Ecological specialization, rather than the island rule, explains morphological diversification in an ancient radiation of geckos

Héctor Tejero-Cicuéndez[1]*#, Marc Simó-Riudalbas[1]*, Iris Menéndez[2,3], Salvador Carranza[1]

[1] Institute of Evolutionary Biology (CSIC-Universitat Pompeu Fabra), Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain.

[2] Departamento de Geodinámica, Estratigrafía y Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, C/ José Antonio Novais 12, Madrid, 28040, Spain.

[3] Departamento de Cambio Medioambiental, Instituto de Geociencias (UCM, CSIC), C/Severo Ochoa 7, Madrid, 28040, Spain.

* These authors contributed equally.

Correspondence to be sent to: Institute of Evolutionary Biology (CSIC-Universitat Pompeu Fabra), Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain.
E-mail: hector.tejero@ibe.upf-csic.es

ABSTRACT

Island colonists are often assumed to experience higher levels of phenotypic diversification than their continental sister taxa. However, empirical evidence shows that exceptions to the familiar "island rule" do exist. In this study, we tested this rule using a nearly complete sampled mainland-island system, the genus *Pristurus*, a group of sphaerodactylid geckos mainly distributed across continental Arabia and Africa and the Socotra Archipelago. We used a recently published phylogeny and an extensive dataset of morphological measures to explore whether island and mainland taxa share the same morphospace or if they present different dynamics of phenotypic evolution. Moreover, we used habitat data to examine if ecological specialization is correlated with morphological change, reconstructing the ancestral habitat states across the phylogeny to compare the level of phenotypic disparity and trait evolution between habitats. We found that insular species do not present higher levels or rates of morphological diversification than continental groups. Instead, habitat specialization provides insight into the evolution of body size and shape in *Pristurus*. In particular, the adaptation to exploit ground habitats seems to have been the main driver of morphological change, producing the highest levels of disparity and evolutionary rates. Additionally, arboreal species show very constrained body size and head proportions, suggesting morphological convergence driven by habitat specialization. Our results reveal a determinant role of ecological mechanisms in morphological evolution and corroborate the complexity of ecomorphological dynamics in mainland-island systems.

Keywords
Body size; disparity; evolutionary rate; island colonization; morphospace; *Pristurus* geckos.

INTRODUCTION

The life history and population biology of mainland and insular taxa of a specific evolutionary radiation are fundamentally distinct (Foster 1964; Baeckens and Van Damme 2020). In the mainland, communities are often assumed to be complex and composed of many species that share a long history of coevolution (Losos 2009). In such a scenario, most of the ecological niches will be filled, and high levels of interspecific competition are expected (Losos and Ricklefs 2009). These factors, together with higher predation pressures, will tend to limit niche expansion and, consequently, morphological diversification (Yoder et al. 2010). In contrast, insular groups are usually exposed to higher levels of ecological opportunity and thus, they can occupy the new or relatively unexploited adaptive landscapes that islands provide (Schluter 2000; Harmon et al. 2008). As a result, island species may experience increased rates of phenotypic diversification and higher levels of morphological disparity compared to mainland taxa (Whittaker et al. 2008). However, empirical evidence outlines a more complex scenario in which island colonists might not necessarily experience great levels of evolutionary divergence (Rundell and Price 2009), depending on multiple *extrinsic* factors (mostly modulated by the geography or geology of the island), as well as *intrinsic* factors (i.e., the biological characteristics of the group concerned) (Losos 2009, 2010). Thus, ecological specialization is expected to be more pronounced when island colonization results in an expansion into novel ecological contexts, and such specialization might carry morphological changes depending on species and system-specific factors (Schluter 2000; Losos and Ricklefs 2009).

Whether ecological specialization follows island colonization or not, the study of habitat occupancy is essential to understand the evolution of associated traits and the structuring of ecological communities (Mahler et al. 2010). In particular, specialization in substrate use can promote morphological diversity through deterministic body size evolution and diversification (Reynolds et al. 2016). Moreover, microhabitat use can be strongly correlated with convergent phenotypic evolution resulting in recurrent ecomorphs beyond the effect of history and clade membership (Moen et al. 2016).

Arid regions, generally considered relatively depauperate in terms of animal diversity, have been successfully inhabited by some vertebrate groups and harbor especially high levels of reptile diversity. Among reptiles, geckos are particularly prominent due to their outstanding diversity in ecological features, exhibiting a wide variety of morphological and behavioral adaptations (Gamble et al. 2015). Afro-Arabian geckos have been recently prominent in studies of the role of arid biomes in generating biodiversity (Metallinou et al. 2012, 2015; Šmíd et al. 2015, 2017; Garcia-Porta et al. 2017; Machado et al. 2021). However, the outcomes of morphological diversification in these animals have only been properly investigated within the genus *Hemidactylus,* which is the best-studied Arabian reptile group with well-resolved taxonomy and reliably reconstructed biogeographic history (Carranza and Arnold 2012; Gómez-Díaz et al. 2012; Šmíd et al. 2013a, 2013b, 2015, 2017, 2020; Vasconcelos and Carranza 2014). In particular, two recent studies including continental and insular taxa from the Socotra Archipelago proved that the genus *Hemidactylus* conforms to the "island rule" at least regarding body size evolution (Garcia-Porta et al. 2016a, 2016b). In contrast, the geckos of the genus *Pristurus*, which have also colonized and diversified within the same archipelago, seem to show lower rates of body size diversification than other insular genera, but also compared to their continental relatives (Garcia-Porta et al. 2016a). Despite these preliminary results, a more nuanced analysis of the morphological evolution in *Pristurus*, including undescribed diversity, morphological and ecological data, is still lacking. Interestingly, besides having colonized the Socotra Archipelago, *Pristurus* geckos occupy a variety of habitats, including rocky and sandy surfaces, gravel plains, and trees (Arnold 2009; Badiane et al. 2014).

Here we use a recently inferred phylogenetic assessment of Afro-Arabian reptiles including undescribed diversity, together with an extensive morphological sampling and detailed ecological information, to explore the morphological evolution in *Pristurus* geckos. Specifically, we test alternative scenarios of body size and shape evolution in this genus, to determine the role of island colonization and ecological specialization in generating the morphological diversity observed. The independent diversification of both insular and continental taxa, the ecological and behavioral diversity, and the unique phenotypic dataset compiled in this study, make this group of geckos an exceptional system to investigate keystone dynamics in evolutionary biology such as the "island rule" and ecological adaptation, and their impact on morphological evolution.

