Mutualism influences species distribution predictions for a bromeliad-breeding anuran under climate change

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Abstract   Ecological niche models, or species distribution models, have been widely used to identify potentially suitable areas for species in future climate change scenarios. However, there are inherent errors to these models due to their inability to evaluate species occurrence influenced by non-climatic factors. With the intuit to improve the modelling predictions for a bromeliad-breeding treefrog (*Phyllodytes melanomystax*, Hylidae), we investigate how the climatic suitability of bromeliads influences the distribution model for the treefrog in the context of baseline and 2050 climate change scenarios. We used point occurrence data on the frog and the bromeliad (*Vriesea procera*, Bromeliaceae) to generate their predicted distributions based on baseline and 2050 climates. Using a consensus of five algorithms, we compared the accuracy of the models and the geographic predictions for the frog generated from two modelling procedures: (i) a climate-only model for *P. melanomystax* and *V. procera*; and (ii) a climate-biotic model for *P. melanomystax*, in which the climatic suitability of the bromeliad was jointly considered with the climatic variables. Both modelling approaches generated strong and similar predictive power for *P. melanomystax*, yet climate-biotic modelling generated more concise predictions, particularly for the year 2050. Specifically, because the predicted area of the bromeliad overlaps with the predictions for the treefrog in the baseline climate, both modelling approaches produce reasonable similar predicted areas for the anuran. Alternatively, due to the predicted loss of northern climatically suitable areas for the bromeliad by 2050, only the climate-biotic models provide evidence that northern populations of *P. melanomystax* will likely be negatively affected by 2050.

Key words: Atlantic Forest, biotic interactions, climate change, *Phyllodytes melanomystax*, species distribution models.

INTRODUCTION

Changes in precipitation and temperature regimes worldwide have resulted in species altering their phenological life-history events (e.g. timing of breeding events) or shifting their distributional ranges (Bellard *et al.* 2012; Araújo *et al.* 2013). However, for most taxa, and particularly in the biodiverse tropics, extensive historical information on species distribution is either unavailable or imprecise, which makes it impossible reliably evaluate how climate change has affected species distribution on a biogeographical scale. In these circumstances, researchers make use of predictive tools to compare the differences between species' current ranges and their predicted climatically suitable areas in order to assess the potential effects of climate change on species distribution (Araújo & Luoto 2007; Silva *et al.* 2014; Vasconcelos 2014; Vasconcelos & Nascimento 2016).

These tools are commonly known as ecological niche models (ENMs) or species distribution models (SDMs).

Ecological niche models are important tools for understanding the whole-range geography and ecology of species (Araújo & Peterson 2012). These methods generally consider the climatic preferences of a species across its known points of occurrence to generate the potential geographic ranges within a bioclimatic envelope (Elith & Burgman 2002). These models assume that climate has a major influence on species distribution limits (see the review in Araújo & Peterson 2012). Though widely used in a range of fields within biology, ENMs are known to generate errors due to their inability to evaluate cases of species presence and/or absences associated with evolutionary processes, dispersal limitations, and biotic interactions with other species (Vasconcelos *et al.* 2012 and references therein). However, these issues may not necessarily represent true errors if a clear conceptual application is defined prior to the use of the ENM (Araújo & Peterson 2012). For instance,

errors of commission (i.e. the model predicts species presence where it is not recorded) may represent either predictions of interest (if the goal is to identify potential or abiotically suitable areas of a species for occurrence in the future climate change scenario) or areas with environmental conditions suitable for a rare species if the knowledge on its geographic distribution is incomplete (e.g. Araújo & Peterson 2012; Vasconcelos & Nascimento 2016).

Conceptually, the term species distribution model (SDM) implies that the geographic distribution of the species is the quantity being modelled rather than the climatic niche (i.e. the potential climatically suitable area) considered in the designation of the ENMs (Araújo & Peterson 2012). Therefore, species distribution modelling must include steps that transform estimated areas from potential areas (e.g. ENMs) to actual areas so as to aid in the accurate reconstruction of distributions (Peterson & Soberón 2012). Therefore, SDMs are usually benefited when non-climatic variables are implemented into the modelling process (e.g. Araújo & Luoto 2007; Bateman *et al.* 2012), but this task is not straightforward: the decision over whether to include specific non-climatic variables requires case-specific considerations based on the auto-ecology of the species (Triviño *et al.* 2011).

