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Residence time, expansion toward the equator in the invaded range and native range size matter to climatic niche shifts in non-native species

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ABSTRACT

Aim Identifying climatic niche shifts and their drivers is important for the accurate prediction of the risk of biological invasions. The niches of non-native plants and birds have recently been assessed in large-scale multispecies studies, but such large-scale tests are lacking for non-native reptiles and amphibians (herpetofauna). Furthermore, little is known about the factors that contribute to niche shifts when they occur. Based on the occurrence of 71 reptile and amphibian species, we compared native and non-native realized niches in 101 invaded ranges at a global scale and identified the factors that affect niche shifts.

Location Global except the Antarctic.

Methods We assessed climatic niche dynamics in a gridded environmental space that allowed niche overlap and expansion into climatic conditions not colonized by the species in their native range to be quantified. We analysed the factors that affect niche shifts using a model-averaging approach, based on generalized linear mixed-effects models.

Results Approximately 57% of the invaded ranges (amphibians, 51%; reptiles, 61%) showed niche shifts ($\geq 10\%$ expansion in the realized climatic niche). Island endemics, species introduced to Oceania and invaded ranges outside the native biogeographical realm all showed a higher proportion of niche shifts. Niche shifts were more likely for species that had smaller native range sizes, were introduced earlier into a new range or invaded areas located at lower latitudes than the native range.

Main conclusions The proportion of niche shifts for non-native herpetofauna was higher than those for Holarctic non-native plants and European non-native birds. The ‘climate-matching hypothesis’ should be used with caution for species undergoing niche shifts, because it could underestimate the risk of their establishment.

Keywords

Climate match, ecological niche models (ENMs), expansion towards equator, native range size, niche shifts, non-native species, realized climatic niche, residence time.

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INTRODUCTION

Niche conservatism refers to the tendency of a species' ecological niche to be conserved over space and time, an assumption

that is increasingly invoked in evolutionary, ecological and conservation studies (Peterson, 2011). In particular, it is a pivotal assumption for ecological niche models (ENMs), which depict Grinnellian species niches by correlating species' geographical

occurrences with environmental variables (i.e. 'climate matching' with climate variables only) and use them to project the potential distribution of species in time and space (Guisan & Thuiller, 2005; Pearman *et al.*, 2008; Soberón & Nakamura, 2009; Peterson *et al.*, 2011; Araújo & Peterson, 2012; Liu *et al.*, 2013). There is still, nonetheless, considerable debate on the climatic niche conservatism of species (Losos, 2008; Peterson & Nakazawa, 2008; Wiens *et al.*, 2010; Peterson, 2011; Pearman *et al.*, 2014).

Non-native species offer excellent model systems for examining niche conservatism and evolution within a short time-scale through comparisons of climate attributes between the native and invaded ranges (Sax *et al.*, 2007; Peterson, 2011; Schulte *et al.*, 2012). Several studies have identified shifts in the realized climatic niches of non-native species (Fitzpatrick *et al.*, 2007; Broennimann & Guisan, 2008; Beaumont *et al.*, 2009; Gallagher *et al.*, 2010), demonstrating the limited capacity of climate-matching approaches in predicting the potential geographical extent of invasion. In this context, a robust framework serving to formalize, quantify and statistically test for niche shifts of non-native species in environmental space has recently been developed (Warren *et al.*, 2008; Broennimann *et al.*, 2012; Petitpierre *et al.*, 2012).

Assuming that a species has colonized all suitable conditions in its native range, the realized niche quantified in its invaded range can be divided into three parts (Petitpierre *et al.*, 2012): niche stability, the part of the niche in which the species occurs in both its native and invaded ranges; niche expansion, where the species newly occurs in the invaded range; and niche unfilling, where the species occurs only in its native range. As biological invasions are recent and ongoing processes, niche unfilling is likely due to dispersal limitations in the invaded range. Thus, only niche expansion towards a climate that is available but not colonized in the native range (i.e. an analogous climate) can be unambiguously considered as niche shifts. Based on such a framework, two studies have suggested that climatic niche shifts are rare for non-native plants (< 15% of 50 species displaying niche shifts, i.e. $\geq 10\%$ expansion in realized climatic niche; Petitpierre *et al.*, 2012) and birds (29% of 28 species showing niche shifts; Strubbe *et al.*, 2013). Whether the same patterns of niche shifts are found in other organisms remains unknown.

