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Research article

Arthropod traits as proxies for abundance trends in the Azorean Islands

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Human activities drive ecological transformation, impacting island ecosystems from species diversity to ecological traits, mainly through habitat degradation and invasive species. Using two unique long-term datasets we aim to evaluate whether species traits (body size, trophic level, dispersal capacity and habitat occupancy) can predict temporal variations in the abundance of endemic, indigenous (endemic and native non-endemic) and exotic arthropods in the Azores Islands. We found that body size is crucial to predict arthropod abundance trends. Small-bodied herbivorous arthropods showed a decrease in abundance, while large-bodied indigenous arthropods increased in abundance, mainly in well-preserved areas. Also, large-bodied exotic arthropods increased in abundance across the entire archipelago. Moreover, endemic canopy dwellers increased in abundance, while endemic ground-dwellers decreased in abundance. Simultaneously, exotic arthropods showed the opposite result, increasing in abundance in the ground while decreasing in abundance in the canopy. Finally, habitat influenced both endemic and exotic spider abundance trends. Endemic spiders that occupy solely natural habitats experienced a decline in abundance, while exotic spiders in the same habitats increased in abundance. Our study underscores the significance of arthropod species traits in predicting abundance changes in island ecosystems over time, as well as the importance of monitoring species communities. Conservation efforts must extend beyond endangered species to protect non-threatened ones, given

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the increased extinction risk faced by even common species on islands. Monitoring and restoration programs are essential for preserving island ecosystems and safeguarding endemic arthropod populations.

Keywords: Arthropod populations, environmental degradation, oceanic islands, population trends

Introduction

In times marked by anthropogenic activities, humans have triggered five key transformations: climate change, pollution, overexploitation of natural resources, land-use alterations with associated loss of habitat area, contiguity and quality, and biological invasions (Sala et al. 2000, Pievani 2014, IPCC 2021). These transformations lead to the disruption of many biodiversity facets, including the decrease in abundance of both rare and common species (Pievani 2014, WWF 2022). Importantly, species are not equally prone to different threats. Certain characteristics or traits predispose species to decline while other traits will favor the maintenance or even the spread of species (Merckx et al. 2018, Wong et al. 2019, Chichorro et al. 2022a). Such traits correspond to phenotypical and functional characteristics that can describe and predict interactions, vulnerabilities, population trends and extinction risk within human-modified environments (Baeckens et al. 2023, Martins et al. 2023, Schleuning et al. 2023). Habitat breadth and life-history traits (e.g. offspring number and size) emerge as universal traits to predict extinction risk and population trends in many terrestrial taxa (Chichorro et al. 2022a). When affected by human activities, animals with slow growth and low reproductive rates are at a higher risk of abundance declines and extinction (Merckx et al. 2018, Chichorro et al. 2022a, Baeckens et al. 2023, Martins et al. 2023). Likewise, despite being energetically expensive, a high dispersal ability (e.g. flying capacity) increases the probability to reach favorable habitats and render species more resilience to the effects of rapid habitat degradation and loss (Kehoe et al. 2020, Chichorro et al. 2022a, b). Moreover, omnivore species have a more flexible diet compared to strictly carnivores and herbivores, which make them more resilient to food web disruptions caused by human-induced disturbance (Kehoe et al. 2020, Munstermann et al. 2021, Reuter et al. 2023). Therefore, trait-based approaches are valuable tools to provide insights on populations and ecosystem health.

Arthropods, the most diverse animal group, face alarming threats with recently documented losses in species richness, abundance and biomass as well as functional diversity (Hallmann et al. 2017, Saunders et al. 2020, Harvey et al. 2023). For instance, estimates point that over 30% of all insect populations are endangered and 45% are in decline (Wagner et al. 2021, Raghavendra et al. 2022). Climate change can shift distribution and abundance patterns, behavior and phenology, potentially disrupting pollination networks and food webs (Hallmann et al. 2017, Sallé et al. 2021, Harvey et al. 2023). The transformation of natural habitats into anthropogenic landscapes exposes arthropods to harmful pesticides, habitat loss or degradation, which can reduce their abundance and taxonomical and functional diversity (Wong et al. 2019, Uhler et al. 2021, Harvey et al. 2023). Moreover, invasive species may also have a negative impact on habitat structure and quality, further exacerbating the challenges by introducing novel competitors, predators and pathogens (Florencio et al. 2013, Borges et al. 2020, Wong et al. 2020, Harvey et al. 2023).

Despite this alarming scenario, we still lack the necessary insight into which species are declining and why (Cardoso et al. 2011a, Cardoso and Leather 2019). Depending on the taxon and habitat, results vary widely (Martins et al. 2023) and should be seen as a complex interplay of multiple factors, including species traits that influence their susceptibility to anthropogenic change. Therefore, unraveling the effects of species traits on arthropod population trends is crucial to design conservation strategies tailored to arthropod needs, providing evidence for long-term species survival amid human activities (Blüthgen et al. 2016, Staab et al. 2023). This is especially relevant in oceanic island ecosystems, where arthropods are often the only protagonists of many ecosystem functions such as predation, herbivory, pollination and decomposition (Russell and Kueffer 2019). Yet, studies have primarily investigated declining arthropod populations in continental ecosystems, with more knowledge gaps existing regarding arthropod diversity trends on islands.

Oceanic islands are famed for their smaller area size, odd biodiversity compared to continental settings and fragile ecological balance (Triantis et al. 2010, Whittaker et al. 2017). Hence, islands are vulnerable and in urgent need of effective conservation to address the profound challenges posed by anthropogenic activities (Norder et al. 2020, Fernández-Palacios et al. 2021, Nogué et al. 2021). In this context, oceanic islands are home to a large number of arthropod species, a substantial proportion of which are endemic, with evolutionary traits and ecological legacies that cannot be found anywhere else (Russell and Kueffer 2019). These arthropod species are now severely affected by the land-use changes and species invasions (Ferreira et al. 2016, Whittaker et al. 2017). As a consequence, numerous island endemic arthropods are classified as endangered or critically endangered by the International Union for Conservation of Nature (IUCN), underscoring their vulnerability to population decline and extinction (Russell and Kueffer 2019, Montgomery et al. 2020, Borges et al. 2022a).

