

Risk of biological invasions is concentrated in biodiversity hotspots

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Understanding the locations of potential invasion hotspots and the extent to which they overlap with biodiversity hotspots is crucial for prioritizing efforts to reduce the impacts of alien species on global biodiversity. Using ensembles of species distribution models based on climate, anthropogenic predictors, vegetation, and water resources, we predict global potential invasion hotspots for alien herpetofauna (reptiles and amphibians). On average, when subjected to current and future climate scenarios, potential richness of alien herpetofauna per grid cell (the minimum unit of our spatial variables for modeling and projecting) in biodiversity hotspots is nearly 1.4 times higher than in other regions. Furthermore, potential invasion hotspots are projected to occupy a large proportion of the total area within biodiversity hotspots. These results suggest that biodiversity hotspots are at greater risk from alien herpetofaunal invasions than are other regions. Our results provide key information for globally targeting early detection and rapid-response programs to help prevent or mitigate future impacts of alien herpetofauna on biodiversity.

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Biological invasions are increasing as a result of international trade and globalization, posing a major threat to global biodiversity and ecosystem functioning (Simberloff *et al.* 2013; Blackburn *et al.* 2014). Understanding where potential invasion hotspots are located (Ibáñez *et al.* 2009; O'Donnell *et al.* 2012; Duursma *et al.* 2013), and the extent to which they overlap with biodiversity hotspots (Bellard *et al.* 2014), is crucial for prioritizing conservation efforts to prevent or mitigate future biodiversity impacts of alien species.

“Invasion hotspots” may be defined as areas with environmental conditions suitable for numerous alien species (O'Donnell *et al.* 2012); thus, they are areas with high innate invasibility. Several studies have used species distribution models (SDMs) to project potential invasion hotspots for alien plants at regional or continental scales (Ibáñez *et al.* 2009; O'Donnell *et al.* 2012; Duursma *et al.* 2013). Yet few studies have identified potential invasion hotspots globally for an entire taxonomic class or quantified how these invasion hotspots are distributed with respect to biodiversity hotspots under current or projected future climatic conditions.

Biodiversity hotspots include 35 geographic regions defined as having high levels of plant endemism and major habitat loss (Mittermeier *et al.* 2011), although these regions have high endemism in other taxa as well. Collectively, this makes these areas of great conservation

importance. Indeed, these geographic regions cover only 15.9% of Earth's land surface but contain 22,939 terrestrial vertebrate species (77% of the world's total) and 152,000 plant species (over 50% of the world's total) (Mittermeier *et al.* 2011). These areas harbor a total of 12,717 vertebrate species endemic to the hotspots, as well as 60% of mammals, 63% of birds, and 79% of amphibians, all designated as “threatened” by the International Union for Conservation of Nature. Biodiversity hotspots have raised public awareness of different threats to biodiversity, such as habitat loss, overharvesting, climate change, and alien species (Bellard *et al.* 2014). Determining the extent to which invasion risks are concentrated in biodiversity hotspots may facilitate cost-effective strategies for preventing or otherwise managing alien invasions at global or regional scales.

SDMs can be powerful tools for predicting potentially suitable environments for alien species (Ibáñez *et al.* 2009; Bellard *et al.* 2013; Guisan *et al.* 2013). Species' niches are typically modeled using climate data either from a species' native geographic range or from its native and invaded ranges together; these modeled niches are then mapped globally to identify areas potentially susceptible to further invasion under present or future climate scenarios (Ibáñez *et al.* 2009; Bellard *et al.* 2013; Li *et al.* 2014). Ideally, SDMs should include factors other than climate – such as anthropogenic activities, vegetation, and water resources – that potentially determine both the native and invaded distributions of a species (Ficetola *et al.* 2007; Dalby *et al.* 2014; Cardador *et al.* 2016). Human-mediated dispersal facilitates not only introductions of alien species outside of their native range but also range expansion within invaded ranges (Pyšek *et al.* 2010; Liu *et al.* 2014). In addition, many alien species are more likely to establish or spread in human-modified environments (Ziska and

