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Stable isotopes and diet uncover trophic-niche divergence and ecological diversification processes of endemic reptiles on Socotra Island

Natalia Martín[a,b], Sergi Martínez[a], Eudald Pujol-Buxó[a], Amador Viñolas[c], Gustavo A. Llorente[a], Carola Sanpera[a], Raquel Vasconcelos[d,e], Salvador Carranza[e], Xavier Santos[d,*]

[a] Departament de Biologia Animal, and Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Barcelona, Spain.

[b] Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional. (CIIDIR Oaxaca), Instituto Politécnico Nacional (IPN). Hornos 1003, Col. Nochebuena, Santa Cruz Xoxocotlán, 71230, Oaxaca, México.

[c] Museu de Ciències Naturals de Barcelona. C/ Passeig Picasso s/n. 08003 Barcelona, Spain.

[d] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Universidade do Porto, Campus Agrário de Vairão, R. Padre Armando Quintas 7, 4485-661 Vairão, Portugal.

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

[*] Corresponding author: Xavier Santos. E-mail: xsantossantiro@gmail.com

Abstract: Ecological diversification on islands typically results in divergence of ecological niches. As diet is a major component of species niches, we hypothesize that sister species within island monophyletic groups diversify in their dietary preferences. We have examined this hypothesis in two *Haemodracon* and four *Hemidactylus* species endemic reptiles of from Socotra Island (Yemen), corresponding to two independent colonization events. Convergence i.e., similar dietary patterns of phylogenetically unrelated species, was also examined. Trophic niches were studied by the analysis of carbon and nitrogen stable isotopes combined with faecal samples. We collected tail tips (for isotopes) and faecal pellets during two visits in 2013 and 2014 to Socotra. Specific trophic niche widths inferred from stable isotopes were estimated from ellipse-based metrics, whereas interspecific differences were compared by linear mixed models and examined in a phylogenetic framework. From faecal samples, diet variation among species was quantified by the Bray-Curtis index. Isotope and dietary interspecific divergence was compared with Mantel tests. For both isotopes, models detected interspecific differences between sister species i.e., trophic niche divergence and also interspecific similarities of distant lineages that use similar microhabitats i.e., ecological convergence. We did not find any phylogenetic signal neither in the interspecific differences in $\delta^{13}C$ nor in $\delta^{15}N$ isotopic values; thus species phylogenetically more closely related did not have more similar isotopic niches. The Mantel test demonstrated similar interspecific divergence using isotopes and faecal samples. In a phylogenetic context, trophic-niche interspecific comparisons highlight some mechanisms that are driving ecological diversification and speciation of Socotra Island.

Key words: ecological diversification, endemism, reptile, Socotra, stable isotopes, trophic niche.

1. Introduction

Islands have long been recognized as natural laboratories to study the patterns of species diversification (Parent and Crespi, 2006; Grant and Grant, 2008; Losos and Ricklefs, 2009; Algar et al., 2013). Colonization of islands represents the opportunity for colonizers to find new resources unconstrained by mainland biota, then facilitating diversification in novel directions (Losos and Ricklefs, 2009). The degree of such a diversification can be mediated by inherent islands characteristics such as geological history, geographic location, size, and isolation time (MacArthur and Wilson, 1967; Del Arco et al., 2006; Fernández-Palacios et al., 2011). The absence of top predators, low species richness and short trophic chains are common rules on islands (MacArthur and Wilson, 1967; Losos and Ricklefs, 2009) that ultimately reduce antagonistic interactions and may facilitate ecological diversification. Ecological diversification and speciation on islands typically results in divergence of ecological niches (Nosil, 2012). Defined as the ways in which organisms obtain resources and interact with the environment, the ecological-niche concept has multiple components being diet and habitat use two major axes (Schoener, 1989). Thus, description of the realized niche (i.e. the subset of fundamental niche where species are restricted due to their interspecific interactions; Soberón and Nakamura, 2009) among phylogenetically related species may illustrate which are the drivers of ecological divergence and increase our understanding of mechanisms that govern intra-island speciation (Diamond, 1986; Losos, 2010). Independent lineages in islands (i.e. those resulted from independent colonization events) can develop similar diversification modes producing consistent patterns of eco-morphological convergence (Losos et al., 1998). This similarity among phylogenetically independent lineages could evidence similar evolutionary processes in response to

island environmental factors (Montaña and Winemiller, 2013), for example related to exploitation of a limited set of available food and habitat resources.

In this study, we have described and compared the isotopic signature of six reptile species inhabiting Socotra, by the quantification of carbon and nitrogen stable isotope ratios. Stable isotope analysis (SIA) is a widespread tool in studies of diet composition, trophic interactions, habitat use, and migration (Layman et al., 2007; Caut, 2013). SIA quantifies the ratio between any given element and its stable isotope. Comparisons can then be made between isotopic ratios in tissues of different organisms to make dietary or trophic level inferences. The most commonly used elements are carbon (C) and nitrogen (N); the carbon isotope ratio ($\delta^{13}C$) changes minimally through food webs (Rounick and Winterbourn, 1986), whereas the nitrogen isotope ratio ($\delta^{15}N$) of a consumer enriched by $\sim 3‰$ relative to that in the diet (Minagawa and Wada, 1984). Thus, $\delta^{13}C$ shows original carbon source of a consumer' nutrients (e.g. type of habitat), and $\delta^{15}N$ estimates consumer relative trophic position (Post, 2002). SIA provides insights into trophic relationships among organisms, and hence it has been an important advance in food-web ecology dynamics (Layman et al., 2012). However, isotopic ratios can vary according to a number of environmental and physiological factors, notably the C3/C4 photosynthetic pathway of plant species (higher $\delta^{13}C$ values for C4 plants; Rounick and Winterbourn, 1986) and precipitation rates (higher $\delta^{13}C$ values in more arid zones; Kohn, 2010). SIA is an indirect characterization of organisms' diet, and interpretation of isotope data is exposed to potential ambiguity (Layman et al., 2012). Hence, environmental variation of sampling sites and additional data sets particularly diet analysis are necessary to provide answers for questions regarding trophic ecology of organism (Layman and Post, 2008). For this reason, we also examined faecal pellets from a subsample of reptiles used in the isotope study. Isotope and diet studies in

parallel are adequate tools to examine dietary niche segregation (e. g. in cichlid fishes; Genner et al., 1999; Hata et al., 2015) and convergence (cichlids and centrarchids; Montaña and Winemiller, 2013).

This study was conducted in Socotra Island, the main island of an archipelago of continental origin located in the northern part of the Indian Ocean and isolated from Arabia in the Red Sea and Gulf of Aden around 30-17 Mya (Autin et al., 2013). The island show an elevational / climatic gradient (arid in lowlands and more humid in mountains), and two main lithologies, namely granitic and limestone (Fig. 1). Almost all reptile species in Socotra are endemic (29 out 31; Razzetti et al., 2011; Sindaco et al., 2012; Vasconcelos and Carranza, 2014), with phylogenetic studies demonstrating a number of independent colonizers from the mainland that diversified on the island, which then over time led to the current endemic species (Gómez-Díaz et al., 2012; Badiane et al., 2014). Because of their low metabolic rate and resistance to dryness and, in some groups, to salinity (e.g. geckos), reptiles are the second most capable vertebrate group of colonizing islands after birds (Carranza et al. 2000). For this reason, they represent a good model group to understand evolutionary patterns and processes of island colonization and diversification (Losos and Ricklefs, 2009; Camargo et al., 2010). The six gecko species studied, two species of the genus *Haemodracon* Bauer et al., 1997 and four species of the genus *Hemidactylus* Oken, 1817, conform two monophyletic lineages based on independent colonization events and further intra-island diversification (Gómez-Díaz et al., 2012; Simó, 2012). *Haemodracon* is an endemic Socotran genus and only these two species have been described. In contrast, *Hemidactylus* is a widespread genus on the world with seven species occurring in the island; from these species, only four were selected for this study according to their phylogenetic relatedness within a single colonizer event (Gómez-Díaz et al., 2012).

Within an historical context, the description of their trophic niches is expected to contribute to understand how the reptile ecological diversification occurred in Socotra. Specifically we tested the hypothesis that there was trophic diversification between phylogenetically related species, and eventual convergence between phylogenetically unrelated ones.

