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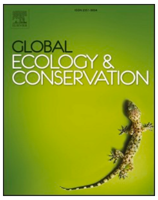

Original research article

Table for two: Diet composition differences of allopatric and sympatric populations of island geckos

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ABSTRACT

Oceanic islands are exciting models for studying how evolutionary processes and environmental variables can jointly contribute to speciation and community assembly over time. In this context, the Cabo Verde archipelago serves as a simplified natural laboratory, harbouring a group of endemic reptile species that are descended from a single common ancestor, with sympatric species exhibiting wide morphological variation, particularly for size, and competing for limited food resources. This framework allows for the exploration of how the diet composition of closely related and spatially overlapping species is influenced by competition. This is exemplified by the two endemic wall geckos, *Tarentola gigas* and *Tarentola raziana,* which occur in sympatry on Raso Islet, with the latter also occurring in allopatry on Santa Luzia Island, due to the human-mediated extinction of *T. gigas*. DNA metabarcoding of faecal pellets was used to compare the diets of both sympatric and allopatric populations. It revealed significant differences in diet composition between both populations of *T. raziana*, with significantly lower prey richness and niche breadth in the Santa Luzia population. Differences observed in sympatric species were due to a higher incidence of vertebrates and plants in the diet of *T. gigas*, while differences between the allopatric populations of *T. raziana* were due to a higher incidence of plants and a lower incidence of invertebrates in the population of Santa Luzia, compared to Raso. These results suggest that competition has played an important role in structuring the stable coexistence of these species in sympatry, promoting extreme morphological discrepancies that allowed resource partitioning. In addition, this study reveals unexpected dietary differences within the allopatric population of *T. raziana* on Santa Luzia, suggesting a niche shift in response to the absence of a direct competitor that may influence the reintroduction planning of *T. gigas*. Hence, this work highlights

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the importance of understanding the mechanisms of resource partitioning for conservation efforts and management, especially for fragile island ecosystems.

1. Introduction

Trophic interactions are one of the main factors shaping natural communities and population dynamics (Gravel et al., 2011; Warren et al., 2015). In small and isolated ecosystems such as oceanic islands, typically characterised by extreme environmental conditions and unique habitats, these trophic networks are often simplified with a low number of species and limited trophic links (Gil et al., 2020; Lopes et al., 2019; Warren et al., 2015). In the case of islets, their small size can even lead to closer links between terrestrial and marine trophic webs (Lopes et al., 2019). Moreover, islands typically host a high number of endemic and often threatened species with unique adaptations, that coexist and coevolved in such restricted space, by occupying distinct ecological niches (Dufour et al., 2018; Tamar et al., 2019). Compared with mainland areas, island communities are typically more vulnerable to species-level extinctions due to environmental and habitat changes, loss of genetic diversity, introduced species, and the limited potential and realised range sizes of insular species. Thus, small alterations, such as a decrease in the availability of prey species, may drastically affect the equilibrium of the ecosystem (Whittaker et al., 2017). This makes oceanic islands excellent models for studying evolutionary and ecological dynamics.

Cabo Verde is an arid oceanic archipelago of ten islands and several islets within the Macaronesia biogeographical region (Fig. 1A), with ages between 2–26 million years, My (Ancochea et al., 2015). This archipelago, within the Mediterranean biodiversity hotspot (Mittermeier et al., 2011), hosts a remarkable reptile biodiversity, including a total of 32 endemic terrestrial reptile taxa from three genera (Vasconcelos et al., 2013; Vasconcelos et al., 2020). Among these, geckos within the genus *Tarentola* are estimated to have originated from a single colonisation event from the Canary Islands approximately 7.7 My ago, followed by the beginning of radiation around 6 My ago (Carranza et al., 2000; Vasconcelos et al., 2010). Their diversification within Cabo Verde has resulted in 12 endemic species and four subspecies (Vasconcelos et al., 2010; Vasconcelos et al., 2012), some of which co-occur in pairs across the islands of the archipelago. Although the Canary Island ancestor was most likely of medium size, in Cabo Verde there is a very marked size difference between sympatric species (Carranza et al., 2000; Vasconcelos et al., 2012). This contrast is particularly evident in the northern islands with the case of the giant wall gecko *Tarentola gigas* (Bocage 1875), locally abundant on Raso and Branco islets, but

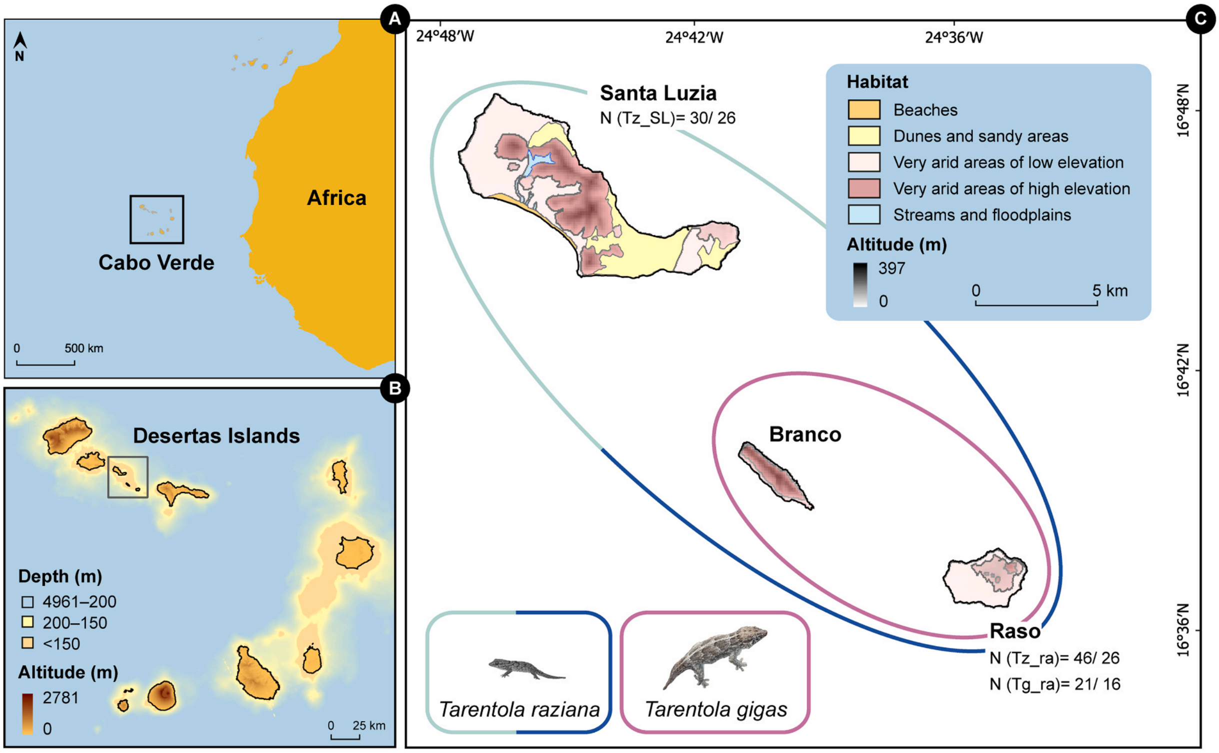

Fig. 1. Study area and species. A) Geographic location of the Cabo Verde Archipelago. B) Desertas Islands, depicting elevation and bathymetry. C) Habitat types and distributions of the three *Tarentola* populations (*T. raziana* from Santa Luzia in light blue, Tz_SL, from Raso in dark blue, Tz_ra, and *T. gigas* from Raso, Tg_ra in pink), showing the number of faecal samples (N) extracted, and used in the analyses, respectively (Geographic Coordinate System, Datum WGS84).