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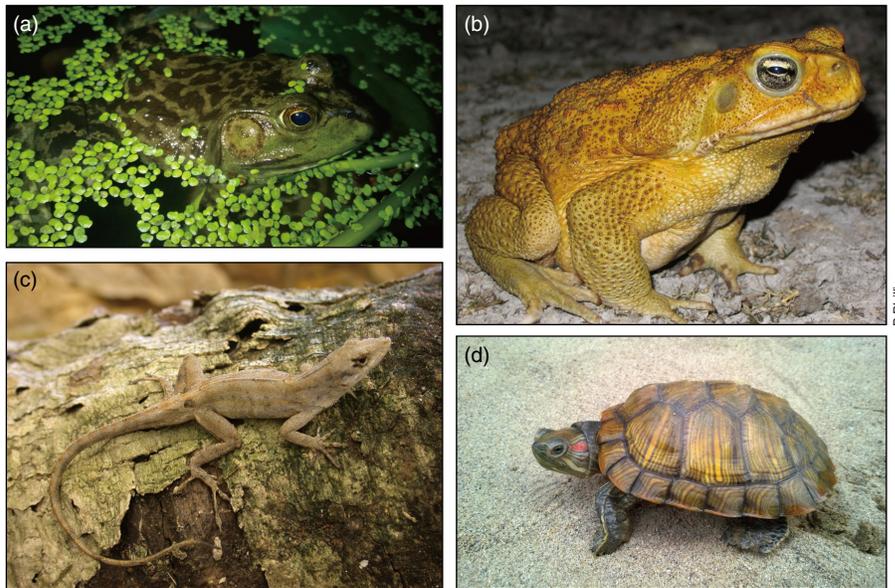


Figure 1. Four species of invasive herpetofauna. (a) The American bullfrog (*Lithobates catesbeianus*) is responsible for spreading the chytrid fungus that has caused amphibian population declines and is a predator and competitor of many small vertebrates; (b) the cane toad (*Rhinella marina*) has poisoned native predators in Australia; (c) the brown anole (*Anolis sagrei*) outcompetes and consumes native lizards; and (d) red-eared sliders (*Trachemys scripta*) hybridize with and compete with native turtles.

Dukes 2014). Vegetation structure and productivity can strongly affect microclimates and therefore distributions of species (Ferber *et al.* 2014). Moreover, environments with higher primary productivity may support larger populations and communities of animals, suggesting that this measure may be useful as a surrogate for biotic interactions at a site (Wisz *et al.* 2013). Finally, water resources may affect distributions of species by affecting habitat suitability. Water also facilitates dispersal of some species, given that many alien species expand their ranges through waterways (Ricciardi 2007). To date, climatic factors have commonly been included in SDMs, but other variables (eg anthropogenic activities) are rarely incorporated for predicting invasion risks (Elith 2013).

Here we use SDMs and an updated version of a comprehensive global database of reptile and amphibian introductions (Kraus 2009) to predict inherent invasion risks for established (eg having a wild reproducing population) alien herpetofauna at a global scale. Alien herpetofauna include several of the most notorious globally invasive species, such as the American bullfrog (*Lithobates catesbeianus*), cane toad (*Rhinella marina*), brown anole (*Anolis sagrei*), and red-eared slider (*Trachemys scripta elegans*) (Figure 1). Alien herpetofauna can have serious ecological, evolutionary, and societal impacts in their invaded ranges (Kraus 2009, 2015). Their ecological impacts are diverse and include predation on rare species, poisoning of predators, competition with natives, spreading novel parasites, secondary disruption of food webs, and modification of ecosystem functioning (Kraus 2009, 2015).

Herpetofaunal invasions can also cause genetic contamination or introgression via hybridization with natives, as well as evolutionary changes in morphological, physiological, or behavioral traits. Some alien herpetofauna even adversely affect human health, economies, or quality of life (Kraus 2009).

