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Island spider origins show complex vertical stratification patterns in Macaronesia

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Abstract

1. Spiders are among the most diverse and yet threatened groups of arthropods in Macaronesia. Found in most habitat types, they occupy the vertical gradient of native forests from ground to canopy level.
2. We hypothesize that their vertical distribution is influenced by the colonization origin. As introduced species should arrive using shipping containers and similar means, they should mostly occupy the lower levels in the gradient, with potential negative effects on the indigenous epigean fauna.
3. Spiders were sampled from epigean to arboreal microhabitats (maximum height varying between 2 and 4 m) on 45 sites across five islands belonging to three archipelagos. The mean and range of vertical stratification were obtained for each captured species. These values were then compared between different colonization origins at Macaronesian and archipelagic levels.
4. Native non-endemic species were found at significantly higher vertical strata than both endemic and introduced species. Likewise, native non-endemics had a larger vertical range. These patterns were largely replicated across archipelagos, although there were exceptions.
5. Overall, introduced species do not seem to occur mostly at lower strata in the native forests of Macaronesia (at least in the studied vertical range) but seem to be vertically restricted in most settings with the exception of Madeira.

KEYWORDS
Araneae, introduced species, islands, microhabitat, native habitat, verticality

INTRODUCTION

In many islands, native habitats have been extremely reduced by historical human-mediated change and degradation (Ewers et al., 2006; Fernández-Palacios et al., 2021; Kueffer & Kinney, 2017), with most of the endemic diversity now restricted to the remaining montane forests.

The Macaronesian islands (Azores, Madeira and Canary Islands) have suffered massive anthropogenic impacts, but they still host a large diversity of endemic flora and fauna in their unique native forests, which occur mostly between 500 and 1200 m altitude (Elias et al., 2016; Fernández-Palacios, 2013; Gouveia, 2005). Although most of these areas are now protected (Borges et al., 2005; del Arco Aguilar et al., 2010; Gouveia, 2005), their biota may still be under pressure from key biodiversity erosion drivers, such as climate change and the spread of introduced, often invasive species (Borges, Santos, et al., 2020; Fernández-Palacios & Whittaker, 2008; Ferreira et al., 2016; Gouveia, 2005). In the case of arthropods, at least 39% of all recorded species in the Azores, 19% in Madeira and 8% in the Canary Islands are thought to have been introduced due to human activities (Borges, Aguiar, et al., 2008; Borges, Lamelas-Lopez, Andrade, et al., 2022; Oromí & Báez, 2010). By establishing populations in the habitat matrix that envelops protected sites, vagrant individuals of introduced species can then venture into the areas of native forests (Borges, Lamelas-Lopez, Andrade, et al., 2022; Borges, Rigal, et al., 2020; Borges, Ugland, et al., 2008; Gouveia, 2005). As introduced species might compete with indigenous species for resources, or directly predate or parasitize them (Borges & Wunderlich, 2008; McNatty et al., 2009), it is important to document how they differ from the latter in their ecological traits, such as their micro-habitat preferences, and this way better understand possible negative interactions (Boieiro et al., 2018; Rigal et al., 2018; Whittaker et al., 2014).

Studies conducted on Azorean native forests have shown that introduced species better succeed to establish at the soil level, whereas canopies still seem to be dominated by indigenous (endemic and native non-endemic) species (Borges & Wunderlich, 2008; Florencio et al., 2016; Gaspar et al., 2008). However, for Madeira and the Canary Islands archipelagos, these patterns are still poorly understood, with studies on invasiveness mostly focusing on epigean species (Arndt & Perner, 2008; Boieiro et al., 2018; Lobo & Borges, 2010). Overall, few studies have investigated how introduced arthropods have invaded the vertical gradient in Macaronesia native forests and what their vertical stratification can tell us about their impact on the indigenous arthropod fauna.

In Macaronesia, spiders are some of the best studied groups of arthropods (Arnedo et al., 2001; Borges & Wunderlich, 2008; Cardoso et al., 2010; Crespo et al., 2014) being ubiquitous predators that occur in great numbers in different microhabitats of native forests (Boieiro et al., 2018; Crespo et al., 2014; Gaspar et al., 2008). Some endemic species are known to have experienced species reductions and extinctions in the past (Cardoso et al., 2010; Crespo et al., 2022), making spiders good monitoring organisms in this system (Borges, Cardoso, Kreft, et al., 2018; Gaspar et al., 2010).

