Elevated human footprint on islands promotes both introduction and extinction probability of insular reptiles at opposite ends of geographic, evolutionary and ecological continua.

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Abstract

The Anthropocene is marked by unprecedented changes to species ranges worldwide. Introduced species expand their native range into new geographic regions while extinction-prone species experience severe native range contraction. Introductions and extinctions are both caused by how species respond to human influence within their native ranges. The question arises if the opposite response in distributional change is due to introduced and extinction-prone species falling at opposite ends of geographic, evolutionary and ecological trait continua. Here, we assess the factors that explain the introduction and extinction-prone status for 3111 squamate reptile species native to the western hemisphere, of which 142 species have been introduced elsewhere and 483 species are threatened with extinction. We first asked what geographic regions contained the most introduced and extinction-prone species and if these species are evolutionarily related. We then tested the opposite ends hypothesis for several species characteristics. Our results show that the native ranges of introduced and extinction-prone reptiles are skewed towards island regions and that significant phylogenetic signal exists for these two groups, indicating they are not a random selection of the reptiles that have evolved in the western hemisphere. Species whose native ranges were more insular and were more influenced by humans were more likely to be introduced or extinction-prone. Evolutionary factors did not explain species status, but multiple geographic and ecological factors supported the opposite ends hypothesis. Introduced species were positively associated with herbivory and omnivory and had large and complex ranges, whereas extinction-prone species were generally carnivorous with small and simple ranges. In addition, introduced species produced larger clutches and extinction-prone species had relatively small body sizes. In the Anthropocene, the naive ranges of introduced and extinction-prone species are situated in the same human-impacted regions, but species range characteristics and functional traits determine whether species ranges expand or contract in the continuing face of global change.

Introduction

In the Anthropocene, humans have altered species distributions and reassembled global biogeographic patterns that arose naturally across eons of evolution (Alroy 2015, Capinha et al. 2015, Ceballos et al. 2017). The "winners" of the Anthropocene are introduced species, which expand into new geographic regions through human-vectored dispersal and establishment (Colautti and MacIsaac 2004). The "losers" are the extinct and threatened species that have experienced severe native range retraction often because of human-associated stress factors such as overharvesting, pollution, and land-use change (Vitousek et al. 1997, Sax and Gaines 2008, Böhm et al. 2013, Young et al. 2016). Species that are introduced to other regions benefit from having native ranges that encompass high human populations because of increased likelihood of intentional (e.g. via pet trade) or unintentional (e.g., as stowaway) human-aided dispersal (Latella et al. 2011, Liu et al. 2014, Su et al. 2016). After introduction, species with suitable functional traits are better able to utilize novel food sources and endure local climatic regimes (Mahoney et al. 2015, Monaco et al. 2020). In contrast, extinction-prone species generally are ecological specialists, characterized by narrow dietary and climatic niches and poor dispersal abilities due to their geographic restriction to mountain tops, islands, or isolated nature reserves in a matrix of anthropogenic land use (Kotiaho et al. 2005, Böhm et al. 2016). Hence, introduced and extinction-prone species appear to be each other's antipodes in many characteristics that cause opposite distributional responses in the Anthropocene. This raises the question if these winners and losers are at opposite ends of the same geographic, evolutionary and ecological trait continua (Jeschke and Strayer 2008, Blackburn and Jeschke 2009). Testing the opposite ends hypothesis requires identification of functional traits, native geographic range characteristics, and phylogenetic

63 clustering associated with introduced and extinction-prone species, followed by an analysis to
64 determine the (dis)similarity between these two groups.

65 The few studies that test the opposite ends hypothesis show variable results. For instance,
66 extinction-prone and successfully introduced plants (Bradshaw et al. 2008, Pandit et al. 2011,
67 Schmidt et al. 2012) and crayfish (Larson and Olden 2010) were on opposite extremes of the same
68 trait axes associated with body size, fecundity, genetic diversity and generalist versus specialist
69 habitat use. Conversely, studies on birds, fishes (Jeschke and Strayer 2008, Blackburn and Jeschke
70 2009) and reptiles (Tingley et al. 2016) found different set of traits to characterize either extinction-
71 prone or introduced species. Furthermore, such comparative studies generally lack an (in-depth)
72 phylogenetic and geographic perspective on species introduction and extinction probabilities,
73 possibly obscuring or exaggerating observed effects by not accounting for phylogenetic
74 interdependence of species.

75 Nonoverlapping phylogenetic clustering of introduced and extinct species is expected under
76 the opposite ends hypothesis because many species characteristics exhibit phylogenetic signal.
77 Phylogenetic clustering of extinction-prone species has been detected in plants (Davies et al. 2011,
78 Loza et al. 2017), fish (Adeoba et al. 2019), bumblebees (Arbetman et al. 2017), birds, and
79 mammals (Fritz and Purvis 2010). In addition, moderate to strong levels of phylogenetic signal
80 have been found in traits associated with introduction and/or invasion success (Cadotte et al. 2009),
81 dispersal capacity (Park and Potter 2015), native range size (Pigot et al. 2018), and fecundity (Allen
82 et al. 2017) for plants (Cadotte et al. 2009, Yessoufou et al. 2016, Pyšek et al. 2017), fish (Alcaraz
83 et al. 2005), and birds (Su et al. 2016). However, the proposed reasons for this phylogenetic signal
84 vary considerably between studies. For instance, Fritz and Purvis (2010) ascribe phylogenetic
85 signal to the distribution of life-history traits associated with attractiveness, making species
86 sensitive to over-harvesting. In contrast, Davies and colleagues (2011) detected a phylogenetic

87 signal for extinction risk that is unrelated to the distribution of specific traits, but associated with
88 young, recently diversified lineages within a single geographic region. Overall, there is compelling
89 evidence that the predisposition to becoming introduced or extinct is phylogenetically clustered
90 and should be considered when testing for opposite ends of the trait continua.

