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Do Island Spiders Descend From Trees? – A Tale of Island Colonisation and Niche Expansion

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ABSTRACT

Aim: Oceanic islands are known for being home to drastically different communities compared to the mainland, as their isolation and limited area significantly favour clades able to travel long distances over water. On spiders, this happens mainly, although not exclusively, through ballooning whose propensity is unevenly distributed across species and requires specific conditions, possibly influencing their microhabitat distribution. However, once reaching the islands, colonisers might shift their preferences towards microhabitats with less competition. In this study, using Macaronesian spiders as models, we aim to test whether: (1) the closest mainland relatives to island endemics occupy higher vertical strata; (2) island endemics show niche shift and expansion towards lower vertical strata (lower vertical distribution and larger range compared to their closest mainland relatives); (3) active hunters show a larger vertical niche shift and expansion than web-weavers.

Location: Macaronesia (Azores, Madeira and Canary Islands).

Taxon: Spiders (Arachnida: Araneae).

Methods: We selected the closest relatives from a comprehensive phylogenetic tree encompassing Iberian and Macaronesian forest spiders. We tested our hypotheses using null models and paired Wilcox non-parametric tests followed by linear models.

Results: The mainland lineages did show higher average verticality than expected by chance. However, despite showing a significantly larger vertical range, and contrary to our expectations, island endemics display higher average verticality than their mainland lineages. Furthermore, hunters showed an increase in mean verticality, while web-weavers tended to be those decreasing, with both guilds showing no differences in the variation of vertical range separately.

Main Conclusions: Spiders living in higher layers in mainland forests have a higher probability of reaching oceanic islands; yet, not all show a preference to grab opportunities at ground level. Although this is possibly due to the presence of ground-dwelling competitors/predators or the past extinction of epigean species, the transition observed further supports the colonisation filter favouring more arboreal species.

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1 | Introduction

Oceanic islands are well known for their disharmonic communities, often being composed of unique assemblages that greatly differ from those of the mainland (Simberloff 2000; Denslow 2003; Fernández-Palacios et al. 2021). One of the reasons to explain this pattern is related to the different ability of taxa to cover long distances (Mayr and Diamond 2001; Dennis et al. 2012).

In the case of spiders, many groups use their silk to sail in the wind, a phenomenon known as ballooning (Bonte et al. 2003; Bell et al. 2005). This enables spider species to colonise suitable habitats far from the source (Thomas 1996; Thorbek et al. 2002). All this makes ballooning ability the main trait related to long-distance dispersal ability, with which groups of spiders can often reach isolated island systems (Szymkowiak et al. 2007; Gillespie et al. 2012; Fisher et al. 2014).

Ballooning propensity differs greatly among spiders (Guerra et al. 2025), and lifestages (Blandenier 2009; Rossi et al. 2021). This depends on morphological traits such as body size (Dean and Sterling 1985; Larrivée and Buddle 2011; Rossi et al. 2021) but also on life-history traits such as preferred microhabitat (Bell et al. 2005). This is particularly true in forest systems, as optimal conditions for ballooning include the presence of ascendant warm air currents and atmospheric electric fields that enable the spider to take off into the air (Montes and Gleiser 2025). Such conditions tend to happen among the canopy's vegetation (Bell et al. 2005; Morley and Robert 2018), hence climbing to higher heights on vegetation has been associated with ballooning behaviour (Thorbek et al. 2002; Bonte et al. 2003; Buzatto et al. 2021).

Given that oceanic islands and archipelagos can be very isolated from the mainland, colonising spiders may tend to be the best dispersers, that is, arboreal web-weaving species that often disperse by ballooning (Blandenier 2009; Larrivée and Buddle 2011). However, there is an increasing number of accounts of ground-dwelling spider groups previously unknown to balloon that do so as juveniles (Buzatto et al. 2021; Rossi et al. 2021) which are ecologically less studied due to being harder to identify taxonomically. Still, the occurrence of ballooning in these groups seems associated with climbing vegetation by the juveniles (Rossi et al. 2021), which points to the importance of arboreal habitats for dispersal to occur. It has also been proposed that some spider groups have been able to disperse long distances over the water through rafting (Buzatto et al. 2021; Crespo et al. 2021). Between islands of oceanic archipelagos, this means of dispersal has been associated with massive landslides, in which mats of vegetation serve as rafts that help their inhabitants to colonise new islands (García-Olivares et al. 2017; Noguerales et al. 2024). Although ground-dwelling spiders that rarely balloon as adults might also colonise islands (e.g., Arnedo et al. 2001; Crespo et al. 2021), the majority of successful colonisers in forest systems should be arboreal dwellers. Despite this, how much of the contribution to island spider communities comes from arboreal ancestors or those living in other strata is still unknown and in need of a proper evaluation (but see Soto et al. 2017). If indeed the majority of these successful colonisers are arboreal they might be prone to shift and expand their vertical niche into the unoccupied lower strata due to ecological release (Herrmann et al. 2021). With time, species that expand their vertical niche might then specialise in certain microhabitats to reduce competition with sympatric species (Blackledge et al. 2003; Arnedo and Hormiga 2021). However, not all species are equally likely to change their preferred microhabitat. Due to the need for proper anchor points and vegetation structure (Uetz 1991; Rypstra et al. 1999; Amaral Nogueira and Pinto-da-Rocha 2016) by web-building groups to build the intricate structures necessary to catch their prey, these might be less likely to colonise the forest litter (but see Arnedo and Hormiga 2021). Despite this, at a community level, spiders should occupy the entire vertical gradient (e.g., Arnedo and Hormiga 2021), even if species are unevenly distributed.

