



RESEARCH PAPER



Rapid niche shifts in introduced species can be a million times faster than changes among native species and ten times faster than climate change

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Abstract

Aims: As global temperatures rise, the survival of many species may hinge on whether they can shift their climatic niches quickly enough to avoid extinction. Previous analyses among species and populations suggest that species' niches change far slower than rates of projected climate change. However, it is unclear how quickly niches can change over the timeframe most relevant to global warming (decades instead of thousands or millions of years). Here, we use data from introduced species to assess how quickly climatic niches can change over decadal timescales.

Location: Global.

Methods: We analyse climatic data from 76 reptile and amphibian species introduced into the USA. We test for a relationship between species climatic-niche values in their native and introduced ranges. We also quantify niche shifts in introduced populations relative to their native ranges and the rate of change associated with these shifts. We then compare these rate estimates to those estimated among species and to projected rates of future climate change.

Results: Remarkably, niche shifts in introduced species are roughly a million times faster than niche shifts among species in their native ranges and roughly 10 times faster than rates of projected climate change.

Main conclusions: Our results demonstrate that dramatic and rapid niche shifts are possible, although these may be limited in species' native ranges by biotic interactions and other factors.

KEYWORDS

amphibians, climate change, introduced species, niche conservatism, niche shift, reptiles

1 | INTRODUCTION

As global temperatures rise, many species are becoming threatened (e.g., Thomas et al., 2004; Urban, 2015; Wiens, 2016) and these species may need to rapidly shift their geographic ranges or climatic niches to avoid extinction (e.g., Holt, 1990; Moritz & Agudo, 2013; Williams, Shoo, Isaac, Hoffmann, & Langham, 2008). However, shifting geographic ranges may be difficult for numerous species, either

because dispersal is limited by natural or anthropogenic factors (e.g., occurring on mountaintops, islands or isolated nature preserves) or because rates of dispersal are too slow (e.g., Loarie et al., 2009; Schloss, Nunez, & Lawler, 2012). In these cases, the speed at which species can shift their climatic niches may be critically important for their survival (where a "niche shift" or "niche change" is any change in the realized climatic niche, whether evolutionary or not, following Guisan, Petitpierre, Broennimann, Daehler, & Kueffer, 2014).

Unfortunately, recent analyses of rates of change in species' realized climatic niches show that these rates are far slower than projected rates of anthropogenic climate change (typically by >100,000 fold). These rates are based on phylogenetic analyses of divergence in niche variables over time among closely related species and populations, with timescales from thousands to millions of years (Jezkova & Wiens, 2016; Quintero & Wiens, 2013). Yet, these analyses also revealed that these climatic niche shifts appear to be faster over shorter timescales (e.g., potentially caused by rapid change over short time-scales and subsequent long-term stasis). Therefore, it is unclear how quickly climatic niches might change over the timescales that are relevant to anthropogenic climate change (i.e., decades). Here, we use climatic data from introduced species as one line of evidence to assess rates of climatic niche change at the decadal timescale, based on how quickly climatic niches can change between native and introduced populations (with niche change measured as divergence in introduced populations beyond the niche values in the native range; see Figure 1).

Numerous studies have used data from introduced species to test the extent to which climatic niches are conserved or labile (e.g., Broennimann et al., 2007; Peterson, 2003; Petitpierre et al., 2012). Several analyses have shown that climatic niches are similar between populations of species in their native and introduced ranges (e.g., Peterson, 2003; Petitpierre et al., 2012), and that niche models based on species' native ranges can potentially predict their spread in the introduced range (e.g., Thuiller et al., 2005). More generally, concordance between realized climatic niches in species' native and introduced ranges may provide evidence of niche conservatism (e.g., Petitpierre et al., 2012; Wiens & Graham, 2005). This pattern of niche conservatism has also been used to support the use of niche modelling for predicting impacts of anthropogenic climate change on species distributions and persistence (e.g., Petitpierre et al., 2012),

an approach that assumes niche divergence will be negligible over the timeframe of prediction. Nevertheless, many other studies have instead shown frequent deviations between climatic distributions of species in their native and introduced ranges (e.g., Atwater, Ervine, & Barney, 2018; Broennimann et al., 2007; Colautti & Barrett, 2013; Early & Sax, 2014; Fernández & Hamilton, 2015; Gallagher, Beaumont, Hughes, & Leishman, 2010; Lauzeral et al., 2011; Parravicini, Azzurro, Kulbicki, & Belmaker, 2015). Recent authors have also suggested that changes in introduced populations can potentially shed light on how species might respond to climate change (e.g., Fernández & Hamilton, 2015; Guisan et al., 2014; Monahan & Tingley, 2012; Moran & Alexander, 2014). Yet few studies, if any, have explored how quickly climatic niches change in introduced species and how this speed might compare to rates of anthropogenic climate change and to rates of niche change among species. Of course, introduced species may not fully reflect how species will respond to climate change in their native ranges (Fernández & Hamilton, 2015; Guisan et al., 2014; Moran & Alexander, 2014). Nevertheless, they can offer insights into a more specific (and very relevant) question: how quickly can climatic niches change over timescales relevant to global warming?

