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Threatened and invasive reptiles are not two sides of the same coin

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Abstract

Aim The ‘two sides of the same coin’ hypothesis posits that biological traits that predispose species to extinction and invasion lie on opposite ends of a continuum. Conversely, anthropogenic factors may have similar effects on extinction and invasion risk. We test these two hypotheses using data on more than 1000 reptile species with either threatened or invasive statuses.

Location Global

Methods We used Hierarchical Bayesian models to determine whether biological traits and anthropogenic factors were correlated with whether a species was: (i) listed as Threatened vs. Least Concern on the IUCN Red List, and (ii) successful vs. unsuccessful at establishing a viable population once introduced outside of its native geographic range. The ‘two sides of the same coin’ hypothesis predicts that model coefficients for each trait should be opposite in sign between these two models.

Results Seventy-three percent of model coefficients describing 10 aspects of a species’ life-history, ecology, biogeography, and environmental niche breadth were opposite in sign between the two groups; however, most effect sizes for variables that showed contrasting relationships were small and/or uncertain. The only exception was body size: larger-bodied species were more likely to be threatened, whereas smaller-bodied species were more likely to be invasive. As predicted, human population density across a species’ native geographic range was positively correlated with both threat and invasion probabilities. Other anthropogenic variables did not have strong analogous effects.

Main conclusions The assumption that threatened and invasive species lie on opposite ends of a continuum, while consistent with life history-theory, appears to be an oversimplification. Our results do suggest, however, that anthropogenic variables can be important predictors of a species’ fate, and should be more routinely incorporated in trait-based analyses of extinction and invasion risk.

INTRODUCTION

Anthropogenic activities homogenize biodiversity by increasing extinction risk, while simultaneously facilitating the transition of species through each stage of the invasion pathway (Romagosa *et al.*, 2009; Blackburn *et al.*, 2011; Schmidt *et al.*, 2012). Identifying biological traits that influence a species' response to anthropogenic activities is thus a shared goal of conservation and invasion biology (Fisher & Owens, 2004; Bradshaw *et al.*, 2008). Indeed, both disciplines are concerned with understanding the factors that determine the fate of small populations (Blackburn & Jeschke, 2009; Blackburn *et al.*, 2009). General rules of thumb developed from trait-based analyses can be used to predict extinction or invasion risk of poorly-known species, providing a rapid, cost-efficient approach to the allocation of limited conservation resources (Bradshaw *et al.*, 2008; Böhm *et al.*, in press).

Traits that predispose species to become either threatened or invasive are often assumed to lie on opposite ends of a continuum: trait values that render a species more vulnerable to extinction are thought to be opposite in sign to those that facilitate invasion, and vice-versa (Bradshaw *et al.*, 2008; Jeschke & Strayer, 2008; Schmidt *et al.*, 2012). The assumption that threatened and invasive species are 'two sides of the same coin' (Jeschke & Strayer, 2008) has strong links to life-history theory (Jeschke & Kokko, 2008), which posits that species can be classified along a fast-slow continuum (i.e., that invasive species have fast life histories and threatened species have slow ones). Most trait-based analyses have examined the characteristics that influence whether a species becomes threatened or invasive in isolation, and thus provide limited inference regarding the validity of that hypothesis (Bradshaw *et al.*, 2008; Jeschke & Strayer, 2008). Furthermore, studies that have jointly analyzed traits that influence a species' fate have produced equivocal results. Studies of plants (Bradshaw *et al.*, 2008; Pandit *et al.*, 2011; Schmidt *et al.*, 2012) and crayfish (Larson & Olden, 2010) support the 'two sides of the same coin' hypothesis, whereas studies of fishes and birds (Jeschke & Strayer, 2008; Blackburn & Jeschke, 2009) contradict it. However, these tests have either failed to account for shared evolutionary history among species (Blackburn & Jeschke, 2009), arguably used inappropriate source pools for contrasting invasive with non-invasive species (Bradshaw *et al.*, 2008; Jeschke & Strayer, 2008; Larson & Olden, 2010; Pandit *et al.*, 2011), examined traits individually with