To attain this general aim, the specific objectives and questions were: (i) to describe the carbon and nitrogen isotopic ratios of two *Haemodracon* and four *Hemidactylus* endemic geckos from Socotra Island; (ii) to examine whether isotopic signatures are related to habitat selection (expectation of lower δ^{15}N ratios in vegetation habitats for the foreseeable presence of more herbivorous arthropods which would be in lower trophic levels; Layman et al., 2012), elevation (expectation of lower δ^{13}C values at higher wetter altitudes; Kohn, 2010), and soil lithology (expectation of higher δ^{13}C values in limestone than igneous ground due to the rich carbon composition and sea origin; Jardine et al., 1989), as sources of isotopic variation; (iii) within a phylogenetic comparative framework, to examine the phylogenetic signal of the trophic niche diversification within the six species studied; and (iv) to compare whether isotope and dietary interspecific differences are related.

Material and methods

2.1. Study area

The Socotra Archipelago is located in the northern part of the Indian Ocean, 230 km NE of the Horn of Africa and 350 km south of Ras Fartak, on the Arabian coast (Fig. 1). It has a total area of 3,625 km^2, and it is composed of a large main island, Socotra, and three islets, Samha, Dharsa, and Abd al Kuri. This archipelago is a fragment of the Gondwana Supercontinent, isolated in the Indian Ocean around 17-30

Mya (Autin et al., 2013). In 2008, Socotra was recognized as a World Natural Heritage site by the United Nations Educational, Scientific and Cultural Organization (UNESCO, 2014), because of its singularity and endemism rate of flora and fauna. For example, there are about 825 species of vascular plants, 307 of which are regarded as endemic (Miller and Morris, 2004). Similarly, there is a high level of endemism of fauna (Van Damme, 2009; Batelka, 2012). The lithology of Socotra Island consists of igneous stones basically located on the Haggar Mountains, and limestones occupying the rest of the island (Scholte and De Geest, 2010). Overall, the climate corresponds to the boundaries of the monsoonal precipitation regime with mean annual rainfall being 216 mm (Scholte and De Geest, 2010) and mean annual temperatures ranging between 17.9°C and 28°C (Batelka, 2012). However, there is climatic variation along the altitudinal gradient with arid climate up to 1000 m elevation and semi-arid conditions due to the presence of fog and mist brought by sea winds from 1000 m to the top Haggar Mountains at 1500 m. Accordingly, Socotra has a remarkably diverse vegetation cover, with 19 land-cover classes (Král and Pavlis, 2006) and homogeneous land units (Attorre et al., 2014), arranged on a geo-altitudinal gradient (De Sanctis et al., 2013). In summary, De Sanctis et al. (2013) identified four main vegetation zones each of them including several types of woody, shrub and herbaceous vegetation types: 1) between 0 and 200 m altitude, an arid coastal plain on alluvial substrata with shrubland and grassland communities; 2) between 200 and 400 m, a transition zone; 3) between 400 and 1000 m, an arid limestone zone interspersed with hills and plateaus; and 4) between 1000 and 1500 m, a semi-arid upper zone of the Haggar mountains on a granitic substratum.

2.2. The reptile community and species sampling

There are 31 reptile species, 29 of those endemic to the archipelago (Razzetti et al., 2011; Sindaco et al., 2012; Vasconcelos and Carranza, 2014). Phylogenetic studies have fixed the historical relatedness of Socotran to Arabian and Malagasian reptiles (Schätti and Utiger, 2001; Nagy et al., 2003; Sindaco et al., 2012; Gómez-Díaz et al., 2012; Badiane et al., 2014). Recent phylogenic studies suggested old colonization events from mainland and further intra-island speciation (Gómez-Díaz et al., 2012; Badiane et al., 2014).

Stable isotopes and diet were described in two groups of phylogenetically related endemic species, all of them with nocturnal activity. The first group is composed of two species of the endemic Socotran gecko genus *Haemodracon* (*H. riebeckii* [Peters, 1882]; and *H. trachyrhinus* [Boulenger, 1899]; Supplementary Materials S1) which diversified on the island (Simó, 2012). The second group is composed by four gecko species of the globally distributed genus *Hemidactylus* (*H. dracaenacolus* Rösler and Wranik, 1999; *H. granti* Boulenger, 1899; *H. inintellectus* Sindaco et al., 2009; and *H. pumilio* Boulenger, 1903; Supplementary Materials S1). These *Hemidactylus* species form a monophyletic lineage resulting from intra-island speciation with a common ancestor that originated by vicariance from Arabian mainland taxa ca. 14 Mya (Gómez-Díaz et al., 2012). Other independent *Hemidactylus* transmarine colonization events arrived more recently to Socotra (e.g. *H. oxyrhinus* Boulenger, 1899; *H. forbesii* Boulenger, 1899; and *H. homoeolepis* Blanford, 1881; Vasconcelos and Carranza, 2014); the lack of samples and their independent origin were the reason to exclude these species from analyses.

Field sampling was conducted between March and April in 2013 and 2014. Two to four researchers systematically visited 34 sites throughout the island (Fig. 1). Sites were chosen randomly in order to cover an altitudinal gradient, different habitat types,

and the two main lithologies of the island. Reptiles were collected by hand or noosing, and tail tips of 87 specimens of the six focal species were collected for isotopic analyses. Each reptile specimen was identified to species level, sexed and measured (SVL, snout-vent length, accuracy= 0.5 mm). These specimens were gently palpated in the abdomen, and pellets were collected from 59 of them. Major microhabitat type (i. e. cliff, ground and vegetation) and geographic coordinates of each individual were registered for further analyses. Cliff was assigned to geckos found on vertical positions of big rocks and stony walls, and ground to specimens found on the ground or under stones. Vegetation was assigned to geckos found on tree trunk or branches tree and shrub. We acknowledge that this is a broad microhabitat classification; however in Socotra there is relatively little microhabitat specialization among lizards compared to that found in the tropics. Given the more generalist nature of the lizards in Socotra, these broader categories seemed more useful when trying to detect different nitrogen ratios for geckos found on vegetation due to the particular consumption of herbivorous prey. Tail tips and pellets were transported to the laboratory for further analyses at the Department of Animal Biology of the Universitat de Barcelona. All specimens were released to the exact place of capture.

2.3. Laboratory procedures

Tail tips were used for the analysis of carbon and nitrogen stable isotopes (hereafter $\delta^{13}C$ and $\delta^{15}N$). Since the carbon isotope ratio $^{13}C/^{12}C$ (expressed in standard delta notation as $\delta^{13}C$) changes minimally (circa 1‰) as carbon moves through food webs (Rounick and Winterbourn, 1986), it is commonly used to identify the source of carbon in the tested individuals and ultimately at the base of the food web. In contrast, the nitrogen isotope ratio $^{15}N/^{14}N$ ($\delta^{15}N$) in consumer's tissues is typically considered to

be enriched by circa 3‰ relative to that in the diet (Minagawa and Wada, 1984). It is thus commonly used to estimate trophic position along food chains with increase between 2 - 6‰ per trophic level (Caut, 2013). Thus, $\delta^{13}C$ can be used to track the original sources of consumer nutrients, and $\delta^{15}N$ can be used to estimate a consumer relative trophic position, i.e. higher $\delta^{15}N$ indicates higher trophic position (Post, 2002). The data have not been corrected for diet-tissue discrimination since all the samples were from the same tissues (tail tip). We acknowledge that it can be intra- specific (size/age-related) differences in the discrimination factor within a single tissue (Steinitz et al., 2015). To minimize such issues, we excluded any lizards with regrown tails from the study.

In the laboratory, tail tips were cleaned, dried and cut to very small pieces. Subsamples were weighed to the nearest µg (0.25-0.5 µg) and placed into tin capsules for $\delta^{13}C$ and $\delta^{15}N$ analyses. Analyses were carried out at the Serveis Científico-Tècnics (Universitat de Barcelona, Spain) by means of a Thermo-Finnigan Flash 1112 (CE Elantech, Lakewood, NJ, USA) elemental analyzer coupled to a Delta-C isotope ratio mass spectrometer via a CONFLOIII interface (Thermo Finnigan MAT, Breman, Germany). Stable isotope ratios were expressed in conventional notation as parts per thousand (‰), using: $\delta X = ((R_{sample}/R_{standard}) - 1) * 1000$, where X is ^{15}N, ^{13}C and R is the corresponding ratio $^{15}N:^{14}N$, $^{13}C:^{12}C$. Reference materials from the International Atomic Energy Agency (IAEA CH6, IAEA CH7 and USGS 24 for C, and IAEA N1, IAEA N2 and IAEA NO3 for N) were inserted every 12 samples to calibrate the system and compensate for any drift over time. $\delta^{15}N$ values are expressed relative to atmospheric nitrogen (VAIR) and $\delta^{13}C$ values are expressed relative to Pee Dee Belemnite (VPDB). Replicate assays of standards indicated analytical measurement errors of ±0.1‰ and ±0.2 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. For animals, there is a

strong effect of lipid content on $\delta^{13}C$, resulting in lipid-rich tissues showing lower carbon isotope ratios (Post et al., 2007). These authors suggest that C:N ratios higher than 4 for terrestrial animals indicate high lipid content on the tissues analysed; in these cases, lipid extraction would have little influence on the $\delta^{13}C$ values. In the Socotran geckos examined, C:N ratios were similar among species and never exceeded 3.5 (Table 1), indicating low lipid content of tail tip samples.

