Another brick in the wall of European subterranean spider knowledge: adding Macaronesian species and their traits to the picture

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Author contribution

DPS, NMH, and SM conceived the study. DPS, PC, AB, MP, LC, KT, GN, NMH, and SM compiled traits and/or curated data. SM analysed the data. DPS, NMH, and SM wrote the first draft. All authors contributed to the writing with suggestions and critical comments.

Conflicts of Interest

No conflicts of interest are declared by the authors.

Abstract

Caves and other subterranean ecosystems impose highly selective environmental filters, driving the evolution of convergent and specialized traits in subterranean organisms. Here, we present the first comprehensive checklist and trait database for subterranean spiders of Macaronesia, thereby filling a significant knowledge gap relative to continental Europe. We compiled data through direct morphological measurements and literature review, covering 64 morphological and ecological traits for 61 species (14 families) from Macaronesia, along with 66 additional species in continental Europe not included in the previous checklist. After accounting for taxonomic changes, the checklist of European subterranean spiders now lists 637 species, of which 278 are considered to be obligate subterranean-dwellers (troglobionts). Functional trait analyses using n-dimensional hypervolumes revealed moderate overlap in the functional space of continental Europe and Macaronesian subterranean spiders ($\beta\_total = 0.47$), driven primarily by differences in trait richness rather than the replacement of functional space, with the Macaronesian spiders occupying a smaller functional space than the continental European ones. The Macaronesian assemblage showed more regular (even) niche occupation but similar overall functional dispersion compared to Europe, suggesting lower functional redundancy yet comparable trait diversity. These findings suggest that similar environmental pressures drive functional convergence in cave faunas despite geographic, geological (karstic vs. volcanic), and taxonomic differences. The expanded trait database is a valuable resource for ecological and conservation research, highlighting the need for continued exploration and protection of subterranean biodiversity on oceanic islands.

Keywords: Arachnida, functional diversity, Macaronesia, speleology, subterranean biology, troglobiont

Introduction

Subterranean ecosystems—such as caves, aquifers, and fissure systems—are considered harsh environments for organisms to establish in, as they impose strong environmental filters on colonizing taxa from the surface species pool (Fernandes et al., 2016). Subterranean animals have evolved a wide array of morphological, physiological, and behavioral adaptations to survive the conditions imposed primarily by the absence of sunlight and the resulting scarcity of food resources, which shape the typically small and species-poor biological communities found underground (Howarth & Moldovan, 2018; Lunghi et al., 2024). As a result, subterranean communities are typically depauperate in species but are notable for high endemism and unique adaptations (Deharveng & Besos, 2019).

Spiders (Araneae) and other arthropods, such as beetles (Coleoptera), millipedes (Diplopoda), isopods (Isopoda), and pseudoscorpions (Pseudoscorpiones), have successfully colonized the subterranean domain multiple times throughout their evolutionary history (Deharveng & Besos, 2019). These groups play critical ecological roles in subterranean ecosystems, acting as apex predators (e.g., spiders and some beetles), primary decomposers (e.g., isopods and millipedes), and important contributors to nutrient cycling and food web structure (Fernandes et al., 2016; Mammola & Isaia, 2017; Deharveng & Besos, 2019). Their diversity and functional adaptations highlight the ecological significance of arthropod assemblages in subterranean ecosystems.

Despite advances in continental cave biology, the subterranean fauna of oceanic islands such as those in Macaronesia has historically received less attention. These archipelagos offer a unique opportunity to study evolutionary processes in isolated environments and to fill critical gaps in the biogeography of subterranean arthropods (Oromí et al., 1991; Oromí, 2004; Borges et al., 2012). Research on subterranean spiders in Macaronesia gained momentum in the late 20th century. In the Canary Islands, interest in cave spiders increased notably in the early 1980s with the establishment of the Group of Speleological Researchers of Tenerife (GIET - Grupo de Investigaciones Espeleológicas de Tenerife, Spain), which focused on biological analyses of caves and species descriptions (Oromí & Martín, 1990). Initial investigations in the Azores began in 1987 through expeditions funded by the National Geographic Society and led by researchers from La Laguna University (Tenerife) and the University of Edinburgh (Scotland, UK), exploring caves on Terceira, Pico, and São Jorge islands. These efforts led to the discovery of the first troglobiont species in the archipelago, the spider *Rugathodes pico* (Merrett & Ashmole, 1989) (Merrett & Ashmole, 1989; Oromí et al., 1990).

