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Research article

Environmental and morphological drivers of mutualistic plant–lizard interactions: a global review

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Plant–lizard interactions are still poorly studied, despite lizards are known to interact with flowering plants in many parts of the world. They are commonly reported on islands although the number of documented interactions has also increased in mainland, mostly in isolated environments. In this study, we first performed a global review to explore whether lizard–flower and lizard double mutualistic interactions in continents occur in environments similar to those of islands. Then, we aimed at explaining the factors driving the current distribution of such interactions worldwide. To do this, we considered four environmental factors (latitude, altitude, rainfall and temperature), and phylogeny and body size of lizards that may influence flower visitation. Furthermore, we investigated for the first time the functional role (legitimate visit versus florivory) of lizards in plant reproduction and the conditions under which each type of interaction occurs. Finally, we explored the factors influencing the distribution of lizard double mutualisms worldwide. We recorded a total of 452 lizard–flower interactions (ca 3.4% and 0.1% of the extant lizard and plant species, respectively). Lizard–flower interactions were more frequently recorded on islands (79%) regardless of phylogeny and lizard body size, whereas in mainland the number of interactions increased with altitude. Our analyses also revealed that only 20% of all interactions confirmed pollination effectiveness and a strong association of the type of interaction with environmental factors and species traits. Regarding the distribution of lizard double mutualisms, we found a positive effect of island and rainfall, but a decrease in their occurrence with latitude, altitude, temperature and body size. We predict that mutualistic plant–lizard interactions will be increasingly documented, especially in isolated environments (both on islands and continents), which will help us to better understand the biological patterns of this phenomenon and the mechanisms underlying them.

Keywords: body size, double mutualism, florivory, frugivory, Lacertilia, nectarivory, phylogeny, pollination effectiveness

Introduction

Interactions between plants and lizards (Squamata: Sauria/ Lacertilia), specifically those in the families Gekkonidae and Lacertidae, are frequently reported on islands (Traveset and Sáez 1997, Olesen and Valido 2003, Hervías-Parejo et al. 2020). The low species richness and, thus, a weak interspecific competition, together with a low predation level, may explain the high densities that some taxonomic groups such as lizards achieve on insular systems (i.e. the so-called density-compensation phenomenon, MacArthur et al. 1972). In turn, high densities of lizards on islands, where their favorite arthropod food is scarce, lead to trophic niche expansion ('ecological release' sensu Cox and Ricklefs 1977) which has been reported for a high number of island vertebrate species. Considering specifically the expansion in the relationships with other species, the term was extended to 'interaction release' (sensu Traveset et al. 2015). Thus, for instance, taxa that are typically insectivores in mainland are found to include flower resources and fruits in their diet on islands.

Mutualistic plant–lizard interactions, however, are not restricted to islands, and indeed such interactions are increasingly being reported in continental areas (Fuentes 1976, Acosta et al. 1996, Galindo-Uribe and Hoyos-Hoyos 2007, Gomes et al. 2014, Wester 2019). When mainland lizards face shortage of arthropods, in stressed, isolated or harsh environments (e.g. deserts, rock outcrops, high-altitude zones, cliffs), they also expand their dietary niche to include nectar and fruits in the same way as do insular lizards (Gomes et al. 2014, Novosolov et al. 2018). Nevertheless, it has never been investigated whether plant–lizard interactions in continents occur under environmental conditions similar to those of islands, and which are the environmental drivers that determine such interactions.

The same lizard species can sometimes feed first on the flowers of a plant and subsequently on its fruits, acting as a double mutualist (sensu Olesen 2003, Hansen and Müller 2009). Double mutualist animal species have been documented most frequently on islands, and more often in the tropics than in temperate zones (Fuster et al. 2019), although the environmental factors that shape such a distribution are still unknown.

Herbivorous lizards (> 90% plant volume in diet; Cooper and Vitt 2002) are generally associated with warm (to maintain high body temperatures) and arid climates, and the consequent water deficit (Gomes et al. 2014). By foraging for nutrients on plants to supply their energy and water requirements, lizards are more likely to visit flowers and eat fruits (van Marken Lichtenbelt 1993). Moreover, seasonal differences in environmental conditions, such as rainfall, may regulate resource abundances, and thereby influence the amount of plant matter in the diet of some lizards (Robinson 1987). Therefore, temperature and rainfall seem to be important factors explaining the distribution of plant–lizard interactions. These phenomena might be more prevalent in the lowest latitudes and altitudes, according to the general lizard distribution patterns (Heatwole 1982, McDiarmid et al. 2012). Herbivorous lizards also possess digestive and morphological adaptations for processing leaves, such as large digestive system, and herbivory level in general is correlated with an increase of body size (but see Espinoza et al. 2004). In contrast, lizards feeding on flowers and fruits lack such specializations to process these items which are more easily digested than leaves (Zimmerman and Tracy 1989, Cooper and Vitt 2002). Indeed, recent studies have shown that body size and frugivory in lizards are weakly correlated, and fruit consumption is also common among small-sized species (Hervías-Parejo et al. 2019, Valido and Olesen 2019). Now that more data on plant–lizard interactions are available, we can determine if body size influences flower visitation and fruit consumption. We predict, for instance, that smaller lizards (e.g. juveniles) can access a wide range of corolla sizes more easily than larger lizards (e.g. adult males), whereas the latter can be the main fruit consumers. Such intraspecific variation in lizards may have implications for the reproductive success of plants (Fuster and Traveset 2020).

From a plant's perspective, by consuming nectar and fruits, lizards may act as effective pollinators and dispersers if they visit the flowers and disperse the seeds to suitable sites for germination and growth, respectively (Traveset and Sáez 1997, Hansen and Müller 2009). The quantity component of pollination effectiveness is estimated as the frequency of floral visits and their duration whereas the quality component is quantified as fruit and/or seed set (Schupp et al. 2017). Pollination effectiveness is the product of the quantity and quality components and has proven to be a robust way to estimate the contribution of pollinators to plant fitness in a range of species (Hervías-Parejo and Traveset 2018, Cozien et al. 2019).

In this study, we wanted to improve our understanding of the drivers (both environmental factors and the effect of lizard body size) explaining interactions of lizards with plants. Specifically, we asked the following three questions: 1) Are lizard–flower interactions associated with adverse environmental conditions? If so, we expected these interactions in mainland occurring in environments similar to those of islands. We also expected such interactions to be more prevalent in low latitudes and altitudes and in warm and arid climates; 2) What empirical evidence is available showing that lizards act as true pollinators? Despite the importance of this process in the reproductive cycle of plants, we expected that only a small fraction of studies assessed pollination effectiveness; 3) Which factors drive the type of interaction (pollination versus florivory)?; and 4) What is the frequency of lizard double mutualistic interactions and under what conditions are they found? We predicted them to be more common on islands as this phenomenon has also been more prevalent in such ecosystems for other animal taxa (Fuster et al. 2019).