MATERIALS AND METHODS

Phylogenetic and ecological data

We used a recently published phylogenetic tree of Afro-Arabian squamates (Tejero-Cicuéndez et al. 2021). This tree contains all the species of *Pristurus* for which there exists genetic data, including some species currently in the process of being described, resulting in a total of 30 species. We extracted the *Pristurus* clade from the squamate tree, both for the consensus and for 1,000 trees randomly selected from the posterior distribution generated in the cited study. Using a sample of posterior trees allowed us to take into account the phylogenetic and temporal uncertainty in the subsequent analyses.

Each species was defined as insular (present in the Socotra archipelago) or continental (present in mainland Africa or Arabia). For habitat specialization, each species was categorized based on substrate preferences into one of three groups: ground-dwelling, rock climber, or arboreal (Arnold 1993, 2009). Additionally, the ground-dwelling species were divided into "soft-ground" (sandy surfaces) and "hard-ground" (gravel plains) categories to further characterize the morphological adaptations to each type of ground habitat. Nevertheless, the disparity dynamics and rates of trait evolution were estimated with the original categorizations (mainland - island and the three habitat states) which, due to the limited number of species, were more appropriate for the analyses.

Ancestral reconstructions

We studied island colonization and habitat specialization through time by reconstructing ancestral states across the phylogeny. First, we fit several models of character evolution across the phylogeny in order to select the best-fit model for insularity and for habitat evolution. With such a purpose, we used the function *fitDiscrete* from the R package geiger v2.0 (Pennell et al. 2014; R Core Team 2019). We fit three models: an equal-rates model (ER), a symmetrical model (SYM), and an all-rates-different model (ARD). We selected the best-fit model in each case based on the Akaike information criterion, correcting for small sample size (AICc; Akaike 1973). We then used the function *make.simmap* from the R package phytools (Revell 2012), which simulates plausible stochastic character histories after fitting a continuous-time reversible Markov model for the evolution of the character states assigned to the tips of the tree. We run 1,000 simulations with the previously selected model of character evolution (ER model for both traits). Additionally, we randomly selected 100 trees from the posterior distribution, and we ran 100 stochastic character histories on each of them for both traits (insularity and habitat).

Phenotypic data

For the 30 species included in the phylogenetic tree, a total of 697 specimens were examined and measured, with a minimum of one, a maximum of 56, and a mean of 23 specimens per species (Table S1). All vouchers were obtained from the following collections: Institute of Evolutionary Biology (CSIC-UPF), Barcelona, Spain (IBE), Natural History Museum, London, UK (BM), Museo Civico di Storia Naturale, Carmagnola, Turin, Italy (MCCI), Università di Firenze, Museo Zoologico "La Specola", Firenze, Italy (MZUF), Oman Natural History Museum (ONHM), Laboratoire de Biogéographie et Écologie des Vertébrés de l'École Pratique des Hautes Etudes, Montpellier, France (BEV), and National Museum Prague, Czech Republic (NMP). The following measurements were taken by the same person (MSR) using a digital caliper with accuracy to the nearest 0.1 mm: snout-vent length (SVL; distance from the tip of the snout to the cloaca), trunk length (TrL; distance between the fore and hind limb insertion points), head length (HL; taken axially from tip of the snout to the anterior ear border), head width (HW; taken at anterior ear border), head height (HH; taken laterally at anterior ear border), humerus length (Lhu; from elbow to the insertion of the forelimb), ulna length (Lun; from wrist to elbow), femur length (Lfe; from knee to the insertion of the hindlimb) and tibia length (Ltb; from ankle to knee). Tail length was not measured because most of the specimens had regenerated tails or had lost it.

Morphological differentiation

As body size and shape evolution might be affected by island colonization and/or ecological specialization, we characterized the morphospace occupied by each species to compare the effect of each trait on the morphological breadth and differentiation. This allowed us to investigate whether island colonists are morphologically distinct from their mainland relatives (the island rule) and likewise whether the differential habitat use is reflected in species morphology. For each species, the mean of each morphological variable was calculated and $\log_{10}$-transformed in order to improve normality and homoscedasticity prior to subsequent analyses. We then performed a phylogenetic regression of each trait on snout-vent length (SVL) to remove the effect of the body size on the other variables. The residuals of these regressions were used to implement a phylogenetically controlled principal component analysis (pPCA) using the functions *phyl.resid* and *phyl.pca* from the R package phytools with the method set to 'lambda' (Revell 2012). We used the principal components representing 75% of the cumulative proportion of variance as shape variables. Additionally, we performed a principal component analysis (PCA) with the shape data from all the specimens measured, after correcting for body size through regressions on SVL similarly to our processing of the species data. We generated per-species boxplots of size and shape variation with the specimen data. We used the function *phenogram* from the R package phytools (Revell 2012) to map and visualize size and shape variation across the species trees, and we further visualized the 2D shape morphospace. For all these visualizations, we categorized the species according to insularity (mainland or island) and to habitat use (ground, rock or tree) separately, to have a detailed perspective of the extent of the morphospace occupied by each category.

Exploring differences in phenotypic disparities

Since one of the main possible outcomes of island colonization and/or ecological specialization is the increase in phenotypic disparity, we tested this assumption following previous research on other geckos (Garcia-Porta et al. 2016b) and defining disparity as the average squared Euclidean distance between all pairs of species in a group for a given continuous variable (Harmon et al. 2008), in our case body size (SVL) and two variables of shape (pPC1 and pPC2). We did this for both discrete traits (insularity and habitat use), with the aim of testing whether disparity is higher in island species than in the mainland, and, in the

light of our results of morphological differentiation, whether ground-dwelling species are significantly more disparate than species in the other habitats. We first calculated the observed disparity ratios (island/continent and ground/no-ground) for each morphological variable, using the function *disparity* from the R package geiger (Pennell et al. 2014). In the case of higher disparity in the island or in ground species (disparity ratio island/mainland or ground/no-ground higher than 1), we then compared the observed ratios with a null distribution of disparity ratios obtained from 10,000 simulations of the evolution of a continuous character according to a Brownian motion model across the phylogeny. These simulations were performed by applying the function *sim.char* after estimating the empirical rate parameter for body size and shape from the best-fit model (Brownian motion) with the function *fitContinuous*, both from the package geiger (Pennell et al. 2014). This approach allowed us to test, in the case of an observed higher disparity in island or ground species, whether this is a significant increase considering the rate of evolution of the character, or rather this is not evidence of effectively increased disparity.

