1   Elevated human impact on islands increases the introduction and extinction status of native insular

2   reptiles.

3

4   Jesse, Wendy A.M.*[1]

5   Ellers, Jacintha[1]

6   Behm, Jocelyn E.[2]

7   Costa, Gabriel C. [3]

8   Hedges, S. Blair [2]

9   Helmus, Matthew R.[2]

10
11   * Corresponding author
12

13   [1]Department of Ecological Science, Vrije Universiteit Amsterdam, De Boelelaan 1085

14   Amsterdam, NL 1081 HV

15   [2]Department of Biology, Temple University, 1925 N. 12th Street Suite 502, Philadelphia, PA

16   19122

17   [3]Department of Biology and Environmental Sciences, Auburn University at Montgomery,

18   Montgomery, AL, 36124, USA

1 **Elevated human impact on islands increases the introduction and extinction status of native**

2 **insular reptiles**

3

4 **Abstract**

5 Species ranges are changing in the Anthropocene, the ranges of introduced species are expanding,

6 while extinction-prone species are contracting. Introductions and extinctions are both caused by

7 how species respond to human impacts, but it is unknown why the ranges of some species expand

8 and some contract. Here, we test that this opposite response of human impact is due to introduced

9 and extinction-prone species falling at opposite ends of geographic, evolutionary, or ecological

10 trait continua. We constructed a database of native range maps, traits, phylogenetic relationships,

11 and the introduction and extinction-prone status of squamate reptiles with ranges native to the

12 Western Hemisphere. Across >3,000 snake and lizard species (88% of known native squamates),

13 142 had been introduced elsewhere and 483 were extinction-prone (i.e., extinct, vulnerable,

14 threatened). To explain variation in status, we first tested if the same human-impacted regions in

15 the Americas contained the native ranges of species of either status. Second, we tested for

16 phylogenetic signal in species status. Finally, we tested the explanatory power of multiple trait

17 continua. The native ranges of introduced and extinction-prone reptiles were clustered in island

18 regions with high human impact vs. mainland regions with lower human impact. Phylogenetic

19 signal was weak for status, but introduced and extinction-prone species were clustered in different

20 clades. All geographic and ecological traits that explained both statuses supported the opposite

21 ends hypothesis. Introduced species had larger, edgier ranges, while extinction-prone species had

22 smaller, simpler ranges. Introduced species were mostly herbivorous/omnivorous, while

23 extinction-prone species were mostly carnivorous. Introduced species produced larger clutches,

24 while extinction-prone species were smaller in body size. In the Anthropocene, the naive ranges of

25   introduced and extinction-prone species are in the same human-impacted regions where trait

26   continua, having opposite effects, determine whether species ranges expand or contract in the

27   continuing face of global change.

28

29   **Introduction**

30   In the Anthropocene, humans have altered species ranges and reassembled global biogeographic

31   patterns that arose naturally across eons of evolution (Alroy 2015, Capinha et al. 2015, Ceballos et

32   al. 2017). Range contraction and expansion varies across species due to human impact (Pacifici et

33   al. 2020). However, the ultimate "winners" of the Anthropocene are introduced species, which

34   expand into new geographic regions through human-driven dispersal and establishment (Colautti

35   and MacIsaac 2004). While the "losers" are the extinct and threatened species that have

36   experienced severe native range contraction due to human impacts like overharvesting, pollution,

37   climate change, and land-use change (Vitousek et al. 1997, Sax and Gaines 2008, Böhm et al. 2013,

38   Young et al. 2016). Most introductions and extinctions have occurred since the mid 20th Century,

39   a period considered to be the start of the Anthropocene epoch where multiple indicators of human

40   impact accelerated (IPBES 2019, 2023, Waters and Turner 2022).

41   The reasons for the opposite responses of introduced and extinction-prone species to human

42   impact are multitiered. Species that get introduced to other regions often have native ranges that

43   overlap with dense human populations increasing likelihood of intentional (e.g., pet trade) or

44   unintentional (e.g., stowaways) human-aided dispersal (Latella et al. 2011, Liu et al. 2014, Su et

45   al. 2016, Perella & Behm 2020). After introduction, species with suitable functional traits tend to

46   be more successful in utilizing novel food sources and endure local climatic regimes (Mahoney et

47   al. 2015, Monaco et al. 2020). In contrast, extinction-prone species generally are ecological

48   specialists, characterized by narrow dietary and climatic niches and poor dispersal abilities due to

49   their geographic restriction to mountain tops, islands, or isolated nature reserves in a matrix of

50   anthropogenic land use (Chichorro et al. 2019, Kotiaho et al. 2005, Böhm et al. 2016). Hence,

51   introduced and extinction-prone species appear to be not only each other's antipodes in how they

52   respond to human influence but also in many characteristics that could explain their opposite range

53   responses in the Anthropocene. This raises the question if these winners and losers are at opposite

54   ends of geographic, evolutionary, and ecological trait continua (Schmidt et al. 2021, Jeschke and

55   Strayer 2008, Blackburn and Jeschke 2009). Testing this introduced-extinct opposite ends of the

56   same trait continua hypothesis (also generically termed the two-sides-of-the-same-coin hypothesis

57   in the literature) requires data on functional traits, native range characteristics, and geographic and

58   phylogenetic clustering associated with introduced and extinction-prone species that are analyzed

59   to determine the causes of dissimilarity between the two groups.

60   The studies that have tested the introduced-extinct opposite ends hypothesis show variable

61   results. For instance, extinction-prone and successfully introduced plants (Bradshaw et al. 2008,

62   Pandit et al. 2011, Schmidt et al. 2012), fish (Liu et al. 2017), mammals (Pacifici et al. 2020) and

63   crayfish (Larson and Olden 2010) were on opposite extremes of the same trait axes such as body

64   size, fecundity, longevity, genetic diversity, intraspecific trait variation, and habitat specialization.

65   However, not all traits showed the opposite pattern. Other studies on birds and reptiles have found

66   little evidence for the opposite-ends hypothesis even though different groups of traits characterized

67   either extinction-prone or introduced species (Jeschke and Strayer 2008, Blackburn and Jeschke

68   2009, Tingley et al. 2016, Marino & Bellard 2023). Furthermore, such comparative studies

69   generally lack an (in-depth) phylogenetic perspective on species introduction and extinction

70   probabilities, which is needed because nonoverlapping phylogenetic clustering of introduced and

71   extinct species is expected under the hypothesis because many traits or characteristics of species

72   exhibit phylogenetic signal (Schmidt et al. 2021). Moderate to strong levels of phylogenetic signal

73   have been found in traits associated with introduction and/or invasion success (Cadotte et al. 2009,

74   Park and Potter 2015), native range size (Pigot et al. 2018), and fecundity (Allen et al. 2017,

75   Yessoufou et al. 2016, Pyšek et al. 2017, Alcaraz et al. 2005, Su et al. 2016). Also, phylogenetic

76   clustering of extinction-prone species has been detected in various taxa (Davies et al. 2011, Loza

77   et al. 2017, Adeoba et al. 2019, Arbetman et al. 2017, Fritz and Purvis 2010, Tonini et al. 2016).

78   Overall, there is compelling evidence that the predisposition to becoming introduced or extinct is

79   phylogenetically clustered and should be considered when testing for the opposite ends hypothesis.

80   How species respond to human influence is assumed to be related to native geographic

81   range characteristics associated with range expansions and contractions. Island-living may be an

82   important characteristic determining species status. Islands have high human population densities

83   and are subjected to disproportionate levels of human impact (Kier et al. 2009), thus insular species

84   might be more likely to be introduced or go extinct than mainland species. Islands are hotspots of

85   species loss (Myers et al. 2000, Mittermeier et al. 2011) and provide unique environments that

86   select for functional traits that naturally determine major range expansions or contractions. Insular

87   species have evolved through processes of oversea colonization, followed by often rapid adaptive

88   diversification (Cowie and Holland 2006, Hedges 2006). Thus, insular species are selected to be

89   efficient dispersers and quick adapters to available niche space, which could favor survival of

90   human-vectored dispersal events (Poe et al. 2011). Indeed, post-introduction ecological niche shifts

91   can occur for introduced species that originate from oceanic islands (Liu et al. 2014, Stroud 2021).