Identifying the factors that contribute to niche shifts between invaded and native ranges will not only help to clarify the debate but will also be of fundamental importance for our understanding of species distributions and their responses to changing environments, e.g. through ENM predictions. It has been hypothesized that realized niche shifts can result from both (1) changes in dispersal limitations and biotic interactions between native and invaded ranges and (2) introduction history and rapid evolution (Pearman *et al.*, 2008; Alexander & Edwards, 2010). First, for species with restricted native ranges (such as those endemic to islands or mountains), shifts in realized niches are most likely to result from dispersal limitation (including extrinsic dispersal limitation, e.g. barriers to dispersal, and intrinsic dispersal limitation, e.g. a species' ability to disperse) in

the native range (Alexander & Edwards, 2010). Realized niche shifts would similarly be more likely for species introduced into lower-latitude areas (Alexander & Edwards, 2010). It is hypothesized that the low-latitude boundary of a species' geographical range is determined by its tolerance to the biotic pressures that arise from more complex biotic interactions (Darwin, 1859; Normand *et al.*, 2009). Because species richness tends to be greater toward the equator, greater competition and predation pressures would be expected in low-latitude areas, resulting in more complex biotic interactions there. A boundary expansion towards lower latitudes in the invaded range than in the native range may thus contain climates that were not colonized in the native range due to limiting biotic pressures, which are more likely to cause realized niche shifts.

Second, it is hypothesized that the realized climatic niche would tend to shift as a function of residence time in the invaded range (Gallagher *et al.*, 2010; Peterson, 2011). The invaded range will expand with increasing residence time (Wilson *et al.*, 2007; Williamson *et al.*, 2009), thus becoming increasingly likely to include climatic habitats that were excluded by biotic interactions and dispersal limitations in the native range. With increasing residence time, a species would also be more likely to evolve adaptations to climatic conditions not found in the native range (non-analogue) and to expand its fundamental niche (Peterson, 2011). In addition, multiple introductions of a non-native species from different source populations in the native range may facilitate the admixture of previously isolated native populations and increase the genetic variation in invading populations (Kolbe *et al.*, 2004). Such added genetic variation may promote the capacity of a population in the invaded range to respond to selection in new environments, favouring the occurrence of fundamental niche shifts (Pearman *et al.*, 2008; Alexander & Edwards, 2010).

Although the ecological and evolutionary drivers of niche changes cannot easily be disentangled from observational data, a necessary first step when using such data is nevertheless to assess whether niche changes occur and in what proportions. However, niche-change studies across many species and over large areas remain scarce. Here, we assess shifts in realized climatic niches for non-native terrestrial reptile and amphibian species (non-native herpetofauna) by comparing the realized niches between the invaded and native ranges, using empirical distribution data and identifying the factors that could affect niche shifts in invaded ranges.

As ectothermic organisms, reptiles and amphibians depend on external heat to increase their body temperature and become active. Climate affects all important aspects of reptile and amphibian biology, including growth, development, foraging and the timing of hibernation and breeding (Vitt & Caldwell, 2009). Temperature and precipitation are both considered to have marked effects on the distribution, range size and species-richness patterns of reptiles and amphibians (Araújo *et al.*, 2008; Aragón *et al.*, 2010; Whitton *et al.*, 2012). Many reptile and amphibian species have been introduced into new ranges via the pet and food trades, through deliberate introduction for personal aesthetic pleasure or aquaculture and the deliberate or

accidental release of pets and aquarium specimens (Kraus, 2009). Unlike the introduction of non-native plants and mammals, however, the widespread introduction of herpetofauna is only recent, and the introduction histories of most species have been documented in relatively great detail (Kraus, 2009). These provide a unique opportunity to examine the effects of introduction history (the number of introduction events and the residence time since arrival) on niche shifts. In this paper, we ask the following questions: (1) How frequent and important are shifts in realized climatic niche in non-native herpetofauna within their invaded ranges at a global scale? (2) What factors promote shifts in realized climatic niche in the invaded ranges? We tested for possible associations between niche shifts and native range size, island-endemic identity, the direction of latitudinal expansion in the invaded range, the number of introduction events and the residence time since arrival.

Assessing and explaining the magnitude of realized climatic niche shifts would allow a better understanding of species' responses towards changing environments and would facilitate more efficient management strategies for invasive species.

MATERIALS AND METHODS

Data on occurrences of non-native herpetofauna

We obtained data on successfully introduced amphibian and reptile species from the database of Kraus (2009), which is widely used in studies of non-native herpetofauna (Tingley *et al.*, 2011; van Wilgen & Richardson, 2012). Subsequently, we validated the data and determined the final species list (Text S1 in Supporting Information). If taxonomic inconsistencies were found, they were resolved by further literature review.

Occurrence data for each species were obtained from various databases and published references (Table S1). Here, native and invaded ranges within the same biogeographical realm can be clearly distinguished (Kraus, 2009). We therefore distinguished, in our dataset, invaded ranges within the same biogeographical realm from those outside the native biogeographical realm. A total of 68,459 location records in native ranges (range: 14–8741 records) and 15,973 records in introduced ranges (range: 10–2740 records) were collected for 71 species of non-native reptiles and amphibians. Previous studies have been conducted at a coarse resolution (grid cells of 30 arc-minutes = c. 50 km × 50 km; Petitpierre *et al.*, 2012; Strubbe *et al.*, 2013). Given that certain fine-scale niche shifts might not be detected at such a resolution (Petitpierre *et al.*, 2012), we integrated our data into grid cells at both a finer resolution (10 arc-minutes = c. 16 km × 16 km) and the same coarse resolution (30 arc-minutes) after removing duplicate observations in the same geographical cell.