91 Native geographic range characteristics associated with range expansions and contractions
92 should underlie how species respond to human influence. In particular, island-living may be an
93 important characteristic determining the likeliness of introduction and extinction. Islands generally
94 have high population densities and are subjected to disproportionate levels of human influence
95 (Kier et al. 2009), thus insular species are much more likely to be introduced or go extinct than
96 mainland species. Islands are prime locations of species loss (Myers et al. 2000, Mittermeier et al.
97 2011) and also provide unique environments that select for traits that naturally determine major
98 range expansions or contractions. Insular species have evolved through processes of oversea
99 colonization, followed by often rapid adaptive diversification (Cowie and Holland 2006, Hedges
100 2006, 2011). Thus, insular species are selected to be efficient dispersers and quick adapters to
101 available niche space, which could favor survival of human-vectored dispersal events (Poe et al.
102 2011). Indeed, post-introduction ecological niche shifts occur often for introduced species that
103 originate from oceanic islands (Liu et al. 2014). In contrast, adaptive radiations cause island biota
104 to be highly specialized, extremely suited to exploit a narrow ecological niche within island
105 environments (Losos 2009, Mahler et al. 2010, 2013). This level of specialization leaves island
106 endemics sensitive to human-caused (a)biotic change and thus prone to extinction (Jantz et al.
107 2015).

108 In this study, we used a phylogenetic comparative approach to identify (dis)similarities in
109 introduced and extinction-prone species characteristics. We used a comprehensive dataset of 13
110 characteristics of 3111 squamate reptiles (lizards and snakes) native to the western hemisphere

(Figure 1). Of these, 142 species have been introduced to at least one location somewhere in the world and 483 species are threatened with extinction according to the International Union for the Conservation of Nature (IUCN). Reptiles are particularly suitable to test opposite responses to human influence, as reptiles are species-rich in the western hemisphere and are greatly impacted by human activities (Young et al. 2016, Jesse et al. 2018). We analyzed this data set to ask: 1) Are islands of the western hemisphere disproportionate sources of introduced and sinks of extinction-prone species? 2) Can we detect phylogenetic signal among introduced and extinction-prone species? 3) For which geographic, evolutionary and ecological trait continua are introduced and extinction-prone species positioned at opposite ends?

Methods

Data compilation

Squamate phylogeny

To robustly test for (dis)similarities in introduced and extinction-prone species characteristics across western hemisphere squamates, a phylogenetic tree of all species was needed. Thus, we began our data compilation by updating a global, smoothed, and interpolated phylogeny of squamates from the TimeTree of life project (Kumar et al. 2017), previously used in (Marin et al. 2018, Rapacciuolo et al. 2019) with species synonyms from The Reptile Database (Uetz, P., Freed, P. & Hošek 2012) to match up with the spatial range dataset that we obtained on western hemisphere squamates (see "Geographic data" below). Any species not in the phylogeny and not in the spatial dataset was removed from further data compilation and not included in our analyses. This phylogeny of 3111 species (Figure 2) was used to calculate phylogenetic signal among

134 introduced and extinction-prone species and included in multivariable phylogenetic generalized
135 linear models (PGLMs).
136
137 Species introduction and extinction-prone status
138 The response variables in our analyses were based on species statuses of squamates across the
139 western hemisphere. We constructed a binomial variable to indicate whether a species was
140 introduced into some area of earth or not and a response variable that indicated if a species was
141 extinction-prone in its native range or not. To determine introduction status, we cross-referenced
142 3111 species from the phylogeny for which we had spatial native range data (see "Geographic data"
143 below) with published invasive species databases, such as the Global Register of Introduced and
144 Invasive Species, the Global Invasive Species Database and the Invasive Species Compendium, as
145 well as several multispecies scientific studies (e.g., Kraus 2009, Powell et al. 2011, 2012, Mahoney
146 et al. 2015, Krysko et al. 2016, Tingley et al. 2016, Helmus et al. 2017; see Supplement S1 for the
147 full list of references). For all species that did not match with these databases, we performed a
148 Google query for each species using the search term "*Species name* AND introduced OR exotic
149 OR invasive OR alien OR nonnative OR non-indigenous" to look for species-specific literature
150 that indicates it as introduced regardless of whether an exotic population is currently extant. We
151 excluded species for which introduction records were not scientifically published, uncertain or
152 debated. To estimate extinction risk, we reviewed IUCN records for all species with spatial native
153 range data (accessed August 2018). Species that were "vulnerable", "endangered", "critically
154 endangered", "extinct in the wild", and "extinct" were all categorized as extinction-prone, and
155 species with "near threatened" and "least concern" status were considered to be not threatened with
156 extinction, consistent with the categorization by IUCN (IUCN Standards and Petitions

Subcommittee 2019). Of the 3111 species, 349 of category "data deficient" and 494 of category "not assessed" were excluded from the analyses (see "Analyses" below).

Geographic data

Distributional range maps for 3463 reptile species were compiled from the IUCN (IUCN Redlist 2021) and the Caribherp Caribbean island databases (Hedges 2021) and edited to only include polygon shapes of native ranges of squamates in the western hemisphere which also appeared in the phylogenetic tree. The resultant dataset included 3111 species. This difference in the number of species between datasets was caused by the mismatch between phylogeny and geographic ranges and removal of duplicate ranges, taxonomic synonyms, exotic ranges, and non-squamate species. We used these range polygons to calculate independent covariates (italicized subheadings below) for our statistical analyses.

Range size and complexity

Species range characteristics are thought to influence introduced and extinction-prone status. For each species, we calculated native range size and complexity. First, range area (m^2) and range perimeter (m) were estimated with the "areaPolygon" and "perimeter" functions, respectively, from the geosphere R package (Hijmans 2019). Size was estimated as range area and complexity was estimated as a normalized perimeter where range perimeter values are standardized for circularity by dividing the measured perimeter of species range by a hypothetical perimeter of a circle with the same surface area (variation of method proposed by Cox (1927) and Polsby and Popper (2017):