Material and methods

Literature review

A literature review was conducted using the engines Web of Science (WOS: www.webofknowledge.com) and Google

Scholar (https://scholar.google.com), and the following combination of key words and Boolean operators: ('lizard' OR 'gecko' OR 'reptile' OR 'vertebrate') AND ('flower visit*' OR 'pollinat*' OR 'nectar' OR 'nectarivor*' OR 'florivor*' OR 'flower' AND 'diet' OR 'feed') OR ('seed' OR 'fruit' AND 'diet' OR 'feed' AND 'double mutualism'). All plant–lizard interactions included in previous reviews by Godínez-Álvarez (2004) and Fuster et al. (2019), plus all published articles from 2004 to 2022 (last search on 05/07/2022) were considered in our dataset (Supporting information).

Here, lizards were regarded as legitimate visitors if they contacted the reproductive organs of the flowers while foraging for floral rewards or insects, thus increasing plant fitness (Faegri and Van der Pijl 1966). By contrast, lizards were considered as florivores if they damaged or consumed the floral structures, such as petals or even the whole flower (McCall and Irwin 2006; Fig. 1). Some species, for example *Podarcis lilfordi* on Na Redona (Balearic archipelago) which is a legitimate flower visitor of *Lavatera maritima* (pers. obs.), can eat the flowers of the same species they visit under dry conditions when other food resources are scarce. In such cases (< 10%), we only considered the legitimate visitation behavior of the species.

For each interaction obtained in the literature, we recorded: lizard species and family, plant species and family, area (island – either oceanic or continental – versus mainland), island and archipelago or country name, GPS coordinates, latitude and altitude (from Google Earth: www.google.com/intl/es/earth; when not specified in the article), mean annual rainfall and mean annual temperature (from Foreca: www.foreca.es; when not specified in the article), biome (according to WWF classification: www.worldwildlife.org), biogeographical zone (Afrotropical, Australasia, Indomalaya, Nearctic, Neotropical, Oceania, Palearctic), type of interaction (legitimate visit, florivory or unknown), if pollination effectiveness was experimentally assessed in the study (yes/no), and whether a double mutualism interaction was indicated by presence of both pollination and seed dispersal interactions in the same pair of interacting species (yes/no). We also included maximum snout–vent length (hereafter SVL) of lizards, obtaining data from Meiri (2018). To illustrate the global distribution of all reported mutualistic plant–lizard interactions, we used QGIS ver. 3.4.14 (QGIS Development Team 2020).

Statistical analysis

We tested the hypothesis that the frequency of occurrence (FO) of lizard–flower interactions is influenced by area (island versus mainland), environmental factors (latitude, altitude, rainfall and temperature) and/or SVL of lizards using phylogenetic mixed models. For this, we used 'ape' (Paradis et al. 2004) and 'MCMCglmm' (Hadfield 2010) R packages (ver. 4.1.2, www.r-project.org), and adjusted data to a Gamma distribution, with area, environmental factors and SVL as predictor variables. Altitude was square-root transformed, and mean annual rainfall, temperature, and maximum SVL were log-transformed to achieve normality. We fitted both phylogenetic models, including biogeographical zone and phylogeny from Pyron et al. (2013) as random effects, to take distribution and phylogenetic relationship between species into account (de Villemereuil and Nakagawa 2014), and also fitted models without phylogenetic structure with biogeographic region as the only random effect. The different models were compared using deviance information criterion (DIC; lowest values are the best) that measures the quality of the adjustment made by the model, using the function *DIC_bayesbr* of the R package 'bayesbr' (Melo and Mayrink 2021). We used the locations where a lizard–flower interaction was observed as sampling units (n = 188).

To assess whether the type of interaction (legitimate visit versus florivory), is explained by area (island versus mainland), environmental factors (latitude, altitude, rainfall and temperature) and/or SVL, we used multiple logistic regression models (GLM, binomial family) with the R function *glm* (package 'stats'; www.r-project.org). To compare the fit of different regression models we used the Akaike information criterion (AIC, the model with the lowest AIC offers the best fit), using the R *model.sel* function ('MuMIn' package; Barton 2022). The plant–lizard interaction was the sampling unit (n = 452).
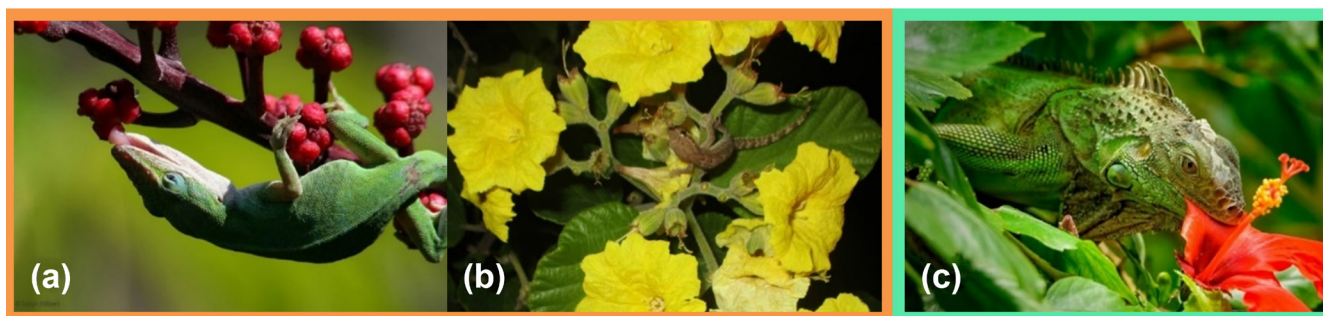

Figure 1. Types of lizard–flower interactions. From left to right: legitimate visits: (a) *Anolis carolinensis* feeding on *Schefflera actinophylla* nectar, in the island of Hawaii (photo L. Hillbert); and (b) *Phyllodactylus galapagensis* foraging for insects on *Cordia lutea* flowers in the island of Santa Cruz, Galápagos, Ecuador (photo S. Hervías-Parejo); and (c) florivory: *Iguana iguana* eating the petals of a *Hibiscus* flower in the island of Curaçao, Lesser Antilles (photo K. L'amour).

The conditions under which double mutualisms occur were investigated using generalised linear mixed models (binomial GLMMs) with area (island versus mainland), latitude, altitude, rainfall, temperature and SVL as predictor variables and biogeographic region as random effect (function *bglmer*, R package 'blme', Chung et al. 2013). Model performance was evaluated using the AIC ('MuMIn' package; Barton 2022). The plant–lizard interaction was the sampling unit (n = 452).

Results

Lizard–flower interactions on islands versus mainland

Of the 304 records resulting from our literature search, we found 162 studies reporting a total of 452 plant–lizard interactions (Supporting information) involving 173 lizard species of 20 families (ca 3.4% and 46.5% of the extant lizard species and families, respectively, www.reptile-database.org/db-info/taxa.html#Sau) and 311 plant species of 106 families (ca 0.1% and 26.2% of the extant plant species and families, respectively, www.theplantlist.org/1.1/browse/A). Lizard species forage on flowers worldwide, most records being from tropical and subtropical regions and, specifically, from 91 islands (41 archipelagos) and 31 continental countries (Table 1, Fig. 2).