Climatic variables

Eight climatic variables from the WorldClim database, which is widely used in large-scale studies of species distributions

(Hijmans *et al.*, 2005), were used to depict the realized climatic niche of each species: mean diurnal temperature range, annual temperature range, minimum temperature of the coldest month, mean temperature of the warmest quarter, annual precipitation, precipitation seasonality, precipitation in the driest quarter, and precipitation in the warmest quarter. These variables describe the energy and water factors that define the primary physical requirements of amphibians and reptiles and are widely used for determining the geographical distributions of amphibians and reptiles (Araújo *et al.*, 2008).

Quantifying the dynamics of realized climatic niches

The extent of the study area has important effects on niche comparisons. The spatial and temporal extent of the study area should be sufficiently broad to allow the optimal coverage of the spatial footprint of all suitable environmental conditions and to incorporate the range of factors that typically affect species' ranges, such as geographical barriers, climates, historical events and phylogeographical phenomena (Barve *et al.*, 2011; Soberón & Peterson, 2011). We used biogeographical realms to define native and invaded extents, following the definition of Olson *et al.* (2001): Afrotropics (including Madagascar), Australasia, Indo-Malay, Nearctic, Neotropics, Palaeartic and Oceania. Several species were distributed in two or more native realms. The native realm for such species was defined as the realm where the midpoint of its latitudinal and longitudinal ranges was located.

We quantified the dynamics of climatic niches in analogous climates (i.e. the climates that are available in both native and invaded extents; see Fitzpatrick & Hargrove, 2009) between the native and the invaded ranges for every species at both coarse and fine resolutions. Non-analogue climates were excluded from the analyses, because niche extrapolations in this case are difficult to interpret (Fitzpatrick & Hargrove, 2009; Guisan *et al.*, 2012; Petitpierre *et al.*, 2012). We gridded the species' occurrences in the native and invaded ranges and, to retain sufficient statistical power, we only included species occurring in ≥ 10 grid cells in either their native (range: 11–1200 grid cells) or invaded (range: 10–695 grid cells) ranges in our analyses.

Species data were projected onto the first two axes of a principal components analysis (PCA), depicting a multivariate climatic space calculated with the eight climatic variables (Fig. S1). Following previous studies (Broennimann *et al.*, 2012; Petitpierre *et al.*, 2012; Strubbe *et al.*, 2013), we did not include additional axes because the first two explained a large proportion of the total climate variation (Fig. S1, Tables S2 & S3). We used two PCA calibration approaches (both referred to as PCA_{env} in Broennimann *et al.*, 2012). A first PCA was calibrated on climate factors distributed in the native extent only, and a second was calibrated on the native and invaded extents. Correlations between the first two PCA axes and climate factors vary depending on the extent used for the PCA calibration (Table S3). Species occurrences were then transformed into species density using a kernel smoother in the gridded PCA environmental space (at a resolution of 100 × 100 cells) (Broennimann

et al., 2012). This approach reduces the risk that a difference between the number of native and introduced records would cause an analytical bias in our results. The same gridding and smoothing procedure was applied to the entire climate available in the native and invaded extents. This approach allowed species occupancy to be defined by correcting species densities through the incorporation of the differences in environmental availability between native and invaded ranges (Broennimann *et al.*, 2012). The niche overlap between native and invaded ranges was quantified with Schoener's *D* (Warren *et al.*, 2008; Broennimann *et al.*, 2012), varying between 0 (no overlap) and 1 (total overlap). This approach has been suggested as the most accurate of numerous methods for evaluating realized niche dynamics (Broennimann *et al.*, 2012). It also allows niche conservatism to be tested through a one-sided niche-similarity test based on *D* (Broennimann *et al.*, 2012).

D does not reveal the detailed nature of the niche changes. Therefore, we also quantified three more specific components of niche change: unfilling, niche stability and niche expansion (Petitpierre *et al.*, 2012). Unfilling corresponds to the portion of niche space colonized only in the native range, stability to the portion colonized in both native and invaded ranges and expansion to the portion colonized only in the invaded range. These indices were measured in the climatic space shared between the native and invaded extents in order to avoid detecting niche shifts due to climatic non-availability in the native range. Note that in both the native and invasive extents, marginal climates with densities below 25% were not included to reduce the heterogeneity in climate availability between native and invaded extents. The results were similar for different proportions of the intersection of the species densities (75%, 80%, 85%, 90%, 95% and 100%; Fig. S2). The same R functions as in Petitpierre *et al.* (2012) were used for the entire procedure.