In the early 1990s, Jörg Wunderlich conducted an extensive study on Macaronesian spiders. He described numerous species from Madeira, including *Centromerus sexoculatus* (Wunderlich, 1992) and *Centromerus anoculus* (Wunderlich, 1995)—the only two troglobiont spiders currently reported from the archipelago—and as many as 19 cave-dwelling species from the Canary Islands (Wunderlich, 1992, 1999, 2011). In Cape Verde, extensive cave exploration was carried out between 1997 and 1999 by the Speleo Club of Torres Vedras (ECTV- Espeleo Clube de Torres Vedras, Portugal) and the GIET team, during which two still-undescribed troglobitic spiders belonging to the families Hahniidae and Theridiidae were discovered (Hoch et al., 1999). This pioneering fieldwork paved the way for further research into the high diversity and endemism of subterranean spiders in Macaronesia, providing valuable insights into evolutionary processes such as speciation and adaptive radiation on oceanic islands (e.g., Arnedo et al., 2007; Dimitrov & Ribera, 2007; Macías-Hernández et al., 2024).

Building on this legacy, we present an updated checklist of subterranean spiders in Macaronesia, complementing the existing checklist and trait database of subterranean spiders in continental Europe (Mammola et al., 2018, 2022), and release a new trait database for all species included in the checklist. For the latter, we followed the recently proposed template of 64 morphological and ecological traits for European cave spiders (Mammola et al., 2022). Additionally, we take this opportunity to update the European database by including missing species—5 species described since 2023, 3 species previously overlooked, and 58 species from the Dinaric karst currently under description.

To illustrate the dataset, we constructed a functional space (following Mammola et al., 2021a) for subterranean spiders in Macaronesia, mapping the position of species and families within this multidimensional space. We also explore the extent of functional convergence between subterranean spider communities in Macaronesia and continental Europe. Our objectives are to quantify the extent of this convergence and to highlight unique adaptations and diversity patterns specific to Macaronesian faunas. Despite limited similarity in their taxonomic composition, we hypothesize that strong environmental filtering—especially darkness, spatial constraints, and food scarcity—should drive convergence in functional traits between species in Macaronesia and continental Europe.

Materials & Methods

Study area – Macaronesian subterranean habitats

The Macaronesian biogeographical region is located in the northeastern Atlantic Ocean and comprises the Azores, Madeira, Selvagens, Canary Islands, and Cape Verde (Fernández-Palacios et al., 2024). These archipelagos share common geological characteristics, having all formed from the accumulation of primarily volcanic materials that emerged between the Tertiary and Quaternary periods. As a result, they lack developed karstic landscapes and, consequently, true caves (Oromí, 2004). In this context, lava tubes represent the majority of macro-caverns and are predominantly found in geologically young areas with recent volcanic activity, such as many of the Azores and Canary Islands (Oromí et al., 2021).

Other widespread volcanic shallow subterranean habitats include networks of small to medium-sized interconnected voids and spaces within the shallow underground—commonly referred to as the *milieu souterrain superficiel* (MSS; Mammola et al., 2016). The MSS is an important habitat in the Canary Islands due to its extensive distribution across the archipelago (Macías-Hernández et al., 2024). Numerous troglobiont species have been described from this environment since its discovery by the GIET team in the 1980s (Oromí et al., 1986), especially following the improvement of Juberthie's MSS pitfall trap by López & Oromí (2010).

Pyroclastic deposits are also known to harbor subterranean taxa due to their capacity to retain humidity, even at high altitudes (Macías-Hernández et al., 2024; Oromí et al., 2018). In contrast, deep subterranean habitats such as volcanic pits are less common but tend to reach greater depths and persist longer over geological timescales compared to lava tubes. These habitats are more typical of mature islands (Macías-Hernández et al., 2024).