Although biotic variables are argued to largely influence the species distribution on a local scale (e.g. Willis & Whittaker 2002), this assumption seems to be more evident only for negative species interactions, such as competition and amensalism (Araújo & Rozenfeld 2014). Thus, biotic variables that reflect positive interactions (e.g. mutualism and commensalism) are manifested across scales (Araújo & Rozenfeld 2014) and are usually helpful in broad-scale studies on improving SDM predictions and generating the potential geographic ranges of species (Araújo & Luoto 2007; Bateman *et al.* 2012; de Araújo *et al.* 2014). Though they sometimes fail to improve the algorithms' ability to predict species distribution, biotic interactions in SDMs can still produce different range predictions than climate-only modelling (e.g. Silva *et al.* 2014).

This study investigates how mutualism influences the SDM predictions for a bromeliad-breeding frog and considers both baseline and future climate change scenarios. Many bromeliads live in low-nutrient environments in which they could derive nutrients from sources such as frog faeces through the absorption of specialized foliar trichomes (Romero *et al.* 2010). Meanwhile, some anurans are dependent on the rainwater accumulated in the rosettes of bromeliads to deposit eggs where tadpoles will develop (e.g. Giaretta 1996; Haddad & Prado 2005; Peixoto & Pimenta 2010). Hence, some anurans are completely dependent on bromeliads for reproduction; this is

true of the genus *Phyllodytes* (Hylidae) (Haddad & Prado 2005). For this reason, we investigate how climatic suitability across the geographic range of a widely distributed bromeliad (*Vriesea procera*) in which the *Phyllodytes* species are most commonly found (Giaretta 1996; Schineider & Teixeira 2001; Ferreira *et al.* 2012) influences SDM predictions of the range of the treefrog *Phyllodytes melanomystax* (Hylidae). Specifically, we intend to answer the following questions: (i) does the implementation of climatic suitability for the bromeliad as a new predictor improve the accuracy of the treefrog distribution model? and (ii) does the implementation of this plant's climatic suitability into the treefrog distribution model generate different range predictions for the treefrog compared to a climate-only modelling approach? To answer these questions, we generated ENM predictions for these two mutualistic species and implemented climatic suitability for the bromeliad into a new climate-biotic model (SDM) for the treefrog. We also evaluated how the effects of global climate change may affect the treefrog distribution by 2050. To do so, we projected the ecological niche of both mutualistic species into future climate change scenarios and, again, implemented future climatic suitability for the bromeliad to predict the geographic extent of the treefrog by 2050.

MATERIALS AND METHODS

Species data collection

Phyllodytes melanomystax is a Hylidae treefrog endemic to the Atlantic Forest domain and restricted to the Brazilian states of Bahia and Sergipe in the northeastern region of the country. Specimens tend to be found in habitats consisting of coastal sandy plains covered by herbaceous and shrubby vegetation commonly known as *restinga* forests (Peixoto & Pimenta 2010; Haddad *et al.* 2013; Xavier *et al.* 2015). The individuals of this species, as well as other *Phyllodytes* species, are often associated with bromeliads (Bastazini *et al.* 2007; Camurugi *et al.* 2010; Dabés *et al.* 2012; Haddad *et al.* 2013) because they depend on bromeliad axils for breeding, egg laying, larval development, and foraging (Haddad & Prado 2005; Ferreira *et al.* 2012). The most common bromeliad species in which these frogs are found is *V. procera* (Bromeliaceae) (Giaretta 1996; Schineider & Teixeira 2001; Ferreira *et al.* 2012). This bromeliad is widely distributed along the Atlantic coast, from northeastern to southern Brazil, and is found in different vegetation types, including ombrophilous, semideciduous, and deciduous forests (Forzza *et al.* 2014). The other bromeliad species (Bromeliaceae) that *Phyllodytes* species rely on have a similar (*Aechmea nudicaulis*) or smaller (*Aechmea blanchetiana*, *Aechmea aquilega*) extent of occurrence across the same geographic range of *V. procera* (Forzza *et al.* 2014). Many factors affect the amount of occurrence records available: *V. procera* is the most common bromeliad in which *Phyllodytes* species are found; the geographic range of this

bromeliad overlaps the distribution range of the other bromeliads; and the surveys in open-access digital databases (see next paragraph) did not return enough unique occurrence records for the distribution model for the bromeliads *A. aquilega*, *A. blanchetiana*, or *A. nudicaulis*. Therefore, we used only the occurrence records of *V. procera* as the biotic variable in the climate-biotic modelling of *P. melanomystax* (see ahead).