$$normalized\ perimeter_i = \frac{(2\pi r)_i}{2\sqrt{\pi * (\pi * r^2)_i}}$$

179 Low values indicate more circular ranges and high values indicate deviations from a circular range.
180 Species with high range complexity values thus have ranges that are unevenly spread across a
181 landscape and/or include many geographic boundaries (e.g., multiple islands).
182
183 *Species insularity*
184 For each species we calculated its degree of insularity as the portion of a species range located on
185 oceanic islands. We intersected species range polygons with a map of the continental mainland of
186 North and South America (GADM 2018), enabling us to identify the mainland continental ranges
187 for all species. Based on the area difference between the total species range and the continental
188 range, we were able to infer the insular fraction of a species range. An insularity value of 1 indicates
189 exclusive island living (i.e., island endemic) and values of 0 indicated that species only occur on
190 the continental mainland.
191
192 Evolutionary data
193 *Genus age*
194 Genus age has been associated with adaptability of species, and can be indicative of whether
195 species has been part of a recent radiation or has been able to persist for a long time (Davies et al
196 2011, Title & Burns 2015). Genus age was determined by calculating the branching-time from the
197 most recent common ancestor of the genus (i.e., the crown age) with the 'AssessMonophyly' and
198 'branching.time' functions from the 'ape' R package. Of 280 western hemisphere genera, 212 were
199 monophyletic, 65 were monotypic (a genus containing 1 species) and 3 were paraphyletic
200 (*Epicrates*, *Leposoma*, *Homonota*). For monotypic genera, we took the branching-time from the
201 most recent node connecting the focal tree tip as genus age. The intruder or outlier clades in
202 paraphyletic genera were all monophyletic or monotypic for which we could obtain a reliable age.

After close examination of the paraphyletic genera, we concluded that division into smaller clades would not benefit our analysis nor significantly change our outcomes. We thus used the most recent common ancestor of paraphyletic genera for further analysis.

Evolutionary range expansion rate

The rate at which a clade has expanded its range in the past has been suggested to be a proxy for the potential of its species to do so in the present (Title & Burns 2015). We summed the species range areas for all the species within the same genus to represent the cumulative range area that a genus has spread into since the time of speciation from the most recent common ancestor. Cumulative range area was divided by the focal genus age to calculate the average evolutionary range expansion rate of geographic spread for all congeners.

<u>Ecological data</u>

Functional traits

We obtained data on functional traits thought to be related to opposite distributional responses to human influence (Jeschke and Strayer 2008, Blackburn and Jeschke 2009, Tingley et al. 2016). Natural log-transformed values of clutch size and maximum body size, as well as two categorical variables for diet (herbivorous, carnivorous, and omnivorous) and reproductive mode (binomial: oviparous and (partially) viviparous), were included as independent variables in PGLMs. These trait data were from Rapacciuolo et al. 2019.

Seasonality and elevation

The environment that a species has adapted to in their native range may be associated with distributional changes in the Anthropocene. We used Principal Component Analysis (PCA) to

227 extract composite variables that explain the climatic variation experienced among species. We
228 calculated the median of all 37 climatic variables in WorldClim and ENVIREM raster layers per
229 species range (Fick and Hijmans 2017, Title and Bemmels 2018). All range medians were
230 subsequently included in a scaled PCA in R, of which the first two principal components were
231 selected, and explained a cumulative proportion of 70% of the median environmental variation
232 among all species ranges. The first axis (PC1) aligned with climatic seasonality variables such as
233 annual temperature range, diurnal temperature range, and seasonal variation in potential
234 evapotranspiration (PET), and the second axis (PC2) aligned with two elevation-derived variables
235 from the ENVIREM dataset: terrain roughness and topographic wetness (indicative for the
236 catchment of water in a watershed) (Title and Bemmels 2018; See Supplement S2 for biplot).
237
238 *Climatic niche differentiation*
239 Species with little ability to adapt to a changing climate should be more extinction-prone, while
240 those with high adaptive potential should be more likely to establish in a new environment once
241 introduced. To estimate a species' adaptive capacity, we assessed the climatic variability in species'
242 ranges as indication of the various climatic regimes a species has adapted to. We calculated the
243 standard deviations of the 37 WorldClim and ENVIREM climatic variables per species range and
244 included these as new variables in a scaled PCA. PC1 of this PCA (explaining 63% of all variation)
245 was positively correlated to variability for all climatic variables (See supplement S3). Thus, PC1
246 score per species was taken as a value for climatic variability in a species range, which was
247 positively correlated with log-transformed range area ($r = 0.65$, $t_{3054} = 47.45$, $P < 0.001$), i.e.,
248 species with large ranges experience high levels of climatic variation. We used the residuals of this
249 linear relationship to reflect climatic niche differentiation relative to a species range size, indicating

250 disproportionate climatic niche diversification/uniformity as a measure of adaptive capacity
251 (hereafter referred to as climatic niche differentiation).
252
253 Anthropogenic data
254 *Human footprint and number of ports*
255 Unlike the previous species traits and characteristics described above where we expect introduced
256 and extinction-prone species to be at opposite ends of the continua, anthropogenic metrics are
257 expected to show positive relationships with both introduced and extinction-prone status, because
258 both processes are (likely) human-mediated. We determined the number of ports (incl. harbors,
259 seaports, and major terminals) per native range area (World Port Index; National Geospatial-
260 Intelligence Agency 2017) as a proxy for the level of seaborne trade to and from the species native
261 range. While trade clearly increases introductions directly, it also should increase extinctions
262 indirectly by indicating increased potential of introduced predators, pathogens and competitors.
263 We also calculated the median human footprint index (Venter et al. 2016) for every species range,
264 which varies between 0 to 50 and is a compilation of several human pressures, including the amount
265 of built environment, population density, agriculture, and several types of terrestrial and
266 waterborne infrastructure. Like the number of ports, we expected human footprint to increase both
267 introductions and extinctions. The number of ports and human footprint index were not
268 significantly correlated ($r=-0.02$, $t_{2988}=-0.98$, $P=0.33$), and therefore both were included in the
269 statistical analyses.
270
271 ***Analyses***
272 We first asked if islands are sources of introduced and sinks of extinction-prone species.
273 We made maps of squamate species richness and proportions of introduced and extinction-prone

richness in relation to total species richness using 1 km^2 grid cells. This fine grain represents the relevant scale for the occurrence of introduction and extinction particularly on islands, because many islands are small. Further, the Caribherp island database has explicitly made ranges at this fine scale resolution (Hedges 2021). We then calculated the proportion of species with introduced or extinction-prone status whose ranges were found only on the mainland, mainland and islands, or only islands; and tested if our species insularity covariate explained introduced and extinction-prone status with chi-squared tests.