univariate techniques (Blackburn & Jeschke, 2009), or have been limited in geographic and taxonomic scope (Larson & Olden, 2010). In addition, the ‘two sides of the same coin’ hypothesis has not been evaluated in reptiles. Independent studies suggest that geographic range size and body size show opposing relationships in threatened (Tingley *et al.*, 2013; Ducatez *et al.*, 2014; Böhm *et al.*, in press) vs. successfully established (Mahoney *et al.*, 2015) reptile species, but these studies differ markedly in the spatial scale at which they were conducted, as well as the species and traits they considered.

Previous comparisons of threatened and invasive species have also failed to account for anthropogenic factors that directly influence the probability that a species will succumb to either fate (Cardillo *et al.*, 2004; Pyšek *et al.*, 2010; Murray *et al.*, 2014). In contrast to species-level traits, we predict that many anthropogenic factors will have similar effects on invasion and extinction risk. For example, species that occupy urbanized landscapes and are sympatric with high human population densities may be introduced in greater numbers (Cassey *et al.*, 2004; Tingley *et al.*, 2010) and may be more likely to establish in human-modified environments where they are typically released. Similarly, species that are associated with urban habitats and large human populations may be at greater risk of extinction in their native ranges due to factors such as exploitation and habitat loss (Cardillo *et al.*, 2004).

International trade in species can also reduce the viability of wild populations through overharvesting, while increasing propagule pressure and thus invasion potential (Romagosa *et al.*, 2009). Jeschke & Strayer (2008) and Schmidt *et al.* (2012) contrasted traits of threatened and invasive species and found that species-level traits were stronger predictors of invasion success than extinction risk. They speculated that anthropogenic threats may be more important in determining extinction risk than establishment success or pest status, but this hypothesis has not been explicitly tested.

Here we overcome many of the limitations of previous tests of the ‘two sides of the same coin’ hypothesis, using data on extinction risk and invasiveness of reptile species from across the globe. Unlike most previous tests of this hypothesis (Bradshaw *et al.*, 2008; Jeschke & Strayer, 2008; Larson & Olden, 2010; Pandit *et al.*, 2011), we directly compare successful and unsuccessful introduced

species, allowing us to decouple characteristics associated with establishment from those linked with earlier and later stages of the invasion pathway (Blackburn & Jeschke, 2009). Additionally, we examine the related hypothesis that anthropogenic factors that facilitate invasion success are the same as those that lead to a high risk of extinction.

METHODS

Threatened vs. non-threatened species

We contrasted threatened vs non-threatened species (as in other tests of the ‘two sides of the same coin hypothesis’; e.g., Jeschke & Strayer, 2008) so that we could directly compare correlates of extinction with those of invasion, which was a binary response variable (see *Successful vs. unsuccessful invaders*). We included in our analysis all species listed by the International Union for Conservation of Nature (IUCN) as Endangered or Critically Endangered (hereafter ‘threatened’), as well as a single random sample of Least Concern (‘non-threatened’) species as a control group (Böhm *et al.*, 2013). Data Deficient, Vulnerable, Near Threatened, and Extinct species were not considered. Globally, there are far fewer crocodile and turtle species than there are snakes and lizards, and this disparity is even larger when we exclude threatened species. We therefore retained all Least Concern crocodiles and turtles in our analyses to make our findings generally applicable to all reptile species. Least Concern snakes and lizards were randomly sampled in proportion to their representation within threatened squamates, such that we ended up with an equivalent number of non-threatened and threatened species overall. However, due to missing trait data for some species, final sample sizes differed slightly between threatened ($n = 422$) and non-threatened ($n = 419$) groups. The final dataset (Appendix S1 in Supporting Information) included 20 crocodilians, 650 lizards, 377 snakes, and 151 turtles.