Checklist compilation

We compiled a checklist of subterranean spiders in Macaronesia based on knowledge accumulated over more than 40 years of field surveys in caves and other subterranean habitats, complemented with a thorough bibliographic survey. In the checklist, we included species that are described, or under description, focusing exclusively on those that carry out at least part of their life cycle in subterranean ecosystems. Conversely, we excluded "accidental species" (Trajano & de Carvalho, 2017), namely surface-dwelling spiders accidentally occurring underground. We classified each species listed in the checklist into two ecological categories:

i) Troglophiles, namely species able to maintain stable subterranean populations or prone to inhabit subterranean habitats, being, however, associated with surface habitats for some biological functions or able to maintain surface populations too; and

ii) Troglobionts, for species strictly bound to subterranean habitats.

We are aware this is a somewhat artificial ecological classification that oversimplifies real cases (see Ashby & Maddox, 2005). The ultimate product is an artificial categorization, which will work well for clear-cut cases but may fall short when the association of a species with the subterranean domain is less strict. Still, we provided it to offer a rough indication of the affinity of species for the subterranean medium and consistency with previous checklists on subterranean spiders (Mammola et al., 2018; 2022).

We also took the opportunity to update the checklist and trait database for species in continental Europe, updating taxonomy and incorporating newly described species, previously overlooked species, and those currently under description (the latter are identified up to the genus level [morphospecies] and will have their names updated in future database revisions).

Trait compilation

We here use the definition of "trait" as in the World Spider Trait database (Lowe et al., 2020; Pekár et al., 2021), whereby a trait is considered any phenotypic characteristic measured at the individual or species level, including morphological, anatomical, ecological, and behavioral attributes. We gathered 64 morphological and ecological traits for every species and morphospecies included in the checklist. These traits are the same ones used to describe the functional space of European subterranean spiders. A detailed description of each trait and its functional significance can be found in Mammola et al. (2022). In brief, we collected morphological traits related to body size and subterranean adaptation, as well as ecological traits such as functional guild, foraging strategy, prey range, and type of habitats occupied within the cave. For each species, we collected traits through both direct measurements and literature data (primarily taxonomic descriptions), using individuals of both sexes when available. All measured specimens are stored at the Department of Zoology of the University of La Laguna DZUL collection (species from the Canary Islands), at the DTP – Dalberto Teixeira Pombo arthropod collection (University of the Azores, Angra do Heroísmo, Portugal) (species from the Azores), and at the Croatian Biospeleological Society Collection in Zagreb (undescribed species from the Dinaric karst). We obtained literature through species-specific online searches in the World Spider Catalog (2025) and Google Scholar.

Data Analysis

We conducted all analyses using R version 4.1.0 (R Core Team, 2024). Following the same approach as in Mammola et al. (2022), we generated a visual representation of the trait space for subterranean spiders, mapping the position of each species and family from Macaronesia and continental Europe. First, we selected a subset of traits from the complete trait matrix, representing: i) Species body size and overall morphology (Average body size, Sexual size dimorphism, and Prosoma shape); ii) Morphological adaptation to the subterranean conditions, including binary (Presence/absence of Eyes, Eye regression), continuous (Femur elongation, Profile reduction, Anterior median eyes [AME], Anterior lateral eyes [ALE], Posterior median eyes [PME], and Posterior lateral eyes [PLE]), ordinal (Pigment), and categorical (AME type) traits; and iii) Hunting strategy (all binary variables referring to diet, hunting strategy, and food specialization). Then, we carried out data exploration on this trait matrix following Palacio et al. (2022). As a result of data exploration, we log-transformed all continuous traits to homogenize their distributions. We also standardized all traits to mean = 0 and standard deviation = 1 to ensure comparable ranges among traits.