recently extinct on Santa Luzia Island, and the Raso wall gecko *Tarentola raziana* Schleich, (1984), occurring across all islands of the Desertas Island group (Santa Luzia Island, Branco and Raso islets; Vasconcelos et al. 2013), the two species representing the largest and smallest geckos in the archipelago, respectively (Vasconcelos et al., 2012). These belong to two sister clades that diverged approximately 4.5 My ago (Vasconcelos et al., 2010). The *T. gigas* clade comprises tendentially larger species than the ancestral species, whereas species in the *T. raziana* clade are generally similar in size to the ancestral species (Vasconcelos et al., 2012). Therefore, building from a historical phylogenetic signal for size differentiation, the two species most likely further diverged in opposite directions accentuating this size discrepancy. Both species are nocturnal and syntopic on Raso and Branco (Vasconcelos et al., 2013), having access to the same limited resources and being subjected to the same climatic pressures, thus creating the potential for competition between them.

The competitive exclusion hypothesis suggests that two coexisting species cannot completely overlap in their ecological niche (Gause, 1934). Thus, it has been suggested that syntopic reptile species should rapidly diverge in their ecological niche as a response to competition (Amorim et al., 2017; Dufour et al., 2017). This is often emphasised by variations in morphological features that allow differential resource use and subsequent resource partitioning (Schoener, 1974; Williams, 1983). This can be achieved through, either consuming different food items (e.g., Crested Butte bumblebees (Pyke, 1982)) or using the same limiting resource in different ways (e.g., Bimini Island *Anolis* (Schoener, 1968)). These ecological differences should favour the long-term coexistence of species and thus the diversity of the communities (Pianka, 2011). Understanding dietary niche partitioning among evolutionary and ecologically related and co-occurring species is important for the development of a general understanding of community assembly and co-evolution (Arrizabalaga-Escudero et al., 2018; Kartzinel et al., 2015; Schmack et al., 2021). This is greatly facilitated within systems where it is possible to characterise dietary habits within allopatric populations of one or both species. Such a sampling framework allows for a greater understanding of the extent to which the diet composition of geographically overlapping species is influenced by competition. On the island of Santa Luzia, the Raso wall gecko occurs without the presence of the giant wall gecko, providing an appropriate comparative framework for interpreting the diet of *T. raziana* when there is no competitor. Previous morphological analyses of faecal contents have suggested that *T. raziana* feeds mainly on arthropods (Mateo et al., 2016; Schleich, 1987), while *T. gigas* appears to feed on a mix of arthropods, plants, birds, reptiles and fish remains arthropods (Mateo et al., 2016; Schleich, 1980; Schleich, 1987). However, the trophic competition between them has never been explored in detail. The diet of *T. gigas* has recently been characterised on the islands of Branco and Raso through metabarcoding of faecal pellets, highlighting a strong trophic link with seabirds, and revealing the importance of plant species within its diet (Lopes et al., 2019; Pinho et al., 2018).

Herbivorous reptiles tend to be larger in insular ecosystems (Meiri, 2008; Van Damme, 1999). Shift to plant consumption may also lead to changes in the structure and function of the digestive system, such as longer gastrointestinal tracts and the development of caecal valves (Pafilis et al., 2016; Sagonas et al., 2015). These morphological adaptations are even observed in omnivore species when compared to strictly insectivorous reptile species (Herrel et al., 2004). Elongation of the intestine allows for slower gut passage times and longer exposure to digestive enzymes, thus increasing the digestive efficiency and nutrient absorption of fibrous plant items (Dearing, 1993; Pafilis et al., 2016), which can be difficult to digest due to their thick cell walls when compared to animal items (Holland et al., 2020). These adaptations may allow larger island reptiles to optimise energy intake by expanding their trophic niche towards plant matter and enhance survival in resource-limited island habitats (Sagonas et al., 2015), which may be the case for *T. gigas*.

DNA-based non-invasive studies can provide a large amount of data at different trophic levels with less time investment, disturbance and more cost-effectively, compared to alternative approaches (Pompanon et al., 2012; Taberlet et al., 2012). Additionally, compared to conventional methods, DNA-based approaches provide for improved taxonomic resolution, detection of rare prey species and detection of soft, small prey that can be undetectable by classical methods after digestion (Symondson, 2002). This is particularly important when studying endangered or near-threatened species such as the Cabo Verdean *Tarentola* geckos. Besides highlighting specific trophic relationships, such data can additionally shed light on species coexistence and the partitioning of food resources. Here we use DNA metabarcoding of faecal pellets to investigate how diet composition varies among sympatric populations of *T. gigas* and *T. raziana* on Raso Islet, and the allopatric populations of *T. raziana* from Santa Luzia Island and Raso. We predict that *T. gigas* and *T. raziana* will compete for some resources, but with evidence of resource partitioning and dietary specialisation. Furthermore, we predict that any specialisation toward plants will be accompanied by gastrointestinal adaptations, thus providing stronger support for dietary differences as an evolved response. Between the two allopatric populations of *T. raziana,* we expect to observe a signal of ecological release with the Santa Luzia population through dietary niche expansion, in response to the absence of the competitor. Moreover, by contributing to the general understanding of competition theory, the knowledge gained on the ecological needs of these two species can support local conservation actions, such as guiding the reintroduction of *T. gigas* on Santa Luzia.

2. Methods

2.1. Study area

The Desertas island group is located within the northwest of the Cabo Verdean archipelago and is composed of Santa Luzia Island, together with the Branco and Raso islets (Fig. 1). These islands are currently uninhabited and were designated as nature reserves in 1990 and marine protected areas in 2003. The Desertas, together with São Vicente, are thought to have been connected during lower sea levels in the Pleistocene (Fig. 1B; Ancochea et al. 2015) and share most elements of their fauna and flora (Arechavaleta et al., 2005; Gomes et al., 2023; Romeiras et al., 2019; Vasconcelos et al., 2015). Santa Luzia has an area of approximately 35 km^2, with a landscape of arid lowlands, mountainous areas, streams and floodplains, and sandy areas (Fig. 1C; Diniz and Matos 1994). Raso, with an area of less than 6 km^2, is characterised by flat and low-altitude arid zones, small intermittent streams (Fig. 1C), and vegetation mainly composed of patches of grasses (Freitas et al., 2015; Gomes et al., 2023).