Most spider species are not evenly distributed along the vertical gradient in forests (from ground to canopy). Some species are preferentially associated with specific vertical layers (i.e. microhabitats), which is linked to their foraging strategy and preferred prey (Blackledge et al., 2003; Domènech et al., 2022; Yanoviak et al., 2003). On islands, successful colonizers may occupy a wider range of niches than on the mainland (Blackledge et al., 2003; Costa et al., 2008; Gillespie, 2005), sometimes showing intraspecific niche variation and expansion (Cotoras et al., 2021). Instead, species that evolve in sympatry might have specialized in different niches (Blackledge et al., 2003; Gillespie, 2005).

The so-called ‘verticality’ of the preferential microhabitat might also be related to other species' traits. In the case of spiders, species in lower, epigean micro-habitats often disperse using cursorial movements, whereas arboreal species more often disperse by aerial means involving ballooning (Bell et al., 2005; Malumbres-Olarte et al., 2021). The lower dispersal ability of species can affect gene flow, and the isolation of the populations can favour speciation (Gillespie et al., 2008; Suárez et al., 2022). Indeed some of the biggest radiations in Macaronesia have occurred within epigean spider clades, the best example being the genus *Dysdera* (Arnedo et al., 2001; Crespo et al., 2021). However, this might make epigean species more vulnerable to environmental changes (Chichorro et al., 2022), including higher competition with introduced congeners, especially if indigenous species are also habitat specialists and have small ranges (Boieiro et al., 2018; Malumbres-Olarte et al., 2021).

Adding to the natural vulnerability of epigean indigenous species, introduced spiders are, in principle, more likely to also be epigean, as they benefit from human transportation through shipping by using crates, containers or similar means (Nentwig & Kobelt, 2010). One can, therefore, expect that introduced species will more likely colonize epigean micro-habitats, where many of the indigenous, including endemic, species occur.

In this work, we aim to test whether indigenous (endemic and native non-endemic) and introduced species differ in their vertical distribution along an epigean-canopy gradient to understand (i) how introduced species succeeded in colonizing Macaronesian forests, and (ii) how their micro-habitat preference might lead to increased pressure over their endemic and native non-endemic counterparts.

We investigate if species with different colonization origins (endemic, native non-endemic and introduced) differ: (i) in their preferred vertical stratum (mean verticality), (ii) in their vertical range (standard deviation of verticality) and (iii) if these potential differences vary between archipelagos. For our first objective, at the Macaronesia level, we expect to find a higher proportion of introduced species at lower vegetation levels (soil and herbaceous vegetation), while endemic and native non-endemic species should be found on all strata. For the second objective, we explore two alternative hypotheses: (a) endemic and introduced species should have smaller ranges when compared to native non-endemic, as endemic species should be more specialized in particular niches and so be more vertically restricted, while introduced species should be less adapted to the native forest and so be restricted in the range of microhabitats they were able to colonize (Borges & Wunderlich, 2008), or (b) native non-endemic and introduced species might have larger vertical range compared to endemics due to higher plasticity and ability to survive a broader range of environmental conditions (Borges, Ugland, et al., 2008; Borges & Wunderlich, 2008;

Gillespie et al., 2008). For the last objective, in Madeira and the Canary Islands, we expect higher specialization of endemic species, as these not only had more evolutionary time to adapt to certain micro-habitats, both archipelagos being older than 14 Myr (Fernández-Palacios et al., 2011), but also given the high local species richness we expect spider species to partition the vertical space more finely to avoid competition (Cardoso et al., 2010; Triantis et al., 2012). For the Azores, a more isolated and younger archipelago with a known depauperate arthropod fauna, introduced spiders should show high overlap with indigenous species and high vertical range (Whittaker et al., 2014), due to less competition in most strata and lower stratification of the forest canopy (Borges, Ugland, et al., 2008; Fernández-Palacios, 2010).