Since the trait matrix is a mixture of continuous, binary, ordinal, and categorical traits, we estimated functional dissimilarity among species with a Gower distance (Gower, 1971). In calculating Gower distance, we attributed equal weight to traits encompassing similar functions within the three groups of traits defined above. This approach resulted in a high-quality hyperspace, with limited distortion of original functional distances among species [quality of 0.99 based on the approach by Maire et al. (2015)]. We visualized the trait space as the first two axes of a Principal Coordinate Analysis using the trait dissimilarity matrix as input data. For graphical visualization, we estimated the density of species on the ordination diagram with a kernel density.

Finally, we tested for convergence in the functional space of subterranean spiders in Macaronesia versus continental Europe. For this, we used the three axes of the Principal Coordinate Analysis to construct n-dimensional hypervolumes (*sensu* Blonder et al. 2014) for the two pools of species. We computed hypervolumes using a Gaussian kernel density estimator and a default bandwidth for each axis (Blonder et al. 2018), as implemented in the function *hypervolume_gaussian* in the package 'hypervolume' version 3.0.1 (Blonder 2022). We characterized the estimated hypervolumes with functions from the R package 'BAT' version 2.7.1 (Cardoso et al. 2015, 2021), calculating their dispersion and regularity (Mammola & Cardoso 2020). We measured the dissimilarity between the two hypervolumes using the *kernel.beta* function (Mammola & Cardoso 2020). This estimation decomposes the two processes underlying overall dissimilarity (β_total) among hypervolumes (Carvalho & Cardoso 2020): the replacement of trait space between hypervolumes (β_replacement), and the net differences between the amount of trait space enclosed by the two communities (β_richness).

Results & Discussion

Subterranean spiders in Macaronesia by numbers

The checklist of Macaronesian subterranean spiders includes 61 species—of which three are currently under description—belonging to 14 families (Figure 1). The most species-rich family is Linyphiidae, with 15 species shared among different genera, especially *Lepthyphantes* (four spp.), *Centromerus* (three spp.), and *Troglohyphantes* (three spp.). Note, however, that preliminary genetic data place the Canarian *Troglohyphantes* in an unrelated Linyphiidae lineage, indicating they probably belong to a separate, still undescribed genus. In second place, Dysderidae is represented by 14 species, all within the genus *Dysdera*, which underwent a large adaptive radiation, especially in the Canary Islands (Arnedo et al. 2007; Macías-Hernández et al. 2016). Pholcidae is the third most species-rich family (13 species, 3 genera), with the majority of species belonging to the genus *Spermophorides* (6 spp.) and *Pholcus* (6 spp.), and a single species from the monospecific genus *Ossinissa*. All other families consist of fewer than three species. Linyphiidae and Dysderidae comprise, for the most part, specialised species only found in subterranean habitats and showing traits such as the loss of eyes, appendage elongation, and depigmentation (Arnedo et al. 2007), whereas many Pholcidae are generalist species exhibiting a low degree of morphological specialisation to subterranean life (Huber 2018). Concerning the distribution by island, subterranean Dysderidae species seem to occur exclusively in the Canary Islands, whereas other species-rich families such as Pholcidae and Linyphiidae are represented to different extents in almost all archipelagos.

The Selvagens Islands and Cape Verde exhibit much lower family and species richness of subterranean spiders—there are still no records of cave spiders in Cape Verde—compared to other islands (Figure 1B), which may be partly due to research bias, as both archipelagos remain poorly studied. In the case of the Selvagens Islands, another contributing factor could be their small geographic area and the resulting limited availability of subterranean habitats. The islands experience high erosion and have unfavorable conditions for supporting troglobitic fauna, with only one cave known on Selvagem Grande (Oromí, 2004), and two known troglophile spiders. In contrast, Cape Verde is the second-largest archipelago in terms of surface area (4,033 km²) and contains multiple caves, but in general is poorly explored.

Another factor driving cave spider diversity in Macaronesia could be the degree of island nature preservation and habitat intactness. For instance, family and species richness is slightly higher in Madeira compared to the Azores (Figure 1B), even though the surface area of the latter is almost three times larger, and the Azores has a greater number of caves (Pereira et al., 2015) and therefore more habitat availability (Oromí et al., 2021), which can be positively correlated with cave arthropod diversity (Borges et al., 2012). However, many of these cavities in the Azores are located in areas heavily impacted by human activity and land-use change. Although a new legal framework for the conservation of Azorean caves has recently been established (Regional Legislative Decree No. 10/2019/A of 22 May; Resolution of the Regional Government Council No. 163/2024 of 4 November 2024), these subterranean habitats have historically received limited attention in conservation strategies, and ongoing efforts are needed to ensure their effective protection (Borges et al., 2012).

