 < TSS < 0.75$, and poor $TSS < 0.40$.

Dispersion and extrapolation on the accuracy of SDMs predictions

To assess the effects of dispersal processes on the temporal predictability of SDMs, the Kruskal-Wallis test was conducted to compare medians of the three measures of prediction accuracy between SDMs with and without dispersal limitation, followed by post-hoc pairwise comparisons among model treatments using Tukey's HSD test when differences were found. To assess the effect of model extrapolation, the predictive accuracy of analogue climates and no-analogue climate areas was computed using a geographical stratification of the validation data set according to the climatic novelty reclassification of the study area (see *Quantifying emergence of no-analogue climates*), and compared through a Mann-Whitney test. All analyses were performed in R v. 3.1.2 (R Core Team 2014).

RESULTS

Predicted shifts of suitable climates

The spatially explicit correlation between monthly values of climatic variables from generated climate surfaces and from CRU-TS v3.10.01 Historic Climate Database were generally high for all three recent past periods (mean Pearson $r = 0.84$; Appendix S5), reflecting a good fit with the recent climatic history of the study area. All five bioclimatic variables showed

significant changes between 1965–1969 and 2005–2009. Temperature seasonality, mean temperature of wettest quarter, precipitation seasonality, and precipitation of coldest quarter experienced significant increases; while annual precipitation showed a significant decrease (Friedman repeated measures analysis of variance on ranks, all $P < 0.001$). Over the last 40 yr, the suitable climates for *R. darwinii* predicted by SDMs have shifted their range upward and southward (Fig. 2), resulting in increases in the climatically suitable area by 46% on average under no dispersal limitations (Fig. 3).

Identifying dispersal limitations

The MigClim output allows distinguishing between suitable habitats that are accessible from suitable habitats that are not accessible due to dispersal limitations (Fig. 2). This geographic area where dispersal limitations were identified was also consistent with populations of *R. darwinii* that were identified as potential recent local extinctions (2000–2014). SDMs that explicitly incorporated dispersal constraints restricted the upward extensions, resulting in decreases in the range areas by 35% or 12% over the last 40 yr using minimum and maximum dispersal capacity scenarios for dynamic SDMs, respectively. These contrasting patterns in predicted range size changes (a metric usually used to assess extinction risk under climate change scenarios) between simple SDMs and dispersal-constrained SDMs were significantly different (Kruskal-Wallis test $H = 16.29$, $P < 0.001$; Fig. 3).

Dispersal constraints on accuracy of SDMs predictions across time

Model accuracy estimated using temporal independent data set (i.e., current presences and absences) was significantly lower than using a subset of the calibration data set (i.e., historical occurrences), independently of dispersal constraints (Kruskal-Wallis test $H = 36.31$, $P > 0.01$). Performance of no-dispersal constraints SDMs was poor to good, with the median AUC estimated for SDMs without dispersal process projections was 0.71 (with 25th percentile = 0.67, 75th percentile = 0.75), which corresponds to poor to fair accuracy; and the median TSS was 0.42 (with 25th percentile = 0.35, 75th percentile = 0.49), which corresponds to poor to good accuracy. For SDMs with dispersal constraints the median AUC estimated was 0.74 (25th percentile = 0.71, 75th percentile = 0.79) for the minimum dispersal capacity scenario and 0.76 for the maximum dispersal capacity scenario (25th percentile = 0.73, 75th percentile = 0.80; Fig. 4), which corresponds to overall fair to good accuracy. This performance improvement was also reflected in the TSS median of 0.49 (25th percentile = 0.44, 75th percentile = 0.56) for the minimum dispersal capacity scenario and 0.52 for the maximum dispersal capacity scenario (25th percentile = 0.45, 75th percentile = 0.60;

