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**Dispersal processes and environmental extrapolation on  
predictive accuracy of species distribution models when  
transferred in time.**

**Tesis**

Entregada a la Universidad de Chile  
en cumplimiento parcial de los requisitos para optar al grado de

**Magíster en Ciencias Biológicas**

Facultad de Ciencias

por

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“Nor need we fear that this philosophy, while it endeavours to limit our enquiries to common life, should ever undermine the reasonings of common life, and carry its doubts so far as to destroy all action, as well as speculation. Nature will always maintain her rights, and prevail in the end over any abstract reasoning whatsoever. Though we should conclude, for instance, as in the foregoing section, that, in all reasonings from experience, there is a step taken by the mind which is not supported by any argument or process of the understanding; there is no danger that these reasonings, on which almost all knowledge depends, will ever be affected by such a discovery. If the mind be not engaged by argument to make this step, it must be induced by some other principle of equal weight and authority; and that principle will preserve its influence as long as human nature remains the same. What that principle is may well be worth the pains of enquiry.”

— David Hume

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## ABSTRACT

Anthropogenic 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. Common issues for accurate predictions of Species Distribution Models (SDM) across time are model extrapolation and realistic incorporation of dispersal capacities. We investigated the consequences of these issues on the success of predicting recent (1970-2010) climate-driven changes in the distribution of Darwin's frog *Rhinoderma darwinii*. We built SDMs that incorporate dispersal processes and compared their predictions with predictions from SDMs without dispersal limitations. We generated new dataset of bioclimatic variables for three time periods (1970, 1990, 2010), and calibrated SDMs with historical occurrences (1950-1975) fitted to 1970s climate, and projected them to conditions of the 2010s. Accuracy of models was assessed through AUC, sensitivity and specificity rates, contrasting binary model predictions across time against current presences/absences. The incorporation of dispersal capacity enhanced accuracy, reducing the false presence rate in model predictions, and this was consistent with discrimination of suitable but inaccessible habitat. This enhancement also had consequences on range size changes over time, a metric commonly used to assess extinction risk from climate change. Comparing the climates of 1970 and 2010, the area of current climates that was absent in the 1970s (no-analogue climates) represents 39% of the study area (35°-46°S;71°-75°W). As a consequence models showed a high degree of environmental extrapolation, leading to a decrease in accuracy of model predictions for no-analogue climate areas compared to analogue ones. Our results highlight the consequences of two acknowledged issues of species distribution forecasts on the accuracy of SDM predictions, proposing ways to improve model predictability and reduce uncertainties of over-simplistic full/no dispersal scenarios, hoping to provide more reliable information for conservation decision makers.

## RESUMEN

Desarrollar modelos que permitan predecir de manera confiable los efectos del cambio climático sobre la biodiversidad es una prioridad para su gestión. Problemas comunes a la precisión predictiva de los Modelos de Distribución de Especies (MDE) al transferirlos en el tiempo son la extrapolación ambiental y una incorporación realista de las capacidades de dispersión de las especies. Investigamos las consecuencias de tales problemas sobre el éxito al predecir cambios recientes en la distribución de la ranita de Darwin *Rhinoderma darwinii* (1970-2014). Construimos MDEs que incorporan explícitamente procesos de dispersión biológica, comparando sus predicciones con las de MDEs que no los incorporan. Para esto, generamos capas bioclimáticas para tres periodos (1970, 1990 y 2010), y calibramos los MDEs ajustando las ocurrencias históricas (1950-1975) y proyectándolas al clima más reciente. La precisión de los modelos fue evaluada contrastando predicciones binarias de los modelos a través del tiempo, con presencias y ausencias actuales (2000-2014). La incorporación de procesos de dispersión mejora la precisión, reduciendo la tasa de falsas presencias de las predicciones, lo cual es consistente con la discriminación de hábitats adecuados pero inaccesibles. El espacio climático de 2010 que no se encontraban en 1970 (no-análogos climáticos) representa el 39% del área de estudio (35°-46°S;71°-75°O). Como consecuencia, las transferencias temporales de los modelos presentaron un alto grado de extrapolación, resultando en una disminución en la precisión de las predicciones en áreas no-análogas climáticas respecto de áreas análogas. A partir de estos resultados se proponen alternativas para mejorar la precisión de las predicciones temporales de los MDEs, reduciendo incertezas de escenarios demasiado simplificados de dispersión, y haciendo un llamado a comunicar las áreas geográficas donde los MDEs sean extrapolados. Con esto esperamos se proporcione información más fiable de los efectos del cambio climático a los tomadores de decisiones de conservación.





## 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 et al. 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 decisions (Guisan et al. 2013). The most commonly used tools to forecast climate-driven changes of species distribution are Species Distribution Models (SDM), 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; Araújo and Rahbek 2006, Dobrowski et al. 2011, Rapacciuolo et al. 2012), and therefore their utility to decide how scarce funds should be allocated in large-scale conservation projects (Sinclair et al. 2010).

There are some shortcomings regarding the temporal predictability of SDMs. These include, but are not limited to, the lack of species-environment equilibrium due to dispersal limitations and the emergence of novel environments outside the range of conditions used to calibrate the models (i.e. model extrapolation to no-analogue climates, Rapacciuolo et al. 2012). However, the consequences of these shortcomings 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 for the need to assess the effects of dispersal constraints on predictive performance of SDMs over time (Eskildsen et al. 2013, Miller and Holloway 2015).

Dispersal is a key process in range dynamics (Davis et al. 1998), 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 versus unlimited dispersal). Incorporating dispersal processes could allow distinguishing the suitable area that is accessible from which that is not, a critical issue to predict range shifts successfully (Soberon and Peterson 2005,

Barve et al. 2011); by doing so it is expected to result in more accurate projections of range shifts (Miller and Holloway 2015).

