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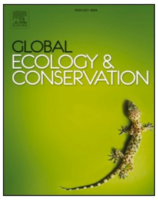

Original Research Article

Beyond native habitats: Indigenous arthropods adapted to mid-elevations find refuge in exotic forests

Sébastien Lhoumeau [a,*,1], Guilherme Oyarzabal [a,2], Paulo A.V. Borges [a,b,c,3]

[a] University of Azores, CE3C—Centre for Ecology, Evolution and Environmental Changes, Azorean Biodiversity Group, CHANGE —Global Change and Sustainability Institute, School of Agricultural and Environmental Sciences, Rua Capitão João d'Ávila, Pico da Urze, Angra do Heroísmo, Azores 9700-042, Portugal
[b] IUCN SSC Atlantic Islands Invertebrate Specialist Group, Angra do Heroísmo, Portugal
[c] IUCN SSC Species Monitoring Specialist Group, Angra do Heroísmo, Portugal

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ABSTRACT

In island ecosystems, extensive land-use changes since human colonisation has transformed native habitats into agriculture and exotic forests, raising concerns about the long-term persistence of indigenous biodiversity. This study explores the distribution of relict populations of indigenous arthropod species in exotic forests on Terceira Island (Azores) and identifies the ecological and environmental drivers shaping their presence. Using standardized SLAM (Sea, Land, and Air Malaise) traps and pitfall traps data from native and exotic forest plots, we investigated the distribution and abundance of 85 indigenous arthropod species across 15 orders, of which 65 were recorded at least once in exotic forests. We modelled the effects of species traits and biogeographic variables on species abundance and presence in exotic forests. Elevation emerged as the dominant predictor in both models, with species associated with mid-elevation habitats (300 – 500 m a.s.l.) showing higher abundance and occurrence in exotic forests, while high-elevation specialists (above 500 m a.s.l.) were largely absent. Endemic species generally had lower relative abundances in exotic forests compared to native non-endemics, even when their overall elevational range was broad. These results suggest that species historically present in mid-elevation zones find refuge in exotic forests. While relict populations may offer a degree of resilience and restoration potential, their long-term persistence is uncertain, particularly under climate change scenarios that limit available habitat at higher elevations. Conservation strategies should therefore recognize the role of exotic forests as transitional refuges and prioritize their management and restoration of native forests, especially in non-protected and privately-owned landscapes.

1. Introduction

Native habitat loss and land-use changes are among the most significant anthropogenic drivers of global biodiversity loss and

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* Correspondence to: University of the Azores, Rua Capitão João d'Ávila, Pico da Urze, Angra do Heroísmo, Azores 9700-042, Portugal.
E-mail address: 2022113906@uac.pt (S. Lhoumeau).

[1] https://orcid.org/0009-0006-7241-6269

[2] https://orcid.org/0000-0001-7332-9788

[3] https://orcid.org/0000-0002-8448-7623

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decline (Borges et al., 2019; Davison et al., 2021; Sala et al., 2000). Over the past few centuries, natural landscapes have undergone rapid and extensive transformations (Altieri, 2007; Samper, 2010). Their spatio-temporal magnitude often exceeds the capacity of many species to adapt (Garant, 2020), resulting in degradation of native habitats (Nešić and Bjedov, 2021), population declines (Spooner et al., 2018), and species extinctions (Di Marco et al., 2018). However, the ecological impacts of habitat degradation are not always immediate, as many species continue to persist temporarily in degraded or suboptimal habitats before eventually disappearing (Halley et al., 2016; Spalding and Hull, 2021). This time lag between the disappearance of the species' native habitat and the extinction of the species is a phenomenon known as extinction debt (Kuussaari et al., 2009; Tilman et al., 1994; Triantis et al., 2010).

One primary mechanism through which land-use change influence negatively biodiversity is habitat fragmentation (Haddad et al., 2015). The breaking of continuous native habitats into mosaics of altered and often isolated patches reduces ecological connectivity, thereby disrupting species dispersal, reproduction, and gene flow between populations (Holyoak and Heath, 2016; Peacock, 2025). Fragmentation has particularly severe consequences for species with limited dispersal ability, specialized habitat requirements, or small population sizes (Ewers and Didham, 2005). These negative effects are amplified in island ecosystems, where endemic species are naturally range-restricted and often lack alternative habitats (Aparício et al., 2018; Burkey, 1995; Oyarzabal et al., 2025a). In such contexts, habitat fragmentation often creates “islands within islands” (Watling and Donnelly, 2006), further isolating populations and elevating their risk of extinction (Struebig et al., 2011). Many island endemics species found in these fragmented ecosystems are already listed as threatened according to the IUCN Red List (Oyarzabal et al., 2025b), highlighting the urgency for targeted conservation actions and the designation of additional protected areas.

The Azores archipelago is one of the most remote group of volcanic islands in the North Atlantic. Despite its isolation, since human colonisation in the 15th century, the original native vegetation has been drastically reduced, with only small and highly fragmented patches restricted to high elevation and remote areas (Borges et al., 2005; Lhoumeau et al., 2025a). Elias et al. (2016), described several distinct vegetation belts across elevations above sea level (a.s.l.): low-land forests (below 300 m a.s.l., hereafter low-elevation forests), submontane forests (between 300 and 600 m a.s.l., hereafter mid-elevation forests), montane forests (between 600 and 900 m a.s.l., hereafter high elevation forests) and altimontane, sub-alpine and alpine scrublands (above 900 m a.s.l.). At low and mid-elevation of islands such as Terceira (the third largest island of the archipelago), native vegetation has been extensively replaced by agriculture areas (mostly pastureland), exotic tree plantations of *Cryptomeria japonica* and *Eucalyptus* spp. and secondary woodlands dominated by the invasive *Pittosporum undulatum* (Lhoumeau et al., 2025a; Lourenço et al., 2011; Pavão et al., 2024).

These exotic forests are novel human-created ecosystems that differ structurally and functionally from the original vegetation (Lhoumeau et al., 2025a). Yet, despite their anthropogenic origin, some of these forests continue to host populations of indigenous (endemic and native non-endemic) arthropod species (Cardoso et al., 2009; Tsafack et al., 2021). Recently, Tsafack et al. (2021) highlighted the ecological significance of exotic forest patches for arthropod biodiversity on Terceira Island, showing that even small, lowland stands of exotic trees can harbour rare endemic species. While native forests, particularly those at high elevations, remain irreplaceable strongholds for Azorean endemics (Borges et al., 2005; Fernández-Palacios et al., 2011; Lhoumeau and Borges, 2023), these findings suggest that endemics with broader ecological tolerances or historical lower elevation distributions are still able to thrive in exotic forests.

The presence of indigenous arthropods in novel exotic forests raises significant conservation and ecological questions. These species are often considered to be biogeographic relict populations, i.e. the remnants of once broader distributions that have survived the large-scale transformation of their native habitats (Habel et al., 2010). Their continued existence may reflect a degree of ecological tolerance or adaptability but could also be a transient phase in a longer trajectory of decline, consistent with the concept of extinction debt (Ewers and Didham, 2005; Triantis et al., 2010). In this context, such populations might not represent true resilience but instead signal delayed extinction in habitats that no longer support viable long-term survival (Kuussaari et al., 2009). Moreover, these populations are nowadays facing new challenges as multiple pressure on biodiversity occur at low and mid-elevation (Cardoso et al., 2009), including the competition with novel introduced species (Borges et al., 2020; Walsh et al., 2012). Despite that, biogeographic relict populations of indigenous arthropods might survive due to functional trait resilience (Oyarzabal et al., 2025a) providing tolerance due to broad intrinsic Grinellian niche, or even a niche shifting, due to plasticity (Cheptou et al., 2017).

Identifying the drivers that shape the distribution of these relict populations is essential for assessing biodiversity persistence in human-modified landscapes. These may include biotic and abiotic variables such as species traits or habitat characteristics. Among the most relevant variables are elevation and site occupancies, body size, trophic guild, dispersal ability and vertical stratification. Elevation is known as a key driver of arthropod diversity and distribution on islands, as it shapes climatic conditions and vegetation structure. Many high-elevation endemic species having narrow ecological tolerances (Gillespie and Roderick, 2002; Hodkinson, 2005). Thus, species historically associated with mid-elevations may be more likely to persist in exotic forests, which are typically located within this altitudinal range. In parallel, species with broader site occupancy (i.e., those recorded within extensive areas) are expected to exhibit greater ecological flexibility and, consequently, higher chances of persistence in transformed habitats (Hanski and Ovaskainen, 2000). Body size also plays an important role, as smaller-bodied species generally require fewer resources and may more readily exploit microhabitats in fragmented or modified environments (Gaston and Blackburn, 1996; Gibb et al., 2015; Oyarzabal et al., 2025a). Trophic guild reflects dietary specialization, and generalist feeders are expected to better tolerate exotic vegetation compared to herbivores or parasitoids that rely on specific hosts (Basset et al., 2012; Novotny et al., 2006). Dispersal ability is especially relevant in fragmented landscapes, with good dispersers more likely to reach and establish in isolated or novel habitats such as exotic forests (Clobert et al., 2009). Finally, vertical stratification in forest layers may influence vulnerability to forest alteration, as species inhabiting the canopy or intermediate strata may be better adapted to the changed structural complexity of exotic forests, whereas ground-dwelling species may be more negatively affected (Basset et al., 2015; Costa et al., 2023; Lhoumeau and Borges, 2025).

In this study, we investigate the occurrence and distribution of biogeographic relict populations of indigenous arthropod species within mid-elevation exotic forests on Terceira Island in the Azores. Specifically, we address two main questions:

1. What is the current distribution of relict populations of indigenous arthropods within these exotic forest habitats?
2. Which ecological and environmental factors primarily influence this distribution?

We hypothesize that the presence of populations of biogeographic relict species in exotic forests is primarily shaped by their historical elevational range, with species adapted to mid-elevation habitats being more likely to persist. Furthermore, we predict that species´ ecological traits such as dispersal ability, trophic guild, body size, and vertical stratification, will influence their capacity to survive in these non-native forest ecosystems. Specifically, generalist and highly mobile species are expected to have a greater likelihood of persistence in exotic stands.