Differences in tempos of phenotypic diversification

In order to test the effect of insularity and ecological specialization in the tempo of phenotypic evolution, we fitted different models of character evolution across the phylogeny in which the evolutionary rates of body size and shape might or might not differ between categories (i.e., between island and mainland, and between ground, rock and tree habitats). For body size, we used the R package OUwie (Beaulieu and O'Meara 2021) to fit three alternative models: BM1 (Brownian motion single rate, i.e., assuming one single rate regime for all lineages in the phylogeny), OU1 (Ornstein-Uhlenbeck single-rate value with a phenotypic optimum and a selective pressure towards it), and BMS (Brownian motion multi-rate model, with different rate values for each of the regimes specified, i.e., island different from mainland lineages, and differences between habitats). Similarly, we studied the rates of phenotypic evolution for body shape, but in this case we fitted multivariate models including the first two principal components resulting from the phylogenetic PCA (pPC1 and pPC2; 77% of the variance, see Results section). We used the package mvMorph (Clavel et al. 2015) to fit four alternative models: BM1, OU1, and BMM (analogous to BMS in the OUwie package), and OUM (multi-rate Ornstein-Uhlenbeck model). We fitted these models in the 1,000 stochastic character maps generated for the consensus tree, and also in the 100 character maps on each of the 100 posterior trees used to reconstruct ancestral states (see above Ancestral reconstructions). We then selected the best-fit models based on the AICc distributions and means, and we extracted the distributions of rate values estimated for each regime (island, mainland, ground, rock and tree) in the multi-rate models, to unravel the effect of each trait in morphological rates. All the visualizations of the disparity and phenotypic rate analyses were built with the R packages ggplot2 (Wickham 2011), patchwork (Pedersen 2020), and cowplot (Wilke 2020).
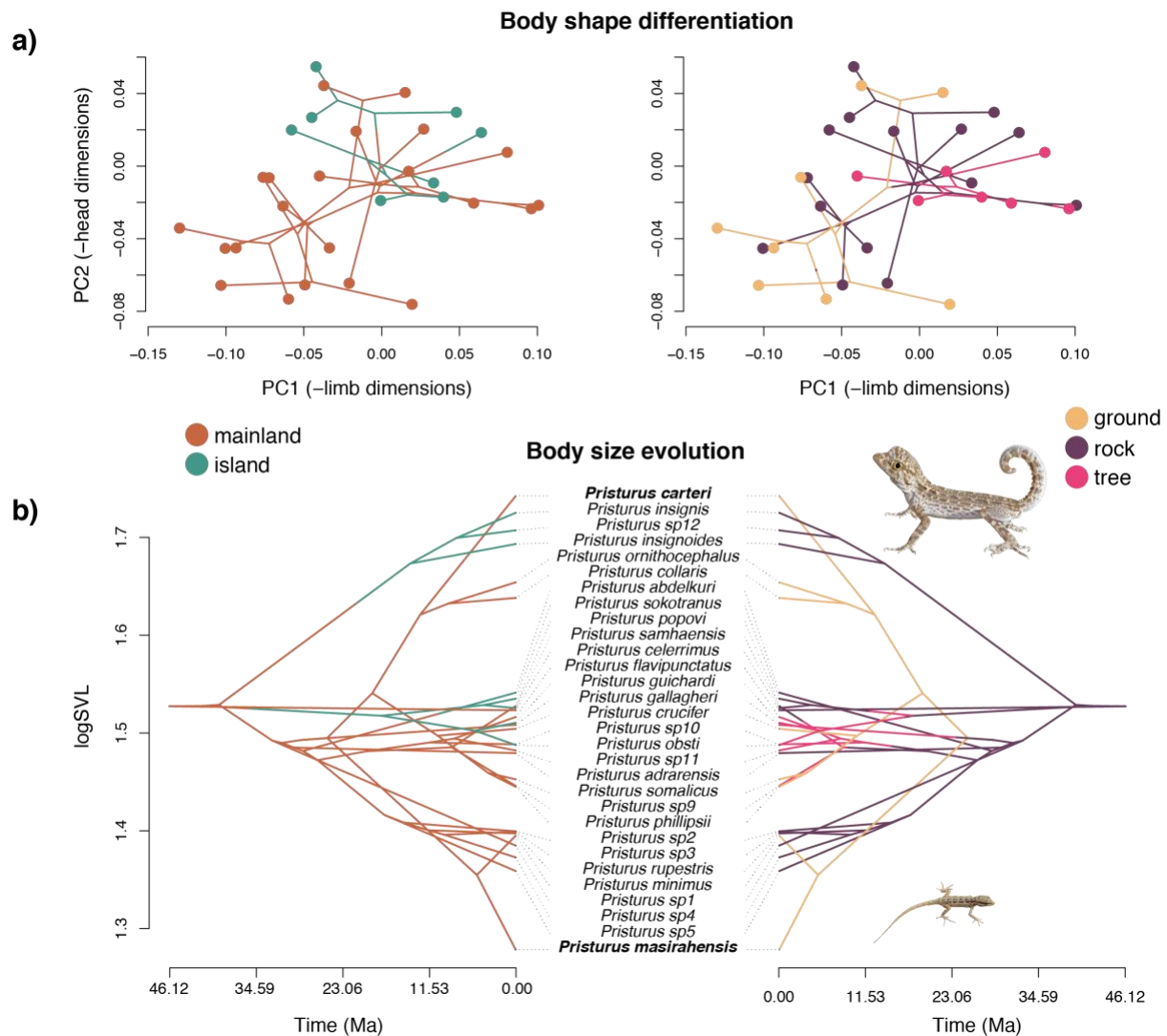
RESULTS

Ancestral reconstructions and morphological variation

The ancestral reconstructions following an equal-rates model (ER), with the probabilities of each state in ancestral nodes (island and mainland; ground, rock, and tree) can be found in the Supplementary Material (Fig. S1). The ecological reconstruction shows rocky habitats as the ancestral state in *Pristurus*, with several transitions to arboreal habitats and one colonization of the ground in the ancestor of the clade known as "Spatalura group" (Arnold 1993, 2009; Fig. S1B). One of the subclades of this group later colonized more compact, harder

substrates, shown in our more detailed analysis separating soft- and hard-ground species (Fig. S1).