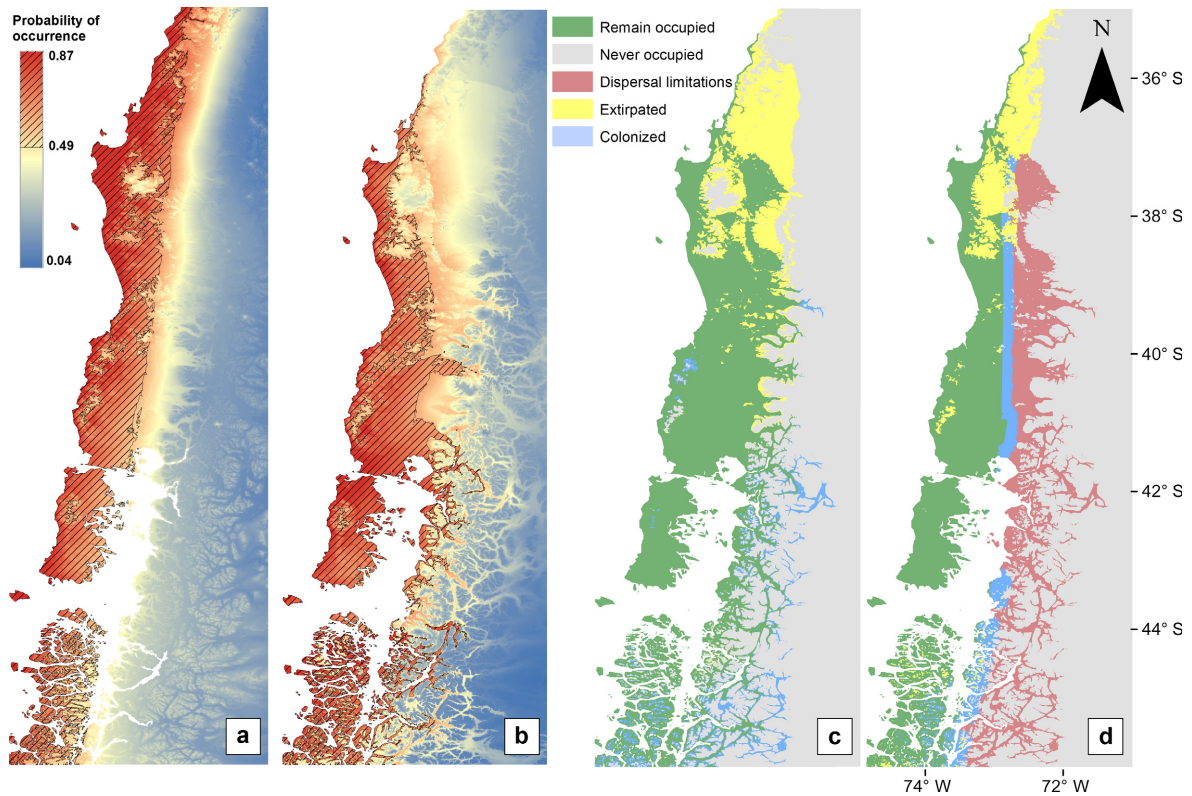


Fig. 2. (a) Maps showing predicted suitable climates for baseline (1965–1969) and (b) predictions for current climatic conditions (2005–2009) through temporal transference of species distribution models without dispersal limitations (hatched area indicates probability of occurrence greater than the cut off threshold). Differences in predicted range change for the last 40 yr (1970–2010) for *Rhinoderma darwinii* using (c) simple species distribution models and (d) dispersal-constrained SDMs that incorporate dispersal capacity. Range change categories following Engler and Guisan (2009), defined for simple species distribution models projections using presence–absence predicted distributional changes since 1970–2010 using geographic intersections. [Color figure can be viewed at wileyonlinelibrary.com]

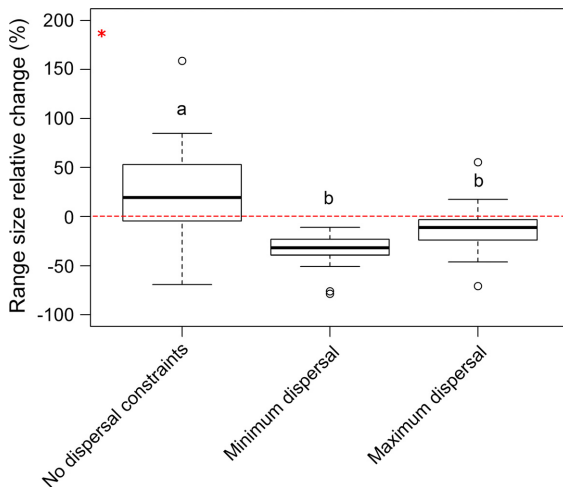


Fig. 3. Boxplot (median, 25th, and 75th percentiles) showing the consequences of dispersal constraints on predicted range size change (%) over 40 yr (1970–2010) for *Rhinoderma darwinii*. Different letters above boxes indicate statistical differences in model accuracy between different modeling treatments. [Color figure can be viewed at wileyonlinelibrary.com]