Additions to the subterranean spider species in continental Europe

We update the list of species (and trait information) for spiders in continental Europe, adding 77 new species to the list, of which 61 are undescribed species from the Dinaric karst—one of the largest karst landscapes in the world and the largest hotspot of subterranean biodiversity globally (Culver et al. 2021). We also made several taxonomic changes and removed some doubtful species. The new checklist (including Macaronesian species) now lists 637 species, of which 278 are considered troglobionts.

Trait database

We collected traits for all species for which adult specimens were available to us. The trait database is available in Figshare (https://doi.org/10.6084/m9.figshare.16574255.v3) as a tab-delimited file (.csv) and in Excel format (.xlsx). We refer to Mammola et al. (2022) for a lengthy description of each trait and its functional meaning.

Comparison between subterranean spiders in Macaronesia and continental Europe

Using a selection of mostly complete traits from the trait matrix, we mapped the position of each species and family in the trait space (Figure 2), obtaining a quantification of the functional spread of this trait space and its redundancy (e.g., if multiple species fall within highly sampled areas of the trait space). The overall organization of the trait space is similar to that of the trait space for European cave spiders (*cfr.* Mammola et al., 2022: Fig. 4). Several families are isolated in specific regions of the trait space, suggesting the expression of unique combinations of functions and ecological strategies.

Hypervolume analysis revealed that the functional space of continental European and Macaronesian subterranean spiders moderately overlapped in a multidimensional space (β_{total} = 0.47; Figure 3). This degree of overlap suggests an effect of environmental filtering in shaping subterranean ecosystems, leading to some general convergence in the functionality of spider communities in these environments (Cardoso 2012; Mammola et al., 2024). Differences between the two functional spaces were primarily driven by net differences in the amount of trait space enclosed by the two hypervolumes ($\beta_{richness}$ = 0.30), rather than by functional replacement ($\beta_{replacement}$ = 0.17). This dominance of $\beta_{richness}$ in shaping the pattern indicates that, although trait profiles are similar between Macaronesia and continental Europe, the frequency of the most abundant traits differs substantially.

The functional space of subterranean spiders in Macaronesia was more even than that of continental Europe (regularity: 0.28 vs. 0.14), possibly due to lower redundancy in species functions and greater filling of functional niches (Martínez et al., 2022) in the former. Both trait spaces, however, were similarly dispersed (dispersion: 0.34 vs. 0.31), suggesting that the broader space of functionalities has been similarly explored in both regions.

The specific drivers underlying these patterns are likely multifaceted and may relate to taxonomic similarities and differences between the two species pools, as well as other factors. First, 9 of the 61 species listed in the checklist for the Macaronesian region are also found in continental European subterranean habitats, contributing to some of the observed overlap in functional space (Figure 1A). These species occur in circum-Mediterranean countries and typically inhabit the twilight zones of caves (e.g., *Loxosceles rufescens*, *Metellina merianae*, *Steatoda grossa*, and two species of *Tegenaria*), as well as the alien species *Eidmannella pallida*, which can likely exploit caves opportunistically across different climatic regions (Nicolosi et al., 2023).

Second, it appears that the two regions have undergone somewhat different evolutionary radiations. In continental European caves, the most significant radiation involves Linyphiidae—especially the highly speciose genus *Troglohyphantes* (Deeleman-Reinhold et al., 1978; Isaia et al., 2017)—along with Nesticidae and Leptonetidae (Mammola et al., 2018, 2022). In contrast, although Linyphiidae are also speciose in the Canary Islands, there has been a major radiation of *Dysdera* in this archipelago, which contributes unique functionalities that are scarcely present in continental Europe—with the notable exception of the Dinaric karst, where other genera of Dysderidae are highly diversified (Platania et al. 2020; Adrián-Serrano et al. 2024).

