Patterns of diversification in islands: A comparative study across three gecko genera in the Socotra Archipelago ☆

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A B S T R A C T

In this study we used the complete fauna of geckos of the Socotra Archipelago to test whether the three gecko genera co-occurring in the islands (*Pristurus*, *Hemidactylus* and *Haemodracon*) produced similar outcomes of morphological and climatic diversification. To test this, we produced a time-calibrated tree of 346 geckos including all 16 endemic species of the archipelago and 26 potential close-relatives in the continent. Our dating estimates revealed that most of the diversity of geckos in the archipelago was the consequence of *in situ* diversification. However not all genera shared similar patterns of diversification. While in *Hemidactylus* and *Haemodracon* this involved great differences in body size and low levels of climatic diversification (mostly involving sympatric distributions), an opposite pattern appeared in *Pristurus* in which most of the diversification involved shifts in climatic envelopes (mostly involving allopatric and parapatric distributions) but almost no size differentiation. Consistently with this, *Pristurus* was the only genus in which rates of size diversification in islands were substantially lower than in the continent. This illustrates how different groups can greatly differ in their patterns of intra-island diversification and highlights the importance of taxon-dependent factors at determining different patterns of diversification in the same insular context.

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1. Introduction

One of the most typical outcomes of intra-island diversification is the emergence of adaptive radiations, usually driven by resource partitioning among closely related species coexisting in the same island (Losos and Ricklefs, 2009; Schluter, 2000). In these cases, disruptive selection on resource use traits often leads to the examples of extreme morphological diversification so often observed in islands (Schluter, 2000).

Yet, evidence shows that not all groups radiating in insular environments produce high levels of phenotypic diversification (Rundell and Price, 2009). Indeed, phenotypic divergence may not necessarily be the outcome when diversification, instead of involving the partitioning among local resources (or α-niche diversification), takes place across different climatic envelopes (or β-niche diversification), typically involving parapatric or allopatric scenarios (Ackerly et al., 2006). This would allow the

accommodation in the same island of multiple species with similar phenotypes and non-overlapping distributions (Harmon et al., 2008; Rundell and Price, 2009).

A number of factors may determine whether groups take the path of diversifying at the small scales (typically involving phenotypic differentiation) and/or at large scales (across different climatic envelopes). On one hand, the physical features of islands provide different patterns of environmental heterogeneity, which in turn can determine different extents of resource partitioning and climatic differentiation. For instance, as island area is often correlated with the diversity of vegetation, islands with different areas will likely provide different opportunities for microhabitat specialization (Losos and Parent, 2009). Moreover, different lengths of the altitudinal gradient in islands will obviously determine different opportunities for altitudinal diversification (Whittaker et al., 2008).

On the other hand, physiological or morphological constrains in the insular groups may also lead to different climatic or phenotypic evolvabilities (i.e. the ability to evolve into different phenotypes or into different climatic envelopes), which can be translated into various degrees of climatic or phenotypic differentiation. For instance,

if all traits involved in partitioning among local resources tend to be evolutionarily conserved, diversification among different habitats may be the most likely observed pattern (Ackerly et al., 2006). Alternatively, if these traits are labile enough, this can facilitate the possibility of different resource use between closely related species in the same habitat, which often leads to high levels of phenotypic differentiation (Ackerly et al., 2006; Emerson and Gillespie, 2008).

The main goal of the present study is to use the complete fauna of endemic geckos of the Socotra Archipelago as a case study to explore whether independent cases of intra-island diversification share common outcomes in terms of morphological and climatic diversification (defined in this study as differentiation across different portions of the environmental space provided by the islands). When we detect different patterns of diversification it is also our aim to explore how island-dependent or taxon-dependent factors modulate such differences.

The Socotra Archipelago is situated in the northwest Indian Ocean (at 110 km from Somalia and 450 km from Yemen; Fig. 1) (Damme and Banfield, 2011). This archipelago once formed part of Arabia and detached completely from its southern margin around 20 Ma ago (the upper age limit of the deposits associated to the rift process that separated the islands from the continent) (Fournier et al., 2010; Watchorn et al., 1998). Two main islands, Socotra and Abd al Kuri, and two little islets, Darsa and Samha, nowadays form the archipelago. Socotra is the easternmost and largest of the islands (3620 km^2) and with a maximum altitude of 1500 m, it is also the most geographically, biologically and ecologically diverse. The second largest island, Abd al Kuri (130 km^2), is the westernmost island of the archipelago and with a maximum altitude of 700 m, presents a more homogeneous habitat. Darsa and Samha are very small islets that until very recently were likely connected to the island of Socotra (Fig. 1).

The archipelago contains an endemic fauna of geckos consisting of 16 species distributed in three genera that belong to three different families: the genus *Pristurus* (family Sphaerodactylidae) constituted by seven diurnal species, one endemic to Abd al Kuri (introduced in some coastal harbors of Socotra), five endemic to Socotra and one endemic to Samha and Darsa; the genus *Hemidactylus* (family Gekkonidae) constituted by seven strictly nocturnal species, two of them endemic to Abd al Kuri, four endemic to Socotra and one present in Socotra, Samha and Darsa; and finally

the genus *Haemodracon* (family Phyllodactylidae) which contains two strictly nocturnal species, one endemic to the island of Socotra and another one present in Socotra and Samha islands (Razzetti et al., 2011).

These three genera have independently arrived and diversified within the same islands. This provides an excellent opportunity to study whether closely related groups (all of them geckos), diversifying in similar island environments, converge into similar patterns of phenotypic and climatic diversification.

2. Material and methods

2.1. Taxon sampling, DNA extraction, amplification and phylogenetic analysis

In order to detect intra-island diversification events across the three island genera, we took a phylogenetic approach and produced a time-calibrated molecular phylogeny that included all the 16 species of geckos endemic to the archipelago, 26 species occurring in Africa and Arabia, which previous studies showed as close relatives to the Socotran geckos (Badiane et al., 2014; Gamble et al., 2012; Gómez-Díaz et al., 2012; Šmíd et al., 2013) and a wide representation of geckos obtained from GenBank (Table S2).

Having all island species and potential continental close relatives in the same phylogeny allowed us to make sure (as far as possible with current available data) that no continental species fell within any insular clade (which would render it paraphyletic, turning potential cases of *in situ* speciation events into a situation of two independent colonization events). The additional geckos obtained from GenBank were used to place different calibration points across the phylogeny (all external to the Socotra Archipelago) and calculate divergence times while limiting potential problems of biased and/or low sampling across the phylogeny (Venditti et al., 2006).