The main sources for the point occurrence data on *P. melanomystax* were two open-access digital databases (the Global Biodiversity Information Facility, or GBIF; www.gbif.org, and the SpeciesLink project; http://splink.cria.org.br) and the amphibian collections from Brazilian institutions known as the Museu Nacional/Universidade Federal do Rio de Janeiro (Rio de Janeiro, Rio de Janeiro) and the Museu de Zoologia da Universidade Federal da Bahia (Salvador, Bahia). We included additional *P. melanomystax* records available from the following Brazilian collections: the Museu de Zoologia da Universidade Estadual de Santa Cruz (Ilhéus, Bahia), the Museu de Zoologia da Universidade Estadual de Feira de Santana (Feira de Santana, Bahia), and the Universidade Federal do Rio Grande do Norte (Natal, Rio Grande do Norte). We also considered the amphibian collections from the Universidade Estadual do Sudoeste da Bahia (Vitória da Conquista, Bahia) and the Universidade Federal da Paraíba (João Pessoa, Paraíba), but there were no *P. melanomystax* records available in these collections. The representative records of the distribution of *V. procera* were obtained only from the aforementioned open-access digital databases (GBIF and SpeciesLink). After removing duplicate, imprecise, and/or erroneous records (see protocol in Vasconcelos & Nascimento 2014), we were able to obtain 26 unique occurrence records for *P. melanomystax* and 216 unique records for *V. procera*. These records were applied in the modelling process (Appendices S1 and S2).

Modelling procedure

We used five modelling methods to build the ENMs and SDMs: boosted regression trees, or BRTs (Friedman 2001), the generalized linear model, or GLM (McCullagh & Nelder 1989), the generalized additive model, or GAM (Hastie & Tibshirani 1990), random forests, or RFs (Breiman 2001), and support vector machines, or SVMs (Vapnik 1995). These models are generally classified into two types (*sensu* Rangel & Loyola 2012): (i) statistical methods (GAM and GLM), which have best-practice applications when to the goal is to incorporate the consequences of the interaction between factors for the distribution of species; and (ii) machine-learning methods (BRT, RF, and SVM), which work well when the researcher wants to describe the actual (not potential) geographic distributions when all, or almost all, populations are known. These methods are known to produce reasonably reliable results, so descriptions, applications, and comparisons of model performances can be found in Elith *et al.* (2006), Elith and Graham (2009), Araújo *et al.* (2011), Vasconcelos (2014), and Naimi and Araújo (2016). For each model run, we entered 20% of the sample records as a *random test percentage*, meaning that 80% of the dataset was used for calibration (training) and the remaining 20% was used for model evaluation. This procedure was replicated ten times using random subsampling without replacement (Naimi & Araújo 2016). The models were evaluated by the two accuracy metrics most traditionally used in the SDM literature. The first is the area under the receiver operating characteristics (ROC) curve (or simply AUC: area under the curve), which is a threshold-independent statistic that is considered a highly effective measure for the performance of ordinal score models whose area under the curve (AUC) ranges from 0 to 1 (Allouche *et al.* 2006). AUC values of 0.5 represent a model no better than random, whereas a value of 1 indicates perfect model discrimination between presence and absence records (Elith & Burgman 2002). The second metric is the true skill statistic (TSS), a threshold-dependent statistic that takes into account both omission and commission errors, which is not affected by prevalence (i.e. the proportion of presence sampling points), and which ranges from -1 to 1 (Allouche *et al.* 2006). Values close to -1 indicate a model no better than random, and values close to 1 indicate a perfect fit (Allouche *et al.* 2006).