Second, we asked if there was phylogenetic signal among introduced and extinction-prone species. The level of phylogenetic signal among introduced and extinction-prone species was determined with the phylo.d-function for binomial data ('caper' package). The observed distributions of introduced and extinction-prone species was compared to 1000 permutations of a random trait distribution and a clumped trait distribution assuming Brownian trait evolution.

Finally, we tested the opposite ends hypothesis by asking which ecological, geographic and evolutionary characteristics predict introduction and extinction-prone species status. To do this, we used multivariate phylogenetic generalized linear models (PGLMs) to test the dichotomous variables of introduction and extinction status against all predictor variables (see text above) with logistic error term and Firth's penalized likelihood correction ('phyloglm' function, 'phylolm' package). Two separate PGLMs with introduction and extinction status as dependent variables were performed with range insularity as the sole independent factor, because of collinearity issues between insularity and most other predictors (Supplement S4). All other predictor variables had relatively low levels of collinearity ($r \leq |0.60|$ and VIF < 3.0). Prior to all analyses, we scaled the continuous variables (mean = 0, sd = 1), so model estimates represented effect sizes. All analyses were executed in R statistics, version 4.0.3 (R Development Core Team 2021) within the R studio environment (R Studio Team 2021).

Results

The geographic distributions of introduced and extinction-prone species were strikingly different from the distribution of all reptiles in the western hemisphere (Figure 1). For instance, the native ranges of the 142 introduced species in our dataset spanned most of the western hemisphere and were more prevalent in North America and the Caribbean than South America, opposite to the cumulative distribution of all reptiles (Figure 1A,B). In contrast, the ranges of the 483 extinction-prone species in our dataset were much more localized and concentrated to specific endangered ecosystems and mountainous regions such as the Andes, the Pampas, Mesoamerican cloud forests and the Caribbean (Figure 1C).

The native ranges of introduced and extinction-prone species were similar to each other in that these species were often found on islands. Of all species in our dataset, 16% were island endemics; 32% had ranges encompassing both island and mainland regions, and a majority of 52% had native ranges only on the mainland, primarily Amazonia (Figure 1A). In contrast, 91% of the introduced reptiles had an association with island-living, either as island endemics (44%) or with oceanic islands in their native range (47%, Figure 1B). On many islands, >50% of the native species have been introduced elsewhere, making islands key sources of introduced reptiles globally. Similarly, island endemics constituted 41% of the extinction-prone species, and on many islands >30% of species are threatened with extinction (Figure 1C). This clear overrepresentation of island endemics in introduced ($\chi^2 = 47.83$, df = 1, $P < 0.001$) and extinction-prone reptile groups ($\chi^2 = 164.67$, df = 1, $P < 0.001$) indicates that islands are simultaneous sources and sinks of biodiversity in the Anthropocene.