Here, we estimate rates of change in climatic niche variables in introduced populations and compare these to rates of niche divergence among native species and to rates of anthropogenic climate change. We focus on 76 exotic reptile and amphibian species in the USA. This study system offers several advantages. First, introduced reptiles and amphibians have been relatively well-documented in the USA, and a survey including most exotic species and the timing of their introductions is available (Kraus, 2009). Second, most introductions occurred between 50 and 100 years ago (Kraus, 2009), similar to the timescale in studies of projected anthropogenic climate change. Third, these species offer a large sample size without being

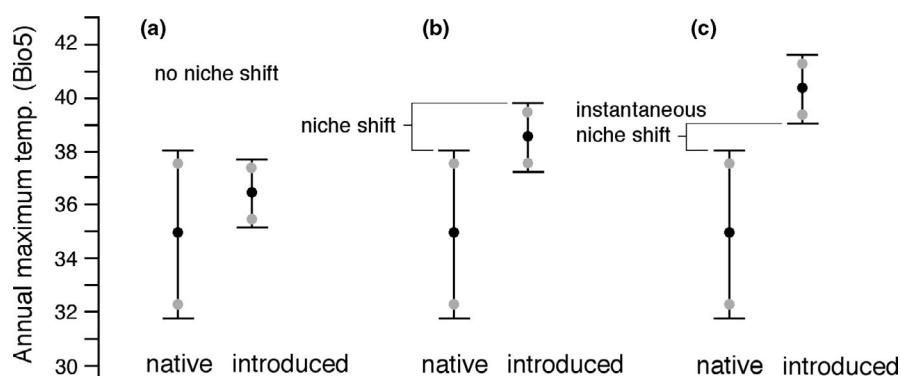


FIGURE 1 Three hypothetical examples illustrating how niche shifts were inferred for a given introduced species. Thick lines indicate the range of values for a climatic variable among localities in each range (native and introduced). Black dots indicate means, grey dots indicate the 10th and 90th percentiles. (a) When the values in the native and introduced ranges overlap fully, no niche shift is inferred. Note that mean values between the native and introduced ranges can differ substantially, even when the values overlap fully (this issue also applies to multivariate analyses). (b) A niche shift is inferred when some values in the introduced range are outside those in the native range. The niche shift is the absolute difference between the most extreme value in the introduced range and the closest value in the native range. A larger niche shift is inferred using the percentiles. (c) An instantaneous niche shift is the minimum absolute difference between the values in the native and introduced ranges, and is only inferred when there is no overlap between the native and introduced ranges. This shift is considered “instantaneous” because it must have occurred when the species was introduced. A much larger instantaneous niche shift would be inferred using the difference between percentiles.



unmanageable (e.g., contrasting with ~25,000 exotic plant species in the USA; Pimentel, Zuniga, & Morrison, 2005). Fourth, the USA spans a broad range of climates and habitats (from arctic to tropical), avoiding potential biases associated with a single climatic regime. Fifth, rates of change in climatic niche variables have been estimated for >300 reptile and amphibian species in their native ranges, and compared to rates of anthropogenic climate change (Quintero & Wiens, 2013), providing both sets of rates for comparison to rates in introduced species. These analyses suggest that future climate change will be >100,000 times faster than typical rates of niche change among species. We note that there have been numerous studies on introduced reptiles and amphibians, including studies of their climatic niches and niche shifts (e.g., Li, Liu, Li, Petitpierre, & Guisan, 2014; Liu et al., 2017; Mahoney et al., 2015; While et al., 2015). However, to our knowledge, no previous study has estimated rates of niche change between native and introduced populations and compared them to rates of niche divergence among species and to rates of anthropogenic climate change.

In this study, we compare rates of niche change in introduced population to rates of niche change among species and projected rates of anthropogenic climate change. We first amassed locality data representing the native and introduced ranges of each species (Appendix S1) and obtained climatic data (Appendix S2) for four key climatic variables. We then tested for relationships between climatic niche values in the native and introduced ranges among species (Appendix S3). We next identified niche shifts as cases in which (for a given species and climatic variable) values in the introduced range were outside the set of values in the native range (Figure 1), and the extent of these niche shifts (i.e., the difference between the most extreme value in the introduced range and the closest value in the native range). We then estimated the timeframe over which these niche shifts occurred. Finally, we estimated rates of niche change based on these two values. We then compared these rates to rates of niche change among native species and rates of anthropogenic climate change. Our results show that climatic niche shifts are widespread among these introduced reptile and amphibian species, and that they can be dramatically faster than rates of niche change among native species and faster than rates of projected climate change.

2 | MATERIALS AND METHODS

2.1 | Selection of introduced species

We included most introduced, established species of reptiles and amphibians in the USA (including Alaska and Hawaii), starting from the extensive summary of Kraus (2009). These included 14 amphibians (all anurans [frogs and toads]) and 62 non-avian reptiles (one crocodilian, six turtles, 52 lizards, three snakes). However, we acknowledge that newly introduced species are recorded frequently, making a comprehensive sampling a constantly moving target. Regardless, our study clearly includes a large sample size of introduced, established species. By “established” we mean species that are reproducing successfully in their introduced range. We included

introductions of species from outside the USA and introductions between different parts of the US (i.e., different states). The latter are no less biologically relevant, and many parts of the USA are more geographically distant from each other than many countries are. However, we did not include introductions between different parts of the same state, given the practical difficulty of distinguishing native and introduced localities in these cases.

2.2 | Locality and climatic data

We initially searched GBIF (www.gbif.org), HerpNet (www.herpnet.org) and VertNet (www.vertnet.org) for georeferenced localities for each species in its native and introduced ranges. These were supplemented with localities from the primary literature, especially for exotics (e.g., using Kraus, 2009). For several species, carefully vetted climatic data for native ranges were already available (Quintero & Wiens, 2013). In all cases, we ensured that localities in the native range were consistent with the known native geographic range, using published maps and online resources (e.g., amphibians: IUCN, 2014; reptiles: Uetz & Hošek, 2014). We focused on sampling each species' entire native range, including diverse latitudes, longitudes and elevations (and we added localities from the literature in some cases where representation in these databases appeared inadequate). Climatic data for each locality are presented in Appendix S1 and summarized in Appendices S2 and S3.