Studies of arthropod abundance, richness and functional traits have been valuable to understand island dynamics (Whittaker et al. 2014, Rigal et al. 2018, Macías-Hernández et al. 2020, Chichorro et al. 2022a). For instance, in the particular case of the Azores archipelago, the extinction of island endemic beetles has been shown to be more common in large-bodied and habitat specialist species (Terzopoulou et al. 2015). At the same time, the native forest seems to be characterized by small-bodied native non-endemic species, while only arthropods with great dispersal ability (flight and ballooning capacities) can occupy both native forests and human-altered habitats (Rigal et al. 2018). Since exotic species have different functional traits than indigenous species, they can maintain certain ecosystem functions, even in human-altered habitats (Rigal et al. 2018). Moreover, exotic spider species tend to occur across all vertical strata of native forests, hence possibly competing within the micro-habitats with endemic species (Costa et al. 2023).

Here, we aim to assess, in an insular context, whether functional traits can predict changes in arthropod abundance over time, and whether or not these relationships vary between different taxonomic, biogeographic and trophic groups. To answer these questions, we use two unique datasets of long-term arthropod monitoring data sampled in the Azores over

Table 1. Azorean arthropod species traits, their associated hypothesis and references. Summary of our obtained results for traits predictions for species abundance trends.

Trait	Variable type	Hypothesis	References	Obtained results
Body size	Continuous. Species mean body length. Values for each species were standardized by the arthropod order	Large-bodied species would be more vulnerable to human activities since they tend to have lower population densities, greater resource needs (e.g. larger food requirements or larger home ranges) and longer life cycles	Purvis et al. 2000, Chichorro et al. 2022b	Large-bodied indigenous and exotic arthropods increased in abundance on Terceira island and throughout the Azores, respectively. In contrast, small-bodied endemic and indigenous herbivores increased in abundance throughout the Azores
Vertical stratum (Verticality)	Continuous. Average vertical stratum (AVS) of species vertical stratum, from ground level to the highest point sampled in the vegetation. Ranging from zero to one. It indicates, from ground to canopy level, where the species was sampled at a higher proportion	Forest canopy species would be less vulnerable to human activities compared to those occupying only the ground level or all the available vertical stratum as they often have less competition from exotic species and have higher dispersal ability	Rocha-Ortega et al. 2019, Van den Broeck et al. 2019, Gaona et al. 2021, Chichorro et al. 2022a, b, Mawan et al. 2022, Costa et al. 2023, Zhang et al. 2023	On Terceira island, endemic canopy-dwellers increased in abundance while endemic ground-dwellers decreased in abundance. In contrast, exotic ground-dwellers increased in abundance while exotic canopy-dwellers decreased in abundance throughout the Azores
Habitat occurrence	Categorical, with three levels: presence in anthropogenic habitat, presence in natural habitats or presence in both habitat types. Indicates the species capacity to inhabit impacted and/or natural/not-impacted habitats	Species that would be capable of occupying anthropogenic habitats would be less vulnerable while species that occupy only natural habitats would be more vulnerable	Campomizzi et al. 2008	Endemic spiders inhabiting only natural habitats decreased in abundance. At the same time, exotic spiders inhabiting both natural and anthropogenic habitats, also decreased in abundance
Trophic group	Categorical, with four levels: carnivore, herbivore, omnivore or fungivore. It indicates the trophic level of the species and its diet	Carnivores would be more affected by disturbance than species at lower trophic levels as they suffer from the synergistic effects of environmental disturbance and cascading effects from lower trophic levels	Kehoe et al. 2020, Munstermann et al. 2021, Chichorro et al. 2022a, Reuter et al. 2023	Trophic groups have not predicted changes in abundance of any of the arthropod groups or species origin explored
Dispersal ability	Categorical, with four levels: ballooning, crawling, flying or phoretic; and binary, with low dispersal (crawling and phoretic) and high dispersion (ballooning and flying). Indicates the species capacity and way of dispersal	Species with low dispersal ability (e.g. crawling) would be more vulnerable, and thus are more likely to fall in abundance owing to human activities since they do not have effective mechanisms to find new, suitable habitats	Kehoe et al. 2020, Chichorro et al. 2022a, b	Dispersal ability have not predicted changes in abundance of any of the arthropod groups or species origin explored

the past 25 years. We pose five hypotheses (Table 1). First, that abundance trends will be related to species' body size, predicting that large-bodied species will decline in abundance through time, while small-bodied species will increase or maintain their abundance. Second, for vertical stratum occupancy, we expect that ground-dwelling species will lose abundance compared to those species that occupy only the forest canopy. Third, for species habitat occurrence, species in both anthropogenic and natural habitats will not decrease their abundance compared to those that occupy only one of these habitat types. Fourth, for trophic groups, predatory species are expected to decline in abundance, while herbivorous and omnivorous species will maintain or increase their abundance. Fifth, for dispersal ability, species with lower dispersal capacity will lose abundance, while species with higher dispersal abilities will maintain or increase their abundance (Table 1).

Material and methods

Study area

We carried out this study in the Azores archipelago, which encompasses nine volcanic islands and several islets and seamounts. The archipelago is located in the northern Atlantic Ocean, approximately between 37° and 40° N latitude and 24° and 31° W longitude, spread along a distance of approximately 615 km from east to west. The archipelago is divided into three distinct island groups: western (Corvo and Flores), central (Faial, Pico, São Jorge, Graciosa and Terceira) and eastern (São Miguel and Santa Maria). On all islands, the climate is characterized as temperate oceanic with high levels of relative atmospheric humidity, which can reach 95% in the elevated native semi-tropical evergreen laurel forest (Elias et al. 2016, Borges et al. 2022a, b, c). Human presence on these islands, dating back to the 15th century, has significantly altered the landscape (Norder et al. 2020). The once-pristine native forests have given way to exotic tree plantations, agricultural and pastoral fields and urban settlements. Consequently, the original native forest currently occupies a mere 5% of the archipelago total land area, primarily confined to the remote and elevated regions of difficult access (Gaspar et al. 2008, Triantis et al. 2010, Elias et al. 2016, Borges et al. 2022d).

