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ORIGINAL PAPER

Native range climate is insufficient to predict anuran invasive potential

Lilian P. Sales · **Raoni Rebouças** · **Luís Felipe Toledo**

Abstract Niche conservatism explains biological invasions worldwide. However, a plethora of ecological processes may lead invasive species to occupy environments that are different from those found within native ranges. Here, we assess the potential invadable areas of the world's most pervasive invasive amphibians: the cane toad, *Rhinella marina* + *R. horribilis*, and the North American bullfrog, *Lithobates catesbeianus*. The uncontrolled spread of such voracious, large-bodied, and disease-tolerant anurans has been documented to impact native faunas worldwide. To disentangle their invasion-related niche dynamics, we compared the predictive ability and distributional forecasts of ecological niche models calibrated with information from native, invaded and pooled (native + invaded) ranges. We found that including occurrences from invaded ranges improved model accuracy for both studied species. Non-native occurrences also accounted for 54% and 61% increase in the total area of potential distribution of the cane toad and bullfrog, respectively. Besides, the latter species occupied locations with climatic conditions that are more extreme than those found within its native range. Our results indicate that the occupancy of environments different from those found in native ranges increases the overall potential distribution of the studied invasive anuran species. Therefore, climate information on native ranges alone is insufficient to explain and anticipate the distributional patterns of

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invasion of cane toads and bullfrogs, underestimating predictions of potential invadable distribution. Moreover, such an observed expansion of realized niches towards occupancy of climates not found within native ranges also has clear implications for invasion risk assessments based on climate modelling worldwide.

Introduction

The origins and mechanisms of the spread of non-native species have long interested ecologists. The past couple of decades, however, have experienced a renewed interest in the general causes of biological invasion from the geographical perspective of species range dynamics and climatic niches shifts (Broenni-mann et al. 2012; Guisan et al. 2014; Sales et al. 2017). The tendency of several invasive species to retain their fundamental climatic niches (i.e., niche conservatism hypothesis; Wiens and Graham 2005; Peterson 2011), suggests that climate-related evolutionary constraints pose long-term and stable constraints to species geographic distributions (Peterson 2011; Pyron et al. 2015), which may be preserved during biological invasions.

Occupancy of environments that are different from native ranges, however, can arise from different processes, such as competitive release, artificial selection or even the truncated nature of the realized niche itself (Guisan et al., 2014). Interaction with superior competitors, for example, can prevent the occupancy of potentially suitable regions (Soberón and Peterson 2005). Therefore, the absence of competitive exclusion on invaded ranges can cause an observed expansion of realized niches (Bolnick et al. 2010). Niche expansion can also be the outcome of eco-evolutionary dynamics that drive changes in species' fundamental niches (Tingley et al. 2014), a process that usually does not happen within the timespan of anthropogenic biological invasions (Peterson 2011). Furthermore, domestication of wild species and the selection of individuals possessing traits on the extremes of phenotype distributions may also expand observed realized niches (Yanar et al.

2019). Regardless of the mechanism, not accounting for potential niche shifts during biological invasions often leads to underestimated invasion risk assessments (Jiménez-Valverde et al. 2011).

In this work, we compared the niche dynamics related to the invasion of two voracious, large-bodied, and disease-tolerant amphibians: the cane toad, the species complex formed by *Rhinella marina* (Linnaeus, 1758) + *R. horribilis* (Wiegmann, 1833) and the North American bullfrog (hereafter, bullfrog), *Lithobates catesbeianus* (Shaw, 1802). These species are included among the most pervasive invaders among all taxa (Lowe et al. 2000), due to the well-documented impact they pose on native faunas (Nori et al. 2011; Barbosa et al. 2017). Effects of cane toads and bullfrogs on native faunas span from increased predation and competitive exclusion (e.g., Snow and Witmer 2010), interference with the communication of other frog species (Both and Grant 2012; Forti et al. 2017), and induced morpho-physiological change of native predators (Phillips and Shine 2006a, b). In addition, their invasion has been associated with the co-introduction of lethal pathogens, such as chytrid fungus and ranavirus (Schloegel et al. 2009; O'Hanlon et al. 2018; Brunner et al. 2019), which have been linked to amphibian population declines and extinctions around the world (Scheele et al. 2019, 2020).

To understand the mechanisms that underlie the biological invasions of the cane toad and the bullfrog, we disentangled potential niche dynamics, comparing the environment occupied in native and invaded ranges, while mapping invadable areas. Specifically, we test for (i) differences in the niches of native *vs* non-native populations, while also (ii) looking for their mechanistic drivers. Also, we evaluate (iii) if models calibrated with native occurrences can accurately predict non-native occurrences, and (iv) the effect of including non-native records in models of species' potential distribution. Using such an approach, we aim to bring light not only to observed patterns but also to the mechanisms that control and facilitate the spread of invasive species.