Climatic and elevational data for each locality were obtained from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) at a resolution of ~1 km². This database consists of temperature and rainfall data from weather stations from 1950 to 2000, spatially interpolated and averaged. This time period (or earlier) encompasses most introductions analysed here (Appendix S4) and precedes the major increases in global mean annual temperature (above the pre-industrial average) associated with global warming (IPCC, 2014). Climatic data for more recent time periods (i.e., subsequent to the introductions and niche shifts) would not necessarily be relevant to our study. Locality data were screened again to find and remove outliers in elevational distributions in the native range (e.g., lowland species with a single locality >2,000 m). After the final screening, we had an average of 117 unique localities per species within the native range (range = 4–1130) and 22 for each introduction to each region (range = 1–899). Some species were separately introduced to more than one part of the USA (e.g., both Florida and Hawaii) and these were generally treated as separate units. Many species are known from very few localities in their introduced range (e.g., recent introductions), but as only demonstrably established introductions are included here, these introductions were just as relevant to understanding niche shifts as those known from hundreds of localities. Some species are known from relatively few localities in their native ranges, but these were generally species with very small native ranges (such that a few localities should accurately capture the climatic variation across the entire species range).

We focused on four standard climatic variables: annual mean temperature (Bio1), hottest annual (e.g., summer) temperatures (Bio5),

coldest annual (e.g., winter) temperatures (Bio6) and annual precipitation (Bio12). Annual temperature and precipitation are important descriptors of overall climate (e.g., tropical vs. temperature; mesic vs. arid) and are widely used in studies of climate change. In contrast, these temperature extremes (Bio5, Bio6) are generally considered to be crucial in determining where species can occur and persist, because these will be the hottest and coldest temperatures that species are potentially exposed to. We used only annual precipitation because this should be more relevant than precipitation over shorter time periods (e.g., arid and mesic regions are defined based on annual precipitation, not precipitation in particular time periods). These four variables were used in previous analyses of rates of niche change and climate change in vertebrates (Quintero & Wiens, 2013) and other taxa (Jezkova & Wiens, 2016). Thus, the use of these variables allowed direct comparison of these three sets of rates, which was the main goal of our study. We also note that it is possible that including other variables might also show rapid niche shifts in introduced species (or not), but this would not overturn our results for the variables we did include.

For most analyses, we used maximum and minimum values of annual mean temperature (Bio1) and annual precipitation (Bio12), as well as maximum values of maximum temperature (Bio5) and minimum values of minimum temperature (Bio6). We did not include lowest hottest temperatures or highest coldest temperatures, as it seems unlikely that these would be generally important in influencing species distributions.

We did not perform multivariate analyses of the climatic data for introduced species (e.g., PCA) because the units and corresponding rate estimates would then be unique to these analyses and not comparable between analyses. Thus, multivariate analyses would not allow us to accomplish our primary goal of comparing rate estimates from introduced populations to those from species in their native ranges and to rates of climate change. Furthermore, we were most interested in climatic variables relevant to global warming (e.g., warmer annual mean temperatures, hotter summer temperatures), and not composite multivariate variables combining relevant and less relevant variables. Therefore, multivariate analyses were not appropriate here and would actually obfuscate the patterns of interest. Finally, we note that our inferences from single variables cannot be overturned by those from multivariate analyses. For example, if we show that an introduced population of a given species experiences much higher maximum annual temperatures than it does in its native range, this remains true regardless of whether other climatic variables (e.g., annual mean temperatures) do not show the same pattern, and regardless of whether different climatic variables are correlated or not. Again, multivariate analyses would make it very difficult to disentangle rates for relevant and non-relevant variables, whereas our analyses directly estimate rates in the relevant variables.

2.3 | Comparing climates in native and introduced ranges

We performed phylogenetic linear regression analyses comparing climatic extremes in the native and introduced ranges across all

76 species (data and methods in Appendix S3). We performed six analyses, one for each variable (see above). For species introduced to two or more US regions, we averaged values between these regions to obtain a single estimate for the introduced range for each species, but just for this analysis (having two introduced data points for a single species would be problematic, especially for the phylogenetic analyses). Given niche conservatism, we predicted significant positive relationships, as previously found for maximum latitudes for 35 reptile and amphibian species introduced in the USA (Wiens & Graham, 2005). This would indicate that (for example) species native to tropical regions become established primarily in tropical US regions and temperate species in temperate regions.

2.4 | Climatic niche shifts and rates

Here, we describe the baseline methodology used to estimate niche shifts and rates of change in introduced populations. We then evaluated the consequences of changing this methodology for mean rate estimates in Appendix S5. We use “niche shift” and “niche change” rather than “niche evolution”, to emphasize that many niche shifts may not involve evolutionary adaptation, including niche shifts among species.

To estimate niche shifts for a given climatic variable, we first identified cases in which species had values in the non-native distribution that were outside the range of values in the native distribution (Figure 1). These cases are summarized in Appendix S4. We focused on these cases because a non-native population could be within the native climatic niche, but the native and non-native populations might still differ substantially in mean values (Petitpierre et al., 2012). For example, a newly introduced population might be within the native niche for a given variable but have a very different mean value relative to the native geographic range, simply because that population was introduced at a site that differed from the mean value of the native range (Figure 1a). There is no reason to expect any species to be introduced to a site that corresponds to the exact mean value of its native geographic range for all climatic variables. Therefore, a difference between mean values in the native and introduced ranges may not represent a niche shift at all (note: this issue would also apply to centroids or almost any method for summarizing variation among localities within the native and introduced ranges, not just means). To avoid this problem, we only considered niche shifts to be cases in which climatic niche values in the introduced populations were entirely outside the range of values from the native geographic distribution (Figure 1b). For a given variable, a climatic niche shift was therefore considered to be the difference between the most extreme value in the introduced range and the closest value in the native range (Appendix S4). Note that using quantiles to remove potential effects of outliers in the native and introduced ranges would have similar consequences to using means (i.e., artificially increasing the frequency and magnitude of inferred niche shifts). We performed such analyses in Appendices S5 and S6, and confirmed that the frequency and rate of inferred niche shifts generally increased. Therefore, our main analyses used the more



conservative approach for inferring niche shifts. We also focused on the absolute amount of non-overlap between native and introduced ranges, not the non-overlap divided by the niche width of the exotic or native range (i.e., “niche expansion” and “niche unfilling” of Guisan et al., 2014). Niche width is not necessarily relevant to how quickly species can occupy novel climatic conditions.

