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Darwin's Naturalization Conundrum in the Azores: Scale-Dependent Patterns of Arthropod Invasion

Guilherme Oyarzabal¹  | Pedro Cardoso^{2,3}  | François Rigal^{1,4}  | Mário Boeiro^{2,5,6}  | Ana M. C. Santos^{1,7,8}  | Isabel R. Amorim^{5,6}  | Jagoba Malumbres-Olarte^{1,3}  | Ricardo Costa^{1,3}  | Sébastien Lhoumeau¹  | Gábor Pozsgai¹  | Rosalina Gabriel¹  | Paulo A. V. Borges^{1,6,9} 

¹University of the Azores, CE3C—Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity Group & CHANGE—Global Change and Sustainability Institute, School of Agricultural and Environmental Sciences, Angra do Heroísmo, Azores, Portugal | ²CE3C—Centre for Ecology, Evolution and Environmental Changes, CHANGE—Global Change and Sustainability Institute, Faculty of Sciences, University of Lisbon, Lisbon, Portugal | ³LIBRe—Laboratory for Integrative Biodiversity Research, Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland | ⁴Institut Des Sciences Analytiques et de Physico Chimie pour L'environnement et les Matériaux UMR5254, Comité National de la Recherche Scientifique -, University of Pau et des Pays de l'Adour, Pau, France | ⁵University of the Azores, CE3C—Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity Group & CHANGE—Global Change and Sustainability Institute, Angra do Heroísmo, Azores, Portugal | ⁶IUCN SSC Atlantic Islands Invertebrates Specialist Group, Angra do Heroísmo, Azores, Portugal | ⁷Terrestrial Ecology Group (TEG-UAM), Departamento de Ecología, Universidad Autónoma de Madrid, Madrid, Spain | ⁸Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, Madrid, Spain | ⁹IUCN SSC Species Monitoring Specialist Group, Angra do Heroísmo, Azores, Portugal

Correspondence: Guilherme Oyarzabal (guilhermeoyarzabal@gmail.com)

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ABSTRACT

Aim: To test the mechanisms governing the assembly of exotic arthropods within endemic-rich island communities by evaluating Darwin's naturalization conundrum, which predicts that invasion success occurs through either functional dissimilarity from native species (Naturalization Hypothesis) or functional similarity with them (Pre-adaptation Hypothesis).

Location: Azores archipelago, Portugal, North Atlantic Ocean.

Methods: We analysed long-term spatial and temporal data from two standardized monitoring programmes in Azorean native forests: the BALA project (spatial dataset) and the SLAM project (temporal dataset). The dataset included more than 100 species of spiders and beetles sampled across multiple islands over two decades. Using functional trait approaches, we quantified exotic–endemic community structure across spatial and temporal scales and compared observed patterns with null expectations to assess functional similarity or dissimilarity.

Results: Across both datasets, most Standard Effect Sizes (SES) values clustered around zero, indicating that exotic assemblages were largely indistinguishable from null expectations relative to endemic communities. This neutral pattern was consistent for exotic spiders across all spatial and temporal scales, providing no support for either Darwinian hypothesis. Exotic beetles, however, showed weak but detectable functional overdispersion at broader spatial scales and through time, suggesting limited and context-dependent support for the Naturalization Hypothesis. Overall, the pattern found is consistent with stochastic processes that appear to dominate exotic–endemic functional relationships, although this cannot be demonstrated directly from SES values alone.

Main Conclusions: Our results suggest that deterministic competition plays a minor role in structuring exotic arthropod assemblages in Azorean native forests. Instead, landscape-level processes, particularly the pressure from surrounding anthropogenic habitats and environmental filtering linked to forest fragmentation, likely shape invasion dynamics. These findings highlight

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1 | Introduction

Human activities are accelerating the transport, introduction, establishment, and spread of exotic species worldwide (exotic as a broad term for an introduced, alien, non-indigenous, or non-native species living outside its original distributional range (Pergl and Pyšek 2020)), reshaping community assemblages across terrestrial, freshwater, and marine ecosystems (Blackburn et al. 2011; Dafforn 2025; Luo et al. 2021; McGeoch et al. 2010; Rivera-Estay et al. 2024). Oceans and mountain ranges should act as major dispersal barriers for many taxa, however human transport increasingly bypasses these constraints (Dafforn 2025; Laiolo et al. 2023; Suárez et al. 2022). Indeed, purposefully or not, a global trade under a profit-driven economy has led to the rapid transportation of organisms across continents and oceans, accelerating species movements far beyond natural rates (Dafforn 2025; He et al. 2024; Marino et al. 2024; Rivera-Estay et al. 2024). In turn, exotic species introductions can change native interaction networks (e.g., competition, predation, parasitism, mutualism) and may increase pathogen transmission, shifting ecosystem functioning and reduce ecosystem services (He et al. 2024; Marino et al. 2024; Rivera-Estay et al. 2024).

On islands of all sizes, native species are often highly vulnerable to the establishment of exotic species (Whittaker et al. 2017). Due to small populations, limited geographic ranges, along with long periods of isolation, insular communities are often considered less complex and diverse compared with their continental counterparts (Whittaker et al. 2017). Moreover, this vulnerability is frequently greater on small and remote islands (e.g., the Azores), where limited area and high edge-to-interior ratios further constrain native species (Fernández-Palacios et al. 2021; Gill et al. 2023; Russell and Kueffer 2019; Whittaker et al. 2017). For instance, invasive predators (e.g., cats, rats), herbivores (e.g., goats, European rabbits), and plants (e.g., Australian boxwood, kahili ginger) frequently displace, outcompete, directly eliminate or cause cascading effects that endanger native fauna and flora, while the absence of natural predators, parasites or other antagonists, allows exotic species to proliferate unchecked (Gill et al. 2023; Gizicki et al. 2018; Gómez-Alceste and Rando 2024; Kueffer et al. 2010).

Among exotic taxa on islands, arthropods may often drive the loss of native species diversity and ecosystem processes (Ferrante et al. 2023; Kehoe et al. 2020; Oyarzabal et al. 2024). The success of exotic arthropods on islands is linked to the presence of biological and functional traits that promote the dispersal and/or establishment of these species in new environments (Oyarzabal et al. 2024; Rigal et al. 2018). Indeed, functional traits provide an understanding of species' ecological strategies, which reflect their adaptations, interactions, and impact within communities (Cadotte et al. 2011; Violle et al. 2007). Thus, distinct functional traits of exotic species may confer competitive advantages (Oyarzabal et al. 2024; Rigal et al. 2018), while native species may lack the behavioural and life-history traits needed to cope with novel competitors, predators, and pathogens (Jezierski et al. 2024;

Wyatt et al. 2008). Anthropogenic activities, such as deforestation, habitat fragmentation, or urbanization, create invasion-prone conditions that favour exotic species, ultimately leading to their ecological dominance on island ecosystems (Oyarzabal et al. 2024; Suárez et al. 2022). For instance, the invasive green lynx spider (Oxyopidae, *Peucetia viridans* (Hentz, 1832)) in the Canary Islands competes with native arthropods while altering pollination networks, creating cascading effects that threaten endangered plant-pollinator mutualisms (Arango et al. 2012; Suárez et al. 2024). Also, the Argentine ant (Formicidae, *Linepithema humile* (Mayr, 1868)) exhibits supercolony-specific expansion patterns, disrupting nutrient cycling, outcompeting native arthropod species, and even preying upon seabird nestlings (Boeiro et al. 2018; Castro-Cobo et al. 2021). Moreover, in the Azores Archipelago, arthropod species are commonly classified and distinguished as endemic (restricted to the archipelago), native non-endemic (naturally occurring but also present elsewhere), or exotic (introduced through human-mediated dispersal) (see Methods and Borges et al. 2006; Borges, Lamelas-Lopez, et al. 2022; Borges, Lamelas-López, et al. 2022; Borges and Wunderlich 2008; Oyarzabal et al. 2024). Because endemic species represent the most evolutionarily distinct and locally adapted component of the indigenous fauna, examining their functional relationships with exotic species provides a useful framework for understanding how recipient community characteristics influence invasion success.

In this way, one of the central questions in exotic species introduction is identifying the traits that allow certain species to successfully establish and spread as invaders. However, the success of an exotic species also depends on the characteristics of the native species present in the recipient community (Oyarzabal et al. 2024; Rigal et al. 2018). Based on an original observation of De Candolle (1855), Charles Darwin, in his book "On the Origin of Species", already questioned why some exotic species were more successful in becoming colonizers or invasive (Darwin 1859). He proposed the Naturalization Hypothesis, which predicts that biotic filtering should regulate the invasion of a given exotic species, where those species phylogenetically and/or functionally distinct (not closely related) from native species are more likely to succeed in the new habitat, avoiding competition (Darwin 1859; Jiménez-García et al. 2023). Darwin also identified an alternative situation, known as the Pre-adaptation Hypothesis, which predicts an environmental filter, where invasions are only successful for those exotic species that are phylogenetically and/or functionally similar (closely related) to the native species, mainly due to their shared evolutionary history and hence the way they interact with and are influenced by the environment (Darwin 1859; Jiménez-García et al. 2023).

This apparent conceptual paradox for species invasion, known as Darwin's naturalization conundrum (Diez et al. 2008), has sparked extensive research and is usually dependent on the spatial and temporal scales at which it is examined (Arjona et al. 2025; Ma et al. 2016; Park et al. 2020). At small spatial scales, in which interactions between species are more common, the successful invaders would be more often functionally different from the

native community, supporting the Naturalization Hypothesis (Arjona et al. 2025; Cadotte et al. 2018; Jiménez-García et al. 2023; Thuiller et al. 2010). In contrast, at larger spatial scales, individuals and species distributions are mostly driven by environmental conditions, and so the Pre-adaptation Hypothesis would be supported (Arjona et al. 2025; Cadotte et al. 2018; Thuiller et al. 2010). When considering the time scale, there would be the opposite pattern, in which an initial or short-term interaction may favour functionally similar species, while a long-term interaction would favour functionally distinct species (Arjona et al. 2025; Cadotte et al. 2018; Jiménez-García et al. 2023; Thuiller et al. 2010). However, this more than 160-year-old puzzle remains unresolved, with studies producing mixed results, since the complexity stems from variations across scales, invasion stages, and ecological factors (Arjona et al. 2025; Cadotte et al. 2018; Jiménez-García et al. 2023; Thuiller et al. 2010).