While the inclusion of dispersal processes in mechanistic models usually requires information that is lacking for most species (e.g. dynamic range models; Schurr et al. 2012), alternative dynamic SDMs which need little species knowledge 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). Species with limited dispersal capacity may be expected to be more vulnerable to climate change, since those species won't 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 et al. 2012). The study of Dobrowski et al. (2011) on temporal predictability of SDMs suggested that dispersal-limited species would have lower predictive accuracy over time than species with high dispersal capacity, but the consequences of explicitly incorporating dispersal processes remain untested.

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 and has received scarce attention (Fitzpatrick and Hargrove 2009). 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 dataset to assess the accuracy of model predictions over time (model evaluated at a time window different than the calibration time, using observed presence/absence data), Dobrowski et al. (2011) found that model predictions for no-analogue areas had similar accuracy to those of analogue areas 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 temporal predictability of climate-based

SDMs, measured as the accuracy of predictions over time. We addressed two questions: (1) Can the incorporation of dispersal constraints in SDMs improve the temporal predictability of SDMs? and (2) Are environmental extrapolations of SDMs to no-analogue climates leading to decreased temporal predictability? We hypothesize that a) 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 b) as it is not possible to characterize fully the relationship between environment and species distribution from the realized niche (i.e. occurrence data), geographic areas where no-analogue climates have arisen will experience not only higher uncertainties, but also lower temporal predictability than climate analogue areas. We tested our hypotheses using observed distributional data of Darwin's frog (*Rhinoderma darwinii*), a species with 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 already changing (Jacques-Coper and Garreaud 2015).

## METHODS

Based on historical occurrence records (1950-1975) and data on observed climatic change over the last 40 years, 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/absence 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 low net displacement (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); 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 main threats (Soto-Azat et al. 2013a, 2013b).

The study area covers central and southern Chile and adjacent areas of Argentina (35°-46°S; 71°-75°W, Figure 1). In this area the greatest decrease in precipitation is expected to occur along with the greatest increase in temperature; it is also where most vulnerable ecosystems of Chile occur (Santibañez et al. 2013). It spans about 37,000 km<sup>2</sup> and is characterized by a highly irregular topography, including the Pacific Coast Range, the western slope of the Andes Range and part of the fiords of northern Patagonia. Its territory includes the Chilean Winter Rainfall-Valdivian Forests, a recognized biodiversity hotspot (Mittermeier et al. 1999).

### Occurrence data

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 include additional non-published records. Historical occurrence records for the species were restricted to all archived specimens found in museums around the world that were collected between 1950 and 1975 (Soto-Azat et al. 2013a; ti), while current presences and absences (i.e. sites prospected but no individual found) included georeferenced records from individuals captured between 2000 and 2014 from 35 field campaigns across the entire historical distribution of *R. darwinii* carried out between 2008 and 2014 (tf). The historical dataset included 97 records, corresponding to 28 unique occurrences (i.e. information regarding a single cell in a grid-based georeferenced data with ~1x1 km resolution); the present-day dataset 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. Details on georeferenced records are available in Table S1.