The pPCA analysis of body shape resulted in two first components explaining 77% of the total variance: pPC1 (61% of the variance) mainly representing limb dimensions (variables Lhu, Lun, Lfe, Ltb), and pPC2 (16% of the variance) mostly representing head proportions (variables HL, HW, HH) (Fig. 1a; Fig. S2 and Table S2; see Fig. S3 for body size and shape differentiation using the specimen data and PCA). The morphospace occupied by mainland species is notably larger than that occupied by island species, and they overlap almost completely (Fig. 1a left, Fig. S2). When visualizing the phylomorphospace along with habitat categories, we observe a wide portion occupied by the ground-dwelling species, especially in pPC2 (head dimensions) (Fig. 1a right). These eight species of the "Spatalura group" essentially occupy almost as much of the morphospace as all the rest of the species together, with morphologies specialized to arboreal habits localized in a narrow area, especially for head proportions (Fig. 1a right). We found a similar pattern for body size. Body size variability of island species is completely contained in the range occupied by mainland species (Fig. 1b left). On the contrary, ground-dwelling species show a size variability higher than all the species from other habitats together, being the largest and the smallest species of *Pristurus* specialized to ground habitats (Fig. 1b right). As with head proportions, arboreal species have apparently constrained body sizes, being restricted to specific intermediate values within the genus' size range.

When separating ground species into hard- and soft-ground habitats, we observed a clear morphological differentiation, especially in body size. Hard-ground species seem to be highly specialized, with some of the largest body sizes of the genus, long limbs and large heads (Fig. S4).

Figure 1. Morphological variability in *Pristurus*, with insight from insularity (left) and habitat use (right). a) Morphospace with phylogenetic relationship between the species, showing body shape differentiation. b) Traitgram showing body size (SVL) through time on the summary phylogenetic tree of *Pristurus*, mapped by the discrete categories of land occupancy (left) and by ecological specialization (right). Photos (proportional to species' SVL): *Pristurus carteri* (top) and *P. masirahensis* (bottom), the largest and smallest species of the genus, respectively.

Phenotypic disparity

We found that the morphological disparity in the island is lower than in the mainland for the three variables, with disparity ratios island/mainland below 1 (SVL: 0.88; pPC1: 0.52; pPC2: 0.53). When comparing disparity between ground and no-ground habitats, we found a higher observed disparity in ground for body size (SVL) and head proportions (pPC2), with disparity ratios ground/no-ground of 2.25 for SVL, 0.86 for pPC1, and 2.47 for pPC2. Furthermore, both for size and head proportions, the increased disparity in ground habitats was significant compared with the null distribution of simulated disparity ratios (p_{size} = 0.03; p_{head} = 0.01; Fig. 2).
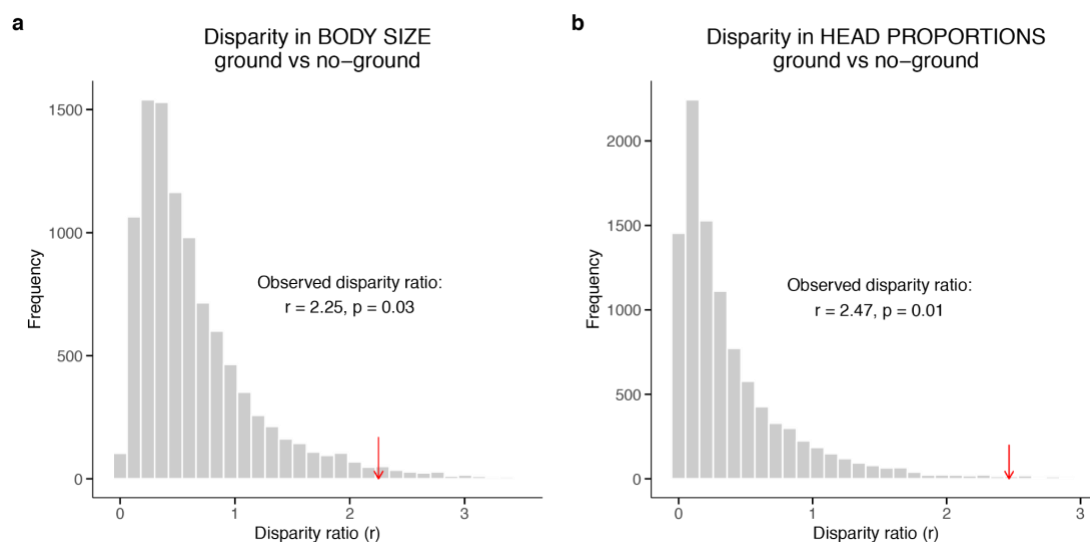
Figure 2. Observed (red arrows) and simulated (gray bars) ratios of phenotypic disparity between ground versus no-ground habitats. a) Body size disparity ratios. b) Head proportions (pPC2) disparity ratios.

Rates of morphological evolution

For body size, a multi-rate Brownian motion model (BMS) was the best fit both for insularity and for ecological specialization (lowest AICc; Fig. 3a), suggesting differences in the rate of morphological evolution across discrete categories (i.e., island vs. mainland, and different habitats). For body shape, however, we did not find evidence for differences in evolutionary rates, being the single-rate Brownian motion model (BM1) the best fit both for limb (pPC1) and head (pPC2) dimensions, although the overlap across all models was considerable (Fig. 3b).
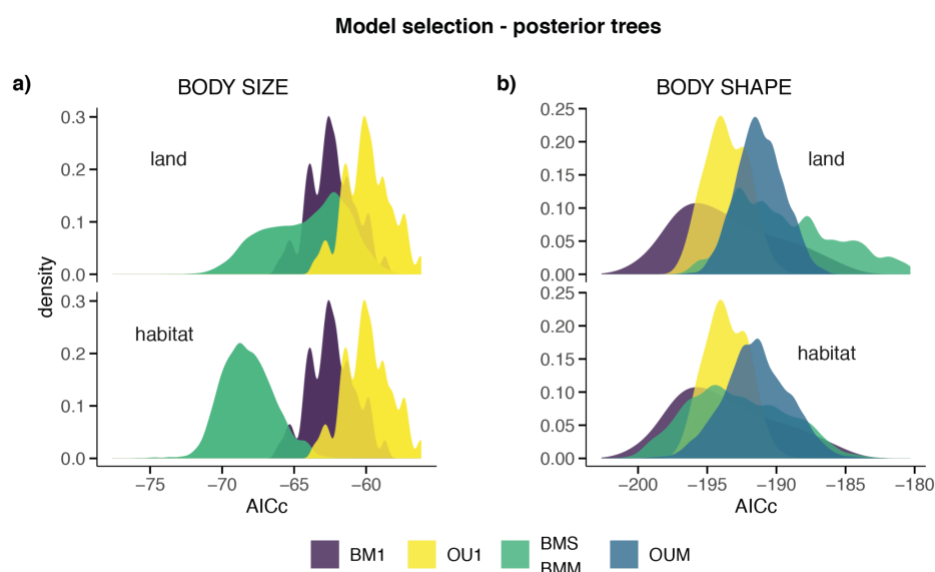