Methods

Study species

Cane toads (*Rhinella horribilis* + *R. marina*) belongs to the family Bufonidae and are large-sized (snout-vent length of adult females ∼ 18 cm), lowland nocturnal species, which occur from sea level up to 1000 m of elevation. Cane toads are the most widely distributed and abundant New World amphibians around the world (Lever 2001), whose native populations are essentially Neotropical, occurring from Mexico to Brazil (Frost 2021). Non-native populations can be found in the Caribbean and Pacific Islands and southeastern Asia and Australia (Mayer et al. 2015; Pikacha et al. 2015; Tingley et al. 2017; Fig. 1a). Cane toads' generalist diet includes invertebrates and small vertebrates (Meshaka Jr and Powell 2000; Heise-Pavlov and Longway 2011; Pamintuan and Starr 2016), with recorded cannibalism in experimental conditions (Crossland et al. 2011). Reproductive rates

are high and clutch sizes comprise up to 30,000 eggs (Zug and Zug 1979; Lever 2001).

Recent evidence suggests the existence of two distinct species (*Rhinella horribilis* and *R. marina*) throughout the geographical distribution originally attributed to *Rhinella marina* (Acevedo et al. 2016). Such taxonomic rearrangement hinders the precise definition of the origin of translocated populations. Furthermore, all the literature on the recently revalidated *R. horribilis* can be found under *R. marina* so that it is not possible, using the methods we have in hand, to differentiate which populations were used for each translocation event. Therefore, we consider the monophyletic *Rhinella marina* + *R. horribilis* species complex as a single lineage of cane toads. We caution that our methods and results must be evaluated acknowledging that we are referring to this species complex.

Bullfrogs (*Lithobates catesbeianus*) belong to the family Ranidae and are also large-sized and nocturnal species (snout-vent length of adult females ∼ 16 cm; Howard 1981), considered the largest frog in North

Fig. 1 Cane toads (upper panel) and bullfrogs (lower panel) native and non-native distribution around the world. Dark-green-colored silhouettes indicate occurrences within species' native distribution, defined according to polygons of extent of occurrence provided by the International Union for the Conservation of Nature, while pale-pink silhouettes represent non-native occurrences. This figure represents a subset of the total occurrence dataset, to differentiate global invasion patterns
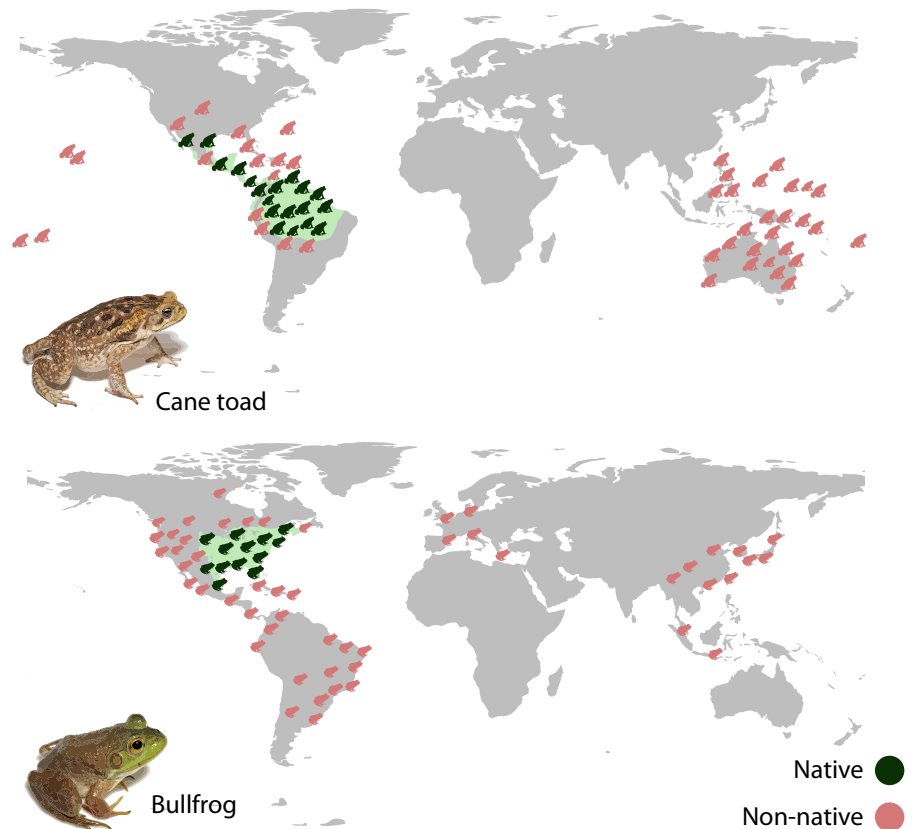
America and among the largest true frogs in the world (D'Amore 2012). Native bullfrog populations occupy vast areas of the Nearctic region, being recorded in the eastern United States, Canada, and Mexico (Fig. 1b). Non-native populations are also found worldwide once the species was introduced in all continents except Antarctica (D'Amore 2012). Bullfrogs' feeding habits are generalist and opportunistic; most of the diet is composed of invertebrates and small vertebrates (Simon and Toft 1991; Jacowski and Orchard 2013), including other frogs and cannibalistic behaviour (Stuart and Painter, 1993; Toledo et al. 2007; Leivas et al. 2012). Offspring production is also abundant, where females can lay more than 20,000 eggs per clutch (Howard 1978).