92   However, island adaptive radiations may also cause island biota to be highly specialized, dispersal-

93   limited, and extremely suited to exploit a narrow ecological niche within island environments

94   (Losos 2009, Mahler et al. 2010, 2013). This level of specialization leaves island endemics

95   sensitive to human-impact and thus prone to extinction (Jantz et al. 2015).

96   In this study, we used a phylogenetic comparative approach to identify dissimilarities in

97   introduced and extinction-prone species characteristics. We built a dataset of 3111 squamate

98   reptiles, which is 84% of all known lizards and snakes native to the Western Hemisphere (Fig. 1).

99   We identified 142 species that had been introduced to at least one location somewhere in the world

100   and 483 species threatened with extinction according to the International Union for the

101   Conservation of Nature (IUCN 2021, Cox et al. 2022). Reptiles of the Americas are particularly

102   suitable to test opposite responses to human influence, as reptiles are species-rich in the Western

103   Hemisphere and are greatly impacted by human activities (Young et al. 2016, Jesse et al. 2018,

104   Gleditsch et al. 2023). We asked: 1) Are islands of the Western Hemisphere disproportionate

105   sources of introduced and sinks of extinction-prone species? 2) Can we detect phylogenetic signal

106   among introduced and extinction-prone species? 3) For which geographic, evolutionary, and

107   ecological trait continua are introduced and extinction-prone species positioned at opposite ends?

108

109   **Methods**

110

111   ***Data compilation***

112   Squamate phylogeny

113   We updated a global, smoothed, and interpolated phylogeny of squamates from the TimeTree of

114   life project (Kumar et al. 2017), which contained 9378 worldwide species previously built in Marin

115   et al. (2018) and Rapacciuolo et al. (2019). Species synonyms were identified and cleaned using

116   the Reptile Database (Uetz, P., Freed, P. & Hošek 2012) to match up with IUCN native range

117   polygons (see "Geographic data" below). Species not in the phylogeny and not in the spatial dataset

118   were not analyzed. Specifically, the IUCN listed 3519 Western Hemisphere species of which 3463

119   had native range distributions available. Intersecting the phylogeny with the range polygons,

120 resulted in a phylogeny of 3111 of species (Fig. 2, 88% of known Western Hemisphere species).

121 We analyzed this subset of species for phylogenetic signal in introduced and extinction-prone

122 status. Of these 3111 species, 2936 had IUCN native range maps and data on traits. We analyzed

123 this subset of species in multivariable phylogenetic generalized linear models (PGLMM) to test if

124 introduced and extinction-prone species fall at opposite ends of the same trait continua.

125

126 <u>Species introduction and extinction-prone status</u>

127 The response variables in our analyses were based on species statuses of squamates across the

128 Western Hemisphere. We constructed a binomial variable to indicate whether a species was

129 introduced anywhere on earth, and a response variable that indicated if a species was extinction-

130 prone or not. To determine introduction status, we cross-referenced 3111 species from the

131 phylogeny for which we had spatial native range data (see "Geographic data" below) with

132 published invasive species databases, such as the Global Register of Introduced and Invasive

133 Species, the Global Invasive Species Database, the Invasive Species Compendium, and others (e.g.,

134 Powell et al. 2011, Mahoney et al. 2015, Tingley et al. 2016, Helmus et al. 2017, Behm et al. 2022;

135 see Table S1 for the full list of references). For all species that did not match with these databases,

136 we performed a Google query using the search term "*Species name* AND introduced OR exotic

137 OR invasive OR alien OR nonnative OR non-indigenous" to look for species-specific literature.

138 We excluded species for which introduction records were not scientifically published, uncertain,

139 or debated. Extinction risk was taken from IUCN records (accessed August 2018). Species that

140 were "vulnerable", "endangered", "critically endangered", "extinct in the wild", and "extinct" were

141 all categorized as extinction-prone. Of the 3111 species, 349 of category "data deficient" and 494

142 of category "not assessed" were excluded from the analyses (see "Analyses" below).

143

144   <u>Geographic data</u>

145   Distributional range maps for 3463 reptile species were compiled from the IUCN and Caribherp

146   databases (Hedges 2021, IUCN 2021) and edited to only include polygon shapes of native ranges

147   of squamates in the Western Hemisphere that also appeared in the phylogenetic tree. The resultant

148   dataset included 3111 species. This difference in the number of species between datasets was

149   caused by the mismatch between phylogeny and geographic ranges and removal of duplicate

150   ranges, taxonomic synonyms, exotic ranges, and non-squamate species. We used these range

151   polygons to calculate covariates (italicized subheadings below) for our statistical analyses.

152

153   *Range size and shape*

154   For each species, we calculated native range size and shape. Range size was estimated as range

155   area in km^2. Range shape was estimated as the inverse of the normalized perimeter of the range,

156   which is calculated as range perimeter divided by the perimeter of a circle with the same area as

157   the range (Patton 1975). While there are many metrics of range shape, most use some equation that

158   includes a measure of range perimeter and area often expressed as a ratio (Krummel et al. 1987,

159   Kupfer 2012). We chose normalized range perimeter (i.e., also termed edge diversity index,

160   perimeter-area ratio shape index) because it is an intuitive metric indicative of range edginess

161   versus compactness that is widely used and statistically independent of range size (Frazier and

162   Kedron 2017). Values closer to one indicate ranges with many edges such as those that include

163   multiple geographic boundaries. Values closer to zero are more compact and circular. Range size

164   and shape were estimated with the "areaPolygon" (m^2) and "perimeter" (m) functions from the

165   geosphere R package (Hijmans 2019). We expected that a species is more likely to be introduced

166   if it has a larger range with more edges. Larger ranges means there is more area for the species to

167   hitchhike along transportation networks. Similarly, more edges means the species is distributed

168   across multiple islands, found near coastlines, in river valleys, and more people live near water

169   (Small & Nicholls 2003). In contrast, we expected extinction-prone species to have small and

170   simpler ranges, confined to a single or few populations.

171

172   *Species insularity*

173   For each species we calculated its level of insularity as the portion of a species range located on

174   oceanic islands. We intersected species range polygons with a map of the continental mainland of

175   North and South America (GADM 2018), enabling us to identify the mainland continental ranges

176   for all species. Based on the area difference between the total species range and the continental

177   range, we were able to infer the insular fraction of a species range. An insularity value of 1 indicates

178   exclusive island living (i.e., island endemic) and values of 0 indicated that species only occur on

179   the continental mainland. We expected both introduced and extinction-prone species to be native

180   to islands because islands are highly populated and impacted by humans compared to the mainland.

181

182   Evolutionary data

183   *Genus age*

184   Genus age was determined by calculating the branching-time from the most recent common

185   ancestor of the genus (i.e., the stem age) with the 'AssessMonophyly' and 'branching.time'

186   functions ('ape' R package). Of 280 Western Hemisphere genera, 212 were monophyletic, 65 were

187   monotypic (i.e., a genus containing one species) and three were paraphyletic (*Epicrates*, *Leposoma*,

188   *Homonota*). The intruder or outlier clades in paraphyletic genera were all monophyletic or

189   monotypic, thus the distribution of genus ages was unaffected. We expected genus age to positively

190   associated with introduced status, and negatively associated with extinction-prone status because

191 of its observed relationship to niche volumes and range expansions (Davies et al. 2011, Title &

192 Burns, 2015).

193

194 *Evolutionary range expansion rate*

195 We summed the species range areas for all the species within the same genus to represent the

196 cumulative range area that a genus has spread into since the time of divergence from the most

197 recent common ancestor. Cumulative range area was divided by the focal genus age to calculate

198 the average evolutionary range expansion rate of geographic spread for all species within a genus.