Successful vs. unsuccessful invaders

Data on the establishment success of introduced reptile species were taken from a previously published database (Kraus, 2009). These data have been used in previous analyses of invasion success (Bomford *et al.*, 2008; Amiel *et al.*, 2011; Ferreira *et al.*, 2012; Poessel *et al.*, 2012; Liu *et al.*, 2014;

Mahoney *et al.*, 2015), and represent the most complete collation of reptile introductions available.

Many species recorded in Kraus (2009) have been introduced to multiple jurisdictions. Here we consider a species successful if it established a viable population in at least one jurisdiction to which it was introduced. This resulted in 193 successfully established species and 164 unsuccessful species.

To account for the fact that some species have been introduced more than others, we included either (i) the total number of locations to which a species has been introduced, or (ii) the total number of introduction attempts (summed across all locations; Bomford *et al.*, 2008). The two measures were positively correlated, but the latter was a stronger predictor of establishment success, and was retained for further analyses. Using the former measure produced qualitatively similar results. We also re-ran our analyses excluding propagule pressure as a covariate, as some previous tests of the ‘two sides of the same coin’ hypothesis have not controlled for its effect (e.g., Larson & Olden, 2010).

We refer to successfully established species as ‘invasive’ for brevity, but acknowledge that the term invasive typically implies an ability to spread widely (Blackburn *et al.*, 2011) or have adverse ecological or economic impacts (Davis & Thompson, 2001). Taxonomy followed the Reptile Database (Uetz & Hallermann, 2008).

Species-level traits

We investigated whether the probability of a reptile species becoming either threatened or invasive was correlated with the following groups of species-level traits:

Life-history and ecology

We started with a life-history trait database collected from primary sources and maintained at Utah State University (Myhrvold *et al.*, 2014), which includes data on adult snout-vent length (SVL), clutch size, and number of clutches per year for select reptile species. We augmented this database by including diet type, reproductive mode, presence or absence of parthenogenesis, and annual fecundity (clutch size * clutches per year). When possible, we incorporated missing life-history data using a

combination of primary and grey literature (see Mahoney *et al.* 2015). We gave priority to the primary literature and averaged values from multiple sources when more than one value was found.

For SVL, we prioritized data in the following order: females, sex not given, and males. In cases where we had either clutch size or the number of clutches per year but not both, we derived complete annual fecundity estimates using multiple imputation with conditional models in a Bayesian framework [R package *mi* (Su *et al.*, 2011)].

The majority of threatened reptile species have been listed by the IUCN on the basis of their extent of occurrence or area of occupancy (Red List Criterion B) (Böhm *et al.*, in press). Thus, failing to account for range size could lead to spurious conclusions regarding the importance of other predictor variables. We therefore included range size as a covariate in our analyses of extinction risk – we did not seek to make inferences regarding its effects. Because the majority of reptile species are listed on the basis of Criterion B, it was not possible to run a second analysis excluding all Criterion B species.

We estimated native geographic range size using equal-area Behrmann projections of IUCN extent of occurrence range maps. When an IUCN range map was not available for a species, we used range maps from WWF Wildfinder (www.worldwildlife.org/pages/wildfinder), or manually georeferenced range maps from published literature. These range maps were also used to calculate the spatial and environmental attributes described below. While these maps undoubtedly contain errors at local spatial scales, these errors are expected to have negligible effects on our general conclusions given the global scale of our analyses. Furthermore, these maps were derived by species experts with the best available information.

Geographic origin

We used two variables to describe a species' geographic origin: (i) distance to the equator (defined as the absolute value of the latitude of the native geographic range centroid), and (ii) insularity (i.e., whether a species' native geographic range occurred exclusively on one or more islands). Islands were

defined as any location that was not on a major continent: Asia, Africa, Australia, North America, and South America (Blackburn & Duncan, 2001). Island endemics were scored as 1, whereas all other species were scored as 0.