Data collection

We collected geo-referenced occurrence data for cane toads (*R. marina* + *R. horribilis* species complex) and bullfrogs (*L. catesbeianus*) from different online repositories, namely: the Global Biodiversity Information Facility (GBIF; www.gbif.org), the VertNet (www.vertnet.org), the Biodiversity Information Serving Our Nation (BISON; www.bison.usgs.ornl.gov), the Berkeley Ecoinformatics Engine (Ecoengine; www.ecoengine.berkeley.edu), and the iNaturalist (www.inaturalist.org). Records were downloaded (date of search: February 3rd 2020, no DOI was generated) using the function *occ()*, then collapsed into the same string using the function *fixnames()*, both from the R package *spocc* (Scott et al. 2016). Additional data for *L. catesbeianus* were extracted from Both et al. (2011) and Hanselmann et al. (2004). All geographic coordinates positioned exactly in centroids of political polygons were ignored, as well as duplicates, incomplete coordinates, and those that were georeferenced to museum locations. Data cleaning was based on the suite of *coord_* functions from R package *scrubr* (Chamberlain 2016). In addition, all records were individually quality-checked, according to available literature (Hanselmann et al. 2004; Both et al. 2011) and to our own experience.

Species' native ranges were defined according to polygons of extent of occurrence considered "native" by the International Union for the Conservation of Nature [henceforth, IUCN range maps] (IUCN 2020). Such polygons are useful to identify current distributional limits of species (Sales et al. 2017), as well as to inform conservation planning, wildlife management and monitoring (Rodrigues et al. 2006). To account for border uncertainty, we added a 200 km buffer to IUCN range maps. This 200 km threshold is above the known dispersal abilities of most amphibians and was chosen as a conservative attempt to distinguish invasion from climate niche tracking (Urban 2020). By doing so, *invasion* is considered here as a process in which a species occupies territories that are widely distant from native ranges, most likely intentionally introduced or otherwise anthropogenically-driven. In contrast, *climate tracking* occurs when a species colonizes areas that are adjacent to the species' native distribution and that became available due to recent environmental change, as defined by Urban (2020). This buffer around the species' current extent of occurrence, therefore, intends to accommodate the uncertainty related to potential recent range expansion due to climate niche tracking. All occurrence records located outside this expanded polygon were considered non-native. To minimize problems related to spatial autocorrelation (Broennimann et al. 2012; Strubbe et al. 2015), we randomly removed occurrences less than 0.5 degrees from each other from the full dataset (both native and non-native ranges), using the function *ecospat.occ.desaggregation()* from R package *ecospat* (Broennimann et al., 2016). A total of 495 occurrence records were included for the cane toad (231 native and 264 non-native), while the bullfrog dataset comprised 1164 records (830 native and 334 non-native) (Fig. 1, Supporting occurrences *Ocorr_supp.csv*).

Ecological niche models

We predicted the potential invadable areas for cane toads and bullfrogs using climate-calibrated ecological niche models (Broennimann and Guisan 2008; Jiménez-Valverde et al. 2011). Climate information for the contemporary conditions encompassed a time range of 30 years (1960–1990) and was downloaded from WorldClim version 1.4 (www.worldclim.org/data/v1.4), using the function *getData()* from the *raster* R package (Hijmans and van Etten 2016), as 10′ resolution gridded files. Here, we used *bioclimatic variables*, which are derived from monthly temperature and precipitation values but adjusted to express situations that likely influence species' ranges

(Hijmans et al. 2005), such as annual trends, seasonality and extreme climatic events. Prior to calibrating ecological niche models, we tested for multicollinearity among predictors using a stepwise approach (Naimi et al. 2014). At first, we calculated the variance inflation factor (VIF) for all variables. Then, a pairwise correlation matrix identified highly correlated variable pairs. Correlation values above 0.7 were highlighted and the variable with the highest VIF was then excluded from the pair, using the function *vifstep()* from *usdm* R package (Naimi et al. 2014). This procedure was repeated until all the strongly correlated variables were excluded, which resulted in eight predictors for bullfrogs' models (BIO2, BIO7, BIO8, BIO9, BIO10, BIO13, BIO15, BIO18) and nine for cane toads (BIO2, BIO3, BIO4, BIO8, BIO13, BIO14, BIO15, BIO18, BIO19).