199 We expected this metric to be negatively associated to extinction-prone status based on previous

200 relationships found for reptiles (Title & Burns 2015), and positively associated with introduced

201 status because squamate lineages that were successful colonizers of ancient Caribbean islands also

202 tend to have more introduced species (Poe et al., 2011).

203

204 <u>Ecological data</u>

205 *Functional traits*

206 We obtained data on functional traits hypothesized to be related to opposite distributional responses

207 to human influence (Jeschke and Strayer 2008, Blackburn and Jeschke 2009, Tingley et al. 2016).

208 Trait data were from Rapacciuolo et al. (2019). Specifically, we expected clutch size, viviparity,

209 omnivory, and body size to be positively (negatively) associated with introduction (extinction-

210 prone) status. Natural log-transformed values of clutch size and maximum body size, as well as

211 two categorical variables for diet (herbivorous, carnivorous, and omnivorous) and reproductive

212 mode (binomial: oviparous and (partially) viviparous), were included as independent variables in

213 PGLMs.

214

Seasonality and elevation

215

216 We used a Principal Component Analysis (PCA) to extract composite variables that best explain

217 the climatic variation experienced by species. First, we calculated the median of all 37 climatic

218 variables in WorldClim and ENVIREM raster layers (30 arcsecond resolution, ca. 1km^2) per

219 species range (Fick and Hijmans 2017, Title and Bemmels 2018). Subsequently, we included all

220 range medians in a scaled PCA in R, of which the first two principal components, together

221 explaining 70% of median environmental variation, were selected. The first axis (PC1) aligned

222 with climatic seasonality variables such as annual temperature range, diurnal temperature range,

223 and seasonal variation in potential evapotranspiration, and the second axis (PC2) aligned with two

224 elevation-derived variables from the ENVIREM dataset: terrain roughness and topographic

225 wetness (indicative for the catchment of water in a watershed) (Title and Bemmels 2018; See Fig.

226 S1). We expected extinction probability to be higher for species associated to isolated mountain

227 ranges (e.g. Guirguis et al., 2023) and introduced species to be associated with seasonal climates

228 with broad environmental tolerances (e.g. Tingley et al. 2016).

229

Climatic niche differentiation

230

231 We assessed the climatic variability in species ranges as indication of a species' adaptive capacity

232 to various climatic regimes, expecting introduced species to have a high capacity and extinction-

233 prone species to have a low capacity. We calculated the standard deviations of the 37 WorldClim

234 and ENVIREM climatic variables per species range and included these in a scaled PCA. PC1 of

235 this PCA (explaining 63% of all variation) was positively correlated to variability for all climatic

236 variables (Fig. S2). Therefore, the PC1 score per species was taken as a value for climatic

237 variability per species range, which was positively correlated with log-transformed range area (r =

238 0.65, t_{3054} = 47.45, $P < 0.001$), that is, species with large ranges experience high levels of climatic

239 variation. We used the residuals of this linear relationship to reflect climatic niche differentiation

240 relative to a species range size.

241

242 <u>Anthropogenic data</u>

243 *Human footprint and number of ports*

244 As a general indicator of human impact within species ranges, we calculated the median human

245 footprint for every species range (30 arcsecond resolution, ca. $1km^2$), which is a compilation of the

246 amount of built environment, population density, agriculture, and several types of terrestrial and

247 waterborne infrastructure (Venter et al. 2016). The median value was calculated across all pixels

248 within each species range. We expected positive associations of human footprint with both

249 introduced and extinction-prone status. We used the number of sea ports as a human impact

250 indicator of propagule pressure to and from native ranges. Firstly, ports can serve as points of

251 species export, positively affecting introduction status (Hulme, 2009). Number of ports in the

252 native range also explains naturalization success of anole lizards (Latella et al. 2011). Secondly,

253 ports can serve as points of entry of exotic species (Schneider et al., 2021), also promoting

254 extinction-prone status, because native species become subjected to negative species interactions

255 form these exotics. We determined the number of ports (incl. harbors, seaports, and major

256 terminals) per native range area (World Port Index; National Geospatial-Intelligence Agency 2017)

257 as a proxy for the level of seaborne trade to and from the species native range. Number of ports

258 and human footprint index were not significantly correlated (r=-0.02, t_{2988}=-0.98, *P*=0.33), and

259 therefore both were included in the statistical analyses.

260

261 ***Analyses***

262   All analyses were performed in R. We first asked if islands are sources of introduced species and

263   sinks of extinction-prone species. We made maps of squamate species richness and proportions of

264   introduced and extinction-prone richness in relation to total species richness using 1 km^2 grid cells.

265   We then calculated the proportion of species with introduced or extinction-prone status whose

266   ranges were found only on the mainland, mainland and islands, or only islands; and tested if species

267   insularity explained introduced and extinction-prone status with chi-squared tests.

268   Second, we asked if there was phylogenetic signal among introduced and extinction-prone

269   species indicating clustering in clades of species with similar status. The level of phylogenetic

270   signal among introduced and extinction-prone species was determined with a metric D that tests

271   for signal in binomial data (phylo.d in caper, Orme et al. 2013). We chose this metric because it

272   exhibits statistically robust expectations for large trees when the proportion of species with a status

273   value is low, like for our data (Fritz & Purvis 2010). The observed D value for introduced and

274   extinction-prone species were each compared to two null distributions. First, to test if there was

275   any phylogenetic signal in the data that is different from random and indicative of phylogenetic

276   clustering, a distribution of 1000 random D values was generated under a null model permutation

277   that randomized status values among species irrespective of the phylogeny. Second, to test the

278   strength of clustering, a distribution of 1000 D values were generated from a null model that

279   simulated status according to Brownian evolution across the phylogenetic tree. Observed D values

280   different than the random null indicated clustering, while values that fell between the two

281   distributions indicated weak clustering.

282   Finally, we tested the introduced-extinct opposite ends hypothesis by asking which

283   geographic, evolutionary, and ecological trait continua explained introduction and extinction-prone

284   status. The trait continua exhibited phylogenetic signal (Table S2), thus we used binomial

285   phylogenetic generalized linear models (PGLMs) with logistic error term and Firth's penalized

286   likelihood correction (phyloglm in phylolm, Ho & Ane 2014). First, two separate PGLMs with

287   introduction and extinction status as dependent variables were performed with range insularity as

288   the sole independent factor, because of collinearity between insularity and other covariates (Fig.

289   S3). All other covariates had relatively low levels of collinearity (r≤|0.60| and VIF < 3.0). Second,

290   we ran two separate PGLMs with the other covariates not including insularity to test the hypothesis.

291   Prior to all analyses, we scaled the covariates (mean = 0, sd = 1), so model estimates represented

292   effect sizes.

293

294   **Results**

295   The native ranges of introduced and extinction-prone squamate species of the Western Hemisphere

296   were often found on islands (Fig. 1). Across all species, 52% had native ranges only on the

297   mainland, primarily Amazonia (Fig. 1A). In contrast, 91% of the introduced species were either

298   island endemics (44%) or had islands in their native range (47%, Fig 1B), making islands key

299   sources of introduced reptiles globally. Similarly, island endemics constituted 41% of the

300   extinction-prone species (Fig. 1C). This clear overrepresentation of island endemics in introduced

301   ($\chi^2 = 47.83$, df = 1, $P < 0.001$) and extinction-prone reptile groups ($\chi^2 = 164.67$, df = 1, $P < 0.001$)

302   indicates that islands are simultaneous sources and sinks of biodiversity in the Anthropocene.