By addressing these questions, we aim to contribute to a broader understanding of how biodiversity persists in human transformed landscapes, as the observed patterns can reflect actual resilience or are indicative of ongoing biodiversity erosion driven by extinction debt.

2. Materials and methods

2.1. Study area

This study was conducted on Terceira Island (38°43′40″N 27°12′48″W), one of the islands in the central group of the Azores archipelago (North Atlantic, Portugal, Fig. 1). The island hosts a diverse array of habitat types, including the best remnant patches of native vegetation within Azores and many areas of small patches of exotic forest (Borges et al., 2005, 2020; Lhoumeau et al., 2025a). The remaining native forest fragments are mostly located at high elevation (above 500 m a.s.l.) and are dominated by endemic tree species such as *Laurus azorica*, *Ilex azorica* and *Juniperus brevifolia* and the shrubs *Erica azorica*, and *Vaccinium cylindraceum*. In contrast,

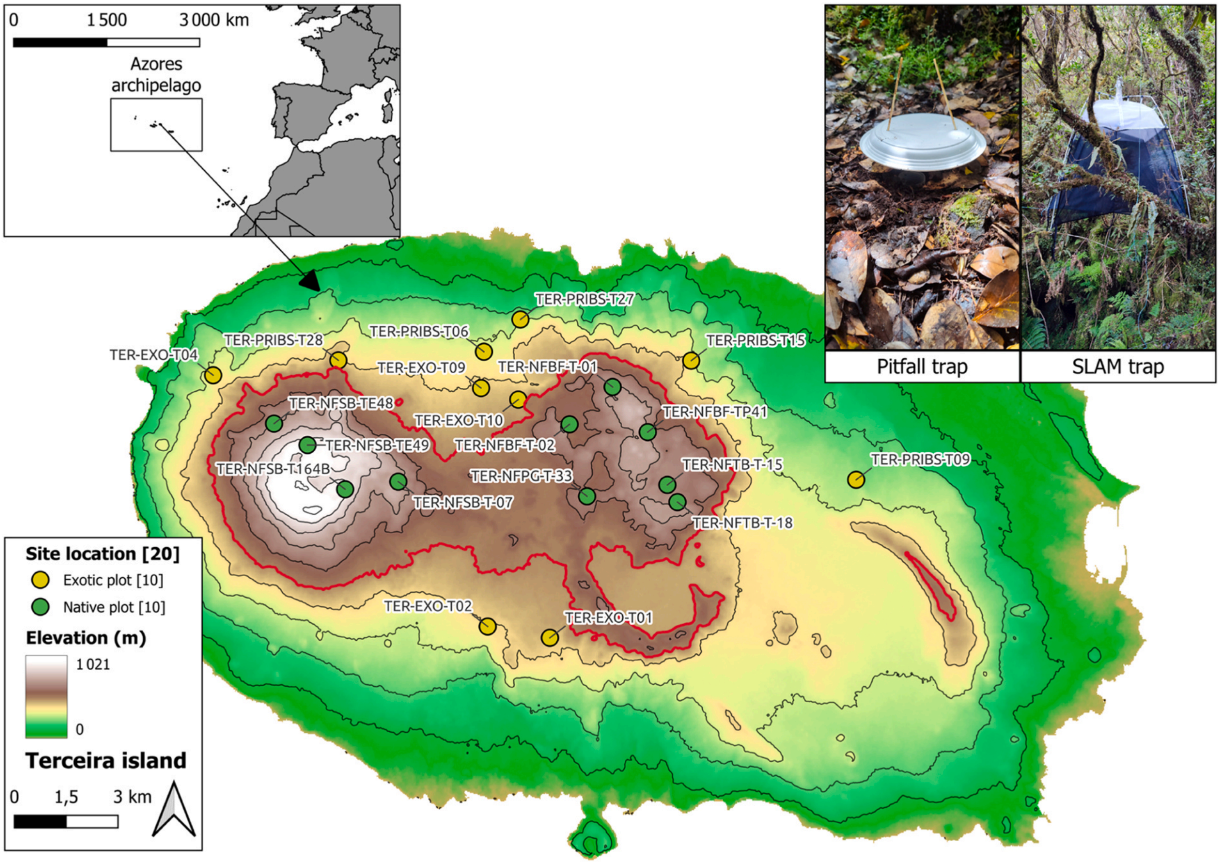

Fig. 1. Map of Terceira Island (Azores, Portugal) showing the spatial distribution of the sampling plots used in this study. A total of 20 plots were surveyed, including 10 in exotic forest stands (yellow circles) and 10 in native forest fragments (green circles). Elevation is indicated by a colour gradient and contour lines at 100-metre intervals (the 500-metre line is red). Inset photos show the sampling methods used: Sea, Land and Air Malaise (SLAM) traps at different strata, and pitfall traps installed at ground level.

exotic forests are primarily found at mid and low elevations (i.e. below 500 m a.s.l.) and are composed of non-native species such as *Cryptomeria japonica*, *Eucalyptus globulus*, *Pittosporum undulatum* and *Acacia melanoxylon*, *P. undulatum* having and invasive status.

Sampling sites (20 × 20 m) for this study were located in both native and exotic forests and were selected to represent a range of elevations and habitat conditions, with a focus on mid-elevation exotic stands where relict arthropod populations were expected to persist (Fig. 1, Table 1). A subset of these sites (n = 15) was included in the long-term monitoring project conducted on the island of Terceira (Borges et al., 2022; Borges et al., 2022b; Costa and Borges, 2021; Lhoumeau et al., 2022b, 2022a). The remaining five sites were originally designed for a study aiming to evaluate vertical stratification in forest arthropod assemblages (Lhoumeau and Borges, 2025).

2.2. *Arthropod data source and pre-processing*

All arthropod data used in this study were sourced from Lhoumeau et al. (2025b). This dataset consists of standardised samples collected using SLAM (Sea, Land, and Air Malaise) traps and pitfall traps across native and exotic forests plots. SLAM traps are effective passive flight-interception traps designed to capture mobile arthropods across multiple forest strata (Borges, 2025). They were deployed at three vertical levels (ground - GRD, understory - UND and canopy - CAN) with at least one vertical meters between each trap (Fig. 2, left). Per site, 14 non-attractive pitfall traps were set up to effectively sample the epigean arthropods fauna (level EPI). The pitfalls were distributed randomly within the 20 × 20 m sampling plots. The plots were subdivided into four subplots, with each subplot containing three or four pitfalls separated by a minimum of two metres to ensure consistent spatial coverage (Fig. 2, right). Further information regarding the design of the sampling can be found in Lhoumeau et al. (2025b).

The collected specimens were identified to the lowest taxonomic level possible by a taxonomic specialist. In the follow-up to earlier studies in these ecosystems, the following classes and orders were targeted: Diplopoda (Chordeumatida, Julida), Chilopoda (Geophilomorpha, Lithobiomorpha, Scolopendromorpha), Arachnida (Araneae, Opiliones, Pseudoscorpiones), and Insecta (Blattaria, Coleoptera, Hemiptera, Hymenoptera-Formicidae, Microcoryphia, Neuroptera, Psocodea, Strepsiptera, Thysanoptera and Trichoptera). In accordance with the most recently published checklist of Azorean arthropods (Borges et al., 2022a), the identified arthropods were classified into three biogeographical categories. The term ’endemic’ is used to describe species that are confined to the Azores archipelago. ’Native non-endemic’ refers to species that occur naturally elsewhere. ’Introduced’ describes species that have been accidentally or deliberately introduced by humans. For the purpose of this study, the focus was exclusively on adult individuals of indigenous species (endemic and native non-endemic). Juveniles were excluded from the dataset, as their identification across all taxa might be unreliable, and they may not accurately reflect stable habitat associations.

2.3. *Statistical analyses and modelling*

To explore the ecological and biogeographic drivers influencing the persistence of indigenous arthropod species in exotic forests, we computed several variables (Table 2). Data on body size, trophic guild and dispersal ability were sourced from recent studies on the species in the Azores archipelago (Oyarzabal et al., 2025a, 2025b; Rigal et al., 2018). Other variables are derived from the published dataset (Lhoumeau et al., 2025b). All compiled data are available in Supplementary Material.

The Model 1 was used to assess the variation in abundance among indigenous arthropod species in exotic forest plots. We selected species that were sampled in both forest types and used the percentage of difference of abundance of the species as response variable (Equation 1).

Table 1
Geographical characteristics of the sampling sites.

Habitat type	Site code	Locality	Decimal longitude	Decimal latitude	Elevation above sea level (m)
Exotic forest	TER-EXO-T01	Mata do Estado	−27.24	38.697	425
Exotic forest	TER-EXO-T02	Matela	−27.26	38.7	394
Exotic forest	TER-EXO-T04	Serreta 400	−27.352	38.765	376
Exotic forest	TER-EXO-T09	Caparica Horses	−27.263	38.762	417
Exotic forest	TER-EXO-T10	Gruta dos Balcões	−27.25	38.759	459
Exotic forest	TER-PRIBS-T06	Caparica	−27.262	38.771	336
Exotic forest	TER-PRIBS-T09	Fontinhas	−27.138	38.738	256
Exotic forest	TER-PRIBS-T15	Agualva	−27.193	38.769	367
Exotic forest	TER-PRIBS-T27	Gruta do Chocolate	−27.249	38.779	271
Exotic forest	TER-PRIBS-T28	Pico Rachado	−27.31	38.769	461
Native forest	TER-NFBF-T−01	Morro Assombrado	−27.219	38.762	680
Native forest	TER-NFBF-T−02	Biscoito da Ferraria	−27.233	38.752	590
Native forest	TER-NFBF-TP41	Pico Alto	−27.207	38.75	673
Native forest	TER-NFPG-T−33	Pico Galhardo	−27.227	38.734	643
Native forest	TER-NFSB-T−07	Lomba	−27.29	38.737	683
Native forest	TER-NFSB-T164B	Caldeira de Santa Bárbara	−27.308	38.735	899
Native forest	TER-NFSB-TE48	Lagoinha	−27.331	38.752	678
Native forest	TER-NFSB-TE49	Lagoa do Pinheiro	−27.331	38.752	927
Native forest	TER-NFTB-T−15	Terra Brava A	−27.201	38.736	637
Native forest	TER-NFTB-T−18	Terra Brava B	−27.197	38.732	679

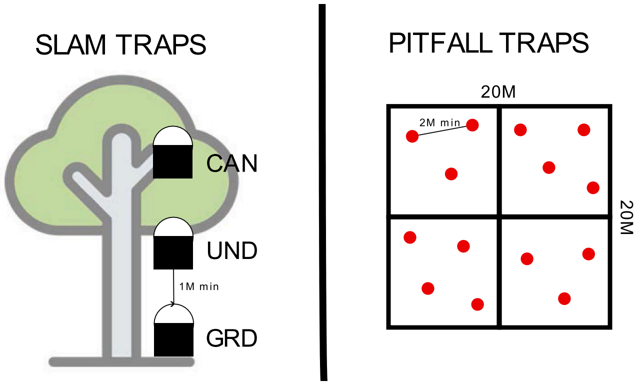

Fig. 2. Sampling design. Left: On a focal tree, three SLAM traps were deployed to sample distinct vertical strata: canopy (CAN), understory (UND), and ground level (GRD), with a minimum vertical separation of 1 m between adjacent traps. Right: Pitfall traps within each 20 × 20 m plot. The plot was divided into four 10 × 10 m subplots, and traps (red circles) were placed at random locations with a minimum spacing of 2 m; each subplot held 3–4 pitfalls, yielding 14 traps per plot.