In this context, island ecosystems and island arthropods may provide particularly valuable systems for disentangling the interplay between Darwin's Naturalization and Pre-adaptation Hypotheses in shaping the distribution of exotic species across spatial and temporal scales (Cadotte et al. 2018; Jiménez-García et al. 2023; Kusumoto et al. 2019; Marx et al. 2016). Dispersal filtering and founder effects constrain the pool of colonizing species, leading to taxonomic and functional disharmony that may increase vulnerability to exotic species introductions (Cadotte et al. 2018; Jiménez-García et al. 2023; Kusumoto et al. 2019; Marx et al. 2016). Furthermore, the severe anthropogenic pressures that characterize many island systems have affected fragile native communities and intensify invasion pressure, making it particularly urgent to improve predictions of introduction success in island environments (Russell and Kueffer 2019).

Building on evidence that land-use change and intensification restructures Azorean arthropod functional trait composition and can create opportunities for exotic taxa (Rigal et al. 2018), we tested two non-mutually exclusive mechanisms commonly invoked to resolve Darwin's naturalization conundrum using trait-based distances. H1—Naturalization (limited similarity): at fine spatial grains and during early establishment, co-occurring exotic species should be functionally more dissimilar from local endemic assemblages than expected, consistent with stronger competitive constraints among functionally similar species. H2—Pre-adaptation (environmental filtering): exotics will be functionally similar to endemic species where abiotic filters dominate (e.g., in harsh or disturbed habitats) or at broader spatial/longer temporal scales, reflecting trait matching to local conditions. We therefore predict scale-dependence: stronger support for H1 in fine-grain, short-term community snapshots, and increasing support for H2 across coarser grains and longer times as filtering and assembly processes accumulate.

2 | Methods

2.1 | Study Location

We conducted this study in the Azores archipelago, which consists of nine main volcanic islands, situated in the northern Atlantic Ocean, approximately between 37° and 40° N and from 24° to 31° W, extending roughly 615 km from west to east (Figure 1).

The archipelago is clustered into three island groups: the western group composed of Corvo and Flores Islands, the central group composed of Faial, Pico, São Jorge, Graciosa, and Terceira Islands, and the eastern group composed of São Miguel and Santa Maria Islands (Figure 1). The climate across the archipelago is temperate oceanic, with high relative atmospheric humidity that often reaches 95% in the native semi-tropical evergreen laurel forests (Borges, Lamelas-Lopez, et al. 2022; Borges, Lamelas-López, et al. 2022; Elias et al. 2016). Since human settlement began in the 15th century, the Azorean landscape has been profoundly transformed, with much of the original native habitat replaced by urban development, exotic tree plantations, and agricultural and pastoral land (Gaspar et al. 2008; Norder et al. 2020). As a result, the original native forest now covers only about 3% of the archipelago's total land area, mostly restricted to remote areas that are difficult to access by humans (Elias et al. 2016; Gaspar et al. 2008; Lhoumeau et al. 2025; Triantis et al. 2010).

2.2 | Data Sampling

We sampled arthropod species through two standardized and long-term monitoring projects in the Azores: (1) the Biodiversity of Arthropods from the Laurisilva of the Azores (BALA project), spanning from 1997 to 2022 (Borges et al. 2006, 2016; Pozsgai et al. 2024); and (2) the Long-Term Ecological Study of the Impacts of Climate Change in the Natural Forest of Azores (SLAM project), running from 2012 to 2025 (Borges, Rigal, et al. 2020; Borges, Lamelas-Lopez, et al. 2022; Borges, Lamelas-López, et al. 2022; Borges 2025; Costa and Borges 2021; Lhoumeau and Borges 2023).

We carried out the BALA project in three phases: BALA I (1997–2004), BALA II (2010–2011), and BALA III (2019–2022). We collected arthropods from low-disturbance native forest fragments across the Azorean archipelago on seven islands, with Corvo and Graciosa excluded due to the absence of native forest patches. Sampling methods included pitfall traps for ground-dwelling arthropods and canopy beating for canopy-dwelling arthropods (up to 3–4 m in height). All our sampling took place during the boreal summer, from June to September. All the data of this project are publicly available (Pozsgai et al. 2024) and further methodological details are available in previous publications (Borges et al. 2006, 2010; Gaspar et al. 2008; Pozsgai et al. 2024; Ribeiro et al. 2005).

For the SLAM project, we collected the data seasonally (every 3 months) from 2012 to 2025 (Borges 2025). Sampling was conducted in ten plots located in Terceira Island and eight plots located in Pico Island, within some of the best-preserved native forest fragments in the Azores with minimal human disturbance. We sampled arthropods using passive flight interception SLAM traps (Sea, Land, and Air Malaise Trap) (Borges, Rigal, et al. 2020; Borges, Lamelas-Lopez, et al. 2022; Borges, Lamelas-López, et al. 2022; Borges 2025; Costa and Borges 2021; Lhoumeau and Borges 2023). Additional methodological details can also be found in the referenced studies (Borges, Rigal, et al. 2020; Borges, Lamelas-Lopez, et al. 2022; Borges, Lamelas-López, et al. 2022; Borges 2025; Costa and Borges 2021; Lhoumeau and Borges 2023). It is important to note that, due to variable sampling durations, all sampling events shorter than 70 days or longer than 110 days were discarded, and remaining abundances were normalized to

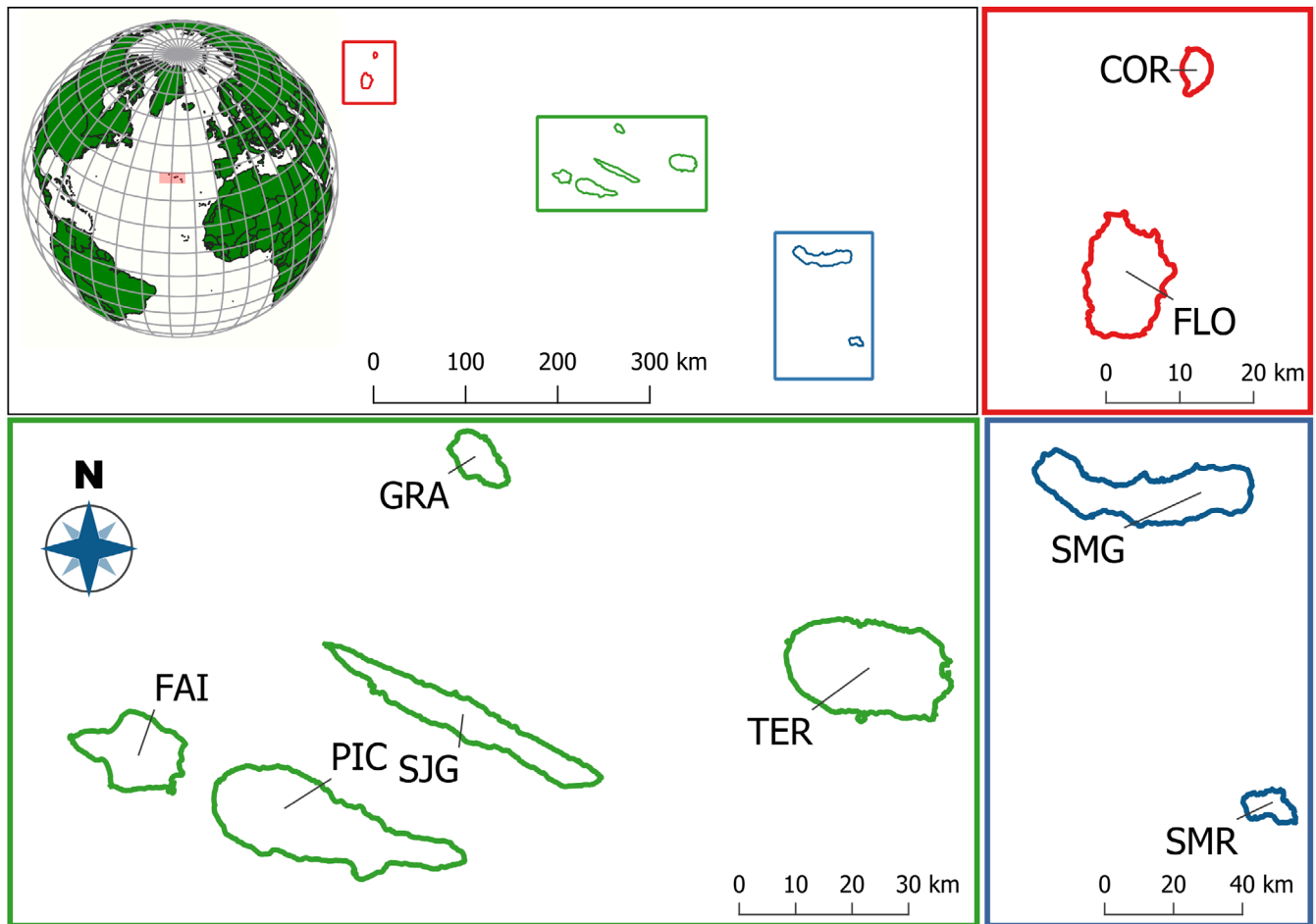


FIGURE 1 | Map of the Azores archipelago. Top left shows the position of the three island groups: Western group—red for Corvo (COR) and Flores (FLO); Central group—green for Faial (FAI), Pico (PIC), São Jorge (SJG), Graciosa (GRA), and Terceira (TER); and Eastern group—blue for São Miguel (SMG) and Santa Maria (SMR). Adapted from Oyarzabal, Pozsgai, et al. (2025).

90 days, resulting in decimal values for SLAM species abundance (see this method description in Lhoumeau and Borges 2023 and in the Supporting Information 1).

2.3 | Species and Traits Data Compilation

We identified arthropods to species level, with nomenclature adhering to the most recent checklist of Azorean arthropods (Borges, Lamelas-Lopez, et al. 2022; Borges, Lamelas-López, et al. 2022). Due to their higher abundance and availability of trait data, only spiders (Araneae) and beetles (Coleoptera) were used in this analysis.