Data sampling

We sampled arthropods following the standardized sampling protocols of two long-term monitoring projects in the Azores: 1) the 'Biodiversity of Arthropods from the Laurisilva of the Azores' (BALA), from 1997 to 2022 (Borges et al. 2006, 2016); and 2) the 'Long Term Ecological Study of the Impacts of Climate Change in the Natural Forest of Azores' (sea, land and air malaise, SLAM), from 2012 to 2022 (Borges et al. 2020, 2022d, Costa and Borges 2021, Lhoumeau and Borges 2023).

We conducted the BALA project in three distinct campaigns, between 1997 and 2004 (BALA I), 2010 and 2011 (BALA II) and 2019 and 2022 (BALA III). We collected arthropods from native forest fragments on seven islands. Corvo and Graciosa were not sampled due to the lack of native forest patches. Two sampling methods were used: pitfall traps to capture ground-dwelling arthropods and canopy beating to capture canopy-dwelling arthropods (maximum height of 3–4 m). All the samplings occurred in boreal summer, between June and September. More details of the methods can be found elsewhere (Ribeiro et al. 2005, Borges et al. 2006, 2016, Gaspar et al. 2008) and data are now openly available (Pozsgai et al. 2024).

We collected the SLAM project data once in each boreal season (spanning three months), continuously between 2012 and 2022. Sampling was conducted in a total of 10 plots, located only on Terceira island. Plots were set in areas that are among the best-preserved native forest fragments, with minimal human disturbance. Arthropods were sampled using passive flight interception SLAM traps at each plot. Each trap had dimensions of 110 × 110 × 110 cm and contained propylene glycol (pure 1,2-propanediol) to capture, kill and conserve the specimens (Borges et al. 2020, 2022d, Costa and Borges 2021, Lhoumeau and Borges 2023). More details of the methods can be found elsewhere (Borges et al. 2020, 2022d, Costa and Borges 2021, Lhoumeau and Borges 2023).

Species and trait data

Most of the collected arthropods were sorted to species level, and nomenclature follows the most recent checklist of Azorean arthropods (Borges et al. 2022a). The remaining specimens that were not identified to species level were sorted to morphospecies and were excluded from the analyses. Also, all Crustacea, Collembola, Diplura, Diptera and Hymenoptera (except Formicidae) species were not considered in this study. Nominated species were then classified according to their biogeographic origin, into the following three categories (Borges et al. 2022a): 1) endemic species, i.e. those exclusive to the Azores; 2) indigenous species, i.e. those that are a combination of endemic and native non-endemic Azorean species, which can also be found in neighboring archipelagos (Madeira and the Canary Islands) and/or in the Mediterranean basin, and which most likely reached the Azores through long-distance dispersal; and 3) exotic species, i.e. those believed to have reached the Azores by human actions (Borges et al. 2006, 2022a, Borges and Wunderlich 2008).

For all sampled species, we selected a total of six functional traits for which we had a priori expectations about how they may respond to increasing habitat disturbance (e.g. body size, dispersal ability), traits that are important in species interaction (e.g. trophic status, specialization) and traits that are common to all arthropod groups encountered in our study (Gossner et al. 2015, Simons et al. 2016, Rigal et al. 2018, Chichorro et al. 2022a) (Fig. 1). The six traits were: 1) body size, which was standardized by the z-score within each order, i.e. average size of the order minus the size of the species divided by the standard deviation of size in the order; 2) vertical stratum that the species occupy in the