In order to find the maximum differences between the six gecko species and to correlate them with differences in isotopic signatures among species, diet remains from pellets were photographed with an Olympus SZX10 stereoscope and identified at least to the Order level. The examination of Coleopteran elytra allowed these items to be identified at Family level. Some Hymenoptera items were classified to Family level by distinguishing between ants (Fam. Formicidae) and other Hymenoptera. Unfortunately, other arthropods could not be identified to a lower taxonomic level due to the exoskeleton fragmentation. The maximum lengths of Coleopteran elytra were measured with the program cellSens Standard 1.6. (2011). Samples were deposited in scientific collections at the Universitat de Barcelona (UB) and the Natural Science Museum of Barcelona (MCNB).

2.4. Data analysis for isotopes

The trophic niche width of each species was assessed by calculating several metrics (Layman et al., 2007): the convex hull area (TA) occupied by all individuals of each group in the $\delta^{15}N$ - $\delta^{13}C$ biplot, and the mean distance to the $\delta^{15}N$ and $\delta^{13}C$ centroid (CD). The latter is the average Euclidean distance of each sample to the ellipse centroid, and provides a measure of the average degree of trophic diversity within a particular species. The application of these metrics can be biased according to sampling size and

the existence of extreme values; for this reason, Jackson et al. (2011) proposed the calculation of the standard ellipse areas (SEA) with a correction for small sample sizes (SEAc). This method applies a Bayesian approach that takes into account uncertainty of the data, and allows at comparing isotopic community metrics between groups (Jackson et al., 2011). For each species, the ellipse centroid is the mean $\delta^{13}C$ and $\delta^{15}N$ values among the samples. Euclidean distances between ellipse centroids for the six species studied (i.e. difference in centroid location) were assessed following Turner et al. (2010). Two centroids occupied different locations (i.e. different trophic niches) if the Euclidean distance between them is significantly greater than zero. We also calculated the eccentricity (E; Turner et al., 2010) that gives insights into differences of the distribution of $\delta^{13}C$ and $\delta^{15}N$ values within a particular species (i.e. a measure of the covariation between both isotopes); thus, E = 0 means a circular ellipse and E = 1 describes a perfect relationship between both isotope values. Interspecific comparisons of these metrics were based on analysis of nested linear models and residual permutation procedures (RPP) implemented by Turner et al. (2010). SEAs were calculated following Jackson et al. (2011) implemented in the R package SIBER (Parnell and Jackson, 2013).

Sampling individuals at different locations can mask the identification of intra-population niche variation (Araújo et al., 2007), and may inflate variation in isotope values when sources vary spatially (Layman et al., 2012). Our aim was to examine variation in isotopic signatures of six reptile species within a phylogenetic comparative framework. Accordingly, knowledge of organisms' natural history can aid in the interpretation of isotope data (Layman et al., 2012). Moreover, several sources of isotope variation, i. e. lithology, altitude, microhabitat, and locality of capture, were considered on statistical analyses. For example, species can segregate spatially by the

soil lithology since the island is mainly composed by two main soil lithologies, namely limestone of marine origin and igneous rocks (Scholte and De Geest, 2010). Isotope values (especially $\delta^{13}C$) can be very sensitive to differences between terrains of marine and terrestrial origin (Harding and Reynolds, 2014). Altitude and microhabitat were animals were collected was considered since some of the species considered segregate spatially according to these factors (Razzetti et al., 2011).

Plant photosynthetic pathways, i.e. C3 and C4 plants, are also source of carbon and nitrogen isotope variation (e.g. C4 species have enriched carbon isotope ratios relative to C3 species; Rounick and Winterbourn, 1986). How C3 / C4 plants are distributed along the geo-altitudinal gradient in Socotra could contribute to better understand the causes of isotope variation in the six reptile species studied. Unfortunately, C3 / C4 plant distribution in Socotra is unknown; likewise, the proportion in which arthropods (the main geckos' prey) are feeding on plants with different isotopic ratio is also unknown. This makes very difficult the predictability of isotopic variation with altitude. In contrast, there is general evidence that $\delta^{13}C$ values increase at smaller precipitation rates within C3 and C4 plants (Weiguo et al., 2005; Kohn, 2010). Accordingly, the potential isotopic variation in lizards placed at different altitudes can be explained by the climatic and altitudinal gradient observed in Socotra.

A complete barcoding analysis of reptile species from Socotra recently demonstrated high levels of cryptic diversity (Vasconcelos et al., 2016). Although we do not know potential ecological or morphological differences between cryptic species, for those species involved in our study, we only used specimens from the more widespread clade.

Differences in $\delta^{13}C$ and $\delta^{15}N$ values among the six species studied were examined by fitting Linear Mixed Models (LMMs) with the package nlme (Pinheiro et

al., 2014). LMMs were conducted separately for $\delta^{13}C$ and $\delta^{15}N$ as both values refers to different trophic and habitat information. As potential fixed effects we included taxa, altitude, soil lithology and microhabitat. Altitude of localities was included as a continuous variable in the models as a potential covariable. The factor lithology was included as a predictor variable with two levels: limestone and igneous. Microhabitat where each reptile was collected was also considered as a categorical predictor with three main types namely cliff, vegetation and ground, given that it could influence isotopic signatures of specimens (Clementz and Koch, 2001). Locality was always included as a random effect in order to account for lack of independence of isotopic signatures of reptiles collected in the same localities. Sex were excluded as a factor from the analysis as a preliminary MANOVA test demonstrated no sexual differences within the six species studied ($F_{2,69} = 2.3$, $P = 0.06$).

In a first step, we fitted a full LMM with all taxa and all potential predictors using maximum likelihood (ML) to subsequently evaluate each fixed effect using likelihood ratio tests (LRTs). Therefore, we dropped from the model only the predictor of interest in each case, obtaining AIC values for the full and simplified models, plus a LRT and a p-value of the simplified model tested against the full model in each case. In a second step, we examined particular effects and their interactions (e. g. the effect of microhabitat on isotope ratios among species located on limestone sites). To conduct these analyses, some species were removed (e. g. *H. pumilio* as it is only present in ground microhabitats and *H. granti* only found in igneous lithologies) before refitting and testing the terms of the model using the same procedures. In all cases we did residual analysis of the models to discard geographic or non-random patterns in the residuals, that is, patterns in the data that would not be explained by the models.

Snout-vent length (SVL) is a potentially interesting variable to be included in LMM analyses since many reptile species show ontogenetic dietary shift, and this can be reflected in variation of $\delta^{13}C$ and $\delta^{15}N$ signatures according to body size. A recent study has demonstrated that for *Hemidactylus* and *Haemodracon* species from Socotra, intra-island diversification resulted in great differences in body size (García-Porta et al., 2016). Within the samples used in our study, the biggest individuals of some species were smaller that the smallest individuals of others (Table 1). In parallel to this morphological differentiation, the studied species experienced habitat segregation (Supplementary Materials S2). For example, within the six species studied, the soil specialists *H. pumilio* were the smallest species, vegetation species had intermediate size, and a cliff species were the largest ones (*H. riebecki*). In order to avoid a collinear effect between SVL and the habitat where species inhabit, we did not consider lizards SVL in the LMM analyses. Analyses of isotopic data were done using R software (R Core Team, 2014).