The model without phylogenetic structure (i.e. biogeographic zone as random effect; DIC = −631.87; $DIC_{null model}$ = −634.59) performed better than that including phylogeny and biogeographic zone as random effects (DIC = −647.63; $DIC_{null model}$ = −649.44), and the analysis showed good convergence (i.e. potential scale reduction factors for the random and fixed effects = 1). The only model that received support by the data included an interaction between two fixed effects (area and altitude), indicating an increase in the frequency of interactions with altitude in mainland areas (Fig. 3).

Lizards as legitimate visitors versus florivores

We found that about half (49%) of the reported lizard–flower interactions were legitimate visits, whereas 39% were florivory cases. For ca. 11% of the records (Supporting information), the type of lizard–flower interaction was not specified and, thus, such records were excluded from the analyses. Foraging for insects on flowers was reported for only three lizard species (< 1%): *P. lilfordi* in the Balearic Islands (Pérez-Mellado et al. 2006), *Gallotia atlantica* in the Canary Islands (Nelson 2010) and *Phyllodactylus galapagensis* in the Galápagos (Hervías-Parejo 2017, unpubl.).

More than half of legitimate visits (54%) were observed in tropical and subtropical moist broadleaf forests and almost one-third of florivory (28%) in deserts and xeric shrublands (Table 1). The most parsimonius model included area, latitude, altitude and SVL (weight AIC = 0.995), and explained 90% of the variation in the interaction type (Table 2). Legitimate visits were less frequent on mainland (20%) than on island (73%; β = −8.66 ± 1.47). Legitimate visits also decreased with latitude (β = −0.04 ± 0.01) and maximum SVL (β = −12.18 ± 1.96) and increased with altitude (β = 0.12 ± 0.03) (Fig. 4). We further explored whether the frequency of legitimate visits and florivory vary with island type (oceanic versus continental), using a Pearson's Chi-squared test with Yates' continuity correction (function *CrossTable* of the R 'gmodels' library; Warnes et al. 2022). We found a significant relationship between the type of interaction and that of island (Chi² = 4.97, df = 1, p = 0.0257; V_{Cramer} = 0.13, CI 95% [0.00, 1.00], n_{obs} = 296); legitimate visits were more frequent on oceanic (77%) than continental islands (63%) (Fig. 5).

Effective pollination has been confirmed in only 20% (90 records) of all plant–lizard interactions, for a total of 23 lizard species (Supporting information). Of such studies, only three plant species: *Guthriea capensis* (F. Achariaceae), *Trochetia blackburniana* (F. Malvaceae) and *Roussea simplex* (F. Rousseaceae) have been documented to be truly dependent for their pollination on lizards, *Pseudocordylus subviridis* (Cozien et al. 2019) and *Phelsuma cepediana* (Hansen and Müller 2009).

Lizards as double mutualists

A total of 25 species (14.6%) from seven families are currently known as double mutualists. Most cases of double mutualisms were found on deserts and xeric shrublands of

Table 1. Percentage of interactions of legitimate visits (LV) and florivory (FL), of pollination confirmed (PC) and of double mutualisms (DM) per area (island versus mainland), for the different biomes (according to WWF classification).

| Biome	Island				Mainland			
	LV	FL	PC	DM	LV	FL	PC	DM
Deserts and xeric shrublands	11.7	7.1	15.9	16.0	88.9	48.8	100.0	99.0
Mediterranean forests, woodlands and scrubs	14.6	25.0	11.0	10.0		1.2		
Montane grasslands and shrublands	0.5	0.0	0.0		11.1	15.1		1.0
Temperate broadleaf and mixed forests	6.8	1.2	0.0			22.1		
Temperate grasslands, savannas and shrublands	0.0	1.2	0.0			5.8		
Tropical and subtropical dry broadleaf forests	10.7	35.7	51.2	26.0		4.7		
Tropical and subtropical grasslands, savannas and shrublands	0.0	2.4	0.0			1.2		
Tropical and subtropical moist broadleaf forests	55.8	27.4	22.0	11.0		1.2		
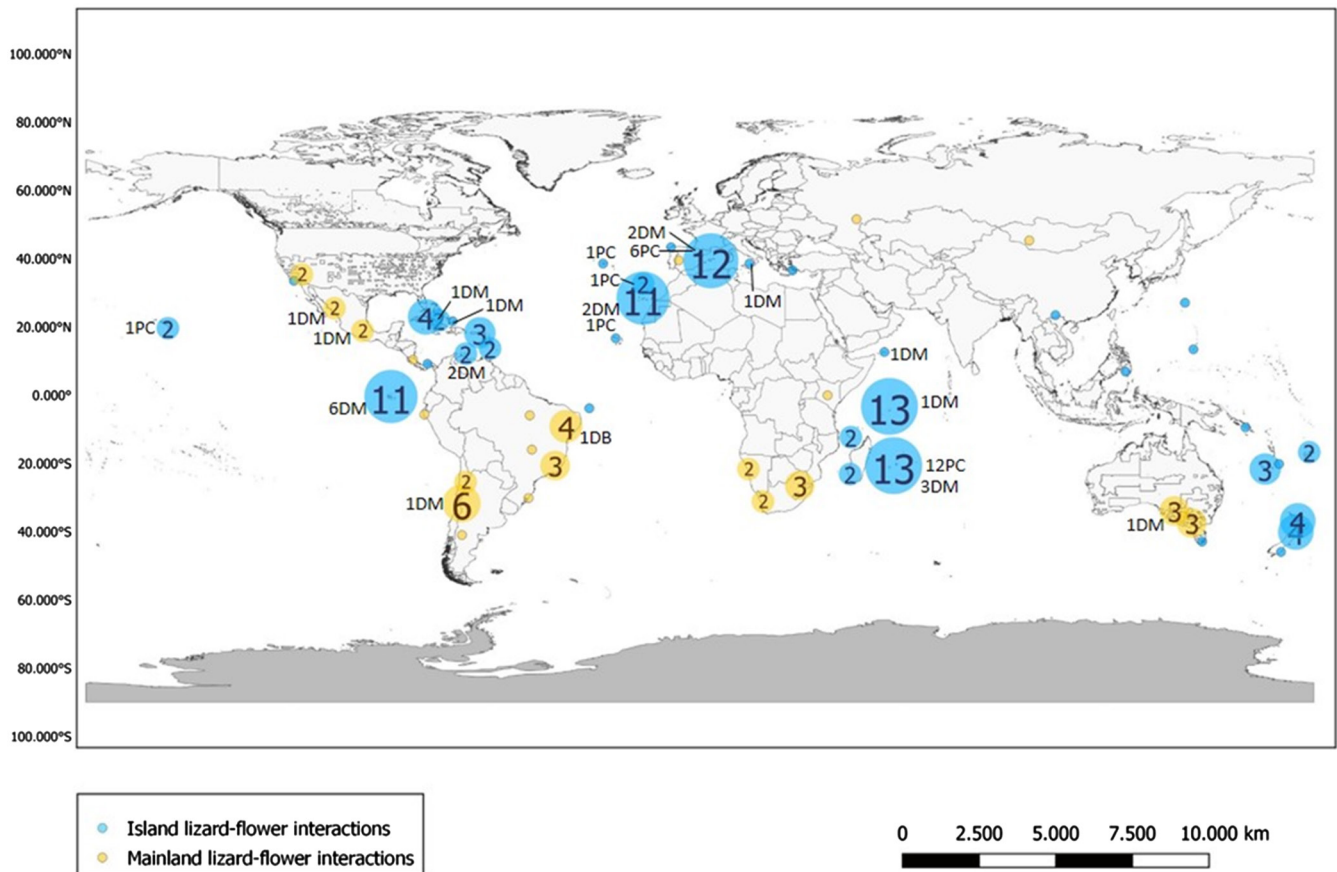
Figure 2. Global distribution (only absent in Antarctica, grey shaded area) of lizard–flower interactions, number of pollination confirmed (PD) and double mutualism (DM). One locality may contain reports about several lizard species (see the interactive and higher resolution version of the map).
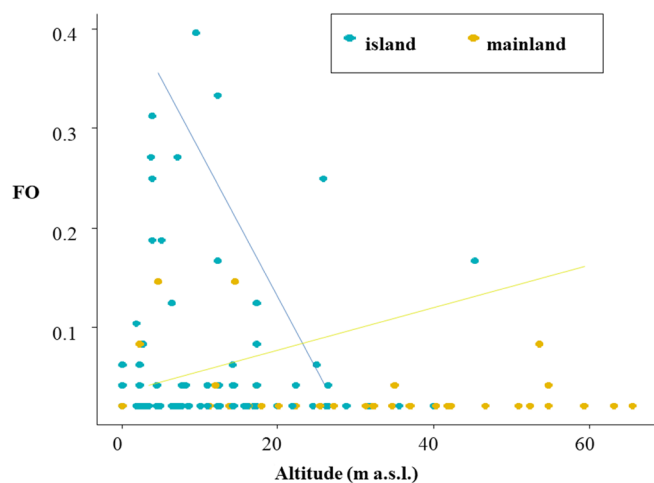