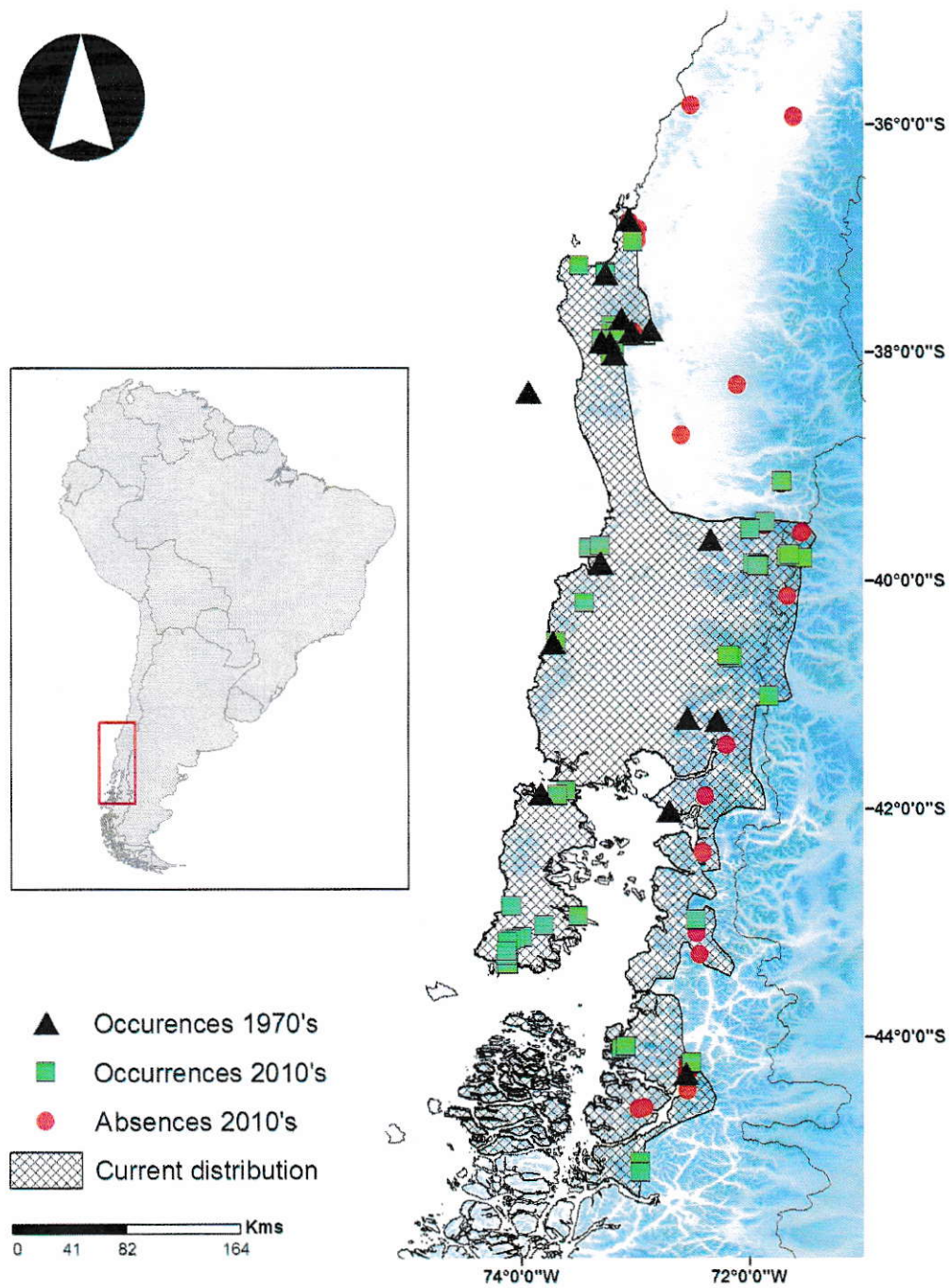


Figure 1. Study area, geographic distribution and location of historical and current presence-absence datasets for *Rhinoderma darwinii*.

### Characterizing recent climate change

Using point data of meteorological stations between 34°-48°S and 70°-75°W, climatic surfaces for three recent past periods (1970; 1990; 2010) were built. Meteorological data encompassed 293 weather stations, and were extracted from the 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-year periods (1965-1969; 1985-1989; 2005-2009). For each period monthly values of each climatic variable were interpolated to generate surfaces using Anusplin v.4.4 (Hutchinson and Xu 2006), which applies the same algorithm used to derive the WorldClim bioclimatic surfaces (Hijmans et al. 2005). Interpolations were fitted at a ~1x1 Km resolution with the second-order spline method using elevation as an independent variable (Hutchinson and Xu 2006, Pliscoff et al. 2014). Finally, surfaces of 19 bioclimatic variables were generated using the dismo package in R (Hijmans et al. 2014). To investigate the observed change in recent climate (last 40 years), we assessed differences between the bioclimatic values of the 1970s and 2010s for a random subset of 10000 grid cells using non-parametric Friedman analysis of variance of ranks for repeated measures.

### Habitat suitability models

Habitat suitability models were fitted using the maximum entropy algorithms implemented in the Maxent software (Phillips et al. 2006), which have better 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). Historical occurrences were randomly subsampled by distance to reduce the effects of spatial autocorrelation (Marino et al 2011), avoiding occurrences that were less than 4 km apart, resulting in a subsample of 24 occurrences, which shows non-significant autocorrelation levels by Moran's I Test (Moran 1950), as well as exceeding the theoretical minimum sample size (i.e. 13) required to obtain good model performance (i.e. AUC > 0.9) in an ideal, balanced and orthogonal world (van Proosdij et al. in press). All models were calibrated using 70% of the dataset points (training data), while

the remaining 30% were used for internal evaluation of model performance (“internal evaluation” [IE] sensu Dobrowski et al. 2011). To reflect the relationship between habitat suitability and local abundance better (Brown et al. 1995) climate variables that were closely related to local abundance 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 *Rhinoderma 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 \*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, “do clamping” was not used; this is the default option in the Maxent software that constrains the upper and lower bounds of future values of environmental variables to the range in which the model was calibrated; Phillips et al. 2006). Fifty replicates were conducted, and using the IE 15 replicates that had the best performance on 1970 projections (i.e. highest Area Under Curve [AUC] values of the receiver operating characteristic ROC function) were selected. The models were projected to 1990 and 2010 for the 15 replicates selected. 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 inputs of dispersal and demographic parameters, maps of initial distribution (1970), and climatic habitat distributions based on changing climate conditions (i.e. environmental steps: 1990 and 2010) it was possible to distinguish suitable climates that were accessible from those which were not. The initial distribution was the potential climate distribution modeled from habitat suitability models fitted and projected on 1970, while the environmental steps were the same climate envelope model projected to 1990 and 2010, 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 Table S2 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 years, 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 twenty years, the CA model produced had a total of 40 annual steps (or “dispersal steps”). 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 past (1970) to present (2010; i.e. the degree of extrapolation in SDM projections over time) we used the Extrapolation Detection tool (ExDet), based on Mahalanobis distances (Mesgaran et al. 2014). The Exdet tool, implemented in the ExDet software, 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 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.



### Assessment of temporal predictability of SDMs

Usually accuracy of SDM projections is assessed using a data-split or a resampled set of the distribution records used to build the models. This involves a limited approach that can overestimate the predictive accuracy (Dobrowski et al. 2011). An emerging and more robust approach to assess the temporal predictability of SDMs is contrasting model predictions across a time period different than that with which the model was originally calibrated with presence/absence data from that new time period (e.g. Pearman et al. 2008, Kharouba et al. 2009, Dobrowski et al. 2011, Rapacciuolo et al. 2012, Watling et al. 2013). 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 ("external evaluation" [EE] sensu Dobrowski et al. 2011). This was done for each of the 15 replicates of the three different model parametrizations separately by calculating three alternative measures of prediction accuracy: i) AUC, the area under the ROC-curve (Fielding and Bell 1997), (ii) sensitivity (i.e., proportion of correctly predicted presences) and (iii) specificity (i.e., proportion of correctly predicted absences), using the SDMTools package (Van Der Wal et al. 2011). 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  $0.50 < AUC < 0.60$ .

### Dispersion and extrapolation on temporal predictability of SDMs

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 (both scenarios), 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 between stratified validation datasets was compared for extrapolation and no extrapolation areas (i.e. analogue climates vs no-analogue climates) using a Mann-Whitney test. All analyses were performed in R v. 3.1.2.