The Macaronesia is a biogeographical region composed of five major archipelagos (Azores, Madeira, Canary Islands, Cabo Verde and Selvagens), being well-known for its endemic biodiversity (Borges et al. 2008, 2022; Florencio et al. 2021; Banco de Datos de Biodiversidad de Canarias 2025; Fernández-Palacios et al. 2024) and numerous evolutionary radiations (Fernández-Palacios et al. 2021). All native forests shared by the archipelagos possess Laurel elements (i.e., the Laurisilva forest), Cabo Verde having forests richer in tropical African Taxa (Fernández-Palacios et al. 2017, 2024; Neto et al. 2020). The forests of the Azores also differ by being mainly restricted to high elevations, being hyper-humid forests, shorter in height and richer in epiphytes with a dense canopy (Elias et al. 2016). This, together with the isolation of the Azores (Triantis et al. 2012; Elias et al. 2016), and the older age of the Canary Islands and Madeira (Van Den Bogaard 2013; Merle et al. 2018; Marques et al. 2020), makes Macaronesia a good study system for analysing colonisation patterns in different settings. This is particularly true when looking at forest spiders, which are well-studied, in terms of macroecology (Borges and Wunderlich 2008; Gaspar et al. 2008; Cardoso et al. 2010), phylogenetics (Macías-Hernández, Domènech, et al. 2020), as well as life-history traits (e.g., Bellvert et al. 2025) such as dispersal ability (Macías-Hernández, Ramos, et al. 2020; Malumbres-Olarte et al. 2021; Suárez et al. 2023) and vertical stratification (from here on verticality) (Macías-Hernández, Ramos, et al. 2020; Costa et al. 2023).

In this study, we aim to compare the verticality of endemic spiders occurring in the native forests of the Azores, Madeira and Canary Islands with that of their closest relatives from the Iberian Peninsula. Our main goals are to test whether: (1) closest mainland relatives to island endemics occupy higher vertical strata when compared to the overall mainland pool; (2) island endemics show niche shift and expansion towards lower vertical strata (lower vertical distribution and larger range compared to mainland relatives); (3) hunters show a larger vertical niche shift and expansion than web-weavers. First, we expect the mainland closest relatives of island species to have higher mean verticality (hereafter mAVG V) than expected by chance from their source, that is, Iberian Peninsula forests, as we do expect the majority of forest taxa ancestors were already living in forests on the continent. Second, we expect lower mAVG V values among single

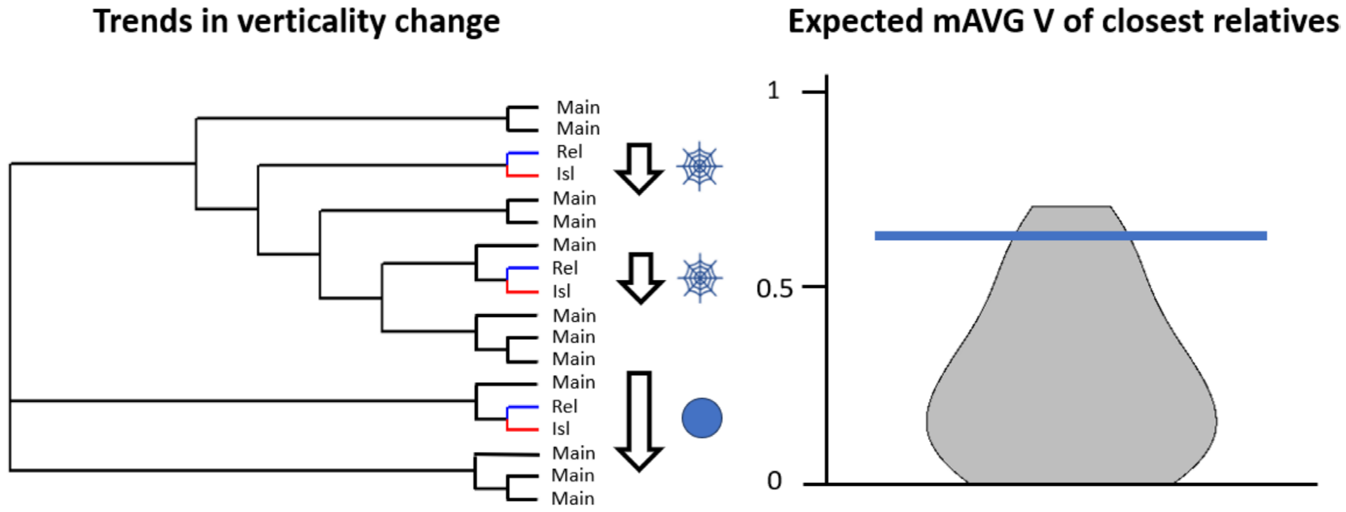

FIGURE 1 | Concept figure resuming the workflows of our study. First, we obtained from the literature a phylogenetic tree encompassing all our species of interest, both from island and from the mainland (Macías-Hernández, Domènech, et al. 2020). Then, we used the tree to identify which are the Mainland species with lower cophenetic distance to Island endemics; On the left, there is an example of a phylogenetic tree with mainland species (Main) in black, island endemics (Isl) in red and mainland closest relatives of island endemics (Rel) in blue. Then, we obtained verticality for mainland lineages and compared it with those expected by random from the pool in grey (example for our first hypothesis); On the right, we have in blue the expected mean of mAVG V of mainland lineages compared to the values from the pool. The arrows in the middle of the figure represent the expected variation in mAVG V values in each pair (example for our second hypothesis), the blue dot referring to a pair of hunters while the web refers to web-weaver pairs. The arrow referring to the hunters is larger as we expect these to have a larger variation than web-weavers (example for our third hipothesis).

archipelago endemics compared to their closest mainland relatives, due to ecological release driven by reduced competition on the island's ground stratum. Meanwhile, the vertical range (hereafter mSTD V) should be higher, as according to our first hypothesis, the availability of habitat along the vertical gradient should be asymmetrically distributed, leading to a range expansion associated with niche shift towards the forest floor. In addition, Macaronesian endemic species occurring in at least two archipelagos (as opposed to single archipelago endemics), should have their mAVG V and mSTD V not statistically different from their mainland relatives. Finally, we expect hunters to show lower changes in mAVG V and higher changes in mSTD V from their mainland relatives compared to web-weavers (see Figure 1 for a summary of our workflow and the hypotheses tested).