We used the extent of the Atlantic Forest as the calibration area when running the models because it is the range of the bromeliad *V. procera*. We selected seven climatic variables as potential predictors to building the distribution models of the bromeliad and the frog. These variables were selected to describe general climatic trends (i.e. mean values), variations in temperature and precipitation over time, and potential physiological limits for the organisms (Nix 1986; Vasconcelos *et al.* 2012). The variables selected were annual mean temperature, temperature seasonality, minimum temperature of the coldest month, temperature annual range, annual precipitation, precipitation seasonality, and precipitation of the warmest quarter. To avoid collinear and redundant climatic variables in the modelling process, we applied the variance inflation factor (VIF) analysis to these variables (Naimi & Araújo 2016). We then removed temperature seasonality and minimum temperature of the coldest month because they produced high VIF values (>10), results which represent collinearity problems for model building (Naimi & Araújo 2016). A new VIF analysis was applied to the remaining five variables, which all presented VIF values lower than 10. They were therefore selected as predictor variables for the model building. These climatic variables were obtained from the WorldClim database at a spatial resolution of ~5 km (Hijmans *et al.* 2005). To project the ecological niche of the species in scenarios for 2050, we used two representative concentration pathways (RCPs) from CO_2 emission scenarios: RCP2.6 and RCP8.5. These two RCPs represent the two extremes of more *optimistic* and *pessimistic* scenarios in terms of CO_2 emmisions (Diniz-Filho *et al.* 2009). RCPs were obtained from three different atmosphere-ocean global circulation models (AOGCMs) of the Intergovernmental Panel on Climate Change (IPCC Fifth Assessment Report), available on the WorldClim portal (http://www.worldclim.org/cmip5_5m): the Community Climate System Model (CCSM4), the New Global Climate Model of the Meteorological Research Institute (MRI-CGCM3), and the Institute Pierre Simon Laplace (IPSL-CM5A-LR).

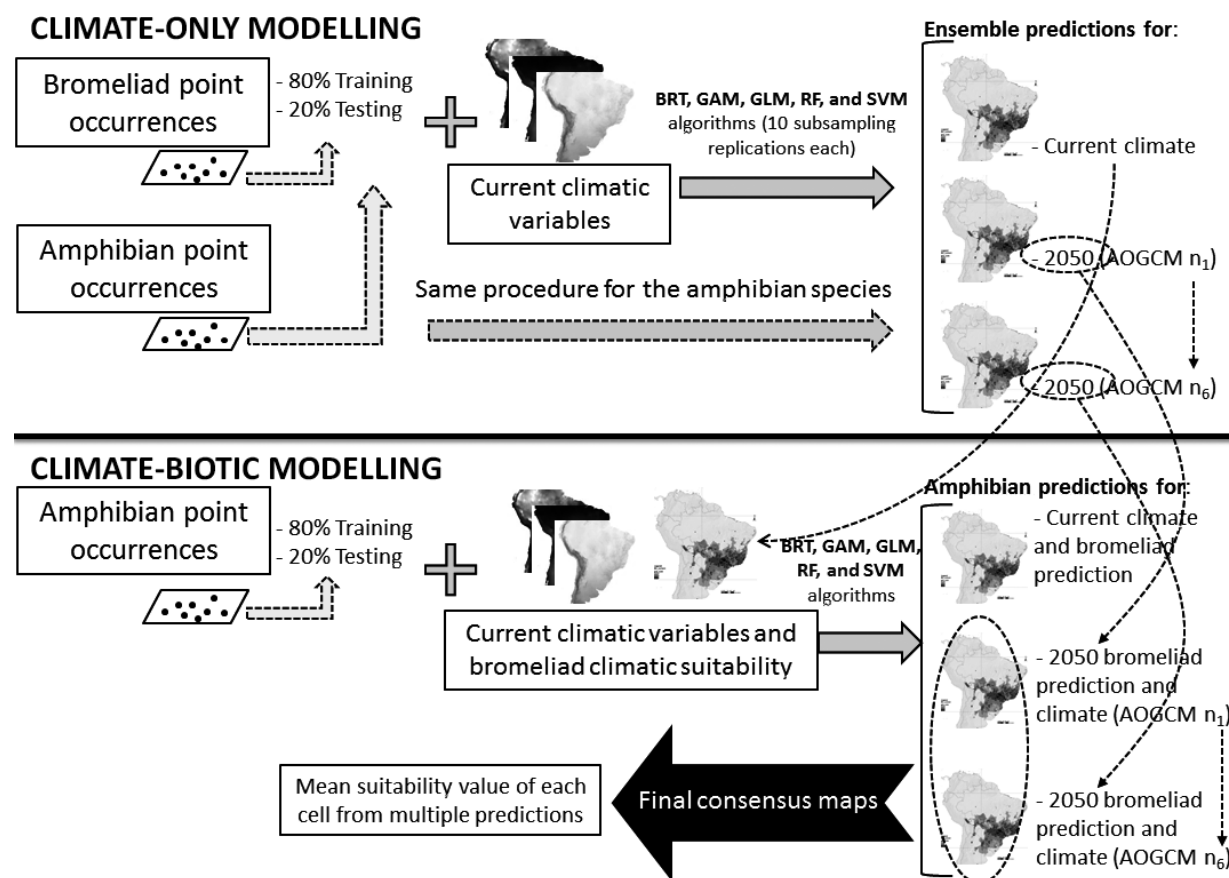We performed two modelling procedures for *P. melanomystax*. They are schematically represented in Figure 1.