## RESULTS

### Predicted shifts of suitable climates

All five bioclimatic variables showed significant changes between 1965-1969 (ti) and 2005-2009 (tf). Temperature seasonality (standard deviation \*100), mean temperature of wettest quarter, precipitation seasonality (coefficient of variation) 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 years, the suitable climates for *R. darwinii* predicted by SDMs have shifted, experiencing upward spread and resulting in increases in the climatically suitable area by 46% on average under no dispersal limitations (Figure 4).

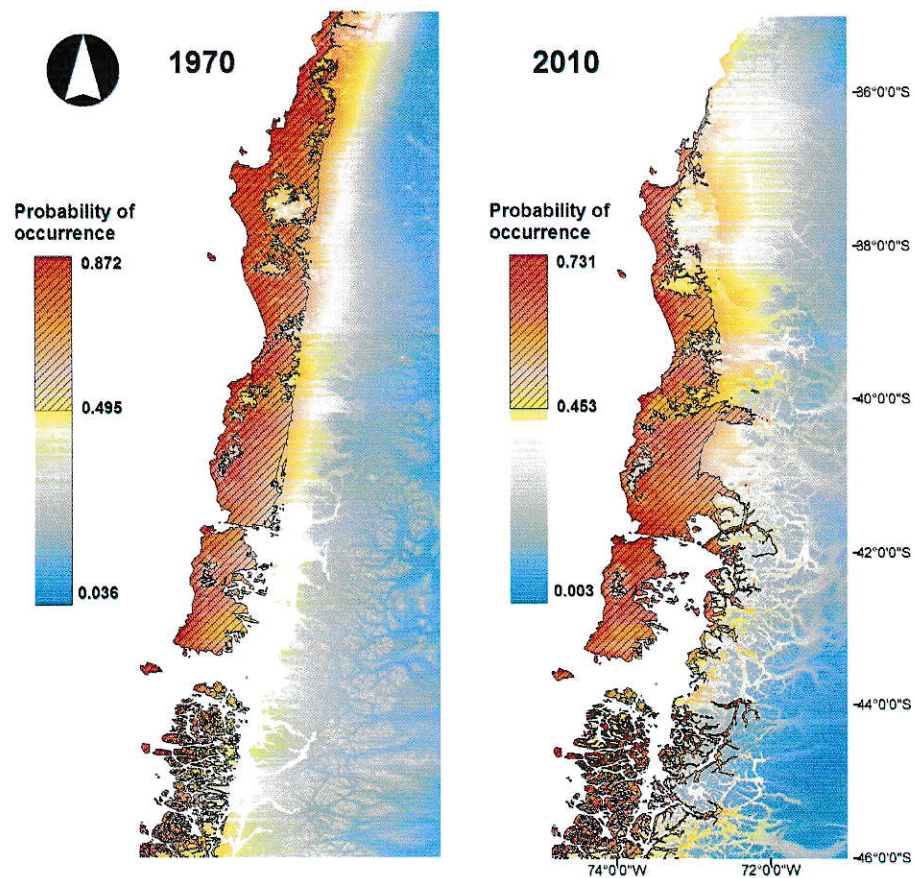


Figure 2. Maps showing predicted suitable climates for 1970 and predictions for 2010 through temporal transference of SDMs without dispersal limitations. Hatched area indicates probability of occurrence probability greater than the cutoff threshold.

### Identifying suitable but inaccessible climates

The MigClim output allows distinguishing between suitable habitats that are accessible from suitable habitats that are not accessible due to dispersal limitations (Figure 3). 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).

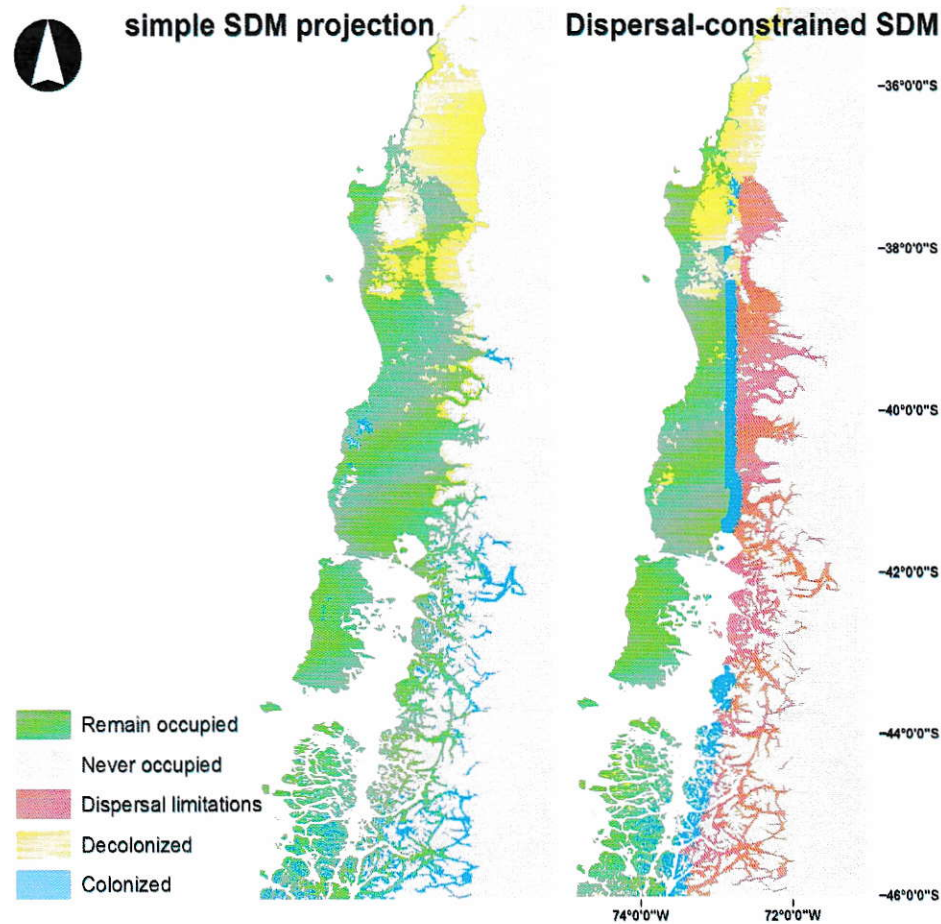


Figure 3. Differences in predicted range change for the last 40 years (1970-2010) for *Rhinoderma darwinii* using simple SDMs and dispersal-constrained SDMs that incorporate dispersal capacity (maximum dispersal rate). Range change categories following Engler & Guisan (2009), defined for simple SDM projections using presence-absence predicted distributional changes since 1970 to 2010 using geographic intersections.