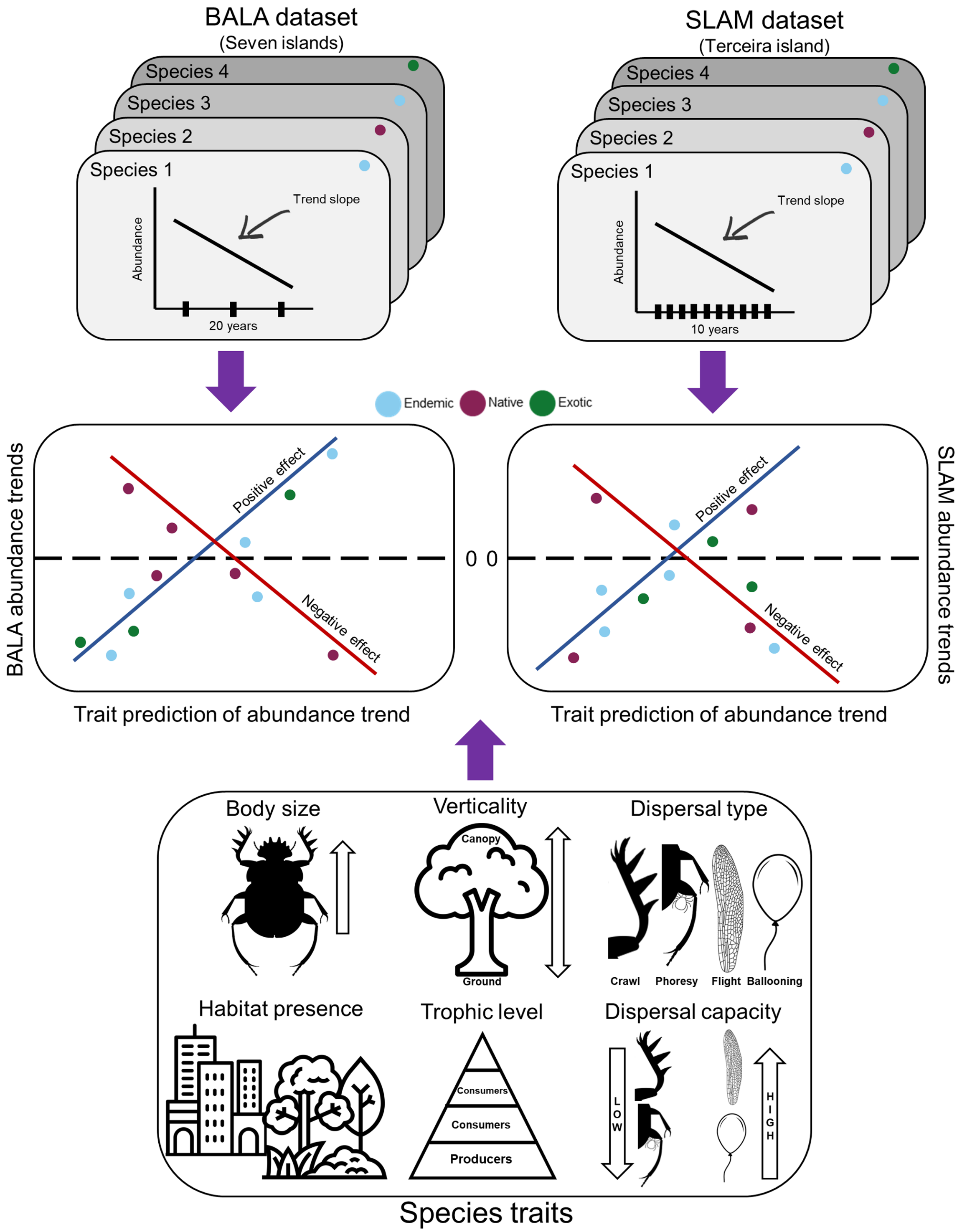

Figure 1. Framework of the steps taken for predicting abundance trends of each arthropod species, taking into consideration their traits. This framework was separated further between different groups of arthropods and their biogeographical origins. Trait figures were obtained from the Noun Project (https://thenounproject.com/).

vegetation (henceforth verticality), expressed as average verticality (AVS), from 0 to 1 where 0 is exclusively ground-dwelling species and 1 is the exclusively canopy-dwelling species; 3) feeding trophic group, expressed in four categories (carnivorous, fungivorous, herbivorous and omnivorous); 4) dispersal ability within and between islands, classified into four categories (ballooning, crawling, flying and phoretic); 5) dispersal capacities: low (crawl, phoretic) or high (ballooning and flying); and 6) habitat occurrence (where species were present) as categorical variables (presence in natural habitat, in anthropogenic habitat or in both natural and anthropogenic habitats) (Table 1). In the case of verticality, we followed the framework described in Costa et al. (2023). Using the BALA databases (I–III), we attributed a verticality score to the sample types, with 0 assigned to pitfalls, 0.5 to beating samples from bushes and 1 to trees. The relative abundance for each species across each stratum in the forest fragments was obtained dividing its abundance by the total number of spiders sampled in that stratum, and the site was standardized for variations in the sampling method. Then, we normalized the values by dividing each species' stratum relative abundance by the sum of its values along all strata within each forest fragment. All these were calculated using the equations described for average verticality in Costa et al. (2023). When we analyzed spiders separately, only three traits were used: 1) body size, 2) average verticality (AVS) and 3) habitat occurrence. Due to the homogeneity of spiders' feeding trophic level (all carnivores) and dispersal ability (only one species was a crawling spider, all others were considered possible ballooners), we removed these traits from the analysis. Moreover, habitat occurrence for spiders only had two levels and these were analyzed as a binary variable (inhabiting only natural habitats or both natural and anthropogenic habitats). Apart from body size, measured on the individuals sampled in these studies, data for the functional traits were compiled from: 1) the Azorean Biodiversity Portal (ABP 2024) or IUCN SSC Atlantic Islands Invertebrate Group Portal (ABP 2024, AIISG 2024); 2) published data, papers and descriptions of particular species; and 3) personal knowledge of the species' natural history by PAVB.

Data preparation

We partitioned the data for the analyses into six different datasets, in which three were the scenario analysis and three were the sensitivity analysis (Supporting information). For the scenario analysis we used the complete BALA dataset (hereafter BALA full) and the SLAM dataset. Since the SLAM data are limited to Terceira island, we also used the BALA data from Terceira only (hereafter BALA Terceira) to compare the results obtained from the two sampling strategies (Fig. 1, Supporting information). For the sensitivity analysis, we used the BALA dataset excluding Pico island (hereafter BALA without Pico), the BALA dataset excluding Terceira island (hereafter BALA without Terceira) and the BALA dataset excluding Pico and Terceira islands (hereafter BALA without Pico and Terceira). Since the native forest is not equally preserved across all Azores islands, we tested the removal of Pico and Terceira, which were the most preserved native forests throughout the archipelago (Tsafack et al. 2023a, Supporting information).

Based on the time length of our datasets (25 years for BALA and 10 years for SLAM) and to improve the reliability of trends and traits analyses, we excluded species with fewer than 10 adult individuals in each of BALA full or SLAM datasets. In this way, we mitigated the potential data noise caused by rare species (Martínez-Núñez et al. 2024), which we considered as those with one or fewer individuals per year in ten years or more. Then, we compiled the abundance of each species per: 1) BALA sampling (BALA I, II and III) and island sites (30), for all BALA datasets and 2) SLAM years (10 years) and sites (10) for the SLAM dataset (Supporting information). In this way, we were able to obtain an abundance trend (slope) of each species in each dataset. Each dataset was further separated into four groups of species: all arthropods, only herbivorous arthropods, only spiders and only beetles, the last two being the most diverse groups of the sampled arthropods. Also, the same groups were studied according to their biogeographic origins: all species together, only endemic species, only indigenous species and only exotic species (Supporting information). Therefore, we had a total of 16 separate analyses for each dataset (four arthropod groups by four biogeographic origins; 64 Bayesian frameworks).

Data analyses

To obtain the abundance trend of each species in each dataset (slope values, β), we fitted null (intercept only) GLMM models with negative binomial distribution and random effect (Goldstein and de Valpine 2022). The response variables were each species abundance (one species per model) and the random effects were specific to each dataset: for BALA full, BALA without Pico, BALA without Terceira and BALA without Pico and Terceira, islands were the random variable (seven islands); and for BALA Terceira and SLAM, sites were the random variables (10 sites). Hence, the intercept of the response variable with a positive estimate indicated a positive abundance trend over time, while a negative estimate value indicated a negative abundance trend over time. GLMM models were performed and Conditional R-squared (delta method, to estimate standard errors of transformations of a random variable, a first-order Taylor approximation (Parr 1983)) were obtained through the 'MuMIn' package (Bartoń 2023) in the R environment (www.r-project.org).