Table 2
Description of the variables used in the two Generalised Linear Mixed Models (GLMMs) that assess the abundance and presence of indigenous arthropod species in the exotic forests of Terceira Island in the Azores.

Variable Name	Description	Type	Used in Model 1	Used in Model 2
Order	Taxonomic order of the species	Categorical	✓ Random effect	✗
Abundance variation	Percentage of difference of abundance of the species within exotic and native forests (see Equation 1)	Numeric	✓ Response	✗
Presence exotic	Binary variable indicating presence (1) or pseudo-absence (0) of the species in exotic forests	Binary	✗	✓ Response
Mean weighted Sampled elevation	Mean elevation (m a.s.l.) of all plots where the species was sampled, weighted by the abundance sampled at each elevation (see Equation 2)	Numeric	✓	✓
Frequency	Proportion of the 20 plots in which the species was sampled	Numeric	✓	✓
Body size	Mean body size of the species (in mm)	Numeric	✓	✓
Trophic	Trophic guild of the species	Categorical	✓	✓
Dispersal ability	Dispersal mean of the species	Categorical	✓	✓
Proportion EPI	Proportion of the standardised abundance of the species sampled on the epigean layer (EPI) (by pitfall traps)	Numeric	✓	✓
Proportion GRD	Proportion of the standardised abundance of the species sampled in the ground layer (GRD) (by SLAM traps)	Numeric	✓	✓
Proportion UND	Proportion of the standardised abundance of the species sampled in the understory layer (UND) (by SLAM traps)	Numeric	✓	✓
Proportion CAN	Proportion of the standardised abundance of the species sampled in the canopy layer (CAN) (by SLAM traps)	Numeric	✓	✓

Equation 1. : Formula used to compute the variation of abundance between exotic and native forests. Results are in percentage and positive values indicate higher abundance in exotic forest. Ab_{EXO} and Ab_{NAT} represent the total abundance of the species sampled respectively in exotic and native plots. Results range on an open interval.

$$Abundance\ variation = \left(\frac{Ab_{EXO}}{Ab_{NAT} - 1}\right) \times 100$$

Equation 2. : Formula used to compute the mean weighted sampled elevation of a species. Results are in meters. $Elev_i$ and Ab_i are respectively the elevation of the samples and the abundance of the species at this elevation. Ab_{TOT} represent the total sampled abundance of the species across all the 20 plots.

$$Mean\ weighted\ sampled\ elevation = \sum_i Elev_i \times \frac{Ab_i}{Ab_{TOT}}$$

To assess potential multicollinearity among explanatory variables, we calculated the Variance Inflation Factor (VIF) for each fixed effect prior to model fitting. The Model 1 is a Linear Mixed Model (LMM). As fixed effects, we included species-level ecological and distributional traits (see Table 2). To account for taxonomic structure and potential phylogenetic non-independence, we included arthropod order as a random effect. The Model 2 aimed to identify the factors predicting whether a species occurs in exotic forests at all. Here, using a Generalized Linear Model (GLM), the response variable was binary (cf Table 2), following a binomial distribution with a logit link. This model included all indigenous species recorded in the study, including those only sampled in native forests. The same set of ecological and biogeographic predictors used in Model 1 was applied here. In this case, order was not used as a random effect due to it adding singularity to the model.

All analyses were conducted in R version 4.5.1 (R Core Team, 2025) using package *lme4* (Bates et al., 2015) to fit the LMM and GLM. Packages *performance* (Lüdecke et al., 2021), *lmerTest* (Kuznetsova et al., 2017) and *car* (Fox and Weisberg, 2019) were used to compute model diagnostics, variables collinearities and p-values. The Zuur method was used to drop the non-significant variables of the models (Zuur et al., 2010). Since the significant variables in the complete models (with all variables) where the same as the drop models (with only significant variables), here we present the results of the complete Model 1 and Model 2.

3. Results

3.1. Sampling of relict arthropod species

The final dataset comprised a total of 85 indigenous arthropod species, distributed across 15 taxonomic orders (see Table 3 for details). These included endemic species, which are limited to the Azores archipelago, and native non-endemic species that naturally occur in the region but have broader distributions. In the course of the present study, 65 species were recorded on at least one occasion in the exotic forest plots; these were therefore classified as relict populations for the purpose of further analysis. In addition, 21 species were only sampled in the ten exotic forest plots. Of the species that were solely sampled in the exotic forest, a mere three (*Athous azoricus, Heteroderes azoricus* and *Tarphius relictus*) are endemic. The remaining 18 are classified as native non-endemics. Among the evaluated species, one is classified as Critically Endangered (CR), seven as Endangered (EN), seven as Vulnerable (VU), six as Near Threatened (NT), eight as Least Concern (LC) and 56 are not evaluated by IUCN.

3.2. Comparison of abundance of relict arthropod species

The percentage ratio of abundance in exotic versus native habitats for the 44 indigenous species sampled in both habitats shows a wide range of responses (Fig. 3). A notable distinction was observed in the patterns exhibited by endemic and native non-endemic species. The range of variation of relative abundance of the 22 endemic species appear to be lower than the 22 native non-endemic. Specifically, six endemic species and seven native non-endemic species exhibited higher abundance in exotic plots compared to native plots. The statistical significance of these patterns was confirmed by a Mann-Whitney test ($W = 124$, p-value $= 0.006$), which demonstrated a significant difference between the two means in abundance (endemics = - 9.57 %, native non-endemics = + 75.69 %, as illustrated by the red dashed line on Fig. 3).

3.3. Elevation as the significant predictor of the variation in the abundance of the relict indigenous arthropod species

The model 1 was used to evaluate the significance of predictors of the variation in abundance among biogeographic relict species sampled in native and exotic forests ($n = 44$ species). The analysis revealed that the mean weighted sampled elevation was the most important factors explaining differences in abundance (Estimate: -1.051 ± 0.173, p-value < 0.001). Species that were predominantly sampled at low elevations were found to be more abundant in exotic forest plots. In contrast, those collected at higher elevations (in average above 500 m a.s.l.) were less abundant or more sporadically represented in exotic forests. Both fixed and random effects (R2 conditional) explained 60.4 % of the variance, indicating a good predictive performance. The pattern is visually summarised in Fig. 4, which shows the predicted effect of the mean weight sampled elevation on species abundance variation.

3.4. Elevation and spatial distribution as the most significant predictor of the presence of indigenous species in exotic forests

Model 2 examined the probability of presence of indigenous species in exotic forest plots, considering all indigenous species sampled during the study, including those found exclusively in a given forest type. Similarly to the previous model, we found that species presence in exotic forests was negatively correlated with its mean weighted sampled elevation (Estimate: -0.036 ± 0.014, p-value < 0.01). Additionally, we also found that the proportion of plots in which the species was sampled was significantly positive for the presence in exotic forests (Estimate: 16.451 ± 6.329, p-value < 0.01). The influence of elevation and the spatial distribution on the

Table 3
List of the indigenous species sampled in the 20 exotic and native forest plots with mention of the taxonomic order and the detailed biogeographic status from (Borges et al., 2022a) and the updated IUCN status of evaluated species from (Oyarzabal et al., 2025b). The species code is mentioned for reference in the following figures. Data are sourced from (Lhoumeau et al., 2025b).