Once climatic niche shifts were quantified, we estimated rates of change based on the maximum timeframe over which these shifts occurred. Specifically, we first determined the oldest successful introduction to the region (e.g., Florida), based on literature summarized by Kraus (2009). We then determined when the species was documented from the specific non-native locality with the extreme value for that variable (e.g., when the relevant voucher specimen was collected). The difference between these dates was the maximum time period over which the niche shift occurred. When the date was determined only to decade, we used the beginning of that decade (1980s = 1980). The final rate of climatic divergence for a given variable was the inferred niche shift divided by the maximum time period over which the shift occurred in the introduced range. By using the maximum timeframe, our estimated rates should be conservative (i.e., yielding lower rates). We included all niche shifts, regardless of how small, to avoid upwardly biasing estimates of mean shifts and rates. Niche shifts, dates and rates are summarized in Appendix S4.

Several species are thought to have colonized Hawaii as stowaways with the original human colonization of the islands (e.g., *Emoia impar*, *Gehyra mutilata*, *Lepidodactylus lugubris*). Kraus (2009) listed a date of “~400” for these introductions. However, subsequent analyses of human colonization revised these estimates to ~1,200–1,290 A.D. (Wilmschurst, Hunt, Lipo, & Anderson, 2011). Therefore, we used ~1,200 A.D. for estimating the maximum time for niche shifts in these species.

To estimate niche shifts, we assumed that when a species was introduced to a region, it initially occurred in climatic conditions similar to its native climatic niche and that shifts occurred subsequently within the non-native range to reach the most extreme value. Given the exact date and locality of the first introduction of each species in each region, the timeframe needed to achieve the most extreme value might be narrowed in some cases, leading to faster rate estimates. This information was available in some cases, but not all. We instead used a consistent, conservative methodology for all species (where “conservative” again means yielding lower rate estimates).

Introduced species might have reached the locality with the most extreme value long before it was documented there (e.g., by a museum specimen). If this older date were known, it would decrease the time between the first introduction to the region and the time it reached this extreme-climate locality (leading to a faster rate estimate). Again, our rate estimates are conservative, yielding lower rate estimates.

We included only introductions that were established in a given non-native region. However, we assumed that once a species was established in a region (e.g., south Florida), it was also established at localities nearby the initial site of introduction (unless other information called this into question). That is, for species

that occur at multiple localities in the introduced range, it would be very difficult to determine whether a species was breeding at every single site where it has been recorded (and for dozens of species). Therefore, this assumption was difficult to avoid for most species, especially if the exact site of introduction was not known with precision.

In some cases, the introduced species was known from a single locality or a small number of nearby localities, all with similar values for the climatic variables. In these cases, there was no uncertainty about when the niche shift occurred, and whether non-native populations with extreme values were established or not, as we only considered populations known to be established in a region. However, these cases were more ambiguous for estimating a rate, as the time is effectively zero. We used a value of 1 year in these cases (the time for a newly introduced population to experience the full yearly range of temperatures at a location). This value is arbitrary but nonetheless conservative, as the actual time frame is instantaneous and a shorter timeframe would yield a faster rate.

The paragraphs above describe our baseline methodology for inferring the mean rate of niche change in introduced populations (on which the Results are based). However, we also explored the consequences of changing these initial assumptions (Appendix S5). These alternative analyses generally gave mean rate estimates within an order of magnitude of the baseline estimates. These alternative analyses included removing instantaneous niche shifts (which decreased mean rates), including species with no niche shifts (decreased) and including only instantaneous niche shifts (increased). We reduced the potential impact of outlier localities by using only the 90th and 10th percentiles to estimate ranges of values in the native and introduced distributions (Appendix S6). Again, this led to more widespread rate shifts, and to generally faster rate estimates.

For the analyses that included only instantaneous niche shifts, we included several species with many non-native localities that also had instantaneous niche shifts, given that there was no overlap between the native and introduced values (Figure 1c). In these cases, we determined the minimum difference between the values of the introduced species in a given region and the closest value in the native range. These niche shifts were also instantaneous, because they occurred simultaneously with the introduction. All instantaneous niche shifts are summarized in Appendix S7: Table S1.

We recognize that there are potentially many other approaches for quantifying niches and niche shifts. However, most of these (such as niche modelling) do not lend themselves to estimating a rate of niche change over time for specific climatic variables, which was our primary goal here.

2.5 | Comparing rates of niche shifts in introduced populations to rates among species and climate change

We compared the rates of niche shifts in introduced populations estimated here to rates of past niche change among species and to

rates of projected climate change that were estimated in a previous study (Quintero & Wiens, 2013). That study estimated rates in 10 families and 306 species of reptiles and amphibians (in their native ranges). Rate estimates for each species were based on finding sister species in well-sampled groups, estimating the best-fitting model of trait evolution for each variable for that group, then using that model to reconstruct trait values across the group's tree. The rate of change for each sister species is the difference between the estimated value in the ancestor of the pair and the species' current value (mean across localities) divided by the age of the species (details in Quintero & Wiens, 2013). These analyses used the same climatic variables used here, but were based on mean values among localities for each species, rather than extremes (used here). However, we performed new analyses to confirm that both mean and extreme values yield similar rate estimates among species (Appendix S8). Rates of niche change are broadly similar across reptile and amphibian clades (Quintero & Wiens, 2013), including species in both tropical and temperate regions. Therefore, use of different sets of species (i.e., the 306 vs. the 76 introduced species) should have little impact on our conclusions. Moreover, there was broad overlap between the clades used in both studies (e.g., both included hylid and ranid frogs, emydrid turtles, alligatorid crocodilians, and chamaeleonid, phrynosomatid, and scincid lizards).