303

304
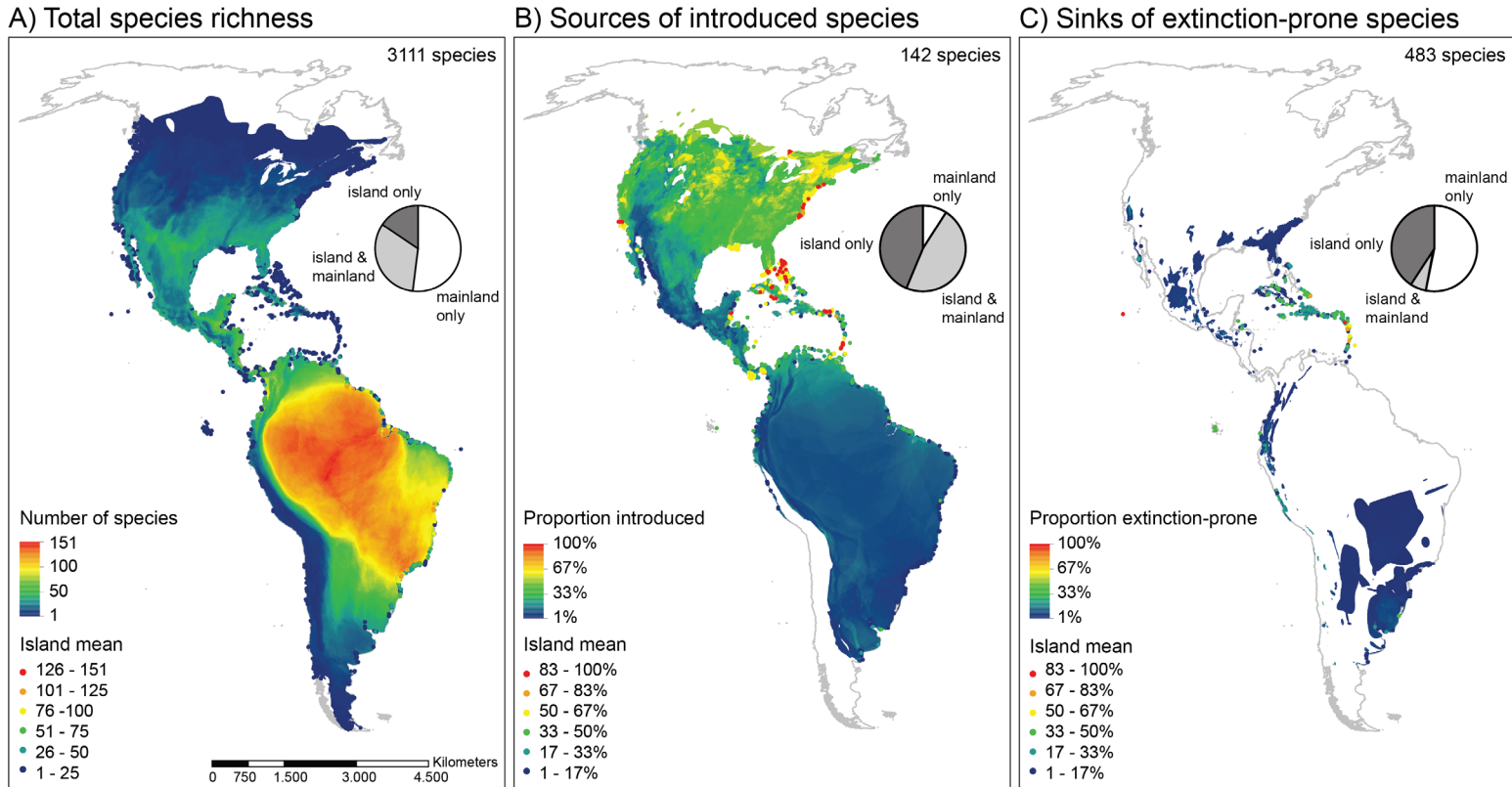
Figure 1. The geographic clustering of the native ranges of introduced and extinction-prone American reptile species indicates islands as sources and sinks of Anthropocene biodiversity.

A) The total of overlapping native species ranges per 1km^2 grid cell provides a map of Western Hemisphere reptile species richness. The 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 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%,

316   (B) 9%, 47%, 44%, (C) 53%, 6%, 41%. All maps were projected as Eckert IV spherical world

317   projection in ESRI ArcMap 10.6.1.

318

319   Introduced and extinction-prone species were phylogenetically clustered across the

320   phylogeny of Western Hemisphere reptiles (Fig 2). The signal for introduced (D = 0.63) and

321   extinction-prone (D = 0.71) statuses both were D < 1 ($P < 0.001$) indicating that statuses more

322   clustered than expected if statuses were randomly distributed across the phylogeny. However, both

323   were D > 0 ($P < 0.001$). Zero is the D value expected under Brownian motion evolution of statuses;

324   thus, the clade clustering of statuses was weak. Introduced and extinction-prone species came from

325   different clades because the composition of the two groups showed little overlap. Of the 142

326   introduced and 483 extinction-prone squamates, only 15 species were included in both categories.

327   Of these 15 species, eight are popular species in the pet trade and threatened with extinction in their

328   native range (e.g., *Cyclura* iguanas).

329

330
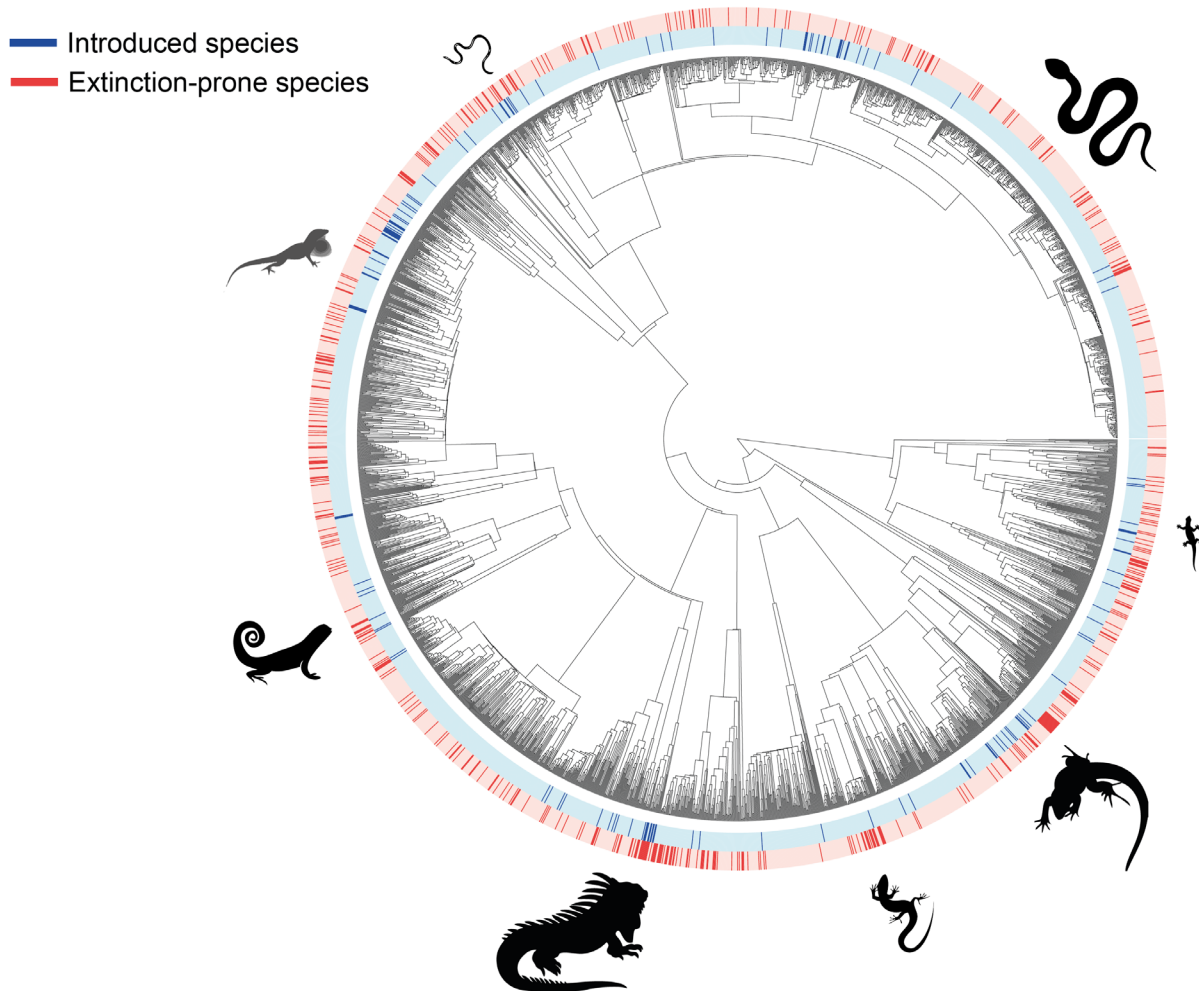
Figure 2. The phylogenetic clustering of introduced and extinction-prone status of American reptiles indicates they are not a random subset of all the reptiles that have evolved in the Western Hemisphere. Introduced species (142) and extinction-prone species (483) are clustered across the Western Hemisphere squamate tree-of-life (3111 species total). Species with an introduced status were those with at least one population established outside of their native range in the Americas. Species with an extinction-prone status were categorized by the IUCN as "vulnerable", "endangered", "critically endangered", "extinct in the wild", and "extinct." Silhouettes are of genera with clusters of introduced and/or extinction-prone species (clockwise: *Boa, Sphaerodactylus, Ameiva, Scincus, Iguana, Cnemidophorus, Anolis, Typhlops*). A metric of