2.2. *Study species*

The Cabo Verde giant wall gecko *Tarentola gigas,* currently one of the largest geckonids in the world (maximum snout-vent length, SVL of 155 mm), is classified as Endangered in the International Union for Conservation of Nature (IUCN) Red List of Threatened species, primarily due to its restricted distribution and exploitation of its prey (Vasconcelos, 2013a). It is divided into two morphologically distinct subspecies, *Tarentola gigas brancoensis* (Schleich, 1984) (mean SVL= 94.80 ± 1.79 mm), found solely on Branco Islet, and *Tarentola gigas gigas* (Bocage, 1875) (mean SVL= 105.47 ± 1.91 mm), found exclusively on Raso Islet (Delgado et al., 2021; Joger, 1984; Schleich, 1984; Vasconcelos et al., 2012). The Raso wall gecko *Tarentola raziana*, the smallest Cabo Verdean wall gecko (mean SVL= 49.30 ± 4.00 mm), is classified as Near Threatened in the IUCN Red List of Threatened species and can typically be found in rocky areas in Santa Luzia, and across the Branco and Raso Islets (Vasconcelos, 2013b). This species is distinguishable from *T. gigas* by its smaller size, its particularly pointed snout and concave forehead, with no tubercles between the eye and the ear opening, and its dark banded dorsal colouration (Vasconcelos et al., 2012). Both species are oviparous, nocturnal, ground-dwelling and frequently syntopic (Vasconcelos, 2013a; Vasconcelos, 2013b; Vasconcelos et al., 2012). Both population of *T. raziana* are morphologically similar and even share mitochondrial and nuclear haplotypes (Vasconcelos et al., 2010; Vasconcelos et al., 2012).

2.3. *Sampling*

Sampling took place during the dry season on Raso (June to August 2016) and Santa Luzia (May 2021). On Raso, transects were performed to cover the island area and a total of 21 and 46 faecal samples were collected for *T. gigas* and *T. raziana*, respectively. On Santa Luzia, transects were carried out in the northwest of the island, where the habitat is mainly characterised by arid lowlands, analogous to Raso (Fig. 1C) and a total of 30 samples were collected for *T. raziana*. The individuals were captured by hand and an abdomen massage was performed to obtain fresh pellets, which were immediately preserved in 96 % ethanol to avoid contamination. Samples were refrigerated at 4 °C as soon as possible and then transported to the CIBIO research centre in Portugal and stored at −20 ºC until further processing. Specimens were measured (SVL to the nearest mm) and photographed to corroborate species identification. Animals were kept in individual tissue bags while others were being processed, to minimise their stress and georeferenced using a GPS device before being released at the same site of their capture.

To further develop a local DNA barcode reference library, newly collected samples of 56 invertebrates and 16 plants from Santa Luzia Island were processed and added to those previously characterised by Pinho et al. (2018) for the Desertas Islands.

2.4. *DNA extraction and sequencing*

DNA extraction of faecal pellets was carried out, including negative controls, using the Stool DNA Isolation Kit (Norgen Biotek Corp., Thorold, ON, Canada), following the manufacturer's instructions. All DNA samples were amplified with three previously validated genetic markers (Pinho et al., 2022; Pinho et al., 2018): IN16STK-1F-mod/IN16STK-1R-mod primers, targeting the mitochondrial 16S gene (Pinho et al., 2018) for invertebrates; g/h primers targeting the short P6-loop of chloroplast trnL (UAA) gene for plants (Taberlet et al., 2007); and the primer pair 12sv5F/12Ssv5R, targeting V5-loop within the mitochondrial 12S gene for vertebrates (Riaz et al., 2011). To avoid the amplification of *T. gigas* and *T. raziana* DNA, a blocking primer for the 12S, previously designed for *T. gigas*, was used (Pinho et al., 2018). Its effectiveness for *T. raziana* was previously validated by comparing PCR amplification with and without the blocking primer, using DNA extracted from the tail tissues with the EasySpin™ kit, following the manufacturer's instructions. All PCRs were performed, including negative controls, with the conditions described by Pinho et al. (2018). Libraries were prepared following the Illumina MiSeq protocol (Illumina, 2013). Samples were sequenced in a MiSeq sequencer (Illumina, San Diego, CA, USA) using the MiSeq Reagent Kit V2 (Illumina, San Diego, CA, USA) for an expected average of 20,000 paired-end reads per PCR product.

Plant DNA for the reference collection was extracted using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following modifications described in Romeiras et al. (2015). Invertebrate DNA for the reference library was extracted from legs or wings, using saline extraction methods following (Carranza et al., 1999). Invertebrate DNA from the reference collection was amplified using two primer sets. The IN16STK primer set, allowing the match with diet items, and the LCO1490/HC02198 primer set, targeting the animal barcode region of the cytochrome oxidase I (COI). PCR conditions used for the latter are described in Folmer et al. (1994). Barcode sequencing was undertaken to assist with taxonomic assignments. Plant DNA was amplified for the chloroplast trnL (UAA) using the primer set c/d (Taberlet et al., 2007) to allow comparison with diet items. All individual-based amplicons were Sanger sequenced.

2.5. *Bioinformatics filtering*

The software package OBITools (Boyer et al., 2016) was used for general sequence processing, which includes the alignment of the sequences obtained and the filtering of sequencing errors, to obtain molecular operational taxonomic units (MOTUs), using pipelines described in Pinho et al. (2018). The MOTUs were compared against known reference sequences in the NCBI Nucleotide Database and our reference collection, using the BLAST+ software (Camacho et al., 2009). Our local database was created using *makeblastdb* and compared against obtained diet sequences using *blastn*. Sequences that had less than 85 % of percent identity value with known species were classified only to the class level, the ones with values between 85 % and 90 % to the order level, while sequences with values between 90 % and 95 % were classified to the family level. Only query coverages above 80 % were considered. Sequences with similarity values above 95 % that match to a single species with coverage above 98 % were classified to the species level. If a sequence matched more than one species with equal similarity values (>95 %) all belonging to the same genus, a genus-level assignment was considered. When a sequence matched more than one species or genus with similar probabilities, only species or genera known to occur in the archipelago were considered, otherwise a higher ranking would be attributed (e.g., family). If more than one MOTU corresponds to the same taxon, a number would be attributed to each different haplotype regardless of the taxonomic resolution (e.g., Poaceae_1 and Poaceae_2). Based on PCR blank counts, all PCR products with less than 300 reads were removed and within the remaining samples, MOTUs representing less than 1 % of the total reads of that PCR product were also excluded. Lastly, MOTUs detected in extraction blanks were identified as contaminations and removed from the corresponding batch of samples (e.g., human, fungi).