Figure 3. AICc distributions from the model fitting for a) body size and b) shape evolution of the genus *Pristurus*. These results correspond to model fitting on 100 stochastic character maps (insularity in the top panels and habitat in the bottom) on 100 trees from the phylogenetic posterior distribution. BM1: Brownian motion single rate. OU1: Ornstein-Uhlenbeck single rate. BMS (OUwie) / BMM (mvMorph): Brownian motion multi-rate. OUM: Ornstein-Uhlenbeck multi-rate. For body size, the best supported model is a Brownian motion with rate

8

heterogeneity across categories. For body shape, a single-rate Brownian motion model was the best-fit, although there is an extensive overlap across all models.

We extracted the rates of body size evolution from the Brownian motion multi-rate models, and we found that island species present lower rates than mainland species (Fig. 4a top). For ecological specialization, we found increased rates of body size evolution in the ground-dwelling species relative to the other habitats, with arboreal habitats showing the lowest rates (Fig. 4a bottom). We also extracted per-category rates of body shape evolution according to the BMM model in mvMorph, even though the multi-rate models were not the best supported, and we found a similar scenario, in which shape evolution (both for limbs and for head proportions) would be notably faster in ground-dwelling species (Fig. 4b bottom). Results from the analyses performed with the 1,000 stochastic character maps on the consensus tree and with the 100 maps on each of 100 posterior trees lead to the same conclusions, so we show the ones from the posterior trees on the main text. Results from analyses with the consensus tree can be found in the Supplementary Material (Fig. S5).
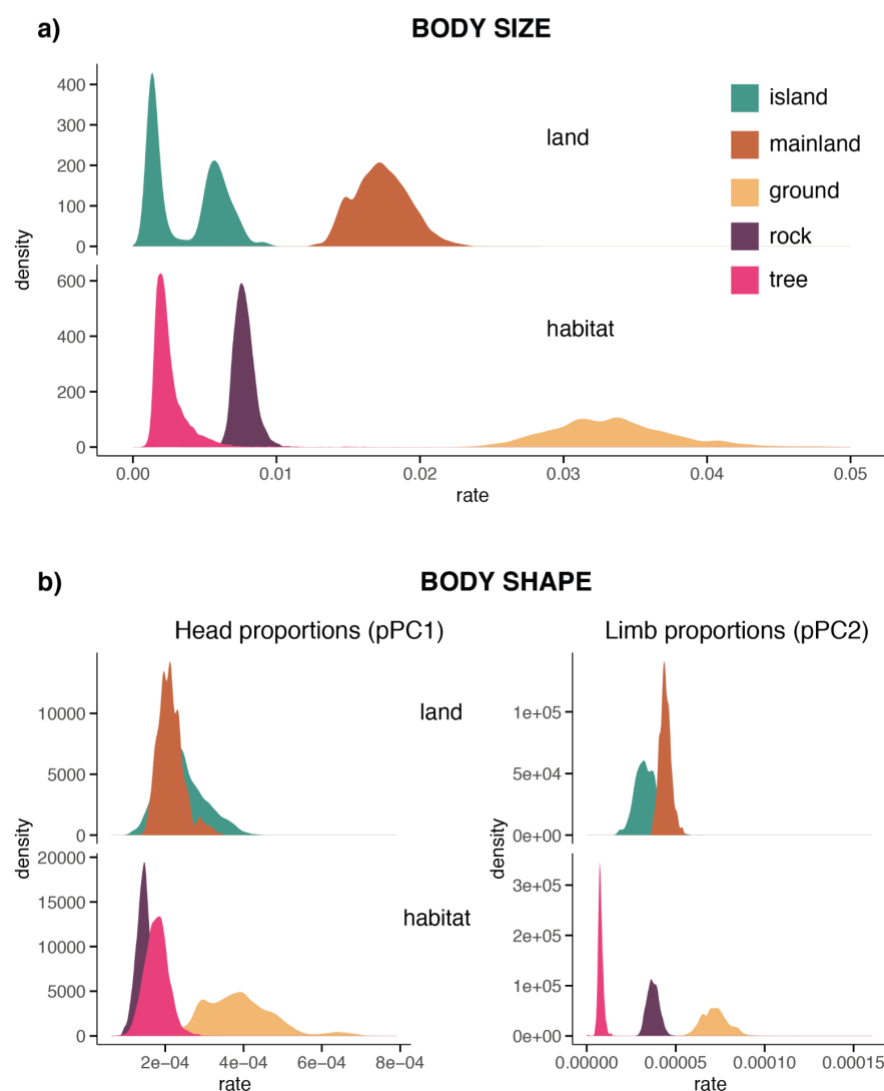
Figure 4. Rates of a) body size and b) body shape evolution in the genus *Pristurus*, extracted from multi-rate Brownian motion models fitted on a total of 10,000 character maps (100 stochastic character maps on 100 posterior trees) of land occupancy (island vs. mainland) and habitat use (ground, rock, and tree).

DISCUSSION

The present study represents the first comprehensive comparative work on the genus *Pristurus*, including undescribed diversity and extensive morphological (size and shape) and ecological data. We tested the relative roles of island colonization and ecological specialization in the evolution of the phenotypic diversity observed within the genus. We did not find evidence for the validity of the 'island rule' in this radiation of geckos, since island species do not present a notably different morphology, higher disparity, nor increased rates of morphological evolution, relative to species in the continent. On the contrary, ecological specialization emerges as a determinant factor in generating morphological diversity, with the colonization of ground habitats as the main driver of phenotypic divergence. Our results reveal a complex scenario in which different morphological traits interact with ecological characteristics of the species in different ways, suggesting a differential relevance of body size and shape proportions for the adaptation to specific habitats.