Fig. 4), which corresponds to overall good accuracy. Accuracy of SDM projections over time was higher when dispersal limitations were incorporated and these differences were statistically significant (both AUC and TSS Kruskal-Wallis tests $H > 6.98$, $P < 0.05$; Fig. 4), but pairwise comparisons showed that only SDM projections with maximum dispersal capacity outperform projections of SDMs without dispersal constraints (Fig. 4). Also, both dynamic SDM projections (maximum and minimum dispersal capacity) exhibited significantly greater sensitivity values than SDM projections that do not incorporate dispersal processes (Kruskal-Wallis test $H = 12.19$, $P < 0.01$; Fig. 4). Otherwise, no significant differences in model specificity were found, independently of the SDM framework (Kruskal-Wallis test $H = 2.12$, $P = 0.34$; Fig. 4).

Environmental extrapolation on accuracy of SDMs predictions across time

No-analogue climates have arisen in 39% of the study area over the last 40 yr, including both projected suitable

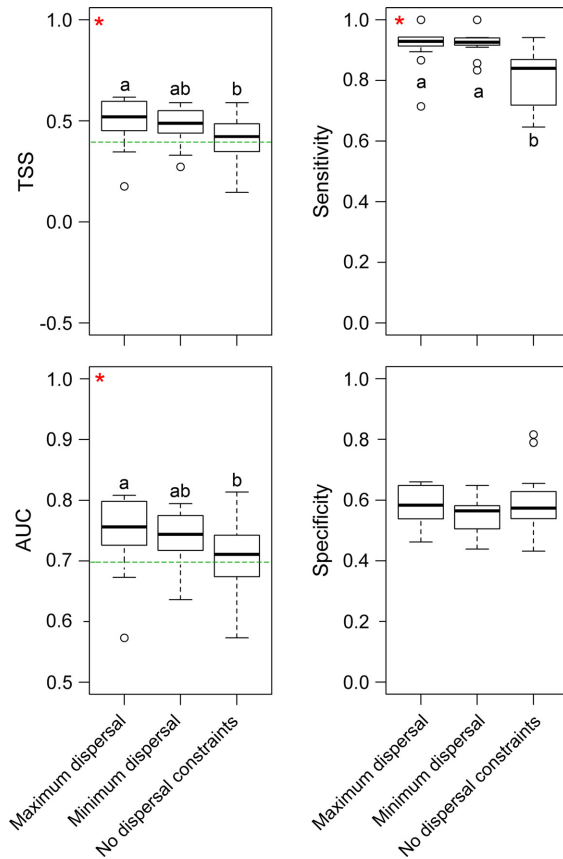


FIG. 4. Boxplot (median, 25th, and 75th percentiles) of different measures of accuracy of species distribution model predictions over time of Darwin's frog (*Rhinoderma darwinii*), for each modeling framework (maximum dispersal, minimum dispersal, and no-dispersal constraints). Significant effects of dispersal processes are denoted by a star. Different letters above boxes indicate statistical differences in model accuracy between different modeling treatments. TSS, True Skill Statistics; AUC, Area Under the ROC Curve. [Color figure can be viewed at wileyonlinelibrary.com]

and non-suitable habitats for *R. darwinii* (Appendix S7). Thereby, SDMs had to extrapolate into 2010 climatic conditions unrepresented in the calibration data set to be projected. The climatic novelties reported by the ExDet tool only occurred in the range of univariate variation (i.e., exceeding the range of values of at least one climatic variable that occurred under the initial climatic conditions), with novel combinations between covariates not being observed. We found that no-analogue climate samples showed significantly lower performance (all Mann-Whitney U from the three dispersal scenarios and two performance indexes < 63 , all $P < 0.05$) and sensitivity values (all Mann-Whitney test $U < 29$, and $P < 0.001$) than analogue samples, but no significant differences in model specificity were observed (all Mann-Whitney $U > 74$, and $P > 0.1$), independently of the SDM framework (Fig. 5; for detailed U statistics and P values of analogue vs. no-analogue areas, see Appendix S6 in the Supporting Information).