We fitted a Bayesian framework, weighted by Conditional R-squared values obtained for each species, to assess how changes in species abundance trends (response variable) could be predicted by species traits (explanatory variables) (Fig. 1). Distinct random effects were chosen to fit each framework for each dataset, being either the arthropod order and/or the species origin (Supporting information). For instance, when we analyzed all arthropods, both order (each arthropod order) and origin (endemic, native non-endemic or exotic) were used as random effects. At the same time, when indigenous arthropods were analyzed, order was used as previously (each arthropod order) but origin was only endemic or native non-endemic, as random effects (Supporting information). All Bayesian frameworks were built with the help of the 'jagsUI' package (Kellner and Meredith 2021) in the R environment, with five simultaneous chains, default priors, one million interactions, 800 000 burn-ins and 10 thins. Variables were considered to be significant when 97.5% of the credible intervals (CRI) were either positive or negative, not passing through zero (Hespanhol et al. 2019).

Results

Data overview

Our dataset included information on 156 arthropod species, of which 56 were endemic, 40 native non-endemic and 60 were exotic species. Eighty-six species were exclusive to the BALA project (33 endemic, 14 native non-endemic and 39 exotic) and 10 were exclusive to the SLAM project (two endemic, three native non-endemic and five exotic). For general abundance trends, from the BALA full dataset, endemic species showed 15 species with positive and 39 with negative trends; native non-endemic species showed 16 species with positive trends and 21 with negative trends; and exotic species showed eight species with positive trends and 47 with negative trends. From the SLAM dataset, endemic species showed 13 species with positive trends and nine with negative trends; native non-endemic species showed 11 species with positive trends and 15 with negative trends; and exotic species showed one species with positive trends and 20 with negative trends.

Hereafter we present the significant (when CRI does not pass through zero) and not-significant (when CRI does pass through zero) predictions of the fixed effects (the explored traits) from the scenario analysis. To interpret our results, it is important to note that the traits predict the abundance trends based on a probability. Hence, traits can predict even lower or higher abundance trends compared to the ones we found. The standard deviation of fixed effects, and standard deviation of random effects from the scenario analysis, along with the results of the sensitivity analysis, can be found in the Supporting information.

Body size and abundance trends

Body size was an important trait for predicting species abundance trends, with different groups having positive or negative predictions. Large-bodied indigenous arthropods increased in abundance while small-bodied ones declined in abundance on Terceira island (SLAM $\beta_{BodySize}$: 0.202–5.287 CRI) (Fig. 2A). Similarly, large-bodied exotic arthropods increased in abundance throughout the Azores (BALA full $\beta_{BodySize}$: 0.606–4.539 CRI) (Fig. 2B). On the other hand, large-bodied herbivorous arthropods decreased in abundance, while small-bodied ones increased in abundance (BALA full $\beta_{BodySize}$: −7.461 to −0.916 CRI) (Fig. 2C). The same pattern can also be seen in endemic herbivorous (BALA full $\beta_{BodySize}$: −14.758 to −1.321 CRI, Fig. 2D) and indigenous herbivorous (BALA full $\beta_{BodySize}$: −11.486 to −1.935 CRI, Fig. 2E).

Verticality and abundance trends

The vertical stratum average was also an important predictor of arthropod abundance trends. Endemic arthropods with a higher average verticality (AVS) (i.e. mostly occupy the canopy) increased in abundance in Terceira island, while the ones that occupy the ground level decreased in abundance (BALA only Terceira β_{AVS}: 1.504–42.300 CRI, Fig. 3A). In contrast,

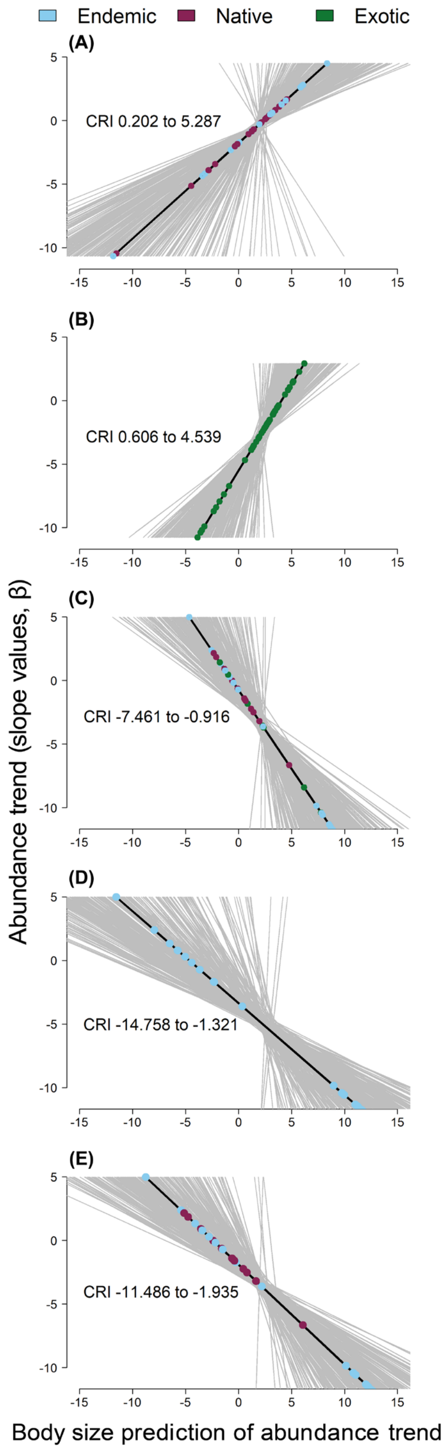

Figure 2. Relationship between abundance trends (dots, the obtained species slope values) and the body size predictions of abundance (species predicted slope values). Black lines show the posterior means and gray lines show estimation uncertainty, based on 300 random posterior distributions of the Bayesian predictions, as a way to depict the prediction uncertainty. (A) All arthropods, SLAM; (B) exotic arthropods, BALA full; (C) all herbivorous arthropods, BALA full; (D) endemic herbivorous arthropods, BALA full; (E) indigenous herbivorous arthropods, BALA full. CRI indicates the credible intervals of 97.5%.

exotic arthropods inhabiting the ground level increased in abundance throughout the whole archipelago, while exotic canopy-dwelling species decreased in abundance (BALA full β_{AVS}: −16.146 to −0.788 CRI, Fig. 3B).