Factors influencing realized climatic niche shifts

Range size was measured as the number of occupied 10-arc-minute grid cells, using HAWTH'S TOOLS in ARCGIS (Beyer, 2004; Gallagher *et al.*, 2010). Island endemics, i.e. species whose native range only included islands, were represented by a binary variable. The number of successful introduction events and the year of the first successful introduction of non-native species were obtained from Kraus (2009). Residence time was determined as the number of years since the first successful introduction in the invaded biogeographical realms. Expansion towards the equator or towards the pole (hereafter, equatorward and poleward expansion, respectively) in the invaded realms was defined by quantifying cases where the high- and low-latitude distribution limits in the invaded extents were, respectively, higher and lower than in the native extent. In all other cases, the expansion towards the equator and towards the poles was set to zero (no expansion).

Statistical analyses

We used multimodel inference based on information theory (Burnham & Anderson, 2002) to investigate the effects of these

factors on the occurrence of niche shifts ($\geq 10\%$ expansion, 1; others, 0). This approach allows more reliable inferences from an entire set of models and is preferable to selecting a single best model (Burnham & Anderson, 2002). The full model is a generalized linear mixed-effects model (GLMM) with a logit link and binomial error distribution, with niche shifts as the response variable and the six factors as predictor variables. We included the invaded and native realms as random factors (Gallagher *et al.*, 2010); all other variables were treated as fixed effects. To avoid potential statistical issues arising from phylogenetic non-independence, we evaluated the phylogenetic signal in the niche shifts for amphibians and reptiles separately (Table S4). We obtained data on phylogenetic distances from published supertrees (Table S4). We estimated Pagel's λ phylogenetic signal using a maximum-likelihood approach, and tested for its significance compared to a Pagel's λ of zero with a likelihood-ratio test. We performed these analyses using the package PHYTOOLS (see Table S4). Because we found no significant relationship between phylogeny and climatic niche shifts (Table S4), we did not consider phylogeny any further in models.

Because we were interested in the relative importance of an individual factor, we excluded models with interaction terms from the calculation of relative variable importance and thus created 63 models ($2^6 - 1$) representing all possible combinations of six predictor variables. We compared the alternative models using the Akaike information criterion adjusted for small samples (AIC_c). We calculated the relative importance of a predictor by summing the Akaike weights across all of the models in which the predictor appeared. We calculated the model-averaged parameter estimate for each predictor and its variances with Akaike weights (Table S5) (Burnham & Anderson, 2002). We report those models that were within two AIC_c units of the highest-ranked models (i.e. $\Delta AIC_c \leq 2$; Burnham & Anderson, 2002). We used the 'lmer' function in the LME4 package to perform the GLMM analysis and used the 'dredge' and 'model.avg' functions in the MuMIn package to perform the model-averaging analysis. All analyses were conducted in R (R Development Core Team, 2011). The full analytical procedure is shown in Fig. S3. The data used are shown in Table S6.

RESULTS

Realized climatic niche shifts

Our sample at the finer resolution comprised 101 invaded ranges for 71 species of non-native reptiles (46 species) and amphibians (25 species), including 53 invaded ranges within the native realm and 48 invaded ranges outside the native realm (Table S2). At the coarser resolution, the sample size was reduced to 58 invaded ranges for 36 species.

Globally, there were no differences in the niche shifts, niche overlap and niche unfilling in the invaded ranges at the same resolution between different extents or between different resolutions based on the same extent (Table S7a–c). These results

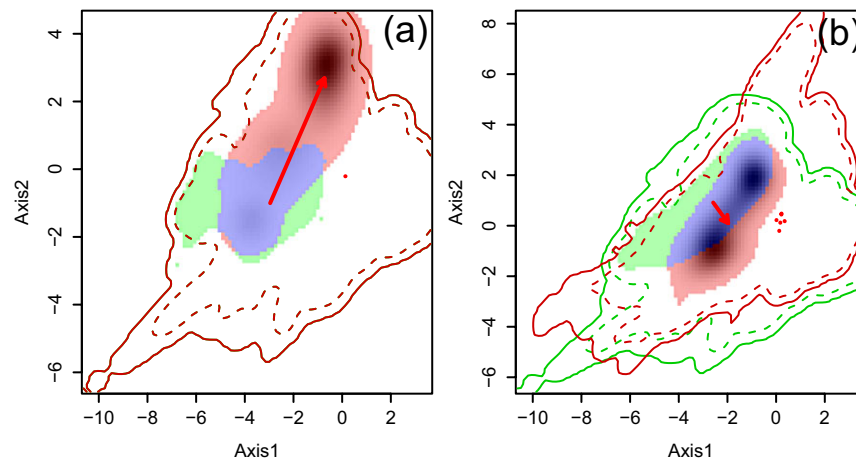


Figure 1 Examples of climatic niche dynamics between native and invaded ranges: (a) the American bullfrog (*Lithobates catesbeianus*) introduced within the native biogeographical realm (Nearctic) and (b) the red-eared slider (*Trachemys scripta elegans*) introduced from the Nearctic to the Palearctic. The solid and dashed contour lines indicate 100% and 75%, respectively, of the available (background) environment (green, native climatic background; red, invasive background). Green area, unfilled; blue area, stability; red area, expansion. The solid arrows (dashed arrows) represent the change in the centre of the species niche (climatic space) between the native and invaded ranges [the dashed line in panel (a) is superimposed, as the introduction event occurred in the same biogeographical realm].