MATERIALS AND METHODS

Study sites

In this study, we used data collected from five islands belonging to three Macaronesian archipelagos, [the Azores (Pico and Terceira Islands), Madeira (Madeira Island) and the Canary Islands (La Gomera and Tenerife Islands)] where humid forests dominated by Laurel elements occur (Fernández-Palacios et al., 2011; Neto et al., 2020) (see Appendix S1 for a detailed description of the studied forests). On these islands, 50 × 50 m plots were established in native forest sites, six in Pico, 10 in Terceira, 12 in Madeira, seven in La Gomera and 10 in Tenerife (see Cicconardi et al., 2017; Malumbres-Olarte et al., 2019, 2020, 2021). For Terceira and Tenerife 10 sites were selected based on the presence of pristine forest within the framework of NETBIOME project (see Cicconardi et al., 2017). For the other islands, the sites sampled were chosen to study the influence of distance-decay between sites on patterns of alpha and beta diversity (for more details see Borges, Cardoso, Fattorini, et al., 2018; Malumbres-Olarte et al., 2021). All plots were set up inside fragments of native mesic forests dominated by endemic trees and shrubs (Borges, Cardoso, Fattorini, et al., 2018; Malumbres-Olarte et al., 2019, 2020, 2021).

Sampling protocol and identification

The analysed dataset was built from collections of spider specimens using the COBRA (Conservation Oriented Biodiversity Rapid Assessment) sampling protocol (Borges, Cardoso, Kreft, et al., 2018; Cardoso, 2009). This protocol has demonstrated its effectiveness to study patterns at large scales—for islands, archipelagos and mainland spider communities (Domènech et al., 2022; Emerson et al., 2017; Malumbres-Olarte et al., 2021). The core version of COBRA (see Appendix S2 for sampling details) consists of nocturnal active aerial search, net sweeping, vegetation beating and pitfall trapping (for more details see Cardoso, 2009; Borges, Cardoso, Kreft, et al., 2018). Sampling was performed in 2012 in Terceira, in 2013 in Tenerife and 2016 in the remaining islands. All islands were sampled between April and September, targeting the period of maximum arthropod richness in these forests (Malumbres-Olarte et al., 2021).

All spiders were identified to species level and we considered only adults for analysis. Morphological identification was confirmed with the mitochondrial cytochrome c oxidase 1 and the nuclear 28 s rRNA genes, for all species except the following: *Argyrodes incertus* Wunderlich, 1987; *Dipoenata longitarsis* (Denis, 1962); *Oxyopes kraepelinorum* Bösenberg, 1895; *Pardosa hortensis* (Thorell, 1872); and *Tenuiphantes leprosoides* (Schmidt, 1975) (for more details see Emerson et al., 2017; Malumbres-Olarte et al., 2021). Species names were checked for updated nomenclature using the R package ‘arakno’ (Cardoso & Pekar, 2022).

Colonization origin (endemic, native non-endemic and introduced) was obtained from the latest published species lists for these archipelagos (Borges, Lamelas-Lopez, Stüben, et al., 2022; Cardoso & Crespo, 2008; Macías-Hernández, 2010; Suárez & Oromí, 2018), as well as from the expertise of the authors on the local arachnofauna and consulting their known distribution in the World Spider Catalog (World Spider Catalog, 2022). We followed the criteria of Borges, Lamelas-Lopez, Stüben, et al. (2022) for the classification of species into different colonization origins, considering also the distribution of species in non-native habitats (Borges et al., 2010). For species that were considered with different origins in different archipelagos, we considered them in both groups (e.g. endemic and introduced) for the analysis of the dataset at the Macaronesia level. Macaronesian endemics were considered native non-endemic, as their large distribution should make them show patterns more similar to native non-endemic species than to archipelago endemics.

All voucher specimens are deposited at EDTP—Entomoteca Dalberto Teixeira Pombo, Campus de Angra do Heroísmo, Portugal, and data from Azores and Madeira can be assessed in Malumbres-Olarte et al. (2019, 2020).

Verticality metrics

Two metrics of verticality were calculated for each species at each site where it occurred: the mean verticality or preferred vertical stratum (hereafter AVG V), being the stratum along the vertical gradient where the species should most often occur, and its associated standard deviation (hereafter STD V) as a measure of vertical range, meaning the distribution of the species along the gradient. The AVG V is adapted from Macías-Hernández et al. (2020). Details of the calculation are given below. First, 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). Scores were then divided by 3 to obtain AVG V values ranging from 0 (for more epigean species) to 1 (for more arboreal species). Next, the relative abundance of the species was calculated for each method (i.e. score) as follows:

$$p_{ijk} = \frac{n_{ijk}}{N_{jk}} \tag{1}$$

where n_{ijk} and p_{ijk} are the abundance and relative abundance of the species i for the score j in the site k, respectively, and N_{jk} is the total abundance of spiders of the score j at the site k. Relative abundance was preferred over raw values, as different sampling methods yield different total abundances (i.e. the most abundant species in sweeping may have the same abundance as a species of intermediate abundance in beating). We then normalized the relative abundances to obtain a proportion summing to 1 across the vertical gradient as follows:

$$qijk = \frac{pijk}{\sum_{j=1}^{4} pijk} \tag{2}$$

where q_{ijk} is the normalized relative abundance. The mean verticality of a species at a given site was then calculated as follows:

$$AVG\_V_{ik} = \sum_{j=1}^{m} qijk \times S_j \tag{3}$$

where *AVG* V_{ik} is the mean verticality of the species *i* in site *k* and S_j is the score for method *j*, and *m* being the number of unique scores. We calculated the standard deviation as follows:

$$STD\_V_{ik} = \sqrt{\sum_{j=1}^{m} qijk \times (S_j\_AVG\_V_{ik})^2} \tag{4}$$

Finally, for a given species, the values *AVG* V_{ik} and *STD* V_{ik} were averaged across all sites *k* where the species occurred to obtain the species-level values mAVG V and mSTD V at the Macaronesia and archipelago levels (see Figure 1 for the overall trait-space and how these would match our hypothesis at the Macaronesia level).

Statistical analysis

To verify if the spider species diversity was properly sampled in our study area, we estimated the values of sampling coverage and completeness using the Jacknife1 (P-corrected) estimator (Chao & Jost, 2012; Heltshe & Forrester, 1983; Lopez et al., 2012) calculated for the entire dataset and each archipelago. Species present only in one site (uniques) were discarded from further analysis to try to prevent the influence of rare, and pseudo-rare species on our results (Borges, Ugland, et al., 2008). The verticality values of mAVG V and mSTD V obtained were then compared between groups of different colonization origins using Kruskal–Wallis tests (KW), as they did not fulfil the statistical assumptions for analysis of variance (ANOVA). This was done both at Macaronesian and archipelago levels. When the overall KW was statistically significant at alpha <0.1, Dunn's tests were performed to identify statistically significant pairwise differences between colonization origins (see Appendix S3 for information on colonization origin). An alpha <0.1 was used as we found several tests between this value and 0.05 to be worth further analysis and discussion. To test if the different colonization origins were