341   phylogenetic signal that indicates clustering (D = 0) or a random distribution (D = 1) for introduced

342   was D = 0.63 (P < 0.001 compared to both distributions) and for extinction-prone was D = 0.71 (P

343   < 0.001).

344

345   Range insularity was positively related to both introduction (0.39 ± 0.08, z = 4.45, *P* <

346   0.001) and extinction probabilities (0.54 ± 0.05, z = 10.52, *P* < 0.001; Fig. 3A). Range insularity

347   showed strong collinearity with other variables in our analyses, most prominently with range area

348   (r = -0.39, t = -23.3, *P* < 0.001), diet type (Kruskal-Wallis: χ^2 = 18.2, df = 2, *P* < 0.001; bias towards

349   omnivory), and human footprint (r = 0.46, t = 29.1, df = 3056, *P* < 0.001) (see Fig. S3 for pairwise

350   correlations). This indicates that island-living can be seen as a trait "syndrome": a set of

351   correlations among individual traits and species-level characteristics (e.g., Poe et al. 2011).

352   Therefore, in our PGLM analyses range insularity was excluded from the set of trait continua used

353   to test if introduced and extinction-prone species are positioned at opposite ends. After exclusion

354   of range insularity from the models, human footprint was the only other explanatory variable that

355   was positively related to introduction and extinction probability (Fig. 3B). The underlying cause

356   of this is likely to be the significantly higher human footprint in species ranges located on oceanic

357   islands than on the mainland (t = 22.03, df = 653.79, *P* < 0.001; Fig. 3C), as well as in the ranges

358   of introduced and extinction-prone species compared to other Western Hemisphere reptiles (t =

359   3.76, df = 145.41, *P* < 0.001 and t = 11.94, df = 579.02, *P* < 0.001, respectively; Fig. 3C).

360   All the trait continua that explained both statuses supported the opposite ends hypothesis

361   (Fig. 3B). Native ranges of introduced species were larger (0.78 ± 0.14, z = 5.58, *P* < 0.001) and

362   more edgy (0.74 ± 0. 12, z = 6.32, *P* < 0.001). Extinction-prone ranges were smaller (-0.86 ± 0.07,

363   z = -12.64, *P* < 0.001) and relatively circular (-0.15 ± 0.05, z = -2.83, *P* = 0.005). Introduced and

364   extinction-prone species had opposing diets. Introduced species were herbivorous (1.27 ± 0.47, z

365   = 2.70, P = 0.007) or omnivorous (0.68 ± 0.28, z = 2.39, P = 0.02) compared to carnivorous (i.e.,

366   carnivory was the contrast in the PGLMs). Conversely, extinction-prone species were carnivorous

367   rather than herbivorous (-2.19 ± 0.41, z = -5.37, P < 0.001) or omnivorous (-1.70 ± 0.22, z = -7.62,

368   P < 0.001). Seven of the tested trait continua were uninformative, but two others explained a single

369   status (Fig 3B). As expected, introduced species had larger clutches (0.25±0.12, z=-2.10, P=0.04),

370   but unexpectedly, extinction-prone species were smaller (-0.11±0.04, z=-2.63, P=0.008).

371

372
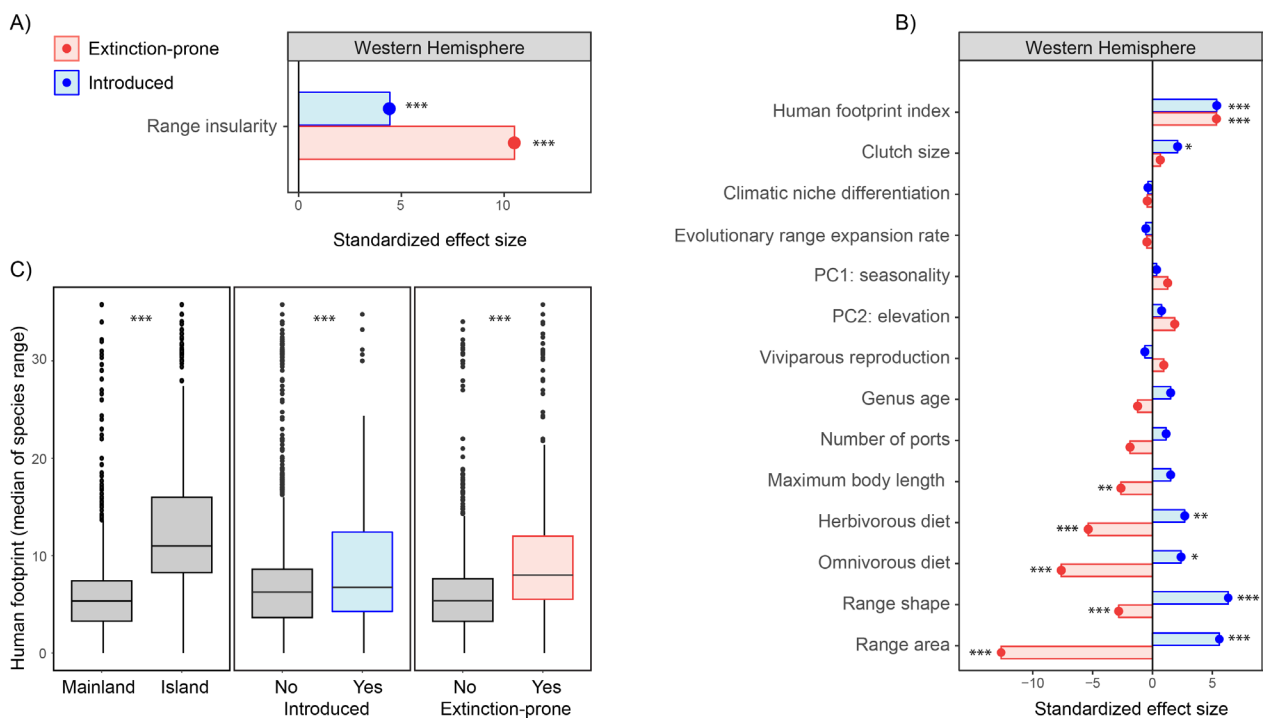
Figure 3. Elevated human impact to islands increases introduction and extinction status of insular lizards and snakes situated at opposite ends of trait continua. A) Across Western Hemisphere squamate reptiles, species with more insular ranges were more likely to be introduced or extinction-prone. B) Species with introduced or extinction-prone status fell on opposite ends of the trait continua that explained both statuses. C) The native ranges of island endemics (Island) are more impacted by humans than continental species (Mainland), and the native ranges of species

379 with introduced or extinction-prone status are also more impacted. In A and C, range insularity was

380 the proportion of a species native range found only on islands and ranged between 1 (island

381 endemics, Island in C) and 0 (continental species, Mainland in C). In A and B, bars are standardized

382 effect sizes (coefficient/SE). In A, separate univariate logistic PGLMMs for introduced or

383 extinction-prone status were fit only to insularity. In B, separate multivariate PGLMMs were fit to

384 a traits based on species geography, evolution, and ecology. In C, the three panels are box plots of

385 the observed data and significance assessed with separate logistic PGLMMs on the data plotted in

386 each panel ($P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$).