Genomic DNA was extracted from ethanol-preserved tissue samples using the Qiagen DNeasy Blood & Tissue Kit (Qiagen, Valencia, CA, USA). Up to six loci were PCR-amplified and sequenced (in both directions): one mitochondrial fragment of the gene encoding the ribosomal 12S rRNA (*12S*; primers 12Sa and 12Sb – Kocher et al., 1989), and five nuclear fragments of the genes encoding the acetylcholine receptor M4 (*acm4*; primers
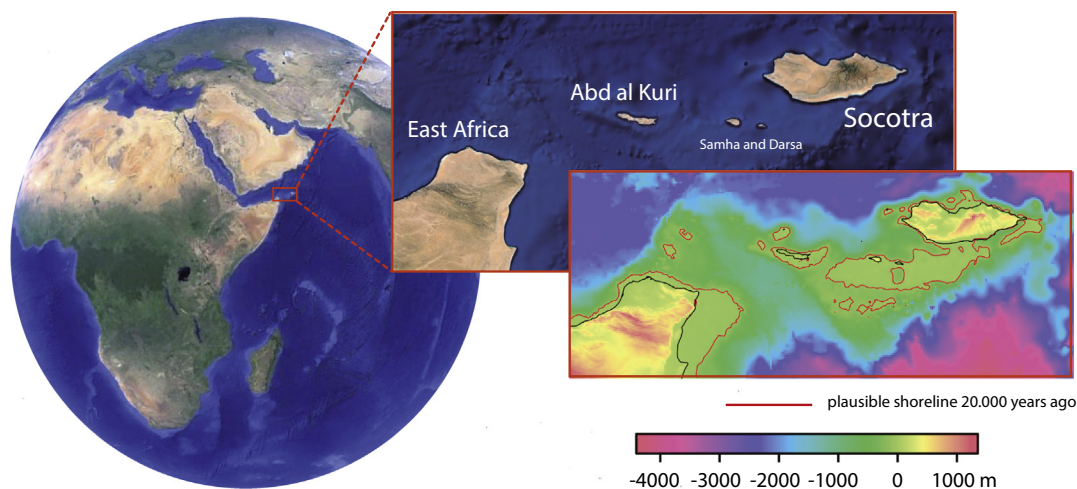

Fig. 1. Map showing the geographic location of the Socotra Archipelago. The upper right map shows an enlarged view of the archipelago and the names of the main islands that constitute it. Map source: Google Earth 2014 (data: SIO, NOAA, US Navy, NGA, GEBCO, image: Landsat). The lower right map provides a visualization of the ocean-floor bathymetry of the region on which we highlight (in red) the portion of topography lying above −120 m. This constitutes a plausible reconstruction of the paleo-shorelines of 20,000 years ago, when sea levels dropped around 120 m from the present-day level (Siddall et al., 2003). Map generated with data from GEBCO (www.gebco.net). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

tg-F and tg-R – Gamble et al., 2008), the oocyte maturation factor Mos (*cmos*; primers FUF and FUR – Gamble et al., 2008), a short fragment of the recombination-activating gene 1 (*rag1*; primers F700 and R700 – Bauer et al., 2007), the recombination-activating gene 2 (*rag2*; primers PyF1 and PyR – Gamble et al., 2008) and phosducin (*pdc*; primers PHOF2 and PHOR1 – Gamble et al., 2008). These genes have been widely used in other large-scale phylogenetic studies of Gekkota (Gamble et al., 2012, 2011, 2008) and were therefore the ones preferred in this study. The primer sequences and PCR conditions used for the amplification of the six loci can be found in Table S1.

We also searched all species of geckos existing in GenBank for which at least three of the genes amplified in this study were available. We then retrieved the longest sequence for each species with the additional requirement that all sequences had to be 200 bp or more to be selected. After this procedure, our sequence dataset included 346 species, 42 of which were sampled and sequenced in this study and 304 were obtained from GenBank (Table S2).

Each gene was then aligned using two procedures: the ribosomal coding *12S* was aligned by means of MAFFT v.7 (Katoh and Standley, 2013) with the Q-INS-i strategy. The protein coding genes (*acm4*, *cmos*, *rag1*, *rag2* and *pdc*) were aligned by means of the translation alignment algorithm implemented in the software Geneious (Drummond et al., 2010). The final alignment consisted of a total of 2259 bp distributed in each gene as follows: *12S* (390 bp), *acm4* (453 bp), *cmos* (375 bp), *rag1* (303 bp), *rag2* (345 bp) and *pdc* (393 bp).

Best-fitting models of nucleotide evolution were inferred using PartitionFinder v.1.1.1 (Lanfear et al., 2012) with the following settings: branch lengths linked, only models available in BEAST evaluated, BIC model selection criterion applied, all partition schemes analyzed. Each gene was set as an independent partition. Three-partitions with the GTR+I+G model of sequence evolution for each scheme were selected: p1, *12S* gene; p2, the nuclear genes *acm4* and *pdc*; and p3, the nuclear genes *cmos*, *rag1* and *rag2*.

Phylogenetic analyses were conducted by means of the package BEAST v1.7.5 (Drummond and Rambaut, 2007) and relied on four independent Markov Chain Monte Carlo (MCMC) that converged on similar posterior estimates. Each chain was run for 100,000,000 generations with parameters and trees sampled every 5000 generations. These runs were combined using LogCombiner v1.7.5 (included in the package BEAST) after excluding, as burning, a suitable amount of generations in each one (from 10% to 30%). Tracer v.1.5 (Rambaut and Drummond, 2007) was used to confirm convergence and good mixing of each MCMC chain. We then calculated the summary tree as the maximum clade credibility tree with median node heights using the TreeAnnotator v1.7.5 program (also included in BEAST package), setting the posterior probability limit to 0.5. Moreover we randomly sampled 1500 trees from the posterior distribution of trees generated by our BEAST analyses. This allowed us to incorporate the topological and branch lengths uncertainties in some of the phylogenetic comparative analyses (see below).

2.2. Estimation of divergence times and detection of in situ diversification events

Five calibrations were used to estimate branch lengths in units of time (see Fig. 2):

1. The minimum age for the radiation of *Sphaerodactylus* in the Caribbean was set to 20 Ma based on an amber fossil of this genus from the Dominican Republic (Daza and Bauer, 2012). The maximum age of this radiation was set, conservatively, to a soft maximum of 70 Ma. This was done by means of a gamma distribution ($\alpha = 2$, $\beta = 10$).

2. The age of the Tien Shan–Pamir uplift in western China, around 10 Ma, was used to calibrate the split between *Teratoscincus scincus* and the clade formed by *T. przewalskii* and *T. roborowskii* considering that this split originated via vicariance as a result of this geologic event (Macey et al., 1999). A normal distribution with a mean positioned at 10 Ma and a standard deviation of 1 Ma was chosen to set the calibration prior of this node.

3. The age for the diplodactyloid radiation in New Caledonia was set to a soft maximum of 37 Ma. This is based on several lines of evidence (geological and biological) that show that the island was submerged until this approximate time (Nattier et al., 2011; Pillon, 2012; Papadopoulou et al., 2013; Garcia-Porta and Ord, 2013). A normal distribution with a mean at 20 Ma and a standard deviation of 10 Ma was used to set the prior of this calibration point.

4. The split between *Phelsuma ornata* from the island of Mauritius and *P. inexpectata* from the island of Reunion was set to a soft maximum of 8.9 Ma based on the age of the oldest rocks of Mauritius (the oldest island in the Mascarenes, including both Mauritius and Reunion) (Moore et al., 2011). This prior was set by means of an exponential distribution with an offset of 0 and a mean at 3 Ma.

5. Finally, the deepest split in the diplodactyloid radiation of New Zealand was set to a minimum of 19 Ma based on the oldest fossils of geckos in the Archipelago (Lee et al., 2009) with a conservative soft maximum of 65 Ma. This was set by means of a gamma distribution ($\alpha = 3$, $\beta = 7$).

Intra-island diversification events in the archipelago were detected by placing the dating estimates and confidence intervals [95% highest posterior densities (HPDs)] of all splits separating two insular species in the timeframe of the geological evolution of the archipelago.