All spider and beetle species were categorized into biogeographic origin groups following the Azorean arthropod checklist (Borges, Lamelas-Lopez, et al. 2022; Borges, Lamelas-López, et al. 2022). In the Azores, the indigenous species pool comprises two distinct categories: endemic species and native non-endemic species (Oyarzabal et al. 2024). Endemic species are those exclusively found in the Azores, representing the deepest evolutionary integration with local ecosystems, the longest residence times, and the strongest local adaptations. Native non-endemic species also occur naturally in neighbouring Macaronesia archipelagos (Cape Verde,

Canary Islands and Madeira) and/or in the Mediterranean basin, having most likely reached the Azores through long-distance dispersal rather than human mediation. Exotic species are those believed to have been introduced to the Azores through human activities, including cosmopolitan species, invasive species, and species known to have arrived via anthropogenic vectors (Borges et al. 2006; Borges, Lamelas-Lopez, et al. 2022; Borges, Lamelas-López, et al. 2022; Borges and Wunderlich 2008; Oyarzabal et al. 2024).

For the purposes of testing Darwin's naturalization conundrum, we deliberately compared exotic species exclusively against endemic species, excluding native non-endemics from the primary analysis. This decision was motivated by three endemic species factors: (i) their longer evolutionary history in the archipelago; (ii) stronger local adaptations; and (iii) a greater interest from a conservation and extinction risk (Oyarzabal, Boieiro, et al. 2025). These aspects provide the most stringent test of functional divergence or convergence between exotics and the indigenous biota. Including native non-endemics would conflate species with different colonization histories and dispersal abilities, potentially obscuring the signals of Darwin's hypotheses. Throughout this manuscript, references to "endemic" species refer strictly to Azorean endemics, and comparisons are made between exotics and endemics unless otherwise stated.

We selected different functional traits for spiders and beetles that would be relevant to explore Darwin's conundrum (Table 1). These traits reflect habitat occupancy and response to disturbance (e.g., body size), capacity for island colonization and establishment (e.g., dispersal ability) and characterize the nature of their interaction with other species (e.g., trophic group) (Chichorro, Correia, and Cardoso 2022; Gossner et al. 2015; Oyarzabal et al. 2024; Rigal et al. 2018; Simons et al. 2016). We obtained all these traits from either previous works performed in the Azores (Macías-Hernández et al. 2020; Rigal et al. 2018; Wallon et al. 2024), from data available at the Azorean Biodiversity Portal and the IUCN SSC Atlantic Islands Invertebrate Specialist Group Portal (ABP 2025; AIISG 2025), or from the personal knowledge of species' natural history by PAVB. Moreover, most of these traits were recently compiled in a complete database of Azorean arthropod traits (Oyarzabal et al. 2026). In the Supporting Information 1, species names are also designated by internal morphospecies codes (e.g., "mf102"). These codes serve as unique identifiers that link each species to its corresponding Linnaean binomial nomenclature, as well as to its respective functional trait values (Oyarzabal et al. 2026).

2.4 | Data Structuring

To comprehensively investigate different facets of functional diversity of spiders and beetles, we partitioned our data into two distinct datasets. Hereafter, the BALA project data (data from seven islands) will be referred to as the *Spatial dataset* and the SLAM project data (data from 14 years) will be referred to as the *Temporal dataset*. The Spatial dataset encompasses seven islands of the Azores archipelago, offering insights at a broader biogeographic scale, and the Temporal dataset focuses on the Azorean islands with the best-preserved native forests (Terceira and Pico Islands), allowing for an analysis on a fine temporal scale, within a relatively stable and intact ecosystem.

We structured the data to investigate the functional distances between groups of species within the Azorean functional space for both beetles and spiders. We compared functional distances for: (i) exotic spiders vs. endemic spiders (see the analyses below), and (ii) exotic beetles vs. endemic beetles. We also divided each dataset by different levels of complexity (Table 2). In this way, we could consider the importance of time within the Spatial dataset and the importance of space in the Temporal dataset. Functional data were used in its raw form, with no previous transformation before calculating interspecific distances (see below and in Supporting Information 1).

2.5 | Data Analyses

We performed all data management, statistical analyses, and visualization procedures presented here using the R programming environment (R Core Team 2025) (version 4.4.3). R scripts can be found in Supporting Information 2.

Functional distances for all pairs of spider species and all pairs of beetle species recorded in our dataset, (Spatial and Temporal datasets), were calculated using the Gower distances (Gower 1966), without incorporating any abundance-weighted

functional diversity indices. The Gower distance metric was chosen due to its ability to handle mixed types of data, like continuous and categorical traits, making it particularly suitable for our trait matrix, which included morphological (e.g., body size), ecological (e.g., verticality, dispersal ability), and trophic (e.g., diet composition) attributes. We obtained the Gower distance values using the "ade4" package (Dray and Dufour 2007).

To explore Darwin's conundrum for both spiders and beetles separately, we used two metrics to quantify pairwise functional distances between pairs of con-ordinal species of different origin, co-occurring at a given spatial and temporal scale. The first metric was the mean pairwise distance (MPD) that computes the arithmetic mean over the functional distance for all possible pairs of con-ordinal species belonging to different origins (exotics vs. endemics). The second metric estimates the mean nearest-neighbour distance (MND) by calculating the arithmetic mean of the minimum functional distance between con-ordinal species of a given origin with all the con-ordinal species of other origin (same exotics vs. endemics). We further tested whether MPD and MND values were lower or higher than expected by chance using null models. At each spatial and temporal scale, we implemented a label-randomization null model for MPD and MND, where species identities are randomly reassigned to exotic and endemic groups while preserving the general observed richness within spiders and beetles (Fridley et al. 2004).

We computed the Standard Effect Sizes (SES) for MPD/MND calculated at each spatial and temporal scale tested above, defined as the difference between the observed value and the null mean divided by the null standard deviation. For this obtained SES, we calculated two Monte Carlo *p*-values: *p* *upper* which is the probability of obtaining a null value greater than or equal to the observed ($SES \geq 2$ is an indicator of trait overdispersion and dissimilarity, supporting the Naturalization Hypothesis) and *p* *lower* which is the probability of obtaining a null value less than or equal to the observed ($SES \leq -2$ is an indicator of trait clustering and similarity, supporting the Pre-adaptation Hypothesis; Park et al. 2020, 2024). To prevent zero *p*-values, we performed 999 simulations and included the observed outcome to bring the total to 1000. If values of SES fall within -2 and $+2$, we consider a neutral assembly process with exotic species being randomly distant from endemics.

To evaluate whether assemblages exhibited an overall tendency toward functional clustering or overdispersion, we first tested whether the distribution of SES values significantly deviated from zero using a two-sided Wilcoxon signed-rank test. This non-parametric test assesses whether the median SES differs from the null expectation of zero, thereby detecting a general directional shift in functional distances across transects, islands, seasons, or years, independent of individual extreme values. A significant positive deviation indicates a community-wide tendency toward higher-than-expected functional distances, consistent with functional overdispersion and supporting the Naturalization Hypothesis, whereas a significant negative deviation indicates lower-than-expected distances, consistent with functional clustering and supporting the Pre-adaptation hypothesis. Only after establishing the presence or absence of such a global trend did we

TABLE 1 | Definition and general hypothesis of the traits of Azorean spider and beetle species included in the analysis of Darwin's conundrum (see also Oyarzabal et al. 2026).

Trait		Arthropod group		Definition and description of the trait	General trait hypothesis	References
Adult body size average	Numerical (mm)	Spiders and beetles		Mean body length of adults (males and females) in millimetres (mm). Spiders were measured from the closest point of the chelicera in the prosoma to the end of the abdomen (excluding abdomen appendages). Beetles were measured from the tip of their head to the end of the abdomen (excluding head and abdomen appendages)	Body size may mediate species' responses to environmental change and resource requirements. Large-body species may exhibit lower ecological flexibility than small-body species. Larger species may also have lower dispersal rates but greater competitive strength, consuming more resources. Smaller species may colonize microhabitats more readily	Chichorro, Correia, and Cardoso (2022); Chichorro, Urbano, et al. (2022); Oyarzabal et al. (2024), Purvis et al. (2000)
Average verticality	Numerical (0-1)	Spiders and beetles		Mean vertical stratum occupancy values (ranging from 0 to 1) describe how a species is distributed across vegetation heights from ground level (0) to the uppermost sampled layer, the canopy (1)	The vertical stratification of arthropod species may influence their response to environmental change. Canopy-dwellers can be buffered from ground-level habitat change, whereas ground-dwellers are more exposed to ground-level habitat change	Chichorro, Correia, and Cardoso (2022), Chichorro, Urbano, et al. (2022), Costa et al. (2023), Kehoe et al. (2020), Oyarzabal et al. (2024), Rocha-Ortega et al. (2019), Zhang et al. (2023)
Dispersal ability	Binary (0 = low; 1 = high)	Spiders and beetles		Summary of each species' dispersal ability based on its range and mode of movement. Species capable of ballooning or flying are classified as high dispersers (1), while those that disperse primarily by crawling are classified as low dispersers (0)	Species with high dispersal ability are likely less affected by habitat fragmentation and climate change than low-dispersing species. High-dispersal species better colonize isolated or disturbed habitats and track environmental change, a key factor on islands, also being able to move to another patch in case there is a high level of competition	Gossner et al. (2015), Kehoe et al. (2020), Oyarzabal et al. (2024), Rigal et al. (2018)
Trophic level	Nominal (three levels)	Beetles		Describes the primary diet of each species based on known food sources: (i) Carnivores – feed exclusively on animals; (ii) Herbivores—feed on algae, lichens, soft plant tissues, and/or woody plant parts; and (iii) Omnivores—consume more than one of the above food types or feed on detritus and/or excrement	Arthropod species at higher or more specialized trophic levels—such as strict carnivores—tend to be more sensitive to environmental changes and habitat disturbances than those at lower or more generalist trophic levels	Chichorro, Correia, and Cardoso (2022), Chichorro, Urbano, et al. (2022), Kehoe et al. (2020), Munstermann et al. (2021), Oyarzabal et al. (2024), Reuter et al. (2023)

(Continues)

TABLE 1 | (Continued)