2 | Methods

2.1 | Sampled Spider Community

The island endemic spiders used in this study result from sampling performed in 45 plots in the native forests of three Macaronesian archipelagos [the Azores (Pico and Terceira Islands), Madeira (Madeira Island) and the Canary Islands (La Gomera and Tenerife Islands)] (Malumbres-Olarte et al. 2021; Costa et al. 2023). These 50 × 50 m plots were established inside native mesic forests (Borges et al. 2018; Malumbres-Olarte et al. 2019, 2020, 2021). The core version sampling protocol implemented (COBRA) (Cardoso 2009), targets 4 different strata, each with a specific sampling technique: forest floor with pitfall traps; short/herbaceous vegetation with net sweeping; trunks and foliage up to ca. 2 m high with nocturnal active aerial search; and canopy foliage with beating vegetation between 2 and 3 m onto a sheet cloth (for more details on sampling see Malumbres-Olarte et al. 2019, 2020, 2021; Costa et al. 2023). Species colonisation origin (introduced, native non-endemic and endemic to Macaronesia) was obtained from the most up-to-date published species lists for these archipelagos (Cardoso and Crespo 2008; Banco de Datos de Biodiversidad de Canarias 2025; Borges et al. 2022), as well as from our expertise. For our analyses, we considered only island endemic species, as introduced and native non-endemics, might not have had time to properly adapt to the insular system, and so might retain the same microhabitat they occupy in continental areas. Only adult species and morphospecies identified through morphology and confirmed with genetics (mitochondrial cytochrome c oxidase 1) were considered to obtain verticality. For the island dataset, to properly identify island endemics, only individuals identified at the species level were considered (Costa et al. 2023).

The pool of potential mainland relatives was obtained from a total of 16 1-ha plots distributed in white-oak (*Quercus* L.) woodlands in six Spanish National Parks across the Iberian Peninsula (Crespo et al. 2018). Spiders were sampled using the same sampling protocol (COBRA) as for the islands. Although sampling was still implemented relatively close to the ground (around 3 m high), previous research has shown that community composition differences within the canopy of Mediterranean forests are rather small (Cardoso and Crespo 2008). As the vertical gradient was sampled using the same sampling methods we can trust the verticality values to be comparable among islands and continental areas.

To verify if the spider species pool was properly sampled, we estimated sampling coverage and completeness using the Jackknife

1 (P-corrected) estimator (Heltshe and Forrester 1983; Chao and Jost 2012; Lopez et al. 2012) using the R package 'BAT' (Cardoso et al. 2015). To confirm if the species names were up to date on their nomenclature, we used the R package 'arakno' (Cardoso and Pekár 2022). All voucher specimens for Macaronesian species are deposited at EDTP—Entomoteca Dalberto Teixeira Pombo, Campus de Angra do Heroísmo, Portugal, and data from Azores and Madeira can be accessed in Malumbres-Olarte et al. (2019, 2020), data from the Canary Islands being also in the Instituto de Productos Naturales y Agrobiología (IPNA-CSIC), Tenerife, collection. Iberian Peninsula specimens are deposited in the Museum of Zoology, Barcelona (MZB).

2.2 | Identification of Closest Relatives of Island Species

Cophenetic distance (pairwise distance between species pairs from the phylogenetic tree using its branch lengths) (Cardona et al. 2013) was calculated with the package 'ape' (Paradis and Schliep 2019) using the phylogenetic tree constructed by Macías-Hernández, Domènech, et al. (2020), which includes the species pool from the Iberian Peninsula (373 ssp.) and all studied island endemics (85 ssp.). The mainland closest relatives (see Table 1) were selected using the lowest cophenetic distance between island endemics and species present in the Iberian Peninsula dataset, using a maximum of five decimal points.

To check if our dataset and tree gave us actual close relatives, we verified if Island endemics belonged to the same family and genus as their Mainland close relatives. We also checked the proportion of the potential continental pool (species in the same family) that was assigned as a close relative, to check if the dataset was high in poorly sampled families. Island endemics with the same pool of Mainland closest relatives occurring in the same archipelago are hereafter considered as the same Island lineage representing one colonisation event, while all their respective Mainland closest relatives are hereafter referred to as Mainland lineages (see Table 1).

2.3 | Obtaining Verticality Metrics

We obtained two metrics of verticality: average verticality, a continuous value along the vertical gradient where the species should most often occur (mAVG V), and its standard deviation as a measure of the range of the species along the gradient (mSTD V). The calculation of these metrics follows the approach described by Costa et al. (2023). A score between 0 and 3 was assigned to each sampling method (0 for pitfall, 1 for sweeping, 2 for active aerial search, and 3 for beating) in a way that higher values of mAVG V would be related to higher strata, and then divided by 3 to vary between 0 and 1. Next, the relative abundance of the species in each method and plot was calculated and normalised to obtain a proportion summing 1 across the four methods. For each species in each plot, we obtained the average verticality (AVG V value) and standard deviation (STD V value). These were then averaged among all the plots where each species occurred, obtaining one value of mAVG V and mSTD V for each species across the full dataset. The calculation was implemented separately for the island and the Iberian Peninsula datasets. The verticality values for all Mainland close relatives belonging to the same Mainland lineage (see Table 1) were averaged to obtain one mean verticality and one vertical range per lineage as a proxy of the verticality of the true continental sister species related to Island lineages (see Table 1).

2.4 | Phylogenetic Signal of Verticality Traits

It is probable that in some cases, the true closest mainland relative to island species was not included in our dataset; thus, to test if verticality is phylogenetically conserved among the mainland species pool, we calculated the phylogenetic signal of both verticality traits using Pagel's λ statistics (Pagel 1999) assuming a Brownian motion (BM) model of trait evolution. The existence of phylogenetic signals in verticality traits will ensure that, although the true mainland closest relatives were not included in our analyses, the verticality variation might be explained by the phylogenetic relatedness of the species included in the mainland dataset. Values of Pagel's λ close to 0 indicate phylogenetic independence and a value of 1 indicates that species' traits are distributed as expected under BM (Münkemüller et al. 2012). The statistical significance of λ was assessed based on a comparison of the likelihood of the observed λ against the likelihood of a model that assumes complete phylogenetic independence (Pagel 1999), using the *phylosig* function in the 'phytools' *R* package (Revell 2012). These analyses were repeated with and without species considered uniques (rare species sampled only at one plot), to test if these influenced verticality patterns of closely related taxa.