Namely, a node separating two island species with a HPD interval overlapping in more than 50% the oceanic stage of the archipelago (the period comprised between 20 Ma and the present, when the islands were already detached from the continent) was considered as an intra-island speciation event. Any other interval distribution was interpreted as non-informative. Given that the two islets of Samha and Darsa were until very recently connected to the big island of Socotra (Fig. 1) and share most of their reptilian faunas with Socotra (with only a single endemic), the split separating *P. sokotranus* (from Socotra) and *P. samhaensis* (from Darsa and Samha) was considered an intra-island speciation event (given that according to our dating estimates, likely took place when both islets were connected to Socotra).

2.3. Exploring climatic diversification

Climatic diversification, as defined in this study, does not necessarily reflect diversification across different fundamental niches (Pearman et al., 2008) but solely implies differentiation across different portions of the environmental space provided by the islands. With this goal in mind, throughout this section, climatic envelopes are used as mere proxies that conveniently integrate a number of ecological and spatial components of the distribution of the different species (e. g. altitudinal span, latitudinal or longitudinal ranges).

We calculated climatic envelopes from the species occurrence data published in Razzetti et al. (2011), which are the result of 215 diurnal and nocturnal transects including mainly Socotra but also Abd al Kuri, Samha, and Darsa Islands, based on time-constrained systematic sampling surveys (Razzetti et al., 2011). Only original data were used and included 834 localities with a mean and a minimum of 52 and 5 localities per species, respectively. To lower the amount of spatial autocorrelation in our data,
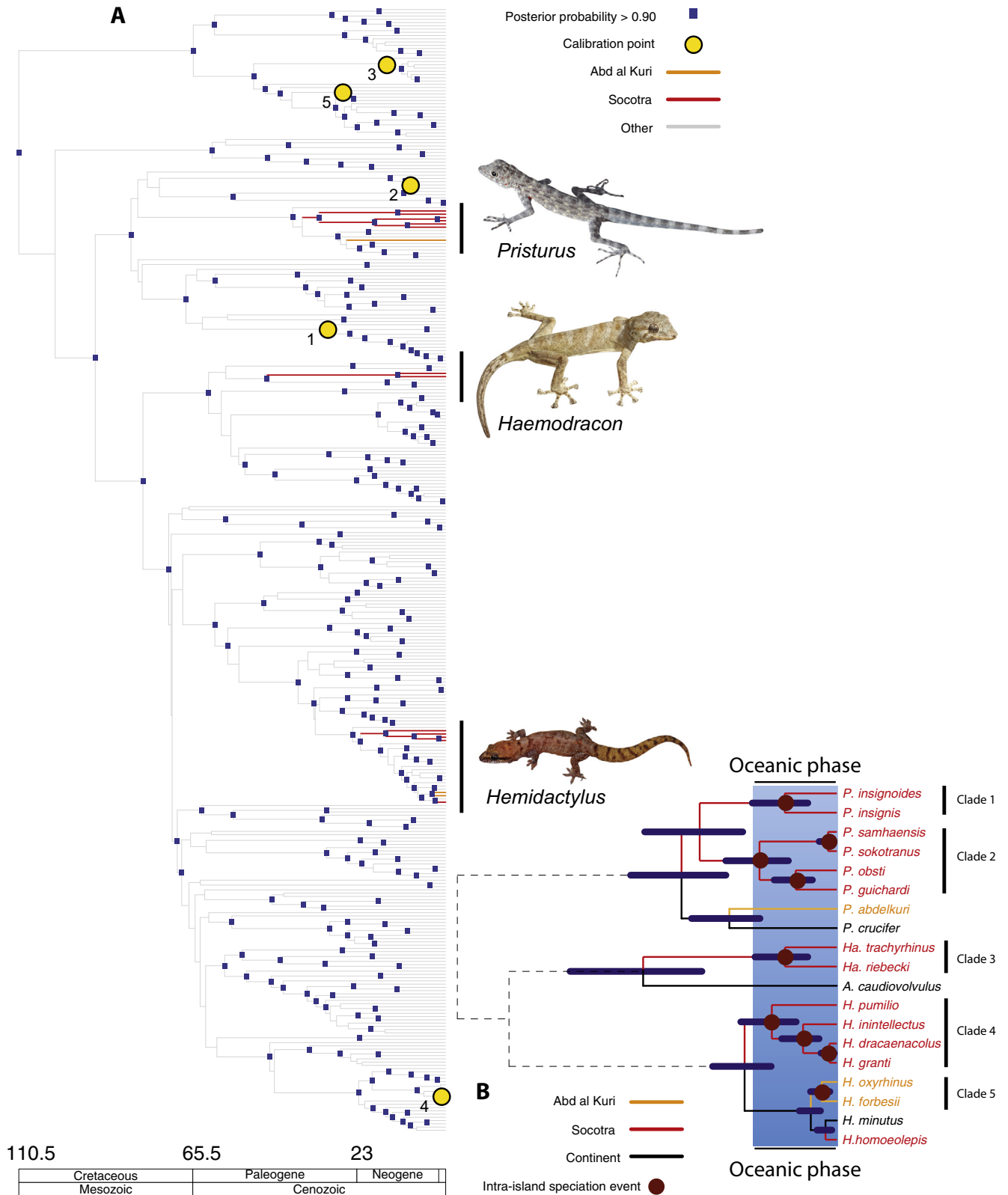
Fig. 2. (A) Time-calibrated tree informed by six genes and including 346 species of geckos. The colored branches refer to all branches associated to species from Socotra (red) and Abd al Kuri (orange). The small blue rectangles highlight all nodes presenting posterior probabilities higher than 0.90. Yellow circles refer to the calibrations used in the analysis (with numbers matching those provided in the text). Also shown are the pictures of one representative of all three genera occurring in the islands, from up to down: *Pristurus insignis*, *Haemodracon riebeckii* and *Hemidactylus pumilio* (photo credits: Roberto Sindaco). (B) Time-calibrated tree showing all branches and nodes related to the Socotra Archipelago, including all nodes separating island lineages and the most recent mainland–island splits recovered in our tree. Blue bars depict the 95% posterior density intervals for all nodes. The blue rectangle depicts the period during which the islands were separated from the continent and isolated by ocean (oceanic stage, from 20 Ma to present). Species from Socotra are shown in red and species from Abd al Kuri are shown in orange. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

these localities were subsequently downsampled by applying a grid of 1×1 km on the archipelago from which we randomly extracted a single locality per species and cell. This resulted in 555 localities with a mean and a minimum of 34.68 and 5 locations per species respectively. Climate in the archipelago was informed by 19 Bioclim variables available in the WorldClim database (http://www.worldclim.org) at 30 arc s of spatial resolution (Hijmans et al., 2005). In order to facilitate the interpretation of the multivariate climatic space, these were subsequently reduced to six following the "PCA-based clustering" method described in Dormann et al. (2013). The ones selected were: Bio 1 (annual mean temperature), Bio 3 (Isothermality), Bio 4 (temperature seasonality), Bio 7 (temperature annual range), Bio 14 (precipitation of driest month) and Bio 16 (precipitation of wettest quarter) and their values were obtained by retrieving all cell values at a resolution of 1×1 km in each of the six climatic rasters (Fig. S2).

We used the "PCA-env" ordination technique (Broennimann et al., 2012) to characterize the climate space of the archipelago and the climatic envelope of each species in it. This method essentially projects the climatic variables existing in the archipelago and the climatic variables associated to each of the species into the multivariate space defined by a principal component analysis (PCA). These are subsequently combined in a metric to obtain the environmental occupancy of each species (derived in Broennimann et al., 2012). We also obtained a point estimate of the niche position for each species by calculating the mean values on the first and the second PCA axes.