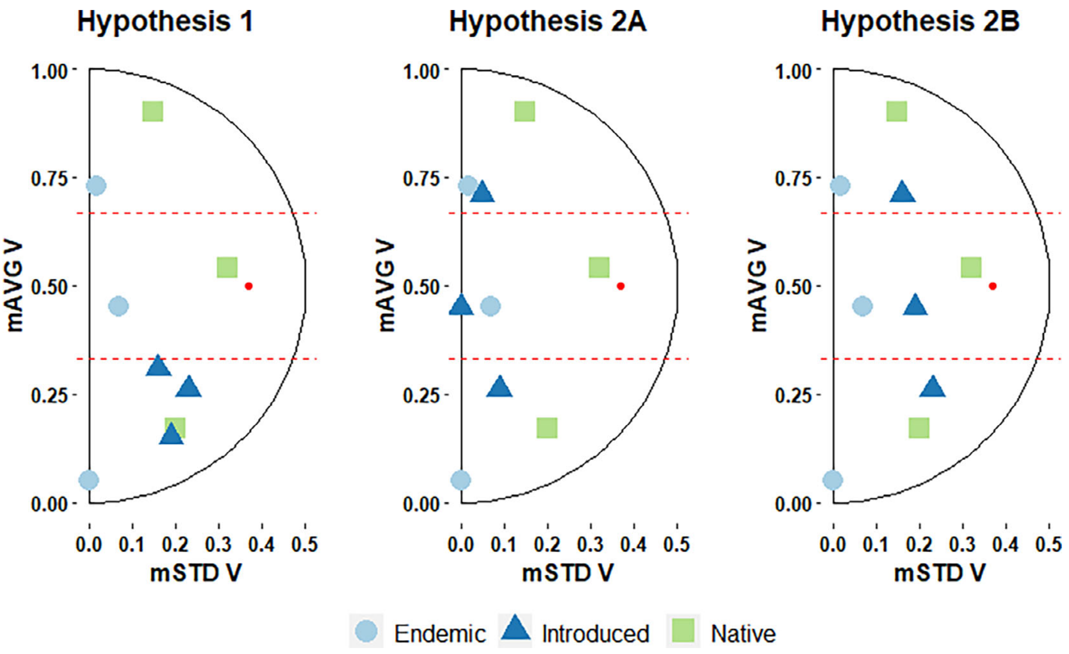

FIGURE 1 Theoretical space of the verticality values that can be obtained, with the *y*-axis showing the possible values for mAVG V (preferred vertical stratum) while mSTD V (vertical range) is represented on the *x*-axis. mAVG V varies between 0 (species only in pitfall) and 1 (species only in beating), while mSTD V varies between 0 (only in one method) and 0.5 (species equally in beating and pitfall). The shaped dots represent theoretical species that form patterns that explain the hypothesis we want to verify at the Macaronesia level. The red dot marks the coordinates of a hypothetical super-generalist (mAVG V = 0.5 and mSTD V = 0.37), which would be any species that would have the same relative abundance at all the strata sampled, and so a normalized relative abundance of 0.25 for each method (summing to 1–100% of the specimens captured) was considered for the calculation. Red dotted lines divide species according to their mAVG V corresponding to the microhabitats of vegetation until knee level sampled by sweeping (mAVG V = 0.33) and higher vegetation and tree trunks sampled by AAS (mAVG V = 0.67).

preferentially associated with either the epigean or the arboreal stratum, we applied one-sample Wilcoxon signed rank tests to quantify if the mAVG V values were significantly above (arboreal species) or below 0.5 (epigean species). All statistical analyses were performed using the R software version v.4.1.0 (R Core Team, 2021).

RESULTS

General patterns

A total of 10,609 adult specimens were identified as belonging to 123 species in 23 different spider families. Sampling completeness was higher in the Azores and Madeira (58%) than in the Canary Islands (53%). Sampling coverage was always above 90%. From the initial dataset, 43 specimens belonging to 21 species were considered uniques (mostly endemic species) as they occurred only at one site in the whole dataset and so were removed from further analyses. The remaining included a total of 102 species in 22 families, most being endemic (59), with only 28 native non-endemic and 16 introduced. *Steatoda nobilis* (Thorel, 1875) was the only species for which we considered a different colonization origin between archipelagos, endemic (Madeira) and introduced (the Azores and the Canary Islands). The reasons behind this decision were: it being considered probably introduced in the Canary Islands (Macías-Hernández, 2010; Suárez & Oromí, 2018) and its presence in different continents and its occurrence in both native and non-native habitats in the Azores.

The Canary Islands are the archipelago with the most species sampled with a total of 57 (including 32 endemics, 21 native non-endemic and four introduced) followed by Madeira with 34 species (14 endemics, 15 native non-endemic and five introduced) and the Azores with 31 species (13 endemics, six native non-endemic and 12 introduced). Linyphiidae were the most species-rich family in all the archipelagos, although closely followed by Theridiidae in the Canary Islands and Madeira.

Vertical stratification of species of different colonization origins

At the Macaronesia level, native non-endemic species had the highest median value of AVG V [0.67, Interquartil range = 0.22 (from here on IQR)], followed by endemic (0.54, IQR = 0.58) and introduced (0.53, IQR = 0.40). Introduced species did not show significant differences from either of the other two categories (see Figure 2a). Only native non-endemic species had AVG V significantly above 0.5 (*p*-value = 0.0298). At the archipelago level, the result was again of no significant differences between the three colonization origin groups. Native non-endemic species showed the highest median AVG V values (AZO: 0.53, IQR = 0.32; CAN: 0.51, IQR = 0.43; MAD: 0.73, IQR = 0.25). In Madeira (see Figure 2d) these were followed by endemic (0.58, IQR = 0.24) and then introduced species (0.33, IQR = 0.56), and in the Azores and the Canary Islands (Figure 2b,c) by introduced (AZO: 0.53, IQR = 0.32; CAN: 0.51, IQR = 0.43) and finally by endemic (AZO: 0.49, IQR = 0.58; CAN: 0.51, IQR = 0.67). Native non-endemic species had AVG V significantly above 0.5 both in Madeira (*p*-value = 0.0473) and in the Canary Islands (*p*-value = 0.0327).