2.6. Data analysis

The frequencies of occurrence (FO) of each of the three diet item groups (plant, invertebrate, vertebrate) were estimated for the two sympatric populations from Raso (*T. gigas* – Tg_ra, and *T. raziana* – Tz_ra from hereafter) and *T. raziana* in allopatry on Santa Luzia (Tz_SL from hereafter). To test for potential differences in proportions of each diet item group between populations, FOs were compared using two-proportion z-tests with the function *prop.test* in R software version 4.2.2 (R Core Team, 2023).

Since it was not possible to achieve species-level taxonomic resolution for several MOTUs, family-level identification was used for the subsequent analysis. The FOs of each prey family were calculated for each population. To visualise and compare the relative abundance and evenness of families present in the diet of each gecko population, rank-abundance curve plots were generated using the *rankabundance* function from the BiodiversityR package (Kindt and Coe, 2005). To visualise the dietary networks at the family level for the three populations bipartite networks were generated using the package bipartite v2.17 (Dormann et al., 2008).

Resource richness and niche breadth were compared among the three populations, at the family level, through rarefaction curves. Richness values were estimated for the double of species with the lower sample size and considered to significantly differ if there was no overlap in the 95 % confidence intervals (Chao et al., 2020). This was performed and visualised using the functions *iNEXT* and *ggiNEXT*, respectively, from the INEXT package (Hsieh et al., 2022). Dietary niche overlap at the family level between the allopatric population of *T. raziana* (Tz_ra vs Tz_SL) and sympatric populations of *T. gigas* and *T. raziana* (Tg_ra vs Tz_ra) were calculated using Pianka's index (Pianka, 1973). This index ranges from 0 to 1, where 0 indicates no common resources and 1 complete overlap in resource use. To test if the obtained dietary niche overlap differed from what would be expected by chance, null models were performed based on the RA3 randomisation algorithm (Lawlor, 1980), generating 10,000 null matrices that were to compare with our observed data, using the EcoSimR package (Gotelli et al., 2015). Additionally, to evaluate prey-use differences between the three populations, non-metric multidimensional scaling (NMDS) was used. Samples were ordinated according to diet similarity in the two-dimensional space using the function *metaMDS* from the vegan package (Oksanen et al., 2022) based on a Jaccard distance matrix.

Lastly, generalised linear models (GLM) were carried out to test for significant differences in diet composition between sympatric (Tg_ra vs. Tz_ra) and allopatric (Tz_ra vs. Tz_SL) populations, at the MOTU, family, and order levels. GLMs for multivariate presence/absence data were fitted by implementing the *manyglm* function of the mvabund package (Wang et al., 2022). The complementary log-log distribution presented the best fit and was used for subsequent testing. In addition to population, SVL was included as a covariate to test whether differences in diet composition were influenced by size. Size had no significant effect on diet composition, so the analysis was performed with population as the only covariate.

The significance of the GLMs was tested using the *anova.manyglm* function. The same function was then implemented with the argument p.uni= 'adjusted' to perform univariate tests, identifying which prey items were responsible for differences in diet composition between species and populations.

2.7. Gastrointestinal comparisons

To conduct preliminary comparisons of gut length for *T. raziana* and *T. gigas* individually. Five specimens of each species were opened from the collections of the National Museum of Natural History and Science of Lisbon (MUHNAC), with the permission of the curator (Table S1). These specimens were originally collected on Raso Islet in 1970. The SVL of the individuals was measured to the nearest mm, as well as the length of the small intestine (SI) and large intestine (LI).

The normality of the data was assessed using the Shapiro–Wilk test with the function *shapiro.test* from the stats package (R Core Team, 2023). To test for correlations between SVL and SI and LI lengths for each species the Pearson correlation coefficient (r) was calculated using *cor.test* function of the stats package (R Core Team, 2023). To test for significant differences between correlation values of the two species a Fisher's r-to-z comparison was used by applying the *paired.r* function of package psych (Revelle, 2023).

3. Results

3.1. Diet composition

The final dataset comprised 68 samples (Tz_SL= 26, Tz_ra= 26, Tg_ra= 16) with a total of 279,007 reads. Across all samples from both species, a total of 114 MOTUs were identified (Tz_SL= 30, Tz_ra= 68, Tg_ra= 55) from eight taxonomic classes (Tz_SL= 6, Tz_ra= 6, Tg_ra= 8), 42 orders (Tz_SL= 18, Tz_ra= 27, Tg_ra= 29) and 66 families (Tz_SL= 20, Tz_ra= 41, Tg_ra= 38; Table S2). For Tz_SL, the most frequent families identified were Zygophyllaceae and Fabaceae (Fig. 2A), namely the MOTUs *Zygophyllum simplex* L. (FO = 65.38 %) and *Lotus brunneri* (FO= 38.46 %). For the diet of Tz_ra, the most frequent family observed was Rhinotermitidae (Fig. 2A), namely the MOTU *Reticulitermes* sp. (FO= 57.69 %). The most frequent families in the diet of Tg_ra were Plumbaginaceae and Fabaceae (Fig. 2A), namely *Limonium brunneri* (Webb ex Boiss.) (FO= 75 %) and *Lotus brunneri* Webb (FO= 56 %) MOTUs, respectively.

The occurrence of the three taxonomic diet groups (plants, invertebrates, vertebrates) differed between species and populations. Plants proportions differed significantly between populations ($\chi^2_{\text{Tz\_ra vs Tz\_SL}}$= 11.53, $p = 0.001$; $\chi^2_{\text{Tz\_ra vs Tg\_ra}}$= 4.67, $p = 0.03$), with higher frequencies in the diets of Tz_SL (FO$_{\text{Tz\_SL}}$ = 100 %) and Tg_ra (FO$_{\text{Tz\_ra}}$ = 94 %) than in Tz_ra (F$_{\text{Tg\_ra}}$ O= 58 %). Invertebrates had similar frequencies in the sympatric populations (FO$_{\text{Tz\_ra}}$= 62 % vs FO$_{\text{Tg\_ra}}$= 50 %) and lower frequency for *T. raziana* in allopatry