Figure 3. Variation in the frequency of occurrence (FO) of lizard–flower interactions with area (island versus mainland) and altitude. FO values were standardised dividing the frequencies by the highest value. To increase the resolution of the figures, we excluded *Phelsuma borboni* from Reunion (FO = 1, interacting with 49 plant species).

Central America mainland, and in tropical and subtropical dry broadleaf forests (71%) and in tropical and subtropical moist broadleaf forests subtropical and Mediterranean forests, woodlands and scrubs of islands (27.6%) (Table 1). The model using area, environmental factors and species traits received overwhelming support from the data (weight AIC = 0.997) and indicated that the presence of double mutualisms is higher on islands ($\beta = 0.34 \pm 0.63$) than on the mainland, and that it increased with rainfall ($\beta = 1.08 \pm 0.35$) while it decreased with latitude ($\beta = -0.07 \pm 0.02$), altitude ($\beta = -0.01 \pm 0.02$), temperature ($\beta = -2.21 \pm 2.72$) and SVL ($\beta = -0.50 \pm 0.59$) (see model selection summary in Table 2).

Discussion

Despite their global distribution (only absent in Antarctica; Fig. 2), lizard–flower interactions are known for a relative low fraction (ca 3.4%) of the total Lacertilia species in the world (Uetz et al. 2022), involving a total of 173 species so far documented. These species belong to 20 (46.5%) of the 43 extant families in that suborder which includes the so-named lizards, geckos, skinks, iguanas and chameleons.

Table 2. Model selection summary of eight candidate models explaining variation in the occurrence of legitimate visits versus florivory by lizards, and of double mutualisms involving lizards.

Models	df	LogLik	AICc	Delta	Weight
Legitimate visits versus florivory					
1. Interaction type ~ area + latitude + altitude + SVL	5	−87.19	184.55	0.00	1
2. Interaction type ~ area + latitude + SVL	4	−108.91	225.93	41.38	0
3. Interaction type ~ area × SVL	4	−128.07	264.24	79.69	0
4. Interaction type ~ area × altitude	6	−128.07	268.35	83.81	0
5. Interaction type ~ area + latitude + altitude + rainfall + temperature + SVL	7	−152.86	320.05	135.50	0
6. Interaction type ~ area	2	−181.88	367.79	183.24	0
7. Interaction type ~ SVL	2	−211.82	427.67	243.12	0
8. Null	1	−272.04	546.08	361.54	0
Double mutualisms					
1. Double_mutualism ~ area + latitude + altitude + rainfall + temperature + SVL	8	−106.12	230.16	0.00	1
2. Double_mutualism ~ area + SVL	4	−129.83	267.78	39.05	0
3. Double_mutualism ~ latitude + rainfall	4	−142.78	293.66	64.94	0
4. Double_mutualism ~ area + latitude + rainfall + temperature	6	−142.14	296.49	67.76	0
5. Double_mutualism ~ altitude + rainfall + temperature	5	−148.49	307.13	78.40	0
6. Double_mutualism ~ rainfall	3	−162.70	331.46	102.73	0
7. Double_mutualism ~ area	3	−164.04	334.14	105.41	0
8. Null	2	−173.12	350.27	121.54	0

In relation to the previous review on pollination by lizards (Godínez-Álvarez 2004), we documented up to a fourfold rise in the number of Lacertilia species interacting with flowers, as a result of an increase by 165% in the number of studies on islands (from 35 to 95 lizard species) and by 3450% in mainland (from 2 to 71 lizard species). These values support the claim that the phenomenon may be even more widespread, but simply has not received much attention yet (Hernández-Teixidor et al. 2020, Hervías-Parejo et al. 2020). Despite this limitation, this study is the first providing data on environmental factors and lizard species traits that could explain the current distribution of plant–lizard interactions.

Are flower–lizard interactions associated to adverse environmental conditions in mainland?