Arthropod group			General trait hypothesis		References
Trait	Data type	Definition and description of the trait			
Iridescence	Binary (0 = absent, 1 = presence)	Express the carapace iridescence property (change of body colour depending on the angle of view or the angle of illumination) of a species	Beetles	Iridescence capacity may enhance survival or reproductive success by influencing visual signalling, camouflage, or predator avoidance. It can also indicate functional roles under island conditions (e.g., signalling in low-light habitats, thermoregulation)	Doucet and Meadows (2009), Seago et al. (2009), Wallon et al. (2024)
Body colour	Nominal (four levels)	Express the carapace colour of a species. Black; Blackish; Greyish; or Reddish-Brown	Beetles	Differences in carapace colour among beetle individuals may reflect adaptations to environmental conditions or selective pressures, such as temperature regulation, habitat type, or predation. Colour variation may reflect thermoregulatory needs and crypsis, influencing fitness across microclimates and substrates	Doucet and Meadows (2009), Seago et al. (2009), Wallon et al. (2024)
Prosoma size	Numerical (mm)	Express the length of the prosoma (cephalothorax). This body part contains key organs for locomotion and sensory processing. Its size reflects overall body robustness, strength, and potential metabolic rate	Spiders	Species with larger prosoma have greater predatory capacity and mobility, allowing them to capture larger prey or inhabit more structurally complex environments	Macías-Hernández et al. (2020)
Tibia I size	Numerical (mm)	Express the length of the first tibia (part of the front leg). It is often involved in prey detection, web handling, and locomotion. Its size can indicate sensory reach and mechanical strength	Spiders	Species with longer tibia I may be more efficient hunters or web manipulators, providing an advantage in prey capture or habitat exploration	Macías-Hernández et al. (2020)
Chelicerae fang size	Numerical (mm)	Express the length of the chelicerae fang. It is the main tool for prey capture and venom inoculation	Spiders	Species with larger chelicera fangs could subdue faster, larger or more resistant prey, offering a competitive advantage in habitats with diverse prey availability	Macías-Hernández et al. (2020)
Dispersal frequency	Nominal (three levels)	Express the dispersal frequency as (i) occasional, (ii) rare or (iii) frequent. It may reflect how often a species moves between habitats or patches of habitat	Spiders	Species with higher dispersal frequency are less affected by habitat fragmentation and are more capable of exploiting new or disturbed habitats due to higher gene flow, colonization ability, and resilience to environmental change	Gossner et al. (2015), Kehoe et al. (2020), Oyarzabal et al. (2024), Rigal et al. (2018)

(Continues)

TABLE 1 | (Continued)

Arthropod group			General trait hypothesis	References
Trait	Data type	Definition and description of the trait		
Diel activity	Numerical (0–1)	Describes the time of day when a species is most active, ranging from 0 to 1. Exclusive diurnal species were classified as 0 and exclusive nocturnal species are classified as 1	Diel activity influences how individuals interact with their environment. Compared to strictly nocturnal species, those with strictly diurnal activity may be more vulnerable to environmental impacts due to greater exposure to extreme temperatures and a higher likelihood of encountering predators	Ockendon et al. (2014), Rigal et al. (2018), Wallon et al. (2024)
Type of capture web	Binary (0/1)	Express whether the species uses the web to capture prey. This may influence prey type, capture success, and microhabitat use	Different prey capture strategies confer functional advantages depending on habitat structure—for example, orb webs are favoured in open, aerial spaces, while active hunting are advantageous in the ground layers	Macías-Hernández et al. (2020)

further dissect the pattern by quantifying the number and proportion of individual transects exhibiting extreme SES values ($SES \geq 2$ or $SES \leq -2$). Finally, we performed a Linear Model (LM) to check the effect of the passage of time (years of sampling) on the obtained MPD SES and MND SES for spiders and beetles.

It is important to note that to evaluate the sampled transects (Spatial Model 2, Temporal Model 2, see above), we needed at least the presence of one exotic and one endemic species. Therefore, we could not obtain the SES values for all transects since some of them were composed of only exotic or only endemic species (see Results).

3 | Results

3.1 | Data Overview

Our dataset included information on a total of 108 species in the Spatial dataset (BALA project) and 130 species in the Temporal dataset (SLAM project). The Spatial dataset was composed of 39 spider species (Araneae, 15 endemic and 24 exotic) and 69 beetle species (Coleoptera, 11 endemic and 58 exotic). The Temporal dataset was composed of 47 spider species (Araneae, 15 endemic and 32 exotic) and 83 beetle species (Coleoptera, 11 endemic and 72 exotic).

3.2 | Spatial Scale Approach to Darwin's Conundrum

Looking into the differences in spiders' functional diversity across the Azores, exotic spider species showed a neutral assembly, being neither more distant nor closer to endemic species than expected by chance ($SES \approx 0$, not > 2 nor < -2 , Figure 2A). Hence, we did not find any support for Naturalization or Pre-adaptation of exotic spider species when comparing them with endemic spiders.

For the beetles' functional diversity across the Azores, exotic beetle species showed a neutral assembly in most of our analysis, only being significant for overdispersion/dissimilarity between exotics and endemics on BALA II (MPD, $SES = 2.22$, $p = 0.026$; MND, $SES = 2.89$, $p < 0.01$, Figure 2B). Moreover, although showing a significant difference, the values on BALA ALL (MND, $SES = 1.95$, $p = 0.038$) and on BALA III (MND, $SES = 1.85$, $p = 0.038$) did not show a $SES > 2$. This indicates that exotic beetles are neither more distant nor closer to endemic beetles than expected by chance. In this way, we found support for the Naturalization Hypothesis for exotic beetles in only one of our cases explored with the spatial data (Figure 2B).

In the fine spatial scale, based on the analyses of MPD and MND SES values across all transects (BALA All, BALA I, BALA II, and BALA III), our results reveal a predominantly neutral assembly pattern for both exotic spiders and beetles at the fine spatial scale. Most SES values clustered around zero, indicating that exotic species are neither functionally distant nor similar to endemic species beyond random expectation, with a limited number of transects exhibiting extreme SES deviations.

TABLE 2 | Description of the models used to explore Darwin's conundrum. Data were divided into two datasets, Spatial (BALA project data) and Temporal (SLAM project data). Within each dataset, we explored the functional distance between exotic species and endemic species of spiders and beetles.

Dataset model	Scale and variables	Description
Spatial Model 1	Scale: Archipelago. Data partitioning: (i) All data on spiders and beetles (BALA ALL = BALA I, II and III); (ii) All data on spiders and beetles from 1997 to 2004 (BALA I); (iii) All data on spiders and beetles from 2010 to 2011 (BALA II); (iv) All data on spiders and beetles from 2019 to 2022 (BALA III)	Investigation of Darwin's conundrum looking into seven islands of the Azores archipelago through the BALA data. Here, we test the extent to which the archipelago's endemic, and exotic species pool are functionally over disperse/dissimilar over the 20 years of BALA and for each campaign (I, II, and III). We test one value of MND and MPD between species pools of different origin
Spatial Model 2	Scale: Archipelago transects. Data partitioning: (i) All data per transect and per island on spiders and beetles (BALA ALL = BALA I, II and III); (ii) All data per transect and per island on spiders and beetles from 1997 to 2004 (BALA I); (iii) All data per transect and per island on spiders and beetles from 2010 to 2011 (BALA II); (iv) All data per transect and per island on spiders and beetles from 2019 to 2022 (BALA III)	Investigation of Darwin's conundrum looking into each sampling site (transect) across seven Azorean islands sampled in the BALA project. Here, we test to which extent endemics and exotic species are functionally over disperse/dissimilar at local scale (transect level). Hence, we test a unique value of MND and MPD for each sampled transect in each island
Temporal Model 1	Scale: Islands. Data partitioning: (i) All data on spiders and beetles from Terceira and Pico Islands (SLAM ALL); (ii) All data on spiders and beetles from Terceira Island (SLAM Terceira); (iii) All data on spiders and beetles on Pico Island (SLAM Pico)	Investigation of Darwin's conundrum looking into the whole SLAM data, and into Terceira and Pico Islands data separately, from 2012 to 2025. Here we did not count for island particularities or species interactions within sampling sites, only test to which extent endemics and exotic species are functionally over disperse/dissimilar at a temporal scale. Hence, a unique value of MND and MPD was obtained for each variable
Temporal Model 2	Scale: Islands sampled sites. Data partitioning: (i) All data per sampling site on spiders and beetles from Terceira Island (SLAM Terceira); (ii) All data per sampling site on spiders and beetles from Pico Island (SLAM Pico)	Investigation of Darwin's conundrum looking into Terceira and Pico Islands separately, from 2012 to 2025 and for each sampling site. Here, we test to which extent endemic and exotic species are functionally over disperse/dissimilar at local scale (sampling site). Hence, we test a unique value of MND and MPD for each sampled site in each island

For spiders, from the 91 available transects, six transects showed MPD SES > 2, while only one transect had MND SES > 2, with no transects below -2 for either metric (Figure 3A and Figure 3B). The median MPD SES was approximately 0.19, with a Wilcoxon signed-rank test confirming a marginal departure from zero ($p = 0.055$). At the same time, the median MND SES was approximately 0.40, with the Wilcoxon test confirming a significant departure from zero ($p = 0.012$).

Similarly, for beetles, from the 90 available transects, 11 transects had MPD SES > 2 and four transects showed MND SES > 2, again with no values below -2 (Figures 3C and 3D). Despite the rarity of extreme deviations, the overall distribution of MPD SES values showed a consistent positive shift. This pattern was even more pronounced, with a median MPD SES of approximately 0.59 and with Wilcoxon signed-rank test confirming that this distribution was significantly greater than zero ($p < 0.001$).

At the same time, the median MND SES was approximately 0.78, with Wilcoxon test confirming that this distribution was significantly greater than zero ($p < 0.0001$). This indicates a marginal but consistent tendency toward functional overdispersion between exotic and endemic beetles.

Despite these results, we did not find a strong signal of Naturalization nor Pre-Adaptation of exotic spiders and exotic beetles within the fine spatial scale of BALA transects.