We calculated overlap among the climatic envelopes of the different species of the same genus inhabiting the same island by means of the Schoener's D metric applied to the environmental occupancies of each of the species (Broennimann et al., 2012; Schoener, 1970; Warren et al., 2008). This metric varies from 0 to 1 (no overlap to complete overlap between species). To produce null distributions of the D values of each of the pairwise species comparisons we generated 1000 sets of random occurrence points for each species in their respective islands, always maintaining the same number of localities existing per species. We then recalculated the D metric for all pairwise comparisons using the random sets of species localities and we calculated the probability of our empirical value to be equal or smaller given the distribution of 1000 simulated D values.

All calculations and data manipulations described in this section were conducted in R (R Development Core Team 2014) using the packages "raster" (Hijmans and van Etten, 2014), "dismo" (Hijmans et al., 2012), "ade4" (Dray et al., 2007), "adehabitat" (Calenge, 2006), "sp" (Pebesma and Bivand, 2005), "phytools" (Revell, 2012) and a modified version of the R scripts provided by Broennimann et al. (2012) (available from http://www.unil.ch/ecospat/home/menuinst/tools–data/tools.html).

2.4. Exploring morphological diversification

2.4.1. Characterization of the morphological variation

To explore phenotypic diversification we focused on phenotypic traits that in lizards typically reflect microhabitat or resource specialization. These include body size, head shape, limb lengths and trunk proportions: body size determines patterns of resource use in many vertebrates, strongly correlating with prey size preference (Fisher and Dickman, 1993; Moen and Wiens, 2009; Woodward and Hildrew, 2002) and with microhabitat use (Losos, 2009), head shape determines resource partitioning by enabling different bite forces (Losos, 2009) and finally limb lengths and trunk proportions are often correlated with the partitioning of the habitat structure (Goodman et al., 2008; Losos et al., 2001, 1997; Ord and Klomp, 2014; Tulli et al., 2011).

We characterized these traits for each of the 16 species of endemic geckos in the archipelago by means of 18 different measurements (Table S5): Body size was measured as the length between the snout and the opening of the cloaca (snout vent length = SVL), head shape was characterized by its length measured from the snout to the auricular opening (HL), its maximum width (HW), its maximum height (HD), the width at the level of the nasal openings (HWN), the head depth at the level of the nasal openings (HDN), the inter-nasal distance (IND), the distance from the anterior margin of the orbit to the nasal opening (END), the distance between the auricular opening to orbit (EED), the inter-orbital distance (IOD) and the orbital diameter (OD). Body proportions were measured as the axilla to groin distance (AGL) and the body amplitude at the level of the scapular and pelvic girdles (ASG and APG, respectively). Regarding limb proportions, forelimbs were measured as the length of the brachium (BL), length of the ante brachium (AL), and hindlimbs proportions were quantified as the thigh length (TL) and the crus length (CL).

All measurements were taken by the same person (JGP) three times using a digital caliper (to the nearest 0.1 mm) with the average of the three replicates used as the final value. These were then $\log_{10}$-transformed to improve the normality and homoscedasticity of our data. A total of 201 specimens were measured, with a mean of 12.6 specimens per species and a minimum of four specimens per species.

We characterized the morphospace occupied by all insular species by means of a PCA conducted on the correlation matrix. We then examined the proportion of variation explained by each component and the loadings of each variable. As body size (measured as snout-vent length; SVL) was the variable that explained most of the morphological variation in the geckos of Socotra Archipelago (see results), and all other measurements were highly correlated with it, we opted for retaining SVL as our best proxy to phenotypic variation. All analysis and data manipulations described in this section were performed in R using the package "stats".

2.4.2. Body size differentiation and rates of evolution

To test whether species resulting from intra-island diversification events differed in their body sizes, we compared the SVLs of all species in all clades resulting from intra-island diversification events in three different ways: we first conducted pairwise permutational ANOVAs on the SVL between the species of each clade to assess whether these significantly differed in body size. Secondly we compared the body size overlap between species by computing the density curve of the SVLs distributions of each species by means of a Kernel density function and computed the area overlap between the two curves (Bello et al., 2013). This overlap ranged from 0, in the case of completely dissimilar species, to 1, in species for which SVLs overlapped completely. All these analyses were performed with custom R scripts relying on the package "stats" (Appendix A).

Moreover we also explored whether the different extents of SVL diversification observed in different genera and islands (see Section 3) were associated with different rates of evolution among island groups and between island and mainland groups. To this end, we compiled the maximum SVL for most of the species of Sphaerodactylidae, Phyllodactylidae and Gekkonidae represented in our phylogeny. The data were obtained mainly from Meiri et al. (2011) and complemented from Arnold (1980), Carranza and Arnold (2012) and Moravec et al. (2011), with the values for the Socotran species obtained from this study. We calculated the rates of body size evolution assuming a Brownian motion (BM) process. In this process character change occurs as a random walk along each branch of a phylogenetic tree and the rate of evolution (rate parameter σ^2) is defined as the variance of the normal distribution from which each step of character displacement is sampled.

(Felsenstein, 1985; Collar et al., 2005; O'Meara et al., 2006; see Eq. (2) in Butler and King, 2004).

With the function "BrownieREML" from the R package phytools (Revell, 2012), we fitted two alternative BM models: a model that assumed a single rate parameter across all the lineages in the phylogeny (model 0), and a model that assumed that different clades of the tree could potentially evolve according to different rate parameters (model 1). To compare rates of evolution between different island clades and between island clades and their continental close relatives, in model 1 we defined the following clades: the five island clades involved in intra-island speciation events (see Section 3), a clade formed by 9 continental species of *Pristurus* (which were compared to clades 1 and 2 of Socotran *Pristurus*), the continental species of the Arid clade of the genus *Hemidactylus* (which were compared to clades 4 and 5 of Socotran *Hemidactylus*), the exclusively continental genus *Asaccus*, and the continental species of the genus *Tarentola* (both Phyllodactylidae, which were compared to clade 3 of Socotran *Haemodracon*). Lastly we defined an additional clade that included the rest of the geckos, which provided an estimate of the average rate of body size evolution for geckos.

These clades were defined on each of the 1500 trees obtained from the posterior distribution of the BEAST analysis and therefore rates integrated the topological and branch length uncertainties of our phylogenetic analysis. We fitted model 0 and model 1 on each tree and both were evaluated and compared using their computed second-order Akaike's information criterion (AIC_c) (Akaike, 1998).

Finally we visualized climatic and morphological diversification by computing the absolute values of the standardized independent contrasts (Felsenstein, 1985) for body size and for the two first axes of climatic variation and plotted them against each other.

3. Results

3.1. Phylogenetic analyses

We recovered 73% of nodes of the maximum clade credibility tree with a posterior probability (pp) greater than 0.90 and 66% of the nodes with a pp greater than 0.95 (Fig. 2). The phylogenetic relationships depicted by our maximum clade credibility tree were generally consistent with previous published phylogenies of Gekkota (Gamble et al., 2012, 2011, 2008; Pyron et al., 2013) (Fig. S1). According to our dating estimates the crown radiation of Gekkota dates from 80 to 150 Ma, which is in the range of most of the estimates provided by previous studies (90–133 Ma in Vidal and Hedges, 2009; 78–95 Ma in Wiens et al., 2006; 84–104 Ma in Hugall et al., 2007; 85–206 Ma in Gamble et al., 2008; 118–167 in Gamble et al., 2011; 52.4–101 Ma in Jones et al., 2013).