Our review confirmed that lizard–flower interactions are most common on islands, supporting the hypothesis of an interaction release phenomenon described in these ecosystems for other vertebrates such as birds (Traveset et al. 2015). The low availability of arthropods on islands seems to force lizards to expand their niches, feeding upon plant resources (Olesen and Valido 2003). More than half (51.6%) of the mainland species that interact with flowers live in Neotropical deserts and xeric shrublands; many of the plants here produce flowers during the dry season, thus lizards probably forage on
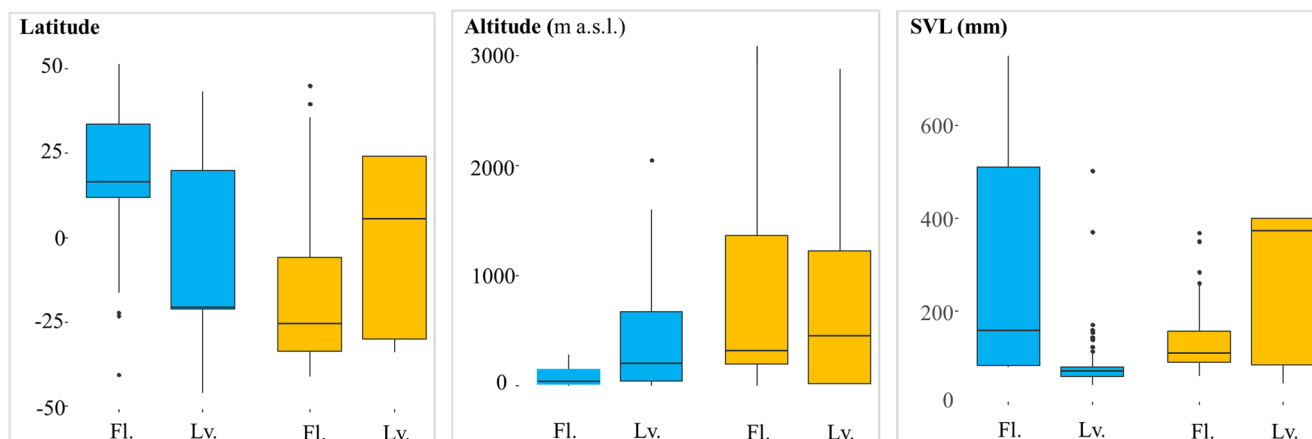

Figure 4. Relationship between the type of the interaction (Fl: florivory, Lv: legitimate visit) and, from left to right, latitude, altitude and maximum snout–vent length (SVL) grouped by area (island versus mainland). Horizontal line in box represents median value, the bottom and top whiskers represent the lower and upper quartile and the dots represent outlier values. Blue boxes correspond to island, while orange boxes correspond to mainland.
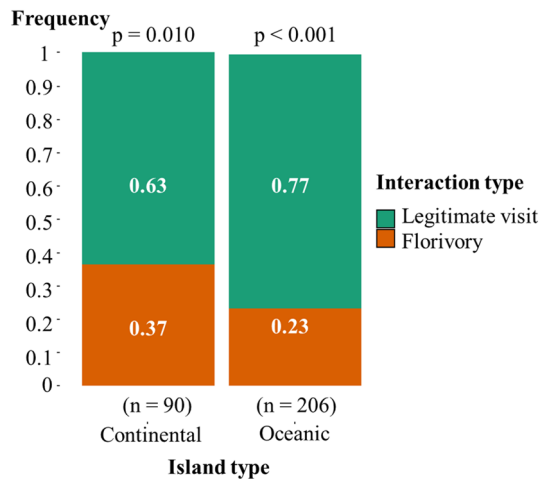
Figure 5. Association between the type of lizard–flower interaction (legitimate visit versus florivory) and the type of island (oceanic versus continental island).

flowers to obtain energy and water (Nagy 1973, van Marken Lichtenbelt 1993, Blázquez and Rodríguez-Estrella 2007). The interactions of mainland lizards with flowers were more frequent at high altitudes (75% above 1000 m a.s.l.), which might also indicate a strong resource limitation. For instance, *P. subviridis* visits the flowers of *G. capensis* in the dry rocky environment of Sentinel Peak (2750 m a.s.l. Maloti-Drakensberg World Heritage Site, South Africa), where there is a relative scarcity of insects (Cozien et al. 2019). Five species (*Liolaemus eleodori*, *L. poecilochromus*, *Paralaudakia stoliczkana*, *Phymaturus punae* and *Sceloporus torquatus*) even interact with flowers, feeding upon them in all five cases, above 3000 m in deserts and xeric shrublands and montane grasslands of Argentina and Mexico (Supporting information). The fact that lizards in such high-elevated habitats acted as florivores might indicate that they obtain more of such resources by feeding on the entire flowers and not just on the nectar and pollen (Albuquerque et al. 2018). These harsh and somehow isolated environments indeed resemble conditions faced by vertebrates on islands (Brown 1978). The finding supports the hypothesis of lizard–flower interactions in mainland being associated with adverse environmental conditions. Variation in the frequency of occurrence of interactions was not explained by genetic similarity, as distantly related lizard species interacted with flowers with similar frequency. Therefore, factors other than phylogenetic relatedness may influence these interactions, for instance a common evolutionary history due to overlap in resource use and/or habitat could determine their ecological similarity or functionality, as found in other systems (Olesen et al. 2012, Ramm et al. 2020).

Functional role of lizards on flowers and factors determining it

Our review revealed that more legitimate visits were recorded on islands compared to mainland, and mostly in the tropics

(66.5%, Table 1). A high fraction (44%) of legitimate visits has actually been reported on two islands of the Indian Ocean, Reunion and Mauritius. This is why the role of lizards as legitimate visitors showed to decrease with latitude. A general trend of fog precipitation and rainfall interception with increasing altitude is common on islands, and such island-scale abiotic variables appear to be an important determinant of arthropod community structure (Hamann 1979, Prada et al. 2009). This pattern could explain the increase observed in the number of legitimate visits by lizards with altitude.

There is an asymmetric use of flowers across Lacertilia families. Thus, for instance, while 24 Gekkonidae species have been found to interact with flowers, the Sphenodontidae and Opluridae families are represented by only one species in the dataset (*Sphenodon punctatus* and *Oplurus cuvieri*, respectively). The reason may simply be that the family Gekkonidae contains 1331 species, which contrasts with the few species in the other two families (one and eight species, respectively; Uetz et al. 2022). However, morphological constrains and differences among families may also determine their ability to access flowers (Zug et al. 2001). This study reveals that species with small body sizes are more likely to act as legitimate visitors than as florivores. Indeed, all interactions with flowers involving Gekkonidae were legitimate, and species in this family are the smallest in body size (mean SVL = 68.7 mm), whereas species with mean SVL greater than 150 mm were mostly florivorous (e.g. 95% Teiidae, 61% Scindidae, 79% Iguanidae and 100% of species in all other families).

To date, there is still little evidence showing that lizards act as effective pollinators (Traveset and Sáez 1997). More pollination exclusion experiments need to be carried out in a larger variety of systems to better understand the functional role of lizards in plant reproduction. Some authors suggested that lizards might not be exclusive pollinators, because pollen does not adhere to their snout/vent properly (Ortega-Olivencia et al. 2012, Fuster et al. 2020). Nevertheless, some *Phelsuma* species have specialised to feed on nectar and insects associated with flowering plants (Staub 1988). For instance, *P. cepediana* is one the few pollinators, if not the only, of *T. blackburniana* and *R. simplex* in Mauritius; although *T. blackburniana* is visited by other taxa such as hymenopterans and birds, the most effective pollinator is the gecko (Hansen et al. 2007). In the case of *R. simplex*, none of the insect species that interacted with the flowers touched the anthers (Hansen and Müller 2009). Likewise, for *G. capensis* in South Africa, animal taxa other than lizards (*P. subviridis*) were observed visiting the flowers but none of them was confirmed as effective pollinator, and pollinator exclusion experiments showed that the absence of insects decreases reproductive success by only 4% (Cozien et al. 2019).