3.3 | Temporal Scale Approach to Darwin's Conundrum

Looking into the differences in spiders' functional diversity across time in the Azores, exotic spider species also showed a neutral assembly, being neither functionally distant nor closer

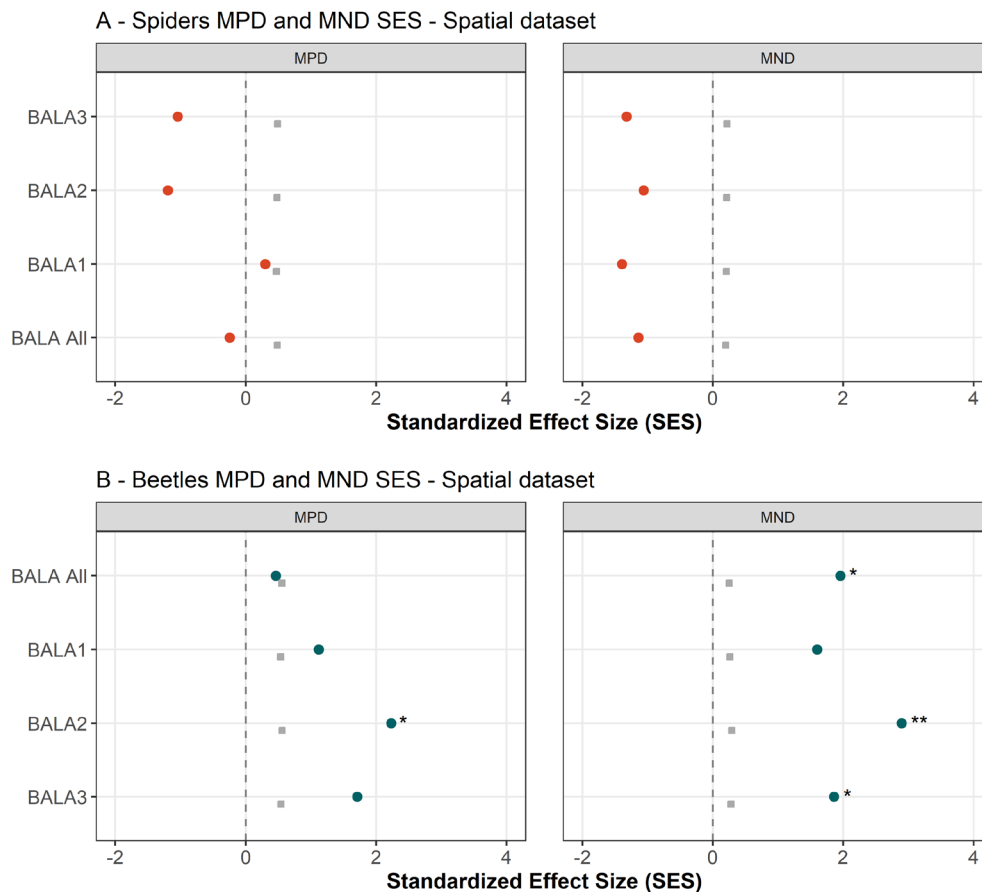


FIGURE 2 | Darwin's conundrum test of functional diversity similarity across the Azores using the Spatial dataset (BALA project) for (A) spider species and (B) beetle species. Coloured dots indicate the Standard Effect Sizes (SES) for spiders (orange) and beetles (green). Island-specific characteristics and species interactions within sampling transects were not considered; therefore, a single value of mean pairwise distance (MPD) and mean nearest-neighbour distance (MND) was obtained for each variable: BALA All—all data (1997–2022); BALA I—1997–2004 data; BALA II—2010–2011 data; and BALA III—2019–2022 data. Grey squares indicate the mean of the null models. Black stars indicate a significant difference between the null mean obtained and the SES of MPD or MND.

to endemic species than expected by chance ($SES \approx 0$, not > 2 nor < -2 , Figure 4A). Moreover, we did not find any positive or negative significant trend for MPD and MND SES through years (Figure 5A). Hence, we did not find any support for Naturalization or Pre-adaptation of exotic spider species when comparing them with endemic spiders.

For the beetles' functional diversity across time in the Azores, exotic beetle species showed a significant functional overdispersion/dissimilarity compared to endemics on SLAM All (MND, $SES = 2.08$, $p = 0.024$, Figure 3B), and in SLAM Terceira (MND, $SES = 2.35$, $p < 0.015$, Figure 4B). Pico island temporal data, though, showed neither values of $SES > 2$ nor $SES < -2$. Moreover, we did not find any positive or negative significant trend for MPD and MND SES through years (Figure 5B). In other words, we found support for the Naturalization Hypothesis for exotic beetles in the temporal data, mainly in Terceira island (Figures 4B and 5B).

In the fine scale, the functional assembly patterns of exotic spiders versus endemic spiders across the temporal sampling sites reveal a predominantly neutral assembly, with most MPD and MND SES values clustering near zero. Out of 120 sampling sites records analysed across the three temporal scales (SLAM All, SLAM Terceira, and SLAM Pico), only 10 sampling sites

exhibited MPD SES values > 2 , while no sampling sites showed SES values below < -2 . Similarly, for MND SES, only seven sampling sites exceeded the threshold of > 2 , with no values below < -2 (Figure 6A,B). Despite the rarity of extreme SES values, the overall distribution of MPD SES showed a weak but detectable positive shift, with a median SES of approximately 0.166. A Wilcoxon signed-rank test confirmed that this distribution was significantly greater than zero ($p < 0.001$), indicating a marginal but consistent tendency toward functional overdispersion across sampling sites. This pattern was mirrored, though more pronounced, in MND SES, where the median was 0.46 and the Wilcoxon signed-rank test confirmed that this distribution was significantly greater than zero ($p < 0.0001$; Figure 6A,B). Despite that, we find no strong support for either Naturalization or Pre-adaptation of exotic spiders.

When comparing exotic beetles with endemic beetles, the analysis of MPD and MND SES values across all sampling sites and temporal scales also reveals a predominantly neutral assembly pattern. Most SES values clustered around zero, indicating that exotic species are neither consistently functionally distant from nor similar to endemic species beyond random expectation. Only a limited number of sampling sites exhibited extreme SES deviations (> 2). For beetles, 20 sampling sites showed MPD SES

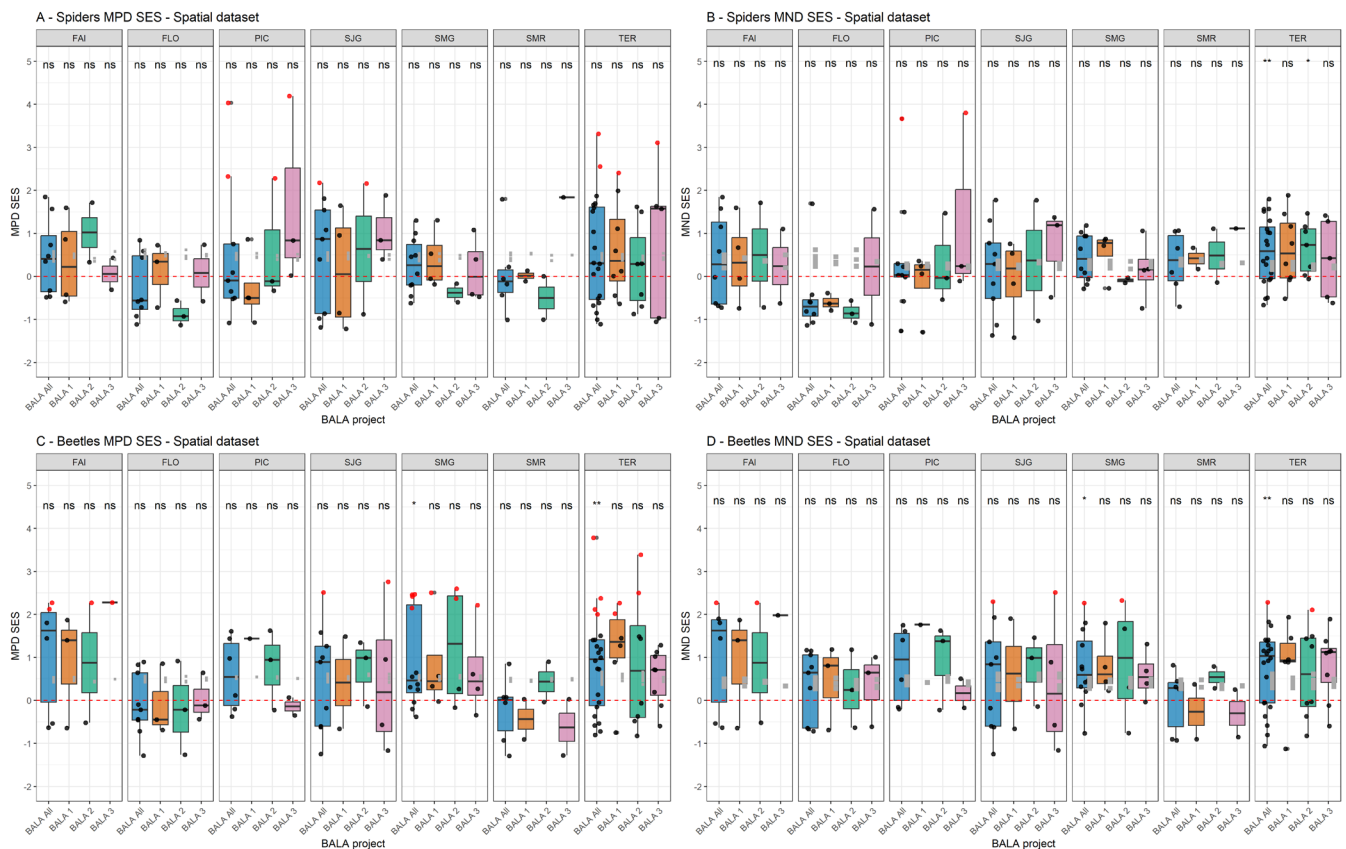


FIGURE 3 | Darwin's conundrum test of functional diversity similarity across each Azorean island using the Spatial dataset (BALA) for (A) spider species MPD, (B) spider species MND, (C) beetle species MPD species and (D) beetle species MND. Island-specific characteristics and species interactions within sampling sites were considered; therefore, a single value of mean pairwise distance (MPD) and mean nearest-neighbour distance (MND) was obtained in each sampled transect, in each island, for each variable: BALA All—all data, blue boxplot; BALA I—1997-2004 data, orange boxplot; BALA II—2010-2011 data, green boxplot; and BALA III—2019-2022 data, pink boxplot. Grey squares indicate the Standard Effect Sizes (SES) of the null models. Red dots indicate values of MPD or MND > 2. Black stars indicate a significant difference while “ns” indicate no significant difference between the null mean obtained and the SES of MPD or MND. Islands names are FAI, Faial; FLO, Flores; PIC, Pico; SJG, São Jorge; SMG, São Miguel; SMR, Santa Maria; TER, Terceira.