We estimated potential invadable areas using ecological niche models (ENMs) calibrated with climate data associated with the species' occurrence data, following acknowledged standards (Araújo et al. 2019). Species-specific study areas were built by limiting our background to a bounding box of species environmental points, plus an additional 10 degrees to each bound, thus only encompassing regions that are probably accessible to species via migration (Barve et al. 2011). Environmental layers were, then, cropped to adjust to the study extent and 10,000 background/ pseudo-absence points were sampled one per cell, with no replacement (Barbet-Massin et al. 2012). To assess the environmental conditions associated with species' occurrences, we used *Maxlike*, a widely used presence-only method known to be well-suited in estimating species' potential distribution (Jiménez-Valverde et al. 2011). The output parameters of *Maxlike* have formal relationships with the classical *Maxent* software (Fitzpatrick et al. 2013; Merow and Silander Jr, 2014), plus the added benefit of directly estimating the probability of occurrence using presence-only data (Royle et al. 2012). We chose to use such a presence-only method because invasion risk assessments must not rely on true absence information, which is often biased by sampling effort (Guillera-Arroita et al. 2015).

Model accuracy was evaluated using a repeated sub-sampling procedure where 25% of occurrence records were randomly selected for model validation and the remaining 75% were used for model training.

This procedure was repeated 30 times for each modelling method per species. Two metrics were used to assess model accuracy: (i) the true skill statistic (*TSS*) (Allouche et al. 2006), and (ii) the area under the receiver operating characteristic curve (*AUC*) (Fielding and Bell 1997). While AUC is a threshold-independent metric, measuring TSS relies on selecting an environmental threshold where presences and absences are discriminated from each other. By using multiple evaluation metrics, we also explored the sensitivity of our results to the uncertainty that arises from threshold-based metrics (Leroy et al. 2018). Then, we selected a threshold that maximized TSS (Liu et al. 2005) to convert continuous predictions of climate suitability into binary maps. Finally, we used an ensemble forecasting procedure to generate a consensus prediction for each species by combining individual model outcomes, by weighting averaged suitability predictions by the accuracy of the model.

To test for the effect of the inclusion of non-native occurrences on model outcome, we created different combinations of dataset sub-sampling, namely (i) *Native-native* models trained and validated with occurrences from native ranges; (ii) *Native-invaded* models trained with native occurrences and validated with non-native (invaded) occurrences; and (iii) *Pooled* models trained and validated with both native and non-native (invaded) occurrences to predict the global potential distribution. Using native ranges as the reference, we, thus, consider that environments similar to those found within species' native distributions are *climate analogs*. Likewise, *no-analog* climates are, here, considered those conditions not found within species' native distributions. We caution that this definition may differ from those defined in previous work, in which *no-analog climates* referred to conditions found in different times (Williams et al. 2007), especially future climate change scenarios (Fitzpatrick and Hargrove, 2009). Therefore, we rely on the conditions that currently exist in geographic space and within which species occur, were detected, and are attributed to the native range limits, as defined by the IUCN, as a baseline for the definition of *analog*.

Occupancy of no-analog environments was defined by areas whose suitability depends on the inclusion of non-native occurrences, i.e., are not considered suitable by native-based models. It was calculated as follows:

$$\%Increase = \frac{100 * noanalog}{Noanalog + analog}$$

where *analog* indicates the number of cells predicted as suitable from native-based models, and *noanalog* indicates cells that are only predicted as suitable when non-native occurrences are included. Results referred to total potential distribution are given in km², considering a WGS84 projection.

Niche equivalence and similarity tests

To test for the equivalence and similarity of the niches of native *vs* non-native populations, we extracted the climate information referred to species occurrences. In Broennimman et al. (2012), the authors compared several ordination methods for quantifying niche overlap and found that, among the methods they evaluated, the PCA-env calibrated on the pooled background most accurately estimated the simulated niche overlap. Therefore, we used the PCA-env, via function *dudi.pca()* from R package *ecospat*, to reduce the dimensionality of environmental data (all 19 bioclimatic predictors) from the pooled background, i.e., native plus non-native ranges (a definition also based on IUCN polygons of extent of occurrence classified as "native"), to the first two axes of the principal component analysis (PCA), which accounted for 75% of the variation in the data. Then, we compared the climate spaces of areas that are occupied by populations (native *vs* non-native) to the pooled background of environmental conditions, using the functions *ecospat.grid.clim.dyn()*, *ecospat.niche.equivalency.test()*, *ecospat.niche.similarity.test()*, also from the *ecospat* R package. Niche overlap between native and non-native ranges was measured by Schoener's *D* index, which ranges from no overlap, 0, to complete overlap, 1 (Schoener 1974; Warren et al. 2008).