Our results show that, while the island endemic *Haemodracon* is monophyletic, the Socotran species of *Pristurus* and *Hemidactylus* are polyphyletic implying more than a single colonization event of these genera into the archipelago. Yet most of the splits separating insular species took place once the islands detached from the continent ("oceanic stage" of the islands, in the last 20 Ma) and are consistent with intra-island speciation events.

More specifically, we recognize five clades with nine instances of intra-island speciation events: two in *Pristurus* (clades 1 and 2), one in *Haemodracon* (clade 3), and two in *Hemidactylus* (clades 4 and 5) (Fig. 2). However not all intra-island clades produced equal numbers of intra-island splits: clades 1 and 3 in Socotra and clade 5 in Abd al Kuri produced a single intra-island split while clades 2 and 4 in Socotra produced three intra-island splits each one (Fig. 2). The only exception of an insular split not being *in situ* is the deepest split in the Socotran *Pristurus*, which according to our estimates took place before the islands detached from

the continent (in the "continental stage" of the archipelago). According to this, the split between the *Pristurus* insular clades 1 and 2 would be the consequence of two independent dispersal or vicariant events neither recovered by our phylogeny (Fig. 2) nor by recent published phylogenies (Badiane et al., 2014; Pyron et al., 2013).

Our results also revealed two instances of overseas dispersal events from the continent (mainland–island splits that took place after the last mainland–island contact). One involved *H. homoeolepis*, which arrived to the island of Socotra around 3 Ma while the other involved the ancestor of *H. oxyrhinus* and *H. forbesii*, which arrived to Abd al Kuri around 6 Ma.

3.2. Climatic diversification

Our analyses on the climatic variables of the archipelago indicate a marked climatic variability between and within islands. The first two components of the PCA explain a 61.32% and 34.28% of the total variance respectively (Table S3). PC1 essentially reflects an altitudinal gradient with lower values in this axis corresponding to lower annual mean temperatures, wider annual thermic ranges of variation and higher precipitation. PC2 reflects variation along a longitudinal axis, with lower values in this component corresponding to lower values of isothermality and higher values in temperature seasonality (Table S3; Fig. S2).

The visualization of the climatic space of the islands shows that Socotra and Abd al Kuri have very different climatic envelopes (Fig. S3). Both are clearly separated along PC2 (with higher values in this component corresponding to Abd al Kuri) and show marked differences in their ranges along both axes, reflecting differences in the altitudinal, latitudinal and longitudinal span of both islands. The islands of Samha and Darsa have intermediate climates between Socotra and Abd al Kuri, but are substantially closer to the climate of Socotra.

The comparison of the climatic envelopes between species within the five clades diversifying *in situ* revealed completely different patterns of climatic structuring in different genera. Our analyses detect instances in which sister species completely overlap their climatic envelopes, as in the two sister species of *Haemodracon* in Socotra (clade 3) and the two sister species of *Hemidactylus* in Abd al Kuri (clade 5) (Table 1). In both cases, sister species are widely distributed across their respective islands with completely overlapping distributions (Figs. 3 and S4). This contrasts with the

Table 1
Values of macro-niche (climatic) overlap between species belonging to the five clades resulting from intra-island diversification events (Fig. 2). *P*-values were calculated by means of a null distribution generated by 1000 randomizations of the localities of each of the two species involved in each pairwise comparison. Dark lines separate different island clades.

| Clade	Species comparisons	Climatic overlap	*p*-value
1	*P. insignis vs P. insignoides*	0.122	0.004
2	*P. samhaensis vs P. sokotranus*	0.087	<0.001
2	*P. samhaensis vs P. guichardi*	0.087	0.017
2	*P. samhaensis vs P. obsti*	0.004	<0.001
2	*P. sokotranus vs P. guichardi*	0.674	0.988
2	*P. sokotranus vs P. obsti*	0.091	0.001
2	*P. guichardi vs P. obsti*	0.011	0.001
3	*Ha. riebeckii vs Ha. trachyrhinus*	0.511	0.331
4	*H. pumilio vs H. inintellectus*	0.455	0.197
4	*H. pumilio vs H. granti*	0.196	0.006
4	*H. pumilio vs H. dracaenacolus*	0.354	0.196
4	*H. inintellectus vs H. dracaenacolus*	0.068	0.004
4	*H. inintellectus vs H. granti*	0.022	<0.001
4	*H. dracaenacolus vs H. granti*	0.198	0.096
5	*H. forbesii vs H. oxyrhinus*	0.839	0.996
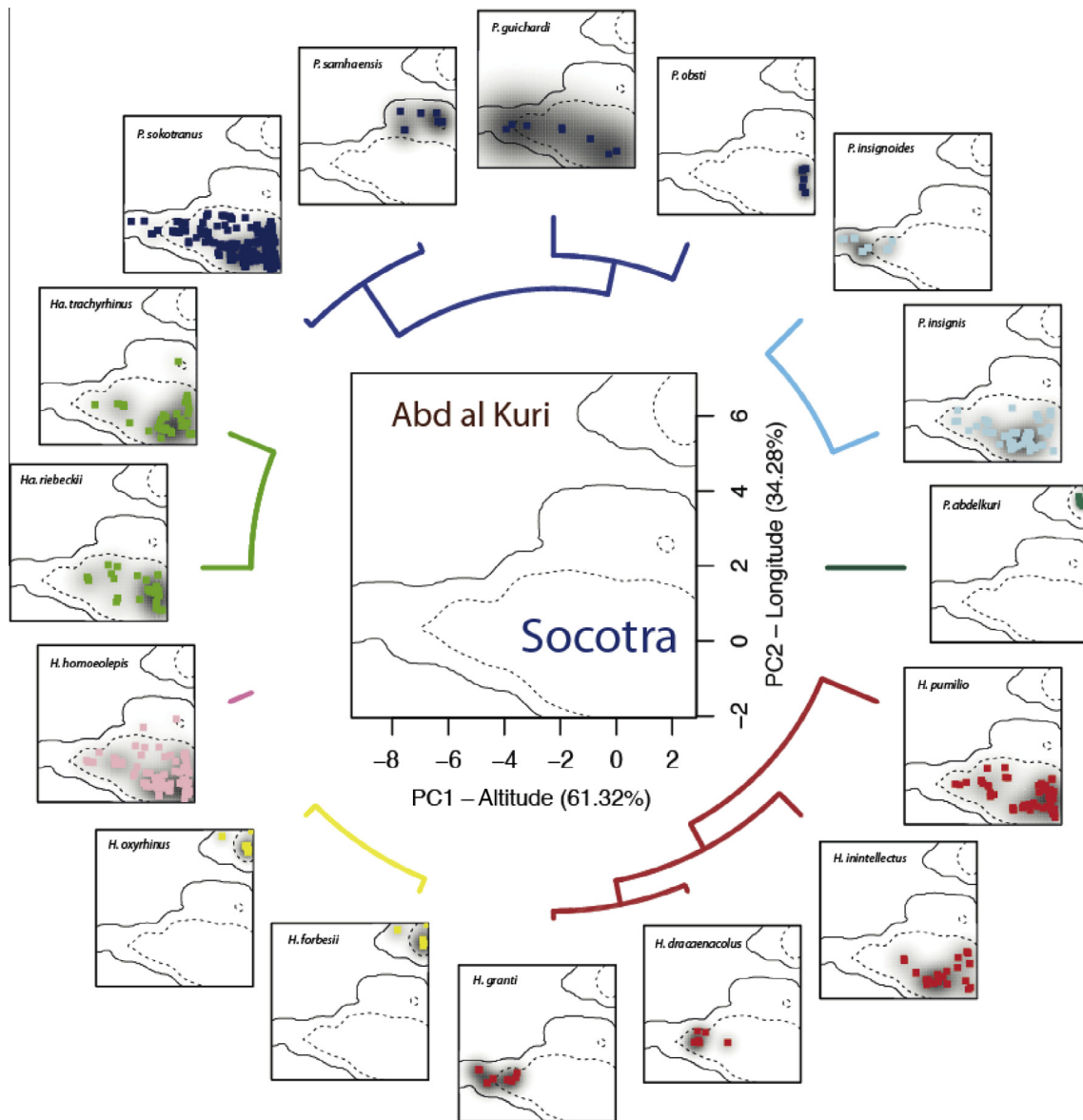
Fig. 3. Visualization of the climatic space occupied by each of the 16 gecko species in the Socotra Archipelago. The squares represent the actual (sampled) values of each species in the climatic space, the grey shading represent the climatic space as interpolated by means of a Kernel density function. The solid and dashed contour lines illustrate, respectively, 100% and 50% of the available (background) climatic space provided by the islands. This space is defined from a PCA performed on six climatic variables (Bio 1, Bio 3, Bio 4, Bio 7, Bio 14 and Bio 16). Different colors highlight the different clades with intra-island splits. Also shown is the phylogenetic structure underlying each clade. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