DISCUSSION

Predicting species range shifts under global climate change is a major challenge for conservation biogeography (Araújo et al. 2005, Botkin 2007, Carvalho et al. 2011). However, the most commonly used approach to forecast range shifts, the habitat suitability models (or ecological niche models), have shortcomings that could limit their predictive accuracy over time (Elith and Leathwick 2009, Franklin 2013). Two key obstacles to predicting range shifts reliably under global change scenarios are (1) lack of incorporation of dispersal processes (Miller and Holloway 2015) and (2) the environmental extrapolation of these models (Fitzpatrick and Hargrove 2009). We demonstrated the consequences of these shortcomings on predictability in time of SDMs using historical data contrasted with current presence-absence data.

Our results offer new insights to predict range shifts reliably. They support with empirical and time-independent results the recognized idea that incorporating dispersal processes would significantly improve the temporal predictability of SDMs (e.g., Pitelka 1997, Midgley et al. 2006, Schurr 2012, Eskildsen et al. 2013, Miller and Holloway 2015). This might help to reduce one of the most common sources of uncertainty of SDM predictions, the difference between full and no dispersal scenarios (Thuiller et al. 2006). Our results showed that model extrapolations could lead not only to higher uncertainties, but also to lower predictive accuracy over time. This is especially relevant as the rise of no-analogue climates is expected to be inevitable, and therefore reporting the geographic distribution of model extrapolation is key to informing conservation decisions better. Our results also support previous reports that model evaluation with non-temporal-independent data (i.e., data-splitting of the calibration data set) provides overly optimistic assessments of predictive accuracy over time; the time-independent data set is the most robust way to assess model accuracy over time (Araújo et al. 2005, Eskildsen et al. 2013).

While SDM forecasts usually show good predictability over time (i.e., $AUC > 0.8$; Kharouba et al. 2009, Dobrowski et al. 2011), the ability to predict changes in occupancy status due to climate change using SDMs that do not incorporate dispersal processes is at best weak (Rapacciuolo et al. 2012, Eskildsen et al. 2013). Two key processes that could limit the accuracy of SDMs in range shift predictions are the persistence of populations in habitats initially suitable and occupied, but that have become unsuitable; and the dispersal capacity to colonize new suitable habitats (i.e., to track climate change; Thuiller 2008, Pöyry et al. 2009, Devicor 2012, Lenoir and Svenning 2015), especially when the suitable habitat has been modified by human activities, reducing landscape connectivity and limiting dispersal processes (Vasudev et al. 2015). Incorporating dispersal processes not only has consequences for