2.5 | Statistical Analysis

To verify if mainland spiders were properly sampled in our study area, we estimated the values of sampling coverage and completeness using the Jackknife1 (P-corrected) estimator (Chao and Jost 2012; Heltshe and Forrester 1983; Lopez et al. 2012), these values were also obtained for the archipelago by Costa et al. (2023). To check if the mainland lineages had higher mAVG V values than expected by random compared to the pool (all the Iberian forest species), we subsampled the entire species pool 1000 times, each subsample with the same number of mainland lineages identified in the study. The observed rank of the mean mAVG V of the mainland lineages was then checked against the 95% quantile of the simulations (one-sided test). This was repeated for both web-weavers and hunters, as they might differ in their original habitat on the mainland. We used the trait data compiled by Macías-Hernández, Ramos, et al. (2020) to classify species according to their hunting strategy, and then used Kruskal–Wallis tests (KW) to test whether those strategies showed different mAVG V of the mainland lineages. When global KW was significant at alpha < 0.1, *post hoc* Dunn's tests were performed to identify statistically significant pairwise differences between groups at alpha < 0.05. To check if overall island endemic species significantly differed in verticality from their respective mainland lineages, we first used paired two-sample Wilcoxon signed rank tests for all the island endemic species. Then, we applied phylogenetic generalised linear models using the *pgls* function from the 'caper' package

TABLE 1 | Key terms and relevant information about each one (Term; Definition—the one used in our study; References—literature of importance for each term used).

	Term	Definition	Sources
Biogeography	Macaronesia endemics	Species whose natural distribution is restricted to the studied Macaronesia archipelagos, but occurring at least in two archipelagos.	Cardoso and Crespo (2008); Borges et al. (2022); Costa et al. (2023); and Banco de Datos de Biodiversidad de Canarias (2025)
	Single archipelago endemics	Species whose natural distribution is restricted to only one of the studied Macaronesia archipelagos.	Cardoso and Crespo (2008); Borges et al. (2022); Costa et al. (2023); and Banco de Datos de Biodiversidad de Canarias (2025)
	Island lineage	Groups of Island endemics that are equally related to the same mainland lineage based on phylogenetic distance.	This study
	Mainland lineage	Groups of Mainland closest relatives equally related to the respective Island lineage based on phylogenetic distance.	This study
	Mainland closest relatives	All species from the mainland dataset that are the closest relative to each of the Island endemics (macaronesia and single archipelago endemics).	Macías-Hernández, Domènech, et al. (2020)
Verticality	Mean verticality (mAVG V)	The abundance weighted mean position of each species along the vertical gradient average across species from different grouping.	Macías-Hernández, Ramos, et al. (2020) and Costa et al. (2023)
	Vertical range (mSTD V)	The abundance weighted standard deviation of the position of each species along the vertical gradient average across species from different grouping.	Costa et al. (2023)
	AVG V diff	Difference observed between the mAVG V of islands endemics and their respective Mainland lineage.	This study
	STD V diff	Difference observed between the mSTD V of islands endemics and their respective Mainland lineage.	This study
	Vertical niche expansion	Realised vertical niche expansion, with island endemic species expanding their presence to more strata along the forest vertical gradient then their mainland closest relatives. This is expressed a positive STD V diff	Herrmann et al. (2021)
	Vertical niche shift	Realised vertical niche shift, with island endemic species shifting their position along the forest vertical gradient then their mainland closest relatives. This is expressed either by a positive AVG V diff if the island endemics move upwards, or by a negative difference if they move downwards.	Herrmann et al. (2021)

(Orme et al. 2023). We used this in order to evaluate the effect of the phylogeny in differences in verticality (AVG V diff and STD V diff) using the presence in one (Azores, Madeira and the Canary Islands) or multiple archipelagos (Macaronesia), and the hunting guild (web-weavers and hunters). Finally, we repeated the process using linear models (LM) using the *lm* function from the 'stats' package (R Core Team 2024) using the presence in one or multiple archipelagos, and the hunting guild as explanatory variables. Finally, we applied emmeans post hoc tests, to evaluate the differences between the factors. All statistical analyses were performed using the R software version v.4.4.0 (R Core Team 2024).

3 | Results

3.1 | General Patterns

From a dataset of 123 species (10,609 adult specimens) collected in Macaronesia native forests, we selected a total of 85 Island endemics (9031 sampled individuals), belonging to 19 different families, for our analyses. The selected species were Island endemic to at least one of the three studied archipelagos (Azores, Madeira and Canary Islands). From these, 17 species were considered Macaronesia endemics (see Table 1), as they are present in at least two archipelagos, while 13 were endemic to the Azores, 17 to Madeira, and 38 to the Canary Islands (Cardoso and Crespo 2008; Banco de Datos de Biodiversidad de Canarias 2025; Borges et al. 2022). Linyphiidae was the family with the largest number of species considered island endemic (28). Hunters were only slightly more diverse than web-builders, constituting nearly 53% of all species.

A total of 8531 adult specimens belonging to 373 species and morphospecies in 39 different families were considered the pool of possible closest relatives of island species present in the Iberian Peninsula forests. Sampling completeness on this dataset was around 48.5%, while sampling coverage was always above 91%. Linyphiidae was once again the richest family, with an overall 66 species, followed by Theridiidae with 40 and Gnaphosidae with 36. Hunters were also the dominant group of this dataset, but were more diverse compared to islands, comprising nearly 70% of all species and morphospecies. mAVG V varied between 0 and 1 for both mainland and island species. mSTD V varied between 0 and 0.499 or 0.333 for mainland and island species, respectively (see Appendices 1 and 2).

Pagel's λ values for both verticality traits were significantly close to 1 (mAVG V and mSTD V: $\lambda = 0.907$, $p < 0.001$), suggesting that verticality is strongly phylogenetically constrained. The same results (mAVG V and mSTD V: $\lambda = 0.928$, $p < 0.001$), were found if uniques were not considered, so these species were kept for the following analyses.

3.2 | Closest Relatives to Island Species

Among the 373 Iberian Peninsula spiders (113 web-weavers and 260 hunters), 97 (26%) were considered one of the Mainland closest relatives of, at least, one of the Island endemics (see Appendix 3). On average, each species had 2.6 relatives assigned as the closest, and represented 19.9% of the species sampled for its family (see Appendix 4). *Philodromus insulanus* Kulczyński, 1905 was the species with the highest number of Mainland closest relatives (14), and for 4 species (2 Pisauridae: *Pisaura acoreensis* Wunderlich, 1992 and *Cladycnis insignis* (Lucas, 1838), 1 Zoropsidae: *Zoropsis rufipes* (Lucas, 1838) and 1 Mysmenidae: *Trogloneta madeirensis* Wunderlich, 1987) only 1 species was sampled for their family in the mainland data. Considering all Island lineages, Mainland closest relatives were assigned to at least 67 different Mainland lineages (36 web-weavers and 31 hunters). A total of 31 pairs of species (corresponding to 14 pairs of Island-Mainland lineages) including the one of *T. madeirensis*, which showed the highest cophenetic distance among all species pairs obtained, were above the third quartile in the cophenetic distance (median = 77.58, Interquartile range = 28.73 [from here on IQR]). All Mainland closest relatives were assigned the same hunting guild as their Island endemics, with the exception of *Canariellanum albidum* Wunderlich, 1987 a web-weaver for which two hunter species were assigned as closest relatives [*Entelecara acuminata* (Wider, 1834) and *Microctenonyx subitaneus* (O. Pickard-Cambridge, 1875)]. However, we considered this transition to be more likely a failure in the sampling than a true change in the hunting guild during island colonisation. Due to this we considered the hunting guilds of Island endemics for all the analyses.