two clades of *Pristurus* from Socotra Island (clades 1 and 2) where all sister species within each clade show extremely diverging climatic envelopes (Table 1 and Fig. 3). This extreme climatic divergence always occurs in allopatric and parapatric scenarios involving segregation along the altitudinal gradient (*P. insignis vs P.insignoides*; Figs. 3 and S4) or along a North-South axis (*P. sokotranus vs P. samhaensis*; Figs. 3 and S4) and along an East-West axis (*P. obsti vs P. guichardi*; Figs. 3 and S4). Finally, in clade 4 of *Hemidactylus* from Socotra Island we find an intermediate pattern between the two above-exposed extremes (Table 1 and Fig. 3): the two most basal branching events (*H. pumilio* and *H. inintellectus*) share the same climate envelope. Both species are widely distributed in the island with completely overlapping ranges (Figs. 3 and S4). However, these two species completely differ from the climate envelopes shown by the species involved in the recent-most intra-island speciation event (*H. dracaenacolus* and *H. granti*), which are restricted to high elevations. In this case, although

H. dracaenacolus and *H. granti* share the same climatic space, both species occur in strict allopatry (Fig. S4).

3.3. Morphological diversification

3.3.1. Characterization of the morphological variation

The PCA conducted on the morphological data, revealed that SVL is the major source of variation among the species in the archipelago. This is essentially reflected in the first component (PC1), which accounted for more than 88% of the total variation (with all loadings in this axis positive and presenting similar values) (Table S4). Based on this analysis, we opted for retaining SVL as our best proxy to phenotypic variation.

Body size differentiation between species within the five intra-island diversifying clades again revealed completely divergent patterns in different genera: *Hemidactylus* and *Haemodracon* (clades 3, 4 and 5) produced extreme levels of size divergence. This size

Table 2
Results of the permutational ANOVAs and dissimilarity analyses between species belonging to the five clades resulting from intra-island diversification events (Fig. 2). Overlap values go from 0 (no body size overlap) to 1 (total body size overlap). Dark and thick lines separate different genera and thin lines separate the different clades diversifying *in situ*.

Clade	Species comparisons	Size overlap	F value	df$_1$	df$_2$	*p*-value
1	*P. insignis vs P. insignoides*	0.41	4.7	1	18	0.057
2	*P. samhaensis vs P. sokotranus*	0.69	5.6	1	50	0.017
2	*P. samhaensis vs P. guichardi*	0.51	13.74	1	43	0.001
2	*P. samhaensis vs P. obsti*	0.23	67.98	1	36	<0.001
2	*P. sokotranus vs P. guichardi*	0.83	2.37	1	55	0.127
2	*P. sokotranus vs P. obsti*	0.54	15.78	1	48	<0.001
2	*P. guichardi vs P. obsti*	0.67	4.39	1	41	0.051
3	*Ha. riebeckii vs Ha. trachyrhinus*	0	1405.04	1	13	0.001
4	*H. pumilio vs H. inintellectus*	0	184.79	1	17	<0.001
4	*H. pumilio vs H. granti*	0	157.67	1	12	0.001
4	*H. pumilio vs H. dracaenacolus*	0	185.89	1	12	<0.001
4	*H. inintellectus vs H. dracaenacolus*	0.14	25.27	1	11	0.001
4	*H. inintellectus vs H. granti*	0.33	14.23	1	11	0.003
4	*H. dracaenacolus vs H. granti*	0.68	0.89	1	6	0.361
5	*H. forbesii vs H. oxyrhinus*	0	221.93	1	18	<0.001

divergence occurred in the unique splits existing in *Hemidactylus* from Abd al Kuri and in *Haemodracon* and in the basal-most split in the *Hemidactylus* from Socotra. This size divergence contrasted with *Pristurus*, which produced negligible levels of size divergence (Fig. 4).

These two different patterns of size diversification were supported by our analyses of body size differentiation and overlap (Table 2). Comparisons within *Haemodracon* and *Hemidactylus* almost always yielded significant differences in size (with the sole exception of *H. dracaenacolus* versus *H. granti*) and low levels of size overlap, ranging from 0% of overlap (in *Hemidactylus* from Abd al Kuri and in *Haemodracon*) to a mean overlap of 19% in *Hemidactylus* from Socotra. Regarding *Pristurus*, permutational ANOVAs produced non-significant or marginally significant results in four, out of seven, size comparisons and the levels of size overlap were substantially higher than in *Hemidactylus* (41% for clade 1 of *Pristurus* and a mean of 58% of overlap for clade 2 of *Pristurus*).

3.3.2. Rates of body size evolution across the three genera and independent contrasts

Model 1, which implied different rate parameters across the phylogeny, had substantially lower AIC$_c$ values than model 0, which assumed a single rate parameter (with 5.30 units of mean AIC$_c$ difference between model 1 and model 0 across the 1500 trees). According to model 1, clades 1 and 2 of *Pristurus* from the Socotra Archipelago exhibit the lowest rates of body size evolution, not only when compared to the other Socotran genera, but also when compared to their closest relatives in the continent and to the average rate computed for the rest of the geckos (Fig. 5). *Hemidactylus* and *Haemodracon* have substantially higher rates than *Pristurus*, but only in *Hemidactylus* from Abd al Kuri and in *Haemodracon* rates are substantially higher than continental groups and the rest of the geckos.

The size and climate contrasts plotted against each other clearly confirmed the existence of radically different patterns of climatic and body size divergence among different genera. At one extreme in *Haemodracon*, *Hemidactylus* from Abd al Kuri and in the basal-most split of the *Hemidactylus* from Socotra (clades 3, 4 and 5), intra-island diversification mostly relied on body size divergence with minimal levels of climatic divergence (Fig. 6). We find the opposite pattern in the clade 1 of *Pristurus* and the two most recent splits in the clade 2 of *Pristurus* and clade 4 of *Hemidactylus* in Socotra in which intra-island diversification relied in climatic divergence and minimal amounts of body size divergence. Interestingly this plot (Fig. 6) also revealed that climatic diversification

only occurs along the altitudinal axis or along the longitudinal axis but not along both axes. Moreover high levels of body size diversification occur only associated to low levels climatic divergence although low levels of climatic divergence may occur associated to low levels of body size divergence.