387

388 **Discussion**

389 Islands contain the most human-dominated ecosystems on earth, and island living today

390 impacts the status of native lizards and snakes across the Western Hemisphere. Our results suggest

391 that native squamate species on islands have a higher likelihood of being either introduced or

392 extinction-prone. We found that phylogeny predicted status, but the signal was weak. Instead,

393 ecological and geographic trait continua best explained status. While species of either status were

394 insular, trait continua oppositely affected introduction vs extinction risk of species to human

395 impact. Below we discuss each of our major results. The results allow for a better understanding

396 of range dynamics under global change and why highly impacted oceanic islands are simultaneous

397 sources and sinks of biodiversity in the Anthropocene.

398

399 <u>Insularity of introduced and extinction-prone species</u>

400 Islands have consistently been found to have more established alien species than the

401 mainland (e.g., Li et al. 2023). What we found here was that islands also generate more introduced

402 species than the mainland. In the Western Hemisphere, squamate species with the most insular

403 native ranges were also most likely to be introduced elsewhere (Fig. 1B, 3A). Such a strong

404 relationship has not been documented before to our knowledge, but we did find two relevant

405 studies. First at the global scale, birds that have been introduced and birds that are extinction-prone

406 due to invasive predatory species often have ranges that encompass islands (Marino & Bellard

407 2023). However, this effect was weak for introduced birds and the authors only studied extinction-

408 prone species impacted by invasives. Second, global spread rates of introduced herpetofauna

409 species are not related to insularity (Liu et al. 2014). However, this study did not compare

410 introduced vs. extinction-prone species and instead looked at how spread rate varied across

411 continents and islands. In sum, insularity seems related to the probability a species is introduced,

412 but not necessarily to how quickly an introduced species spreads.

413   Many of the extinction-prone squamates native to the Western Hemisphere were island

414 endemics, and the more insular a species native range, the more likely it was to be extinction-prone

415 (Fig. 1C, 3A). Globally, island regions are characterized by simultaneous high levels of endemism

416 and extinction risk (Myers et al. 2000, Mittermeier et al. 2012). They are heavily impacted, and

417 most extinctions have and are occurring on islands (Fernández-Palacios et al. 2021). Islands of the

418 Western Hemisphere, like those in the Caribbean, are highly developed and connected by trade

419 (Gleditsch et al. 2023). Thus, we should expect to see a similar influence of insularity on

420 introduction and extinction-prone status for islands in the Eastern Hemisphere that are also highly

421 impacted. The location of a species' native range and how heavily it is impacted by humans are

422 key determinants of a species fate in the Anthropocene.

423

424 Introduced and extinction-prone species trait continua

425   We examined how native range characteristics, functional traits, and human impact

426   influenced status, particularly focusing on range geography, evolutionary history, climate, diet, and

427   life history traits. Human footprint in native ranges significantly raised the chances of a species

428   being introduced or facing extinction, especially for island species (Fig. 3BC). However, we did

429   not detect an association with our other metric of human impact, number of ports in the native

430   range. This is surprising because trade increases propagule pressure of squamates and explains

431   introduced squamates richness (Gleditsch et al. 2023, Mahoney et al. 2015). Port numbers may not

432   well reflect trade pathways for squamates. The pet trade and live-plant trade are the major pathways

433   for squamate introductions (e.g., Perella & Behm 2020). Estimates of the goods produced, and

434   volume traded from within native ranges might better explain introduction and possibly extinction-

435   prone status (Tingley et al. 2016).

436   Consistent with observations in other taxa (e.g., Pacifici et al. 2020), we found that the

437   native range geography of squamates influences both introduction and extinction status. Introduced

438   squamates generally had larger and edgier native ranges, indicative of spatially spread out and

439   disjoint native distributions (Fig. 3B). In contrast, extinction-prone species had smaller and more

440   compact native ranges. The IUCN often uses convex hulls to delineate ranges. This method can

441   cause smaller ranges to be more circular and less edgy, and species with smaller ranges are more

442   likely to be extinction-prone (IUCN 2021). In contrast, any species that has a large and edgier

443   native range is more likely to encounter humans and be introduced by hitchhiking along

444   transportation networks. Edgier ranges indicate abutment to coastlines and river valleys where most

445   of humanity resides (Small & Nicholls 2003). Further, ancient colonization explains recent

446   naturalizations of anole lizards and edgier ranges are also indicative of disjoint distributions derived

447   from ancient long-distance natural colonization events (Poe et al. 2011).

448   The complexity of past and present climatic variation over which the macroevolutionary

449   process has played out to determine the geography and ecology of Western Hemisphere squamate

450   species says nothing about their status today. Climatic niche differentiation—an area standardized

451   metric of the variation in climatic conditions within ranges—did not explain status. Evolutionary

452   range expansion rate—an age standardized metric of how much area species of a genus have

453   expanded into—also did not explain status. Similarly, current climatic conditions of native ranges

454   had no effect on status. Neither did genus age. These negligible effects were unexpected. Measures

455   of climate and evolutionary age do explain native range biodiversity for vertebrates globally,

456   including Western Hemisphere squamates (e.g., Title and Burns 2015; Marin et al. 2018; Wiens et

457   al. 2019). Thus, anthropogenetic changes to ranges are not influenced by current climate

458   conditions, and how species ancestors adapted and responded to past climates. In the

459   Anthropocene, there seems a decoupling of species macroevolutionary range histories from how

460   species ranges are changing today.

461   Functional traits explained status. Squamate species with larger clutches—meaning those

462   with higher reproductive potential—were often introduced. This result is consistent with theory on

463   introduction establishment and vulnerability to stochastic events (Mahoney et al. 2015, Allen et al.

464   2017). Unexpectedly, the reverse was not found. Extinction-prone species did not have smaller

465   clutch size. Viviparous species were neither less-prone to extinction nor more likely to be

466   introduced. The effect of clutch size on introductions is likely accentuated by the pet and wildlife

467   trade (Li et al. 2023). Pet breeders focus on species who reproduce more, and pet introductions are

468   a major invasion pathway for squamates (Perella & Behm 2020; Stringham & Lockwood 2018).

469   Introduced squamates were more herbivorous and omnivorous than extinction prone squamates,

470   which were small and carnivores (Fig. 3B). The positive association between non-carnivores and

471   introduced status is congruent with a global study on reptiles that found herbivores most likely to

472 establish introduced populations (Mahoney et al. 2015), theoretical work that indicates diet

473 generalism predicts invasion success (e.g., Romanuk et al. 2009), and studies of other taxa that find

474 that species with range expansions often have generalist diets (e.g., Pacifici et al. 2020). For

475 extinction-prone species, however, previous work has found that it is the large, herbivorous

476 vertebrates most at risk of extinction, and for reptiles specifically it is the large, herbivorous turtles

477 most at risk (Mahoney et al. 2015, Tingley et al. 2016, Atwood et al. 2020, Senior et al. 2021).