The tendency of island taxa to diverge in morphology compared to their continental relatives is a general pattern in terrestrial vertebrates, especially concerning body size (Lomolino 2005; Benítez-López et al. 2021). In fact, recent studies on Afro-Arabian geckos colonizing the Socotra Archipelago found support for this 'island effect', particularly in the genus *Hemidactylus* (Garcia-Porta et al. 2016a, 2016b). Nevertheless, preliminary results on *Pristurus* geckos failed to find this phenomenon in this genus (Garcia-Porta et al. 2016a). Here we corroborated and extended those preliminary results, incorporating the most complete phylogenetic and morphological sampling within *Pristurus* up to date. We did not find the predicted effects of island colonization in phenotypic diversification. Even though one of the insular clades (the one including *P. insignis*, *P. insignoides* and *P.* sp. 12) has effectively undergone an increase in body size, one of the mainland species (*P. carteri*) is the largest of the genus (Fig. 1b). There is also no apparent divergence in body shape, with limb and head proportions of island species being similar to mainland species (Fig. 1a). Moreover, neither size nor shape disparities observed in the Socotra Archipelago are higher than those of the mainland species. Finally, our results failed to find another expected outcome of island colonization, as is the increase in rates of phenotypic evolution. Species in the mainland show higher rates of body size evolution (Fig. 4a), and our evolutionary model fitting showed no support for differences in shape rates between mainland and island species (BM1 was the best-fit model; Fig. 3a). When extracting the rate values for shape from the multi-rate Brownian motion model, we found little or no difference between mainland and island taxa (Fig. 4b). The lack of an island effect in *Pristurus*, opposed to other similar diversifications of geckos, may indicate the existence of different ecological contexts even in the same physical settings, which would imply different ecological opportunities in the same island (Losos 2010). Namely, some life-history traits, such as being diurnal, may have limited niche expansion in *Pristurus* species in the Socotra Archipelago as a result of ecological interactions with other lizards, while nocturnality may have prevented other geckos such as *Hemidactylus* or *Haemodracon* from suffering that kind of ecological pressure, resulting in a phenotypic divergence of island colonists (Garcia-Porta et al. 2016b; Tamar et al. 2019b). This is consistent with results on global insular vertebrate communities suggesting that the prevalence of the island rule is subjected to system-specific ecological and environmental dynamics (Benítez-López et al. 2021). Furthermore, a recent study on the anole radiation in the Greater Antilles did not find

evidence for an island effect, and instead point to ecological opportunity and key innovations as the drivers of the adaptive radiation (Burress and Muñoz 2021).

Following that reasoning, ecological specialization gives us a much more nuanced insight on *Pristurus* phenotypic evolution. The relationship between habitat use and morphological traits is well recognized in lizards (Goodman et al. 2008; Losos 2009; Higham and Russell 2010). In fact, preceding observations on *Pristurus* geckos suggested that many morphological changes might be functionally associated with shifts in ecology and behavior (Arnold 2009). Our results are consistent with this notion and provide strong evidence that novel ecological opportunities produced high levels of phenotypic disparity associated with increased rates of trait evolution in some forms of *Pristurus*, particularly the species exploiting ground habitats. Even though ground-dwelling species do not show an extremely divergent body shape relative to species inhabiting other habitats (i.e., rocky and arboreal habitats; Fig. 1a), they do comprise the largest and the smallest sizes of the genus (Fig. 1b) and show some extreme values of limb and head proportions (pPC1 and pPC2 respectively; Fig. 1a), as well as they occupy a very large portion of the genus' entire morphospace (Fig. 1a). This extreme variability within ground-dwelling species is reflected in our disparity results. While ground species do not present higher disparity in limb dimensions (pPC1; ratio ground/no-ground < 1), they have more than twice as much disparity as all the rest of the species in body size and head proportions, with these ratios being highly significant compared to the null model generated from simulations of character evolution (Fig. 2). Furthermore, we found increased rates of body size evolution in ground-dwelling species, followed first by rocky and last by arboreal habitats (Fig. 4a). Although rate heterogeneity across habitat categories was not the best-fit model for body shape (Fig. 3b), the rate values extracted from the multi-rate Brownian motion model show a similar pattern, especially for head proportions, with highest rates in ground-dwelling species (Fig. 4b). Taken together, these results point to the existence of a morphological response to the ecological context, especially in body size. This is consistent with the idea that the main driver of morphological divergence, even in an island colonization event, is habitat diversity (Lack 1976; Losos and Parent 2009). If habitat heterogeneity in the Socotra Archipelago is lower than in mainland Africa and Arabia (e.g., no particularly large gravel plains in Socotra), or if the access to those habitats is limited for *Pristurus* geckos in the island and not in the mainland (e.g., due to ecological interactions), phenotypic evolution after island colonization would not be as extreme as expected under the 'island rule' framework. This could imply a tight relationship between morphology and structural habitat, a pattern observed in other Arabian geckos such as *Ptyodactylus* or *Asaccus*, where niche conservatism is associated with a very conserved morphology (Metallinou et al. 2015; Carranza et al. 2016; Simó-Riudalbas et al. 2017, 2018; Tamar et al. 2019a). This would be further supported by the fact that within ground habitats, species show a clear morphological segregation between 'hard' and 'soft' substrates, suggesting a particularly conspicuous specialization to the former (large bodies, long limbs and large heads in the hard-ground species: *P. carteri*, *P. collaris*, *P. ornithocephalus*; Fig. S4). Alternatively, the lack of an island effect might be explained by climatic divergences replacing ecomorphological differentiation, or by a low morphological evolvability (Garcia-Porta et al. 2016a).

Another interesting result is the morphological convergence of arboreal species, especially in body size and head proportions, where they present intermediate values within a very restricted range (Fig. 1). Consistently, we found notably reduced evolutionary rates in body size and head proportions in these species with the multi-rate models (Fig. 4). This might corroborate the idea of adaptive processes leading to a tight relationship between ecological traits and phenotype, since this scenario is expected if a specific habitat constrains the morphology towards optimum values of body size and shape (Moen et al. 2016).