Habitat occurrence and abundance trends

Habitat occurrence was a particularly important trait in predicting changes in endemic and exotic spiders' abundance trends. Endemic spiders inhabiting only natural habitats, i.e. the native forest, had a decrease in abundance (BALA full $\beta_{NaturalHabitats}$: −15.185 to −8.512 CRI, Fig. 4A). In contrast, exotic spider species that occupy both natural and anthropogenic habitats also had a decrease in abundance (BALA full $\beta_{BothHabitats}$: −16.428 to −5.260 CRI, Fig. 4B).

Trophic group and dispersal ability and abundance trends

Neither trophic groups nor dispersal ability were significant predictors of changes in abundance for any of the arthropod groups or species origins examined.

Discussion

Overview of abundance trends

Our study explored the relationship between temporal trends in arthropod abundances and species traits. Overall, our analyses revealed that body size, forest strata occupancy (verticality) and habitat occupancy are significant predictors of changes in arthropod abundance over time, with both positive and negative relations being found, depending on the taxa. These relationships highlight the multifaceted interplay between island forest arthropod traits and their population dynamics and vulnerability. Moreover, our results add more evidence to the expanding knowledge of decline in terrestrial arthropods on islands and continental land masses (Goulson 2019, Cardoso et al. 2020, Staab et al. 2023).

Body size predictions on abundance trends

Body size emerges as a trait that consistently correlates with changes in abundance, with our study adding to this body of literature (Chichorro et al. 2022a, b, Martins et al. 2023, Martínez-Núñez et al. 2024). However, we found different trends depending on the arthropod group. For herbivores and beetles we found a negative trend, indicating a decrease in abundance in large-bodied species and an increase in small-bodied ones, corroborating previous finds from the Azores (Terzopoulou et al. 2015, Rigal et al. 2018). Moreover, this same pattern is also found in continental landmasses, being corroborated by other arthropod communities (Merckx et al. 2018, Martínez-Núñez et al. 2024).

It is important to note that ca 37% of the herbivorous arthropods were beetles (39 out of 105 species). Therefore, our results regarding herbivores may be strongly driven by this single taxon. Despite that, these findings align with the current knowledge that large-bodied species have a higher risk of abundance declines and extinction, probably due to their higher resource requirements (e.g. higher food demands or large home ranges), lower dispersal ability and lower population densities (Hagge et al. 2021, Chichorro et al. 2022a, Martins et al. 2023, Martínez-Núñez et al. 2024). In turn, this may result in a decrease or shrink in body size, as was reported worldwide for many vertebrate and invertebrate animal groups (Martins et al. 2023). Given the past prevalent

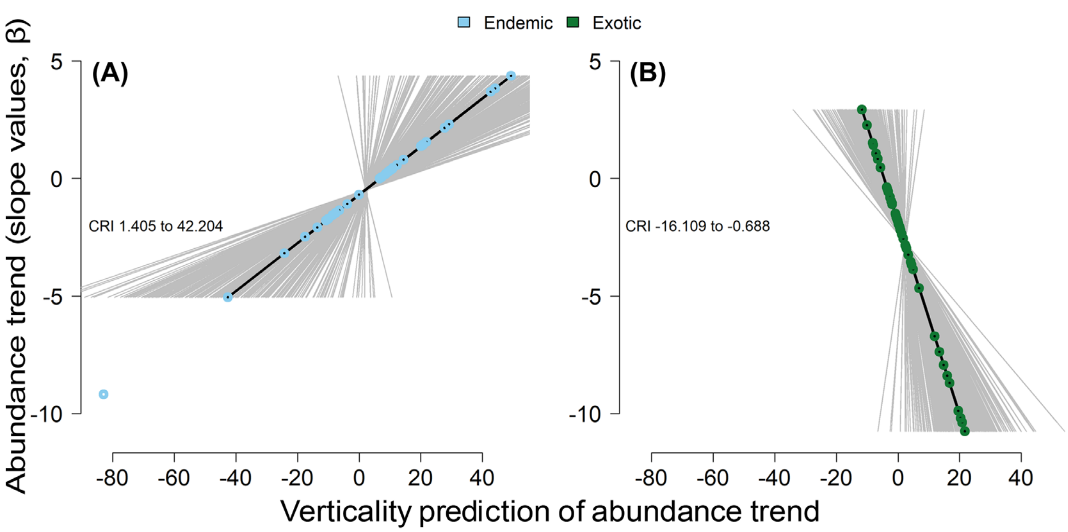

Figure 3. Relationship between species abundance trends (dots, the obtained species slope values) and the verticality predictions of abundance trends (species predicted slope values). Black lines show the posterior means and gray lines show estimation uncertainty, based on 300 random posterior distributions of the Bayesian predictions, as a way to depict the prediction uncertainty. (A) Endemic arthropods, BALA only Terceira; and (B) exotic arthropods, BALA full. CRI indicates the credible intervals of 97.5%.