Third, it is also important to note that our analysis compares the pool of species of Macaronesia and continental Europe, which may be somewhat artificial from a biogeographic standpoint. While continental Europe (and in particular the Iberian Peninsula) is likely the most appropriate reference pool for the Azores and Madeira—the biogeographical context is more complex for the Canary Islands (see, e.g., Martínez et al., 2022). Although the Iberian Peninsula seems to be the most likely source of forest fauna, both due to patterns of wind dispersal colonization (Juan et al., 2000) and the presence of paleo-islands until the end of the last glacial maximum (Fernández-Palacios et al., 2011), alternative routes of colonization cannot be ruled out for lowland dry areas. Some species from the Canary Islands may, in fact, be more closely related to North African fauna, particularly that of Morocco (e.g., Emerson et al., 2000; Carranza et al., 2002; Bidegaray-Batista et al., 2007; Opatova & Arnedo, 2014). However, the current scarcity of data on subterranean spiders from this region limits further analysis—an issue that could be addressed as soon as new data becomes available.

Outlook

We provide an updated account of spider species diversity in subterranean ecosystems across Europe, with a particular emphasis on expanding knowledge from major oceanic islands. In addition, we present species-level trait data for all recorded species—an important resource for advancing research in ecology, evolution, and conservation. Despite these advances, our current understanding remains incomplete, especially in Macaronesia. Several species are still under description or have not been discovered yet, especially for the islands/archipelagos where less sampling has been performed. In the future, both cryptic and conspicuous diversity are likely to be uncovered—especially in poorly studied habitats such as the MSS. Importantly, subterranean habitats on the Macaronesian archipelagos face similar threats to those on the mainland, including forest conversion to pasture in the Azores, damage from tourism and uncontrolled cave visits in Madeira, and sewage pollution in caves of the Canary Islands (O romí, 2004; Borges et al., 2012; Macías-Hernández et al., 2024). Additionally, broader drivers such as climate change, urban expansion, infrastructure development, agricultural runoff, and non-native species introductions further exacerbate the pressures on these subterranean ecosystems, highlighting the urgent need for effective management, long-term monitoring, and enforcement of conservation regulations (Borges et al., 2012). Improved knowledge of species distributions is essential to guide extinction risk assessments and to prioritize conservation efforts. These efforts are further strengthened by the availability of comprehensive species trait datasets (Gallagher et al., 2021).

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Data and code availability

The trait database is available in Figshare (https://doi.org/10.6084/m9.figshare.16574255) as a tab-delimited file (.csv) and in Excel format (.xlsx). We also deposited traits in the Spider Traits Database (https://spidertraits.sci.muni.cz/; Pekar et al., 2021). R code to reproduce the analysis is available on GitHub (https://github.com/StefanoMammola/Cave_Spider_Macaronesia).