4. Discussion

In this study we used all species of endemic geckos existing in the Socotra Archipelago (16 endemic species belonging to three different families) to explore how multiple co-occurring genera diversify in the same islands. Our results reveal contrasting patterns of intra-island diversification: in *Haemodracon* and in *Hemidactylus* diversification events (at least in the earliest splits) were associated with extreme body size divergence and low levels of climatic divergence, while in *Pristurus* and in the latest splits in *Hemidactylus*, splits involved climatic shifts (with sister species always being in allopatry) but minimal amounts of body size divergence.

Such opposite patterns of diversification have already been detected in different insular groups. For instance, Diamond (1986) found that in New Guinea birds tend to diversify into distinct (mostly allopatric) macro-habitats (e.g., along an altitudinal gradient) while maintaining similar micro-niches (e.g., not differing in body size). This pattern of diversification has been reported several times in posterior studies (Schluter, 2000) and has even been proposed as the most general pattern of vertebrate diversification (Streelman and Danley, 2003). However, many studies have posteriorly shown that sometimes the opposite pattern occurs and microhabitat or resource use differentiation (usually involving body size differentiation) may precede the differentiation among different climatic envelopes (Gavrilets and Losos, 2009; Harmon et al., 2008; Losos, 2009; Moen et al., 2009).

In our study we observe these two outcomes of diversification in groups co-occurring in the same island. This suggests that similar environmental contexts do not always determine similar outcomes of diversification and highlights the importance of taxon-dependent factors at determining the patterns of diversification observed in different insular taxa. One of such factors may imply the existence of different body size evolvabilities. Phenotypic evolvabilities have been invoked to explain why different groups fail to diversify phenotypically while others do diversify despite of being exposed to similar levels of ecological opportunity (Losos, 2010). Along these lines, different body size evolvabilities could explain why *Pristurus* did not diversify into the variety of body sizes observed in *Hemidactylus* and *Haemodracon*, and relied so much on parapatric and allopatric scenarios (involving different climatic envelopes). This is consistent with the comparisons between mainland and island rates of body size evolution across the three genera. In *Haemodracon* and in *Hemidactylus*, island taxa maintain or increase the continental rates of body size evolution. This is the expected outcome after island colonization, when groups increase rates of trait evolution as they rapidly fill the novel niches provided by islands in a context of low predatory pressure (Harmon et al., 2008; Losos and Ricklefs, 2009; Schluter, 2000). In *Pristurus*, however, rates of body size evolution were low, not only compared to the other Socotran genera, but also compared to their closest mainland relatives.

A situation of different body size evolvabilities is also supported by the comparison between the different degrees of climatic and morphological diversification shown by *Pristurus* and *Hemidactylus* in Abd al Kuri. It is plausible that the small area and ecological diversity provided by the island of Abd al Kuri (Fig. 1) has limited the chances of diversification in *Pristurus* (which tend to diversify in allopatry rather than along different morphologies, as seen in
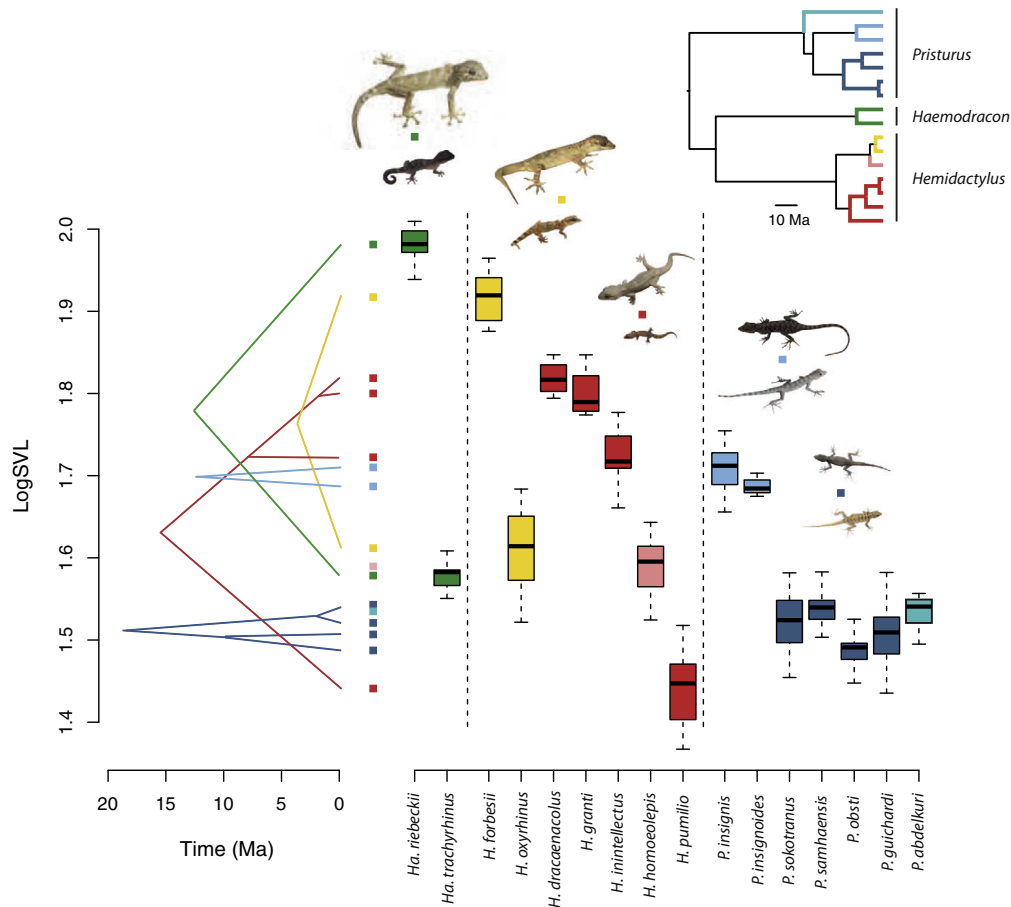
Fig. 4. Body size variation of the 16 species of geckos in the archipelago. The plot on the left side shows body size reconstructed on each of the intra-island diversifying clades in the Socotra Archipelago (each highlighted by different colors). The plot on the right provides a visualization of the ranges of body size variation of each species by means of boxplots. The pictures provide a visualization of the most extreme sizes attained within each clade. From left to right: *Haemodracon ribeckii* (up, photo credit Roberto Sindaco), *Haemodracon trachyrhinus* (down, photo credit Edoardo Razzetti); *Hemidactylus forbesii* (up, photo credit Roberto Sindaco), *Hemidactylus oxyrhinus* (down, photo credit Roberto Sindaco); *Hemidactylus dracaenacolus* (up, photo credit Roberto Sindaco), *Hemidactylus pumilio* (down, photo credit Roberto Sindaco); *Pristurus insignoides* (up, photo credit Roberto Sindaco), *Pristurus insignis* (down, photo credit Roberto Sindaco); *Pristurus obsti* (up, photo credit Roberto Sindaco); *Pristurus samhaensis* (down, photo credit Roberto Sindaco). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Socotra) but has not limited diversification in *Hemidactylus* (which can potentially diversify across different morphologies in sympatric scenarios).