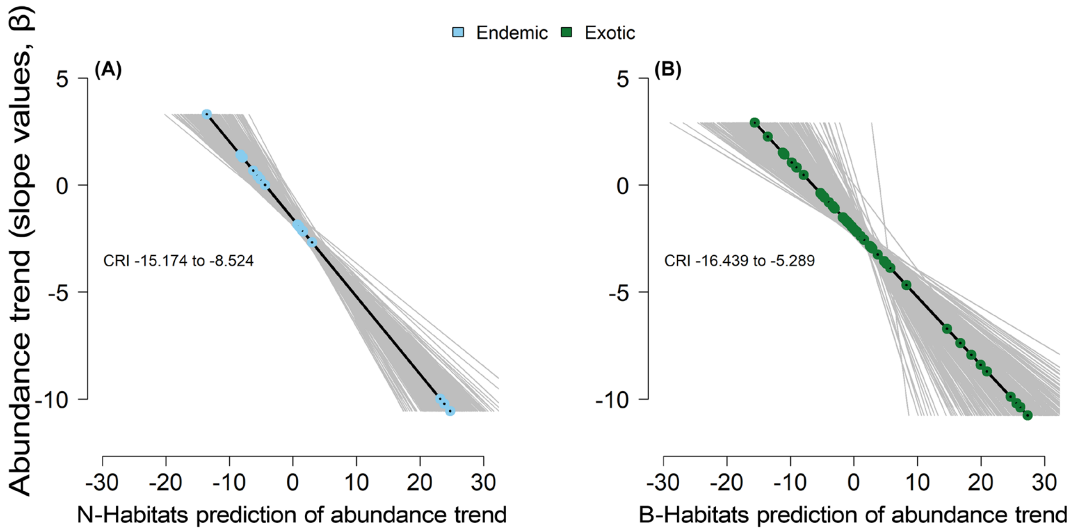

Figure 4. Relationship between abundance trends (dots, the obtained species slope values) and the habitat occupancy predictions of spider abundance trends (species predicted slope values). N-Habitats – presence in only natural habitats, and B-Habitats – presence in both natural and anthropogenic habitats. Black lines show the posterior means and gray lines show estimation uncertainty, based on 300 random posterior distributions of the Bayesian predictions, as a way to depict the prediction uncertainty. (A) Endemic spiders, BALA full and (B) exotic spiders, BALA full. CRI indicates the credible intervals of 97.5%.

habitat and resource loss in Azores (Borges et al. 2006, Triantis et al. 2010, Florencio et al. 2013, Terzopoulou et al. 2015), it is reasonable to expect that large-bodied species would experience more substantial declines than those with more (but less demanding) resource needs (Purvis et al. 2000, Hagge et al. 2021, Martins et al. 2023).

Nevertheless, our findings reveal different abundance trends between indigenous and exotic arthropods. Specifically, large-bodied indigenous species are thriving on Terceira, indicating positive outcomes from forest restoration efforts (Borges et al. 2017). In contrast, large-bodied exotic species are increasing in abundance across the entire archipelago, potentially benefiting from historical land-use changes, in line with previous research (Gaspar et al. 2008, Meijer et al. 2011, Florencio et al. 2013, 2015, Quell et al. 2021).

Verticality predictions on abundance trends

Overall, our results regarding verticality point to three effects occurring: first, canopy endemic species seem to be less impacted in pristine forest remains; second, ground-dwelling indigenous species, outside preserved areas, seem able to persevere in impacted environments; and finally, exotic species seem to be increasing the colonization pressure, mostly in already impacted environments (Borges et al. 2006, Whittaker et al. 2017, Tsafack et al. 2021, Lhoumeau and Borges 2023, Pozsgai et al. 2023, Staab et al. 2023). However, it is important to note that these results should be treated with caution. Colonization status is not trivial or definitive for several species, which could change the interpretation of our results since some species currently classified as native non-endemic might actually be exotic (Borges et al. 2006, Jiménez-García et al. 2023).

In general, the decrease in abundance in ground-dwelling endemic species seems to be mainly caused by a complex interplay between anthropogenic activities, like land-use changes, and the degradation of forest soil structure due to the invasion of plant species, which corroborate previous findings (Gaspar et al. 2008, Meijer et al. 2011, Florencio et al. 2013, 2015). Indeed, the rapid advance of invasive plants in Azorean native forests is changing plant species composition (i.e. decrease in the abundance of bryophytes, ferns and native herbaceous plants) and soil habitat structure, along with soil compaction, which would have a direct impact on epigean arthropods (Ribeiro et al. 2005, Borges et al. 2006, Queiroz et al. 2014). In addition, the continuous colonization of the forest by exotic arthropod species is facilitated by the current native forest being surrounded by a matrix of anthropogenic habitats, which potentially impacts endemic canopy arthropod communities. However, despite this continuous arrival of exotic species to the native forests, the increasing abundance of canopy endemic arthropods indicates a resistance to invasion in native forest canopies of Terceira island, where the well-preserved forest patches may still maintain a complex habitat heterogeneity (Raupp et al. 2010, Swart et al. 2020). Ongoing efforts to reverse trends in habitat degradation in Azorean native forests are in place with three LIFE projects (L'Instrument Financier pour l'Environnement), two of them dedicated to arthropods, but the positive impacts are yet to be demonstrated (Tsafack et al. 2023b).

yOur analysis also revealed that ground-dwelling exotic arthropods gained abundance throughout the whole archipelago (see also Borges et al. 2020). Prior insights from the SLAM project indicated that native forests can act as a barrier to establishment of most airborne exotic species, while the edaphic flora and fauna are the most anthropogenic-impacted ecosystems in the archipelago (Borges et al. 2020, Lhoumeau and Borges 2023). Hence, considering the high rates of human activities in Azores, and that exotic species richness increases as land-use changes intensify (Rigal et al. 2018), together with forest soil habitat degradation, we expected to observe a rise in ground-dwelling exotic abundance. The implications for exotic species would then be a preference for anthropogenic environments (ground level), while displaying diminished abundance in the native forest (canopy level) (Lhoumeau and Borges 2023). We found the same pattern for ground-dwelling indigenous arthropods, albeit only when one of the most preserved islands in the Azores, Terceira, was removed from the analysis (Supporting information). This complements the previous finding on canopy endemic arthropods. While endemic species seem stable in remnants of pristine forest, ground-dwelling indigenous species may struggle but persist along with the ongoing exotic species invasion. Some examples of this struggle could include interactions with the exotic spider *Dysdera crocata*, which might have already caused the disappearance of endemic *Dysdera* spiders (Cardoso et al. 2010). Another example is the highly abundant invasive Diplopoda *Ommatoiulus moreleti*, which is reported to negatively impact the community of endemic millipedes, for instance, on the Canary Islands (Delgado et al. 2013). Furthermore, the effect of the rapid expansion and the changes brought to the soil and understory communities by plants like the Kahili ginger, *Hedychium gardnerianum*, in Terceira still remain mostly unknown (Pereira et al. 2021). Therefore, it is important for future research to go further on the potential effects of specific exotic species, comparing their occurrence on multiple islands and different, pristine or modified, habitats.