478 Thus, there is variation in the extinction-size relationship across vertebrate clades. For squamates,

479 those of small body size may be particularly sensitive to temperature shifts (Herczeg et al. 2007)

480 making them vulnerable to human-caused microhabitat changes caused by land development (Jesse

481 et al. 2018). Due to squamate invasion pathways, it is unsurprising that body size did not affect

482 introduced status. Large squamates are often introduced as pets and smaller squamates introduced

483 via the live plant trade (Powell et al. 2011). However, there is also likely variation in the

484 relationship between squamate body size and introduction across clades (e.g., Latella et al. 2011).

485 More work is needed to tease apart how specific ecological traits of different clades interact with

486 specific invasion pathways and extinction drivers.

487

488 Opposite ends of the same trait continua

489   The trait continua that explained both introduced and extinction-prone status all exhibited

490 an opposite response (Fig 3B). While human footprint in native ranges increased both introduced

491 and extinction-prone status, no geographic, evolutionary, or ecological trait explained statuses

492 similarly. Two traits (clutch size, body size) explained only one of the statuses. Eight out of the 13

493 traits we tested (ca. 60%) exhibited opposite responses that were either significant (herbivorus diet,

494 omnivorous diet, range shape, range area) or weak (body size, number of ports, genus age,

495 viviparity). Other studies also report opposite effect sizes for 50-73% of species-level predictors in

496   animal taxa (Jetschke & Strayer 2008, Blackburn & Jetschke 2009, Tingley et al. 2016). The

497   support for the opposite ends hypothesis seems to find even stronger support in plant studies

498   (Bradshaw et al. 2008, Pandit et al. 2011), although due to their different methodology, the strength

499   of support for the hypothesis is difficult to compare among studies. We suggest a standardized

500   metanalysis on existing studies to test if introduced and extinction-prone species do generally fall

501   at opposite ends of the same trait continua. For Western Hemisphere squamates, there were strong

502   positive associations of status with insularity and human footprint (Fig 3C). Therefore,

503   dissimilarities in species characteristics alone do not provide a full understanding of what makes a

504   species introduced or extinct. A tiered model is needed, in which the level of human impact in the

505   native range of a species determines the likelihood of distributional change, while its ecological

506   and geographic traits determine if the species will expand or contract.

507

508   <u>Implications for insular biodiversity</u>

509   Islands have always served as important steppingstones for overwater dispersal and

510   locations from which many colonizer species originated (e.g., Harbaugh et al. 2009). However,

511   colonization and extinction rates greatly exceed historic background rates of species loss and gain.

512   For instance, in Hawaii, the colonization rate before human settlement has been estimated at 0.03

513   species per 1000 years, increasing to 20 species per 1000 years with the arrival of Polynesians and

514   20000 species per 1000 years over the last two centuries (Ricciardi 2007). While oceanic islands

515   are generally more susceptible to exotic invasion than mainland regions (Dawson et al. 2017), the

516   level of colonization pressure on Hawaii in the last centuries is likely an extreme example.

517   The current rate of species introductions currently surpasses the rate of species extinctions

518   (Ellis et al. 2012). In our dataset, only eight of 483 extinction-prone species were already

519   considered extinct, while a total of 21% of species (483 out of 2268) were threatened with

520   extinction based on IUCN status. This threat level approximates results for all vertebrates, of which

521   18% are at risk of extinction (Atwood et al. 2020) and 32% of terrestrial vertebrates experience

522   range reduction or population decline (also including low concern species) (Ceballos et al. 2017).

523   The discrepancy between extinct and threatened species numbers indicates the existence of an

524   extinction debt: the surplus of species that will go extinct in the foreseeable future, but still

525   contributes to the species richness we see today.

526   The swift influx of colonizers and prospective loss of endemic species leads to significant

527   taxonomic and functional homogenization especially within island biota (Longman et al. 2018).

528   This threatens biodiversity and ecosystem functioning on a small scale, but also poses a threat to

529   global biodiversity because of the profound risk to lose a large portion of diversity on earth. To

530   mitigate island homogenization, screening, biosecurity measures, and targeted protection policies

531   must be better implemented on islands.

532

533   **Acknowledgements**

534

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Appendix

Table S1 list of references used to estimate the introduction status of Western Hemisphere squamates.

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A)

B)