Another possibility may imply that not all genera experience homogeneous amounts of ecological opportunity, even in the same island (Losos, 2010). The fact that *Pristurus* is diurnal and *Hemidactylus* and *Haemodracon* are nocturnal suggests that their ecological contexts, although similar in their physical attributes, may differ in terms of the ecological interactions with other organisms. For instance, the existence of other diurnal lizards such as the lacertid lizard *Mesalina* and the skinks of the genera *Hakaria* and *Trachylepis* may have limited the possibilities of niche expansion in *Pristurus*, but not in *Hemidactylus* and *Haemodracon*, which constitute the only two genera of nocturnal lizards in the islands (Razzetti et al., 2011).

As opposed to *Pristurus*, in *Hemidactylus* and *Haemodracon*, diversification in islands resulted in extreme body size divergences, particularly at the early stages of diversification. This is a common outcome of diversification in islands where groups are released from competition and predation and are able to expand the morphospace often producing extreme phenotypes (Losos and Ricklefs, 2009; Moen and Wiens, 2009). The fact that in both islands such instances of extreme body size divergence take place within the same climatic envelopes, involving sympatric scenarios, is consistent with size-mediated resource partitioning (Moen and Wiens, 2009). In the case of Abd al Kuri, given the small size of

the island, thus limiting opportunities for allopatric speciation, it is plausible that speciation and size divergence could have been simultaneous. This would be the case if size divergence was driven by strong intra-specific competition leading to disruptive selection on body size (Nosil, 2012). In the case of the island of Socotra, its larger area and more complex topography could easily allow a slightly different scenario: speciation in allopatry followed by a secondary contact in which size divergence would take place by character displacement (Grant and Grant, 2009; Stuart and Losos, 2013).

In the clades where successive splits take place, as in *Hemidactylus* from Socotra (clade 4), the extent of body size diversification decreases through time, as has been detected in many other insular groups (Mahler et al., 2010), indicating a progressive saturation of the available niches (Mahler et al., 2010). Such saturation may potentially explain the rapid transition from body size diversification to climatic diversification as intra-island diversification proceeds (Fig. 6).

Finally, our results also show that, aside of intra-island diversification, other processes as dispersal also played a role at producing the patterns of ecological and phenotypic structuration in the Socotra Archipelago. This is the case of the recently arrived *H. homoeolepis*. This species shows a very wide climatic envelope and a distribution that greatly overlaps with most of the other *Hemidactylus* species in Socotra. At the same time it differs
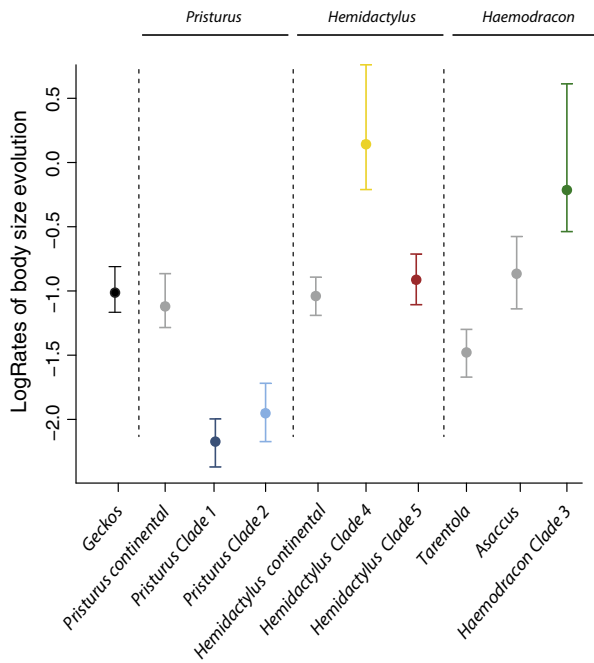
Fig. 5. Plot of the mean relative rates of body-size evolution and their associated 95% confidence intervals for island clades and their continental close relatives, estimated by a Brownian motion model assuming rate heterogeneity along the tree (model 1, see main text for details).
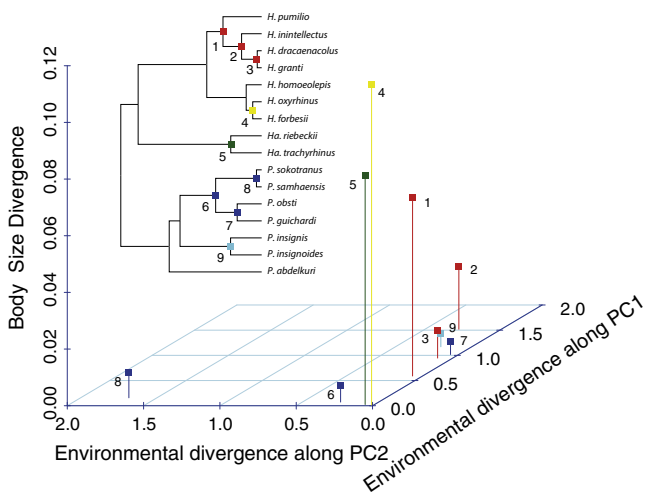

Fig. 6. Plot showing the size and climatic divergences involved in each of the intra-island speciation events that took place within the Socotra Archipelago, as estimated by means of absolute standardized contrasts. Numbers and colors correspond with those in the phylogeny. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

completely in size from all other congeneric species in the island (Fig. 4). A similar case may involve the two distinct clades of Socotran *Pristurus* (big *Pristurus* of clade 1 and small *Pristurus* of clade 2). These, according to our dating estimates, evolved from independent biogeographic origins, are mostly sympatric (sharing similar climatic envelopes) and exhibit highly dissimilar sizes (Fig. 4).

Both cases provide circumstantial evidence for a process of "size assortment", in which inter-specific competition acts as a filter, by means of extinction or failed colonizations, and only allows certain species (with certain traits) to coexist in the same community (Case and Bolger, 1991). Similar patterns consistent with species assortment are not uncommon in insular communities (Case and

Bolger, 1991; Losos, 2009). It is plausible that only species substantially differing in size, such as the big (clade 1) and small (clade 2) *Pristurus*, or substantially differing from all the other species preexisting in the island, as in the case of *H. homoeolepis*, could establish in Socotra. However, given that our analyses did not take into account the sizes of species other than the ones present in the Socotra Archipelago, we cannot rule out a possible size adjustment (e. g. character displacement) after the animals dispersed into (or were isolated in) the islands.

5. Conclusions

In this study we used the complete fauna of geckos of the Socotra Archipelago to test whether the three gecko genera occurring in the islands (*Hemidactylus*, *Haemodracon* and *Pristurus*) followed similar patterns of intra-island diversification. According to our results, different genera showed contrasting patterns of climatic and morphological diversification within the same archipelago. While in the nocturnal *Hemidactylus* and *Haemodracon* intra-island diversification involved great differences in body size and presented a great conservatism in their climatic envelopes, an opposite pattern emerged in the diurnal *Pristurus* in which most of the intra-island diversification involved differences in the climatic envelope but almost no morphological differentiation. Low morphological evolvabilities in *Pristurus* could potentially explain these contrasting patterns. This is consistent with our results on the rates of body size evolution, which show that insular *Pristurus* attain the lowest rates compared of the three insular genera. Moreover, rates of body size evolution in insular *Pristurus* were lower than the rates computed for their continental close-relatives.

Overall this study illustrates how different groups can substantially differ in their patterns of intra-island diversification and highlights the importance of taxon-dependent factors at determining different outcomes of diversification in the same insular environment.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2016.02.007.

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