Observed niche overlap between native and non-native ranges was then compared to random values, using tests of niche equivalence and similarity. The niche equivalence method tests if climatic niches (from native and non-native populations) are indistinguishable from each other (Graham et al. 2004). The rejection of the null hypothesis, therefore, indicates that native and non-native niches are not identical (Broennimann et al. 2012). On the other hand, the niche similarity test asks whether models calibrated on the native range predict invasion occurrences better

than expected by chance (Warren et al. 2008). The null hypothesis in niche similarity tests, thus, refers to niche resemblance, so that its rejection indicates that niches are less similar than expected by chance. We caution that the null hypothesis for niche equivalence is much easier to reject than for niche similarity. We ran 1000 iterations for null hypotheses tests and *p*-values were computed.

Mechanistic links to possible causes of observed differences between native and non-native niches were incorporated by disentangling niche dynamics into the processes of *stability*, *unfilling* and *expansion* (Guisan et al. 2014). Niche *stability* is observed whenever invasion mostly occurs towards regions that are climatically similar to those from the native range. However, niche *unfilling* is expected if environmental conditions from native ranges are available, but unoccupied in the non-native environment (Guisan et al. 2014). Finally, observed niche *expansion* results from occupancy of no-analog climatic conditions.

Thermal and hydric stress tolerance

We characterized the environment within which species are found by assessing the climatic conditions associated with species' occurrence records. To do so, we extracted the values of mean annual temperature (BIO1) and mean annual precipitation (BIO12) associated with each occurrence record from climate raster files referring to current conditions (Supporting occurrences *Ocorr_supp.csv*), obtained from World-Clim version 1.4, also used in the previous analysis. The selection of BIO1 and BIO12 to assess species climatic tolerance is due to their known relationship to the natural history of species (Rödder et al. 2009) as a proxy of thermal and hydric stress. We reiterate that such values are not equivalent to physiological tolerance, which can only be rigorously calculated with manipulative experiments but are conditions that species experience and likely tolerate in the wild. As with any presence-only study at the global scale, however, we were not able to define whether each population associated with each occurrence record is in equilibrium with their surrounding environment, so there is the possibility of eventual occurrence in unsuitable or marginal habitats. Therefore, we recommend that the results of this section are interpreted with caution and as an overview. Thermal and hydric stress tolerance differences among groups (native *vs*

non-native) were tested using a generalized linear model. Residuals and assumptions were checked via graphical analysis.

Results

Including occurrences from invaded ranges improved the accuracy of ecological niche models for both studied species (Table 1). Ecological niche models calibrated across pooled ranges (combining occurrence from both native and invaded ranges, Table 1, column *Pooled*) resulted in models with higher predictive accuracy. Native-based models predicted relatively well the occurrences from native ranges (Table 1, item *Native-native*), but had poor performance predicting occurrences from invaded ranges (Table 1, item *Native-invaded*). The inclusion of non-native occurrences in the modelled ecological niche increased the potential distribution of the cane toad by 51% and by 63% for the bullfrog (Table S1, Fig. 2). In other words, occupancy of climates that are currently absent in native ranges increased potential distribution by $> 10^7$ Km^2 for both species.

Climatic niches from native and non-native populations were different (the *niche equivalence* hypothesis) for both species (Table 1). However, we also found evidence that populations from non-native ranges occupy environments that are more similar than expected by chance to conditions from its native range–the *niche similarity* hypothesis (Table 2), which is corroborated by the high stability (about 94% for both species) observed between native and non-native ranges. Observed values of niche expansion accounted for only 6% and 8% for the cane toad and the bullfrog, respectively. Niche unfilling was relatively low, accounting for less than 1% for the cane toad but up to 8% for the bullfrog.