Environmental niche breadth

To estimate niche breadth, we calculated the standard deviations of mean annual temperature and annual precipitation across a species' native geographic range, using long-term climate grids with ~1 km spatial resolution (Hijmans *et al.*, 2005).

Anthropogenic factors

We calculated three anthropogenic factors that have been shown to correlate with either threat status or invasion success in a wide range of taxa (Cardillo *et al.*, 2004; Sodhi *et al.*, 2008; Pyšek *et al.*, 2010; Murray *et al.*, 2011): (i) habitat loss, calculated as the percentage of a species' native geographic range covered by urban land cover (Balk *et al.*, 2006); (ii) gross domestic product (GDP), averaged across a species' native range using a 1° grid of estimated GDP (Nordhaus, 2006); and (iii) human population density, averaged across a species' native range based on a ~1 km grid (Balk *et al.*, 2006).

Additionally, we hypothesized that the extent to which a species is traded would influence the probability that it would become threatened or invasive. With the exception of species that are listed by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), data on global trade volumes are unavailable. However, the U.S.A. plays a major role in global vertebrate trade (Romagosa *et al.*, 2009; Robinson *et al.*, 2015), and U.S. Fish and Wildlife Service (USFWS) declaration forms that accompany all imports and exports of animals or their products (Form 3-177) provide an unparalleled level of detail on trade frequency and intensity (García-Díaz *et al.*, 2014). These data will of course under-estimate global trade in reptiles (and under-estimate more in some geographic areas than others, e.g., chelonian trade between Asian countries) but can serve as a proxy for the volume of globally traded species (Romagosa *et al.*, 2009).

We requested all importation and exportation records of living and dead reptiles from the USFWS covering the period 1999-2014. Taxa that were not identified to species-level were removed from the USFWS database. From these data, we estimated the total number of animals of each species imported and exported from 1999-2014. The total number of live animals traded was used as a predictor in the model of invasion probability (see *Statistical analysis*), whereas the number of both live and dead animals was used in the model of threat probability.

Statistical analysis

We conducted two separate analyses to determine whether threatened and invasive reptile species are two sides of the same coin. Specifically, we used Hierarchical Bayesian generalized linear models with a binomial error distribution to determine whether 10 species traits (represented by 11 model coefficients due to the categorical nature of our diet variable) and four anthropogenic factors were correlated with whether a species was: (i) threatened vs. non-threatened, and (ii) invasive vs. non-invasive. The ‘two sides of the same coin’ hypothesis predicts that model coefficients for each trait should be opposite in sign between these two models. Models were fit in Stan v2.7.0 (Stan Development Team, 2015) through the R interface ‘rstan’ (R Development Core Team, 2015).

To account for shared evolutionary history among species, taxonomic categories (genus, family, and order) were included as random effects. Snakes and lizards were treated as separate Orders to account for differences in establishment success between these two groups (Mahoney *et al.*, 2015). All other traits were included as fixed effects. Continuous variables were either centered and scaled (by the mean and 2 SDs, respectively) or log-transformed to improve model performance and parameter estimation. Log transformation was used for variables commonly log-transformed in the literature and that exhibit large ranges typical of log-linear data (SVL, range size, total number of introduction attempts). Trade metrics were also log transformed, but required 0.5 to be added to all values due to the presence of zeros in the data.

Variable importance was determined by examining the magnitude of scaled regression coefficients and their 95% credible intervals (CIs). Quadratic relationships for all non-log-transformed continuous variables and two-way interactions were evaluated by examining whether 95% CIs for quadratic and interaction coefficients overlapped zero when they were added to the global model. To avoid overly complex models, we added quadratic relationships one variable at a time, and only tested for interactions between anthropogenic variables and geographic range size. No interaction terms were retained in global models of threat or invasion probability. We built global (i.e. saturated) models for each response variable, as our primary goal was to compare directionality in model coefficients.

