Stability in the Face of Global Decline: A 20-Year Study of Arthropods in an Oceanic Archipelago

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Summary

Insect declines have been reported globally but whilst island ecosystems are potentially facing exacerbated challenges, no long-term studies (LTER) have confirmed this trend. This study utilises the first available LTER data on island invertebrates, targeting epigeal and canopy arthropods from the Azores Archipelago (Portugal), and covering over 20 years in three distinct sampling events from 30 standard sites. We investigate changes in abundance, biomass, and species richness within these arthropod communities, focusing on the proportions of endemic and introduced species, and trends among single-island endemics and forest-dependent endemics.

We reveal no significant declines in overall abundance, biomass, or richness of endemic or non-endemic native arthropod populations, although we observe considerable variability between sampling events in both epigeal and canopy communities. Of the species analysed, 26% experienced declines, 15% increased in abundance, and 59% showed no change. We found minimal evidence for the rapid spread of exotics or their increasing influence in the communities, nor any exotic-driven extirpation of endemic species. Forest-dependent endemic species declined at a lower rate than

anticipated, suggesting that the extinction debt for these species may be less severe than previously thought. The three-decade-long conservation of Azorean native forests may have contributed to these unexpectedly stable populations.

Main

Collectively, oceanic islands harbour disproportionate amounts of biodiversity and in particular, high proportions of endemics compared to continents[1]. However, in addition, oceanic islands also possess some of the world's most threatened biotas[1]. Their vulnerability stems from high levels of anthropogenic exploitation, habitat degradation, and the deleterious influence of introduced species relative to their land area[2,3], which is further exacerbated by the effects of ongoing climate change[4] and the elevated vulnerability of species evolved in isolation[5]. Consequently, the rate of historical and contemporary anthropogenic extinction on islands surpasses that of the continents[6].

Arthropods are fundamental elements of most ecosystems and several recent studies have reported declines[7,8], particularly in relation to insects. Arthropod declines may lead to an accelerating deterioration of ecological functions provided by these organisms[9], diminishing ecosystem services (e.g. pollination, regulation of pests, decomposition) and, ultimately, leading to ecosystem collapse[10]. Despite several studies raising the alarm in terms of insect declines[7,11,12], insect populations do not show a consistently declining pattern, particularly as trends have been found to differ between taxa and functional groups and habitat type[12]. As true for other taxonomic groups, some species may increase in prevalence[8] and the proportion of winners often counterbalances that of the losers[13].

While island biotas are known to be particularly threatened, few studies have tested for insular arthropod declines through time. Thus, the contribution of islands to global insect declines remains unknown. Island endemics in particular are expected to decline[1], with many rare endemic species expected to be threatened with extinction. Yet, mostly because of the scarcity of systematic and standardised sampling of, and long-term databases on, insular arthropods, few of these predictions have received sufficient scrutiny to be able to confirm their generality for arthropods of remote islands. Moreover, since the rate of non-native species introduction on islands may exceed the extinction of endemic species[14], it is key to gain understanding into whether population trends of endemic, native but not endemic (henceforth native), and introduced (or exotic) species follow similar trajectories.

The humid forests of the Azorean Islands (North Atlantic, Macaronesia) form a distinctive habitat type that once covered ~99% of the archipelago. By the second half of the 20th century its area had shrunk to its current range of only 5% of its original size[15]. Due to the legal protection of the most pristine areas, the current area of the forest remnants has not decreased for almost four decades and direct human disturbances have been reduced significantly. Yet, the persisting forest patches are highly fragmented and prone to indirect (mostly anthropogenic) influences, such as the spread of exotic, and potentially invasive, species[16] and climate change[17–19]. Moreover, it remains unclear whether these forest patches are large enough to sustain viable populations of endemic forest-dependent arthropod species and halt the future extinction processes that have been predicted. Hence, our focus herein is primarily on the endemic species that survive in less-than-ideal circumstances, some of which may not present viable populations, contributing to the so-called extinction debt[20]. Notwithstanding the apparent urgency of comprehensive conservation strategies for these imperilled species, the lack of in-depth insight into population trends (Prestonian shortfall[21,22]) of insular arthropods may hamper the development of effective protection measures.

In this study, we utilise a dataset of standardised samples collected in 1999–2000, 2010–2011, and 2020–2023. This unique data series, compiled as part of the “Biodiversity of Arthropods from the Laurisilva of the Azores” (BALA) project[23], provides an opportunity to gain the first detailed insight into whether arthropods are declining in the native forests of remote oceanic islands. Whilst we pay particular attention to species of outstanding conservation importance, such as single-island endemics (SIE) and strict forest-dependent Azorean endemics (FDE) considered to be facing extinction debts[20,24] (Fig. 1), we also scrutinise how exotics change over time in abundance and species richness. Moreover, since the overall trends of arthropod abundances may be differentially influenced by island-wide trends, we also take a simulation approach to investigate the contribution of each individual island towards the overall changes. Our dataset holds a collection of abundance data of ground-dwelling (epigeal henceforth, collected with pitfall traps) and canopy-dwelling (arboreal henceforth, collected by canopy beating) arthropods from 30 repeatedly sampled sites across seven Azorean islands, collected in three distinct archipelago-wide sampling campaigns (B1, B2, and B3, henceforth) from 1999 to 2023.