> 2, while 13 had an MND SES > 2 (Figure 6C,D). At the same time, no sampling sites showed values < -2 for either metric (Figure 6C,D). These extreme values were spatially scattered rather than concentrated in specific locations, suggesting localized rather than systematic assembly processes. Despite the rarity of extreme deviations, the overall distribution of MPD SES values showed a consistent positive shift. For beetles, the median MPD SES was approximately 0.43, with a Wilcoxon signed-rank test confirming a significant departure from zero ($p < 0.001$). At the same time, the median MND SES was approximately 0.59, but still showed a statistically significant positive shift ($p < 0.001$). This indicates a moderate but detectable tendency toward functional overdispersion/dissimilarity across beetle communities, which supports the Naturalization Hypothesis (Figure 6C,D).

4 | Discussion

Across Azorean spatial (BALA) and temporal (SLAM) data, encompassing over 100 spider and beetle species, exotic assemblages showed functional structure that was largely

indistinguishable from null expectations relative to endemic communities. Most Standard Effect Sizes (SES) values explored to test Darwin's naturalization conundrum clustered near zero across space and time windows, implying no consistent shift toward functional divergence (limiting similarity/Naturalization) or convergence (environmental filtering/Pre-adaptation). This neutrality, or even the lack of effects magnitude, was especially consistent in spiders, which provided little evidence for either mechanism across the scales considered. In contrast, beetles showed occasional, context-dependent functional overdispersion/dissimilarity, mainly at specific spatial and temporal scales, reflected in positive shifts in mean pairwise distance (MPD) SES. Although extreme deviations were rare and spatially scattered, the overall trend, particularly over time, provides limited support for the Naturalization Hypothesis. Overall, these findings indicate a lack of consistent deviation from null expectations, suggesting no detectable functional structuring between exotic and endemic assemblages. This pattern is consistent with, but does not directly demonstrate, the predominance of stochastic processes, with only weak and taxon-specific departures from neutrality.

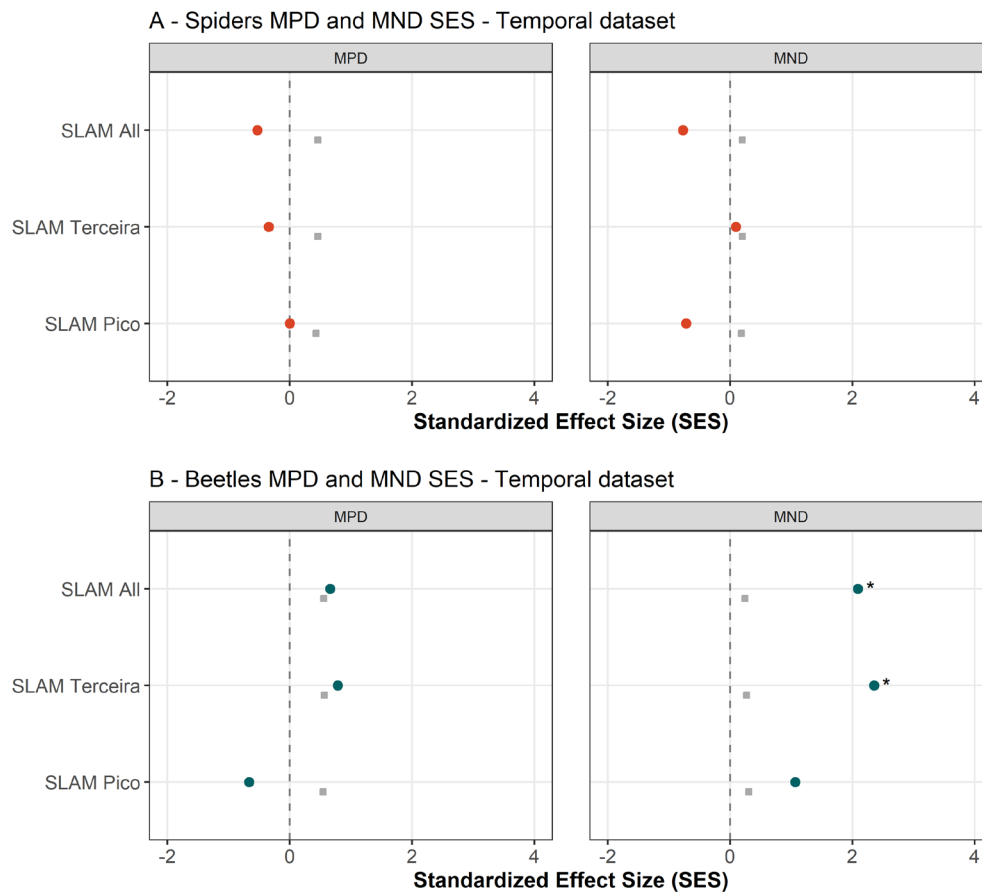


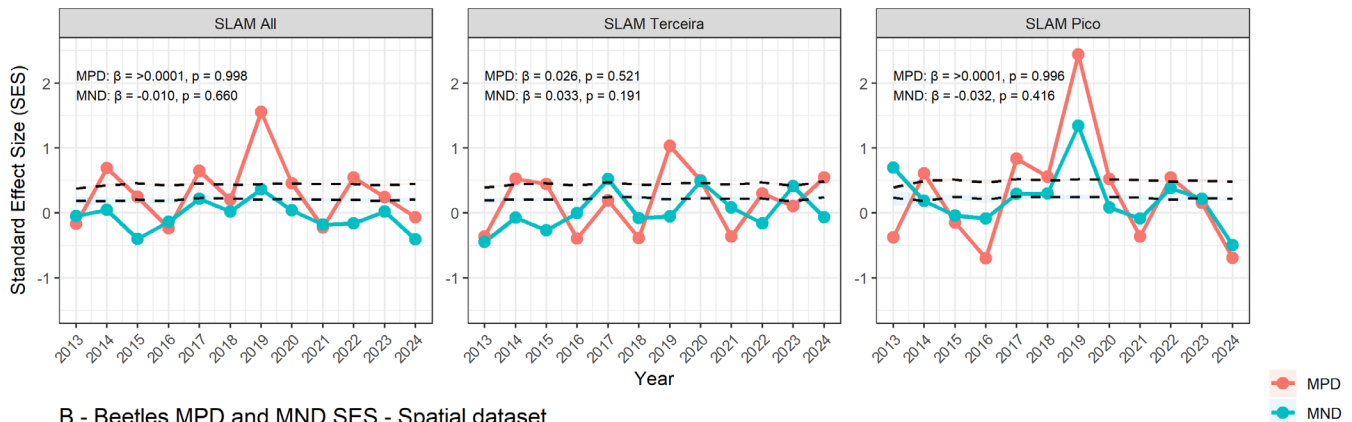
FIGURE 4 | Darwin's conundrum test of functional diversity similarity across the sampled years in Azores and, separately, Terceira and Pico Islands, using the Temporal dataset (SLAM project) for (A) spider species and (B) beetle species. Coloured dots indicate the Standard Effect Sizes (SES) for spiders (orange) and beetles (green). Island-specific characteristics and species interactions within sampling sites were not considered; therefore, a single value of mean pairwise distance (MPD) and mean nearest-neighbour distance (MND) was obtained for each variable through sampled years: SLAM All—all data from Terceira and Pico island; SLAM Terceira—only data from Terceira island; and SLAM Pico—only data from Pico island. Grey squares indicate the mean of the null models. Black stars indicate a significant difference between the null mean obtained and the SES of MPD or MND.

4.1 | Exotic Spiders' Invasion in the Azores Is a Conundrum by Itself: Transient Invaders or Established Residents?

Our study reveals interesting patterns for Azorean spiders, both at small and large spatial and temporal scales. The data indicate no clear deviation from null expectations, with no evidence supporting either hypothesis of Darwin's conundrum for the establishment of exotic spiders in the Azores. It rather indicates that functional assembly at the archipelago scale is largely neutral or stochastic, with limited and spatially sporadic signatures of over- or under-dispersion. These findings align with previous studies that showed an already well-established assemblage of exotic spiders in the Azorean native forest (Gaston et al. 2006; Lhoumeau et al. 2022; Lhoumeau and Borges 2023; Rigal et al. 2013), with likely viable and self-replacing population over multiple life cycles (Divíšek et al. 2025). For instance, cosmopolitan species like *Dysdera crocata* C. L. Koch, 1838 (Dysderidae) and *Ero furcata* (Villers, 1789) (Mimetidae) seem to maintain active populations throughout the years inside the native forest (Lhoumeau et al. 2022; Lhoumeau and Borges 2023).

Our results, though, were unable to clarify the main mechanisms driving the maintenance of these exotic spider populations in the Azores. In this way, it remains unclear how exotic spiders interact with Azorean endemic spiders. On the one hand, evidence for the Naturalization Hypothesis would indicate a functionally distinct exotic fauna, succeeding in habitats not explored by endemics (Darwin 1859; Jiménez-García et al. 2023). On the other hand, evidence for the Pre-adaptation Hypothesis would indicate a functional similarity, with a likely direct competition between exotics and endemics (Darwin 1859; Jiménez-García et al. 2023). As indicated by previous works on this subject (Cadotte et al. 2018; Kusumoto et al. 2019; Marx et al. 2016; Park et al. 2020), Darwin's hypotheses are not mutually exclusive, and thus our results may actually point to a combination of both mechanisms to explain our contemporaneous species assemblages. This pattern may result from partial functional redundancy, likely due to similar dispersal ability, habitat occupancy, and trophic interactions, likely occupying the same microhabitats, maintaining an established population in the native forest (Oyarzabal et al. 2024). However, this interpretation has to be taken cautiously, since inferring competition or interaction from functional trait patterns is challenging (Divíšek et al. 2025).