To reduce collinearity between variables, we first removed all variables with Pearson's correlation coefficients $>|0.7|$ (Dormann *et al.*, 2012). The choice of which variable to use from a correlated pair was determined through exploratory modeling (e.g., univariate models, degree of confounding through more complex model specifications) and via assessments of variance inflation. We retained all variables with variance inflation factors less than 3 (see Appendix S2 in Supporting Information for correlations and variance inflation factors).

We used diffuse univariate normal priors ($\mu = 0$, $\sigma = 100$) for all fixed effects, and expanded normal priors ($\mu = 0$) with uniform hyperpriors (min = 0, max = 100) on σ for all random effects. We estimated posterior distributions using Markov chain Monte Carlo simulation (MCMC) with a No-U-Turn sampler (NUTS). We evaluated MCMC chain convergence following warm-up by using a combination of trace diagnostics, assessments of sample independence (thinning = 10), ratios of the posterior mean standard errors to sample standard deviations ($\leq 1/10$), and estimates of R-hat and effective samples sizes with the aid of shinyStan (Gabry, 2015).

RESULTS

Species-level traits

Comparisons of trait values between threatened and invasive reptiles revealed limited support for the 'two sides of the same coin' hypothesis (Figs. 1, 2). Seventy-three percent (8/11) of model

coefficients describing 10 aspects of species life-history, ecology, biogeography, and environmental niche breadth were opposite in sign between the two groups; however, most effect sizes for variables that were opposite in sign were small and/or highly uncertain (Fig. 3). The only variable that showed somewhat strong and opposing relationships with threat status vs. invasion success was SVL. Larger-bodied species were more likely to be threatened, whereas smaller-bodied species were more likely to be invasive (although 95% CIs for the latter coefficient only excluded zero when propagule pressure was not included as a covariate; Appendix S3 in Supporting Information). Furthermore, the positive relationship between body size and threat status was only apparent after accounting for taxonomy and additional confounding characteristics (cf Figs. 2 & 3).

Variation in precipitation across a species' native geographic range (a measure of environmental niche breadth) and native geographic range size were negatively correlated with threat probability. This latter finding is expected, given that IUCN uses range size to assign threat status. Native geographic range size also was negatively correlated with invasion success (but only after controlling for propagule pressure), whereas parthenogenicity, oviparity, and herbivory (relative to carnivory) were all positively correlated with invasion. However, 95% CIs for the latter two coefficients slightly overlapped zero. Effects of parthenogenicity, oviparity, and herbivory were much more certain when propagule pressure was excluded from the model (Appendix S3).

Anthropogenic factors

Coefficient estimates for anthropogenic variables revealed opposite relationships with threat status vs. invasion success for three of the four variables tested (Fig. 3). However, in all three cases where opposite relationships were evident, at least one coefficient estimate from each model was small and had 95% CIs that overlapped zero. The only variable that did not show an opposing relationship – mean human population density across a species' native geographic range – had a positive linear relationship with invasion success, and a positive quadratic relationship with threat probability. Probability of invasion also increased with propagule pressure, and decreased with the proportion of urban area within a species' native geographic range (although 95% CIs overlapped zero when

propagule pressure was not included in the model). Threat probability decreased non-linearly with GDP (Fig. 3; Appendix S3).

DISCUSSION

We did not find strong support for the hypothesis that trait values that predispose species to become threatened or invasive lie on opposite ends of a continuum. Although nearly 75% of the species-level traits that we considered showed opposite relationships with threat status vs. invasion success, effect sizes for those traits were generally small and/or uncertain. These findings are consistent with the results of previous analyses of Holarctic fish and bird species; both Jeschke & Strayer (2008) and Blackburn & Jeschke (2009) found that ~50% of traits showed opposite relationships in comparisons of trait values between species listed as threatened by the IUCN and species that have established non-native populations. Additionally, effect sizes in both previous studies were weak for traits that differed between threatened and established species, as we observed here. The number of traits that have opposite relationships with threat status vs. invasion success, as well as the magnitude of the observed effects, will clearly depend on the specific traits that are considered. Furthermore, the broad taxonomic and geographic diversity of our analysis, coupled with the coarse resolution of some of the input variables used (e.g., geographic range maps and associated variables) likely contributed to some of the uncertainty in our analyses. Nonetheless, the fact that we contrasted species at opposite ends of the threat continuum (i.e., Least Concern vs Endangered/Critically Endangered species), means that our analyses had a high sensitivity to detect trait differences between threatened and non-threatened species – yet we still find little support for the ‘two sides of the same coin’ hypothesis. The overall consistency between our results and those of Jeschke and Strayer (2008) and Blackburn and Jeschke (2009) suggest that trait values that lead to vertebrate endangerment are not simply the opposite of those that facilitate invasion success.