Importance of lizards as double mutualists

Since the global review on double mutualistic vertebrate species (Fuster et al. 2019), at least eight studies reported new cases involving lizards (Supporting information).

Overall, nine lizard species were added to the previously 15 species already known as double mutualists, representing an increase of 33%.

Double mutualisms are especially prevalent on Neotropical dry forests and xeric habitats, where less pronounced seasonality and almost continuous flowering and fruiting may explain the higher prevalence in this region (Hansen and Müller 2009, Olesen et al. 2018). In temperate zones, *P. lilfordi* from Balearic Islands is the only species reported as double mutualist, though it is true that the interaction of this species with plants has received much attention so far (Supporting information). We confirmed a higher frequency of double mutualisms on islands compared to mainland, as observed by Fuster et al. (2019) in their review involving lizards, mammals and birds. However, double mutualisms involving lizards are also common in desert and xeric shrublands in Central American mainland (Iverson 1977, van Marken Lichtenbelt 1993, Blázquez and Rodríguez-Estrella 2007). Scarcity of other interaction partners in habitats poor in animal diversity such as islands, deserts or other xeric habitats (as these conditions mimic those of islands; sensu 'terrestrial islands', Dillon and Rundel 1990, Downie 1999) may contribute to the engagement of plants and lizards in double mutualisms in such ecosystems (Gomes et al. 2014).

The occurrence of double mutualisms was positively influenced by rainfall. Hence, locations with higher mean annual rainfall reported more cases of double mutualisms, which may be explained by the special conditions of biomes with a dry season, where most double mutualisms were reported, and the positive effect of water on plant flowering and fruiting (Zeppel et al. 2014). Rainfall may also be one of the most important environmental cues influencing the seasonal activities and abundances of tropical insects (Kishimoto-Yamada and Itioka 2015). A priori, the greater the availability of arthropods, the fewer visits to flowers and frugivory by lizards would be expected. However, the abundance of an insect species is also affected by its predators and parasitoids, and interactions between them are often influenced by rainfall and possibly other factors (Itioka and Yamauti 2004). Future studies on plant–lizard interactions could benefit from measuring the abundance of both insects and flowers under different rainfall patterns. Although fruits seem to be a proper food resource, in many cases the flower visiting lizards might not eat the fruit, if available, because it might be too big or too hard to eat; alternatively, the frugivorous lizards might not legitimately visit a flower (if available) because of its small corolla size. Our study suggests that small-sized lizards are those more likely to act as double mutualists.

As observed for legitimate visits, double mutualisms decrease with latitude, according to the general lizard distribution pattern (Heatwole 1982, McDiarmid et al. 2012). Moreover, double mutualisms were more frequently reported at relatively low altitudes (mean $= 435.1 \pm 687.2$) and mild temperatures (mean $= 21.3 \pm 5.9$). Ectotherms living at low altitudes are faced with warmer temperatures and less harsh conditions than those living at high altitudes (Spellerberg 1976). Thus, this result suggests that the more pleasant an environment, the greater probabilities of finding double mutualisms. However, a bias in the research of double mutualisms towards habitats with more pronounced seasonality could also explain, at least partially, this result.

Our study sheds light on the environmental conditions and morphological traits of lizards that explain the distribution of double mutualisms. This phenomenon occurs when two interacting species benefit each other in two different ecological processes (i.e. pollination and seed dispersal), representing a strong dual benefit for both partners (Olesen et al. 2018). The evolutionary consequences of this process should depend on the output of this interaction. For instance, double mutualisms may impose a large risk to both processes if one partner or its performance drops out, with still unknown consequences for community composition and functioning.

The plant families Cactaceae, Fabaceae and Rubiaceae showed to be those that rely mostly on lizards as double mutualists. There is an important number of studies documenting frugivory by lizards upon Cactaceae species in the Brazilian caatinga, where the adverse conditions and low availability of preferred resource (in a similar way as it occurs on islands) forces these lacertids to feed upon plant material (Xavier and dos Reis Días 2015, Gomes et al. 2017). Most frugivory studies probably did not take into account flower visitation and vice versa (Traveset and Sáez 1997, Hervías-Parejo et al. 2019) and, therefore, further effort will allow assessing a more realistic distribution pattern of plant–lizard double mutualisms.

Concluding remarks

Mutualistic plant–lizard interactions are prevalent on tropical and subtropical biomes on islands, arid highlands in mainland and among small-sized lizard species. We predict such interactions will be increasingly documented, especially on mainland isolated environments such as 'terrestrial islands'. Compared to other ectothermic animals (insects), pollination effectiveness by lizards is poorly documented and the attention given to the different lizard species is so far disproportionate. Lizard–flower interactions such as those by *Phelsuma* geckos in Reunion and Mauritius and by *Podarcis* in the Balearic Islands are the best studied. Focusing attention on other species and ecosystems is much needed to assess the importance of these interactions, which in some cases might be essential for plant reproduction and even for community functioning (Torres-Vanegas et al. 2021). Likewise, we expect that more species will be documented in the future as double mutualists, especially opportunistic lizard species that consume both flower and fruit resources and benefit plants doubly by doing so. This review sheds light on certain environmental factors and lizard species traits that explain part of the occurrence of plant–lizard interactions. However, more studies are needed to determine if we are observing a true reflection of a biological pattern. Attention on other environmental drivers and plant species traits is also required to expand our general understanding of the ecology and evolution of mutualisms. All this information will allow assessing

the importance of lizards in the life cycle of plants and will be crucial to develop better conservation strategies of these species and their interactions.

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Author contributions

Esther J. Correcher: Formal analysis (equal); Investigation (lead); Methodology (equal); Writing – original draft (lead); Writing – review and editing (equal). **Sandra Hervías-Parejo**: Conceptualization (equal); Formal analysis (equal); Methodology (lead); Writing – original draft (equal); Writing – review and editing (lead). **Rocío Ruiz de Ybáñez Carnero**: Supervision (lead); Writing – original draft (equal); Writing – review and editing (equal). **Sohan Sauroy-Toucouère**: Investigation (equal). **Anna Traveset**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

A list of all species and interactions is available in Supporting information and a list of all articles from our search result in the Supporting information. An interactive map of the global distribution of lizard–flower interactions and double mutualisms is available at https://drive.google.com/drive/folders/1OtYfI129TK7XeOn2EpGn_QzJqEvc_rqi?usp=share_link.

Supporting information

The Supporting information associated with this article is available with the online version.

References

Acosta, J. C., Ávila, L. J. and Blanco, M. G. 1996. Ecología de *Liolaemus boulengeri* (Sauria: Tropiduridae) en el noroeste de la estepa patagónica (Ing. Jacobacci, Río Negro, Argentina). – Cuad. Herpetol. 9: 100–107.