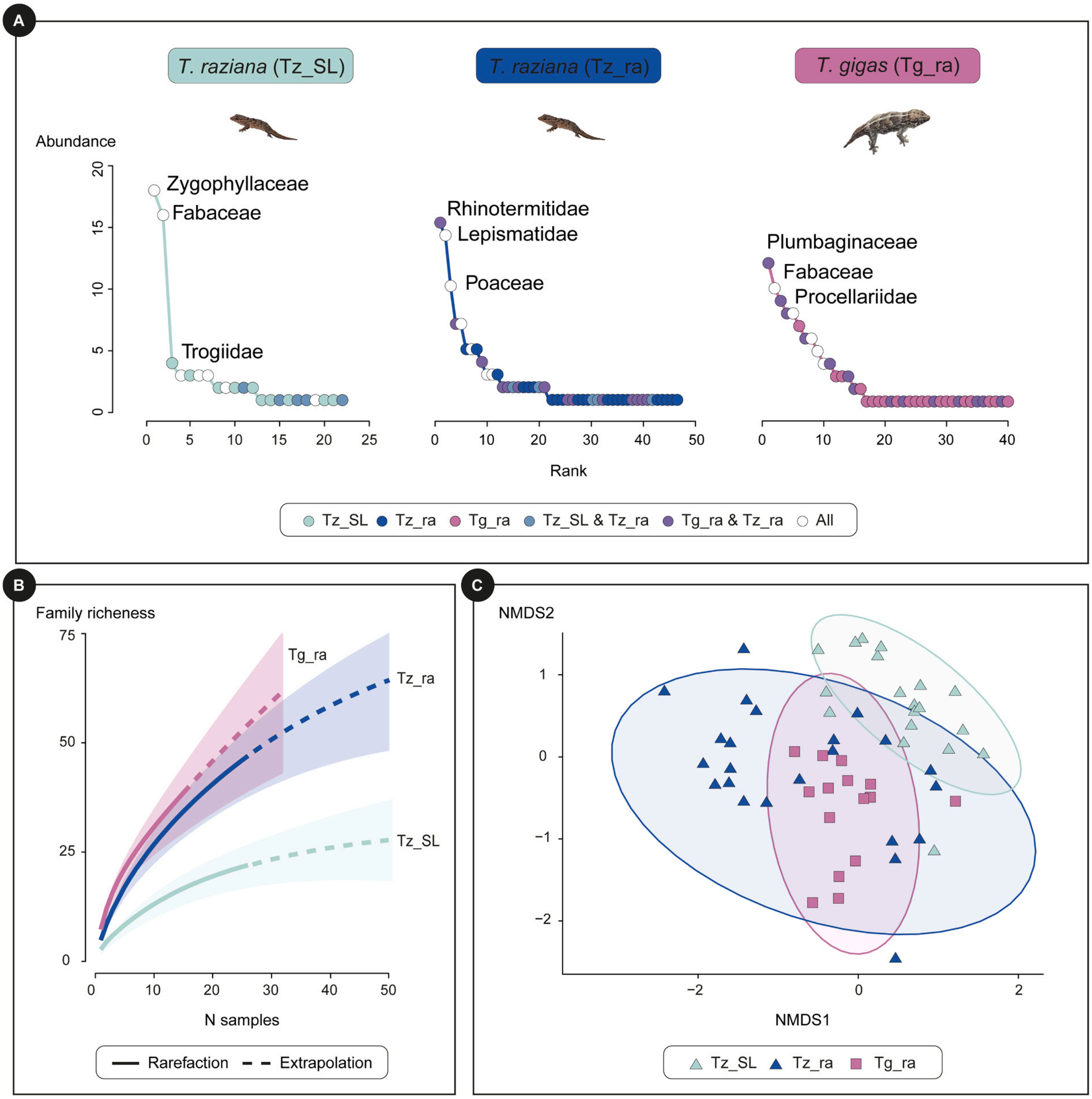

Fig. 2. Diet composition results for the three *Tarentola* populations (*T. raziana* from Santa Luzia, Tz_SL, from Raso, Tz_ra, and *T. gigas* from Raso, Tg_ra). A) Rank abundance curve plots, showing the percentages of the three more abundant diet item families for each population and the common prey items among them. Distinct colours are used to indicate families exclusively present in each population, white if shared by all populations and summed colour if shared by two of them. B) Accumulation curves depicting observed (full line) and extrapolated (dashed line) family richness with their 95 % confidence intervals. C) Non-metric multidimensional scaling ordination (NMDS) of the diet composition. Points closer together correspond to samples with a more similar dietary composition. Ellipses represent the standard error of the dietary composition centroids at 95 % confidence intervals.