Studies of plants (Bradshaw *et al.*, 2008; Pandit *et al.*, 2011; Schmidt *et al.*, 2012) and crayfish (Larson & Olden, 2010), on the other hand, provide stronger support for the ‘two sides of the same coin’ hypothesis. The extent to which this disparity reflects true taxonomic differences in the validity

of the hypothesis is questionable, however, as studies have applied very different statistical approaches (e.g., univariate t-tests vs. multivariate machine learning algorithms), compared different response variables (e.g., establishment success vs. pest status), or used different source pools to contrast invasive and non-invasive taxa (e.g., all species within a family or region vs. only introduced species). As highlighted by Cassey *et al.* (2004) and Blackburn & Jeschke (2009), the latter consideration is critical. Established or pest species typically represent a biased subset of all species in a region or taxonomic group (Tingley *et al.*, 2010; García-Díaz & Cassey, 2014), and thus tests of the ‘two sides of the same coin’ hypothesis will be most informative when studies can control for characteristics associated with earlier or later stages of invasion, as we have done here by comparing successful vs. unsuccessful introduced species.

The trait that differed most between threatened and invasive species in our analysis was body size. Large species were more likely to be threatened, whereas small species were more likely to be invasive. Similar positive relationships between body size and threat status have been found in a wide array of vertebrate taxa, including amphibians (Sodhi *et al.*, 2008), mammals (Cardillo, 2003), birds (Bennett & Owens, 1997), and squamate reptiles (Tingley *et al.*, 2013; Böhm *et al.*, in press). Body size has also been found to correlate negatively with establishment success in insects (Lester, 2005), fishes (Ruesink, 2005), mammals (Jeschke & Strayer, 2006), and herpetofauna (Allen *et al.*, 2013; Mahoney *et al.*, 2015). Blackburn and Jeschke (2009) found that measures of body size (mass and length) had opposite effects on threat status vs. invasion success in birds and fishes as well (although effects were relatively weak for at least one response variable). Collectively, these findings suggest that although there is little support for the ‘two sides of the same coin’ hypothesis in vertebrates overall, there do appear to be weak (but consistent) diametric relationships with body size.

Small body size may facilitate invasion success by reducing the probability that a species is detected by biosecurity personnel, by increasing propagule pressure, or by increasing niche opportunities upon introduction (Mahoney *et al.*, 2015). Alternatively, differences in body size between threatened vs. invasive species may reflect the fact that large species typically exhibit lower reproductive rates,

slower growth rates, and consequently, lower population growth rates, than small species (Pimm *et al.*, 1988; Cardillo, 2003). Thus, large species may be slower to recover from anthropogenic disturbance, and have a reduced likelihood of establishing populations from low numbers of founders (Pimm *et al.*, 1988; Owens & Bennett, 2000). This rationale is consistent with the idea that threatened and invasive species lie at opposite ends of a ‘fast-slow continuum’, in which invasive species have fast life histories and threatened species have slow ones (Jeschke & Strayer, 2008). Nonetheless, other aspects of the fast-slow continuum that we predicted would be important, such as annual fecundity, diet, reproductive mode, and the presence or absence of parthenogenesis, did not conform to the predictions of the ‘two sides of the same coin’ hypothesis (although the latter three variables were correlated with invasiveness). Using a similar dataset, Mahoney *et al.* (2015) also found that reptile establishment success was higher for species with parthenogenesis; however, our findings regarding fecundity and oviparity are at odds with the results of Mahoney *et al.* (2015). This disparity may be due to the fact that we aggregated introductions at the species level, whereas Mahoney *et al.* (2015) treated individual introductions as the unit of analysis. Furthermore, our study considered different covariates, which may have influenced model coefficients and estimates of uncertainty.