Albuquerque, R. L. Protázio, A. S., Cavalcanti, L. B. Q., Lopez, L. C. S. and Mesquita, D. O. 2018. Geographical ecology of *Tropidurus hispidus* (Squamata: Tropiduridae) and *Cnemidophorus ocellifer* (Squamata: Teiidae) in a Neotropical region: a comparison among Atlantic Forest, Caatinga and coastal populations. – J. Herpetol. 52: 145–155.

Barton, K. 2022. MuMIn: multi-model inference. – R package ver. 1.46.0, https://CRAN.R-project.org/package=MuMIn.

Blázquez, M. C. and Rodríguez-Estrella, R. 2007. Microhabitat selection in diet and trophic ecology of a spiny-tailed iguana *Ctenosaura hemilopha*. – Biotropica 39: 496–507.

Brown, J. H. 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. – Great Basin Nat. Memoirs 2: 20–27.

Chung, Y. 2013. A nondegenerate penalized likelihood estimator for variance parameters in multilevel models. – Psychometrika 78: 685–709.

Cooper Jr., W. E. and Vitt, L. J. 2002. Distribution, extent and evolution of plant consumption by lizards. – J. Zool. 257: 487–517.

Cox, G. W. and Ricklefs, R. E. 1977. Species diversity and ecological release in Caribbean land bird faunas. – Oikos 28: 113–122.

Cozien, R. J., van der Niet, T., Johnson, S. D. and Steenhuisen, S.-L. 2019. Saurian surprise: lizards pollinate South Africa's enigmatic hidden flower. – Ecology 100: e02670.

de Villemereuil, P. and Nakagawa, S. 2014. General quantitative genetic methods for comparative biology. – In: Garamszegi, L. (ed.), Modern phylogenetic comparative methods and their application in evolutionary biology. Springer, pp. 287–303.

Dillon, M. O. and Rundel, P. W. 1990. The botanical response of the Atacama and Peruvian Desert floras to the 1982–1983 El Niño event. – Elsevier Oceanogr. Ser. 52: 487–504.

Downie, D. A. 1999. Performance of native grape phylloxera on host plants within and among terrestrial islands in Arizona, USA. – Oecologia 121: 527–536.

Espinoza, R. E., Wiens, J. J. and Tracy, C. R. 2004. Recurrent evolution of herbivory in small, cold-climate lizards: breaking the ecophysiological rules of reptilian herbivory. – Proc. Natl Acad. Sci. USA 101: 16819–16824.

Faegri, K. and Van der Pijl, L. 1966. The principles of pollination ecology. – Pergamon Press, pp. Ix + 248.

Fuentes, E. R. 1976. Ecological convergence of lizard communities in Chile and California. – Ecology 57: 3–17.

Fuster, F. and Traveset, A. 2020. Importance of intraspecific variation in the pollination and seed dispersal functions of a double mutualist animal species. – Oikos 129: 106–116.

Fuster, F., Kaiser-Bunbury, C. and Traveset, A. 2020. Pollination effectiveness of specialist and opportunistic nectar feeders influenced by invasive alien ants in the Seychelles. – Am. J. Bot. 107: 957–969.

Fuster, F., Kaiser-Bunbury, C., Olesen, J. M. and Traveset, A. 2019. Global patterns of the double mutualism phenomenon. – Ecography 42: 826–835.

Galindo-Uribe, D. and Hoyos-Hoyos, J. M. 2007. Relaciones planta–herpetofauna: nuevas perspectivas para la investigación en Colombia. – Univ. Scient. 12: 9–34.

Godínez-Álvarez, H. 2004. Pollination and seed dispersal by lizards: a review. – Rev. Chil. Hist. Nat. 77: 569–577.

Gomes, V. G. N., Meiado, M. V., Quirino, Z. G. M., Araujo, H. F. P. and Machado, I. C. 2017. Synchronous fruiting and common seed dispersers of two endemic columnar cacti in the Caatinga, a dry forest in Brazil. – Plant Ecol. 218: 1325–1338.

Gomes, V. G. N., Quirino, Z. G. M. and Machado, I. C. 2014. Pollination and seed dispersal of *Melocactus ernestii* Vaupel

subsp. *Ernestii* (Cactaceae) by lizards: an example of double mutualism. – Plant Biol. 16: 315–322.

Google Earth 2020. Retrieved from https://earth.google.com/web/@57.47296694,-87.51144142,11050.53912101a,25963948.55775834d,35y,0h,0t,0r.

Hadfield, J. D. 2010. MCMC methods for multi-response generalised linear mixed models: the MCMCglmm R package. – J. Stat. Softw. 33: 1–22.

Hamann, O. 1979. On climatic conditions, vegetation types and leaf size in the Galápagos Islands. – Biotropica 11: 101–122.

Hansen, D. M. and Müller, C. B. 2009. Reproductive ecology of the endangered enigmatic Mauritian endemic *Roussea simplex* (Rousseaceae). – Int. J. Plant Sci. 170: 42–52.

Hansen, D. M., Kiesbüy, H. C., Jones, C. G., Müller, C. B. and Wilbur, H. M. 2007. Positive indirect interactions between neighboring plant species via a lizard pollinator. – Am. Nat. 169: 534–542.

Heatwole, H. 1982. A review of structuring in herpetofaunal assemblages. – In: Scott, N. J. (ed.), Herpetological communities. Wildlife Research Report 13, U.S. Dept Interior Fish and Wildlife Service, pp. 1–19.

Hernández-Teixidor, D., Díaz-Luis, N., Medina, F. M. and Nogales, M. 2020. First record of geckos visiting flowers in the Palaearctic Ecozone. – Curr. Zool. 66: 447–448.

Hervías-Parejo, S. and Traveset, A. 2018. Pollination effectiveness of opportunistic Galápagos birds compared to that of insects: from fruit set to seedling emergence. – Am. J. Bot. 105: 1142–1153.

Hervías-Parejo, S., Heleno, R., Rumeu, B., Guzmán, B., Vargas, P., Olesen, J. M., Traveset, A., Vera, C., Benavides, E. and Nogales, M. 2019. Small size does not restrain frugivory and seed dispersal across the evolutionary radiation of Galápagos lava lizards. – Curr. Zool. 65: 353–361.

Hervías-Parejo, S., Nogales, M., Guzmán, B., Trigo, M. M., Olesen, J. M., Vargas, P., Heleno, R. and Traveset, A. 2020. The potential role of lava lizards as pollinators across the Galápagos islands. – Integr. Zool. 15: 144–148.

Itioka, T. and Yamauti, M. 2004. Severe drought, leafing phenology, leaf damage and lepidopteran abundance in the canopy of a Bornean aseasonal tropical rain forest. – J. Trop. Ecol. 20: 479–482.

Iverson, J. B. 1977. Behavior and ecology of the rock iguana *Cyclura carinata*. – PhD thesis, Univ. of Florida, USA.

Kishimoto-Yamada, K. and Itioka, T. 2015. How much have we learned about seasonality in tropical insect abundance since Wolda (1988)? – Entomol. Sci. 18: 407–419.