Figures

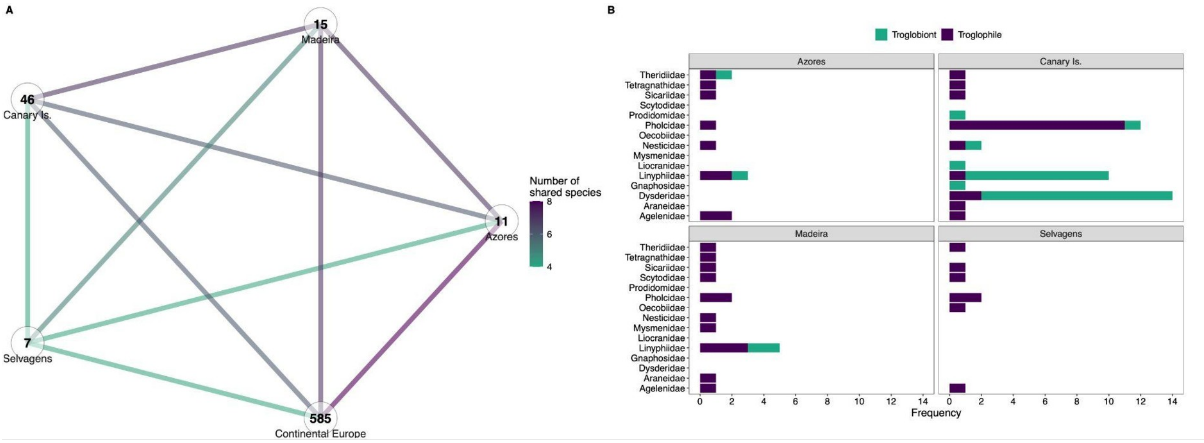

Figure 1. Macaronesian subterranean spiders by numbers. a) Network diagram showing the number of shared species among Macaronesian islands and between the islands and continental Europe. The number inside each dot represents the total number of species on each island and in continental Europe. **b**) Breakdown of species numbers by archipelago and spider family.

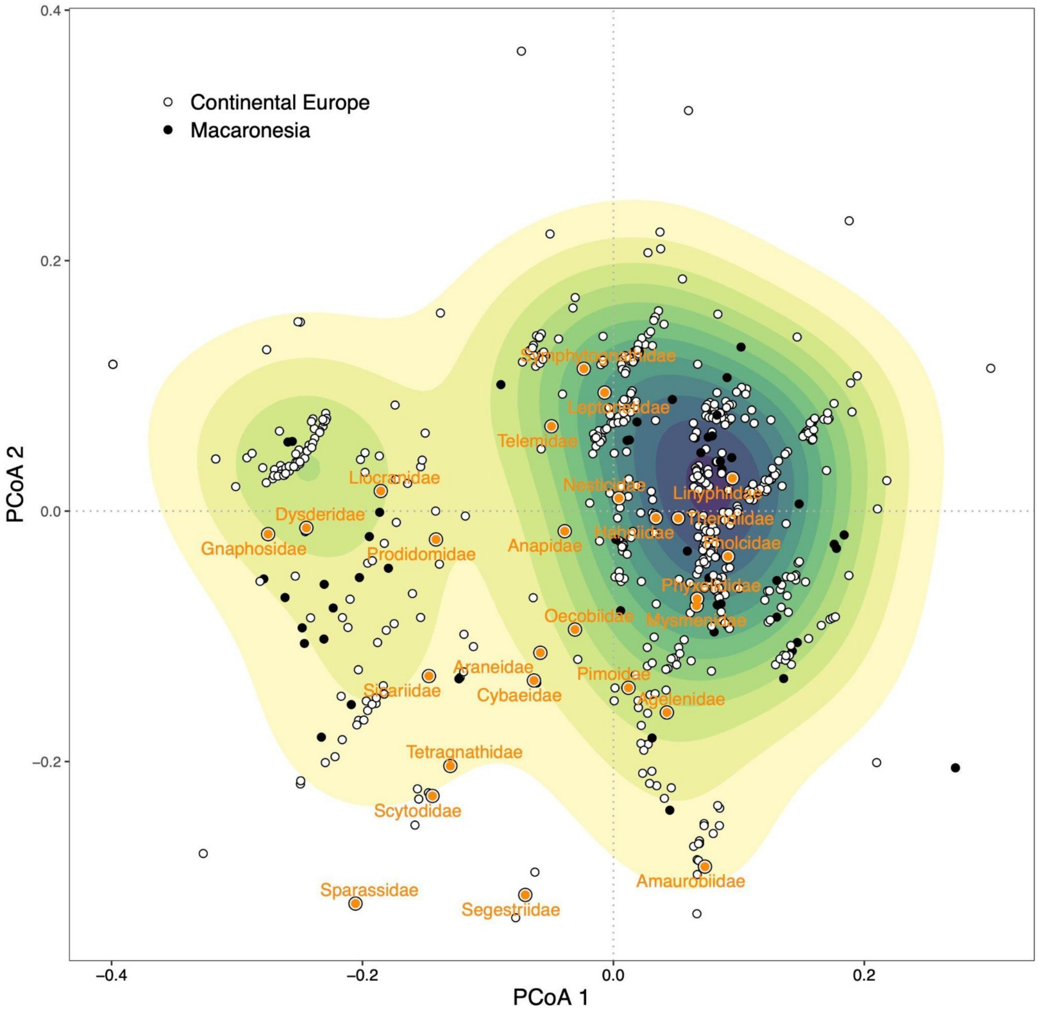

Figure 2. Trait space representation for Macaronesian subterranean spiders. The plot is based on the first two axes of a principal coordinate analysis (PCoA 1 & 2) describing the trait similarity among species. Small black and white dots are individual species, and large orange dots are the centroids for each family. Colour gradient reflects the density of species (higher density in darker areas) and, in turn, highly represented trait combinations.