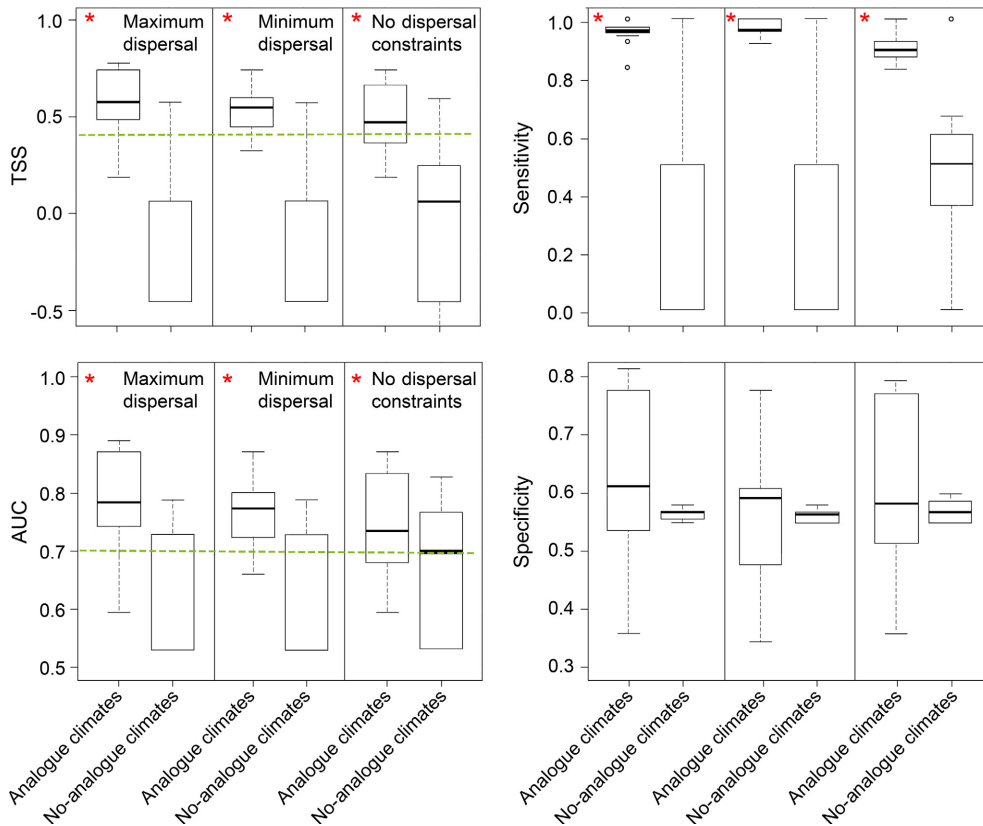


FIG. 5. Boxplot (median, 25th, and 75th percentiles) of different measures of accuracy of species distribution models predictions over time of Darwin's frog (*Rhinoderma darwinii*) computed using stratified validation data set by analogue and no-analogue climate areas for each modeling framework (maximum dispersal, minimum dispersal and no dispersal constraints). Significant effects of model extrapolation are denoted by a star. [Color figure can be viewed at wileyonlinelibrary.com]

reducing the uncertainty of projected range shifts needed in conservation planning (Carvalho et al. 2011, Aben et al. 2016), but also for extinction risk assessments. Usually, SDM projections using full dispersal assumptions overestimate the geographical range area because these models are not able to distinguish an accessible habitat from that one that is inaccessible (Miller and Holloway 2015, Zurell 2016), and therefore might lead to incorrect estimations of extinction risk (Hamann and Aitken 2013). Moreover, the relationship between projected suitable habitat (accessible and inaccessible) and extinction risk is often weak (Fordham 2012), and this apparent weakness could be explained by differences between incorporating or not the dispersal capacity of species when assessing the risk of extinction due to climate change through SDMs. For *R. darwinii*, simple SDM forecasts predicted an increase in potential climatically suitable area. However, dispersal-constrained SDMs predicted decreases in the range area for 14 out of 15 replicates, highlighting that dispersal capacity plays an important role in accurate assessment of extinction risk (Fig. 3). Even more, the results presented here could be considered as conservative because they do not incorporate land use change and its interactions with

climate change (Sohl 2014). If we had included land use change, the results could have shown even greater losses due to the dynamics of forests replacement experienced over the last 40 yr in central and southern Chile (Echeverría et al. 2006, Miranda et al. 2016).

Improvement in temporal predictability when dispersal constraints are included in SDMs is clearly explained by the desirable increase in model sensitivity (i.e., a decrease in false presence predictions). Model sensitivity has been suggested as more critical to model reliability to support conservation decisions than model specificity (Jiménez-Valverde et al. 2011). This is important in conservation management because the former allows more accurate reports of where the species is expected to spread and where the species should not colonize due to dispersal limitations, even though the model predicts suitable climates. The increase in model sensitivity for *R. darwinii* using dispersal-constrained SDMs with respect to projections from simple SDMs is consistent with large areas of habitat that have become suitable, but which *R. darwinii* cannot reach due to dispersal limitations (e.g., high-latitude islands in Patagonian fjords and high altitudes in the Andes; Fig. 2d). However, we did not observe improvements in SDM specificity (i.e., no decrease in false