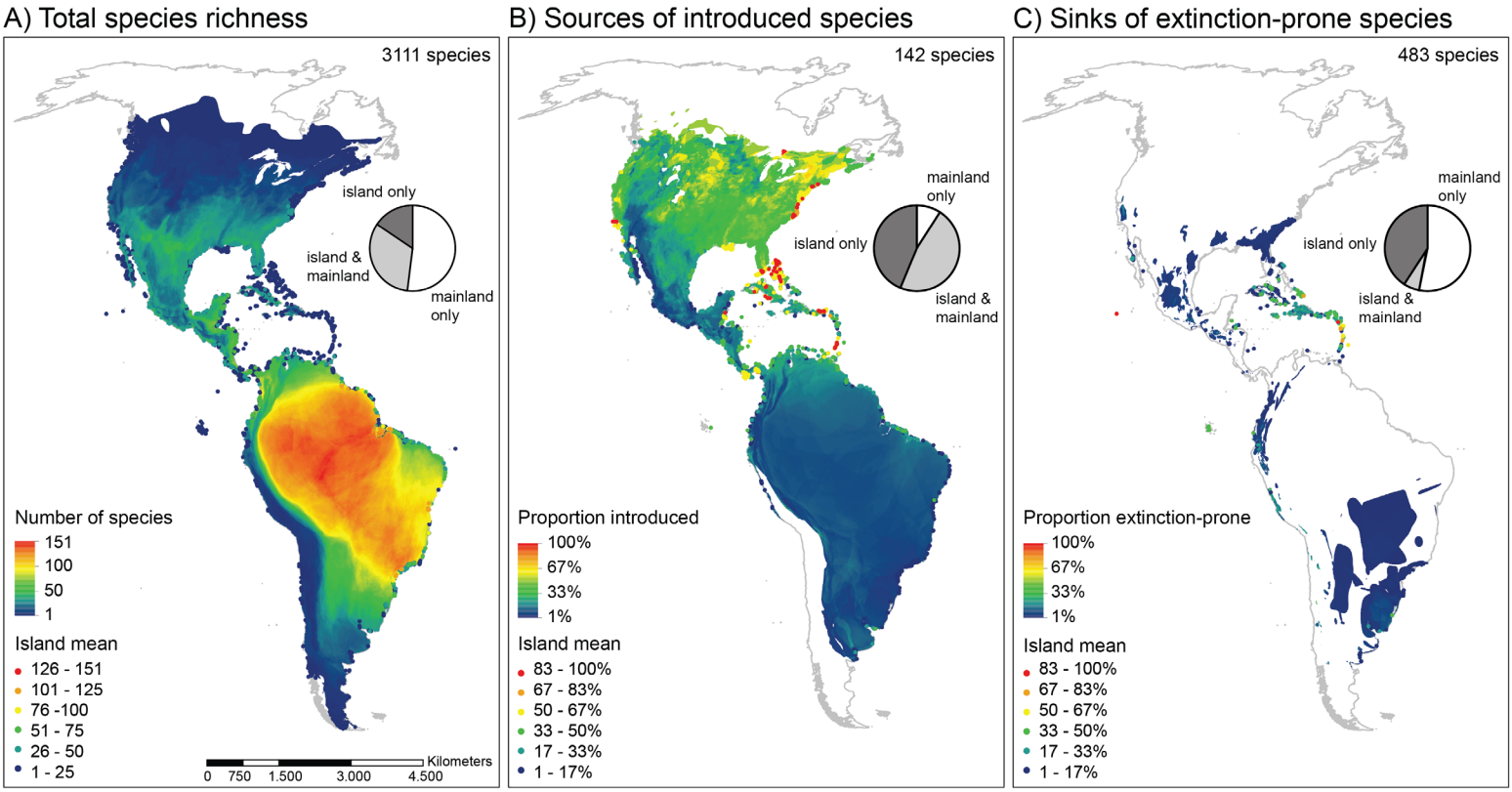

Figure 1. The geographic distribution of reptile species richness in the western hemisphere, and identification of sources and sinks of reptile biodiversity in the Anthropocene. A) The total of overlapping native species ranges per 1km^2 grid cell. Proportions of introduced (B) and extinction-prone (C) richness in relation to total species richness were calculated for all 1 km^2 grid cells inhabited by >1 species. Points in all maps represent mean values per island and were plotted as such to increase visibility. Points follow the same color scheme as the gridded layers. Pie charts represent the geographic context of the species ranges depicted in the respective maps, showing the proportions of species that are restricted to the continental mainland of North and South America (white), partially insular species that inhabit island and mainland areas (light grey), and species that are restricted to oceanic islands (dark grey). Percentages within pie charts are (clockwise, i.e., *mainland only, island and mainland, island only*) (A) 52%, 32%, 16%, (B) 9%,

47%, 44% , (C) 53%, 6%, 41%. All maps were projected as Eckert IV spherical world projection in ESRI ArcMap 10.6.1.

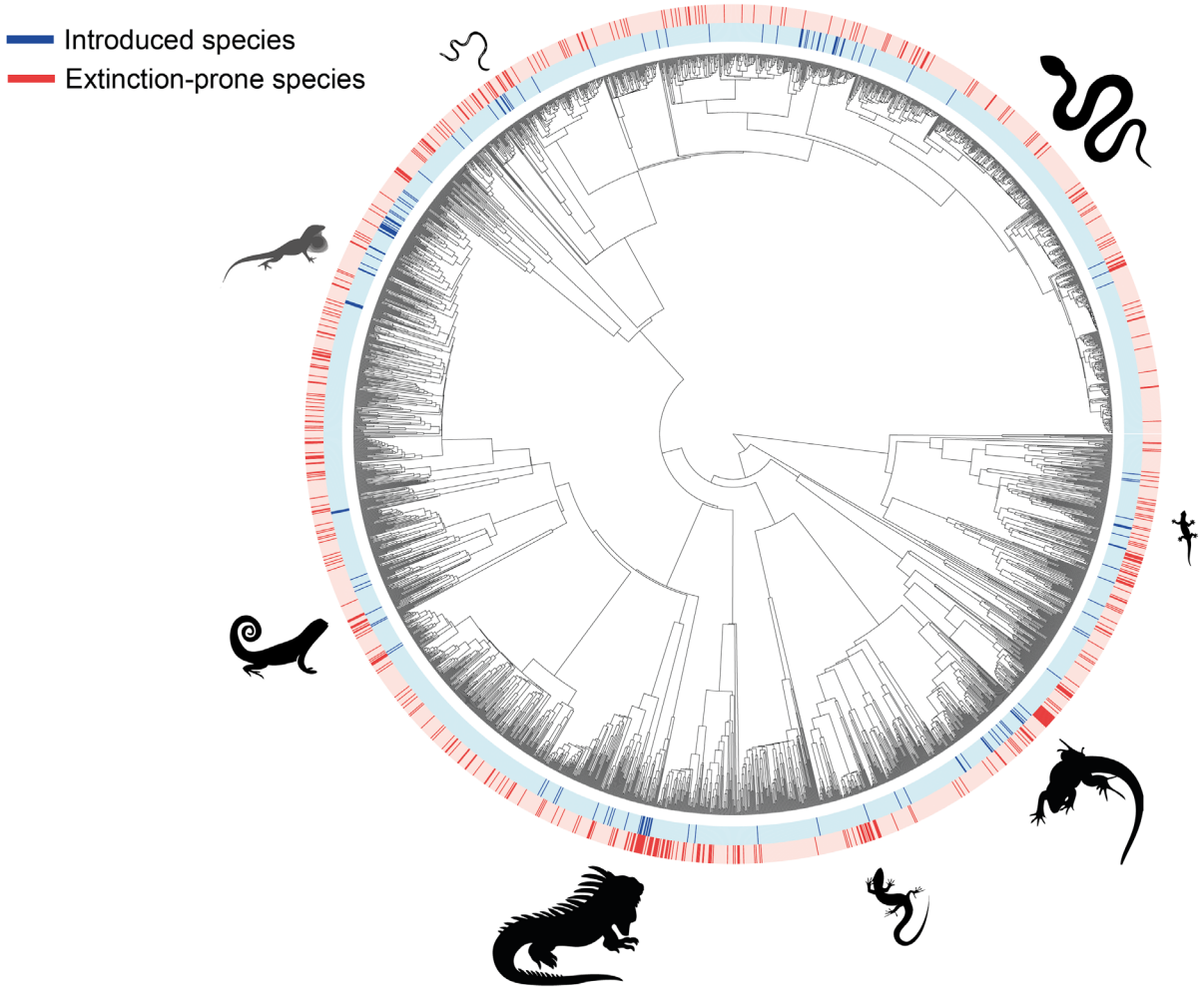

Figure 2. Significant phylogenetic signal among introduced and extinction-prone reptiles. Introduced (142 spp) and extinction-prone reptiles (483 spp) plotted across the tree of life (3111 spp total). Silhouettes are of genera containing proportionally high numbers of introduced and/or extinction-prone species (clockwise: *Boa, Sphaerodactylus, Ameiva, Scincus, Iguana, Cnemidophorus, Anolis, Typhlops*).