Order	Scientific name	Biogeographic status (IUCN Status)	Species code
Araneae	*Acorigone acoreensis* (Wunderlich, 1992)	Endemic (VU)	312
	Canariphantes acoreensis (Wunderlich, 1992)	Endemic (VU)	50
	Gibbaranea occidentalis Wunderlich, 1989	Endemic (NT)	134
	Lasaeola oceanica Simon, 1883	Endemic (LC)	208
	Lathys dentichelis (Simon, 1883)	Native non-endemic	117
	Leucognatha acoreensis Wunderlich, 1992	Endemic (VU)	179
	Macaroeris cata (Blackwall, 1867)	Native non-endemic	198
	Macaroeris diligens (Blackwall, 1867)	Native non-endemic	793
	Microlinyphia johnsoni (Blackwall, 1859)	Native non-endemic	697
	Palliduphantes schmitzi (Kulczynski, 1899)	Native non-endemic	20
	Pardosa acorensis Simon, 1883	Endemic (LC)	17
	Pisaura acoreensis Wunderlich, 1992	Endemic (NT)	39
	Porrhoclubiona decora (Blackwall, 1859)	Native non-endemic	516
	Porrhomma borgesi Wunderlich, 2008	Endemic (VU)	4
	Rugathodes acoreensis Wunderlich, 1992	Endemic (NT)	5
	Savigniorrhipis acoreensis Wunderlich, 1992	Endemic (VU)	181
	Steatoda nobilis (Thorell, 1875)	Native non-endemic	869
	Tenuiphantes miguelensis (Wunderlich, 1992)	Native non-endemic	2
	Theridion musivivum Schmidt, 1956	Native non-endemic	241
	Walckenaeria grandis (Wunderlich, 1992)	Endemic (VU)	421
	Xysticus cor Canestrini, 1873	Native non-endemic	3
Opiliones	*Leiobunum blackwalli* Meade, 1861	Native non-endemic	6
Geophilomorpha	*Geophilus truncorum* Bergsøe & Meinert, 1866	Native non-endemic	26
	Strigamia crassipes (C.L. Koch, 1835)	Native non-endemic	287
Lithobiomorpha	*Lithobius pilicornis pilicornis* Newport, 1844	Native non-endemic	27
Archaeognatha	*Dilta saxicola* (Womersley, 1930)	Native non-endemic	279
	Trigoniophthalmus borgesi Mendes, Gaju, Bach & Molero, 2000	Endemic (EN)	144
Blattodea	*Zetha simonyi* (Krauss, 1892)	Native non-endemic	59
Coleoptera	*Anaspis proteus* Wollaston, 1854	Native non-endemic	78
	Athous azoricus Platia & Gudenzi, 2002	Endemic (EN)	136
	Calacalles subcarinatus (Israelson, 1984)	Endemic (LC)	141
	Catops coracinus Kellner, 1846	Native non-endemic	257
	Cedrorum azoricus azoricus Borges & A.Serrano, 1993	Endemic (EN)	346
	Cephennium validum Assing & Meybohm, 2021	Native non-endemic	283
	Drouetius borgesi borgesi (Machado, 2009)	Endemic (EN)	46
	Dryops algiricus (Lucas, 1846)	Native non-endemic	286
	Heteroderes azoricus (Tarnier, 1860)	Endemic (EN)	540
	Notothecta dryochares (Israelson, 1985)	Endemic (NT)	439
	Ocys harpaloides (Audinet-Serville, 1821)	Native non-endemic	15
	Pseudophloeophagus tenax borgesi Stüben, 2022	Endemic	102
	Psylliodes marcida (Illiger, 1807)	Native non-endemic	395
	Stilbus testaceus (Panzer, 1797)	Native non-endemic	69
	Tarphius relictus Borges & Serrano, 2017	Endemic (CR)	1216
	Trechus terrabravensis Borges, Serrano & Amorim, 2004	Endemic (EN)	222
Ephemeroptera	*Cloeon dipterum* (Linnaeus, 1761)	Native non-endemic	495
Hemiptera	*Acalypta parvula* (Fallén, 1807)	Native non-endemic	159
	Anthocoris nemoralis (Fabricius, 1794)	Native non-endemic	390
	Aphrodes hamiltoni Quartau & Borges, 2003	Endemic (EN)	8
	Campyloneura virgula (Herrich-Schaeffer, 1835)	Native non-endemic	574
	Cinara juniperi (De Geer, 1773)	Native non-endemic	44
	Cixius azoterceirae Remane & Asche, 1979	Endemic (VU)	7
	Cyphopterum adscendens (Herrich-Schäffer, 1835)	Native non-endemic	124
	Eupteryx azorica Ribaut, 1941	Endemic (NT)	465
	Eupteryx filicum (Newman, 1853)	Native non-endemic	1019
	Heterotoma planicornis (Pallas, 1772)	Native non-endemic	535
	Kelisia ribauti Wagner, 1938	Native non-endemic	321
	Kleidocerys ericae (Horváth, 1909)	Native non-endemic	167
	Loricula coleoptrata (Fallén, 1807)	Native non-endemic	530
	Megamelodes quadrimaculatus (Signoret, 1865)	Native non-endemic	254
	Monalocoris filicis (Linnaeus, 1758)	Native non-endemic	476
	Nabis pseudoferus ibericus Remane, 1962	Native non-endemic	230
	Orius laevigatus laevigatus (Fieber, 1860)	Native non-endemic	645
	Pilophorus perplexus Douglas & Scott, 1875	Native non-endemic	784
	Pinalitus oromii J. Ribes, 1992	Endemic (LC)	137
	Saldula palustris (Douglas, 1874)	Native non-endemic	248
	Scolopostethus decoratus (Hahn, 1833)	Native non-endemic	118

(*continued on next page*)

Table 3 (*continued*)

Order	Scientific name	Biogeographic status (IUCN Status)	Species code
	Strophingia harteni Hodkinson, 1981	Endemic (LC)	557
	Trioza laurisilvae Hodkinson, 1990	Native non-endemic	195
Hymenoptera	*Hypoponera eduardi* (Forel, 1894)	Native non-endemic	F2
	Lasius grandis Forel, 1909	Native non-endemic	F1
	Monomorium carbonarium (Smith, 1858)	Native non-endemic	F4
	Tetramorium caespitum (Linnaeus, 1758)	Native non-endemic	F6
Neuroptera	*Hemerobius azoricus* Tjeder, 1948	Endemic (LC)	200
Psocodea	*Atlantopsocus adustus* (Hagen, 1865)	Native non-endemic	205
	Bertkauia lucifuga (Rambur, 1842)	Native non-endemic	374
	Ectopsocus strauchi Enderlein, 1906	Native non-endemic	218
	Elipsocus azoricus Meinander, 1975	Endemic (LC)	184
	Elipsocus brincki Badonnel, 1963	Endemic (LC)	370
	Trichopsocus clarus (Banks, 1908)	Native non-endemic	478
	Valenzuela burmeisteri (Brauer, 1876)	Native non-endemic	625
	Valenzuela flavidus (Stephens, 1836)	Native non-endemic	191
Strepsiptera	*Elenchus tenuicornis* (Kirby, 1815)	Native non-endemic	1680
Thysanoptera	*Ceratothrips ericae* (Haliday, 1836)	Native non-endemic	498
	Hoplothrips corticis (De Geer, 1773)	Native non-endemic	13
Trichoptera	*Limnephilus atlanticus* Nybom, 1948	Endemic (NT)	432

likelihood of occurrence in exotic forests is illustrated in Fig. 5.

4. Discussion

It is imperative to understand the mechanisms through which native species persist in human-modified landscapes to achieve the conservation of biodiversity in increasingly altered ecosystems (Fischer and Lindenmayer, 2007). Following previous findings on Terceira (Cardoso et al., 2009; Tsafack et al., 2021) and Santa Maria islands (Meijer et al., 2011), the present study offers a deeper investigation into the distribution of indigenous (endemic and native non-endemic) arthropod species within exotic forest habitats in the Azores. The primary objective was to identify the ecological and environmental factors that shape the presence and abundance of these species. By combining standardised sampling across forest types with trait-based modelling, we aimed to determine the conditions under which biogeographic relict populations can persist in these novel ecosystems and to assess the influence of biotic and abiotic variables on their current distribution.

We found that species with large range size and with greater abundance at low elevation were more likely to be sampled in exotic forests, whereas those with population with restricted distribution and in average sampled at higher elevation were consistently absent. Hence, our findings support the first hypothesis: species historically associated with mid to low elevation habitats are more likely to persist in exotic forests, highlighting the importance of historical elevational range as a key driver of relict species distribution. However, the second hypothesis predicting that species-level ecological traits such as dispersal ability, trophic guild, body size, or vertical stratification would explain persistence, was not supported. This outcome suggests that historical biogeographic context, rather than functional ecological characteristics, is more likely to be the dominant driver of the current arthropod assemblages in exotic forests of Terceira.

4.1. Historical elevational niche as a driver of relict species persistence

The findings suggest that elevation is the most significant environmental factor influencing the distribution of indigenous arthropod species in exotic forest habitats on Terceira Island. Amongst all the indigenous species included in the present dataset, those with a mean sampling elevation at or below approximately 500 m a.s.l. exhibited high variation in abundance within exotic forest plots. Conversely, species typically associated with higher elevations demonstrated consistently low abundance or were entirely absent from exotic woodlands. It is hypothesised that this elevational pattern may be indicative of a historical distribution. The exotic forests examined in this study are predominantly situated at mid to low elevations, which is below the extent of best-preserved vegetation belts that are now restricted to areas above 600 m a.s.l. (Elias et al., 2016). Consequently, mid-elevation arthropod endemic or native non-endemic species that naturally occur prior to substantial structural change in habitat may be pre-adapted to the abiotic conditions found in these transformed ecosystems. Conversely, species adapted to higher elevations may be unable to persist due to unsuitable microclimates, vegetation structure, or resource availability.

Research on arthropod communities reveals complex patterns of diversity and abundance distribution along elevational gradients. Examples of studies in Alaska, Arizona, and the Azores show that arthropod species composition changes significantly with elevation (De Vries et al., 2021; Haberski et al., 2023; Uhey et al., 2021). However, these patterns of abundance variation vary among functional and taxonomic groups (De Vries et al., 2021; Uhey et al., 2022). Also, it is noteworthy that habitat type interacts with these elevational patterns, with forested habitats exhibiting an increase in cover with elevation (Uhey et al., 2022), while climate factors, vegetation structure, and human disturbance influence arthropod distributions (De Vries et al., 2021; Haberski et al., 2023).