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 years 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  $H=16.29$ ,  $p<0.001$ ; Figure 4).

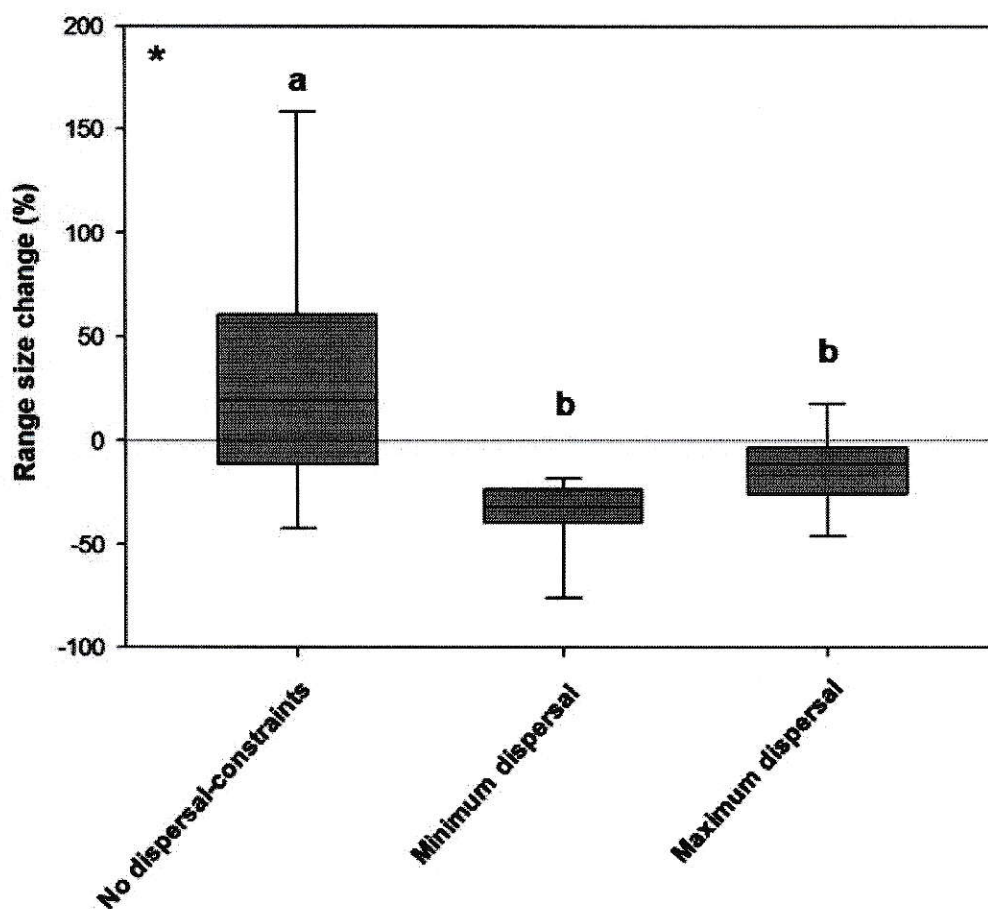


Figure 4. Boxplot (median, 25<sup>th</sup> and 75<sup>th</sup> percentiles) showing the consequences of dispersal constraints on predicted range size change (%) from 1970 to 2010. Significant effects are denoted by \*. Different letters indicate statistical differences in model accuracy between different modeling treatments.

### Dispersal limitations on temporal predictability of SDMs

Model accuracy estimated using EE was significantly less than using IE, independently of dispersal constraints (Kruskal-Wallis test  $H = 36.31$ ,  $p > 0.01$ ; Figure 5). 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 overall poor to fair accuracy (sensu Swets 1988). 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; Figure 5) which corresponds to overall fair to good accuracy (sensu Swets 1988). Accuracy of SDM projections over time (AUC from a time-independent dataset) significantly increased when dispersal limitations were incorporated (Kruskal-Wallis test  $H = 8.44$ ,  $p < 0.05$ ; Figure 5), but pairwise comparisons showed that only SDM projections with maximum dispersal capacity outperform projections of SDMs without dispersal constraints (Figure 5). 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  $H = 12.19$ ,  $p < 0.01$ ; Figure 5). Otherwise, no significant differences in model specificity were found, independently of the SDM framework (Kruskal-Wallis test  $H = 2.12$ ,  $p > 0.34$ ; Figure 5).

### Model environmental extrapolation on temporal predictability of SDMs

No-analogue climates have arisen in >39% of the study area over the last 40 years, including both projected suitable and non-suitable habitats for *R. darwinii* (Figure 6). Thereby, SDMs had to extrapolate into 2010 climatic conditions unrepresented in the calibration dataset 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.