343 Introduced and extinction-prone species were non-randomly distributed across the
344 phylogeny of Western Hemisphere reptiles (Figure 2). The signal for introduced (D = 0.63, $P <$
345 0.001) and extinction-prone (D = 0.71, $P < 0.001$) species was intermediate in strength and
346 significantly different from random and clumped null models based on 1000 permutations. Further
347 multivariate testing was done using phylogenetic generalized linear models to account for
348 phylogenetic non-randomness of observations. While introduced and extinction-prone species
349 exhibited phylogenetic clustering, the composition of the two groups showed little overlap. Of the
350 142 introduced and 483 extinction-prone squamates, only 15 species were included in both
351 categories. Of these 15 species, eight are popular species in the pet trade and threatened with
352 extinction in their native range (e.g., iguanas of the genus *Cyclura*).

353 Range insularity (the proportion of species range overlap with oceanic islands) was
354 positively related to both introduction (0.39 ± 0.08, z = 4.45, $P < 0.001$) and extinction probabilities
355 (0.54 ± 0.05, z = 10.52, $P < 0.001$; Figure 3A). Range insularity showed strong collinearity with
356 other variables in our analyses, most prominently with range area (r = -0.39, t = -23.3, $P < 0.001$),
357 diet type (Kruskal-Wallis: $\chi^2 = 18.2$, df = 2, $P < 0.001$; bias towards omnivory), and human
358 footprint (r = 0.46, t = 29.1, df = 3056, $P < 0.001$) as well as significant correlations with range
359 complexity (negative), parity (association with oviposition), clutch size (negative), climatic niche
360 differentiation (negative), genus age (positive), and evolutionary range expansion rate (negative)
361 (see Supplement S4 for pairwise correlations between all variables). This indicates that island-
362 living can be seen as a trait "syndrome": a set of correlations among individual phenotypic traits.
363 Therefore, in our PGLM analyses range insularity was excluded from the set of trait continua used
364 to test if introduced and extinction-prone species are positioned at opposite ends. After exclusion
365 of range insularity from the models, human footprint was the only other explanatory variable that
366 was positively related to introduction and extinction probability (Figure 3B). The underlying cause

of this is likely to be the significantly higher human footprint in species ranges located on oceanic islands than on the mainland (t = 22.03, df = 653.79, $P < 0.001$; Figure 3C), as well as in the ranges of introduced and extinction-prone species compared to other western hemisphere reptiles (t = 3.76, df = 145.41, $P < 0.001$ and t = 11.94, df = 579.02, $P < 0.001$, respectively; Figure 3C).

Several explanatory variables had significant opposing effects on introduced and extinction-prone status consistent with the opposite ends hypothesis (i.e. diet, range area, and range perimeter in Figure 3B). Native ranges of introduced species were larger (0.78 ± 0.14, z = 5.58, $P < 0.001$) and more complex (0.74 ± 0. 12, z = 6.32, $P < 0.001$) than the ranges of other western-hemisphere reptiles, while extinction-prone ranges were smaller (-0.86 ± 0.07, z = -12.64, $P < 0.001$) and relatively circular (-0.15 ± 0.05, z = -2.83, $P = 0.005$). Extinction-prone and introduced species also had divergent diets, with extinction-prone species adhering to a carnivorous, rather than omnivorous (-1.70 ± 0.22, z = -7.62, $P < 0.001$) or herbivorous diet (-2.19 ± 0.41, z = -5.37, $P < 0.001$), while introduced species were positively related to herbivory (1.27 ± 0.47, z = 2.70, $P = 0.007$) and omnivory (0.68 ± 0.28, z = 2.39, $P = 0.02$; carnivory being the contrast level in the PGLM analysis, not shown). Other predictor variables also showed opposite effects for introduced and extinction-prone species, but did not differ significantly. In total, seven of the predictor variables supported the opposite ends hypothesis (Figure 3B). Finally, clutch size had relatively small single effect with introduced species having larger clutches (0.25 ± 0.12, z = -2.10, $P = 0.04$).