However, one clear exception, is the ground-beetle *Cedrorum azoricus azoricus,* a subspecies previously known to inhabit primarily high-elevation pristine “*Juniperus-Ilex*” montane forests in Terceira Island (Borges, 2018; Borges and Serrano, 1993). Prior ecological

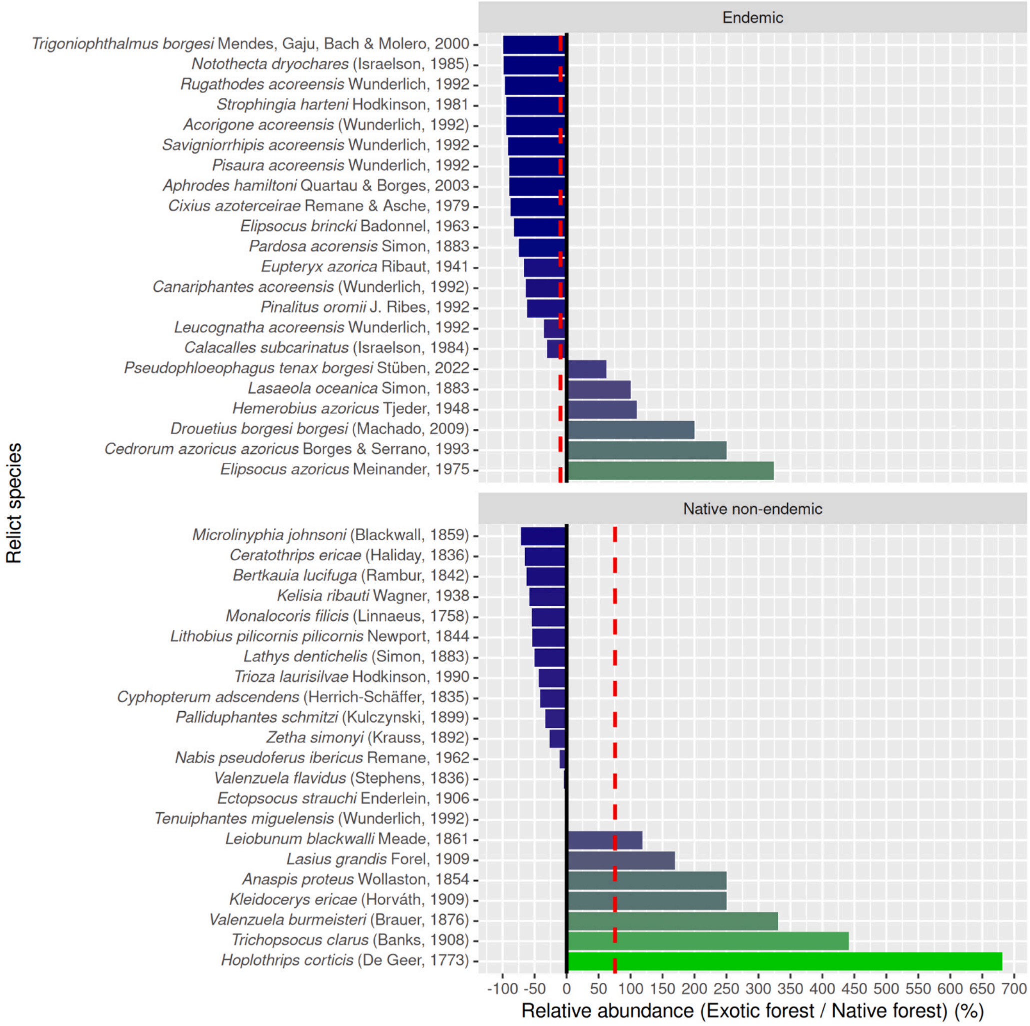

Fig. 3. Relative abundance (%) of 44 relict arthropod species sampled both in exotic and native forests on Terceira Island computed following Equation 1. Bars to the left of the line indicate lower abundance in exotic forests; bars to the right indicate higher abundance in exotic forests. Species are grouped by biogeographic category: Endemic (top panel, n = 22 species) and Native non-endemic (bottom panel, n = 22 species). The red dashed line indicates the mean relative abundance for each group.

models suggested that this beetle had a more restricted distribution than would be expected based on its local abundance at known sites (Gaston et al., 2006). Therefore, the discovery of a previously unknown population comprising a large number of individuals at a mid-elevation site, dominated by exotic vegetation was unexpected. These findings challenge earlier assumptions, as this large-bodied beetle, belonging to an endemic genus (see Borges and Serrano, 1993) was previously considered strictly adapted to dense, hyper-humid native forests confined primarily to ravines and deep valleys (Borges, 2018; Gaston et al., 2006). Furthermore, earlier modelling studies indicated that *C. azoricus azoricus*, having a limited dispersal capability, was particularly vulnerable to habitat fragmentation and the negative effects of degraded landscape matrices (Aparício et al., 2018). The presence of this significant population in such an atypical habitat raises intriguing ecological and conservation questions, suggesting greater adaptability or ecological plasticity than previously recognized, or indicating complex dynamics related to extinction debt and source-sink processes in fragmented island landscapes.

Our findings then suggest that even in highly modified landscapes, elevation continues to structure community assembly. The persistence of indigenous species in exotic forests is strongly constrained by their historical elevational niches given that native habitats extended to low altitudes prior to the 15th century (Elias et al., 2016; Triantis et al., 2010). Consequently, successful relict species are species whose elevational niches historically overlapped with the current location of exotic forests. Another support to this pattern is the current distribution of the endemic species solely found in exotic forests, namely the rare beetle species *Tarphius relictus* that is a low to mid land specialist and only found so far in an isolated patch of *Acacia* spp. in the old part of the island where no native forest is remaining (Borges et al., 2017).

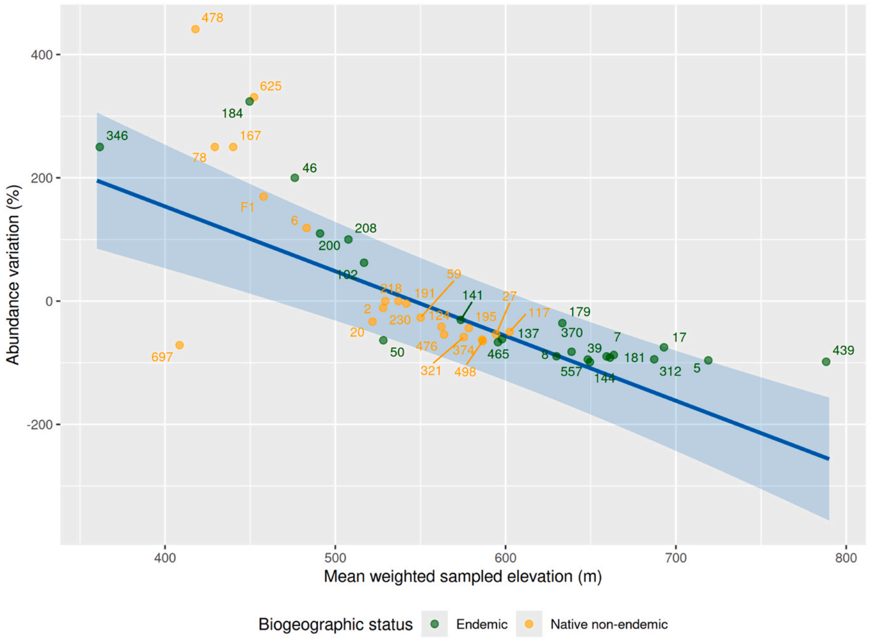

Fig. 4. Effect of the mean weight sampled elevation on the abundance of relict species in exotic forests of Terceira Island. Predicted values were derived from a Linear Mixed Model (LMM) fitted with a Gaussian distribution. Shaded areas represent 95 % confidence intervals. Only relict species recorded in both exotic and native forests (n = 44) were included in the model. Species codes available in the Table 3.

4.2. Ecological profiles of relict species: generalists, specialists, and survivors

Amongst the 44 indigenous species sampled in both forest types, a broad spectrum of responses in terms of relative abundance was observed. These heterogeneous responses suggest that intrinsic species characteristics (ecological or biogeographic) shape their ability to persist in these transformed ecosystems. With a few exceptions like *C. azoricus azoricus*, endemic species appeared to be more negatively affected by habitat change than native non-endemics. This suggests that native non-endemics are more likely to become dominant in the context of forest transformation.

This divergence in species response likely reflects inherent differences in niche breadth, ecological plasticity, and historical distribution patterns. Native non-endemic species, which generally exhibit wider distributions, may possess ecological traits that confer greater flexibility in adapting to novel environmental conditions, such as altered forest structures or microclimates (Grime and Pierce, 2012). This adaptability may explain their higher representation in human-modified habitats. For instance, in our study, 21 indigenous species were sampled exclusively in exotic forest plots—of which only three (*Tarphius relictus*, *Heteroderes azoricus*, and *Athous azoricus*) were endemics, while the remaining 18 were native non-endemics. This pattern suggests that some native non-endemic species may disproportionately benefit from anthropogenic habitat transformations, whereas endemic species, often restricted by specialized habitat and elevational requirements, remain at greater risk (Gaston et al., 2006). It is acknowledged that the colonisation status of certain species may not be definitive, which could lead to alterations in the interpretation of our results as some taxa currently classified as non-endemic indigenous may in fact be exotic (Borges et al., 2006; Jiménez-García et al., 2023).

Nevertheless, exceptions to this trend exist. Some endemic species, such as the wolf-spider *Pardosa acoreensis*, have been observed across a broad range of habitats and elevations in the Azores (Borges and Wunderlich, 2008), reflecting a degree of generalist behaviour not typically associated with insular endemics. These cases illustrate that even species with limited population sizes and localized distributions can, in some instances, adapt to fragmented or novel ecosystems. For example, exotic forest patches ("islands within the island") on Terceira exhibit greater structural heterogeneity than native forests (Lhoumeau et al., 2025a), potentially offering microhabitats suitable for some indigenous species. However, despite their broad habitat use, even widespread endemic species often exhibit lower relative abundance in exotic forests, suggesting that these "mitigation strategies" do not necessarily translate into ecological success. Indeed, exotic forests act as ecological filters, favouring species with certain elevational and spatial traits (Cardoso et al., 2009), and this selectivity is shaped by both species-level ecological traits and past distribution dynamics. As shown by (Gorman et al., 2014) in *Eucalyptus* species, even when endemics occupy varied habitats, they often converge on a narrow suite of functional traits, a phenomenon described as an “endemic syndrome of traits”, which may constrain their resilience in the face of novel environmental pressures.