The cane toad occupied mostly warm (*Mean annual temperature* = 26 ± 4 °C) environments, with a vast array of precipitation conditions, from near zero to almost 800 mm^3 per year (Fig. 3). We observed no differences in temperature, but the environments invaded by the cane toad were drier than those from native ranges (BIO12|Native $_{mean}$ = 2121 ± 63 mm^3; Invaded $_{mean}$ = 1475 ± 62 mm^3; F-stat = 50.1, p-value < 0.001). The bullfrog, on the other hand, mostly occupied temperate environments (*Mean annual temperature* = 14 ± 3 °C), and invaded environments with more extreme climatic conditions (considering precipitation and temperature) than those found within native ranges (Fig. 3). Within its native distribution, the bullfrog occupies environments whose precipitation ranges from zero to < 300 mm^3 per year, while non-native occurrences were found in more humid environments (> 400 mm^3 per year). Environments invaded by the bullfrog were warmer than those from native ranges (BIO1|Native $_{mean}$ = 12.7 ± 2 °C; Invaded $_{mean}$ = 15.2 ± 3 °C; F-stat = 51.5, p-value < 0.001), although some extreme occurrences were found in environments whose temperatures frequently go above -10 °C. The bullfrog also invaded environments that are more humid than those from native ranges (BIO12|Native $_{mean}$ = 959 ± 16 mm^3; Invaded $_{mean}$ = 1222 ± 25 mm^3; F-stat = 82, p-value < 0.001).

Discussion

Anticipating invasion risk is crucial to prevent the harmful effects that exotic species can impose on ecosystems. Here, we assessed the invasion potential of two of the world's worst invasive species: cane toads, *Rhinella marina + R. horribilis*, and bullfrogs, *Lithobates catesbeianus*. These amphibians are large-bodied, prolific breeders, good competitors in all developmental stages and opportunistic feeders (Liu et al. 2015; Heise-Pavlov and Longway 2011; Isaacs and Hoyos 2010), who negatively impact native faunas worldwide (Werner et al. 1995; Wu et al. 2005). Disentangling niche dynamics, we observed evidence for a relatively small niche expansion for both species.
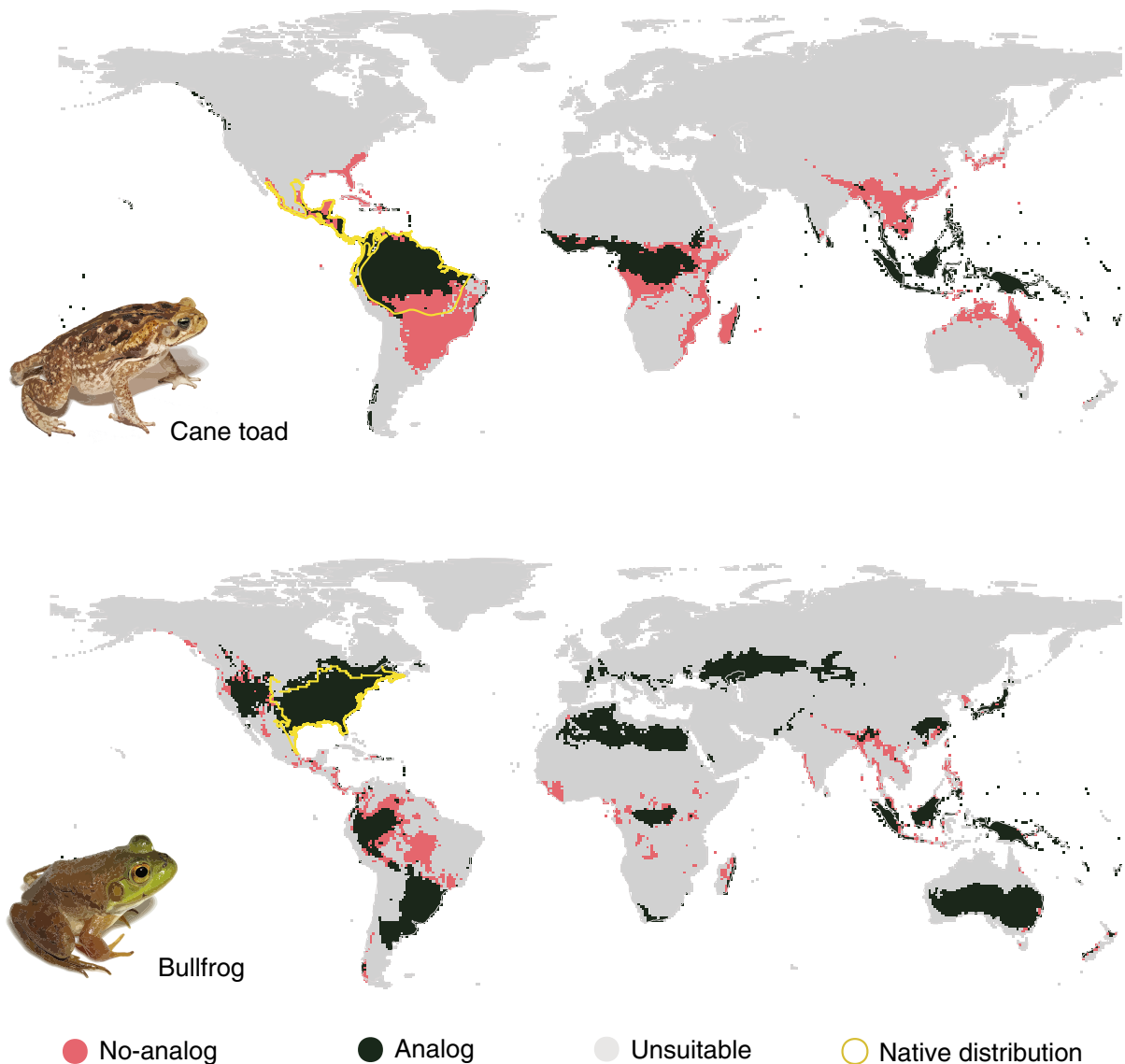
Table 1 Effect of the inclusion of non-native occurrences on the predictive accuracy of ecological niche models, in terms of true skills statistics (*TSS*), of invasive species