Our goal is to determine the susceptibility of different global regions to future herpetofaunal invasions, so as to assist with developing effective biosecurity measures. We evaluate the performance of SDMs, including climate variables alone, as well as SDMs that incorporate both climate and habitat variables. We then use these models to project invasion risk for alien herpetofauna under current and projected future climate conditions. Finally, we quantify the extent to which predicted hotspots of herpetofaunal invasion overlap with recognized global biodiversity hotspots.

Methods and materials

Species occurrence data

We obtained data on successfully introduced amphibian and reptile species from the database of Kraus (2009), which has been updated by one of the authors (FK). We compiled occurrence data from both native and introduced ranges of each species from various databases and published references (for more detailed methods, see WebPanel 1, WebTable 1, and WebFigure 1). We resampled all distributional data and spatial variables to a resolution of 10 arc-minutes. In sum, we used 125,543 grid-cell records, with an average of 450 cells per species, for 279 species of non-native amphibians ($n = 98$) and reptiles ($n = 181$).

Environmental variables

We assessed the performance of two sets of environmental variables: one containing climate variables alone, and the other including climate and habitat variables together. We used eight long-term averaged climatic variables representing annual trends, seasonality, and extremes (WebPanel 1). We downloaded data for the current climate from WorldClim (www.worldclim.org). For future climate projections, we adopted three widely used global circulation models (GCMs: CSIRO-MK3.6.0, IPSL-CM5A-LR, and MIROC5), for two periods (2040–2069 [hereafter “2050s”] and 2070–2099 [hereafter

“2080s”]) under two Representative Concentration Pathways (RCPs: RCP2.6 and RCP8.5). We included data on three habitat variables: human footprint to represent anthropogenic activities; the normalized difference vegetation index (NDVI), which is correlated with net primary productivity and total green biomass, as a vegetation surrogate; and data layers from the Global Lakes and Wetlands Database to quantify the area of open water (WebPanel 1).

Predicting environmental suitability

We predicted potentially suitable environments for each species using an ensemble of five SDM algorithms (BRT, GLM, MARS, MAXENT, and RF) with the biomod2 package in R (WebPanel 1). These algorithms fit statistical relationships between the current geographic distribution of a species and environmental predictors. High environmental suitability values for a particular grid cell indicate a higher relative likelihood of species presence. We used occurrence records from both native and invaded ranges of each species to fit SDMs, and we calibrated models using 70% of the distributional data and projected them onto the remaining 30% of data for evaluation. We assessed the discriminatory ability of models with two measures: the area under a receiver operating characteristic curve (AUC) and the true skill statistic (TSS) (WebPanel 1). AUC ranges from 0 to 1, with values 0.7–0.9 indicating fair to good model performance, and TSS ranges from -1 to $+1$, with values 0.4–0.8 indicating fair to good performance. To make conservative forecasts and minimize extrapolation errors, we restricted model projections to analogous environments: that is, environments sampled by occurrence and background records in both native and invaded ranges (Elith *et al.* 2010). We used an ensemble approach to reduce variation in predictions produced by different SDMs and GCMs (Araujo and New 2007). We excluded from the final ensemble any model with $AUC < 0.8$ and $TSS < 0.6$ (WebPanel 1; Bellard *et al.* 2013).

Quantifying potential invasion hotspots

We summed continuous SDM outputs across species to estimate potential species richness under current and future climates. We also compared results based on presence–absence predictions obtained by thresholding (the process of selecting a threshold for converting continuous model outputs to binary projections of present versus absent) raw SDM outputs into binary predictions (using the threshold maximizing TSS). We compared the potential richness per grid cell between biodiversity hotspots and other regions based on an equal-area grid cell (approximately $10' \times 10'$ at the equator; WebPanel 1). We defined potential invasion hotspots as the top 25% of grid cells holding the highest species richness of alien organisms (O'Donnell

et al. 2012), and we quantified the area shared between these invasion hotspots and biodiversity hotspots under different climate scenarios.