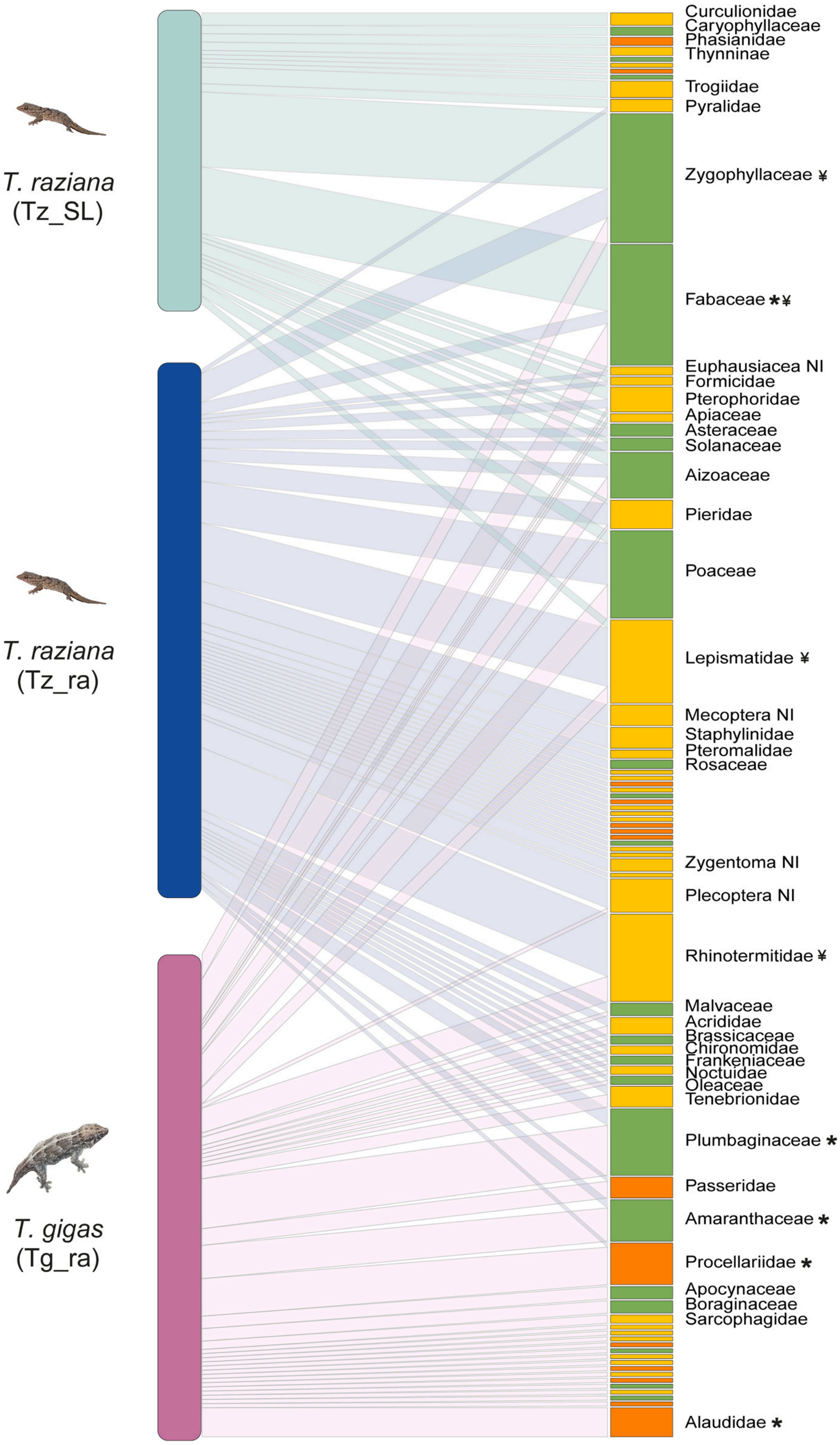

Fig. 3. Bipartite network representing associations among the three *Tarentola* populations (*T. raziana* from Santa Luzia, Tz_SL, from Raso, Tz_ra, and *T. gigas* from Raso, Tg_ra), and their diet items. The predators are on the left and arthropod (yellow), plant (green) and vertebrate (orange) prey families on the right. The width of the connecting bars represents the frequency of occurrence of each family in the pellets of each population. The symbol (*) indicates the families that contributed significantly to differences between sympatric (Tz_ra vs Tg_ra) and (¥) in both *T. raziana* (Tz_ra vs Tz_SL) populations. Only family names with a frequency of occurrence above one are mentioned.

(FO $_{\text{Tz\_SL}}$= 35 %), however none were significant (χ^2 $_{\text{Tz\_ra vs Tz\_SL}}$= 2.77, $p = 0.09$; χ^2 $_{\text{Tz\_ra vs Tg\_ra}}$= 0.17, $p = 0.679$). Vertebrate prey taxa were more frequent in the diet of the giant (FO $_{\text{Tg\_ra}}$= 94 %) than in both Raso wall gecko populations (FO $_{\text{Tz\_SL}}$= 12 %, FO $_{\text{Tz\_ra}}$= 23 %), with significant differences for the species in sympatry but not between *T. raziana* allopatric populations (χ^2 $_{\text{Tz\_ra vs Tz\_SL}}$= 0.53, $p = 0.463$; χ^2 $_{\text{Tz\_ra vs Tg\_ra}}$= 17.06, $p = 3.61\text{e}^{-05}$).

The two species living in sympatry (Tg_ra and Tz_ra) presented no differences in family-level richness, both observed and extrapolated, while *T. raziana* in allopatry presented significantly lower richness values (Tz_SL; Fig. 2B and S1). In sympatry, diet niche overlap (O) at the family level was significantly higher than expected by chance (O $_{\text{Tz\_ra vs Tg\_ra}}$= 0.57, $p < 0.001$; Fig. 2C) and higher than overlap between allopatric *T. raziana* populations (O $_{\text{Tz\_ra vs Tz\_SL}}$= 0.36, not significant).

The multivariate analysis revealed significant differences in the diet composition of the two populations of *T. raziana* at the MOTU, family, and order levels (all with $p = 0.001$; Table S3). Univariate tests showed that differences in diet composition between both populations of *T. raziana* were due to four MOTUs (*Reticulitermes*_1, *Zygophyllum simplex*, Plecoptera_1 and *Thermobia domestica* (Packard 1837)), four families (Fabaceae, Rhinotermitidae, Lepismatidae and Zygophyllaceae; Fig. 3) and five orders (Blattodea, Fabales, Zygentoma, Plecoptera and Zygophyllales), with invertebrate items present exclusively in the Tz_ra diet and plant items in the Tz_SL diet. The multivariate analysis also revealed significant diet composition differences between sympatric populations (Tz_ra vs Tg_ra; $p = 0.001$), mainly due to vertebrate prey taxa (*Alauda razae*, *Bulweria bulwerii* (Jardine and Selby 1828)) and plants species (*Chenopodiastrum murale* (L.) S.Fuentes, Uotila & Borsch, *Limonium brunneri*, *Lotus brunneri*, *Patellifolia procumbens* (Chr.P.Sm.) A.J. Scott, Ford-Lloyd & J.T.Williams), all either consumed exclusively or in higher frequencies by *T. gigas*. The families that contributed significantly to these differences were Alaudidae, Procellariidae, Plumbaginaceae, Fabaceae and Amaranthaceae (Fig. 3) and the Procellariiformes, Fabales and Passeriformes orders. The *p*-value results for the univariate tests are presented in Table 1.

3.2. Gastrointestinal comparisons

Snout-vent length (SVL) and intestinal length (SI, LI) of museum specimens are shown in Table S1. The *T. raziana* and *T. gigas* individuals had an average SVL and standard deviation of 48.90 ± 4.04 and 105.30 ± 11.8, SI of 3.20 ± 0.27 and 11.3 ± 3.14 and LI of 1.62 ± 0.13 and 4.74 ± 0.44, respectively. There was no significant correlation in the relationship between SVL and the two intestine portions for *T. raziana* (r_{SI}= 0.2, $p = 0.74$; r_{LI}= −0.32, $p = 0.6$; Figure S2). For *T. gigas*, there was a marginally significant positive correlation in the relationship between SVL and SI (r_{SI}= 0.88, $p = 0.05$; Figure S2), indicating an increase in SI length with body size, but no significant correlation was observed between SVL and LI length (r_{LI}= 0.72, $p = 0.17$; Figure S2). For LI the Pearson correlation value of *T. gigas* was significantly higher than that of *T. raziana* ($p = 0.03$), however, for SI the results were not significant ($p = 0.19$).

4. Discussion

The present study reveals significant differences in diet composition between *T. raziana* and *T. gigas* living in sympatry on Raso Islet, as well as between the two allopatric populations of *T. raziana* present on Santa Luzia and Raso. These results show that competition had an important role in structuring the stable coexistence of these sympatric species, promoting extreme morphological discrepancies that allowed differential resource use and subsequent resource partitioning. Additionally, this study reveals an unexpectedly high degree of dietary specialisation in the allopatric population of *T. raziana* on Santa Luzia, indicating a niche shift as a response to the absence of a direct competitor.