We used estimated rates of future climate change (from Quintero & Wiens, 2013) based on IPCC (2007) projections for 2080–2099 ("2100" hereafter for brevity), using Emission Scenario A2 (following Beaumont, Hughes, & Pitman, 2008) and six standard General Circulation Models (GCMs): CCCMA-CGCM, CSIRO-MK3, HADCM3, CCSR-NIES, MPI-ECHAM5 and MRICGCM2.3.2. In brief, the rate of future climate change for each locality for each climatic variable was the difference between the estimated value for the 1950–2000 time period and the projected value for the 2080–2099 time period, divided by the overall interval between these time periods (90 years). For each species, the rate was the mean rate across these localities. We used mean values across all 1,265 vertebrate species for all six models (Appendix S9). Use of all species increased sample sizes, and future rates are not based directly on niche characteristics of species. More recent projections (IPCC, 2014) give very similar rate estimates that remain similar across different projection models (Jezkova & Wiens, 2016).

3 | RESULTS

Most climatic variables showed a significant, positive relationship between conditions in the native and introduced ranges (Figure 2; Table 1). Thus, species from tropical regions have generally become successfully established only in tropical regions of the USA (e.g., Hawaii, Florida), and temperate species only in temperate regions (e.g., Kansas, Ohio). These results support an overall pattern of niche conservatism.

Nevertheless, 61.8% of these species had climatic distributions in their introduced ranges that were outside those of their native

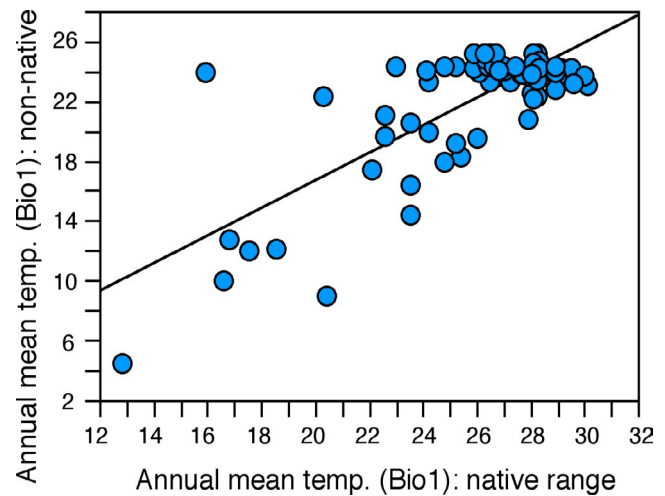


FIGURE 2 Relationship between climatic distributions of species in their native and introduced ranges. This example shows the relationship ($r^2 = 0.587$; $p < 0.0001$) between maximum values of annual mean temperature (maximum Bio1) in the native and introduced ranges for 76 reptile and amphibian species in the USA. Results plotted are for the raw data, but the main analyses are based on phylogenetic regression. See Table 1 for results for all variables and Appendix S3 for methods and data

ranges for one or more climatic variables (amphibians: 11/14; crocodilians: 1/1; turtles 5/6; lizards: 29/52; snakes: 1/3). Some instances might be explained by inadequate sampling in the native range, but sample sizes of localities in the native range were not significantly different between species with and without niche shifts (mean with niche shifts = 102.6; mean without = 139.1; t -test, $p = 0.3567$). Many niche shifts occurred in the two largely tropical regions (Hawaii = 42%, Florida = 24%, of 104 total; Appendix S4), with fewer in temperate regions (e.g., California = 9%, Arizona = 8%). However, this seemed to reflect the overall smaller number of introduced temperate species (Figure 2).

These niche shifts occurred in all variables and were often substantial in their magnitude (Figure 3a; Appendix S4). For example, introduced species often occurred in cooler climates than in their native ranges (mean decrease in coldest annual mean temperature = 2.6°C; mean decrease in coldest winter temperatures = 4.6°C). Many shifts were also into warmer climates (mean increase in annual mean temperature = 2.9°C; hottest summer temperature = 2.4°C). Shifts were also inferred into both drier conditions (mean decrease in annual precipitation = 352 mm/year) and wetter conditions (mean increase = 1,256 mm/year).

These niche shifts occurred at rapid rates (Appendix S4). For example, shifts towards cooler annual mean temperatures occurred at a mean rate of 0.09°C/year (range = 0.001–0.600), and towards coldest yearly temperatures at a mean rate of 1.23°C/year (range = 0.008–6.7). Shifts toward warmer annual mean temperatures occurred at a mean rate of 0.54°C/year (range = 0.105–2.00), and towards hotter maximum temperatures at 0.86°C/year (range = 0.053–4.6). Shifts towards higher annual precipitation occurred at a mean rate of 217.19 mm/year



TABLE 1 The relationship between climatic niche variables in the native and introduced ranges of species

Climatic variable	r^2	t-value	Lambda	p
Minimum Bio1 (mean temperature)	0.461	7.949	0.152	<0.0001
Maximum Bio1 (mean temperature)	0.587	10.263	0.000	<0.0001
Maximum Bio5 (maximum temperature)	0.076	2.470	0.000	0.0035
Minimum Bio6 (minimum temperature)	0.310	5.761	0.642	<0.0001
Minimum Bio12 (annual precipitation)	0.002	-0.352	0.134	0.8835
Maximum Bio12 (annual precipitation)	0.122	3.204	0.000	0.0001

Results are based on phylogenetic regression among species, for 76 species of reptiles and amphibians with one more introduced populations in the USA. Analyses are based on the most extreme values for each variable in the native and introduced ranges of each species, not the means. See Appendix S3 for methods and data. For species with introduced populations in different regions of the USA (e.g., Florida, Hawaii), the extreme values in different regions are averaged to obtain a single value for all introduced populations. All relationships are positive.

per year (range = 4.84–1,008), and towards lower annual precipitation at 20.80 mm/year per year (range = 0.235–184). These mean rate estimates were largely robust to alternative methods (Appendices S5 and S6).