Unlike previous tests of the ‘two sides of the same coin’ hypothesis, we also examined whether anthropogenic variables influenced threat and invasion probabilities. In line with our prediction, human population density had strong, positive effects on probabilities of both outcomes – species with high human densities in their native ranges were more likely to be both threatened and invasive than species from less populated areas. High human population densities have been shown to correlate with a high risk of extinction in global studies of mammals (Cardillo *et al.*, 2004, 2008), birds (Davies *et al.*, 2006), and amphibians (Sodhi *et al.*, 2008), and in New Zealand reptiles (Tingley *et al.*, 2013). Additionally, our finding that invasive reptile species tend to originate from regions with high human population densities accords with the results of Jeschke & Strayer (2008), who found species affiliated with humans were more likely to be invasive. Positive effects of human population density on reptile extinction risk likely reflect more direct impacts of habitat loss, pollution, and/or over-exploitation. Similarly, in the context of invasions, human population density plausibly integrates more proximal

factors, such as propagule pressure and introduction pathways (e.g., pet trade activity) (Pyšek *et al.*, 2010). It is also important to note that potential filtering of species pools caused by historic human activities means that our results likely underestimate effects of human population density on extinction and invasion risk.

Our analyses also revealed effects of additional anthropogenic variables on threat and invasion probabilities. Firstly, we found that GDP within a species' native range was negatively correlated with its threat status. Several studies have found that regions with higher GDP host fewer threatened plant and vertebrate species (Davies *et al.*, 2006; Vamosi & Vamosi, 2008; Holland *et al.*, 2009). Our results build upon these earlier studies by demonstrating that effects of GDP can also be apparent at the level of individual species. This correlation may reflect a greater focus on economic growth at the cost of environmental protection in developing countries, or conversely, the fact that many species that are sensitive to development have already been extirpated from regions with high GDP. Secondly, we found that the extent of urban area within a species' native range was negatively correlated with its invasion success. Thus, sufficient amounts of native habitat may be required to provide enough propagules for species to successfully establish. The fact that GDP and urban extent did not have strong effects on both response variables, however, contradicts our hypothesis that anthropogenic variables have similar effects on threat and invasion probability.

Incorporating anthropogenic variables can not only improve the explanatory power of threat and invasion models (as we have shown here), but may also help resolve contradictions between studies testing the 'two sides of the same coin' hypothesis (Schmidt *et al.*, 2012). Species-level traits may be confounded by anthropogenic variables, or traits may interact with anthropogenic variables to create context-dependent pathways to decline or invasion (Cardillo *et al.*, 2004; Murray *et al.*, 2011). Böhm *et al.* (in press), for example, found that effects of geographic range size on extinction risk depended on a species' proximity to a large population center. Although we found no evidence of interactions between range size and anthropogenic variables, we did find that accounting for propagule pressure shifted coefficient estimates for some species-level traits and generally increased coefficient

uncertainty. Thus, the validity of the ‘two sides of the same coin’ hypothesis may be sensitive to the inclusion of propagule pressure, and future studies should seek to control for its effects. Furthermore, our results demonstrate that despite the fact that anthropogenic variables, such as GDP and human population density, are not causally related to invasion and extinction processes, they can serve as useful surrogates of anthropogenic impact in the absence of more detailed data on introduction effort and key threatening processes (Cardillo *et al.*, 2004; Pyšek *et al.*, 2010).