4.3. Relictual dynamics: extinction debt and source-sink processes

Persistence does not imply long-term stability, it may reflect a classic case of extinction debt (Triantis et al., 2010) and source–sink

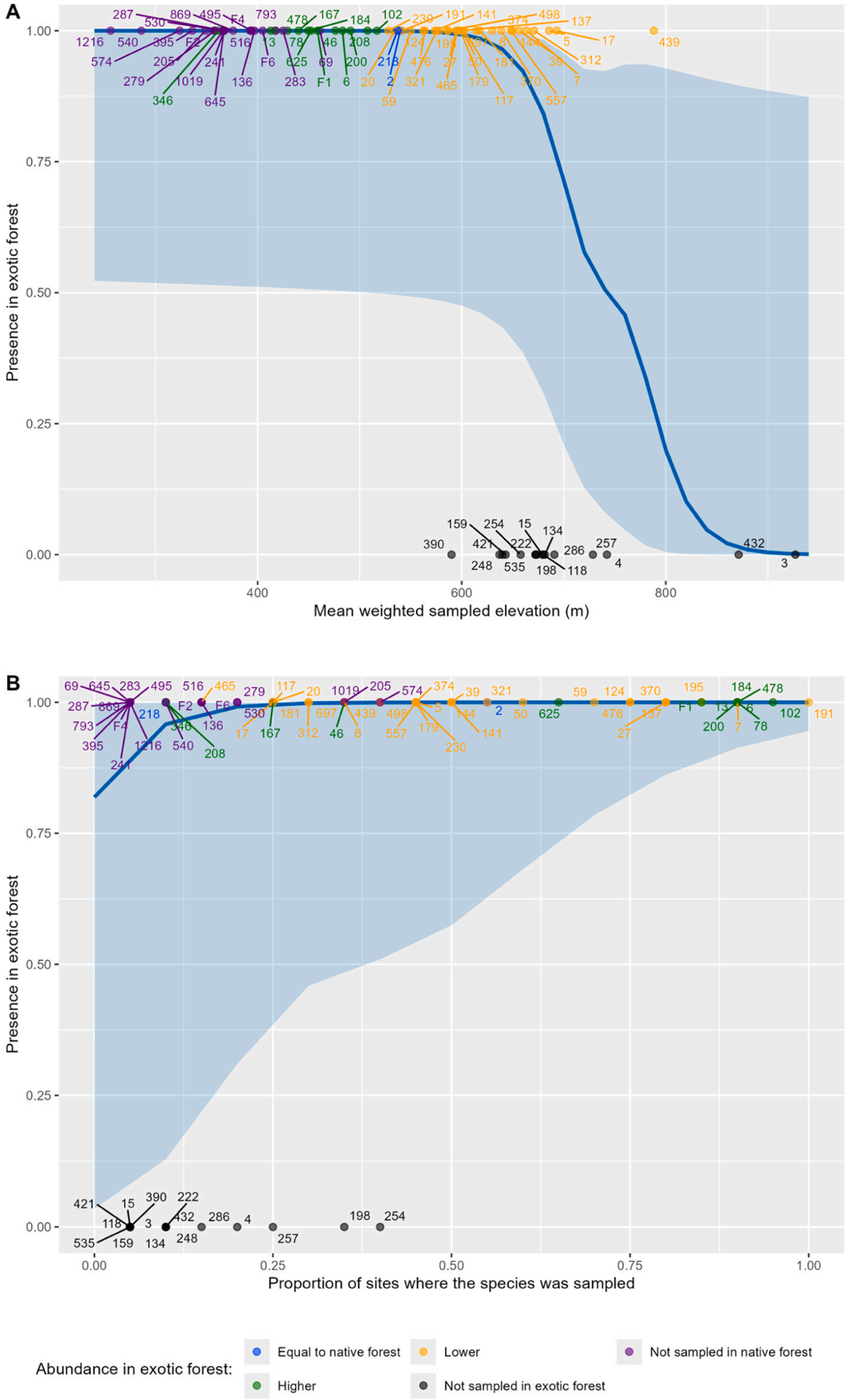

Fig. 5. Effect of the elevation (A) and the spatial distribution (B) on the probability of presence of indigenous arthropod species in exotic forests. Predicted values were derived from a binomial GLM (logit link) including all indigenous species. Shaded areas represent 95 % confidence intervals. Species codes available in the Table 3.

dynamics. Certain high-elevation species, mostly endemics, are occasionally recorded in exotic forests, likely as transient occurrences from adjacent native habitats. Their low abundance and absence from many exotic sites suggest these areas function as ecological sinks—patches where reproduction or survival is insufficient to sustain populations without immigration. This is consistent with the significant negative effect of mean elevation on both abundance (Model 1) and presence (Model 2) in exotic forests. Species primarily associated with higher elevations are simply not tracked into these lower elevation forests in viable numbers.

This situation reveals a dual pressure on community dynamics: while exotic species exert well-known impacts on native ecosystems, indigenous species are also extending into novel forest types, perhaps in search of suitable resources or through passive dispersal. The result may be an increasing biotic homogenization of forest ecosystems where species from different original communities co-occur in modified habitats. This ongoing process may eventually lead to mixed communities of adaptable native and introduced taxa, while more specialized endemics disappear altogether.

4.4. Conservation implications: from remnants to resilience

The presence of indigenous relict arthropod populations in exotic forests of Terceira highlights an important and often overlooked dimension of biodiversity conservation: the value of transformed, non-native, and non-protected ecosystems as transient refuges for native species (see also Fattorini et al., 2012). While these exotic forests are far from ecologically equivalent to native forests, our results suggest that they still host a fraction of the island's indigenous arthropod fauna, particularly species historically associated with mid-elevation zones.

This has three key implications. First, these areas could serve as biological reservoirs or facilitators of recolonization in future restoration efforts, targeting a landscape mosaic management (Brockerhoff et al., 2013). The fact that many species still persist in exotic stands, albeit at altered abundances, indicates that the full collapse of native assemblages has not yet occurred. In such cases, passive or assisted restoration towards native ecosystems might succeed more rapidly than expected if relict populations remain to seed recovery. These systems may also provide ecosystem functions, such as predation or nutrient cycling, that buffer against total ecological degradation.

Second, these findings should reshape how conservation priorities are set in the Azores and similar island systems. With some exceptions (Matela and Fontinhas patches) most of the exotic forest plots in this study lie outside formally protected areas and are often privately owned, making them especially vulnerable to further land-use change. Their status depends largely on landowner decisions, yet they currently play a key role in maintaining opportunities for indigenous to thrive. We argue that these areas should be formally recognized as micro-reserves, Key Biodiversity Areas (KBAs) or designated as conservation-relevant transitional habitats, especially in landscapes where native forests are limited (Fattorini et al., 2024).

Third, under the recently adopted EU "2030 Nature Restoration Law", Member States are legally obliged to restore degraded terrestrial ecosystems, including afforested and semi-natural habitats, by 2030. This regulation provides both a binding mandate and dedicated funding instruments that could be mobilized to (1) integrate exotic forest patches hosting relict arthropod populations into national restoration targets, and (2) incentivize landowners to manage these stands not only for timber or biomass but also for biodiversity recovery and connectivity. For instance, some years ago the exotic forest site where *Tarphius relictus* was found was included in the Natural Protected Area of Terceira Island guaranteeing the long-term persistence of this rare Critically Endangered beetle (Borges and Lamelas-López, 2017).

Nevertheless, caution is warranted. The restricted presence of endemic species in exotic forests, and the sharp decline in their abundance with increasing elevation, emphasizes that exotic forests do not offer full refuge for these taxa. Although endemic species possess genetic or behavioural adaptations that allow them to cope with small and fragmented populations, which is common among island taxa (Vicente, 1999) and may explain their persistence despite habitat degradation, such resilience is not limitless. Ecological thresholds, such as critical minimum population sizes, habitat patch sizes, or disruption of species interactions, could still push these species toward decline or extinction. In fact, endemics confined to higher elevations face a compounded risk under climate change (Ferreira et al., 2019): their suitable climatic range is limited, and no thermal refugee exist above current elevations. Moreover, they face isolation in a fragmented native forest (Aparício et al., 2018). Without intervention, these species may become increasingly restricted, first ecologically, then geographically, and eventually demographically.

The present study highlights the imperative for conservation measures to be implemented across the entire Azorean forest mosaic. A particular set of action must be implemented in secondary, exotic, and transitional forests to gradually converted them toward native vegetation. Delayed biodiversity responses whether due to extinction debt or slow ecological filtering should not be misinterpreted as resilience. Instead, they represent a narrowing window for action. In the face of ongoing climate pressure, land-use change, and biotic homogenization, the presence of relict species in exotic forests offers both a warning and an opportunity to act.

CRediT authorship contribution statement

Borges Paulo A. V.: Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Guilherme Oyarzabal:** Writing – review & editing, Writing – original draft, Validation, Software, Methodology, Formal analysis. **Sébastien Lhoumeau:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03935.

Data availability

Processed data are available as supplementary material. Sources of raw data are mentionned in the manuscript.

References

Altieri, M.A., 2007. Fatal harvest: old and new dimensions of the ecological tragedy of modern agriculture. Sustain. Resour. Manag. Edw. Elgar Lond. 189, 213.

Aparício, B.A., Cascalho, J., Cruz, M.J., Borges, P.A.V., Azevedo, E.B., Elias, R.B., Ascensão, F., 2018. Assessing the landscape functional connectivity using movement maps: a case study with endemic Azorean insects. J. Insect Conserv 22, 257–265. https://doi.org/10.1007/s10841-018-0059-7.

Basset, Y., Cizek, L., Cuénoud, P., Didham, R.K., Guilhaumon, F., Missa, O., Novotny, V., Ødegaard, F., Roslin, T., Schmidl, J., et al., 2012. Arthropod diversity in a tropical forest. Science 338, 1481–1484.

Basset, Y., Cizek, L., Cuénoud, P., Didham, R.K., Novotny, V., Ødegaard, F., Roslin, T., Tishechkin, A.K., Schmidl, J., Winchester, N.N., Roubik, D.W., Aberlenc, H.-P., Bail, J., Barrios, H., Bridle, J.R., Castaño-Meneses, G., Corbara, B., Curletti, G., Duarte Da Rocha, W., De Bakker, D., Delabie, J.H.C., Dejean, A., Fagan, L.L., Floren, A., Kitching, R.L., Medianero, E., Gama De Oliveira, E., Orivel, J., Pollet, M., Rapp, M., Ribeiro, S.P., Roisin, Y., Schmidt, J.B., Sørensen, L., Lewinsohn, T. M., Leponce, M., 2015. Arthropod distribution in a tropical rainforest: tackling a four dimensional puzzle. PLoS One 10, e0144110. https://doi.org/10.1371/journal.pone.0144110.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Borges, P.A.V., 2018. Cedrorum azoricus. https://doi.org/10.2305/IUCN.UK.2018-1.RLTS.T97113324A99166544.en.

Borges, P.A.V., 2025. Best practices for long-term monitoring of island arthropods: insights from the Azores Islands. Discov. Conserv 2, 11. https://doi.org/10.1007/s44353-025-00030-6.