indicated that the realized climatic niche dynamics between invaded and native ranges for non-native herpetofauna were highly consistent despite the use of methods based on different extents or different resolutions. We therefore only report here the results of niche shifts quantified by PCA calibrated on climate availability within the native range extents at fine resolution, due to the larger sample size of invaded ranges and the consistent use of extent (the results of niche shifts by PCA calibrated on native and invaded ranges were similar and are shown in Tables S2 & S6–S8).

Realized climatic niche conservatism (i.e. niche stability) between the invaded and native ranges was observed for 50% (50/101) of these invaded ranges at fine resolution ($P \leq 0.05$ for the similarity test) (Table S2). Niche unfilling ($\geq 10\%$) was observed for 80% (80/101) of the invaded ranges. (See Fig. 1 for the climate niche dynamics between the invaded and native ranges for two notorious globally invasive species.)

At the global scale, the proportion of climatic niche shifts in all invaded ranges was high. Of the 101 invaded ranges (Fig. 2a; Table S2; Fig. S4), 58 showed greater than 10% niche expansion, with 18 ranges displaying niche shifts ($\geq 10\%$ expansion) for amphibians and 40 for reptiles. *Discoglossus pictus*, introduced from the Palearctic into the same realm outside its native range, showed 92.8% expansion, the highest expansion found in an invaded range for amphibians. *Caiman crocodilus*, introduced from the Neotropics into the Nearctic, displayed 90.5% expansion, the highest found for reptiles (Table S2). The proportion of niche shifts in invaded ranges at the global scale did not differ between reptiles and amphibians (chi-square test, $\chi^2 = 0.780$, d.f. = 1, $P = 0.377$). No difference between amphibians and reptiles in the proportion of species showing niche shifts in one or

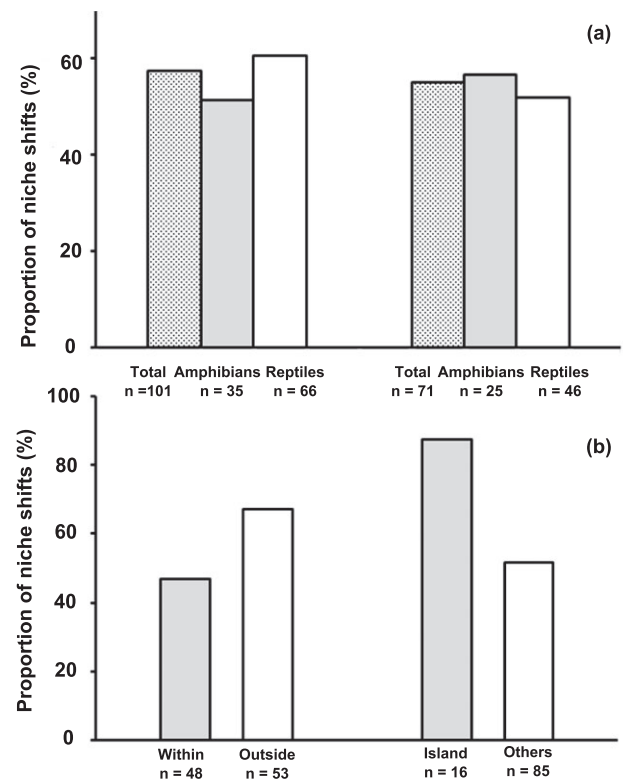


Figure 2 Proportions of invaded ranges or species showing a climatic niche shift ($\geq 10\%$ expansion) for non-native herpetofauna: (a) at the invaded range level (left) and at the species level (right); (b) invaded ranges within the native biogeographical realm and those in different biogeographical realms (left), island endemics and other species (right).

Figure 3 Proportions of invaded ranges showing a climatic niche shift ($\geq 10\%$ expansion) for non-native herpetofauna across each biogeographical realm. The denominator in a pie slice represents the sample size of invaded ranges and the numerator represents the number of invaded ranges showing a climate niche shift, respectively. The size of the slice in the right half of a pie represents the relative sample size between two taxa.