A - Spiders MPD and MND SES - Spatial dataset



B - Beetles MPD and MND SES - Spatial dataset

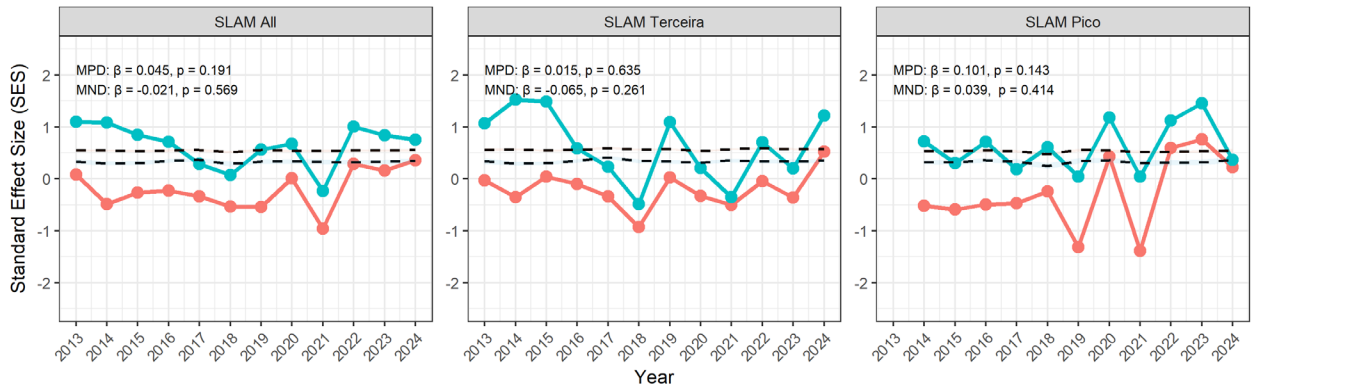


FIGURE 5 | Values of Standard Effect Sizes (SES) of the temporal dataset (SLAM project) obtained for the mean pairwise distance (MPD, orange line) and mean nearest-neighbour distance (MND, blue line) of (A) spider species and (B) beetle species. SLAM All—all data from Terceira and Pico Islands; SLAM Terceira—only data from Terceira Island; and SLAM Pico—only data from Pico Island. Dashed black lines are the values of null model. Orange shadow indicates the Standard Deviation of the MPD null model and blue shadow indicates the Standard Deviation of the MND null model. Note that the values presented in the SLAM All graph are the median values of both SLAM Terceira and SLAM Pico.

Furthermore, competitive interactions might also be masked by the temporal and local persistence of exotics as a result of a continuous flux between a source of exotic species (anthropogenic landscapes) and sink populations (native forest remnants) (Lhoumeau et al. 2022; Lhoumeau and Borges 2023; Oyarzabal et al. 2024). This makes the functional space of native forest colonizers more dependent on the presence/amount of surrounding anthropogenic habitats (Rigal et al. 2018), rather than on the species interactions occurring inside the native forest. Indeed, this process may be facilitated since all remnant native habitats in the Azores are embedded within a matrix of anthropogenic environments, which likely act as perpetual sources of exotic spider individuals (Borges et al. 2008; Elias et al. 2016; Gaspar et al. 2008; Triantis et al. 2010). Future experiments should be designed to better detect colonization dynamics of exotic spiders, which could differ between vagrant individuals and already established species. Such studies would also benefit from incorporating population genetic experiments to quantify dispersal pathways, gene flow, and the demographic connectivity between the likely source and sink populations. Moreover, incorporating juvenile stages, as they are the most likely life stage to disperse and colonize new areas, would therefore provide a more complete understanding of population turnover and establishment processes (Costa et al. 2025; Domènech et al. 2022; Niedobová et al. 2025).

4.2 | Exotic Beetles' Invasion in the Azores Is Dictated by Large Spatial and Time Scales

Across the Azorean archipelago and through time, exotic beetles were mildly but consistently functionally overdispersion/dissimilarity relative to endemics, supporting the Naturalization Hypothesis. Yet at finer spatial and temporal scales, most SES values clustered near zero and showed low magnitude, indicating no strong deviation from null expectations and broadly neutral assembly, with only a subtle shift toward greater exotic–endemic functional distinctness than expected by chance. Hence, our results point against the common expectation of the Naturalization Hypothesis, where overdispersion/dissimilarity is expected to be dominant at finer (local) scales, supported low functional similarity among co-occurring species (Cadotte et al. 2018; Jiménez-García et al. 2023; Park et al. 2020; Thuiller et al. 2010).

Given that most existing studies addressing Darwin's conundrum have focused on plants and vertebrates (Cadotte et al. 2018), with comparatively little empirical evidence from arthropods, our results on beetles gain even more relevance. Most evidence from island ecosystems, largely derived from plant studies, aligns with our findings, indicating that the Darwin's hypotheses are not mutually exclusive but instead depend on ecological context (Arjona et al. 2025; Kusumoto

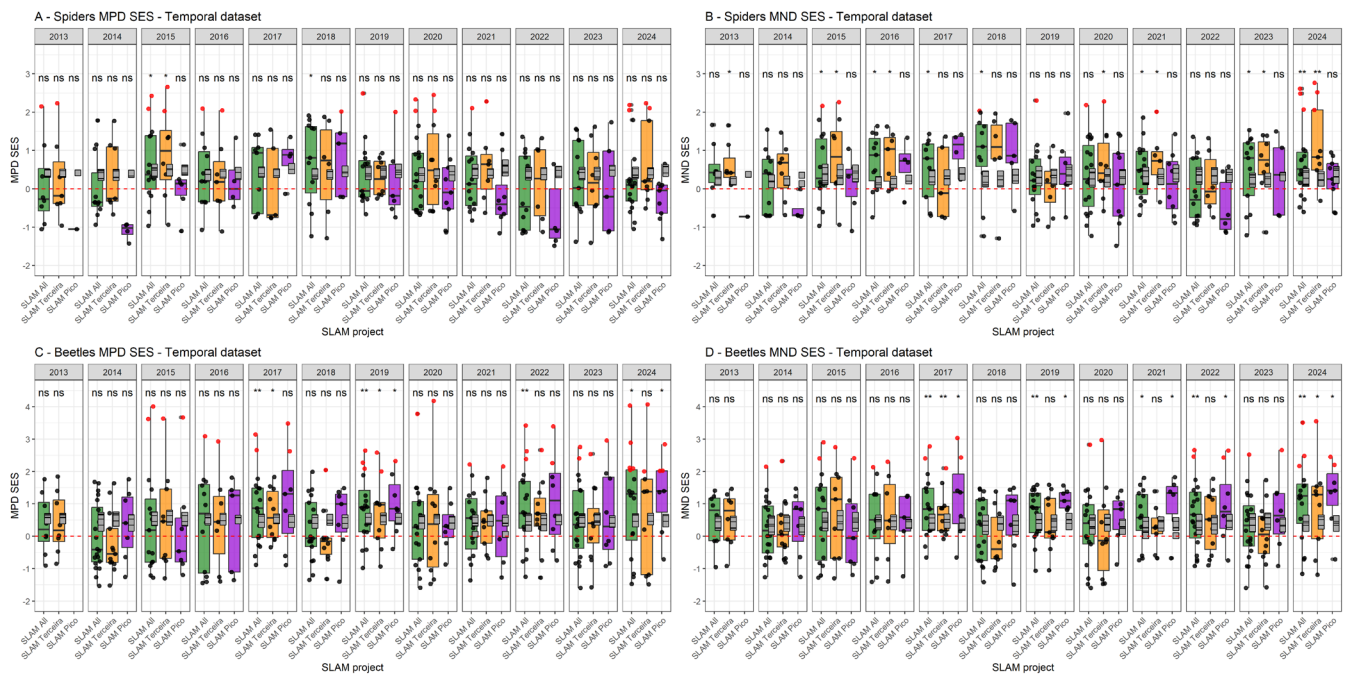


FIGURE 6 | Darwin's conundrum test of functional diversity similarity across the sampled years in Azores and, separately, Terceira and Pico Islands, using the Temporal dataset (SLAM) for (A) spider species MPD, (B) spider species MND, (C) beetle species MPD species and (D) beetle species MND. Island-specific characteristics and species interactions within sampling sites were not considered; therefore, a single value of mean pairwise distance (MPD) and mean nearest-neighbour distance (MND) was obtained in each sampled year and sampling sites, in each island, for: SLAM All—combination of Terceira and Pico Islands data, green boxplot; SLAM Terceira (TER)—only data from Terceira Island, orange boxplot; and SLAM Pico (PIC)—only data from Pico Island, pink boxplot. Grey squares indicate the Standard Effect Sizes (SES) of the Null models.

et al. 2019). For instance, although pre-adaptation, through functional similarity, may still play the dominant role shaping assemblages in the Canary islands, the Naturalization hypothesis for invasive plants is better explained by their functional adaptations to environmental conditions and phylogenetic distance to native species (Arjona et al. 2025). For exotic plants in Japan, Darwin's conundrum mechanisms appear complementary and context dependent, with Pre-adaptation prevailing under strong abiotic filtering and regional similarity while Naturalization prevailing where biotic differentiation and disturbance create niche opportunities (Kusumoto et al. 2019). In this way, our findings show a rather particular trend, where exotic beetles are likely avoiding competition, occupying different habitats at broad spatial and temporal scales, as suggested by other authors (Pozsgai et al. 2023), and not in a finer scale. One parsimonious explanation is demographic: exotic beetles in Azorean native forests often show lower densities and occupy fewer sites than indigenous taxa, which can weaken local interaction signals even when broader-scale distributions imply niche separation (Gaston et al. 2006). Similar to what we previously discussed for spiders, this scale dependence is consistent with a landscape process in which anthropogenic habitats supply repeated supply of immigrants (supporting broader-scale distinctness), while many exotics still struggle to maintain self-sustaining populations in the most pristine native-forest patches (Lhoumeau and Borges 2023).

Moreover, it is important to note that the drastic reduction and fragmentation of the Azorean native forest has not only diminished the available space for endemic beetles but may also have helped the invasion of exotic beetles (Borges et al. 2008;

Lhoumeau and Borges 2023; Oyarzabal et al. 2024). Especially ground-dwelling exotic beetles have been increasing in abundance in disturbed ecosystems that are favourable to their expansion (Oyarzabal et al. 2024). Recent evidence indicates that the archipelago is gradually being invaded and dominated by exotic species, particularly in anthropogenic habitats and degraded areas of native forest (Boeiro et al. 2025; Borges, Santos, et al. 2020; Lhoumeau and Borges 2023; Oyarzabal et al. 2024). Hence, exotic beetles appear to be occupying vacant habitats, either those that were abandoned by endemic species, unable to tolerate the microclimatic and structural changes in the soil caused by land-use disturbance, or those brand-new, created by invasive plants (Borges et al. 2006; Oyarzabal et al. 2024; Oyarzabal, Boeiro, et al. 2025; Oyarzabal, Pozsgai, et al. 2025; Queiroz et al. 2014; Ribeiro et al. 2005).