Borges, P.A.V., Aguiar, C., Amaral, J., Amorim, I.R., André, G., Arraiol, A., Baz, A., Dinis, F., Enghoff, H., Gaspar, C., Ilharco, F., Mahnert, V., Melo, C., Pereira, F., Quartau, J.A., Ribeiro, S.P., Ribes, J., Serrano, A.R.M., Sousa, A.B., Strassen, R.Z., Vieira, L., Vieira, V., Vitorino, A., Wunderlich, J., 2005. Ranking protected areas in the Azores using standardised sampling of soil epigean arthropods. Biodivers. Conserv 14, 2029–2060. https://doi.org/10.1007/s10531-004-4283-y.

Borges, P.A.V., Amorim, I.R., Terzopoulou, S., Rigal, F., Emerson, B.C., Serrano, A.R.M., 2017. Cryptic diversity in the Azorean beetle genus Tarphius Erichson, 1845 (Coleoptera: Zopheridae): an integrative taxonomic approach with description of four new species. Zootaxa 4236. https://doi.org/10.11646/zootaxa.4236.3.1.

Borges, P.A.V., Gabriel, R., Fattorini, S., 2019. Biodiversity Erosion: Causes and Consequences. In: Leal Filho, W., Azul, A.M., Brandli, L., Özuyar, P.G., Wall, T. (Eds.), Life on Land, Encyclopedia of the UN Sustainable Development Goals. Springer International Publishing, Cham, pp. 1–10. https://doi.org/10.1007/978-3-319-71065-5_78-1.

Borges, P.A.V., Lamelas-Lopez, L., Andrade, R., Lhoumeau, S., Vieira, V., Soares, A., Borges, I., Boieiro, M., Cardoso, P., Crespo, L.C., Karsholt, O., Schülke, M., Serrano, A., Quartau, J.A., Assing, V., 2022a. An updated checklist of Azorean arthropods (Arthropoda). Biodivers. Data J. 10, e97682. https://doi.org/10.3897/BDJ.10.e97682.

Borges, P.A.V., Lamelas-Lopez, L., Stüben, P., Ros-Prieto, A., Gabriel, R., Boieiro, M., Tsafack, N., Ferreira, M.T., 2022. SLAM project - long term ecological study of the impacts of climate change in the natural forest of Azores: II - a survey of exotic arthropods in disturbed forest habitats. Biodivers. Data J. 10, e81410. https://doi.org/10.3897/BDJ.10.e81410.

Borges, P.A.V., Lamelas-López, L., 2017. *Tarphius relictus*. https://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T112214780A112214784.en.

Borges, P.A.V., Lamelas-López, L., Tsafack, N., Boieiro, M., Ros-Prieto, A., Gabriel, R., Nunes, R., Ferreira, M.T., 2022b. SLAM project - long term ecological study of the impacts of climate change in the natural forest of Azores: III - testing the impact of edge effects in a native forest of Terceira Island. Biodivers. Data J. 10, e85971. https://doi.org/10.3897/BDJ.10.e85971.

Borges, P.A.V., Lobo, J.M., Azevedo, E.B. de, Gaspar, C.S., Melo, C., Nunes, L.V., 2006. Invasibility and species richness of island endemic arthropods: a general model of endemic vs. exotic species. J. Biogeogr. 33, 169–187. https://doi.org/10.1111/j.1365-2699.2005.01324.x.

Borges, P.A.V., Rigal, F., Ros-Prieto, A., Cardoso, P., 2020. Increase of insular exotic arthropod diversity is a fundamental dimension of the current biodiversity crisis. Insect Conserv. Divers 13, 508–518. https://doi.org/10.1111/icad.12431.

Borges, P.A.V., Serrano, A.R.M., 1993. New taxa of Poecilini (Coleoptera, Carabidae, Pterostichinae) from the Azores. Boll. Mus. Reg. Sci. Nat. 11, 315–329.

Borges, P.A.V., Wunderlich, J., 2008. Spider biodiversity patterns and their conservation in the Azorean archipelago, with descriptions of new species. Syst. Biodivers. 6, 249–282. https://doi.org/10.1017/s1477200008002648.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Ferraz, S.F., 2013. Role of eucalypt and other planted forests in biodiversity conservation and the provision of biodiversity-related ecosystem services. For. Ecol. Manag 301, 43–50.

Burkey, T.V., 1995. Extinction rates in archipelagoes: implications for populations in fragmented habitats. Conserv. Biol. 9, 527–541. https://doi.org/10.1046/j.1523-1739.1995.09030527.x.

Cardoso, P., Aranda, S.C., Lobo, J.M., Dinis, F., Gaspar, C., Borges, P.A.V., 2009. A spatial scale assessment of habitat effects on arthropod communities of an oceanic island. Acta Oecologica 35, 590–597. https://doi.org/10.1016/j.actao.2009.05.005.

Cheptou, P.-O., Hargreaves, A.L., Bonte, D., Jacquemyn, H., 2017. Adaptation to fragmentation: evolutionary dynamics driven by human influences. Philos. Trans. R. Soc. B Biol. Sci. 372, 20160037. https://doi.org/10.1098/rstb.2016.0037.

Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S., Massot, M., 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecol. Lett. 12, 197–209.

Costa, R., Borges, P.A.V., 2021. SLAM project - long term ecological study of the impacts of climate change in the natural forest of Azores: I - the spiders from native forests of Terceira and Pico Islands (2012-2019). Biodivers. Data J. 9, e69924. https://doi.org/10.3897/BDJ.9.e69924.

Costa, R., Cardoso, P., Rigal, F., Borges, P.A.V., 2023. Island spider origins show complex vertical stratification patterns in Macaronesia. Insect Conserv. Divers 16, 886–895. https://doi.org/10.1111/icad.12686.

Davison, C.W., Rahbek, C., Morueta-Holme, N., 2021. Land-use change and biodiversity: challenges for assembling evidence on the greatest threat to nature. Glob. Change Biol. 27, 5414–5429. https://doi.org/10.1111/gcb.15846.

De Vries, J.P.R., Van Loon, E., Borges, P.A.V., 2021. A small-scale analysis of elevational species richness and beta diversity patterns of arthropods on an oceanic island (Terceira, Azores). Insects 12, 936. https://doi.org/10.3390/insects12100936.

Di Marco, M., Venter, O., Possingham, H.P., Watson, J.E.M., 2018. Changes in human footprint drive changes in species extinction risk. Nat. Commun. 9. https://doi.org/10.1038/s41467-018-07049-5.

Elias, R.B., Gil, A., Silva, L., Fernández-Palacios, J.M., Azevedo, E.B., Reis, F., 2016. Natural zonal vegetation of the Azores Islands: characterization and potential distribution. Phytocoenologia 46, 107–123. https://doi.org/10.1127/phyto/2016/0132.

Ewers, R.M., Didham, R.K., 2005. Confounding factors in the detection of species responses to habitat fragmentation. Biol. Rev. 81, 117. https://doi.org/10.1017/s1464793105006949.

Fattorini, S., Cardoso, P., Rigal, F., Borges, P.A.V., 2012. Use of arthropod rarity for area prioritisation: insights from the Azorean Islands. PLoS One 7, e33995. https://doi.org/10.1371/journal.pone.0033995.

Fattorini, S., Dapporto, L., Borges, P.A.V., 2024. Protected areas and insect conservation. In: Pryke, J.S., Samways, M.J., New, T.R., Cardoso, P., Gaigher, R. (Eds.), Protected Areas and Insect Conservation. Routledge, Taylor & Francis Group, New York, pp. 146–158.

Fernández-Palacios, J.M., De Nascimento, L., Otto, R., Delgado, J.D., García-del-Rey, E., Arévalo, J.R., Whittaker, R.J., 2011. A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests: Palaeo-Macaronesia and the Atlantic island laurel forests. J. Biogeogr. 38, 226–246. https://doi.org/10.1111/j.1365-2699.2010.02427.x.

Ferreira, M.T., Cardoso, P., Borges, P.A.V., Gabriel, R., De Azevedo, E.B., Elias, R.B., 2019. Implications of climate change to the design of protected areas: the case study of small islands (Azores). PLoS One 14, e0218168. https://doi.org/10.1371/journal.pone.0218168.

Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. Glob. Ecol. Biogeogr. 16, 265–280. https://doi.org/10.1111/j.1466-8238.2007.00287.x.

Fox, J., Weisberg, S., 2019. An R Companion to Applied Regression, Third. ed. Sage, Thousand Oaks CA.

Garant, D., 2020. Natural and human-induced environmental changes and their effects on adaptive potential of wild animal populations. Evol. Appl. 13, 1117–1127. https://doi.org/10.1111/eva.12928.

Gaston, K.J., Blackburn, T.M., 1996. Range size-body size relationships: evidence of scale dependence. Oikos 479–485.

Gaston, K.J., Borges, P.A.V., He, F., Gaspar, C., 2006. Abundance, spatial variance and occupancy: arthropod species distribution in the Azores. J. Anim. Ecol. 75, 646–656.

Gibb, H., Stoklosa, J., Warton, D.I., Brown, A., Andrew, N.R., Cunningham, S., 2015. Does morphology predict trophic position and habitat use of ant species and assemblages? Oecologia 177, 519–531.

Gillespie, R.G., Roderick, G.K., 2002. Arthropods on Islands: colonization, speciation, and conservation. Annu. Rev. Entomol. 47, 595–632. https://doi.org/10.1146/annurev.ento.47.091201.145244.

Gorman, C.E., Potts, B.M., Schweitzer, J.A., Bailey, J.K., 2014. Shifts in species interactions due to the evolution of functional differences between endemics and non-endemics: an endemic syndrome hypothesis. PLoS One 9, e111190. https://doi.org/10.1371/journal.pone.0111190.

Grime, J.P., Pierce, S., 2012. The evolutionary strategies that shape ecosystems. John Wiley & Sons.

Habel, Jan C., Assmann, T., Schmitt, T., Avise, J.C., 2010. Relict Species: From Past to Future. In: Habel, Jan Christian, Assmann, T. (Eds.), Relict Species. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 1–5.