MacArthur, R. H., Diamond, J. M. and Karr, J. R. 1972. Density compensation in island faunas. – Ecology 53: 330–342.

McCall, A. C. and Irwin, R. E. 2006. Florivory: the intersection of pollination and herbivory. – Ecol. Lett. 9: 1351–1365.

McDiarmid, R. W., Foster, M. S., Guyer, C., Chernoff, N. and Gibbons, J. W. 2012. Reptile biodiversity: standard methods for inventory and monitoring. – Univ. of California Press.

Meiri, S. 2018. Traits of lizards of the world: variation around a successful evolutionary design. – Global Ecol. Biogeogr. 27: 1168–1172.

Melo, J. and Mayrink, V. 2021. bayesbr: beta regression on a Bayesian model. – https://cran.microsoft.com/snapshot/2022-05-30/web/packages/bayesbr/bayesbr.pdf.

Nagy, K. A. 1973. Behavior, diet and reproduction in a desert lizard, *Sauromalus obesus*. – Copeia 1973: 93–102.

Nelson, E. C. 2010. Lizards on *Aeonium lancerottense* in Lanzarote, Canary Islands: a new example of pollination by reptiles? – Bradleya 2010: 15–18.

Novosolov, M., Rodda, G. H., Gainsbury, A. M. and Meiri, S. 2018. Dietary niche variation and its relationship to lizard population density – J. Anim. Ecol. 87: 285–292.

Olesen, J. M. 2003. In Island ecosystems: conservation and molecular approach. – Centre of Biological and Geological Sciences, pp. 45–86.

Olesen, J. M. and Valido, A. 2003. Lizards as pollinators and seed dispersers: an island phenomenon. – Trends Ecol. Evol. 18: 177–181.

Olesen, J. M., Alarcón, M., Ehlers, B. K., Aldasoro, J. J. and Roquet, C. 2012. Pollination, biogeography and phylogeny of oceanic island bellflowers (Campanulaceae). – Perspect. Plant Ecol. Evol. Syst. 14: 169–182.

Olesen, J. M., Damgaard, C. F., Fuster, F., Heleno, R. H., Nogales, M., Rumeu, B., Trøjelsgaard, K., Vargas, P. and Traveset, A. 2018. Disclosing the double mutualist role of birds on Galápagos. – Sci. Rep. 8: 57.

Ortega-Olivencia, A., Rodríguez-Riaño, T., Pérez-Bote, J. L., López, J., Mayo, C., Valtueña, F. J. and Navarro-Pérez, M. 2012. Insects, birds and lizards as pollinators of the largest-flowered *Scrophularia* of Europe and Macaronesia. – Ann. Bot. 109: 153–167.

Paradis, E., Claude, J. and Strimmer, K. 2004. APE: analyses of phylogenetics and evolution in r language. – Bioinformatics 20: 289–290.

Pérez-Mellado, V., Riera, N., Potter, C., Piccolo, V. and Hernández-Estevéz, J. Á. 2006. A complex case of interaction between lizards and plants. The dead horse arum *Dracunculus muscivorus* and the Balearic lizard *Podarcis lilfordi*. – In: Corti, C., Lo Cascio, P. and Biaggini, M. (eds), Mainland and insular lacertid lizards: a Mediterranean perspective. Firenze Univ. Press, pp. 133–160.

Prada, S., Sequeira, M. M., Figueira, C. and da Silva, M. O. 2009. Fog precipitation and rainfall interception in the natural forests of Madeira Island (Portugal). – Agric. For. Meteorol. 149: 1179–1187.

Pyron, R. A., Burbrink, F. T. and Wiens, J. J. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards, amphibaenians and snakes. – BMC Evol. Biol. 13: 93.

QGIS Development Team 2020. QGIS Geographic Information System. – Open Source Geospatial Foundation Project, http://qgis.osgeo.org.

Ramm, T., Roycroft, E. J. and Müller, J. 2020. Convergent evolution of tail spines in squamate reptiles driven by microhabitat use. – Biol. Lett. 16: 20190848.

Robinson, M. D. 1987. Diet diversity and prey utilisation by the omnivorous Namib Desert dune lizard, *Aporosaura anchietae* (Bocage), during two years of very different rainfall. – J. Arid Environ. 13: 279–286.

Schupp, E. W., Jordano, P. and Gómez, J. M. 2017. A general framework for effectiveness concepts in mutualisms. – Ecol. Lett. 20: 577–590.

Spellerberg, I. F. 1976. Adaptations of reptiles to cold. – In: Bellairs, A. d'A. and Barry Cox, C. (eds), Morphology and biology of reptiles, Vol. 3. Linnean Society Symposium Series, pp. 261–285.

Staub, F. 1988. Fauna of Mauritius and associated flora. – Indian Ocean Press.

Torres-Vanegas, F., Hadley, A. S., Kormann, U. G., Jones, F. A., Betts, M. G. and Wagner, H. H. 2021. Tropical deforestation reduces plant mating quality by shifting the functional composition of pollinator communities. – J. Ecol. 109: 1730–1746.

Traveset, A. and Sáez, E. 1997. Pollination of *Euphorbia dendroides* by lizards and insects: spatio-temporal variation in patterns of flower visitation. – Oecologia 111: 241–248.

Traveset, A., Olesen, J. M., Nogales, M., Vargas, P., Jaramillo, P., Antolín, E., Trigo, M. M. and Heleno, R. 2015. Bird–flower visitation networks in the Galápagos unveil a widespread interaction release. – Nat. Commun. 6: 6376.

Uetz, P., Freed, P., Aguilar, R. and Hošek, J. (eds) 2022. The EMBL reptile database.

Valido, A. and Olesen, J. M. 2019. Frugivory and seed dispersal by lizards: a global review. – Front. Evol. 7: 49.

van Marken Lichtenbelt, W. D. 1993. Optimal foraging of a herbivorous lizard, the green iguana a seasonal environment. – Oecologia 95: 246–256.

Warnes, G. R., Bolker, B., Lumley, T. and Johnson, R. C. 2022. gmodels: various R programming tools for model fitting. – https://CRAN.R-project.org/package=gmodels.

Wester, P. 2019. First observations of nectar-drinking lizards on the African mainland. – Plant Ecol. Evol. 152: 78–83.

Xavier, M. A. and dos Reis Días, E. J. 2015. First record of the Brazilian restinga lizard *Tropidurus hygomi* ingesting a fruit of *Melocactus violaceus* (Cactaceae). – Herpetol. Notes 8: 437–438.

Zeppel, M. J. B., Wilks, J. V. and Lewis, J. D. 2014. Impacts of extreme precipitation and seasonal changes in precipitation on plants. – Biogeosciences 11: 3083–3093.

Zimmerman, L. C. and Tracy, C. R. 1989. Interactions between the environment and ectothermy and herbivory in reptiles. – Physiol. Zool. 64: 374–409.

Zug, G. R., Vitt, L. and Caldwell, J. P. 2001. Herpetology: an introductory biology of amphibians and reptiles. – Academic Press.