Many niche shifts were effectively instantaneous, given no overlap in the values of climatic variables between the native and introduced ranges (Figure 3b). Thus, these niche shifts were concomitant with the initial introduction of these species to these non-native regions. Instantaneous shifts were inferred in 23 species (seven amphibians, one crocodilian, three turtles, 12 lizards; Appendix S7: Table S1) and in all variables. Instantaneous shifts were similar in magnitude to the other niche shifts (Figure 3).

Rates of niche change in introduced populations were dramatically faster than rates of change among species, by roughly a millionfold (Figure 4; Appendix S8). For example, for annual mean temperature, the mean rate among 306 reptile and amphibian species is 0.62°C per million years (Quintero & Wiens, 2013). For introduced species that have undergone niche shifts (Appendix S4), mean rates were 0.54°C/year (to warmer mean annual temperatures) and 0.09°C/year (to cooler temperatures). Similarly, annual precipitation changed among species at a mean rate of 104.9 mm per million years (Quintero & Wiens, 2013). Here, niche shifts in extremes of annual precipitation for exotics vary from 217 mm/year (for higher precipitation) to 21 mm/year (for lower precipitation). Differences were similar in magnitude for the hottest and coldest yearly temperatures (Figure 4).

Niche shifts in introduced populations were also faster than rates of projected climate change, by roughly tenfold (Figure 4; Appendix S7: Table S2). Across the geographic ranges of 1,265 vertebrate species (Quintero & Wiens, 2013), the mean rate of projected change for annual mean temperature (Bio1) was ~0.06–0.10°C/year (across six models for projecting future climates; Appendix S9), whereas the mean rate of niche change was 0.54°C/year for introduced species shifting into warmer climates (for Bio1). For hottest annual

temperatures (Bio5), the mean rate of projected change was ~0.04–0.06°C/year, whereas the mean rate of niche change for introduced species for this variable was 0.86°C/year. Similarly, annual precipitation had a mean projected rate of future change of 6.37–9.77 mm/year. For introduced species, mean rates of change in annual precipitation (Bio12) were 217.19 mm/year for increases and 21.44 mm/year for decreases.

4 | DISCUSSION

We examined climatic niche characteristics of 76 reptile and amphibian species with introduced populations in the USA. We found an overall signature of niche conservatism, with significant relationships between most climatic variables in their native and introduced ranges. But within this overall relationship were many deviations between climatic niche values in the native and introduced ranges. These deviations were striking in their magnitude and (most importantly) in their estimated rates of change. Our results suggest that niche shifts in these introduced populations are dramatically faster than niche shifts among species (by roughly a millionfold), and are faster than rates of projected climate change in the next ~100 years (by roughly tenfold). We discuss the implications of these results below.

First, our results may help reconcile the conflicting literature on niche conservatism and lability for introduced species. Previous studies have found conflicting results but examined different sets of species (e.g., Petitpierre et al., 2012 vs. Atwater et al., 2018). Here, we found that both conservatism and lability were widespread in the same set of 76 species. Specifically, climatic niches were broadly similar between native and introduced ranges (Figure 2), but deviations between them were common, often quite large, and occurred over very short timescales. This could be a widespread pattern. We