4.1. Allopatric populations

On Santa Luzia, under reduced interspecific competition, *T. raziana* would be expected to exploit previously unused resources, consistent with ecological release and subsequent niche expansion (Pianka, 2011). However, in contrast to our initial hypothesis, the population from Santa Luzia demonstrated niche contraction rather than expansion, as evidenced by a significantly less diverse diet when compared to the Raso population. This indicates that, without its direct competitor, the Santa Luzia population has narrowed its dietary niche to focus on a smaller set of resources. One potential explanation for this could be in the context of an improved

Table 1

Results of univariate tests. The prey items that significantly ($p < 0.05$) contributed to the differences in diet composition between allopatric (alo, Tz_ra vs Tz_SL) and sympatric (sym, Tz_ra vs Tg_ra) populations, considering three taxonomic levels (Order, Family and MOTUs) are given.

Pop	Order	*p*	Family	*p*	MOTUs	*p*
Alo	Blattodea	0.001	Rhinotermitidae	0.001	Reticulitermes_1	0.001
	Fabales	0.003	Fabaceae	0.001	*Zygophyllum simplex*	0.009
	Zygentoma	0.006	Lepismatidae	0.003	Plecoptera_1	0.017
	Plecoptera	0.017	Plecoptera_1	0.014	*Thermobia domestica*	0.050
	Zygophyllales	0.024	Zygophyllaceae	0.018		
sym	Procellariiformes	0.003	Alaudidae	0.003	*Alauda razae*	0.003
	Fabales	0.007	Plumbaginaceae	0.003	*Bulweria bulwerii*	0.003
	Passeriformes	0.007	Procellariidae	0.003	*Chenopodiastrum murale*	0.003
			Fabaceae	0.011	*Limonium brunneri*	0.003
			Amaranthaceae	0.033	*Lotus brunneri*	0.011
					Patellifolia procumbens	0.043

cost-benefit ratio, either because food items are easier to access due to the lack of the large competitor (as species are generally equally abundant on all Desertas; Gomes et al., 2023), more nutritious or have greater energy potential. The significantly higher frequencies of plants in the diet of Tz_SL, when compared to the Raso population, as well as the plant items (Fabales and Zygophyllales) contributing to the diet composition differences, reflect this specialisation. For instance, pollen and nectar-rich plants such as *Zygophyllum simplex* and plants rich in proteins as in the Fabacea family, highly frequent in the Tz_SL diet, may represent less demanding, easily digestible, and more nutritious food options than ground-dwelling invertebrates (e.g., termites and firebrats, two dietary items that differ significantly between Tz populations), and are consequently favoured by the Santa Luzia population. Similarly, *Bituminaria bituminosa* (L.) C.H.Stirt. of the Fabaceae family was one of the main species in the diet of the highly herbivorous *Gallotia simonyi* (Steindachner 1889) from the Canary Islands (Pérez-Mellado et al., 1999).

Although exhibiting similar frequencies of consumed vertebrates to the SL population, the Raso population shows a greater variety of items (eight for Tz_ra and two for Tz_SL) including seabird MOTUs (*Calonectris edwardsii* (Oustalet 1883) and *Puffinus boydi* Mathews 1912) and several fish species, indicating a diet link with seabird communities and different feeding habits. This most likely results from the ingestion of seabird regurgitations and faeces, a behaviour already reported for *T. gigas* (Schleich, 1980). On the contrary, the vertebrates found in the diet of the Santa Luzia population are certainly of anthropogenic origin (e.g., chicken from waste left by fishermen/ rangers), reflecting mostly opportunistic habits of this population rather than active foraging. The observed results are in line with optimal foraging theory which predicts that as the availability of preferred resources decreases, the dietary niche breath should expand (Perry and Pianka, 1997). Particularly on Raso, the already scarce preferred food items of *T. raziana* may be further restricted due to competition for resources with *T. gigas*. Thus, *T. raziana* individuals may have been forced to expand their diet to include previously overlooked prey items that may be less nutritious (Bonesi et al., 2004), leading to niche expansion with increased competition. In contrast, individuals on Santa Luzia are expected to have easier access to preferred resources, resulting in a more restricted diet, by preying on a small set of high-value resources while avoiding those with an opportunity cost exceeding their value (Parent et al., 2014; Wilson and Yoshimura, 1994). These results justify the reintroduction of *T. gigas* on Santa Luzia on different areas of *T. raziana* occurrence to prelude mutual exclusion.

It is important to note that there may also be alternative competitive pressures acting within Santa Luzia, such as introduced mammals, which are known to be a major threat to reptiles on the island (Geraldes et al., 2016; Medina et al., 2020). The recent eradication of cats on Santa Luzia has led to an exponential increase in the density of mice, which share activity patterns and refuges with *T. raziana* (Pinho and Vasconcelos, pers. comm.). This could pose an additional threat to this already near threatened endemic species, through competition for resources, or even predation. Consequently, it may be of future interest to characterise the diet of the introduced mouse populations on Santa Luzia and evaluate the level of dietary overlap and predation intensity on *T. raziana*.

4.2. Sympatric populations

The two sympatric populations on Raso showed moderate dietary overlap, even though sharing the same limited resources on the small islet of Raso. This suggests that the species were able to establish a stable coexistence by exploiting different resources, confirming our initial hypothesis. As stated by Pianka (1973), species cannot overlap in all basic niche dimensions. On Raso, *T. raziana* and *T. gigas* show high overlap in two dimensions, activity pattern and distribution (Vasconcelos et al., 2013). Therefore, to effectively reduce interspecific competition, it would appear that they have reduced overlap in the trophic dimension through resource partition.

Both species showed similar richness and niche breadth values, indicating that the variety of items consumed is similar. However, diet composition was significantly different between the two, which further supports dietary niche segregation as a mechanism through which competition is avoided (du Preez et al., 2017; Razgour et al., 2011; Westeen et al., 2023). In particular, several plant and vertebrate items contributed significantly to differentiating the diet of the two sympatric species, by presenting significantly higher proportions in the diet of *T. gigas*. Only two (*Passer iagoensis* (Gould 1838) and *Calonectris edwardsii*) out of the 14 vertebrate MOTUs found were shared between species (Table S2). Similarly, despite invertebrates showing similar proportions in both diets, only 12 % of the invertebrate MOTUs were shared between the species when in sympatry (Table S2), highlighting their distinct exploitation of the islet resources. On the other hand, half of the plant MOTUs were shared between the two species, which may reflect their high availability on the Desertas. However, although both species may feed on plants, they can consume different parts of the plant and with different nutritional values, or at different rates or times of the day to avoid competition (Schoener, 1974; Williams, 1983), a pattern that unfortunately cannot be distinguished through DNA metabarcoding.