Results

Model evaluation

All SDMs showed high predictive performance, with $AUC = 0.957 \pm 0.002$ (mean \pm standard error [SE]) and with $TSS = 0.869 \pm 0.005$ for models based solely on climate variables (averaged across species and algorithms). Including habitat variables increased the AUC (0.959 ± 0.002 ; $P = 0.009$, two-tailed Wilcoxon signed-rank test) and TSS (0.873 ± 0.004 ; $P < 0.001$) slightly from climate-only models (WebFigure 2). We only display results using climate and habitat variables together (when models were based on climate variables alone, results were similar; WebFigures 3–20).

Potential invasion hotspots under current and future climates

The distribution of currently established alien herpetofauna was heterogeneous at a global scale (WebFigure 21), with most invasions located in Europe, North America, and the Caribbean. Approximately 187 alien herpetofaunal species established populations in biodiversity hotspots, with the Mediterranean Basin and Caribbean Islands harboring the greatest numbers (WebTable 2), whereas 197 species invaded non-hotspot regions. The average richness of established species per grid cell in biodiversity hotspots (1.534 ± 0.016 species per grid cell) was slightly higher (1.1 times) than in other regions (1.399 ± 0.014) ($Z = 15.951$, $P < 0.001$, two-tailed Wilcoxon rank sum test).

SDM predictions based on analogous climates indicated that the most environmentally suitable areas for alien herpetofauna (based on summing continuous environmental suitability values) were concentrated in western Africa, South and Southeast Asia, Oceania, the Caribbean, eastern South America, the Mediterranean region, and eastern Madagascar under current climatic conditions (Figure 2). Projected suitable areas under RCP2.6 in the 2050s and 2080s were similar to each other (WebFigure 22). Compared to current climatic conditions, the most suitable areas for future invasion were predicted to expand toward the north of South America, center of Africa, and high latitudes in Europe (Figure 2). Certain areas in western South America, countries bordering the Red Sea, and northern and southern Africa were predicted to have slightly reduced risk.

Under current climatic conditions, the potential species richness of alien herpetofauna per grid cell in biodiversity hotspots (25.564 ± 0.029) was higher than in other regions (18.454 ± 0.014), and these differences were predicted to increase in the 2050s (26.791 ± 0.031