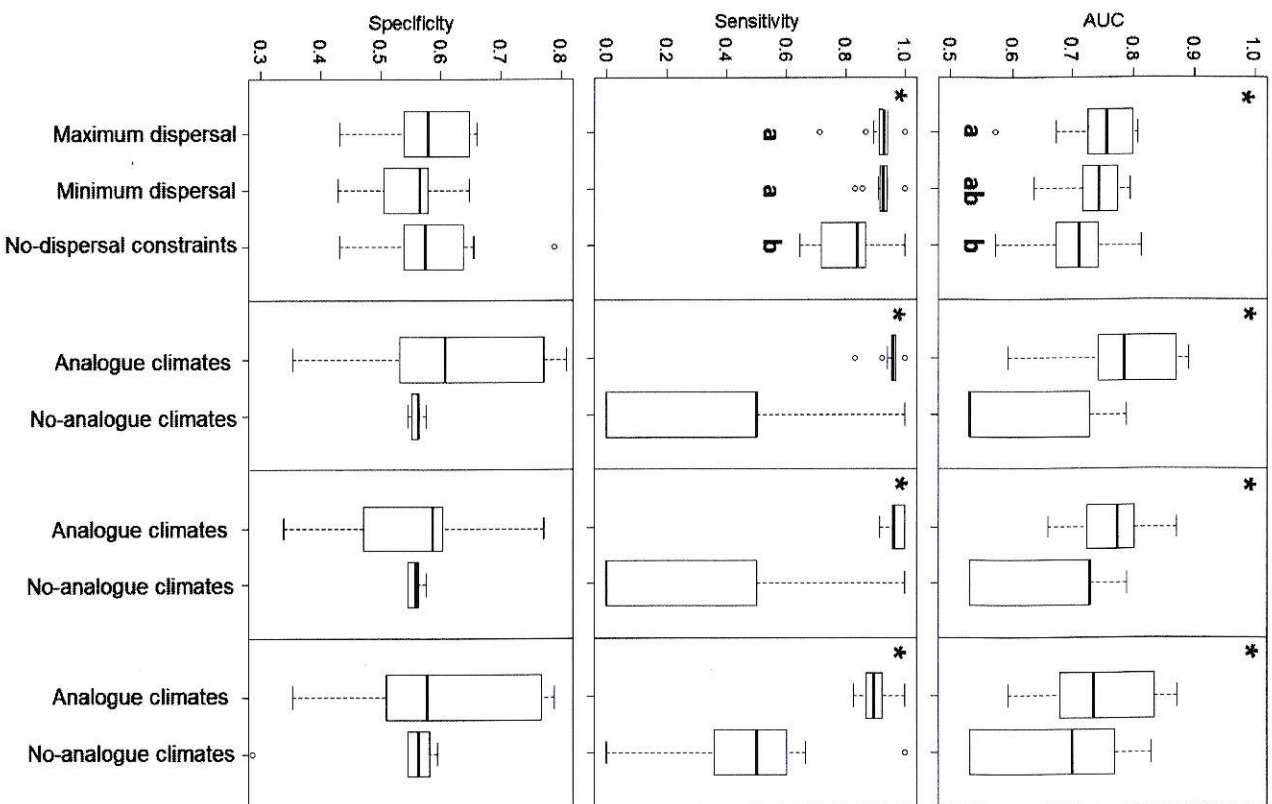


Figure 5. Boxplot (median, 25<sup>th</sup> and 75<sup>th</sup> percentiles) of different measures of accuracy of SDM predictions over time of Darwin's frog (*Rhinoderma darwinii*), for each modeling treatment (maximum dispersal, minimum dispersal and no dispersal constraints) and data stratification (analogue vs no-analogue climates). Significant effects of dispersal processes and model extrapolations are denoted by \*. Different letters indicate statistical differences in model accuracy between different modeling treatments.

We found that no-analogue climate samples showed significantly lower AUC (all Mann-Whitney test  $U < 59$ , all p-values  $< 0.05$ ) and sensitivity values (all Mann-Whitney test  $U < 29$ , all p-values  $< 0.001$ ) than analogue samples, but no significant differences in model specificity were observed (all Mann-Whitney  $U > 74$ , all p-values  $> 0.1$ ), independently of the SDM framework (Figure 5).

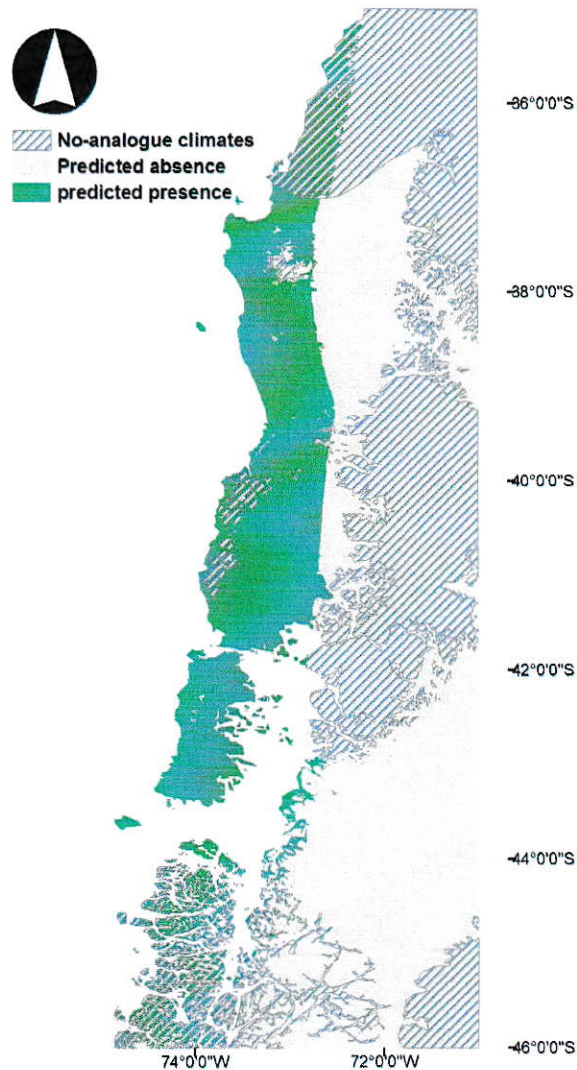


Figure 6. Predicted geographical distribution map for Darwin's frog (*Rhinoderma darwinii*) for 2010 using dispersal-constrained SDM with minimum dispersal capacity; and the extent of model extrapolation (no-analogue climate areas) after 40 years of observed recent climate change (1970-2010).