3.3 | Are Species With Higher Verticality Closely Related to Those on Islands?

As predicted, the mAVG V obtained for the Mainland lineages was significantly higher than expected by chance (mean = 0.412, SD = 0.3; $p < 0.01$) (Figure 2). Considering hunting guilds separately, neither Mainland lineages significantly differed from what was expected by random from the pool and also between themselves. Web-weavers had higher mAVG V, although the latter showed larger median mAVG V [0.554, Interquartile range IQR = 0.331 (from here on IQR) compared to 0.333, IQR = 0.637 of hunters].

3.4 | Do Endemics Lower Verticality and Increase Range?

Island endemics showed significantly higher values of mAVG V compared to their Mainland lineages ($p = 0.007$, Island

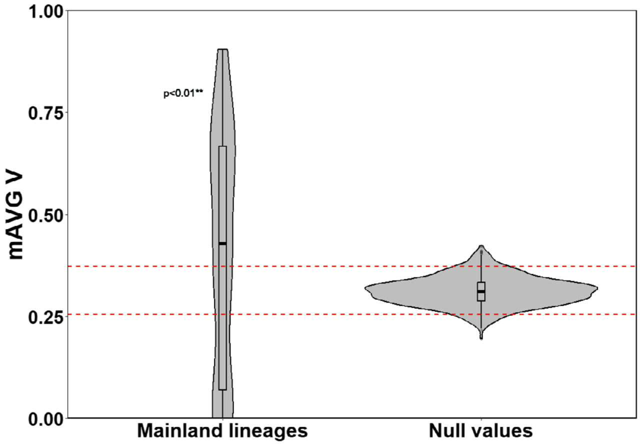

FIGURE 2 | Mean verticality (mAVG V) of 67 identified Mainland lineages and the expectation from null models. Dashed red lines show the 95% confidence interval limits obtained for the null values. The p-value significance obtained for the probability of the mean based on the 1000 samples from the sampled pool is represented next to the Mainland lineages values.

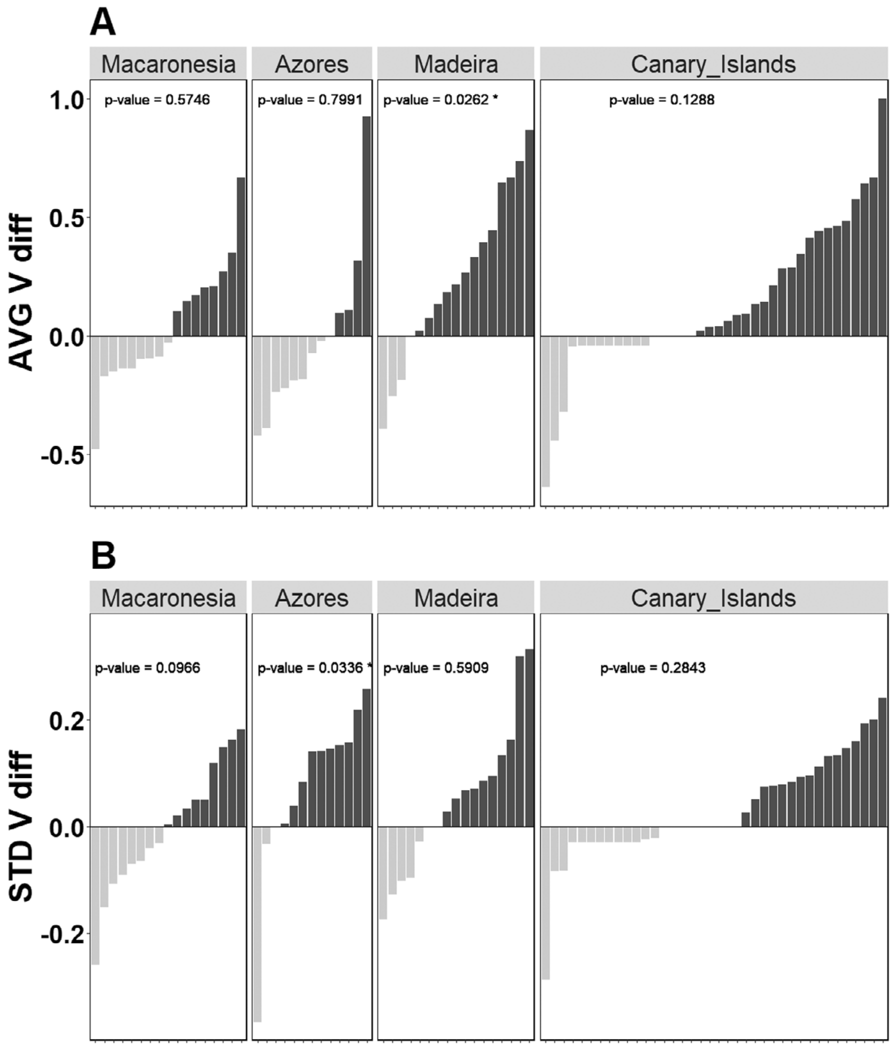

FIGURE 3 | Difference between each Island endemic (each species represented by a bar) and their respective Mainland lineage verticality values (AVG V diff and STD V diff), organised from left to right in each category according to change in (A) mean verticality (AVG V diff), and (B) vertical range (STD V diff). The *p*-values obtained for each variable using the linear models are also represented.

endemics: median = 0.61, IQR = 0.629; respective Mainland lineage: median = 0.337, IQR = 0.626) according to the Wilcox test. Looking to the LM, as predicted Macaronesian endemics showed an effect on AVG diff (LM AVG diff βMacaronesia, $p = 0.575$); however, only Madeira showed a significant effect on AVG V diff (LM AVG diff βMadeira, estimate = 0.266, $p = 0.026$), with no significance being found for either Azores or the Canary Islands (LM AVG diff βAzores, $p = 0.799$ and LM AVG diff βCanary Islands, $p = 0.12988$, respectively) (Figure 3A). The PGLS showed similar results for AVG V diff, only differing for the Canary Islands, which were also significant in the PGLS (LM AVG diff βCanary Islands, estimate = 0.221, $p = 0.01215$ and LM AVG diff βMadeira, estimate = 0.205, $p = 0.035$). No significant differences between factors were found using emmeans tests.