Fig. 1. Schematic representation of the modelling procedure performed in this study.

First, we performed an ENM procedure (i.e. a climate-only approach) that considers the five climatic aforementioned variables for *P. melanomystax* and *V. procera*, which were then projected onto the different climate change scenarios. In the second step, the climatic suitability for *V. procera* was implemented in the SDM procedure for *P. melanomystax* (the climate-biotic modelling approach) jointly with the previous five climatic predictors. This new characterization of the ecological niche of *P. melanomystax* (i.e. considering the five climatic variables and climatic suitability for *V. procera*) was then projected to future climate change scenarios and the plant's climatic suitability in 2050 obtained from the climate-only approach (Fig. 1).

Ensemble forecasting and data analyses

To determine any differences in model accuracy between the climate-only and the climate-biotic modelling approaches for each modelling algorithm (i.e. to determine if the implementation of climatic suitability for the bromeliad as a new predictor improves the accuracy of the tree-frog distribution model), we compared the AUC and TSS values of each of the ten subsampling replicates obtained from the two modelling approaches using the Wilcoxon signed-rank test for related samples (Zar 1999; Bateman *et al.* 2012).

To determine any differences in range predictions for the frog between the climate-only and climate-biotic modelling approaches, we calculated each of the distances between the centroids of the predictions after considering the baseline climate and 2050 predictions for each modelling approach. First, we generated ensemble forecasts for each time slice to reconcile the inherent differences between the modelling methods, the AOGCMs, and the RCPs, thus producing a more robust final prediction (Araújo & New 2007; Loyola *et al.* 2014; Vasconcelos & Nascimento 2016). To produce a consensus map based on the baseline climate of each modelling procedure, the ensemble of projections was calculated by a consensus that considered the mean probability of occurrence per grid cell of the 50 final models with 5 algorithms × 10 replications (e.g. Araújo *et al.* 2011). The consensus for the 2050 time slice considered the mean values per grid cell of the 300 final projections (5 algorithms × 10 replications × 3 AOGCMs × 2 RCPs). To create the representative centre (centroid) of the distributional predicted species range, we generated binary maps from each consensus output using threshold values. We followed Liu *et al.* (2005) and chose the threshold value in which the absolute value of the difference between sensitivity (proportion of accurately predicted actual presence) and specificity (proportion of accurately predicted actual pseudo-absence) is minimized, which is known as the sensitivity-specificity equality approach. Once we

gathered the binary maps from both the climate-only and climate-biotic models, we used the *feature to point* function in ArcGIS 10.1 to locate the centre of gravity (centroid) of the predicted distribution range. We were then able to characterize the distance and direction of the predicted range shifts from the current and 2050 predictions from the two modelling approaches (climate-only *vs.* climate-biotic modelling). General statistics on the total predicted area of the binary maps were also calculated using ArcGIS 10.1. All pre-processing (preparation of species and climate data), processing (model running), and post-processing (model evaluation and confection of ensemble maps) steps were performed in R using the *sdm* package (Naimi & Araújo 2016).

RESULTS

Area under the curve and TSS values from either climate-only or climate-biotic modelling indicate a high predictive power of the models generated for *P. melanomystax* (Tables 1,2) and *V. procera* (Appendix S3). The AUC (Table 1) and TSS values (Table 2) did not differ in their accuracy between the climate-only and climate-biotic approaches.

The predicted climatic suitability for *V. procera* is high throughtout the known occurrence records of the species (Appendix S4); however, under a climate change scenario for 2050, these values tend to decrease in inland areas off the Atlantic coast (Appendix S4). Specifically in northeastern Brazil, where the plant co-occurs with the treefrog, the plant is expected to have a smaller and more fragmented climatically suitable area by 2050, particularly along the rim of its northern distribution (Appendix S4).