## DISCUSSION

Predicting species range shifts under global climate change is a major challenge for conservation biogeography (Araújo et al. 2005, Botkin et al. 2007, Carvalho et al. 2011). However, the most commonly used approach to forecast range shifts, the SDMs, 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: i) no incorporation of dispersal processes in SDMs (Miller and Holloway 2015), and ii) the environmental extrapolation of these models (Fitzpatrick and Hargrove 2009). Here we demonstrated the consequences of these shortcomings on temporal predictability using historical data to predict the present distribution of the dispersal-limited frog *R. darwinii*, assessing the accuracy of predictions contrasted with current presence/absence data.

Our results offer new insights to predict range shifts reliably. They support for the first time with empirical and time-independent results the recognized idea that incorporating dispersal processes would significantly improve the temporal predictability of SDMs (e.g. Pitelka et al. 1997, Midgley et al. 2006, Schurr et al. 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 also showed that model extrapolations could lead not only to higher uncertainties (Dobrowski et al. 2011), 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 better informed conservation decisions. Our results also support previous reports that model evaluation with non-independent data (e.g. data-splitting of the calibration dataset) provides overly optimistic assessments of predictive accuracy over time; the time-independent dataset is the most robust way to assess model accuracy over time (Araújo et al. 2005, Kharouba et al. 2009, Dobrowski et al. 2011, 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 (Rapaccioulo 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 et al. 2008, Pöyry et al. 2009, Devictor et al. 2012, Lenoir and Svenning 2015). Incorporating dispersal processes not only has consequences for reducing the uncertainty of projected range shifts needed in conservation planning (Carvalho et al. 2011), 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), 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 et al. 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.

Improvement in temporal predictability when dispersal constraints are included in dispersal-constrained 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 access due to dispersal limitations (e.g. high latitude islands in Patagonian fjords and high altitudes in the Andes; Figure 3). 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, 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 of a species' range, 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 recently proposed as likely the norm rather than the exception (Early and Sax 2014). Second, another overly pessimistic issue of SDM projections in 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. 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 et al. 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. 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). Moreover, 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 et al. 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. darwinii* appears to live longer. Field studies have recorded adults a minimum of eight years-old (Soto-Azat, pers. comm), while in captivity individuals have survived up to 15 years (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 automatically guarantee equally good performance when these are transferred in time. In spite of decreased predictive accuracy and increased uncertainty of SDMs for no-analogue climate areas, environmental extrapolation seems to be a situation that often cannot be avoided when these correlative SDMs are being transferred in space or time. For this reason, it is strongly recommended to report the degree of environmental extrapolation both for temporal and spatial transference of SDMs (e.g. Elith et al. 2010, Mesgaran et al. 2014) to prevent erroneous or imprecise predictions, or at least communicate where model predictions are reliable and where they are not.

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/full dispersal. This may be more important for dispersal-limited species, which have shown lower temporal predictability than species with high mobility. However, the predictive performance of SDMs significantly decreases in non-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 new dynamic SDMs should include, in addition to dispersal processes, population persistence in unsuitable habitats, thus reporting projected climatic extinction debts and thereby reducing false absences in model predictions.

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## APPENDIX

Table S1. Georeferenced records for *R. darwinii* for both historical (1950-1975) and present-day datasets.

Dataset	Latitude	Longitude	Presence-absence
Historical Dataset	-36.83437	-73.05178	1
	-37.31148	-73.25317	1
	-37.71274	-73.11200	1
	-37.80194	-72.86081	1
	-37.82122	-73.02545	1
	-37.90961	-73.29110	1
	-37.92543	-73.21368	1
	-38.01743	-73.17208	1
	-38.01824	-73.22494	1
	-38.35393	-73.92694	1
	-39.43464	-73.21289	1
	-39.63808	-72.33494	1
	-39.80236	-73.25997	1
	-39.84517	-73.29478	1
	-39.86961	-73.39462	1
	-39.88607	-73.43211	1
	-40.16117	-73.66398	1
	-40.52833	-73.70771	1
	-40.55296	-73.71374	1
	-41.03432	-71.88996	1
	-41.04311	-71.98007	1
	-41.20839	-72.53852	1
	-41.22545	-72.27370	1
-41.22847	-72.26451	1	
-41.46915	-72.93076	1	
-41.86629	-73.82231	1	
-42.01883	-72.69432	1	
-44.32650	-72.55200	1	
Present-day dataset	-35.83300	-72.50805	0
	-35.93611	-71.60738	0
	-36.85260	-73.04167	0
	-36.90967	-73.01728	0
	-36.91013	-73.01607	0
	-36.92058	-72.96992	0
	-37.02125	-72.97117	0
	-37.03293	-73.01263	0
	-37.24473	-73.48612	0
	-37.29798	-73.25164	0
	-37.30058	-73.25038	0
	-37.31148	-73.25317	0
	-37.77235	-73.19883	0
	-37.82122	-73.02545	0
	-37.82487	-73.01365	0
	-37.82600	-73.02467	0
	-37.82785	-73.01005	0
	-37.82894	-73.17269	0
	-37.82925	-73.16339	0
	-37.83083	-73.16167	1
	-37.83150	-73.16228	1
	-37.84153	-72.99883	0
	-37.88992	-73.27578	0
-37.89042	-73.27553	1	
-37.89306	-73.28550	0	