Species	Native-native		Native-invaded		Pooled	
	TSS	*AUC*	*TSS*	*AUC*	*TSS*	*AUC*
Cane toad	0.43	0.73	0.21	0.48	0.73	0.9
Bullfrog	0.52	0.79	0.13	0.37	0.60	0.83

Native-native models were calibrated and tested with occurrences from native ranges, while *native-invaded* models were calibrated with native but tested with invaded occurrences. *Pooled* models included information from both native and invaded occurrences on model calibration and validation. Study species were cane toads (*Rhinella marina + R. horribilis*) and bullfrogs (*Lithobates catesbeianus*)

Fig. 2 Climate suitability and potentially invadable areas for cane toads, *Rhinella marina* + *R. horribilis,* and bullfrogs, *Lithobates catesbeianus*. In this figure, green areas are considered suitable for each species according to distribution models calibrated with occurrences from native ranges only. Pale-pink colours indicate areas that are only considered available when including occurrences from invaded ranges. Empty yellow polygons indicate species' native distribution, according to the International Union for the Conservation of Nature (IUCN 2020)

However, the inclusion of non-native occurrences on ecological niche models improved predictive accuracy and increased estimates of potential distribution for both species. Overall, our results indicate that climatic information from native ranges is insufficient to explain the current invasive distribution of the studied species and that native-based climate modelling may lead to underestimated invasion potential.

We found that cane toads and bullfrogs invade territories with climatic conditions that are not available within their native distributions. Bullfrogs, for example, were recorded in conditions harsher than those from its native range, effectively increasing by 11 °C the thermal amplitude of environments occupied. The occupancy of harsher climates, which are no-analogs to those found within native ranges, can

Table 2 Niche changes and potential mechanisms during the invasion of cane toads and bullfrogs in the world

	Equivalence	Similarity		Expansion	Stability	Unfilling
		E → N	N → E			
Cane toad	0.43	0.4*	0.4*	0.06	0.94	0.01
Bullfrog	0.41	0.4*	0.4*	0.08	0.93	0.08

Equivalence and Similarity (E → N: from exotic to native; N → E: from native to exotic) values refer to estimated niche overlap (as Schoener's *D*), where asterisks indicate rejection of null hypothesis (p-value < 0.05). Expansion and Stability refer to the ratio of the non-native niche that does or does not overlap, respectively, to the native niche. Unfilling represents the proportion of the native niche that is present in non-native ranges yet remains unoccupied