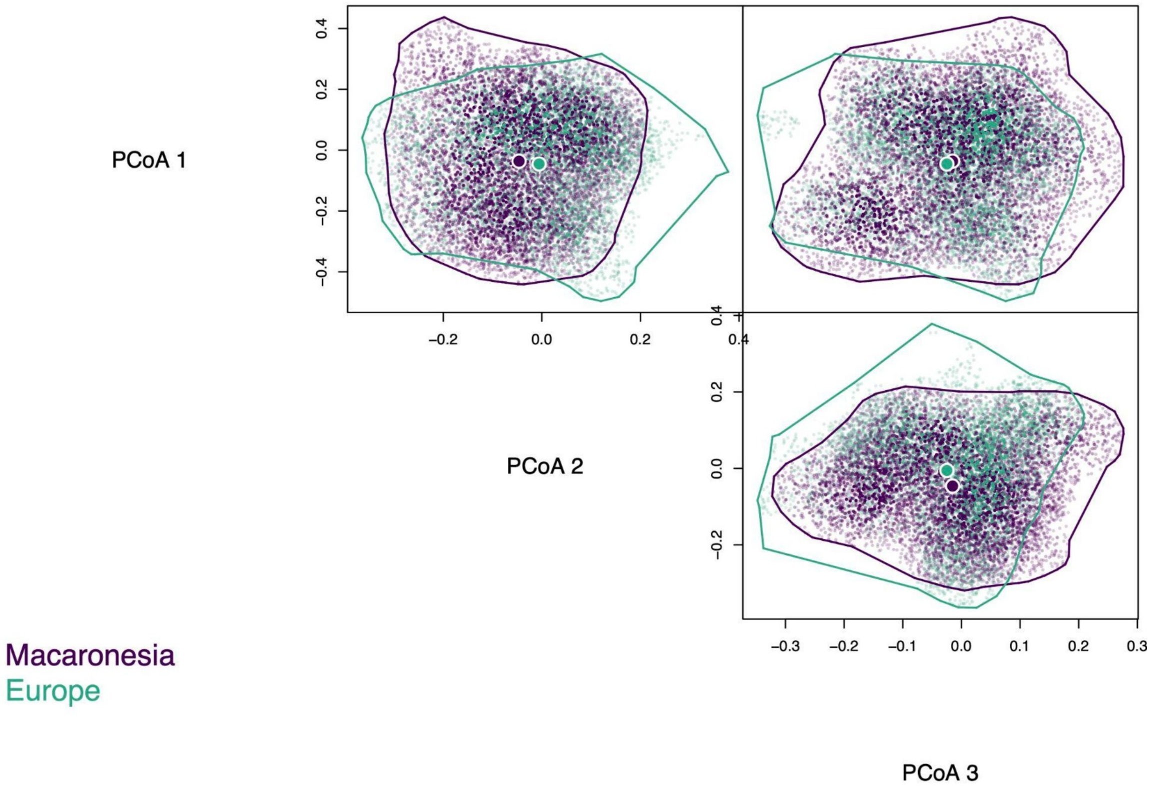

Figure 3. A comparison of the functional space of subterranean spiders in continental Europe versus Macaronesia. For each pair plot, 6000 random points sampled from the estimated 3-dimensional kernel density hypervolumes are shown, and represent the real boundaries of the two hypervolumes. Contour lines are drawn only for visual presentation, using the “alphahull” method. Larger dots represent hypervolume centroids. PCoA refers to the axes extracted from the principal coordinate analysis (Figure 2).