-37.89419	-73.28636	1
-37.90961	-73.29110	0
-38.01158	-73.18225	1
-38.01743	-73.17208	1
-38.03058	-73.20472	1
-38.28658	-72.09952	0
-38.72866	-72.58804	0
-39.13722	-71.71312	0
-39.13894	-71.70967	1
-39.13900	-71.70995	1
-39.14889	-71.71183	0
-39.15092	-71.71506	0
-39.48650	-71.85310	1
-39.48683	-71.85328	1
-39.48694	-71.85292	1
-39.48700	-71.85281	1
-39.51612	-71.86251	0
-39.55036	-71.98803	1
-39.55047	-71.98817	1
-39.57967	-71.53383	0
-39.69815	-73.30187	1
-39.69840	-73.30220	1
-39.71520	-73.40242	0
-39.77497	-71.63925	1
-39.79155	-71.66504	1
-39.80089	-71.52733	1
-39.85315	-71.96065	1
-39.85325	-71.96061	1
-39.85856	-71.93550	1
-39.86367	-71.91728	1
-39.86761	-71.91192	1
-39.86988	-71.91832	1
-39.87022	-71.91175	1
-39.87025	-71.91181	1
-39.87258	-71.91975	1
-39.87261	-71.91367	1
-39.87267	-71.91353	1
-39.87436	-71.92047	1
-39.87483	-71.92164	1
-40.13725	-71.65843	0
-40.19792	-73.43711	1
-40.54800	-73.69117	0
-40.66376	-72.17085	1
-40.66456	-72.17550	1
-40.66798	-72.18556	1
-40.68189	-72.14317	0
-40.68206	-72.14317	1
-41.01469	-71.82191	1
-41.44117	-72.19175	0
-41.83893	-73.60075	1
-41.88080	-73.67605	1
-41.88130	-73.67605	1
-41.88147	-73.67623	1
-41.88197	-73.67557	1
-41.88200	-73.67562	1
-41.88789	-72.38294	0
-42.37586	-72.41082	0
-42.38760	-72.40110	0
-42.85128	-74.08827	1
-42.85308	-74.07853	1

-42.93910	-73.49431	1
-42.97203	-72.46464	1
-43.02533	-73.79739	1
-43.08475	-72.45835	0
-43.12542	-73.98862	1
-43.13892	-74.04710	1
-43.15005	-74.08957	1
-43.16478	-74.12077	0
-43.16478	-74.12077	1
-43.19575	-74.11463	1
-43.24677	-74.12463	1
-43.27587	-72.43217	0
-43.28540	-74.12175	1
-43.29893	-74.11620	1
-43.35332	-74.11199	1
-43.35654	-74.10807	1
-43.35797	-74.11114	1
-43.35878	-74.11147	1
-43.35956	-74.11136	1
-43.35976	-74.13733	0
-43.36118	-74.11108	1
-43.36128	-74.11130	1
-43.36137	-74.11902	1
-43.36150	-74.11058	1
-43.36267	-74.11093	1
-43.36378	-74.12273	0
-44.08778	-73.08242	1
-44.08806	-73.08356	1
-44.08806	-73.08376	1
-44.08919	-73.08369	1
-44.09649	-73.09682	0
-44.09650	-73.09682	0
-44.10821	-73.11854	1
-44.11045	-73.11899	0
-44.23100	-72.50677	1
-44.23210	-72.50663	0
-44.23222	-72.50660	1
-44.23225	-72.50618	1
-44.23303	-72.53877	0
-44.23327	-72.50933	1
-44.23332	-72.50930	1
-44.23340	-72.50922	1
-44.23366	-72.50869	1
-44.23430	-72.50696	1
-44.31407	-72.53257	0
-44.32168	-72.54320	0
-44.46984	-72.54042	0
-44.62046	-72.91927	0
-44.62804	-72.96297	0
-44.63034	-72.96633	0
-45.09967	-72.95541	1
-45.18970	-72.95238	1

Table S2. Published dispersal kernels fitted for amphibian species.

Publication	Specie	Distance [m]	Probability of movement (1 year period)
Kovar et al. 2009	<i>Lissotriton vulgaris</i>	1000	0.0018182014
		2000	0.0000694200
		2500	0.0000205998
		3000	0.0000071912
		4000	0.0000012243
	<i>Mesotriton alpestris</i>	1000	0.0403505354
		2000	0.0137354567
		2500	0.0093302509
		3000	0.0067039344
		4000	0.0038736591
	<i>Triturus cristatus</i> MINIMUM DISPERSAL SCENARIO	1000	0.0000408084
		2000	0.000000904
		2500	0.000000090
		3000	0.000000012
		4000	0.000000000
	<i>Bombina bombina</i>	1000	0.0006589338
		2000	0.0000653491
		2500	0.0000287910
		3000	0.0000143359
		4000	0.0000045353
	<i>Bufo bufo</i>	1000	0.000017796
		2000	0.0124026118
		2500	0.0009243800
		3000	0.0003452872
		4000	0.0001462269
	<i>Rana arvalis</i>	1000	0.0000340830
		2000	0.0000101130
		2500	0.0500623583
		3000	0.0070545444
		4000	0.0033107077
	<i>Rana temporaria</i> MAXIMUM DISPERSAL SCENARIO	1000	0.0017034202
		2000	0.0005479031
		2500	0.0002113160
		3000	0.1094610939
		4000	0.0557328485
Sinsch et al. 2012	<i>Epidalea calamita</i> (Sandy soils- empirical)	1000	0.0437945153
		2000	0.0356519798
		2500	0.0253576971
		3000	0.0192029822
		4000	0.3092340000
	<i>Epidalea calamita</i> (Sandy soils- potential)	1000	0.0907676000
		2000	0.0268259000
		3000	0.0037003600
		4000	0.0009762080
		5000	0.4941060000
Sinsch 2014	<i>Epidalea calamita</i> (empirical)	1000	0.2454920000
		2000	0.1192100000
		3000	0.0584622000
		4000	0.0297608000
		5000	0.3123390000
Tingley et al. 2013	<i>Rhinella marina</i>	1000	0.0964010000
		2000	0.0295630000
		3000	0.0077120800
		4000	0.0003963590
		5000	0.0001411400