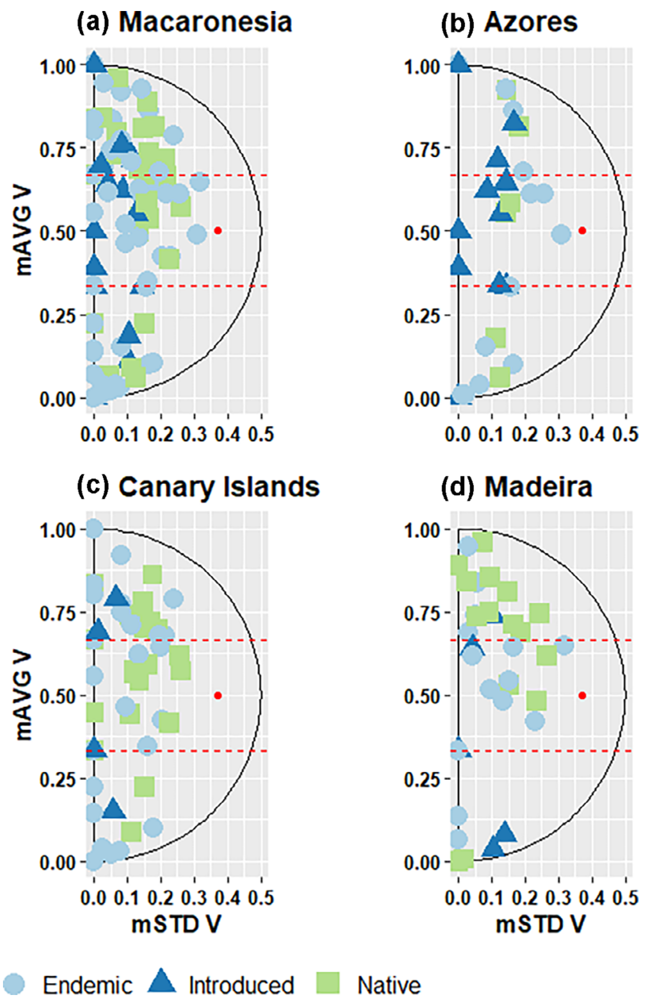

FIGURE 2 Species distribution at the Macaronesian (a) and archipelago levels (b) – Azores, (c) – Canary Islands, (d) – Madeira according to their two verticality values, the *y*-axis representing mAVG V (preferred vertical stratum) values (ranging from 0 to 1) and the *x*-axis representing mSTD V (vertical range) values (ranging from 0 to 0.5). Each point represents a distinct species except in the case of *Steatoda nobilis*, which is represented by two points of different colonization origins according to the archipelago. The red dot marks the coordinates of a hypothetical super-generalist (mAVG V = 0.5 and mSTD V = 0.37), which would be any species that would have the same relative abundance at all the strata sampled, and so a normalized relative abundance of 0.25 for each method (summing to 1–100% of the specimens captured) was considered for the calculation. Red dotted lines divide species according to their mAVG V corresponds to the microhabitats of vegetation until knee level sampled by sweeping (mAVG V = 0.33) and higher vegetation and tree trunks sampled by AAS (mAVG V = 0.67).

Vertical range of species of different colonization origins

At the Macaronesia level and for STD V verticality, native non-endemic species had significantly higher values (0.14, IQR = 0.09) (see Figure 2a), than both endemic (0.08, IQR = 0.16) and introduced (0.06, IQR = 0.10) (*p*-value = 0.0459 and *p*-value = 0.0058, respectively). Looking at the archipelagos separately, in the Azores we found significantly lower values between introduced (0.10, IQR = 0.14) and endemic species (0.16, IQR = 0.14) (*p*-value = 0.0342), but also compared to those of native non-endemic species (0.15, IQR = 0.02) (see Figure 2b), although not significant (*p*-value = 0.0594). In the Canary Islands, native non-endemic species showed significantly higher values (0.14, IQR = 0.06) than endemics (*p*-value = 0.0440 (0.06, IQR = 0.13) (see Figure 2c). The lowest median value was from introduced species (0.03, IQR = 0.05), although these were not significantly different from the rest. In Madeira, none of the colonization origins significantly differed from each other, albeit introduced and native non-endemic species had the highest median values (0.10, IQR = 0.06; 0.10, IQR = 0.14, respectively), and endemics the lowest (0.05, IQR = 0.12).

DISCUSSION

To our knowledge, this is the first time that vertical stratification preferences of spiders across multiple sites and island colonization origins were studied. With this work, we were able to evaluate spider microhabitat choice, which is deeply connected with multiple other aspects of their ecology, such as prey preferences (Blackledge et al., 2003), hunting strategies (Blackledge et al., 2003; Cardoso et al., 2011; Domènech et al., 2022; Samu et al., 1999) and dispersal ability (Domènech et al., 2022; Samu et al., 1999). In this context, our study fills some critical knowledge gaps, regarding the Raunkiaeran shortfall (i.e. lack of knowledge of species traits and ecological functions, see Hortal et al., 2015) for spiders.