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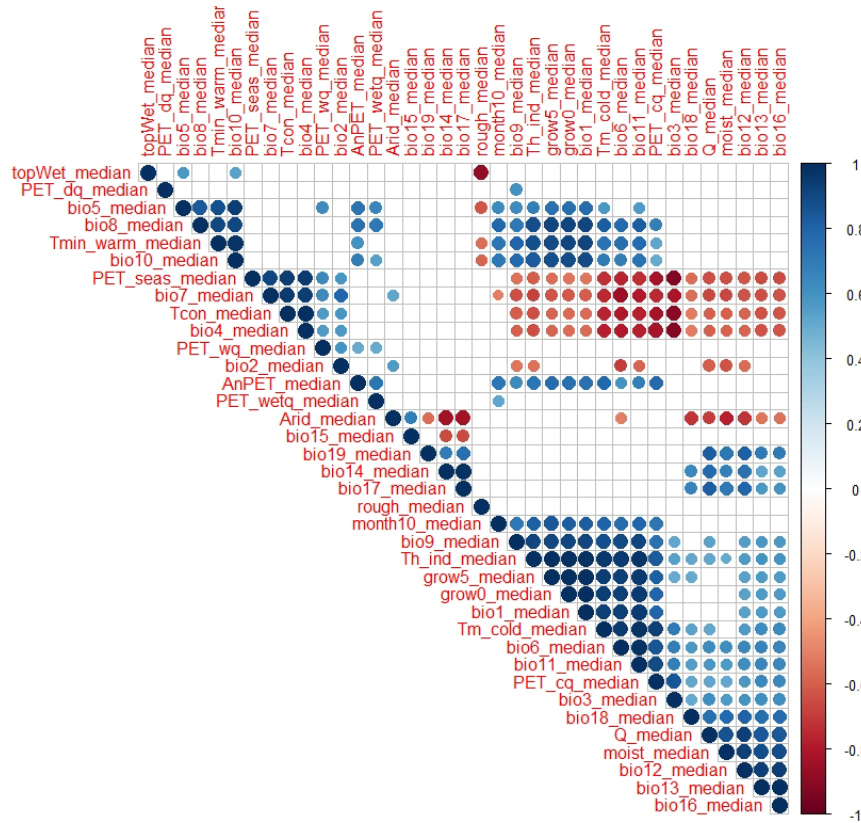
Figure S1. Biplot and correlation matrix including all 37 climatic variables from Woldclim (Fick et al., 2017) and ENVIREM (Title & Bemmels, 2018) databases, which were included a scaled Principal Component Analysis (PCA). From this PCA, two environmental PC axes were derived and included in further analysis. A) Biplot of axis 1 (PC1) and axis 2 (PC2) of a PCAthat shows the variation among the median values of 37 climatic variables in 3061 species ranges. 1 point is 1 species range. PC1 aligns with variables indicating the level of seasonality within a species range (e.g., temperature seasonality; continentality and temperature range, negatively correlated to temperature in the coldest month). PC2 aligns with variables associated with elevational differences (e.g., terrain roughness index; SAGA-GIS topographic wetness index). We inverted both axes compared to the rotation depicted here. B) Correlation matrix of 37 WorldClim and ENVIREM variables for which the median per species range has been calculated. The variables are ordered to maximize congruence. Correlation coefficients > -0.5 and < 0.5 were excluded from this figure for clarity. Dot size indicates the strength of the correlations; the larger the dot, the closer the correlation coefficient is to 1 or –1. Blue dots indicate a positive correlation and red dots indicate a negative correlation among variables, and thus a parallel or opposite direction of the arrows in figure S1A, respectively.
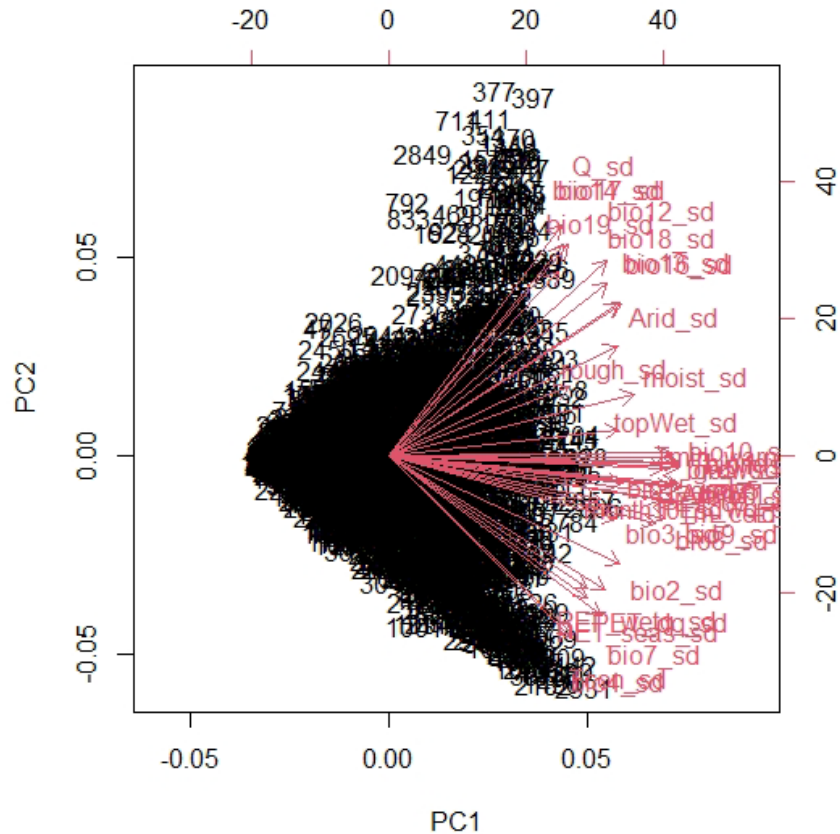
Figure S2. Biplot of WorldClim and ENVIREM climatic variables included in the climatic niche differentiation variable. The standard deviations of 37 climatic variables within 3056 species ranges were included in a principal component analysis (PCA). 1 point is 1 species range. PC1 aligns with all climatic variables, explaining a total of 63% of the overall variation. This means that if a standard deviation of for instance a temperature-based variable is high in a species range (i.e., a species experiences a variety of temperatures), also the standard deviations of other climatic variables increase in the same direction. And when the climatic standard deviations within a species range are high, the PC1 value for that species is also high. As it is expected that larger species ranges have more variable climates, PC1 was regressed against range size, taking the residuals of that relationship (r = 0.65, t_{3054} = 47.45, P < 0.001) as value for disproportional climatic niche differentiation/uniformity.
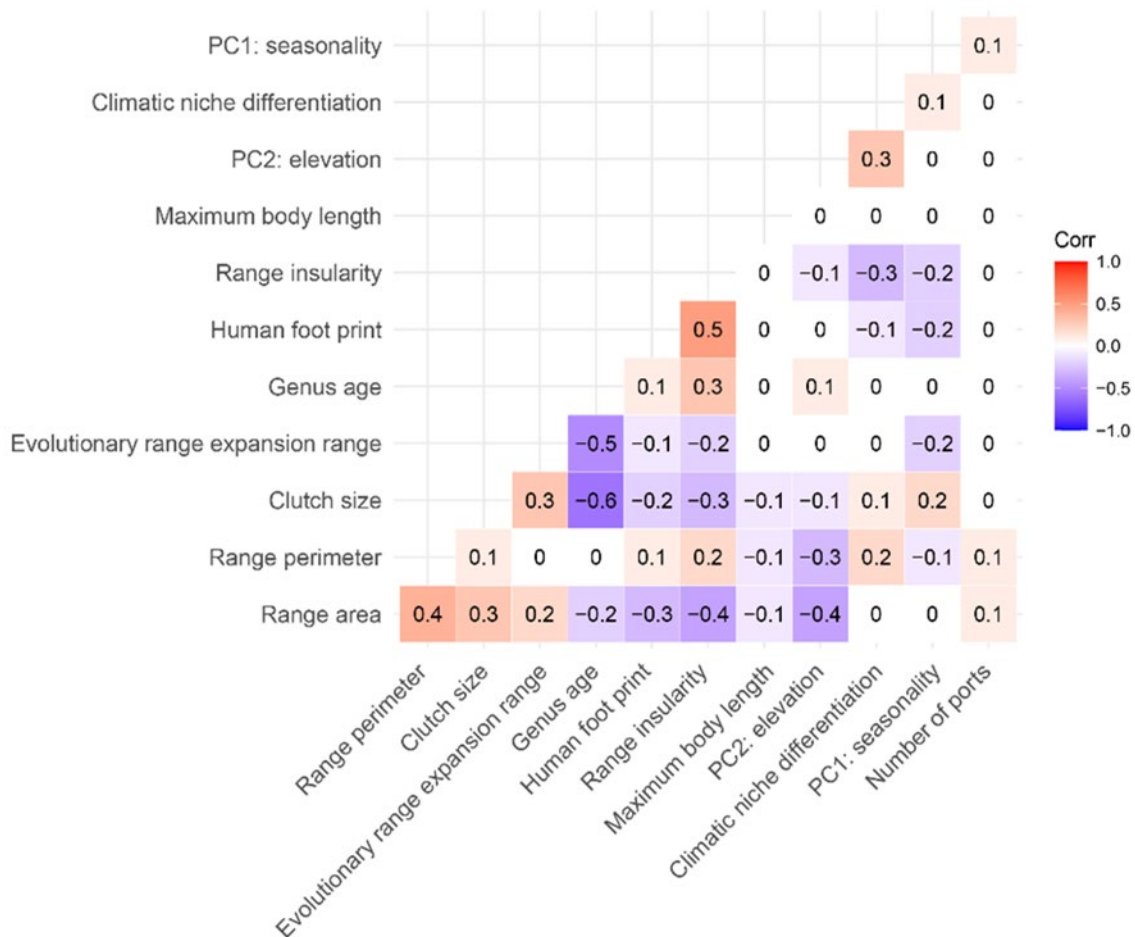
Figure S3. Correlations among predictor variables that were included in phylogenetic generalized linear models. Correlation matrix including all predictor variables. The brighter the color, the stronger the correlation between variables (i.e., closer to 1 or –1). Blue blocks indicate a negative relationship and red blocks indicate a positive relationship. The relatively low correlation coefficients among predictor variables indicate that there are no issues with collinear relationships that bias our model outputs (also indicated by a relatively low Variance Inflation Factor of <3, see main text)

Table S2 Phylogenetic signal of predictor variables. Phylogenetic signal of discrete and continuous predictor variables. Phylogenetic signal is defined as Lamda (λ), ranging between 0 and 1, the higher the value, the stronger the signal ("fitContinuous" and "fitDiscrete" functions in *geiger* R package). We expected phylogenetic signal for some variables: Clutch size, maximum body length, diet type, and reproductive mode were phylogenetically imputed (see Rapacciuolo et al. 2019 for details). Furthermore, two variables were genus-specific variables (stem age, evolutionary range expansion range), hence inherently phylogenetically clustered.

Variable type	Predictor variable	Phylogenetic signal (λ)
Geographic	Range size	0.71816
Geographic	Range shape	0.59037
Geographic	Insularity	0.90954
Ecological	PC1: seasonality	0.81980
Ecological	PC2: elevation	0.70111
Ecological	Climatic niche differentiation	0.59214
Ecological	Diet type	0.94790
Ecological	Maximum body length	0.51557
Ecological	Clutch size	0.94050
Ecological	Reproductive mode	0.98400
Evolutionary	Genus age	1.00000
Evolutionary	Evolutionary range expansion rate	1.00000
Anthropogenic	Human footprint	0.72552
Anthropogenic	Number of ports	0.00007