Island endemics showed significantly higher values of STD V compared to their mainland lineages ($p = 0.005$, Island endemics: median = 0.074, IQR = 0.163; respective Mainland lineages: median = 0.022, IQR = 0.0844). Like previously, Macaronesian endemics did show an effect on STD V diff (LM AVG diff βMacaronesia, $p = 0.097$), and only Azorean spiders showed a significant effect on STD V diff (LM AVG diff βAzores, estimate = 0.073, $p = 0.034$), being non-significant in the case of both Madeira and Canary Islands species (LM AVG diff βMadeira, $p = 0.591$ and LM AVG diff βCanary Islands, $p = 0.284$, respectively) (Figure 3B). For the PGLS, none of the archipelago variables showed a significant effect on STD V diff. For this variable, we also did not find significant differences between factors using emmeans tests.

3.5 | Do Hunters Lower Verticality More Than Web Builders?

Both hunters and web-weavers showed significant influence in AVG V diff (LM AVG diff βHunters, estimate = 0.220, $p < 0.001$ and LM AVG diff βWeb-weavers, estimate = −0.226, $p = 0.001$, respectively), although contrasting ones (Figure 4A). According to the emmeans tests the effect of the two factors was significantly different ($p = 0.001$).

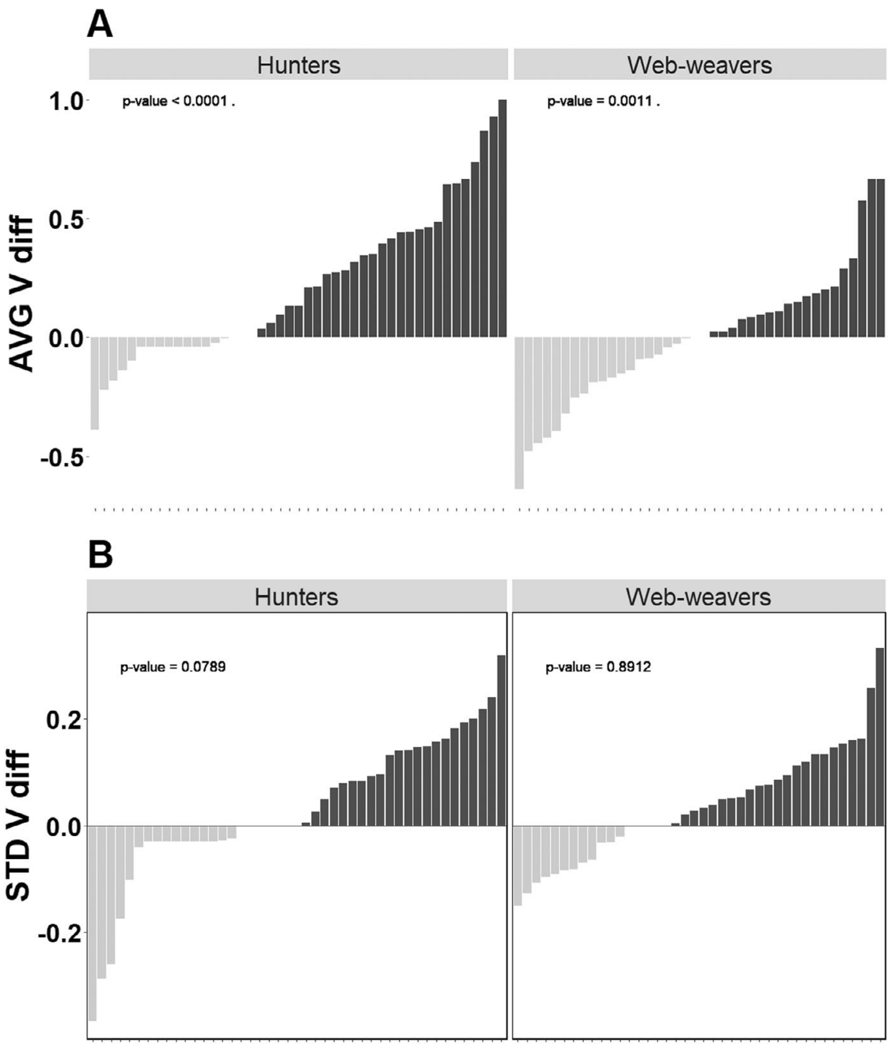

FIGURE 4 | Difference between each Island endemic (each species represented by a bar) and their respective Mainland lineage pairs' verticality values (AVG V diff and STD V diff), organised from left to right in each category (Hunters and Web-builders), according to change in (A) mean verticality (AVG V diff), and (B) vertical range (STD V diff). The *p*-values obtained for each variable using the linear models are also represented.

However, neither of the hunting guilds seemed to significantly influence STD V diff (LM AVG diff βWeb-weavers, $p = 0.891$, and LM AVG diff βHunters, $p = 0.079$) (Figure 4B). Contrary to AVG V diff, no significant differences were found between the factors using emmeans tests. For the PGLS, none of the hunting guilds showed a significant effect on the verticality variables (AVG V diff and STD V diff).