Colonization origin of species along the vertical gradient

Contrary to our predictions for the first hypothesis, it appears that the introduced species were not particularly associated with the lowest-strata (ground and herbaceous vegetation). Indeed, more than half had AVG V values of 0.5 or higher, highlighting their preferences also for trunks and canopy foliage. This is consistent with the idea that island systems have many vacant niches that can be exploited by introduced species (Whittaker et al., 2014), although we cannot rule out the fact that some could be occupying niches left empty by the extinction of indigenous species (Cardoso et al., 2010).

However, these results should be interpreted with caution given that we did not sample the full extent of the canopy, especially in Madeira and the Canary Islands where trees can go up to 30 m (see Appendix S1). As some common introduced species in the herbaceous vegetation of disturbed habitats (Borges & Wunderlich, 2008) may be able to reach the highest strata of the canopy by ballooning, future studies should test whether the pattern we report here holds when the entire canopy range is sampled.

Native non-endemic species were mostly arboreal (AVG V values above 0.5). Unlike endemic species, which tend to have a lower dispersal capacity, and introduced species that have travelled with humans, native non-endemics may be those with the highest dispersal ability (Carlquist, 1974), being found in places as far apart as Terceira (Azores) and Tenerife (Canary Islands). Spiders in higher strata are more prone to ballooning either because they already occupy ideal 'launch pads', or because their lifestyle predisposes them to balloon. Consistent with our findings, Malumbres-Olarte et al. (2021) found that the native forests are richer in frequent ballooners than dry habitats dominated by herbaceous vegetation. This should also hold when comparing arboreal and epigean habitats in native forests, as epigean spiders often lack the conditions to balloon properly in the moist litter of the forest floor (Bell et al., 2005).

However, long distance dispersal is not always linked to high dispersal ability, as small organisms can be, for example, passively transported by birds as it happens with land snails (Whittaker & Fernández-Palacios, 2006). Furthermore, genetic studies are needed to assess the origin of many of the native non-endemic species, as some might be actually introduced species (see Jiménez-Garcia et al., 2023).

Finally, future works should incorporate the verticality of the juveniles, as it is generally at this stage of life that many species disperse by ballooning (Blandenier, 2009; Suárez et al., 2022).

Vertical range of species with different colonization origin

The higher STD V obtained for native non-endemic species supported one of our alternative hypotheses for this trait (see Figure 2a). As speciation takes place, spiders might specialize in terms of prey or habitat (Arnedo et al., 2007; Blackledge et al., 2003; Gillespie et al., 2008). Because island communities are typically impoverished, competition might be lower than on continental areas (Costa et al., 2008; Cotoras et al., 2021), and so many species might tend to be generalists (Gillespie et al., 2008; Macías-Hernández et al., 2016). Native non-endemics matched this profile, showing higher vertical range than even introduced species. Many introduced arthropod species are successful at colonizing mostly anthropogenic habitats (Borges & Wunderlich, 2008; Rigal et al., 2018), which greatly differ from the native forests of Macaronesia. As many of our introduced spiders were found in many sites (see Appendix S4) sometimes in high numbers (Boieiro et al., 2018), their lower vertical range indicates that even the successful invaders are often vertically restricted.

Verticality traits at the archipelago level

Specialization during speciation is more likely to happen in geologically older archipelagos (Gillespie et al., 2008), such as the Canary Islands (22 My) and Madeira (14 My), than in younger ones such as the Azores, which is, for the most part, less than 1 My old (Fernández-Palacios et al., 2011; Marques et al., 2020; Triantis et al., 2012). Our results match this, with native non-endemic species in the Canary Islands having higher vertical range than endemics. However, this was not the case in Madeira, possibly related to the younger age of this island (5 My) when compared to La Gomera and Tenerife (11 and 12 My, respectively) (Fernández-Palacios et al., 2011). Considering that many indigenous spiders from the Canary Islands originated from in situ speciation (Arnedo et al., 2001; Crespo et al., 2021; Emerson & Oromi, 2005; Machado et al., 2017), it is expected that sympatric endemic spiders had to adapt to a finer partitioning of available niche space to avoid competition (Blackledge et al., 2003; Gillespie, 2005). These richer communities might then be more resilient to invasions, which was supported by our results, with the few introduced species present in the archipelago having very low STD V compared to native non-endemic ones.