Habitat occurrence predictions on abundance trends

Habitat occurrence was a crucial trait for the abundance trends in spiders. It is important to note that, in the spiders, habitat occurrence was analyzed as a binary variable: inhabiting only natural habitats or both natural and anthropogenic habitats. Hence, we should exercise caution when interpreting these results. Endemic spiders that strictly inhabit natural habitats are declining in abundance throughout the Azores, while those occurring in both natural and anthropogenic habitats are increasing in abundance. In contrast, exotic spiders present only in natural habitats are increasing in abundance, while falling in abundance when inhabiting both natural and anthropogenic habitats. This pattern may indicate a spread of exotic spiders in natural habitats, with a likely direct competition with endemic spiders (Lhoumeau and Borges 2023). Indeed, previous results show that many exotic spiders are well established in the Azores, even in preserved habitats (Lhoumeau and Borges 2023). Among these populations there are even araneophagic exotic spiders like *Ero furcata*, which inhabit both natural and anthropogenic habitats and could cause further direct impacts on the endemic fauna (Boieiro et al. 2018, Barrantes et al. 2023 , Costa et al. 2023, Lhoumeau and Borges 2023). Consequently, co-occurrence between endemic and exotic spiders may induce the reorganization of ecological networks (Pozsgai et al. 2023), with negative impacts on the endemic species abundance (Martínez-Devesa et al. 2023).

Besides the effects of competition, species presence in modified habitats is also related to species resilience to human activities (Campomizzi et al. 2008). Considering the preference of endemic spiders for natural habitats (Costa et al. 2023), their decrease in abundance may be also linked to land-use changes (Rigal et al. 2018, Borges et al. 2020, Lhoumeau and Borges 2023). For instance, 21 out of the 26 endemic spider species studied here are web-weavers (Cardoso et al. 2011b), which are known for their need of tridimensional vegetation structure and habitat complexity to build their webs, which in turn make them vulnerable to human activities that reduce environmental complexity (Dimitrov et al. 2017, Macías-Hernández et al. 2020, Oyarzabal and Guimarães 2021, 2024). Therefore, habitat occupancy by endemic spiders goes beyond competition and exclusion by exotic spiders, and they are also under constant threat due to habitat structure changes and other human-related drivers of change (Hemm and Höfer 2012, Rocha-Ortega et al. 2019, Gaona et al. 2021, Mawan et al. 2022).

Trophic group and dispersal ability predictions on abundance trends

Contrary to our hypothesis, feeding trophic and dispersal ability seem to not be able to predict the changes in arthropod abundance in Azores. Previous research indicates that trophic level may not predict abundance due to its dependency on the studied taxon, body size and habitat loss (Chichorro et al. 2022a, b). For dispersal ability, though, its inconsistency in predicting abundance trends might be related to the fragmented Azorean landscape (Raupp et al. 2010, Swart et al. 2020). While increasing fragmentation can benefit good dispersers, providing more suitable patches, it may also increase their mortality due to long-distance dispersal requirements (Chichorro et al. 2022a, b). On the other hand, poor dispersers may just avoid unnecessary dispersal events that may lead to an increased mortality (Chichorro et al. 2022a, b). In our case, since most of our data were gathered in the remnants of the Azorean native forest, the effects of dispersal ability may be diluted within the other traits. For instance, considering that good dispersers would also be the ones with large body sizes, our results may indirectly indicate that these species are decreasing in abundance (Chichorro et al. 2022a, b).

Conservation concerns

The Azorean archipelago has experienced a drastic reduction of 95% in its native forest habitats over the past 600 years since human colonization began (Gaspar et al. 2008, Triantis et al. 2010, Elias et al. 2016, Norder et al. 2020). This has led to a loss of species diversity, with a significant extinction debt predicted for arthropods, posing a risk to future endemic species (Triantis et al. 2010, Whittaker et al. 2014, Terzopoulou et al. 2015). Exotic arthropods now dominate the Azorean fauna, comprising 58% of overall arthropod species richness (Triantis et al. 2010, Borges et al. 2022a, Lhoumeau and Borges 2023). However, our results show that not all exotic groups increased in abundance over time, and patterns vary among different arthropod groups. This corroborates previous finds where, for instance, exotic beetles and true bugs were found to exhibit high species turnover, while exotic spiders established stable populations (Lhoumeau and Borges 2023). Therefore, as observed for plants in continental tropical forests (Mungi et al. 2021), the native Azorean forest act as a filter, preventing some exotic species from establishing due to the unsuitability of forest conditions or to the competitive exclusion by native species (Whittaker et al. 2017, Tsafack et al. 2021, Lhoumeau and Borges 2023, Pozsgai et al. 2023, Staab et al. 2023). The ongoing human activities, particularly affecting endemic and indigenous species, are likely to trigger primary and secondary extinction waves, leading to continuous cascading effects on environmental health, stability and the ecological services provided by arthropods (Kehoe et al. 2020, Ferrante et al. 2023). Ultimately, endemic and native non-endemic species seem to persist in the impacted forests, despite facing a significant extinction debt, while exotic species struggle to colonize these due to a lack of suitable habitats and competitive exclusion (Whittaker et al. 2017, Tsafack et al. 2021, Lhoumeau and Borges 2023, Pozsgai et al. 2023, Staab et al. 2023).

Conclusions

Our findings highlight the potential use of arthropod species traits for predicting changes in abundance trends, particularly in island ecosystems. Moreover, all our results are entangled with historical land-use changes, extinction debt of endemic species, spread of exotic species and conservation of Azorean pristine forests (Meijer et al. 2011, Boieiro et al. 2018, Borges et al. 2020, Tsafack et al. 2021). While conservation priorities traditionally tend to focus on mitigating and preventing the extinction of endangered species, it is imperative to also articulate and incorporate protective measures for non-threatened species (Baker et al. 2019, Ceballos et al. 2020). In an island context, even commonly abundant species face elevated extinction risk, and slight declines can result in substantial biodiversity loss (Fernández-Palacios et al. 2021, Ferrante et al. 2023, Lhoumeau and Borges 2023, Pozsgai et al. 2023). Hence, to help ensure the preservation of Azorean native ecosystems, as well as other island ecosystems, it is paramount to increase monitoring and restoration programs targeting different animal and plant taxa (Elias et al. 2016, Mendes et al. 2023). Such actions are pivotal in safeguarding the unique and vulnerable endemic arthropod populations that play crucial roles in the delicate ecosystems of these islands.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.qv9s4mwpf (Oyarzabal et al. 2024).

Supporting information

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

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