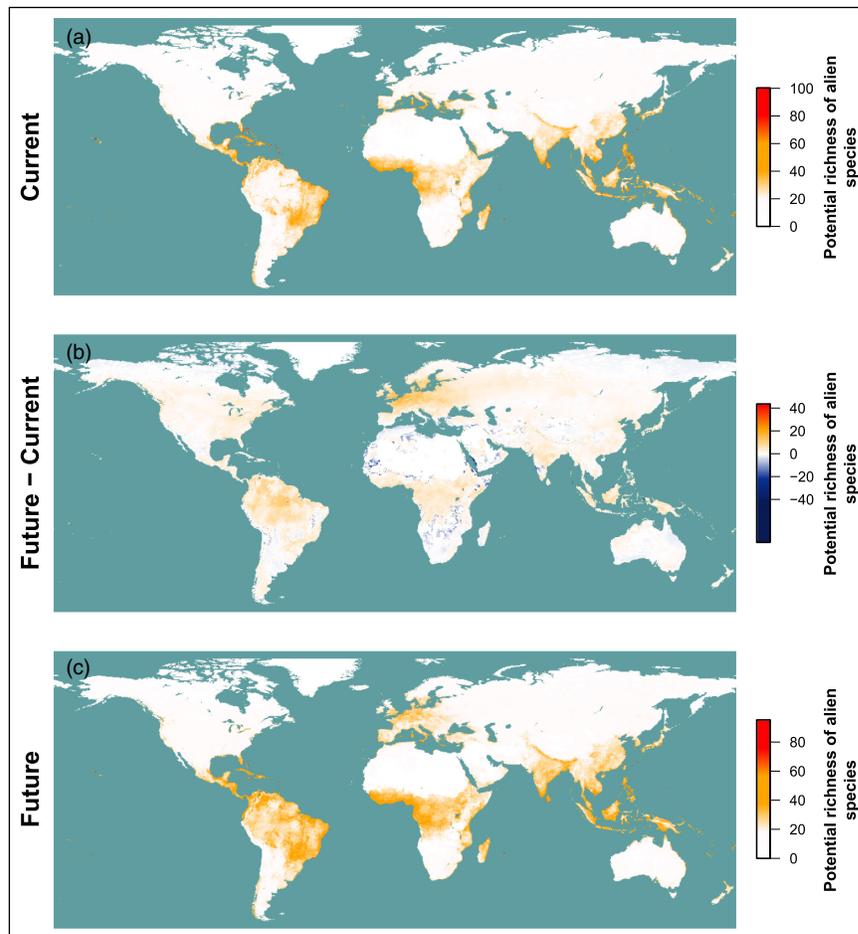


Figure 2. Predicted richness of alien herpetofauna under current and future scenarios modeled using climate and habitat variables together. (a) Richness under current environmental conditions; (b) predicted change in numbers of alien species between the present and the 2080s under low-emissions scenario RCP2.6; (c) projected species richness by the 2080s under RCP2.6.

versus 19.035 ± 0.013) and 2080s (26.800 ± 0.031 versus 19.100 ± 0.013) under RCP2.6. Under all timeframes considered, the potential species richness of alien herpetofauna per grid cell in biodiversity hotspots was nearly 1.4 times higher than in other regions (current climate: $Z = 261.951$; RCP2.6: $Z = 245.057$ in 2050s and $Z = 242.658$ in 2080s; all $P < 0.001$; WebFigure 23).

Potential invasion hotspots (defined as the top 25% of grid cells projected to be suitable for the greatest number of alien herpetofauna) also concentrated in biodiversity hotspots. Approximately 40% of these invasion hotspots (by area) fell within biodiversity hotspots under different hotspot thresholds and climate scenarios (Table 1). Furthermore, potential invasion hotspots based on the top 25% threshold covered a large proportion of the total area of biodiversity hotspots under current climatic conditions (64.4%) as well as under RCP2.6 (58.0% and 57.5% in the 2050s and 2080s, respectively) (Figure 3). Within biodiversity hotspots, the proportion of area shared with an invasion hotspot ranged from 2.1% to

100%, with New Caledonia, Guinean Forests of West Africa, East Melanesian Islands, Caribbean Islands, the Philippines, and the Cerrado predicted to be extremely threatened (Figure 4). The degree of overlap within each biodiversity hotspot slightly decreased with higher threshold values (eg defining potential invasion hotspots as the top 20 or 10% richest grid cells; Figure 4; WebFigures 24–26).

Under the high-emissions scenario (RCP8.5), potential invasion hotspots were predicted in geographic regions similar to those under the low-emissions scenario (RCP2.6); however, the sizes of invasion hotspots in western Africa, northern South America, and Southeast Asia were predicted to shrink (WebFigures 27–33). Potential richness of alien herpetofaunal species per grid cell in biodiversity hotspots was predicted to be 1.4 times than seen in other regions ($Z = 224.426$ in 2050s, $Z = 192.147$ in 2080s; both $P < 0.001$). The absolute and relative extent of overlap between invasion and biodiversity hotspots under RCP8.5 was similar to that under RCP2.6 (Table 1 and WebFigures 29–33).

When projected to both analogous and non-analogous climates (WebFigures 34–37), potentially suitable areas for alien herpetofauna were

projected to increase under current and future climates. For example, the western coast of South America, the southern border of the Sahara, and the coast of India were predicted to become more susceptible to invasion. As compared with predictions based on current climate, most global land areas were predicted to increase in suitability for a richer diversity of alien herpetofauna, especially in Europe. Nevertheless, we urge caution in interpreting these results because of the uncertainties inherent in projecting SDMs to non-analogous climates. Results were similar when environmental suitability values for alien herpetofauna were based on presence–absence predictions (WebFigures 38–73).