Fig. 3 Amplitude of environmental conditions occupied by bullfrogs (green) and cane toads (brown). Mean and extreme values of precipitation (mm × 1000) and temperature (°C) are shown in invaded and native areas, defined according to the International Union for the Conservation of Nature (IUCN 2020)
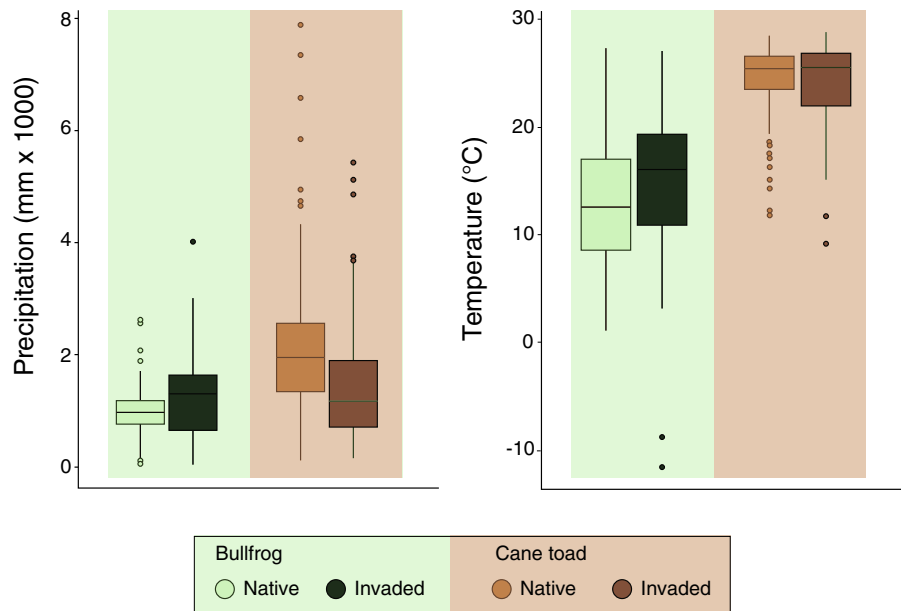
result from eco-evolutionary changes to fundamental niches (Guisan et al. 2014) or simply from the occupancy of suitable but inaccessible areas (Soberón and Peterson 2005; Soberón 2007; Peterson et al. 1999), due to dispersal limitation or competitive exclusion, for example. Regardless of the mechanism, climatic information on native ranges was not enough to explain patterns of invasion, even though niches were statistically similar. Models trained with occurrence data from the native ranges underestimated the invasion potential of areas that are currently invaded. Native-based models were, therefore, unable to accurately predict invasion potential, which has straightforward implications for invasive risk assessments based on ecological niche models.

We also found that cane toads and bullfrogs can potentially colonize vast areas of the globe. However, co-occurrence between them is unlikely because cane toads occur mostly in warm and humid areas, while bullfrogs preferentially occupy drier and colder regions. Cane toads' maps of potential distribution suggest high climatic suitability across the African Congo Basin, the Brazilian Atlantic Forest, the east coast of United States, in Florida, in addition to Sundaland, Phillippines and the Wallacea region in southeastern Asia. If intentional or inadvertent introduction by humans allows colonization of those territories, cane toads may outcompete native counterparts and decimate predators who try to consume them (Phillips and Shine 2006a, b). Such interaction

with native faunas would likely lead to an overall reduction in richness and diversity, mirroring impacts already reported, for example, in Australia (Crossland et al. 2009; Mayer et al. 2015). Failed eradication protocols and the continued spread of cane toads in the Australian continent (Tingley et al. 2017) are, thus, suggestive of the fate of native biodiversity elsewhere under the introduction of this species.

Likewise, bullfrogs' suitable areas span across subtropical ecosystems in South America, such as the mountainous highlands of the Andes and southern Atlantic Forests, as well as temperate portions of Australia, several scattered zones in Asia, most of the eastern United States and even parts of the Amazon, which could potentially be invaded by bullfrogs. Most of the faunas of these regions have experienced no previous contact with bullfrogs, but elsewhere examples of such novel biotic interactions often led to competitive exclusion, favouring the bullfrog (e.g., *Rana boylii* and *Pseudacris regilla*, Kupferberg 1997; *R. aurora*, Lawler et al. 1999).

The large areas predicted as suitable for cane toad and bullfrog raise another conservation flag: the potential co-introduction of emerging infectious diseases, such as those caused by the chytrid fungus, *Batrachochytrium dendrobatidis* (O'Hanlon et al. 2018) and ranaviruses (Ruggeri et al. 2019). There is mounting evidence that bullfrogs co-occur with such pathogens (Rödder et al. 2013), and tolerate their presence (Ribeiro et al. 2019), thus likely acting as vectors for their transmission (Rödder et al. 2013; O'Hanlon et al. 2018). Infectious diseases, especially those caused by the chytrid fungus, were responsible for the decline of hundreds of amphibian populations in the last half-century, representing the greatest loss of biodiversity ever related to a single pathogen (Scheele et al. 2019; 2020).

In conclusion, we found that climatic information on native ranges of cane toads and bullfrogs was not enough to explain their distributional patterns of invasion. The occupancy of climates not found across native ranges increased the potential invadable areas of both species. The high invasion potential of such voracious predators, superb competitors, and lethal disease vectors highlights the urgency of strategies to mitigate their impact on native faunas. Further, we caution that invasive risk assessments based on information from species native ranges, alone, are probably underestimated and unrealistic projections of

impact. Therefore, we suggest the inclusion of environmental information from non-native occurrences on invasion risk assessments based on climate modelling.

Availability of data, material, and code The climate data used in this work can be downloaded at www.ipcc-data.org and in http://worldclim.org/version2. All occurrence records and an example of the R codes used in this work are available as Supporting information.

Declarations

Conflicts of interest The authors declare no conflict of interest.

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