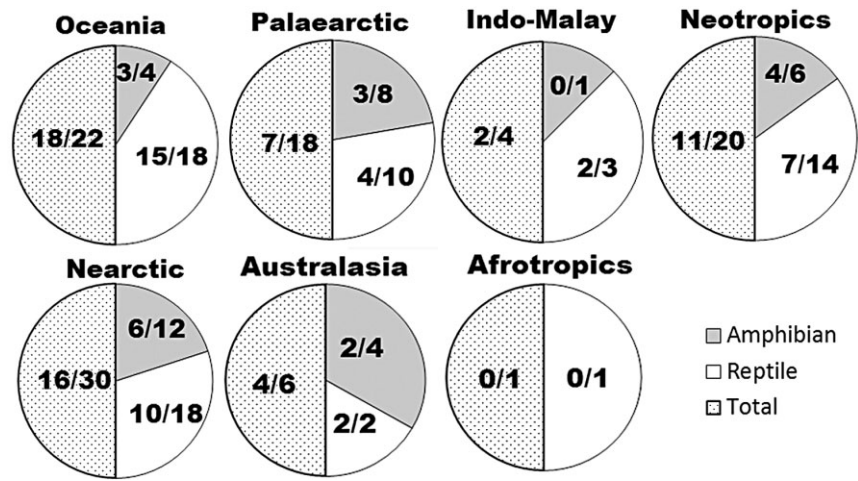


Table 1 The six best models (i.e. $\Delta AIC_c \leq 2$) of the factors influencing niche shifts for 101 invaded ranges of 71 reptile and amphibian invaders worldwide. The models are based on a binomial error structure and a logit link function with climatic niche shifts ($\geq 10\%$ expansion, 1; others, 0) as the response variable, a combination of six factors as explanatory variables and the native and invaded biogeographical realms as random variables. The native realm or invaded realm showed no effects on niche shifts as random variables (for details, see Table S5).

Variables	Model rank					
	1	2	3	4	5	6
Native range size (grid cells)	•	•	•	•	•	•
Residence time (years)	•	•	•	•	•	•
Equatorward expansion in invaded range (degrees)	•	•	•	•	•	•
Poleward expansion in invaded ranges (degrees)	•		•		•	
Number of introduction events		•			•	•
Island-endemic identity (binary variable)			•			•
ΔAIC	0	0.19	0.69	1.17	1.40	1.43
AIC_c	84.39	84.58	85.07	85.56	85.78	85.81
W_i	0.21	0.19	0.15	0.12	0.10	0.10
R^2	0.66	0.66	0.67	0.64	0.67	0.67

•, indicates that a variable is included in the model.

ΔAIC , the difference between each model and the highest ranked model.

AIC_c , Akaike information criterion adjusted for small sample sizes.

W_i (Akaike weights), the relative likelihood of a model given the particular set of best models being considered.

R^2 , Likelihood-ratio based pseudo-R-squared.

more realms was detected at the species level ($\chi^2 = 0.132$, $P = 0.716$), but invaded ranges within the native realm showed a lower proportion of niche shifts than those in different realms ($\chi^2 = 4.239$, $P = 0.04$) (Fig. 2b). Furthermore, island endemics showed a higher proportion of niche shifts than other species ($\chi^2 = 6.964$, $P = 0.008$) (Fig. 2b).

At the biogeographical realm scale, the proportion of niche shifts in invaded ranges varied strongly, ranging from 0 to 75% for amphibians and from 0 to 100% for reptiles (Fig. 3). No difference was found in the proportion of niche shifts among the seven realms (Kruskal–Wallis test, $\chi^2 = 10.986$, d.f. = 6, $P = 0.089$). However, the invaded ranges for species introduced to Oceania showed more niche shifts than those for species introduced to the combination of the other six realms (chi-square test, $\chi^2 = 6.777$, d.f. = 1, $P = 0.009$).

Factors affecting climatic niche shifts

Controlling for the realm into which a species was introduced and the realm to which the species was native, the six best models (i.e. $\Delta AIC_c \leq 2$) contained all predictors (Table 1). Native range size, residence time and equatorward expansion in the invaded range appeared in each of these models. The proportion of the variation explained by predictors in models (pseudo- R^2) ranged from 0.64 to 0.67.

The model-averaging analysis showed that native range size (1.0), residence time (1.0) and equatorward expansion (1.0) had high relative importance values for the realized climatic niche shifts in the invaded ranges (Table 2). The other three variables (poleward expansion, island-endemic identity and number of introduction events) showed lower relative impor-

Table 2 Summary of multiple-model inference for 101 invaded ranges of 71 non-native amphibian and reptile species at a global scale. The model averaging was based on generalized linear mixed models ($2^6 - 1$ models) with a binomial error structure and a logit link function with climatic niche shifts ($\geq 10\%$ expansion, 1; others, 0) as the response variable, a combination of six factors as explanatory variables and the native and invaded biogeographical realms as random variables. The effect of the native (or invaded) realm was significant only in three (or one) of 63 models (for details, see Table S5).