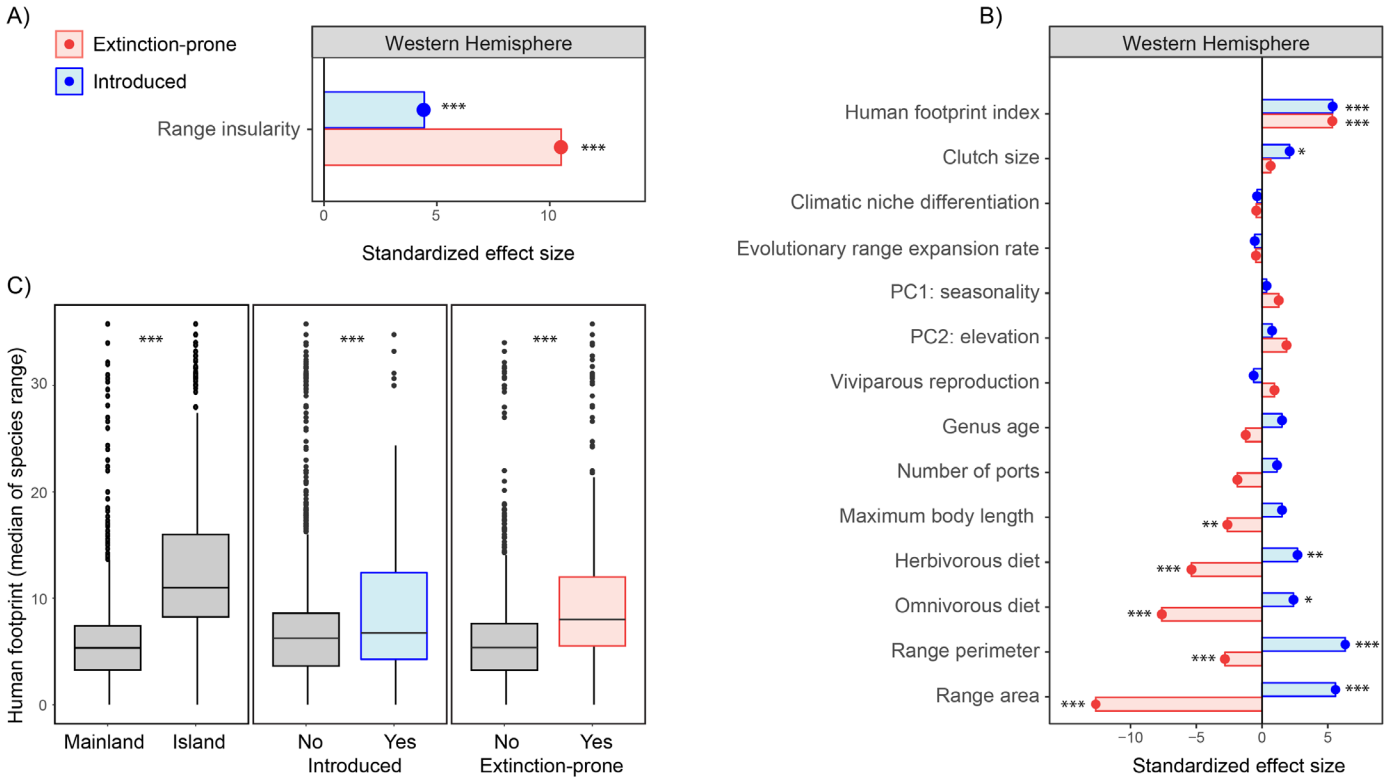

Figure 3. Species functional traits and characteristics as predictors for introduced and extinction-prone status. A) Range insularity is positively related to introduction (blue) and extinction (red) probabilities of western hemisphere reptiles. Bars are standardized logistic PGLM effect sizes (i.e., model estimate/standard error). B) Associations between range and species characteristics with introduction and extinction probabilities. A total of 2936 species, of which 128 were introduced, and 2148 of which 435 extinction-prone, were included in separate PGLM analyses. Bars are ordered according to the level of congruent responses between introduced and extinction-prone species. C) Human footprint is significantly higher within exclusively insular species ranges (range insularity = 1) compared to (partially) mainland ranges (range insularity < 1) and significantly higher for introduced and extinction-prone species compared to other reptiles. $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***).

Discussion

Range insularity and human footprint are important shared characteristics of introduced and extinction-prone species, indicating highly impacted, oceanic islands as simultaneous sources and sinks of biodiversity in the Anthropocene. In addition, we found significant phylogenetic signal among introduced and extinction-prone species, illustrating that these species are not a random draw from the tree of life, but evolutionarily predisposed to success or failure when faced with global change. In contrast to the parallel effects of insularity and human footprint, several ecological and geographic variables affected introduction probability and extinction risk in opposite directions. Our analysis thus shows that while winners and losers of the Anthropocene can inhabit the same geographic areas, their persistence is largely determined by their native range size, range shape, and ecological characteristics that lie on opposite ends of the same trait continua.

Phylogeographic signature of introduced and extinction-prone species

We detected significant phylogenetic signal for both introduced and extinction-prone species groups, indicating that a species' fate in the Anthropocene is partially related to its phylogenetic history. This phylogenetic signal is likely due to the functional traits that clades have evolved and where clades diversified geographically. Previous studies demonstrated that native ranges of exotic fish (Alcaraz et al. 2005) and birds (Blackburn and Duncan 2001) span a wide latitudinal range, and the source distributions of exotic birds are skewed towards northern latitudes (Blackburn and Duncan 2001). However, we found a strong link between insularity of species ranges and introduction status, which to our knowledge has not been established before this study. Reasons for high introduction potential among insular reptiles can be evolutionary, in that insular species are selected to be naturally good dispersers and strong competitors for the limited resources on

421 islands. Evidence for this has been found in Caribbean tree lizards of genus *Anolis* for which a so-
422 called "colonizer body type" has been identified: a set of morphological traits shared by species
423 that recently colonized the islands through human agency and congeners that naturally colonized
424 the islands millions of years ago (Poe et al. 2011). Alternatively, the positive association between
425 insularity and introduction status can also have a contemporary, purely ecological reason, as the
426 high human impact levels on islands increase the probability of being exported elsewhere (Latella
427 et al. 2011, Liu et al. 2014).

428 The association between island-living and extinction-prone status has already received
429 much attention. For instance, all island regions of the world are considered "biodiversity hotspots",
430 characterized by simultaneous high levels of endemism and extinction risk (Myers et al. 2000,
431 Mittermeier et al. 2012). In addition, islands harbor 58% of all critically endangered reptiles (Spatz
432 et al. 2017) and most of the recorded species extinctions occurred on oceanic islands (Sax and
433 Gaines 2008). Potential causes of this correlation between insularity and extinction risk can be that
434 the many endemic species with range-restricted populations are prone to random stochastic
435 extinction events (Fordham and Brook 2010, Smith and Almeida 2020) or insular species may be
436 innately predisposed to fast rates of species turnover (i.e., diversification and extinction). The flora
437 of the South African biodiversity hotspot provides evidence for such predisposition, as young,
438 recently speciated lineages are particularly at risk of extinction, irrespective of human stress factors
439 (Davies et al. 2011); however, we did not find that to be the case for western hemisphere squamates.
440 Hence the location of a species' native range and how heavily it is impacted by humans is a key
441 determinant of species fate in the Anthropocene.

442

443 <u>Introduced and extinction-prone species characteristics</u>

Like Kier et al. (2009) who looked at islands worldwide, our human footprint analysis showed that insular species are subjected to disproportionate levels of human impact. However, we did not detect an association with the number of ports in the native range as a predictor for exotic introductions, while travel movements are a central condition for species introductions (Mahoney et al. 2015). This could be because aerial travel was not taken into account in the number of ports and likely better reflected by human footprint, because air travel volume strongly correlates with population size and infrastructure (Mao et al. 2015).

We found that introduced species generally have large and complex ranges, indicative of an uneven spread across the landscape. However, we did not find indications of exceptional adaptive climatic capacity among introduced species compared to resident native species; a trait that has previously been associated with historic range expansion of western hemisphere passerines (Title and Burns 2015) and rapid climatic niche shift in amphibians and reptiles (Wiens et al. 2019). A potential reason for the high levels of native range complexity (i.e., deviation from a circular range) of introduced species might be that these species follow human impact, which is characterized by a network of irregularly shaped roads and dense settlements (Herold et al. 2003) or that large ranges are more likely to encounter erratic geographic boundaries such as coastlines and mountain ranges. In contrast, extinction-prone species have significantly smaller and simpler range shapes than non-threatened species, often being confined to single point populations. This finding serves as a positive control of our analysis, as range size is one of the main criteria for IUCN to consider a species endangered with extinction (IUCN Standards and Petitions Subcommittee 2019).