The marked body size difference between the two species likely influences prey selection and facilitates resource partitioning. For instance, *T. gigas* presents a stronger trophic link with terrestrial and marine birds and fish, as previously reported by Lopes et al. (2019), than *T. raziana*, and this is most likely favoured by its larger size and expected stronger bite force (Donihue et al., 2023; Herrel et al., 2001). Additionally, this may indicate a strong influence of seabird colony densities of Raso on the body size evolution of *T. gigas*, as suggested by Stadler et al. (2023), promoting the selection of continually larger individuals in the direction of gigantism. Likewise, plants were demonstrated to have a significant role in the diet of *T. gigas* (Pinho et al., 2018), most of which are succulent plants or with succulent parts such as fleshy stems or leaves and fruits (e.g., *Limonium bruneri*). These should be easily consumed by *T. gigas* due to its expected stronger bite, whereas *T. raziana*, most likely relies on more nutritious and easier to consume options such as pollen and nectar. Furthermore, the most frequent invertebrate families in the diet of *T. raziana* on Raso, Rhinotermitidae (Blattodea) and Lepismatidae (Zygentoma), are both mainly composed of small and ground-dwelling individuals. This suggests that *T. raziana* individuals may be more likely to target smaller sized prey, as suggested by Arnold et al. (2008), whereas *T. gigas* requires prey with a higher energetic value to meet its nutritional needs (Pough, 1973).

4.3. Morphological variations

A shift towards herbivory is a common adaptation of insular reptiles of large size, which have proportionately larger intestinal sizes that allow easier plant digestion (Carretero, 2004; Pafilis et al., 2016; Van Damme, 1999). The present results further support this hypothesis, by showing a marginally significant positive relationship between small intestine length and body size for *T. gigas* which is not observed in *T. raziana*. Additionally, the total average ratio between body size and intestinal length was proportionally almost twice in *T. gigas* than in *T. raziana*. This suggests that intestinal length is part of the ontogeny of this species (Pafilis et al., 2016; Sagonas et al., 2015). This allows for longer intestinal transit times and the digestion of difficult items such as vertebrates and plants, which are highly important in the diet of adult T. gigas. This adaptation maximises energy yield, which is essential for large reptiles with high energy requirements (Pafilis et al., 2016). Unfortunately, and as both are protected species, we were only allowed to open five vouchers of each species, which does not provide strong statistical power. However, there is a clear trend that should be investigated further with larger sample sizes. Additionally, differences in diet composition are most likely related to other morphological differences between the two species, that enabled their coexistence (Dufour et al., 2018; Hutchinson and MacArthur, 1959; Schoener, 1970). Our results provide evidence that apart from the phylogenetic signal for size differentiation, reflected in the presumed size discrepancy between the ancestors of the two sister clades (Carranza et al., 2000; Vasconcelos et al., 2010), competition might have favoured character displacement, selecting for individuals with extreme sizes for both *T. gigas* and *T. raziana*. This indicates that, as the availability of preferred resources is reduced due to intraspecific competition, selection might favour individuals who can explore very distinct resources, thereby releasing competitive pressure (Martin and Pfennig, 2009). In the context of ecological specialisation and resource competition, our data suggest that *T. gigas* individuals were most likely selected to be larger than, and *T. raziana* smaller than, their respective ancestral forms (Grant, 1972). This could explain why *T. gigas* and *T. raziana* are the largest and the smallest species within their respective clades, and the only species from these clades that occur in sympatry, representing a possible case of ecological character displacement (Dufour et al., 2017; Grant, 1972). An interesting avenue of future research would be to explore if other morphological features of the head differ among the three populations, which may further explain differences in their trophic niche. Larger reptiles have larger heads, which is inherently related to higher bite force enabling the ingestion of larger and harder prey (Sagonas et al., 2014). In addition, this study could be extended to the islet of Branco, where *T. gigas* and *T. raziana* also occur in sympatry. Yet, this is very difficult to accomplish due to the inherent danger involved in reaching this islet.

4.4. Novel dietary records for T. raziana

The results presented here provide improved knowledge of the dietary composition of the Raso wall gecko. On Raso, the presence of invertebrates and plant material in the faeces of *T. raziana* had already been reported (Schleich, 1987), however, taxonomical identification of the plant items was not possible. More recently, Mateo et al. (2016), described this species to feed exclusively on terrestrial arthropod species. Our results suggest the presence of both invertebrates and plants in the diet, although some items could also be the result of secondary detection (da Silva et al., 2019; Tercel et al., 2021). In this particular case, Mateo et al. (2016) revealed Coleoptera to be the most frequent order in the diet of *T. raziana*, contrary to the present results showing Blattodea and Zygentoma as main items. One possible explanation for this difference could be sampling bias by the presence of easily identifiable chitinous exoskeletons in faeces using a magnifying lens (Brown et al., 2012; Gil et al., 2020). Overall, Zygophyllaceae, Fabaceae and Poaceae were the most frequent plant families in the diet of *T. raziana* on Santa Luzia and Raso populations, corresponding to plants that are abundantly available on the Desertas Islands (Gomes et al., 2023; Lobin, 2015). Most of the invertebrates found in the total diet of *T. raziana* were terrestrial and some were phytophagous. In fact, it was observed that about a third of *T. raziana* samples, on Santa Luzia and Raso, contained both plants and invertebrates, so there is a possibility of indirect consumption of plant items by these geckos (Cuff et al., 2022). On the other hand, two-thirds of Santa Luzia and one-third of Raso samples contained only plant DNA, indicating the importance of direct consumption of these items by this species. The present study also added new arthropod groups to the diet of *T. raziana*, such as Lepidoptera and Psocoptera. Moreover, the present results showed for the first time the consumption of vertebrates by this small gecko, albeit at a lower frequency when compared to its larger competitor. The low frequencies may indicate that vertebrates, or their remains (e.g., regurgitations), are ingested only occasionally and opportunistically and are not a main component of the diet of this species. Analogous behaviour was already observed in *T. gigas* (Schleich, 1980) and other similar-sized species, such as the Selvagens gecko *Tarentola (boettgeri) bischoffi* (Joger, 1984), in the remote Selvagem Grande (Gil et al., 2020).

5. Conclusions

In conclusion, the present study demonstrates resource partitioning facilitating the long-term coexistence of generalist species, and provides valuable insights into the ecological dynamics in island ecosystems. In addition to highlighting specific trophic relationships, these data will help to ensure the sustainable management of the plant, invertebrate and vertebrate communities as a whole. In small and isolated islands these studies are of particular importance, since due to the limited resources the loss of one particular resource can impact the whole network (Lopes et al., 2019; Pinho et al., 2018). Therefore, understanding the mechanisms and outcomes of resource partitioning can provide valuable information for conservation efforts and management (e.g., (Nakashima et al., 2022; Zurdo et al., 2023)), particularly for fragile island ecosystems (Pinho et al., 2018; Schmack et al., 2021).

Ethics Statement

If this manuscript involves research on animals or humans, it is imperative to disclose all approval details.

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Declaration of Competing Interest

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03412.

Data availability

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