Within the context of Darwin's conundrum, our results indicate not only functional overdispersion/dissimilarity between exotic and endemic beetles at fine spatial and temporal scales, but also a potential environmental filtering effect driven by human disturbance, which could indirectly support a Pre-adaptation (Young et al. 2017). Exotic species, equipped with functional traits that favour tolerance to environmental impact, that are efficient dispersers, and have generalist diets, have been able to establish themselves in habitats never occupied by endemic species (Rigal et al. 2018). Thus, land-use change and human disturbance in general in the Azores may not only promote biotic homogenization and the decline of endemic functional diversity but also redefine the ecological structure of the archipelago, as suggested by other authors (Borges et al. 2006; Oyarzabal et al. 2024; Oyarzabal, Boeiro, et al. 2025; Oyarzabal, Pozsgai,

et al. 2025; Queiroz et al. 2014; Ribeiro et al. 2005). This favours the replacement of endemic species by exotics, a process emblematic of the evolutionary tension described by Darwin between adaptive coexistence and competitive exclusion, or rather, Naturalization and Pre-adaptation, respectively (Darwin 1859; Jiménez-García et al. 2023).

4.3 | Contrasting Functional Patterns Between Exotic Spiders and Beetles

Beyond the previously explored dynamics regarding Darwin's conundrum for spiders and beetles, the question remains as to why these two groups yielded such contrasting results. The primary difference is that exotic spiders seem fully established within the Azorean population, whereas exotic beetles appear to be occupying novel niches to avoid competition. Thus, in addition to the ecological aspects provided by trait-based analyses, one may further consider that this fundamental difference lies in the distinct ecosystem functions performed by spiders and beetles.

Spiders are strictly carnivorous animals, known to have experienced strong selective starvation during their evolution (Pekár et al. 2012; Zhang et al. 2025), which may have resulted in substantial intraguild predation and competitive exclusion when microhabitat niches overlap (Harwood and Obrycki 2005; Rickers et al. 2006; Sanders and Platner 2007). Furthermore, the island effect may have selected spider species with high dispersal capacity, which may also limit or simplify their functional diversity (Čandek et al. 2021; Whittaker et al. 2014). Intraguild competition would then drive trait convergence, leading to ecologically equivalent species and the observed neutral assembly (Edwards et al. 2018). However, both in the present study and elsewhere, this mechanism has been demonstrated theoretically rather than empirically for spiders, unfortunately (Edwards et al. 2018). In contrast, beetles are known to have broader diets, with many species exhibiting omnivorous feeding habits; even those that are strictly herbivorous or carnivorous as adults may vary their diet in different life stages and/or due to food availability (Al-Shareefi and Cotter 2019; Eubanks and Styrsky 2005). Consequently, intraguild feeding competition may be minimal, which could have favoured colonization. Moreover, exotic beetles disperse actively through walking or directed flight, which may filter colonizers non-randomly, generating weak functional overdispersion (Iversen et al. 2017; Rundle et al. 2002).

In summary, feeding ecology and dispersal ability may provide plausible and mutually compatible explanations for the contrasting functional patterns observed between exotic spiders and exotic beetles in the Azores. However, direct evidence linking trait composition to the observed contrast remains inconclusive. We acknowledge important limitations, including that functional traits are not directly comparable between spiders and beetles, that our observational design does not allow us to experimentally isolate mechanisms, and that historical factors, such as the previously explored anthropogenic pressure, may also contribute to the observed divergence (Oyarzabal et al. 2024). Future studies that quantify trophic niche overlap or movement ecology approaches to track dispersal pathways would help resolve these uncertainties and provide more direct tests of the mechanisms proposed here (Hock and Mumby 2015; Swanson et al. 2015).

4.4 | Strengthening Inference on Darwin's Naturalization Conundrum in Azorean Arthropods: Priorities for Future Work

Building on the strong multi-scale trait-based foundation provided here, several targeted additions in data, design, and inference can substantially sharpen mechanistic interpretation of exotic–endemic assembly in the Azores and other oceanic islands.

First, integrating phylogenetic/phylogenomic information alongside traits would help distinguish deep evolutionary divergence from recent functional convergence, improving how we interpret “similarity” and “dissimilarity” in the conundrum framework (Arjona et al. 2025; Li et al. 2015; Marx et al. 2016). Second, pairing community trait structure with demographic evidence (occupancy, density, recruitment) would directly test whether neutrality reflects weak interactions or whether it is masked by low abundance and limited occupancy of exotic taxa (Gaston et al. 2006). Third, explicitly quantifying anthropogenic pressure and landscape context would help test whether source–sink dynamics from surrounding human-modified habitats sustain exotic populations within native forest remnants, potentially weakening local interaction signatures (Waddell et al. 2020). In the Azorean context, such processes are likely intertwined with multiple island-level factors, including area, colonization history, land-use change, and current degrees of habitat fragmentation and urbanization (Borges and Hortal 2009; Castanho et al. 2021). While incorporating these dimensions could provide a more comprehensive understanding of invasion dynamics, disentangling their relative effects would require a more complex analytical framework. Fourth, future sampling that consistently includes juveniles and seasonal replication would better separate transient individuals from self-replacing populations and improve inference on establishment dynamics through time (Costa et al. 2025; Domènech et al. 2022; Niedobová et al. 2025). Finally, although the selected traits capture complementary aspects of species morphology and ecology, some degree of trait inter-correlation is expected (Chichorro, Correia, and Cardoso 2022; Chichorro, Urbano, et al. 2022; Mammola et al. 2021). Since our objective was to characterize functional differences between exotic and endemic assemblages, we retained all ecologically relevant traits, following common practice in trait-based community analyses (Chichorro, Correia, and Cardoso 2022; Chichorro, Urbano, et al. 2022; Mammola et al. 2021). While trait inter-correlation may influence functional distances by increasing the weight of certain trait dimensions, patterns of functional similarity or dissimilarity should be interpreted as reflecting overall ecological strategies rather than independent trait axes (Reich et al. 2003). In this way, the future combination of traits with complementary process-sensitive approaches (e.g., co-occurrence/interaction networks, experimental designs across disturbance gradients) would help identify when and where Naturalization vs. Pre-adaptation dominates across spatial grains and invasion stages (Cadotte et al. 2018).

Nevertheless, we advocate that the functional trait-based approach adopted here remains highly informative and appropriate given the ecological questions addressed and the data available. Functional traits are directly linked to species' ecological roles, environmental tolerances, and potential competitive

interactions, making them particularly relevant for assessing invasion dynamics and assembly processes in disturbed island systems including the Azores (Oyarzabal et al. 2024; Oyarzabal, Boieiro, et al. 2025; Rigal et al. 2018). Moreover, several studies have shown that functional metrics can be more sensitive than phylogenetic ones in detecting assembly processes when trait evolution is labile or when phylogenetic signal is weak or inconsistent across traits (Arjona et al. 2025; Cadotte et al. 2018; Park et al. 2020). In this context, our results provide robust evidence that exotic–endemic assemblages in the Azores are predominantly structured by neutral and stochastic processes, regardless of their underlying evolutionary relationships.

5 | Conclusion

Based on the integrated analysis of 20 years of spatial and temporal data of arthropod species in the Azores archipelago, the functional assembly of exotic communities relative to their endemic counterparts is likely to be governed primarily by a neutral process. This main finding is modulated by taxon-specific nuances. Exotic spiders were consistently neutral across all scales, providing no support for either Darwin's Naturalization (functional dissimilarity) or Pre-adaptation (functional similarity) hypotheses, whereas exotic beetles were also mostly neutral but showed a weak, statistically detectable tendency toward functional dissimilarity at broader spatial and temporal scales, suggesting only limited context-dependent support for Naturalization rather than pervasive competitive exclusion.

Taken together, these results indicate that exotic persistence in Azorean native forests is shaped less by strong, direct biotic interactions with endemic species than by broader landscape processes, including land-use change, disturbance-created habitat opportunities, and continued immigration from surrounding anthropogenic environments (source–sink dynamics). From a conservation perspective, maintaining and restoring native forest integrity and reducing fragmentation should therefore be central priorities for safeguarding endemic functional diversity.

Key future challenges are to move from trait patterns to mechanism by integrating: (i) phylogenetic/phylogenomic data to separate deep evolutionary divergence from functional convergence; (ii) demographic evidence (occupancy, density, recruitment—especially juveniles) to distinguish transient visitors from self-sustaining populations; and (iii) explicit landscape metrics (invasive plants pressure, connectivity, and anthropogenic disturbance gradients) to test when and where source–sink dynamics overwhelm local interaction signals. Nonetheless, our results underscore the value of long-term, large-scale functional approaches for guiding conservation action in data-limited island systems.

Author Contributions

Guilherme Oyarzabal: data curation; formal analysis; methodology; validation; visualization; writing – original draft; and writing – review and editing. **Pedro Cardoso:** methodology; validation; writing – review and editing. **François Rigal:** methodology; validation; visualization; writing – review and editing. **Mário Boieiro:** methodology; validation; writing – review and editing. **Ana M. C. Santos:** methodology; validation; writing – review and editing. **Isabel R. Amorim:** methodology;

validation; writing – review and editing. **Jagoba Malumbres-Olarte:** methodology; validation; writing – review and editing. **Ricardo Costa:** methodology; validation; writing – review and editing. **Sébastien Lhoumeau:** data curation; methodology; validation; writing – review and editing. **Gábor Pozsgai:** conceptualization; methodology; validation; visualization; writing – review and editing. **Rosalina Gabriel:** writing – review and editing. **Paulo A. V. Borges:** conceptualization; data curation; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; visualization; writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and R scripts necessary to reproduce the analyses presented in this paper are available in the [Supporting Information](https://doi.org/10.5281/zenodo.21109001) and have been deposited in the Zenodo digital repository (<https://doi.org/10.5281/zenodo.21109001>).

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Supporting Information 1:** ddi70265-sup-0001-Supinfo1.xlsx. **Supporting Information 2:** ddi70265-sup-0002-Supinfo2.docx.