By jointly analyzing correlates of both threat and invasion probability, we have shed new light on the factors that lead to biotic homogenization in a diverse, but poorly understood vertebrate group. Our study also builds on previous tests of the ‘two sides of the same coin’ hypothesis by considering a broad range of species characteristics in a multivariate context, while controlling for shared evolutionary history among species, anthropogenic factors, and biases involved in the introduction stage of the invasion pathway. Despite these statistical and methodological advances, our results accord with those of previous studies of other vertebrate taxa in failing to support the ‘two sides of the same coin’ hypothesis. Thus, the assumption that threatened and invasive species lie on opposite ends of a continuum, while consistent with life-history theory, appears to be an oversimplification.

However, our results do strongly support the findings of previous studies demonstrating that anthropogenic variables can be important predictors of a species’ fate (e.g., Murray *et al.*, 2014). Measures of anthropogenic impact should, therefore, be more routinely incorporated in trait-based analyses of extinction and invasion risk.

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SUPPORTING INFORMATION

Appendix S1. Data on threatened and invasive reptile species.

Appendix S2. Pairwise correlation matrix and variance inflation factors for all covariates.

Appendix S3. Regression coefficients illustrating effects of species traits and anthropogenic factors on reptile invasion success and threat status. Unlike the results presented in Fig. 3 in the main text, the model of invasion probability does not include the total number of introduction attempts (i.e. propagule pressure).

BIOSKETCH

The authors share an interest in how species' traits and human activities influence the dual processes of extinction and invasion in reptile species.

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FIGURE LEGENDS

Fig. 1. Density plots illustrating raw trait differences between invasive and non-invasive reptile species. The inset figure for *animals traded* shows the distributions of the data after removing the highest 10% of values. Note that these comparisons do not account for the random effects structure captured in the coefficients shown in Fig. 3.

Fig. 2. Density plots illustrating raw trait differences between threatened and non-threatened reptile species. The inset figure for *animals traded* and *gross domestic product* shows the distributions of the data after removing the highest 10% of values. Note that these comparisons do not account for the random effects structure captured in the coefficients shown in Fig. 3.

Fig. 3. Regression coefficients describing effects of species traits and anthropogenic factors on reptile invasion success and threat status. Points represent posterior means; lines represent 95% credible intervals. Herbivore was the reference class for *Diet*.

Global Ecology and Biogeography

Fecundity

Global Ecology and Biogeography

Shout-vent length

Human population density

% Urban

Gross domestic product

Absolute latitude

Range size

Precipitation SD

Temperature SD

Animals traded

Threatened

Value

Appendix S2. Pairwise correlation matrices and variance inflation factors for all variables.

Fig. S1. Pearson's correlations between predictor variables included in model of threat probability.

Fig. S2. Pearson's correlations between predictor variables included in model of invasion probability.

Table S1. Variance inflation factors for model of threat probability.

Variable	VIF
Fecundity	1.118852
Snout-vent length	1.284186
Human population density	1.489664
% Urban	1.504543
Gross domestic product	1.057024
Absolute latitude	1.350882
Native range size	1.745141
Precipitation SD	1.751342
Temperature SD	1.578621
Animals traded	1.017689

Table S2. Variance inflation factors for model of invasion probability.

Variable	VIF
Fecundity	1.167215
Snout-vent length	1.431527
Human population density	1.72817
% Urban	2.49996
Gross domestic product	1.56541
Absolute latitude	2.412895
Native range size	2.807832
Precipitation SD	1.721272
Temperature SD	1.368791
Animals traded	1.017689
Number of introductions	1.475663

Appendix S3

Fig. S3. Regression coefficients illustrating effects of species traits and anthropogenic factors on reptile invasion success and threat status. Unlike the results presented in Fig. 3 in the main text, the model of invasion probability does not include the total number of introduction attempts (i.e. propagule pressure). Points represent posterior means; lines represent 95% credible intervals. Herbivore was the reference class for Diet.

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