Curiously, in Madeira epigean indigenous species showed very low values of STD V. A possible explanation for this might be larger differences in microhabitats at lower strata of the forests than among the canopy (Sorensen, 2003). Another factor might be the presence of two introduced species: *Cryptachaea blattea* (Urquhart, 1886), and *Tenuiphantes tenuis* (Blackwall, 1852). These are epigean species with high vertical range, being found on all strata of Madeira forests (see Appendix S4), but in clearly higher proportion on the ground and herbaceous vegetation (Boieiro et al., 2018). Boieiro et al. (2018) suggested that one of the reasons for their success might be the lack of competition with indigenous species. Although our results match this, properly assessing the competition with indigenous species would have to be tested with a broader set of traits, which is beyond the scope of the current work.

In the Azores, as expected we did observe a large overlap in verticality between all categories of colonization origin (Figure 2b). However, we failed to observe high vertical range in introduced spiders. In general Azorean arthropod communities have been described as much poorer due to their isolation, young age and homogeneity of habitats on the islands (Gaspar et al., 2008; Triantis et al., 2012). However, indigenous species showed greater vertical range than introduced (Figure 2b), with *Rugathodes acoreensis* Wunderlich, 1992 being the species that most closely matches the profile of a super-generalist. The low STD V of introduced species observed might be then due to many being vagrants from exotic habitats (Borges, Ugland, et al., 2008; Borges & Wunderlich, 2008), that are not able to establish sustainable populations in a system dominated by well-adapted indigenous generalists.

CONCLUSIONS

The results obtained from our study did not support that introduced spiders occur preferentially in the soil and herbaceous vegetation of Macaronesia native forests. However, we did observe a higher vertical mean and range in native non-endemic species, supporting a higher level of generalism of the species not restricted to just one archipelago. Finally, introduced species in the Azores occurred over the entire vertical range studied, but were more restricted than indigenous species. The two values obtained to characterize the verticality of the spiders sampled were successful at giving us a better insight into the vertical dynamics of the community of spiders from the native forests of Macaronesia. However, our results stress the need for a sampling scheme that documents properly the entire vertical gradient of these forests to verify if the patterns found hold at higher strata, as well as the need to document intraspecific differences among lifestages.

AUTHOR CONTRIBUTIONS

R. Costa: Formal analysis; visualization; writing – original draft; writing – review and editing; investigation; data curation; conceptualization. **P. Cardoso:** Formal analysis; writing – review and editing; methodology; investigation; supervision; conceptualization. **F. Rigal:** Formal analysis; visualization; writing – review and editing; methodology; supervision; conceptualization. **P.A.V Borges:** Writing – review and editing; methodology; investigation; supervision; data curation; conceptualization; project administration; funding acquisition.

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CONFLICT OF INTEREST STATEMENT

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, reference number 10.15468/kcgjfr.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Characteristics of the native forests sampled on the three studied archipelagos (Fernández-Palacios, et al., 2017).

Appendix S2. Sampling methods implemented in the core version of the COBRA protocol used in this study.

Appendix S3. Spider species used in the analysis, family, colonization origin, abundance, preferential vertical stratum (mAVG V) and vertical range (mSTD V) obtained at the Macaronesia level. Information on the archipelago where each species was sampled is coded as follows: Azores—AZO, Madeira—MAD, Canary Islands—CAN. *Steatoda nobilis* (Theridiidae) specimens from Madeira were considered endemic while those in the remaining archipelagos were considered as introduced. Species endemic to Macaronesia were considered as native non-endemic and are signalled with 'ME' in their colonization origin.

Appendix S4. Introduced spider species sampled, islands where they occurred (Terceira—TER, Pico—PIC, Madeira—MAD, La Gomera—GOM, Tenerife—TEN), number of sites where they occurred, sampling methods where they were sampled (Active aerial sampling—AAS, Beating—BET, Pitfall—PIT, Sweeping—SWE) and additional information about the species occurrence in native and non-native habitats (Azores—AZO, Madeira—MAD, Canary Islands—CAN, Non-available—NA). *Metellina merianae* was only considered for Pico, and *Steatoda nobilis* from Azores and Canary Islands. *—species considered as uniques and removed from the analysis.

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