Haberski, A., Rykken, J., Sikes, D.S., 2023. Arthropod communities along an elevation gradient in Denali National Park and Preserve, Alaska: rapidly shrinking tundra hosts a unique assemblage of specialists. Arct. Antarct. Alp. Res. 55. https://doi.org/10.1080/15230430.2023.2178149.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1. https://doi.org/10.1126/sciadv.1500052.

Halley, J.M., Monokrousos, N., Mazaris, A.D., Newmark, W.D., Vokou, D., 2016. Dynamics of extinction debt across five taxonomic groups. Nat. Commun. 7. https://doi.org/10.1038/ncomms12283.

Hanski, I., Ovaskainen, O., 2000. The metapopulation capacity of a fragmented landscape. Nature 404, 755–758.

Hodkinson, I.D., 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. Biol. Rev. 80, 489–513.

Holyoak, M., Heath, S.K., 2016. The integration of climate change, spatial dynamics, and habitat fragmentation: a conceptual overview. Integr. Zool. 11, 40–59. https://doi.org/10.1111/1749-4877.12167.

Jiménez-García, E., Andújar, C., López, H., Emerson, B.C., 2023. Towards understanding insect species introduction and establishment: a community-level barcoding approach using island beetles. Mol. Ecol. 32, 3778–3792.

Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M., Steffan-Dewenter, I., 2009. Extinction debt: a challenge for biodiversity conservation. Trends Ecol. Evol. 24, 564–571. https://doi.org/10.1016/j.tree.2009.04.011.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. J. Stat. Softw. 82, 1–26. https://doi.org/10.18637/jss.v082.i13.

Lhoumeau, S., Borges, P.A.V., 2023. Assessing the impact of insect decline in islands: exploring the diversity and community patterns of indigenous and non-indigenous arthropods in the Azores native forest over 10 years. Diversity 15, 753. https://doi.org/10.3390/d15060753.

Lhoumeau, S., Borges, P.A.V., 2025. Up from the bottom: consistent vertical distance-decay in arthropod assemblage similarity across native and exotic forests in Terceira island (Azores). For. Ecol. Manag 596, 123059. https://doi.org/10.1016/j.foreco.2025.123059.

Lhoumeau, S., Cardoso, P., Boieiro, M., Ros-Prieto, A., Costa, R., Lamelas-Lopez, L., Leite, A., Amorim do Rosário, I., Gabriel, R., Malumbres-Olarte, J., Rigal, F., Santos, A., Tsafack, N., Ferreira, M., Borges, P.A.V., 2022a. SLAM project - long term ecological study of the impacts of climate change in the natural forests of Azores: V - new records of terrestrial arthropods after ten years of SLAM sampling. Biodivers. Data J. 10, e97952. https://doi.org/10.3897/BDJ.10.e97952.

Lhoumeau, S., Cardoso, P., Costa, R., Boieiro, M., Malumbres-Olarte, J., Amorim, I., Rigal, F., Santos, A., Gabriel, R., Borges, P.A.V., 2022b. SLAM project - long term ecological study of the impacts of climate change in the natural forest of Azores: IV - the spiders of Terceira and Pico Islands (2019-2021) and general diversity patterns after ten years of sampling. Biodivers. Data J. 10, e96442. https://doi.org/10.3897/BDJ.10.e96442.

Lhoumeau, S., Elias, R.B., Seidel, D., Gabriel, R., Borges, P.A.V., 2025a. Landscape to microhabitat: uncovering the multiscale complexity of native and exotic forests on Terceira Island (Azores, Portugal). PLOS One 20, e0326304. https://doi.org/10.1371/journal.pone.0326304.

Lhoumeau, S., Leite, A., Parmentier, L., Massard, C., Vounatsi, M., Lucie, G., Borges, P.A.V., 2025b. Vertical distribution of arthropod assemblages in native and exotic forests of Terceira Island (Azores, Portugal). Biodivers. Data J. 13, e154240. https://doi.org/10.3897/BDJ.13.e154240.

Lourenço, P., Medeiros, V., Gil, A., Silva, L., 2011. Distribution, habitat and biomass of Pittosporum undulatum, the most important woody plant invader in the Azores Archipelago. For. Ecol. Manag 262, 178–187. https://doi.org/10.1016/j.foreco.2011.03.021.

Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., Makowski, D., 2021. performance: an R package for assessment, comparison and testing of statistical models. J. Open Source Softw. 6, 3139. https://doi.org/10.21105/joss.03139.

Meijer, S.S., Whittaker, R.J., Borges, P.A.V., 2011. The effects of land-use change on arthropod richness and abundance on Santa Maria Island (Azores): unmanaged plantations favour endemic beetles. J Insect Conserv 15, 505–522. https://doi.org/10.1007/s10841-010-9330-2.

Nešić, M., Bjedov, I., 2021. Habitat degradation: Pressures, threats, and conservation. In: Leal Filho, W., Azul, A.M., Brandli, L., Lange Salvia, A., Wall, T. (Eds.), Life on Land. Springer International Publishing, Cham, pp. 501–514. https://doi.org/10.1007/978-3-319-95981-8_65.

Novotny, V., Drozd, P., Miller, S.E., Kulfan, M., Janda, M., Basset, Y., Weiblen, G.D., 2006. Why are there so many species of herbivorous insects in tropical rainforests? Science 313, 1115–1118.

Oyarzabal, G., Cardoso, P., Rigal, F., Boieiro, M., Santos, A.M.C., Amorim, I.R., Malumbres-Olarte, J., Costa, R., Lhoumeau, S., Pozsgai, G., Gabriel, R., Borges, P.A.V., 2025a. Species traits may predict extinction risk of Azorean endemic arthropods. Insect Conserv. Divers. n/a. https://doi.org/10.1111/icad.12822.

Oyarzabal, G., Pozsgai, G., Tsafack, N., Cardoso, P., Rigal, F., Boieiro, M., Santos, A.M.C., Amorim, I.R., Malumbres-Olarte, J., Costa, R., Lhoumeau, S., Gabriel, R., Borges, P.A.V., 2025b. Threats and conservation status of the endemic terrestrial arthropods of the Azores. Biol. Conserv. 309, 111282. https://doi.org/10.1016/j.biocon.2025.111282.

Pavão, D.C., Brunner, D., Resendes, R., Jevšenak, J., Borges Silva, L., Silva, L., 2024. Climatic drivers and tree growth in a key production species: the case of Cryptomeria japonica (Thunb. ex L.f.) D.Don in the Azores archipelago. Dendrochronologia 85, 126204. https://doi.org/10.1016/j.dendro.2024.126204.

Peacock, M.M., 2025. Negotiating a fragmented world: what do we know, how do we know it, and where do we go from here? Diversity 17, 200. https://doi.org/10.3390/d17030200.

R Core Team, 2025. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rigal, F., Cardoso, P., Lobo, J.M., Triantis, K.A., Whittaker, R.J., Amorim, I.R., Borges, P.A.V., 2018. Functional traits of indigenous and exotic ground-dwelling arthropods show contrasting responses to land-use change in an oceanic island, Terceira, Azores. Divers. Distrib. 24, 36–47. https://doi.org/10.1111/ddi.12655.

Sala, O.E., Stuart Chapin, F., Iii, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774. https://doi.org/10.1126/science.287.5459.1770.

Samper, C., 2010. Biodiversity, Nature and Food Security: A Global Perspective. https://doi.org/10.22004/AG.ECON.125237.

Spalding, C., Hull, P.M., 2021. Towards quantifying the mass extinction debt of the Anthropocene. Proc. R. Soc. B Biol. Sci. 288. https://doi.org/10.1098/rspb.2020.2332.

Spooner, F.E.B., Pearson, R.G., Freeman, R., 2018. Rapid warming is associated with population decline among terrestrial birds and mammals globally. Glob. Change Biol. 24, 4521–4531. https://doi.org/10.1111/gcb.14361.

Struebig, M.J., Kingston, T., Petit, E.J., Le Comber, S.C., Zubaid, A., Mohd-Adnan, A., Rossiter, S.J., 2011. Parallel declines in species and genetic diversity in tropical forest fragments. Ecol. Lett. 14, 582–590. https://doi.org/10.1111/j.1461-0248.2011.01623.x.

Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. Nature 371, 65–66. https://doi.org/10.1038/371065a0.

Triantis, K.A., Borges, P.A.V., Ladle, R.J., Hortal, J., Cardoso, P., Gaspar, C., Dinis, F., Mendonça, E., Silveira, L.M.A., Gabriel, R., Melo, C., Santos, A.M.C., Amorim, I. R., Ribeiro, S.P., Serrano, A.R.M., Quartau, J.A., Whittaker, R.J., 2010. Extinction debt on oceanic islands. Ecography 33, 285–294. https://doi.org/10.1111/j.1600-0587.2010.06203.x.

Tsafack, N., Fattorini, S., Boieiro, M., Rigal, F., Ros-Prieto, A., Ferreira, M.T., Borges, P.A.V., 2021. The role of small lowland patches of exotic forests as refuges of rare endemic Azorean arthropods. Diversity 13, 443. https://doi.org/10.3390/d13090443.

Uhey, D.A., Bowker, M.A., Haubensak, K.A., Auty, D., Vissa, S., Hofstetter, R.W., 2022. Habitat type affects elevational patterns in ground-dwelling arthropod communities. J. Insect Sci. 22. https://doi.org/10.1093/jisesa/ieac046.

Uhey, D., Haubensak, K., Hofstetter, R., 2021. Mid-elevational peaks in diversity of ground-dwelling arthropods with high species turnover on the colorado plateau. Environ. Entomol. 50, 337–347. https://doi.org/10.1093/ee/nvaa166.

Vicente, L., 1999. Evolutionary strategies in insular environments. Nat. Croat. 8, 301.

Walsh, J.C., Venter, O., Watson, J.E.M., Fuller, R.A., Blackburn, T.M., Possingham, H.P., 2012. Exotic species richness and native species endemism increase the impact of exotic species on islands. Glob. Ecol. Biogeogr. 21, 841–850. https://doi.org/10.1111/j.1466-8238.2011.00724.x.

Watling, J.I., Donnelly, M.A., 2006. Fragments as islands: a synthesis of faunal responses to habitat patchiness. Conserv. Biol. 20, 1016–1025. https://doi.org/10.1111/j.1523-1739.2006.00482.x.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.