2.5. *A comparative analysis of intraspecific isotopic differences*

We examined the phylogenetic signal of the isotopic differences between the six species studied. To conduct this analysis we first inferred an ultrametric tree using Bayesian Inference with the software BEAST v.1.8.0 (Drummond and Rambaut, 2007) (Fig. 2). The dataset included 371 base pairs of the 12S rRNA mitochondrial gene for one representative of each one of the six species of geckos included in this study. Three individual runs of $5x10^7$ generations were carried out, sampling at intervals of 10000 generations. Models and prior specifications applied were as follows (otherwise by default): model of sequence evolution for the 12S gene GTR+G (inferred with jModeltest v.0.1.1; Guindon and Gascuel, 2003; Darriba et al., 2012); Yule process tree

prior; random starting tree; base substitution prior Uniform (0,100); alpha prior Uniform (0,10). Posterior trace plots and effective sample sizes (ESS) of the runs were monitored in Tracer v1.5 (Rambaut and Drummond, 2007) to ensure convergence. The results of the individual runs were combined in LogCombiner discarding 10% of the samples and the maximum clade credibility (MCC) ultrametric tree was produced with TreeAnnotator (both provided with the BEAST package). The ultrametric tree was loaded into R (R core team, 2015) using the functions from the package ape (Paradis et al., 2004). Since the tests for phylogenetic signal are poor with a small number of species, we tested for phylogenetic signal using two different indices. We estimated and tested the significance of Pagel's λ (Pagel, 1999) and Blomberg's K (Blomberg et al., 2003) indices using *phylosig* from the *phytools* package (Revell, 2012), which incorporates individual variation (following Ives et al., 2007). We used the implemented randomization tests (5000 iterations) to determine the significance level of both indices.

2.6. Comparisons of diet, stable isotopes and genetic distances of gecko species

From the abundance matrix of the taxonomic prey groups identified in the 59 pellets analyzed, dietary similarities between pairs of individuals were calculated with the Bray-Curtis similarity index. An ANOSIM analysis was further performed based on the Bray-Curtis similarity scores, using 999 random permutations. This test compares how similar diets are among species, by giving a general R-value and further pairwise comparisons between species. A Cluster Analyses was performed to visualize which species have more similar diets.

To evaluate the completeness of the sampling, diversity accumulation curves were calculated for the six species studied. Curves were computed with EstimateS (Colwell, 2013), in order to eliminate the effect of the order in which the data is

included in the analysis (Moreno and Halffter, 2000). Diversity accumulation was calculated by the Chao1 metric (Chao, 1984) which estimates taxa richness identified from pellet analysis. Correlation between predator (reptiles) size (snout-vent length, SVL) and prey sizes (maximum length of coleopteran elytra) was inferred from 33 elytra measured in the laboratory from pellets of four species: *H. riebeckii* (n = 4), *H. dracaenacolus* (n = 13), *H. granti* (n = 3) and *H. inintellectus* (n = 13). We used maximum length of coleopteran elytra as surrogate of coleopteran body length. Based on data from elytra and body size measured from species of the same Families found in pellets, the relative elytra length (and range) averaged 63.58% of the coleopteran size (range 58,41% - 69,36%; A. Viñolas, unpublished data). We used coleopteran elytra as this is the commonest prey type among the six geckos examined (see Results). Due to the low sample size of some species, we pooled all the data in a single correlation in order to get exclusively a general trend of the predator-size vs prey-size relationship.

Diet description is based on the pellets collected from specimens used for SIA. We acknowledge that this subsample is not enough to describe the diet of the six target species, but it is a useful approach to independently corroborate the reliability of intraspecific differences in isotopes. The correlation between diet and stable isotope values of the six gecko species analyzed was performed by Partial Mantel tests using the genetic distance between species as a covariate. To run Mantel test, first similarity matrices between pairs of species in stable isotopes (ISOT), diet (DIET), and genetic distance (GENET) were performed. ISOT was calculated from the individual $\delta^{13}C$ and $\delta^{15}N$ values of geckos using Euclidean Distances between pairs of species. DIET was calculated from the matrix of relative abundances of prey types consumed by gecko species using the Bray-Curtis index. Finally, GENET was calculated as the evolutionary divergence over 37 published sequence pairs of the 12S mitochondrial gene among the

six studied species (Gómez-Díaz et al., 2012; Simó, 2012), and represented the average number of base differences per site among species. There were a total of 376 base pairs in the final dataset. This analysis was conducted in MEGA5 (Tamura et al., 2011). The Partial Mantel test correlation of ISOT and DIET was performed with Passage 2 (Rosenberg and Anderson, 2011). To take into account the phylogenetic relations among species, DIET and ISOT matrices were compared keeping GENET matrix constant.

2. Results

3.1. SVL and microhabitat of the target species

Based on our own data set, the six species varied greatly in body size (see body-size range in Table 1): *H. pumilio* and *H. trachyrhinus* were the smallest species, individuals of *H. inintellectus*, *H. dracaenacolus*, and *H. granti* had intermediate sizes, and *H. riebeckii* was the largest species (Supplementary Materials S2). In terms of habitat preference, *H. pumilio* was a ground-dwelling specialist, *H. trachyrhinus* and *H. dracaenacolus* were mostly or exclusively found on vegetation (i. e. *Cissus* bushes, *Dracaena cinnabari* Balf. f. trees; respectively), and the rest of species largely occupied vegetation or cliff habitats (Supplementary Materials S3). The six species also differed in terms of altitudinal range (Supplementary Materials S4): *H. dracaenacolus* and especially *H. granti* were highland species whereas the rest of species occur on medium-high to lowlands (Razzetti et al., 2011).

3.2. Stable isotope differences

SEAc varied among the six species studied, being *H. trachyrhinus* and *H. pumilio* the species with the largest and *H. dracaenacolus* and *H. granti* the smallest

areas (Table 2; Fig. 3). *Hemidactylus granti* showed the most different SEAc with no overlap with the rest of species. *Haemodracon trachyrhinus* and *H. pumilio* partially diverged with respect to *H. riebeckii*, *H. dracaenacolus* and *H. inintellectus* that almost completely overlapped (Fig. 3). The distance between ellipse centroids was significantly different of 0 for *H. granti* and *H. pumilio* with respect to the rest of species (Supplementary Materials S5).

We also found interspecific differences in MDC and E. Thus, *H. trachyrhinus* and *H. pumilio* had significantly higher MDC values than the rest of species ($p < 0.05$ in all the comparisons), suggesting larger ellipses (Fig. 3). *Haemodracon riebeckii* differed in E respect to *H. trachyrhinus*, *H. granti* and *H. dracaenacolus*, and *H. granti* and *H. inintellectus* also differed ($P < 0.05$ in all the comparisons).

Likelihood ratio tests on LMMs showed that the only significant factor explaining differences for δ^{13}C was Lithology (LRT = 18.96, $P < 0.0001$), whereas Taxa, Habitat and Elevation were not significant ($P > 0.4$; Supplementary Materials S6). Reptile samples collected on limestone had higher δ^{13}C values than those collected on igneous localities. On a second step, we repeated LMMs for sites located in limestone (*H. granti* excluded) and igneous soil (*H. riebeckii* and *H. dracaenacolus* excluded) separately. In these new LMMs, we found interspecific differences both in limestone (LRT = 11.53, $P = 0.02$) and igneous localities (LRT = 9.78, $P = 0.02$; Table 1). On limestone localities, differences among taxa were motivated by high *H. trachyrhinus* and *H. pumilio* δ^{13}C values (Fig. 4a), whereas on igneous localities by low *H. granti* δ^{13}C values (Fig. 4a).

The LMM for δ^{15}N showed that microhabitat and elevation were influential factors (LRT = 5.56, $P = 0.06$; LRT = 4.45, $P = 0.03$ respectively), whereas taxa and lithology were not significant ($P > 0.1$; Supplementary Materials S6). Thus, we repeated

the LMMs excluding lithology and removing *H. granti*, because it was a species with clear altitudinal segregation from the rest (Supplementary Materials S4), and *H. pumilio*, because it was a species almost exclusively found on ground microhabitat (Supplementary Materials S3). In this model, microhabitat maintained a significant effect (Table 1, LRT = 5.66, *P* = 0.02) whereas elevation and taxa did not (*P* > 0.4). Finally, in the LMM conducted with *H. inintellectus* and *H. riebeckii*, the only geckos that were consistently found in two different microhabitats (cliff and vegetation), the only significant effect was Habitat (LRT = 4.38, *P* = 0.04); whereas Taxa, Elevation and the interaction Habitat x Taxa were not significant (*P* > 0.2). For both species, individuals collected on cliff had higher δ^{15}N values than those collected on vegetation (Fig. 4b).