Explanatory variables	Relative importance	Parameter estimate (SE)
Native range size(grid cells)	1.00	-0.007 (0.002)
Residence time (years)	1.00	0.020 (0.008)
Equatorward expansion in invaded range (degrees)	1.00	3.650 (3.520)
Poleward expansion in invaded ranges (degrees)	0.53	0.126 (0.084)
Number of introduction events	0.46	0.021 (0.034)
Island-endemic identity (binary variable)	0.38	1.333 (1.129)

tance, with values ranging from 0.38 to 0.53. The amplitude of niche shifts increased (positive parameter estimates) with increasing residence time, equatorward expansion, poleward expansion, island-endemic identity and number of introduction events, but decreased (negative parameter estimates) with increasing native range size.

The results were similar when the PCA was calibrated using extent data comprising both native and invaded ranges (Table S8a) or when the earliest introduction (2212 years ago for *Macroprotodon cucullatus*; Table S6) was excluded from the sample (Table S8b–c).

DISCUSSION

We detected high proportions of realized climatic niche shifts in invaded ranges at a global scale both for non-native reptiles and for non-native amphibians. The climatic niche shifts were more likely in non-native species with smaller native ranges, those introduced into a new range earlier and those that invaded lower-latitude areas than their native ranges. A recent study of the drivers of climatic niche dynamics (niche expansion, niche overlap and niche unfilling) for European non-native birds (Strubbe *et al.*, 2013) has found that niche overlap was lower for more recently introduced species and that niche unfilling was lower for species that were introduced earlier and more often. The latter study did not detect any significant variables to explain the niche shifts, partly because of the low proportion of niche shifts detected for birds (Strubbe *et al.*, 2013). As far as we are aware, our study is the first to identify the factors that influence realized climatic niche shifts between invaded and native ranges for non-native species.

The results of this study highlight the importance of understanding the factors that influence the realized niche shifts that occur between species' invaded and native ranges. Previous studies have often offered as potential explanations of the observed niche shifts the idea that both evolutionary and ecological changes may take place: changes of the fundamental niche limits and associated evolutionary changes, and changes of the factors – dispersal and biotic interactions – that constrain the occupancy of the fundamental niche in the native range

(Fitzpatrick *et al.*, 2007; Broennimann & Guisan, 2008; Beaumont *et al.*, 2009). It is probable, however, that the observed climatic niche shifts for non-native herpetofauna result more from ecological than from evolutionary processes. The effects that we identified, of residence time and equatorward expansion in invaded range and native range size on the niche shifts, tend to confirm the general hypothesis that climatic niche shifts for non-native species result from changes in dispersal limitations and biotic interactions between native and invaded ranges and from the introduction history (Pearman *et al.*, 2008; Alexander & Edwards, 2010). The high proportion of realized niche shifts in the invaded range implies that many non-native herpetofauna species only occupy, in the native and/or invaded range, a part of the environment that is potentially suitable, because of dispersal limitations and changes in biological interactions.

The proportion of niche shifts in non-native herpetofauna was higher than those in non-native plants and birds (Petitpierre *et al.*, 2012; Strubbe *et al.*, 2013), even when island endemics were excluded from the analysis (Table S7d–f). Clearly, the higher proportion of island endemics was partly responsible for the differences between our study and the two previous studies cited. The introduction histories also showed large differences between the three taxa (median introduction date: non-native herpetofauna, 1917; plants, 1750; birds, 1963). The earlier introduction dates for herpetofauna than for birds might partly explain the higher proportion of niche shifts in the former than in the latter, but this difference in introduction histories does not explain the difference in niche shifts between herpetofauna and plants. Much larger native range sizes may, however, explain the lower niche shifts in plants (mean 35,201; SD 25,143; 10-arc-minute grid cells) compared with the herpetofauna species studied here. Finally, differences in the variables used in the studies might be partly responsible for the differences in niche shifts. All three studies included important climate variables to characterize the realized climatic niches of the studied taxa, but the study on birds also included the human footprint (Strubbe *et al.*, 2013).

Island endemics were more likely to be out of equilibrium with climate, due to the ocean as a barrier to dispersal, and

therefore showed a higher proportion of niche shifts. The higher proportion of niche shifts for invaded ranges in Oceania than in the combination of the other six realms might be due to the difference in native range size. The species introduced to Oceania had smaller range sizes than those introduced to the other realms ($\chi^2 = 4.016$, d.f. = 1, $P = 0.045$), but no differences in residence time ($\chi^2 = 0.039$, $P = 0.843$) or equatorward expansion were detected for introduced species between Oceania and the other realms ($\chi^2 = 0.017$, $P = 0.896$). As a result, species introduced to Oceania may be more likely to exhibit niche shifts than those introduced to other realms.