4 | Discussion

In this study, we explore multiple hypotheses regarding island colonisation and niche expansion of an important and diverse arthropod group, spiders (Arachnida: Araneae). Long-distance dispersal in spiders is thought to be mainly performed through ballooning, and the propensity of species to balloon is considered an essential trait that affects the community and genetic structure of spiders (Gillespie et al. 2012; Carvalho and Cardoso 2014; Suárez et al. 2022). Species-level data on this trait are however challenging to obtain, due to the specific requirements of controlled laboratory ballooning experiments (e.g., Larrivée and Buddle 2011; Carlozzi et al. 2018). Consequently, most studies use family-level classifications (e.g., Carvalho and Cardoso 2014; Malumbres-Olarte et al. 2021) which might have low accuracy, especially on islands (Suárez et al. 2022). In this work, we investigated verticality instead of ballooning propensity. Even if not equivalent (e.g., lycosids (Dean and Sterling 1985; Bonte et al. 2003) and other epigean spiders are known to balloon), it can influence dispersal in forest communities (Sorensen 2003; Gillespie et al. 2012) while being much easier to quantify (Macías-Hernández, Ramos, et al. 2020; Costa et al. 2023). Except for the Azores, the sampled forest in the remaining archipelagos and the Iberian Peninsula normally exceeds 10 m in height. As a result, we are aware that our sampling methods may not effectively capture the upper canopy, potentially overlooking species that occur on these strata. However, we believe that the protocol still adequately samples the vertical gradient where the vast majority of different microhabitats are found. Indeed, it was specifically designed to efficiently sample the community of spiders occurring in a plot in the studied systems. With all this in mind, we believe that, despite the limitations of our sampling, we can still effectively test the main hypothesis of this study.

4.1 | Canopy Spiders Are the Ones Reaching Oceanic Islands

We confirmed our initial hypothesis that Mainland lineages further up in the vertical stratum had a higher probability of reaching the islands (see Figure 2). As previously mentioned, the capacity of spiders to balloon in forest ecosystems is related to their vertical microhabitat, this dispersal mechanism being less likely to occur at ground level in forests (Sorensen 2003). This might also be supported by the fact that the best ballooning species are thought to be web-weavers (Larrivée and Buddle 2011). Our results point towards this hypothesis, as the continental forest pool showed a total species ratio of 0.435 between web-weavers and hunters, while there were more Mainland lineages belonging to web-weavers (36) than to hunters (31). This, more than a higher intra-guild mAVG V, seems to have been the decisive factor for the higher mAVG V of Mainland lineages than expected by random. Indeed, ballooning has been previously considered an important strategy for spiders to colonise isolated archipelagos such as Hawaii (Gillespie et al. 2012), Juan Fernández (Soto et al. 2017), the Caribbean (Čandek et al. 2019, 2021) and Macaronesia (Malumbres-Olarte et al. 2021). However, there is a growing body of evidence pointing towards the occurrence of ballooning performed by ground-dwelling spiders (Guerra et al. 2025) at least as juveniles (e.g., Rossi et al. 2021).

Besides ballooning, the small size and often the resilience to starvation of spiders make them able to arrive on islands through rafting [e.g., *Titanodiops* (Opatova and Arnedo 2014), *Dysdera* (Macías-Hernández et al. 2010; Crespo et al. 2021)]. Rafting has also been pointed out as a possible means for other arthropods [e.g., *Laparocerus* (García-Olivares et al. 2017; Machado et al. 2017) such as *Drouetius* beetles (Machado 2009)], and non-flying vertebrates to arrive on islands (e.g., Pagès et al. 2012). Nevertheless, for most cases of island colonisation by spiders, how species have arrived remains largely uncertain.

Following arrival, the geographical setting often leads to the loss of the dispersal ability of organisms (Gillespie 2005; Čandek et al. 2021), a pattern observed by Charles Darwin in his observation of a high proportion of apterous beetles in Madeira Island, in which high dispersal might be selected against given the amount of inhospitable habitat surrounding islands (Whittaker et al. 2023). It is logical, then, that recent arrivals are more prone to spread across multiple islands (e.g., Čandek et al. 2021), and inhabit the areas of the forest where conditions favourable to long-distance dispersal occur (Costa et al. 2023). This might be the case of Macaronesia endemic spiders, as these taxa show an inter-archipelago distribution.

4.2 | Spiders That Reach the Islands Move Further Up

Contrary to our expectations, in general island species were found to move even further up in the vertical strata compared with their mainland relatives. Of all the studied archipelagos, the Azores was the one closest to our initial hypothesis, with 8 of its 13 endemics showing negative values of AVG diff (see Figure 3A). It is worth noting that the species that showed the highest AVG V diff *Savigniorrhipis acoreensis* Wunderlich, 1992, also has a relative in São Jorge Island, *Savigniorrhipis topographicus* Crespo, 2013 (Crespo et al. 2013) which hunts at ground level. Both, the smaller distance from the mainland and the age of the two older archipelagos, 15 Ma for Madeira (Geldmacher et al. 2000) and 23 Ma for the Canary Islands (Van Den Bogaard 2013), could have increased the opportunities for more species adapted to more ground-dwelling to colonise these islands compared with the Azores.

During the ice age, currently submerged islands close to the Madeira and Canary Islands archipelagos are thought to have been above sea level (Geldmacher et al. 2001; Fernández-Palacios et al. 2011), creating an island chain that facilitated island-hopping from either the Iberian Peninsula or continental Africa (with only 96 km between the Moroccan coast and Fuerteventura) (e.g., Bidegaray-Batista et al. 2007; Amorim et al. 2012). The latest is thought to be the case for the Canary Islands *Dysdera*, which have diversified in the archipelago from just one of the two known colonisation events (Arnedo et al. 2001; Adrián-Serrano et al. 2021). Similarly to our study, Arnedo and Hormiga (2021) have documented a pattern of increasing verticality from mainland to islands in the Juan Fernandez spider genus *Laminacauda*, which seems to be associated with an adaptive radiation of the genus, enabling the coexistence of multiple species in the same forests. However, our results must be interpreted with caution as the possibility that spiders have colonised dry habitats first (either by ballooning or rafting), and then moved into the Laurel forests cannot be fully excluded, as it has been seen in some Macaronesian beetle species (Stüben and Germann 2005; Machado et al. 2017). Furthermore, our analyses were done using Iberian Peninsula taxa, and for some clades the comparison would be more accurately made with taxa from other regions such as North Africa (e.g., Dysdera from the Canary Islands) (Macías-Hernández et al. 2008).