Ultimately, our results provide evidence of the determinant role of habitat specialization in phenotypic evolution. This has important implications for understanding the prevalence of the island rule in the context of differential ecological opportunity and, combined with previous results on other similar systems, shows the complex nature of the relationships between ecological mechanisms and morphology and their reliance on system-specific dynamics. More detailed ecological and morphological data (e.g., dietary habits, geometric morphometrics of head shape) might help for a deeper understanding of the evolutionary dynamics of this and other groups of arid-adapted lizards.

DATA AVAILABILITY STATEMENT
Data and R scripts used for this study will be available in an online public repository.

COMPETING INTERESTS
The authors declare no competing interests.

ACKNOWLEDGEMENTS

REFERENCES

Akaike H. 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov B., Csaki F., editors. Second International Symposium on Information Theory. Budapest (Hungary): Akademia Kiado. p. 267-281.

Arnold E.N. 1993. Historical changes in the ecology and behaviour of semaphore geckos (*Pristurus*, Gekkonidae) and their relatives. Journal of Zoology. 229:353–384.

Arnold E.N. 2009. Relationships, evolution and biogeography of Semaphore geckos, *Pristurus* (Squamata, Sphaerodactylidae) based on morphology. Zootaxa. 21:1–21.

Badiane A., Garcia-Porta J., Červenka J., Kratochvíl L., Sindaco R., Robinson M.D., Morales H., Mazuch T., Price T., Amat F., Shobrak M.Y., Wilms T., Simó-Riudalbas M., Ahmadzadeh F., Papenfuss T.J., Cluchier A., Viglione J., Carranza S. 2014. Phylogenetic relationships of Semaphore geckos (Squamata: Sphaerodactylidae: *Pristurus*) with an assessment of the taxonomy of *Pristurus rupestris*. Zootaxa. 3835:33–58.

Baeckens S., Van Damme R. 2020. The island syndrome. Current Biology. 30:R338–R339.

Beaulieu J.M., O'Meara B. 2021. OUwie: analysis of evolutionary rates in an OU framework. R package, version 2.6.

Benítez-López A., Santini L., Gallego-Zamorano J., Milá B., Walkden P., Huijbregts M.A.J., Tobias J.A. 2021. The island rule explains consistent patterns of body size evolution in terrestrial vertebrates. Nature Ecology and Evolution. 5:768–786.

Burress E.D., Muñoz M.M. 2021. Ecological Opportunity from Innovation, not Islands, Drove the Anole Lizard Adaptive Radiation. Systematic Biology. Advance online publication. https://doi.org/10.1093/sysbio/syab031.

Carranza S., Arnold E.N. 2012. A review of the geckos of the genus *Hemidactylus* (Squamata: Gekkonidae) from Oman based on morphology, mitochondrial and nuclear data, with descriptions of eight new species. Zootaxa. 95:1–95.

Carranza S., Simó-Riudalbas M., Jayasinghe S., Wilms T., Els J. 2016. Microendemicity in the northern Hajar Mountains of Oman and the United Arab Emirates with the description of two new species of geckos of the genus *Asaccus* (Squamata: Phyllodactylidae). PeerJ. 4:e2371.

Clavel J., Escarguel G., Merceron G. 2015. mvMORPH: An R package for fitting multivariate evolutionary models to morphometric data. Methods in Ecology and Evolution. 6:1311–1319.

Foster J.B. 1964. Evolution of mammals on islands. Nature. 202:234–235.

Gamble T., Greenbaum E., Jackman T.R., Bauer A.M. 2015. Into the light: diurnality has evolved multiple times in geckos. Biological Journal of the Linnean Society. 115:896–910.

Garcia-Porta J., Morales H.E., Gómez-Díaz E., Sindaco R., Carranza S. 2016a. Patterns of diversification in islands: A comparative study across three gecko genera in the Socotra Archipelago. Molecular Phylogenetics and Evolution. 98:288–299.

Garcia-Porta J., Simó-Riudalbas M., Robinson M., Carranza S. 2017. Diversification in arid mountains: biogeography and cryptic diversity of *Pristurus rupestris rupestris* in Arabia. Journal of Biogeography. 44:1694–1704.

Garcia-Porta J., Šmíd J., Sol D., Fasola M., Carranza S. 2016b. Testing the island effect on phenotypic diversification: insights from the *Hemidactylus* geckos of the Socotra Archipelago. Scientific Reports. 6:23729.

Gómez-Díaz E., Sindaco R., Pupin F., Fasola M., Carranza S. 2012. Origin and in situ diversification in *Hemidactylus* geckos of the Socotra Archipelago. Molecular Ecology. 21:4074–4092.

Goodman B.A., Miles D.B., Schwarzkopf L. 2008. Life on the rocks: Habitat use drives morphological and performance evolution in lizards. Ecology. 89:3462–3471.

Harmon L.J., Melville J., Larson A., Losos J.B., Oakley T. 2008. The Role of Geography and

Ecological Opportunity in the Diversification of Day Geckos (*Phelsuma*). Systematic Biology. 57:562–573.

Higham T.E., Russell A.P. 2010. Divergence in locomotor performance, ecology, and morphology between two sympatric sister species of desert-dwelling gecko. Biological Journal of the Linnean Society. 101:860–869.

Lack D. 1976. Island biology illustrated by the land birds of Jamaica. Berkeley: University of California Press.

Lomolino M.V. 2005. Body size evolution in insular vertebrates: Generality of the island rule. Journal of Biogeography. 32:1683–1699.

Losos J. 2009. Lizards in an evolutionary tree: Ecology and adaptive radiation of anoles. University of California Press.

Losos J.B. 2010. Adaptive radiation, ecological opportunity, and evolutionary determinism. American Naturalist. 175:623–639.

Losos J.B., Parent C.E. 2009. The speciation-area relationship. In: Losos J.B., Ricklefs R.E., editors. The Theory of Island Biogeography Revisited. Princeton University Press. p. 415–438.

Losos J.B., Ricklefs R.E. 2009. Adaptation and diversification on islands. Nature. 457:830–836.

Machado L., Salvi D., James Harris D., Brito J.C., Crochet P.A., Geniez P., Ahmadzadeh F., Carranza S. 2021. Systematics, biogeography and evolution of the Saharo-Arabian naked-toed geckos genus *Tropiocolotes*. Molecular Phylogenetics and Evolution. 155:106969.