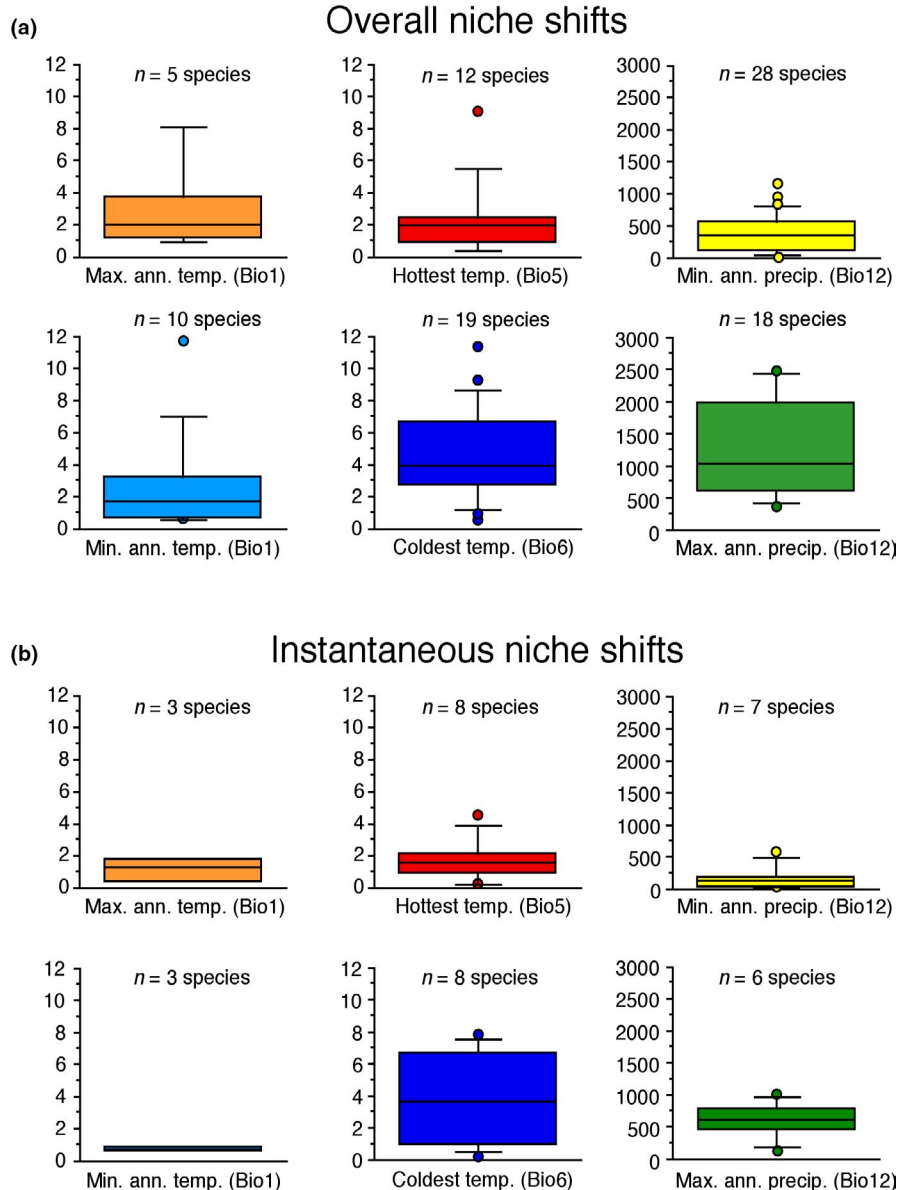


FIGURE 3 Climatic niche shifts in introduced reptile and amphibian species in the USA. (a) Overall niche shifts, showing the difference between extreme values for the variable in the introduced range and the closest value in the native range (indicating median, quartiles, 10th and 90th percentiles and outliers). (b) Instantaneous niche shifts (minimum difference between climatic niche values in species' native and introduced ranges), coincident with each species' introduction. The sample size indicates the number of species, but some species have >1 niche shift for a given climatic variable, associated with their introductions to separate U.S. regions. Also, a single species can have shifts in >1 variable. Note that all shifts are in absolute values, including decreases in temperature (minimum Bio1 and Bio6) and precipitation (minimum Bio12)

show that an overall pattern of niche conservatism across many species can co-occur with rapid and extensive niche change within individual species.

Second, our results show the potential for species to undergo rapid shifts in their climatic niche, roughly tenfold faster than projected climate change (Figure 4). These rapid rates are in striking contrast to those from vertebrate species in their native ranges, which were typically >100,000 times slower than rates of projected climate change (Quintero & Wiens, 2013). Moreover, the absolute magnitude of these changes was substantial, not just the rates (mean increases in annual mean temperature = 2.9°C; mean increase in hottest annual temperatures = 2.4°C).

Why are rates of niche change so fast in introduced species? We think that the primary reason for these rapid rates is that many species can tolerate broader climatic conditions than suggested by their climatic distributions in their native ranges (e.g., wider fundamental

than realized climatic niches; Fernández & Hamilton, 2015). Thus, many species showed instantaneous niche shifts, occurring in climatic conditions entirely outside those of the native range for a given variable (Figure 3b). These species clearly did not adapt evolutionarily to these conditions instantaneously, but instead must have been able to tolerate them before their introduction (although there could still be subsequent adaptation after their introduction; e.g., While et al., 2015). We speculate that biotic interactions in their native ranges may have prevented many species from occupying the full range of climatic conditions that they can actually tolerate. This is consistent with the idea that the spread of introduced species may be facilitated by the absence of species that they interact with in their native ranges, such as competitors, pathogens, and predators (e.g., the Enemy Release Hypothesis; Keane & Crawley, 2002). This hypothesis is potentially supported here by niche modelling analyses of eight diverse species in which instantaneous niche shifts occurred

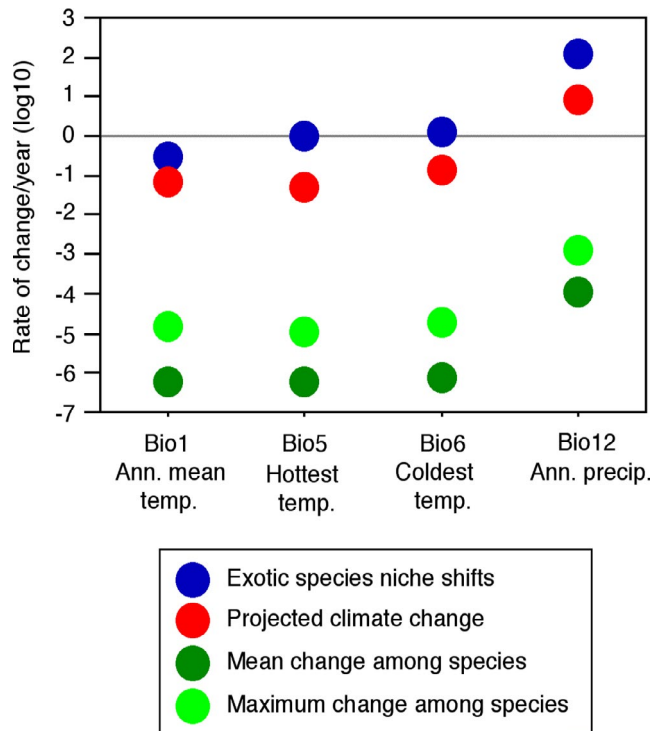


FIGURE 4 Comparison of three rates of change in climatic niche variables. The results show faster rates of niche change in introduced reptile and amphibian species (mean among niche shifts, averaging increases and decreases for Bio1 and Bio12) than mean rates of projected climatic change within the geographic ranges of 1,265 vertebrate species (mean of means across six projections), and mean and maximum rates of change among 306 reptile and amphibian species for each climatic variable. Rates are log 10 transformed and given in °C/year for temperature variables, mm/year for precipitation. Data and standard deviations (generally too narrow to see here) are summarized in Appendix S7: Table 2