When the baseline climate predictions generated for *P. melanomystax* were considered, the climate-only and climate-biotic models generated similar range predictions overall (Fig. 2a,b, Appendix S5), though the range of the climate-only model is more concentrated in the south when compared to the climate-biotic model, which resulted in centroid positions that were relatively far from each other (~449.64 km straight line; note the closed circles in

Fig. 2c,d). However, it is important to note that the climate-biotic model generated a smaller predicted area of the treefrog distribution (~12.61% smaller) when compared to the climate-only prediction (Fig. 2a,b). The differences in the predictions between the two modelling approaches are pronounced by 2050; the climate-biotic model generated a much smaller range size prediction (~63.92% smaller) and centroid positions that were also relatively distant from each other (~316.80 km straight line; see the triangles in Fig. 2c,d). These patterns reflect the loss of suitable predicted areas on the rim of the northern distribution of the treefrog in the climate-biotic approach, but losses are also found in the central-southern predicted area as well (Fig. 2c,d). In summary, the climate-only approach predicts that *P. melanomystax* will experience an increase in predicted climatic suitable area by 2050 relative to the baseline climate, with an associated centroid range shift of 643.12 km northeastward from baseline climate by 2050 (Fig. 2a,c). On the other hand, the climate-biotic model predicts loss of suitable areas in the northern and, to a lesser extent, southern predicted areas by 2050, with an expected centroid range shift of ~154.86 km southward from baseline climate by 2050 (Fig. 2b,d).

Table 2. Mean (±SD) true skill statistic (TSS) values for each modelling algorithm and modelling procedure (TSS$_{C-O}$, climate-only approach; TSS$_{C-B}$, climate-biotic approach), as well as values of the Wilcoxon test (V test) and their associated P-values

	Mean (TSS$_{C-O}$)	Mean (TSS$_{C-B}$)	V test	P-value
BRT	0.9947 ± 0.017	0.9801 ± 0.026	11	0.4164
GAM	0.871 ± 0.20	0.975 ± 0.029	3	0.5840
GLM	0.871 ± 0.20	0.954 ± 0.081	5	0.5896
RF	0.9852 ± 0.023	0.9894 ± 0.022	7.5	0.9980
SVM	0.9897 ± 0.022	0.9894 ± 0.022	5.5	0.9999

BRT, boosted regression trees; GAM, generalized additive model; GLM, generalized linear model; RF, random forest; SVM, support vector machine.

Table 1. Mean (±SD) area under the curve (AUC) values for each modelling algorithm and modelling procedure (AUC$_{C-O}$, climate-only approach; AUC$_{C-B}$, climate-biotic approach), as well as the values of the Wilcoxon test (V test) and their associated P-values

Algorithm	Mean (AUC$_{C-O}$)	Mean (AUC$_{C-B}$)	V test	P-value
BRT	0.9992 ± 0.003	0.9887 ± 0.015	14	0.1056
GAM	0.9315 ± 0.106	0.9837 ± 0.019	3	0.5839
GLM	0.9315 ± 0.106	0.9753 ± 0.038	4	0.4185
RF	0.9918 ± 0.014	0.9964 ± 0.01	5	0.5896
SVM	0.9952 ± 0.01	0.9926 ± 0.017	6	0.8551