Mahler D.L., Revell L.J., Glor R.E., Losos J.B. 2010. Ecological opportunity and the rate of morphological evolution in the diversification of Greater Antillean anoles. Evolution. 64:2731–2745.

Metallinou M., Arnold E.N., Crochet P.-A., Geniez P., Brito J.C., Lymberakis P., Baha El Din S., Sindaco R., Robinson M., Carranza S. 2012. Conquering the Sahara and Arabian deserts: systematics and biogeography of *Stenodactylus* geckos (Reptilia: Gekkonidae). BMC evolutionary biology. 12:258–258.

Metallinou M., Červenka J., Crochet P.A., Kratochvíl L., Wilms T., Geniez P., Shobrak M.Y., Brito J.C., Carranza S. 2015. Species on the rocks: Systematics and biogeography of the rock-dwelling *Ptyodactylus* geckos (Squamata: Phyllodactylidae) in North Africa and Arabia. Molecular Phylogenetics and Evolution. 85:208–220.

Moen D.S., Morlon H., Wiens J.J. 2016. Testing Convergence Versus History: Convergence Dominates Phenotypic Evolution for over 150 Million Years in Frogs. Systematic Biology. 65:146–160.

Pedersen T.L. 2020. Patchwork: The composer of plots. R package version 1.1.1.

14

Pennell M.W., Eastman J.M., Slater G.J., Brown J.W., Uyeda J.C., Fitzjohn R.G., Alfaro M.E., Harmon L.J. 2014. Geiger v2.0: An expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. Bioinformatics. 30:2216–2218.

R Core Team. 2019. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Revell L.J. 2012. phytools: An R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution. 3:217–223.

Reynolds R.G., Collar D.C., Pasachnik S.A., Niemiller M.L., Puente-Rolón A.R., Revell L.J. 2016. Ecological specialization and morphological diversification in Greater Antillean boas. Evolution. 70:1882–1895.

Rundell R.J., Price T.D. 2009. Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. Trends in Ecology and Evolution. 24:394–399.

Schluter D. 2000. The ecology of adaptive radiation. Oxford University Press.

Simó-Riudalbas M., Metallinou M., de Pous P., Els J., Jayasinghe S., Péntek-Zakar E., Wilms T., Al-Saadi S., Carranza S. 2017. Cryptic diversity in *Ptyodactylus* (Reptilia: Gekkonidae) from the northern Hajar Mountains of Oman and the United Arab Emirates uncovered by an integrative taxonomic approach. PloS ONE. 12:e0180397.

Simó-Riudalbas M., Tarroso P., Papenfuss T., Al-Sariri T., Carranza S. 2018. Systematics, biogeography and evolution of *Asaccus gallagheri* (Squamata, Phyllodactylidae) with the description of a new endemic species from Oman. Systematics and Biodiversity. 16:323–339.

Šmíd J., Carranza S., Kratochvíl L., Gvoždík V., Nasher A.K., Moravec J. 2013a. Out of Arabia: A Complex Biogeographic History of Multiple Vicariance and Dispersal Events in the Gecko Genus *Hemidactylus* (Reptilia: Gekkonidae). PLoS ONE. 8:e64018.

Šmíd J., Moravec J., Kratochvíl L., Gvoždík V., Nasher A.K., Busais S.M., Wilms T., Shobrak M.Y., Carranza S. 2013b. Two newly recognized species of *Hemidactylus* (Squamata, Gekkonidae) from the Arabian Peninsula and Sinai, Egypt. ZooKeys.:79–107.

Šmíd J., Moravec J., Kratochvíl L., Nasher A.K., Mazuch T., Gvoždík V., Carranza S. 2015. Multilocus phylogeny and taxonomic revision of the *Hemidactylus robustus* species group (Reptilia, Gekkonidae) with descriptions of three new species from Yemen and Ethiopia. Systematics and Biodiversity. 13:346–368.

Šmíd J., Shobrak M., Wilms T., Joger U., Carranza S. 2017. Endemic diversification in the mountains: genetic, morphological, and geographical differentiation of the *Hemidactylus* geckos in southwestern Arabia. Organisms Diversity & Evolution. 17:267–285.

Šmíd J., Uvizl M., Shobrak M., Salim A.F.A., AlGethami R.H.M., Algethami A.R., Alanazi A.S.K., Asubaie S.D., Busais S., Carranza S. 2020. Swimming through the sands of the

15

Sahara and Arabian deserts: Phylogeny of sandfish skinks (Scincidae, *Scincus*) reveals a recent and rapid diversification. Molecular Phylogenetics and Evolution. 155:107012.

Tamar K., Mitsi P., Carranza S. 2019a. Cryptic diversity revealed in the leaf-toed gecko *Asaccus montanus* (Squamata, Phyllodactylidae) from the Hajar Mountains of Arabia. Journal of Zoological Systematics and Evolutionary Research. 57:369–382.

Tamar K., Simó-Riudalbas M., Garcia-Porta J., Santos X., Llorente G., Vasconcelos R., Carranza S. 2019b. An integrative study of island diversification: Insights from the endemic *Haemodracon* geckos of the Socotra Archipelago. Molecular Phylogenetics and Evolution. 133:166–175.

Tejero-Cicuéndez H., Patton A.H., Caetano D.S., Šmíd J., Harmon L.J., Carranza S. 2021. Reconstructing Squamate Biogeography in Afro-Arabia Reveals the Influence of a Complex and Dynamic Geologic Past. Systematic Biology. Advance online publication. https://doi.org/10.1093/sysbio/syab025.

Vasconcelos R., Carranza S. 2014. Systematics and biogeography of *Hemidactylus homoeolepis* Blanford, 1881 (Squamata: Gekkonidae), with the description of a new species from Arabia. Zootaxa. 3835:501–527.

Whittaker R.J., Triantis K.A., Ladle R.J. 2008. A general dynamic theory of oceanic island biogeography. Journal of Biogeography. 35:977–994.

Wickham H. 2011. ggplot2. Wiley Interdisciplinary Reviews: Computational Statistics. 3:180–185.

Wilke C.O. 2020. cowplot: streamlined plot theme and plot annotations for 'ggplot2'. R package version 1.1.

Yoder J.B., Clancey E., Des Roches S., Eastman J.M., Gentry L., Godsoe W., Hagey T.J., Jochimsen D., Oswald B.P., Robertson J. 2010. Ecological opportunity and the origin of adaptive radiations. Journal of evolutionary biology. 23:1581–1596.