We did not find any phylogenetic signal either in the interspecific differences in δ^{13}C isotopic values (K = 0.256, p = 0.8; λ = 0, *P* = 1.0) or in δ^{15}N isotopic values (K= 0.191, *P* = 0.8; λ = 0, *P* = 1.0). In other words, phylogenetically closer species did not have more similar isotopic niches.

3.3. Diet description and isotope-diet correlation

In total, 160 prey from 10 different arthropod orders were found as prey in gecko pellets: Araneae, Pseudoscorpionida, Chilopoda, Hymenoptera, Heteroptera, Orthoptera, Neuroptera, Homoptera, Blattodea and Coleoptera. The order Coleoptera was the commonest group found in pellets (71 prey, 44.4%), and was represented by seven families (Table 3). *Haemodracon riebeckii, H. dracaenacolus* and *H. inintellectus* were the species with a greatest number of orders represented in their pellets (seven Orders found in the diet within each these three species), while *H. granti* showed the lowest number of groups in its diet (Table 3). *Hemidactylus granti* had the most different diet

since it was the only species that foraged on Cleridae and Histeridae beetles, and did not present Araneae and Chilopoda on its diet (Table 3).

Accumulative curves of diversity for the six species studied showed different shapes (Supplementary Materials S7). For some species, the number of pellets was too low to account for a complete diet (e.g. *H. trachyrhinus*, *H. granti* and *H. pumilio*). Accordingly, more samples would be required to have a complete view of the diet of these geckos. Those species with a bigger sample size, *H. dracaenacolus* and *H. riebeckii* showed low prey diversity; the asymptotic shape of the curve for these two species suggested that the sample size was enough to describe their diet. In contrast, *H. inintellectus* showed the highest diversity in the diet, although the shape of the curve suggested that more pellets were needed to know the complete prey spectrum of this species (Supplementary Materials S7).

The ANOSIM indicated significant interspecific differences in diet (r = 0.081, *P* = 0.02). Pairwise comparisons indicated that pairs with the highest differences were: *H. trachyrhinus - H. pumilio* (*r* = 0.333, *P* = 0.04), *H. riebeckii - H. granti* (r = 0.322, *P* = 0.003), *H. trachyrhinus - H. granti* (r = 0.550, *P* = 0.008) and *H. granti - H. dracaenacolus* (r = 0.268, *P* = 0.001). The cluster tree showed four groups of species according to their diet (Fig. 5)*: (1) H. granti*, (2) *H. pumilio*, (3) *H. trachyrhinus* and finally (4) a group composed by the three biggest reptiles that commonly used vertical environments (*H. riebeckii*, *H. dracaenacolus* and *H. inintellectus*).

The size of elytra ranged between 1-7 mm. As expected, smaller reptile individuals foraged on smaller beetles, whereas the largest individuals foraged generally on bigger prey. The correlation between predator size and prey size was significant (all predators and prey pooled; r = 0.414, *P* < 0.0001). The individual that consumed the largest prey was not *H. riebeckii* but *H. dracaenacolus*. Large individuals also

consumed small prey, this fact meaning that there was some potential competition between species for small prey items.

The Partial Mantel test showed a correlation between DIET and ISOT matrices with GENET matrix keeping constant (R = 0.49, *P* = 0.07, 999 permutations). This means that the isotopic differences among species most probably reflected variation of diet among the six gecko species examined in Socotra.

3. Discussion

4.1. Intraspecific variation in isotope ratios and diets

This study describes for the first time the trophic niche of six endemic lizard species from Socotra using in tandem stable isotope and pellet analyses. The analysis of carbon and nitrogen stable isotopes described a scenario of contrasted trophic niches for some species and considerable overlap for others. The contrast is motivated by the soil lithology of sampling localities (δ^{13}C values) but also by the microhabitat where samples were collected (δ^{15}N values). When the lithology factor was controlled, some species also diverged in their δ^{13}C values suggesting that isotope analyses may contribute to identify interspecific trophic niche variation for Socotran reptiles.

We acknowledge that the isotopic signature of the six reptiles alone may not be sufficient to infer their trophic position and carbon source without an appropriate isotopic baseline, i. e. the isotopic signature of the food resources (Post, 2002). Moreover, the time scale information for tail tip isotopes (the entire life of a gecko for an original tail) versus faecal pellets (the last few days of an individual's diet) is different. Despite these limitations, pellet analyses showed that the six species studied were exclusively anthropophagous. And more importantly, the Mantel test demonstrated that diet similarities between pairs of species were correlated to isotope similarities; this

last result showed parallelism between isotopes and diet despite the time scale differences between both methods. The number of pellets used in this study was unfortunately small in some species (e. g. *H. pumilio*), and diversity accumulation curves suggest that more samples would be needed to know the complete dietary spectrum of the six analyzed species. The diet description was not the objective of this study since examination of pellets has a potential bias of information on reptile dietary studies (Francesco et al., 1997; Pérez-Mellado et al., 2011). However, the pellets examined were enough to identify some dietary differences that in turn were correlated with the isotopic signatures. *Hemidactylus pumilio* and *H. granti* had the most different diets probably related to the contrasted microhabitats (*H. pumilio* is the only typical ground-dwelling species), and altitudinal range (*H. granti* is typically a highland species) occupied by these species. The combination of pellet and stable-isotope analyses showed differences in trophic niche position among the six Socotran geckos studied.

Why *H. granti* showed the most divergent isotopic values? After controlling for lithology, the most likely explanation is that this species only occupies Socotran highlands. According to Schmiedl and Mackensen (2006), $\delta^{13}C$ can vary depending on the microhabitat occupied by the prey consumed by predators following environmental aridity gradients. This seems observed both in C3 and C4 plants (Weiguo et al., 2005; Kohn, 2010). Moreover, $\delta^{13}C$ ratio is higher in arid environments where C_4 plants (higher $\delta^{13}C$ values; O'Leary, 1988; Farquhar et al., 1989) are more abundant as they are more adapted to dry conditions than C_3 plants (lower $\delta^{13}C$ values). Although Socotra shows variation in vegetation types according to a geo-altitudinal gradient (De Sanctis et al., 2013), the distribution of C4/C3 plants and also which plant resources are consumed by gecko's prey are unknown. However, lower $\delta^{13}C$ ratios for plants living in

more humid environments seem a general trend (Kohn, 2010), and moving up to the food web, reptiles that live in more humid habitats are expected to have a lower $\delta^{13}C$ ratio. Taking into account the marked precipitation (rainfall and mist) increase in Socotra with altitude (Batelka, 2012), the lowest $\delta^{13}C$ values for *H. granti* matched the distribution of this gecko at the highest (and more humid) sites of Socotra.

Interestingly, we found a significant effect of $\delta^{15}N$ according to the microhabitats were species were primarily found. These differences accounted for reptiles on cliffs and vegetation (higher values on reptiles collected on cliffs), and this pattern persisted at the intraspecific level (e.g. between *H. riebeckii* and *H. inintellectus* individuals collected on these microhabitats). We acknowledge that plant resources could have disparate nitrogen tissue ratios, which then propagate up the food chain from herbivorous arthropods to geckos. Although we now have information on arthropods found in the diet of the gecko species from this study, we lack information of the plant species fed upon by these various arthropods. $\delta^{15}N$ values consistently differ between trophic levels (Minagawa and Wada, 1984). For this reason, differences at a microhabitat level observed within our study species could indicate consumption of prey types from different trophic position, perhaps related to prey type availability at each microhabitat (e.g. more predatory arthropods in cliffs and more herbivorous arthropods in vegetation). Indeed, our results would indicate that $\delta^{15}N$ values are sensitive enough to detect interspecific differences in microhabitat use among Socotran geckos.

Interspecific differences in microhabitat use and altitudinal segregation has promoted several *Haemodracon* and *Hemidactylus* species to present different isotopic niches. This argument is valid for *H. granti* (altitudinal segregation), *H. pumilio* (ground-dwelling specialist) and *H. trachyrhinus* (small size and vegetation specialist).

The other three species, *H. dracaenacolus*, *H. inintellectus* and *H. riebeckii* have more similar trophic niches. However, the examination of ellipse metrics gives new insights: *H. dracaenacolus* has the smallest ellipse area (surrogate of trophic niche width) that matches its ecological specialization. This gecko is listed as Critically Endangered (IUCN, 2015) as only occurs on a reduced part of the island and lives exclusively on *Dracaena cinnabari* trees (Razzetti et al., 2011). Extensive sampling on *Dracaena* trees across the island indicated that *H. dracaenacolus* and the couple *H. inintellectus*/*H. riebeckii* are not syntopic (authors, unpublished data). Thus, small ellipse area of *H. dracaenacolus* would reflect microhabitat extreme specialization that in turn may be related to ecological segregation among Socotran reptiles in face of evolutionary diversification.