BRT, boosted regression trees; GAM, generalized additive model; GLM, generalized linear model; RF, random forest; SVM, support vector machine.
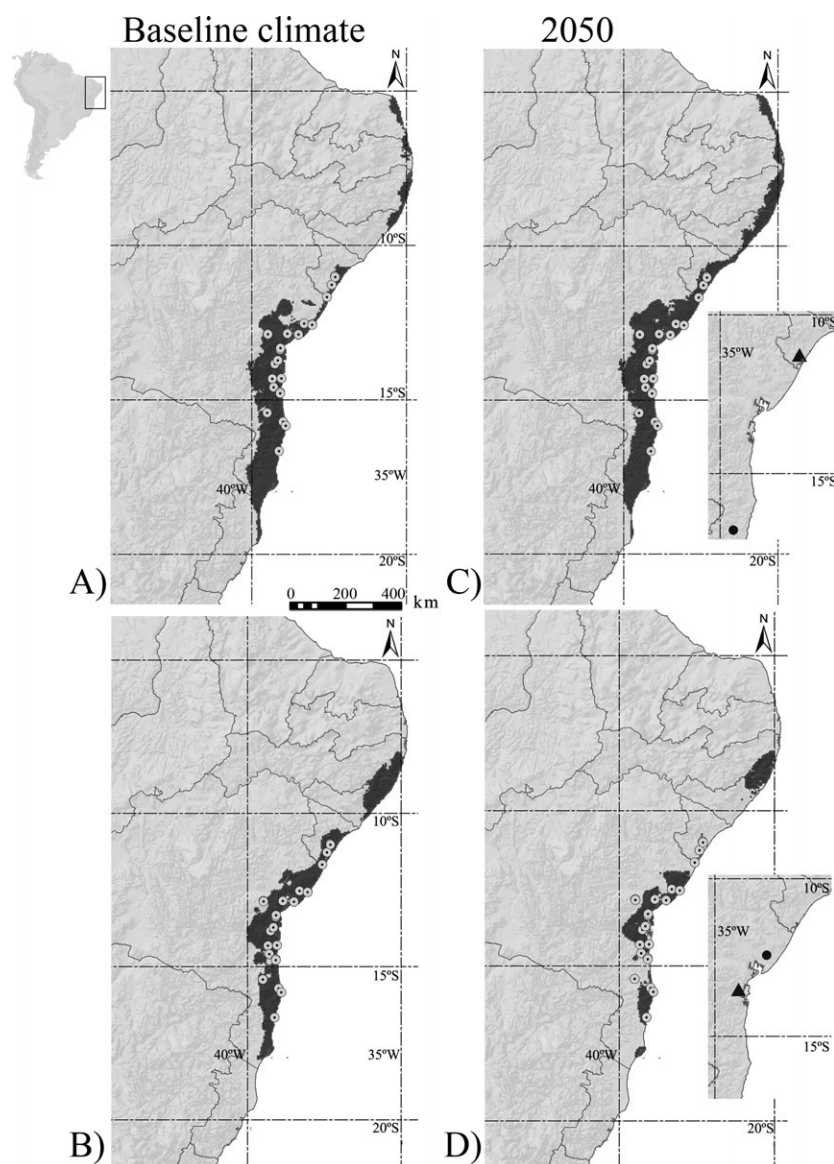
Fig. 2. Distributional suitability for *Phyllodytes melanomystax*. Predictions consider: (a) climate-only modelling and baseline climate; (b) climate-biotic modelling and baseline climate; (c) climate-only and 2050 climate change scenarios; and D) climate-biotic modelling and 2050 climate change scenarios. Circles and triangles showed in (c and d) represent the centroids of the predictions generated for the baseline climate (circles) and for the 2050 (triangles) climate change scenarios.

DISCUSSION

We found that implementing a biotic variable into the treefrog's distribution model did not improve model performance, but the models from both approaches (climate-only and climate-biotic modelling) were found to have high and similar predictive power. Nonetheless, implementing the modelled climatic suitability for the bromeliad into the SDM for *P. melanomystax* produced constrained range predictions, particularly in the 2050 climate change scenario. Similar results were found in a study for an invasive bee in South America that considered the mutualistic bee-flower interaction (Silva *et al.* 2014), and the authors suggested that the biotic variables implemented were not independent on the climatic variables used. In other words, there is a lack of increased model performance when implementing a biotic variable because the biotic variable itself is mainly determined by climate (Silva *et al.* 2014). It is well known that climate is a major driver of species geographic ranges (see review in Araújo & Peterson 2012), so the inclusion of a non-climatic variable may not substantially increase model performance (Silva *et al.* 2014; present study) – rather, the inclusion of a biotic variable may provide: (i) a lower

amount of unexplained variation remaining after the variation explained by climate; (ii) assistance to better define/adjust the predicted geographic limits of treefrog distribution; and (iii) a more concise prediction than the one provided by a climate-only approach. Therefore, although the biotic variable considered herein (climatic suitability for the bromeliad) does not improve the accuracy of models, it provides important information that is not present in other climatic variables, particularly in the 2050 predictions. It was the bromeliad climatic suitability itself that influenced the smaller range size predicted for the treefrog. The dependence of climatic suitability for the bromeliad on the treefrog range predictions was expected, since the treefrog in question directly depends on the bromeliad because of the reproductive requirements of the species (Haddad & Prado 2005).

Projecting the ecological niche for the baseline climate of *P. melanomystax* on a map did not result in major differences between the climate-only and climate-biotic models, though the centroids of the two modelling approaches were reasonably distant from each other. In other words, the maps represented in Figure 2a,b depict similar areas where *P. melanomystax* is expected to occur at present, and these maps consider the predictions generated by both modelling approaches. We believe that the similarities in these predictions are due to the fact that the predicted climatic suitability for the bromeliad (Appendix S4) is much larger and overlaps with the predictions for the treefrog. Therefore, regardless of the far-reaching southern climatic suitability for the bromeliad, these areas are not climatically similar when compared to the known records for the frog. As a result, the different algorithms used during the climate-biotic model run rendered the predicted areas as similar to those generated by the climate-only model with the baseline climate.