Although we have associated arboreal habits with dispersal propensity, this might not be the only reason behind species' presence in arboreal habitats. Indeed, single archipelago endemics greatly outnumber Macaronesia endemics, despite their trend to have increased their mAVG V. Therefore, at least in the case of inter-archipelago dispersal, vertical microhabitat might not be the only relevant factor. We can hypothesise three other possible mechanisms leading to the higher verticality of island spiders. First, the colonisation filter favouring arboreal species might also have filtered for canopy prey, leading to the canopies being richer in other arthropod groups. Indeed, the canopy provides a highly complex and layered environment with numerous microhabitats (e.g., leaves, branches, flowers, bryophyte cushions and lichen mats), which creates opportunities for species specialisation and niche differentiation (Shaw 2004). Second, the presence of other ground-dwelling competitors/predators such as ants (e.g., Gillespie and Reimer 1993), might have favoured the habitat shift of spiders to the canopy, where they might experience less competition (Halaj et al. 1997). Third, we know that, at least for the Azores and Madeira, ground-dwelling spiders are more threatened with extinction (Chichorro et al. 2022; Oyarzabal et al. 2024) with some past extinctions of epigean spiders having possibly occurred (Cardoso et al. 2010). In the absence of anthropogenic extinction data, considering only surviving taxa might fail to explain part of the process that leads to current patterns (e.g., Opatova and Arnedo 2014), and the increasing verticality might be an artefact caused by the current absence of extinct epigean spiders. However, these are hypotheses and do not exclude the possible effect of other factors not accounted for in this study, such as differences in epigean microhabitats between Macaronesia and the Iberian Peninsula.

According to our expectations, island spiders did expand their verticality, supporting a lower microhabitat specialisation of archipelago endemic species. Verticality is a trait that envelops multiple aspects of forest spiders' ecology, such as feeding preferences (e.g., Blackledge et al. 2003), hunting strategies (Cardoso et al. 2011; Domènech, et al. 2022), dispersion means (Sorensen 2003; Domènech, et al. 2022), among others. Although the obtained pattern for island spiders fits well with the available literature mentioning lower specialisation of island species (Fernández-Palacios et al. 2021; Whittaker et al. 2023), as the absence of many competitors and the limited resources available (including area) might favour generalists (e.g., Lister 1976). Despite the young age of the Azores, it was the only one showing an effect in vertical range expansion (see Figure 3B). However, these are the islands with the largest loss of native habitat (Gaspar et al. 2008; Cardoso et al. 2010), which might have led to the extinction of vertically specialised taxa (Oyarzabal et al. 2024). Due to the complexity behind species' vertical patterns, it is to be expected that different processes might be driving the organisation of regional and local communities. For example, in Madeira, ground-dwelling spider communities are majorly dominated by exotic taxa (Boieiro et al. 2018). This might have repercussions for the vertical distribution of endemic species (Costa et al. 2023), restricting many taxa to the canopy of the forest.

4.3 | Hunters Climb Higher While Web-Weavers Go Down

Spider hunting strategy has often been mentioned as having major ecological relevance in how spiders interact with their environment (Cardoso et al. 2011). This might account for the lack of influence of hunting guild on verticality variation shown by our PGLS results, suggesting that the trait is deeply constrained by the phylogeny. Web spiders require attachment points (Uetz 1991) and a particular 3D vegetation structure for web building (Rypstra et al. 1999; Amaral Nogueira and Pinto-da-Rocha 2016). On islands, however, the reduced competition can enable species to occupy different ecological positions in the system (Fernández-Palacios et al. 2021), such is the case in the Hawaii *Tetragnatha* spiny leg clade (Gillespie 1991). Arnedo and Hormiga (2021) also mentioned that *Laminacauda* species presented different webs constructed at different vertical microhabitats, showing ecological stratification of the closely related species, but species adapted to hunting at the ground level also occur. Although examples of web weavers evolving to lose their webs to hunt are known (e.g., Gillespie 1991; Arnedo and Hormiga 2021), overall species already adapted to chase prey without webs might be able to better adapt to a different stratum. In our study, we have seen that hunters increased their mean verticality, although not fully accompanied by an increase in vertical range. This went against our expectations that these species would have some preadaptation of cursorial hunting at ground level, which should include, compared to the canopy, a lower amount of overall spider diversity, and so less competition. However, island species might have instead retained their ancestors' niche (e.g., Crespo et al. 2021), or just fully shifted to a new one without expanding a broader range of ecological settings (e.g., Gillespie 2005; Arnedo and Hormiga 2021). We obtained a slightly larger mAVG V of hunter Mainland lineages compared to the pool, implying these were instead better preadapted to hunting among vegetation.

5 | Conclusions

In this study, we verified that canopy spiders have a higher probability to reach oceanic islands, a pattern driven by their higher verticality associated with ballooning propensity. However, once reaching the islands, spiders seem to expand further up their vertical range, particularly in the older archipelagos, possibly due to the colonisation filter leading to the canopies being richer in other arthropods, the presence of other ground-dwelling competitors/predators in certain islands, and the higher threat of ground-dwelling spiders with some possible past extinctions. Hunting guilds were particularly relevant, as web-weavers seemed to tend to decrease spiders in particular while hunters increased their verticality, both without an expansion in vertical range. This was possibly due to island endemics having retained the vertical niche from their ancestors, already adapted to hunt among vegetation. Importantly, past unrecorded extinctions have certainly changed the natural patterns and might have influenced our findings. However, given the geographical and methodological limitations of this study, future work should focus on better assessments of continental communities to properly sample close relatives, increase ecological information related to the colonisation patterns dispersal ability, and perform a comparison between other islands and continental systems.

Author Contributions

R. Costa: formal analysis (lead), visualisation (lead), writing – original draft (lead), writing – review and editing (equal), investigation (equal), data curation (supporting) and conceptualisation (equal). **N. Macías-Hernández:** formal analysis (supporting), writing – original draft (supporting), writing – review and editing (equal), methodology (equal), investigation (equal), data curation (equal) and conceptualisation (equal). **F. Rigal:** writing – review and editing (equal), methodology (supporting), supervision (equal) and conceptualisation (equal). **P. A. V. Borges:** writing – review and editing (equal), methodology (equal), investigation (equal), supervision (equal), data curation (equal), project administration (equal) and funding acquisition (equal). **P. Cardoso:** formal analysis (supporting), visualisation (supporting), writing – review and editing (equal), methodology (equal), investigation (equal), supervision (equal), conceptualisation (equal), project administration (equal) and funding acquisition (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in GBIF at https://www.gbif.org/dataset/6aa5ac09-2b55-4078-bd2d-ec94fb91850a and http://ipt.gbif.pt/ipt/resource?r=spiders_madeira.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** jbi70093-sup-0001-AppendixS1.docx.