(Appendix S10). The niche modelling results suggest that these species could expand their native ranges into contiguous areas if their ranges were limited only by these climatic variables (but resolving the causes of species range limits is not our primary goal here). In further support of this idea, niche modelling analyses across amphibians (using these same variables) suggest that species typically occupy only ~60% of their climatically suitable ranges within a region (Munguía, Rahbek, Rangel, Diniz-Filho, & Araújo, 2012). Overall, many rapid niche shifts occur because species can tolerate conditions not present in their native ranges, and biotic interactions in the native range offer one potential explanation for why their realized niches may not match their fundamental niches.

Similarly, realized niches of some species in their native ranges might be constrained from matching their fundamental niches by non-biotic factors. For example, some niche shifts involved species native to small tropical islands (e.g., Jamaica, Mauritius). These islands might have a limited range of climatic conditions relative to the mainland (or relative to more heterogeneous islands), potentially preventing species from extending their native ranges into areas with climatic conditions that they could tolerate, and limiting their

realized climatic niches. In our study, 32.6% of the 46 species with niche shifts had native ranges primarily or exclusively on tropical islands. Thus, this factor might help explain some niche shifts, but not all of them.

Importantly, the idea that these rapid climatic niche shifts are associated with differences between realized and fundamental climatic niches does not make these niche shifts irrelevant to future climate change. For example, forecasts of how climate change will impact species' persistence are generally based on their realized climatic niches (e.g., Thomas et al., 2004; Urban, 2015). Thus, our results, which show that species' climatic tolerances are seemingly wider than indicated by their native ranges (and can change rapidly), may indicate greater potential resilience of species to climate change than previously thought. It would be misguided to assume that the only niche changes relevant to global warming are evolutionary changes in the fundamental niche. Indeed, species interactions seem to be the most important cause of local extinctions and declines due to climate change so far (e.g., Cahill et al., 2013; Ockendon et al., 2014). Our results here imply that species interactions might be an important factor limiting rates of climatic niche change in species' native ranges.

Another potential explanation for the rapid rates found here is that rates are simply faster when measured over shorter time scales (e.g., Hunt, 2012). This negative time-rate relationship was found previously for climatic niche shifts among native species and populations (Jezkova & Wiens, 2016; Quintero & Wiens, 2013). Indeed, many niche shifts found here were effectively instantaneous (Figure 3b). An important question is whether the rapid rates in introduced species found here are trivial niche shifts that only yield fast rates because they were measured over very short time-scales. Remarkably, the niche shifts found here are comparable in magnitude to niche differences between closely related species (i.e., regardless of rates). For example, previous analyses (Quintero & Wiens, 2013) found that in 10 of 17 vertebrate clades, median differences between sister species for annual mean temperature were <3.0°C. Here, the mean shift (increase) in annual mean temperatures among introduced species is 2.9°C. This mean shift is also similar to the absolute change expected in mean annual temperature over the next 50 years (Jezkova & Wiens, 2016; based on IPCC, 2007, 2014). Further, most niche shifts were associated with introductions that occurred <100 years ago but >50 years ago (median = 56; Appendix S4). Thus, the timeframe is similar to that typically considered in studies of global warming impacts on species (Thomas et al., 2004; Urban, 2015). In summary, the rapid rates found here are not simply an artefact of small changes over very short time-scales.

Do these rapid niche shifts in introduced species indicate that species may generally be more resilient to climate change than previously thought? One important issue is whether introduced species are representative of all species in a group. Most species here were intentionally introduced (50 of 76; Appendix S2), often in association with the pet trade (44 species), and thus need not have special traits that make their accidental spread more likely. Nevertheless, a recent analysis (Allen, Street, & Capellini, 2017) suggested that introduced

amphibians and reptiles have faster life history relative to non-introduced species (although relatively few non-introduced species were included). Overall, our results show that rapid niche changes have occurred in numerous species of reptiles and amphibians, but whether the potential for such rapid niche change is widespread across all species remains uncertain.

5 | CONCLUSIONS

In conclusion, we find that introduced species can shift their climatic niches far more rapidly than suggested by analyses of species in their native ranges. On one hand, this is good news regarding the potential resilience of species to climate change. On the other hand, most species will experience climate change in their native ranges. Thus, they may contend with the same constraints on niche shifts that they experience now (e.g., species interactions). Therefore, our study should not be taken to imply that there is little danger to species from climate change. Indeed, local extinctions from climate change are already widespread among plant and animal species, suggesting that niche shifts are often insufficient to prevent population extinctions (Wiens, 2016). Nevertheless, our results do demonstrate that extraordinary climatic niche shifts are possible for many species under some conditions. Indeed, numerous species have shown some resiliency to climate change, even as nearby and sympatric species suffered local extinctions (Wiens, 2016). Overall, we suggest that these rapid niche shifts in introduced species should be part of the evidence considered when forecasting the impacts of climate change using similar large-scale climatic data. For example, the standard approach for assessing species vulnerability to climate change (i.e., using niche modelling to examine the future distribution of a species based on its current climatic niche) does not incorporate the potential for rapid niche changes that might allow the species to persist within its current geographic range.

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DATA AVAILABILITY STATEMENT

All data are available as Supplementary Information.

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SUPPORTING INFORMATION

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