The more specialized species communities are, the more dependent they are likely to be on the fate of other species (Araújo & Luoto 2007). This phenomenon may be the main explanation for the differences in the model predictions between the climate-only and climate-biotic procedures obtained for *P. melanomystax* under the climate change scenarios. The potential effects of climate on the distribution of *V. procera* involve projected loss of climatically suitable areas in its northern and central extent of occurrence by 2050 (Appendix S4). Therefore, it follows that the predicted loss of suitable areas for *P. melanomystax* in the climate-biotic modelling involves the northern areas with projected loss for the bromeliad by 2050. This loss manifests as ~63.92% less area predicted as suitable than in the 2050 climate-only model, a difference which provides evidence that the climate-only model depicts

only a partial representation of the species' predicted geographical distribution. Furthermore, the differences in the results between the climate-only and climate-biotic models have direct implications on the establishment of species conservation measures based on climate change scenarios (Araújo & Luoto 2007).

Our results do not corroborate previous studies that found improved models by incorporating biotic variables into SDMs (e.g. Araújo & Luoto 2007; Bateman *et al.* 2012; de Araújo *et al.* 2014). However, our findings do corroborate previous studies that failed to find improved models when implementing biotic variables, yet which recorded constrained predicted ranges (Silva *et al.* 2014 and references therein). Although we did not find improved model performance in the climate-biotic model, the rates of accuracy of the models were high and similar in the two approaches. Because climate is known to be a major determinant of species' geographic ranges (see Araújo & Peterson 2012), we may presume that little variation remains to be explained by non-climatic determinants (such as biotic interactions), so a significant increase in model accuracy in the climatic-biotic model may not be detected. Therefore, if models generated from a different set of predictors of a given species have similarly high accuracies, which model should be considered? We would choose the one that considers the predictors that directly affect the distribution of the species. In our case, it does not matter whether a location is climatically suitable for the occurrence of the frog if the host plant is not there (or is not presumed to be there), so the model containing the host plant becomes the more realistic scenario. There is important information on climatic suitability for the bromeliad that is not addressed in the climatic variables, so implementing a biotic variable helps to adjust the geographic predictions for the treefrog, which, in turn, generates a more concise prediction, particularly for 2050. Additionally, it is important to note some concerns that may hinder the validation of our predictions. First, we used only one bromeliad species (*V. procera*) in which *P. melanomystax* is found. Although this bromeliad is the species in which *Phyllodytes* frogs are most commonly found (Giaretta 1996; Schineider & Teixeira 2001; Ferreira *et al.* 2012), other bromeliads may be more common in specific areas. These other bromeliads include *A. aquilega* in Praia do Forte, part of the city of Mata de São João, state of Bahia in northeastern Brazil (Cunha & Napoli 2016). Thus, the use of additional bromeliad species after considering either all single or stacked plant distributions (e.g. Silva *et al.* 2014) may generate more realistic distribution models for our final predictions. Second, the massive habitat degradation that the Atlantic Forest has suffered (MMA & IBAMA 2011) is an additional threat

to the forest habitat where *P. melanomystax* is found. The implementation of land use scenarios (Tian *et al.* 2014), eco-physiological data on species, or information on population dynamics (Buckley 2013) into correlative/mechanistic models is also a future option for improving model predictions and generating robust information. This is the kind of information required for conservation measures that can mitigate the effects of current global climate change. However, if only point records are available to assess the effects of climate change on biodiversity distribution, the implementation of biotic variables into the modelling process can serve as a helpful option for studies on specialist species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Geographic coordinates (in decimal degrees) used for the modelling process of *Phyllodytes melanomystax*.

Appendix S2. Geographic coordinates (in decimal degrees) used for the modelling process of *Vriesea procera*.

Appendix S3. Mean (±SD) of AUC and TSS values for each modelling algorithm (see methods for algorithms' abbreviation) performed for the bromeliad *Vriesea procera*.

Appendix S4. Distribution suitability of *Vriesea procera* for the: (a) baseline climate; (b) 2050; Predicted range distribution considering the binary threshold 'sensitivity = specificity' (Liu *et al.* 2005, see Methods) for the: (c) baseline climate; (d) 2050.

Appendix S5. Distribution suitability of *Phyllodytes melanomystax* for the: (a) climate-only model and baseline climate; (b) climate-biotic model and baseline climate; (c) climate-only model and 2050; and (d) climate-biotic model and 2050.