Conclusions

Results of this study suggest that regions with the greatest environmental suitability for future invasions by alien herpetofauna are concentrated in global biodiversity hotspots. Potential richness of alien herpetofaunal species per grid cell in these hotspots is

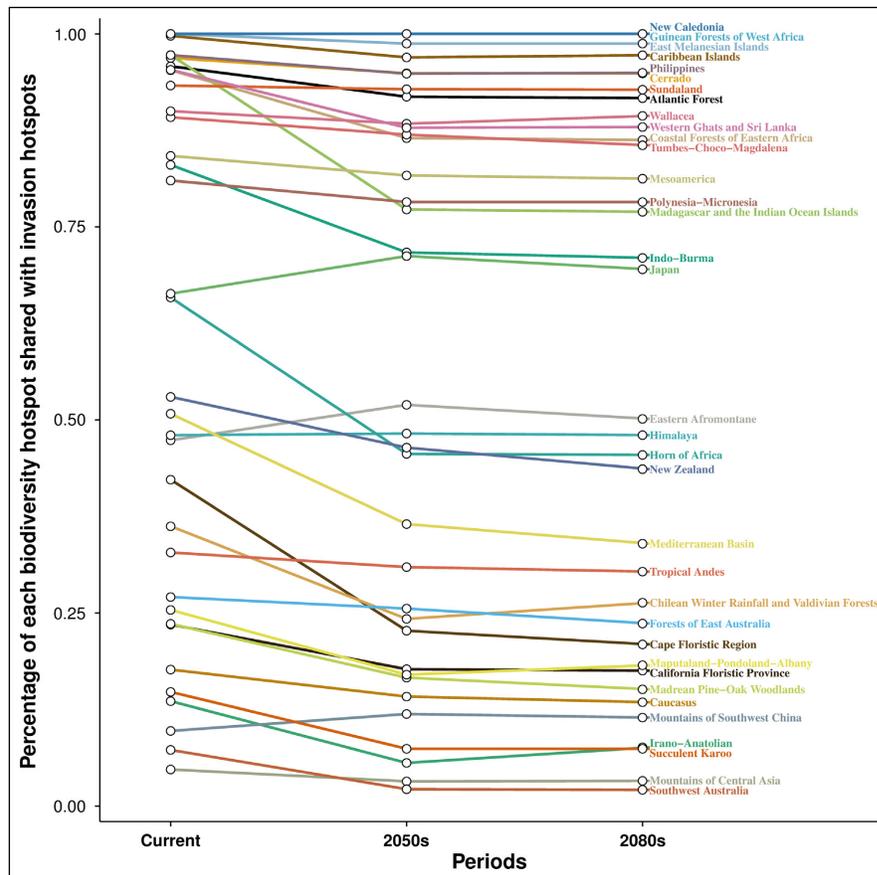


Figure 4. Percentage change in the amount of overlap between biodiversity hotspots and potential invasion hotspots over time for each biodiversity hotspot under RCP2.6. Each biodiversity hotspot is named and has a different color. Invasion hotspots are defined as the top 25% of all the cells with the highest species richness.

By demonstrating that biodiversity hotspots are potentially more threatened by alien herpetofaunal invasions than are other regions, we highlight the conservation gains that may be obtained by adopting protective biosecurity measures in those regions now. We therefore stress the need to consider biodiversity hotspots as priority regions for developing effective biosecurity efforts. Among these regions, our models predict that New Caledonia, the Guinean Forests of West Africa, the East Melanesian Islands, the Caribbean Islands, the Philippines, and the Cerrado are particularly at risk, due to their high overlap with potential invasion hotspots and the small sizes of remaining native habitats. Yet these areas also currently have fewer financial resources to develop biosecurity measures. Awareness of this threat of invasion may allow for proactive development of biosecurity measures in these areas to avoid or minimize future damage to their globally important biodiversity from alien herpetofauna.

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■ Supporting Information

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