4.2. Divergent trophic niches in a phylogenetic framework

The analysis of isotope quantification and faecal samples for the six Socotran geckos support some degree of trophic niche divergence. According to Losos and Ricklefs (2009), sympatry and high population densities reached by island reptile species induce competition for resources; in this scenario, selection may favor adaptations that reduce competition between species, including morphological divergence and resource segregation. Our results support this statement since within the six species studied, we found trophic divergence linked to microhabitat and also altitudinal (vicariance) segregation. For example, *H. dracaenacolus* and *H. granti*, two species with contrasting trophic niches, have parapatric distributions possibly linked to a vicariance process that occurred on the island approximately 2.3 Mya (Gómez-Díaz et al., 2012).

We did not find a phylogenetic signal in the isotopic differences among the six species studied. Thus, isotopic niche similarity between species of different genera suggests that diet diversification is largely uncoupled from the phylogenetic background. Although our sample is small (six species), this conclusion agrees with those regarding the cichlid fish community at the Lake Tanganyika (Muschick et al., 2012). The lack of phylogenetic signal seems a common pattern in evolutionary studies of islands (Losos, 2008) because of the high rates of evolutionary diversification early in the history of the new colonizers (Schluter, 2000). In contrast, phylogenetically unrelated species like *H. riebeckii* and *H. inintellectus* have the more similar trophic niches. They have rather comparable body sizes and were found in vertical microhabitats (cliff and vegetation); this correspondence could suggest evolutionary convergence that explains similarities between these species without having a common phylogenetic origin. Convergent evolution in reptiles has been largely studied in Caribbean *Anolis* lizards (Harmon et al., 2005) for which independent diversification at each island produced a set of convergent (specialist) lizard forms. Patterns of ecological convergence in independent lineages also have provided evidence for adaptation involving morphological feeding traits in fish communities (Montaña and Winemiller, 2012). Futures studies with the whole reptile community in Socotra will examine convergence within independent lineages that colonized the archipelago linking habitat selection, diet and morphology.

Isotopic-niche comparisons of the six gecko species in a phylogenetic framework (Gómez-Díaz et al., 2012; Simó, 2012) uncovered some diversification mechanisms occurring in Socotra during intra-island speciation. Microhabitat, altitudinal and body-size segregation have promoted Socotra to be an island with an amazing and very rich endemic reptile community (29 species; Razzetti et al., 2011;

Sindaco et al., 2012; Vasconcelos and Carranza, 2014) despite its rather small surface area (3,625 km^2) and aridity (Kier et al., 2009). This fact has promoted Socotra to be considered the Galapagos of the Indian Ocean (Van Damme and Banfield, 2011; Hájek and Bezděk, 2012). This study is the first attempt aimed at uncovering the ecological-based mechanisms that have promoted reptile diversification in Socotra.

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Table 1: SVL range (in mm), C/N proportion, and total isotopic mean values and standard error (SE) of $\delta^{13}C$ and $\delta^{15}N$ for the six Socotran lizards examined and grouped by microhabitats where individuals were observed. Sample sizes (n) are also given.

	SVL range (mm)	C:N	Total $\delta^{13}C \pm$ SE	n	Cliff $\delta^{13}C \pm$ SE	n	Vegetation $\delta^{13}C \pm$ SE	n	Ground $\delta^{13}C \pm$ SE	n
Haemodracon riebeckii	66-118	2.92±0.05	-20.86±0.37	12	-20.35±0.54	7	-21.56±0.80	5		
Haemodracon trachyrhinus	23-42	2.99±0.03	-19.56±0.78	13			-19.56±0.50	13		
Hemidactylus dracaenacolus	31-75	2.95±0.02	-20.65±0.18	14			-20.65±0.48	14		
Hemidactylus granti	54-74	3.07±0.01	-23.23±0.28	6	-22.77±0.83	4	-23.47±1.27	2		
Hemidactylus inintellectus	35-64	3.09±0.03	-20.64±0.27	27	-20.63±0.32	22	-20.67±0.80	5		
Hemidactylus pumilio	21-33	3.06±0.02	-19.72±0.57	15					-19.72±0.57	15
			$\delta^{15}N \pm$ SE	n	$\delta^{15}N \pm$ SE	n	$\delta^{15}N \pm$ SE	n	$\delta^{15}N \pm$ SE	n
Haemodracon riebeckii			11.11±0.37	12	11.69±0.59	7	10.31±0.57	5		
Haemodracon trachyrhinus			11.46±0.37	13			11.46±0.35	13		
Hemidactylus dracaenacolus			11.01±0.28	14			11.01±0.34	14		
Hemidactylus granti			5.87±0.59	6	6.71±0.9	4	4.61±0.90	2		
Hemidactylus inintellectus			11.72±0.33	27	12.01±0.35	22	10.98±0.57	5		
Hemidactylus pumilio			9.97±0.48	15					9.97±0.48	15

Table 2: Total area (TA), Standard ellipse areas (SEA), standard ellipse areas corrected for small sample size (SEAc), standard deviation (SD), and ellipse centroids as the $\delta^{13}C$ and $\delta^{15}N$ average values for the six gecko species examined.

| | TA | SEA | SEAc | SD | Centroids | |
					$\delta^{13}C$	$\delta^{15}N$
Haemodracon riebeckii	9.68	5.248	5.549	1.599	-20.858	11.125
Haemodracon trachyrhinus	22.045	11.397	12.647	3.276	-19.562	11.454
Hemidactylus dracaenacolus	4.33	2.331	1.872	0.645	-20.664	11.007
Hemidactylus granti	1.67	3.486	2.261	1.680	-23.040	5.880
Hemidactylus inintellectus	24.655	7.451	7.743	1.465	-20.633	11.715
Hemidactylus pumilio	25.945	12.035	13.371	3.187	-19.720	9.980

Table 3. Number (n) and abundance (%) of prey items per taxa for each studied species. * Coleoptera families; + Hymenoptera family; ° Hymenoptera infraorder. Total number of faecal samples examined is given between brackets.

| Taxa arthropods | *Haemodracon* | | | | | | *Hemidactylus* | | | | | |
| | *H. riebeckii* (n = 19) | | *H. trachyrhinus* (n = 5) | | *H. dracaenacolus* (n = 14) | | *H. granti* (n = 5) | | *H. inintellectus* (n = 13) | | *H. pumilio* (n = 3) | |
	n	%	n	%	n	%	n	%	n	%	n	%
Araneae	11	29.7	4	50.0	8	16.3	−		6	15.8	2	14.3
Pseudoscorpionida	−		−		−		−				7	50.0
Chilopoda	3	8.1	1	12.5	5	10.2	−		1	2.6	1	7.1
Hymnenoptera (total)	4	10.8	−		9	18.4	−		7	18.4	−	
Formicidae +	2		−		8		−		5		−	
Aculeata °	2		−		−		−		−		−	
Other Hymenoptera	−		−		1		−		2		−	
Heteroptera	−		−		−		3	21.4	1	2.6	−	
Orthoptera	2	5.4	1	12.5	1	2.0	−		1	2.6	−	
Neuroptera	2	5.4	−		−		−		1	2.6	−	
Homoptera	−		1	12.5	1	2.0	−		−		−	
Blattodea	1	2.7	−		3	6.1	2	14.3	−		−	
Coleoptera (total)	14	37.8	1	12.5	22	44.9	9	64.3	21	55.3	4	28.6
Curculionidae *	4		1		7		−		13		−	
Tenebrionidae *	5		−	−	1		−		1		1	
Sylvanidae *	1		−	−	4		2		2		−	
Chrysomelidae *	−		−	−	2		−		−		−	
Ptinidae *	−		−	−	3		−		−		−	
Cleridae *	−		−	−	−		1		−		−	
Histeridae *	−		−	−	−		2		−		−	
Other Coleoptera	4		−	−	5		4		5		3	
TOTAL PREY	37		8		49		14		38		14	

Legend of Figures

Figure 1. Location of the Socotra Archipelago, and locations where pellets (faecal analysis) and tail (isotopic analysis) samples were collected from each of the six reptile species studied. The elevations and soil types on Socotra are also depicted.