absence predictions) when dispersal capacity was incorporated. This could be interpreted as a limitation in the ability of SDMs to predict species distributional responses to climate change at the trailing edge of a species' range shift, which is not explained by dispersal constraints. Two alternative explanations compete for false absence predictions. First, SDM projections are probably pessimistic in predicting habitat loss at the trailing edge, because SDMs are based on the realized climatic niche, which can be much narrower than the fundamental niche (Jackson and Overpeck 2000). This is also consistent with non-climatic range limitations, which have been proposed as likely the norm rather than the exception (Early and Sax 2014). Second, another overly pessimistic issue of SDM projections in the face of climate change is the assumption that populations under unsuitable conditions are committed to local extinction (e.g., Thomas et al. 2004). Therefore, these models rarely incorporate persistence of populations when the climate of a given area became unsuitable, which could explain at least part of false absence predictions (but see Dullinger 2012). This highlights the need for incorporating not only dispersal processes in dynamic SDMs, but also population persistence under unsuitable conditions (Schurr et al. 2007, Thuiller 2008), disentangling the effects of misrepresented niche and persistence in unsuitable habitats on the temporal predictability of SDMs. An example of incorporating both processes is presented in Early and Sax (2011), who demonstrated that population persistence could be critical to predict species range shifts. Moreover, García-Valdés et al. (2015) showed that dispersal capacity was the best single predictor not only for colonization but also for extinction rates (along with climate) for most of the 23 species throughout mainland Spain. However, to our understanding, the consequences of incorporating population persistence in temporal predictability of SDMs have not been demonstrated so far (e.g., through time-independent validation of predictions). If persistence has an effect on the predictability of SDMs over time, its effects should be greater in long-lived species because of a greater temporal lag for local extinctions (climatic extinction debts; Devictor 2012), assuming that it is somewhat unlikely that these populations could evolve to adapt to new conditions. Although most amphibians are expected to live for only few years, *R. darwini* appears to live longer. Field studies have recorded adults a minimum of 8 yr old (C. Soto-Azat, *personal communication*), while in captivity, individuals have survived up to 15 yr (Busse 2002); this is a reason why the persistence of populations under unsuitable conditions should be considered in future forecasts of range dynamics for this species.

Current climate conditions are changing, with some climates disappearing and new ones emerging. However, reports of no-analogue climates to take account of prediction uncertainty are still an uncommon practice in species distribution forecasts (Elith and Leathwick 2009). Instead studies typically extrapolate models into no-analogue conditions and assume such extrapolations

are valid (Fitzpatrick and Hargrove 2009). Our results suggest that, similarly to spatial extrapolation (Heikkinen et al. 2012), a good capability of SDMs to predict species distributions under training conditions does not guarantee equally good performance when these are transferred in time. In spite of this, environmental extrapolation seems to be a situation that often cannot be avoided when correlative SDMs are being transferred in space or time. For this reason, our findings demonstrate the importance of environmental extrapolation for temporal transference of SDMs, and is consistent with the recommendations of reporting the degree of environmental extrapolation both for temporal and spatial transference of SDMs (e.g., Elith et al. 2010, Zurell et al. 2012, Mesgaran et al. 2014) to prevent erroneous or imprecise predictions, or at least communicate where model predictions are reliable and where they are not. Bayesian Hierarchical models (e.g., Dynamic Range Models; Pagel and Schurr 2009) have been shown to produce reliable predictions in time (using simulated data; Schurr 2012), with several advantages including the inference of spatiotemporal range dynamics in equilibrium and non-equilibrium conditions, and the capacity of reporting the within-model uncertainty of the predictions. These advantages could be especially relevant in predicting range dynamics when models are transferred in time or space and extrapolated to novel environmental conditions (Schurr 2012).

Significant improvements in temporal model predictability can be obtained when realistic dispersal constraints are included in dynamic SDMs, reducing the uncertainty of the over-simplistic approach of no or full dispersal scenarios. This may be more important for dispersal-limited species, which have shown lower temporal predictability compared to species with high mobility. However, the predictive performance of SDMs significantly decreases in no-analogue climate areas, and as the rise of climatic novelty is inevitable, reporting the geographic distribution of model extrapolation is key to better informed conservation decisions. Studies performing time-independent evaluations of SDM projections over time are needed, since this is a more robust way to assess the predictive accuracy of SDMs in a context of environmental change. Furthermore, the development of novel mechanistic models should include, in addition to dispersal processes, population persistence in unsuitable habitats, thus accounting for local extinction debts or the ability of species to adapt, and thereby reducing false absences in model predictions.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1556/full>

DATA AVAILABILITY

Data associated with this paper have been deposited in Zenodo digital repository: <https://doi.org/10.5281/zenodo.439141>