We found weak evidence for the effects of island-endemic identity on niche expansion in the model-averaging analysis (Table 2). This may have arisen because island-endemic identity was negatively correlated with native range size (Table S9). Due to sea barriers, island endemics had a smaller native range size than others ($\chi^2 = 15.379$, d.f. = 1, $P < 0.001$), which might explain most of the variation in niche shifts resulting from island-endemic identity.

The minor influence of the number of introduction events on niche shifts may result from two factors. First, for certain species, the admixture resulting from multiple introductions of different local populations from the native range might result in offspring with decreased levels of viability or fertility due to the incompatibility of genomes from divergent lineages (Johnson, 2010). Because the hybrids with decreased fitness would be poorly adapted to climate habitats in the hybrid zone compared with their parents, rapid fundamental niche shifts for such hybrids could not occur (also supporting our hypothesis that changes result more from ecological than from evolutionary factors). Second, certain species might have been introduced multiple times into geographically disconnected areas of a realm. Because the introduced populations did not mix, the genetic variation in the populations could not increase, resulting in no effect of the number of introduction events on the niche shifts. Consistent with the results of a previous study of birds (Strubbe *et al.*, 2013), the invaded range size (number of grid cells) was correlated with the number of introduction events in this study ($r = 0.35$, d.f. = 100, $P < 0.001$), suggesting that multiple introductions resulted in a larger invaded range.

One potential explanation for the weak effect of poleward expansion was that the high-latitude boundary of native range for the species with poleward expansion might be less limited by climate. As a result, increasing poleward expansion in invaded ranges might not increase climatic niche expansion. It is known that dispersal (Araújo & Pearson, 2005; Araújo *et al.*, 2008; Baselga *et al.*, 2012) or the conservatism of physiological cold-tolerance (Olalla-Tárraga *et al.*, 2011) determines the high-latitude range boundary for amphibians and reptiles. The distributions of restricted-range species were more likely to be limited by intrinsic dispersal limitation (low dispersal abilities) but less by climate than those of widespread species (Araújo & Pearson, 2005; Baselga *et al.*, 2012). Poleward expansion in invaded ranges for non-native herpetofauna was negatively correlated with the native range size (Table S9), indicating that species with smaller range sizes had greater poleward expansion

in their invaded range. Climatic factors, including cold-tolerance, might pose fewer constraints on the higher-latitude boundary of the native range for these species due to their smaller native range size.

Our results may have important implications for ENM-based predictions of the risk of biological invasion by reptiles and amphibians. 'Climate-matching' between invaded and native ranges and propagule pressure are commonly used to guide risk assessments for initial introductions (Lockwood *et al.*, 2005; Bomford *et al.*, 2009; Guisan *et al.*, 2013). Our results suggested that climate-matching based on ENMs should be applied with caution for species that have small native ranges or those that are introduced into areas at lower latitudes than their native ranges, because realized climatic niche shifts are more likely for these species. In such cases, climate-matching might underestimate the risk of establishment of the non-native species. Because both the fundamental niche and the realized niche are increasingly likely to shift with increasing residence time for established non-native species, ENMs should be rerun in a timely manner based on comprehensive occurrence data from the entire distribution, including both the native range and the new invaded ranges. These updated analyses may produce better predictions of the risk represented by such species (Broennimann & Guisan, 2008; Beaumont *et al.*, 2009; Gallagher *et al.*, 2010).

In conclusion, we found that climatic niche shifts were pervasive among non-native herpetofauna, a pattern that was strikingly different from those of Holarctic non-native plants and European non-native birds. Climate-matching was therefore not warranted as a guide for risk assessments of the initial introductions for non-native herpetofauna. We identified residence time, equatorward expansion in the invaded range and native range size as factors that influence climate niche shifts. These results partly explain how the debate on niche conservation between invaded and native ranges for non-native species can arise (e.g. in terms of differences among the non-native plants, birds and herpetofauna in this study). Our results provide insights into the climatic niche dynamics for both native and invaded ranges. This understanding may facilitate better ENM-based predictions of the risks of biological invasions.

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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.

Table S1 Databases and literature used for occurrence data.

Table S2 Niche change indices based on different extents and resolutions.

Table S3 Ranking of the eight climatic variables by PCA.

Table S4 Significance test for phylogenetic signal.

Table S5 Detailed results of multiple-model inference.

Table S6 Data on niche expansion and six predictor variables.

Table S7 Comparisons of niche dynamics between extents, resolutions and taxa.

Table S8 Multiple-model inference based on the different extent and sample.

Table S9 Spearman rank correlation coefficients among six predictors.

Text S1 Methods for the database of species list.

Figure S1 Correlations between climatic variables and first two components of PCA.

Figure S2 Sensitivity analysis to the marginal climates.

Figure S3 Scheme of the full data analysis procedure.

Figure S4 Climatic niche dynamics for non-native herpetofauna.

BIOSKETCHES

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