Figure 2. Phylogeny of the six Socotra gecko species included in the present study based on sequences of the 12S rRNA mitochondrial gene (see Material and methods). Black points in nodes indicate posterior probability values > 0.95.

Figure 3. Standard ellipse areas based on δ^{13}C and δ^{15}N ratios of the six reptile species studied in Socotra. Each point represents the isotopic values of a sample.

Figure 4: (A) Mean (point) and standard error (box) δ^{13}C values for animals collected on limestone (grey boxes) and igneous (open boxes) ground. Note that some species were only collected on one or the other substrate. (B) δ^{15}N values for *Haemodracon riebeckii* and *Hemidactylus inintellectus* as the only species for which specimens were collected on vegetation and cliff microhabitats.

Figure 5. Cluster dendrogram based on Bray-Curtis diet similarities among six gecko species of Socotra Island. Split points in the cluster indicate the dietary similarity between pairs of species: for example, *Haemodracon dracaenacolus* and *Hemidactylus initellectus* had the more similar diets with a mean similarity index around 70%. Pictures are scaled for the body size of each species.
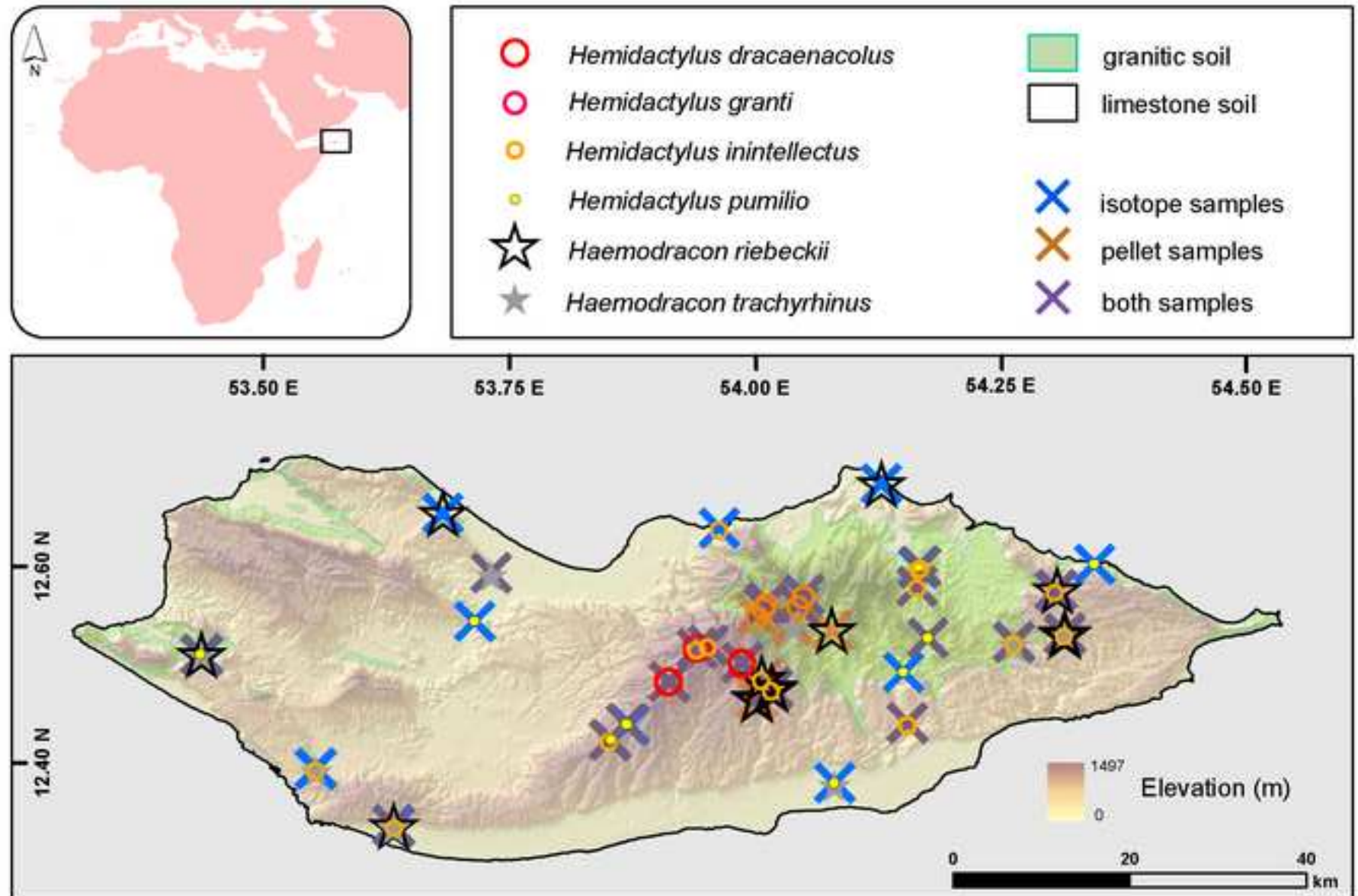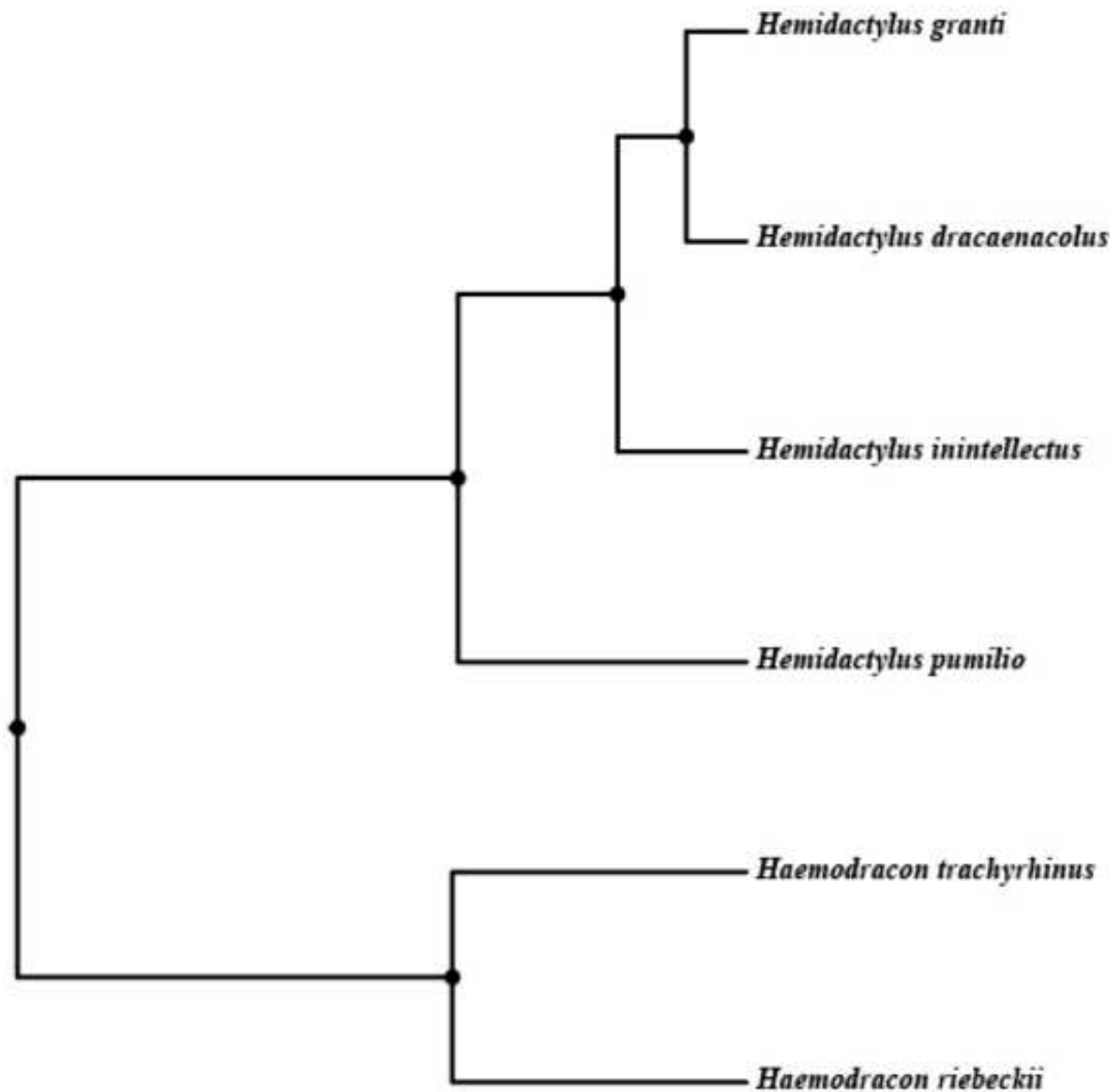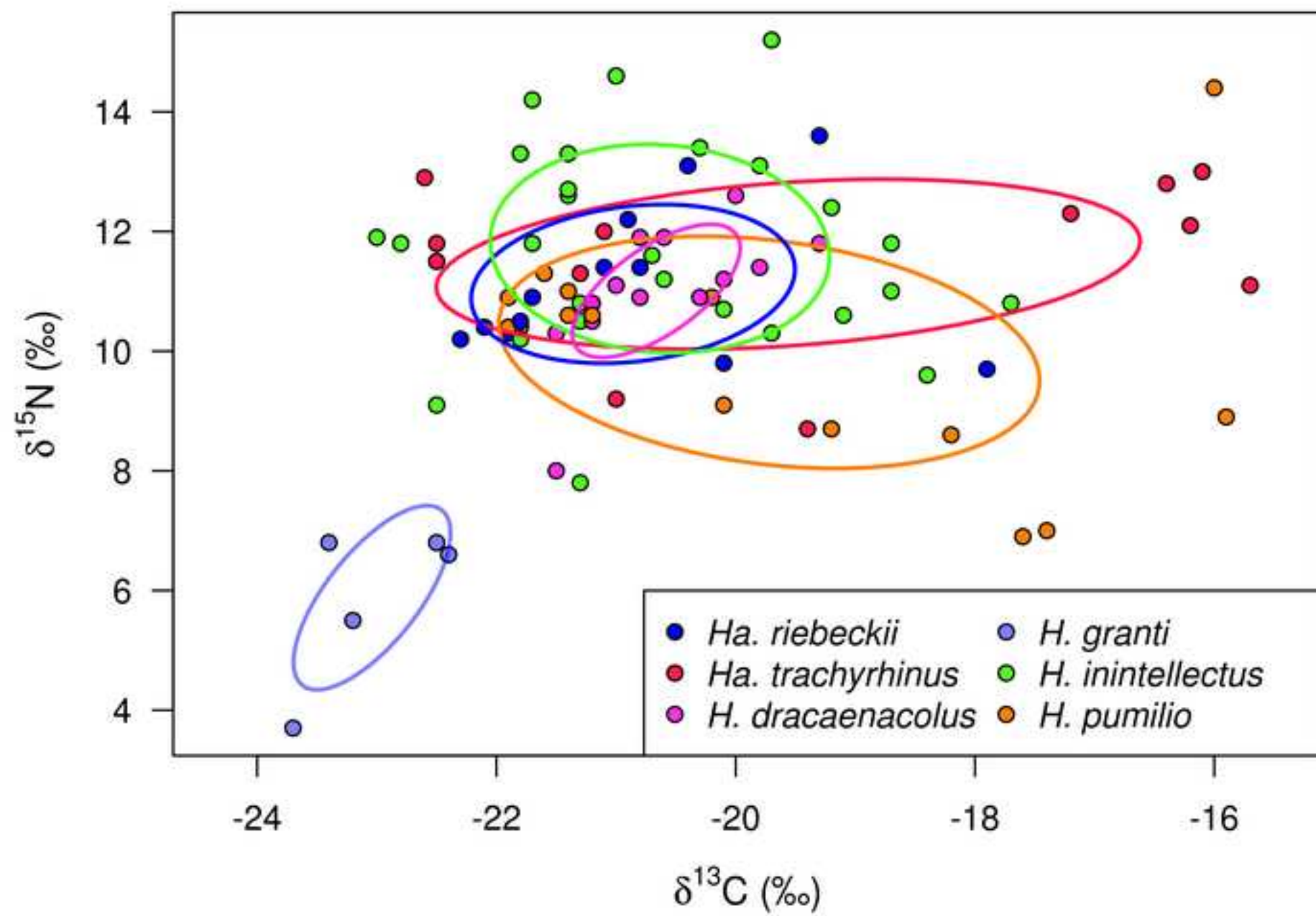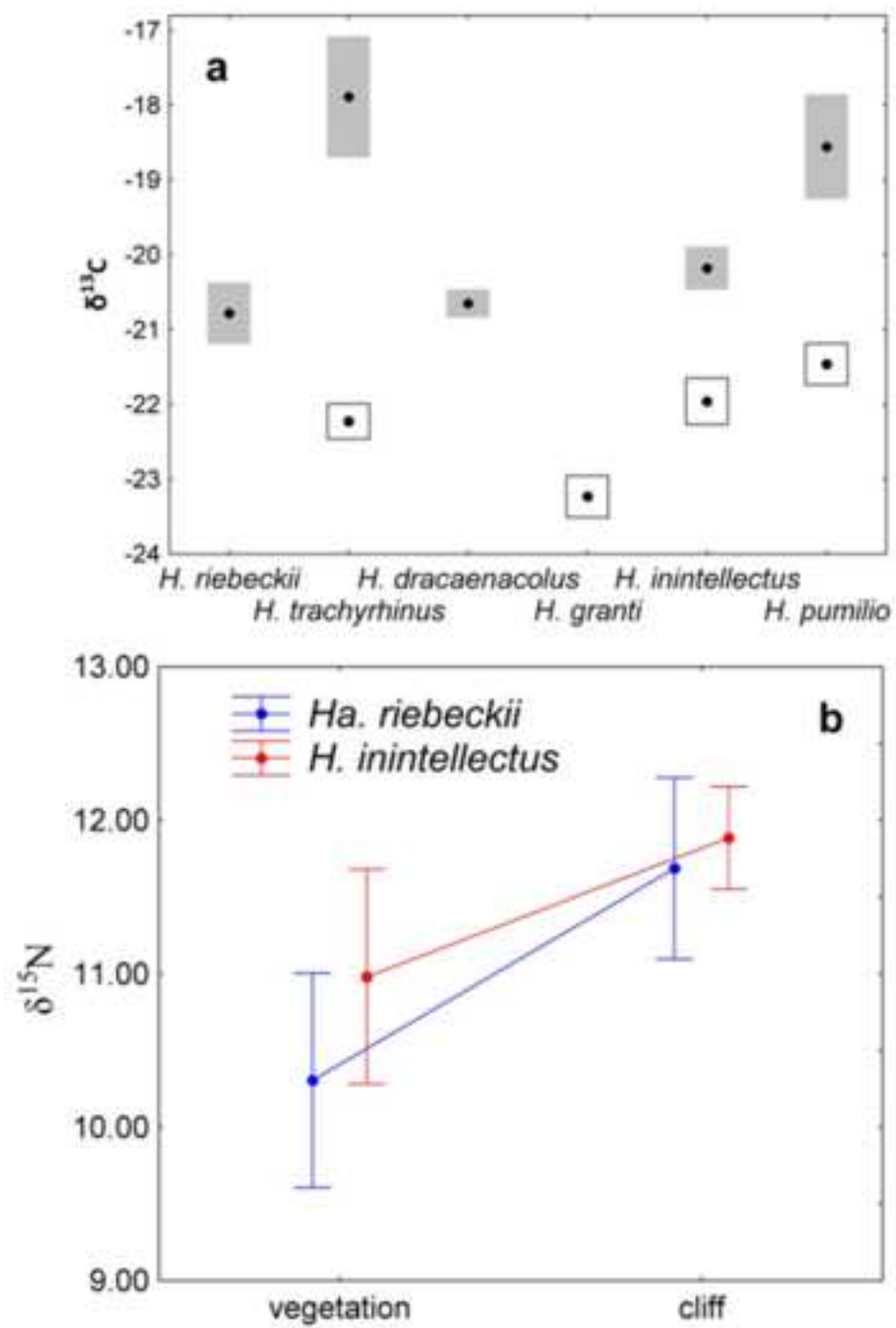
Figure 1

Figure 2

Figure 3

Figure 3. Scatter plot of δ¹³C (‰) versus δ¹⁵N (‰) showing species distributions.

Legend:
- ● *Ha. riebeckii* (blue)
- ● *Ha. trachyrhinus* (red)
- ● *H. dracaenacolus* (magenta)
- ● *H. granti* (purple)
- ● *H. inintellectus* (green)
- ● *H. pumilio* (orange)

Figure 4

Figure 5