Herbivorous and omnivorous diets are overrepresented among introduced species, while carnivory is predominant among extinction-prone species. These results contrast a recent global study across several taxa including reptiles that indicates herbivores to be most at risk of extinction

468 (Atwood et al. 2020). The positive association between herbivory and introduction success are
469 congruent with a modeling study that shows a lower trophic niche level and generalist herbivorous
470 diet to be the most important predictors of introduction success (Romanuk et al. 2009), and with a
471 global study on reptiles that identifies herbivores as most likely to establish exotic populations
472 (Mahoney et al. 2015). However, we expected a positive association between introduction status
473 and carnivory rather than herbivory as most well-known reptile introductions feature carnivorous
474 species, notorious for their impact on native prey populations (e.g., *Boiga irregularis, Boa*
475 *constrictor)* and responsible for most exotic-facilitated species extinctions (Sax and Gaines 2008).
476 Our analysis shows that such introductions do not make up the majority of reptile introductions, at
477 least for those species that originate in the western hemisphere.

478 Introduced species exhibit a single positive association with clutch size, a trait that is
479 associated with fast life-history "r strategies" (i.e., species adhering to r strategies are highly fecund
480 and reach sexual maturity early). Having "fast traits" greatly benefits species establishment and
481 invasive spread in reptiles as these traits facilitate rapid population growth from a small population
482 size and buffer against vulnerability to stochastic events (Mahoney et al. 2015, Allen et al. 2017).
483 In addition, humans may also favor species with large clutches to breed for the pet trade, a major
484 introduction pathway for exotic reptiles (Stringham & Lockwood 2018).

485 We detected a single, negative association between extinction-prone species and maximum
486 body size, contradicting earlier studies that indicated large-bodied reptiles as most threatened, and
487 introduced reptiles as generally small (Mahoney et al. 2015, Tingley et al. 2016). However, these
488 studies included crocodilians and tortoises in their datasets, which are relatively large-bodied
489 compared to squamates (snakes and lizards). A possible reason for the negative association between
490 body size and species endangerment in our study is that small reptiles may be particularly sensitive

491 to temperature shifts (Herczeg et al. 2007) making them vulnerable to human-caused microhabitat
492 and climate change (Jesse et al. 2018).

493 Other possibly important variables for species introduction probability include behavioral
494 traits that correspond to cognitive function. Brain size (Amiel et al. 2011) and behavioral plasticity
495 (Perry et al. 1999; Salazar et al. 2019) have been associated with introduction success, but could
496 not be taken into account in this large-scale and multi-species analysis. Also, reproductive traits,
497 such as the ability of parthenogenesis and long-term sperm storage, could greatly facilitate species
498 establishment in an exotic range (Mahoney et al. 2015), as theoretically only a single pregnant
499 female can establish a viable exotic population.

500

501 <u>Opposite ends of the same trait continua</u>

502 Introduced and extinction-prone reptiles showed opposite species characteristics for seven out of
503 fourteen (50%) of our model variables. Other studies also report opposite effect sizes for 50-73%
504 of species-level predictors in animal taxa (Jetschke & Strayer 2008, Blackburn & Jetschke 2009,
505 Tingley et al. 2016). The support for the opposite ends hypothesis seems to find even stronger
506 support in plant studies (Bradshaw et al. 2008, Pandit et al. 2011), although due to their different
507 methodology, the strength of support for the hypothesis is difficult to compare among studies. In
508 our study, there were strong positive associations of both introduced and extinction-prone species
509 with insularity and human foot print index. Therefore, our results imply that (dis)similarities in
510 species characteristics alone do not provide a full understanding of what makes a species introduced
511 or threatened. To answer this question, we may need to adopt a tiered model, in which the level of
512 human activities in the native area of a species determines the likelihood of distributional change
513 in the species' range, while its eco-evolutionary and geographic characteristics then determine if
514 the species will expand or contract in range.

515

516 Implications for (insular) biodiversity

517 Islands have always served as important stepping stones for overwater dispersal and locations from
518 which many colonizer species originated (MacArthur & Wilson, 1967, Harbaugh et al. 2009).
519 However, colonization and extinction rates greatly exceed historic background rates of species loss
520 and gain (Ricciardi 2007, Loehle & Eschenbach, 2012). For instance, in Hawaii, the colonization
521 rate before human settlement has been estimated at 0.03 species per 1000 years, increasing to 20
522 species per 1000 years with the arrival of Polynesians and 20000 species per 1000 years over the
523 last two centuries (Smith 1985, Loope et al. 1988, Ricciardi 2007). While oceanic islands are
524 generally more susceptible to exotic invasion than mainland regions (Dawson et al. 2017), the level
525 of colonization pressure on Hawaii in the last centuries is likely an extreme example.

526 The current rate of species introductions currently surpasses the rate of species extinctions
527 (Ellis et al. 2012). In our dataset, only eight of 483 extinction-prone species were already
528 considered extinct, while a total of 21% of species (483 out of 2268) were threatened with
529 extinction based on IUCN status. This threat level approximates results for all vertebrates, of which
530 18% are at risk of extinction (Atwood et al. 2020) and 32% of terrestrial vertebrates experience
531 range reduction or population decline (also including low concern species) (Ceballos et al. 2017).
532 The discrepancy between extinct and threatened species numbers indicates the existence of an
533 extinction debt: the surplus of species that will go extinct in the foreseeable future, but still
534 contributes to the species richness we see today.

535 The swift influx of colonizers and prospective loss of endemic species leads to significant
536 taxonomic and functional homogenization (Olden et al. 2006, Clavel et al. 2010, Capinha et al.
537 2015), especially within island biota (Longman et al. 2018). This threatens biodiversity and
538 ecosystem functioning on a small scale, but also poses a threat to global biodiversity because of

539 the profound risk to lose a large portion of diversity on earth. To mitigate this process, this study
540 provides applicable knowledge that can be implemented to prevent species introductions and
541 extinctions via screening and biosecurity measures as well as targeted protection policies.
542

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550

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