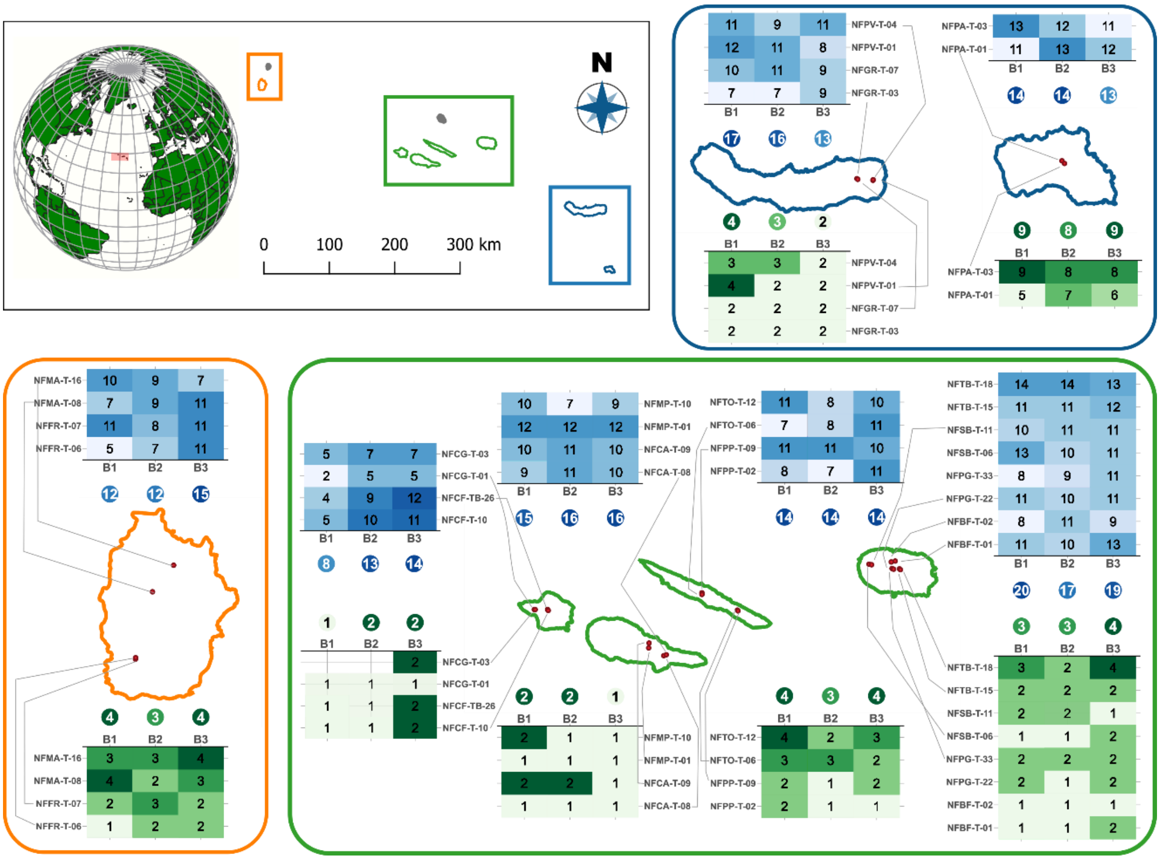

Figure 1. The location of the Azorean Archipelago and the seven sampled islands (top left) in the three island groups (colour-coded as orange, green, and blue for the Western, Central, and Eastern

groups, respectively). Non-sampled island coloured grey. Sampling sites in the three detailed subfigures are indicated with red dots, and arrows linking them to rows in the blue and orange tables show the number of single island endemic species (SIE) or strict forest-dependent endemics (FDE) (respectively) in each sampling campaign. Numbers in circles represent the number of unique SIE/FDE species caught in each BALA sampling campaign (B1-B3) from the entire island. Abbreviations as: FLO – Flores, FAI – Faial, PIC – Pico, SJG – São Jorge, TER – Terceira, SMG – São Miguel, and SMR – Santa Maria.

Results

Changes in overall abundance

The data encompass about 17% of the known Azorean arthropod species described to date, including ~33% of known archipelagic endemic taxa from 15 native forest fragments[25–27]. This corresponds to 30,078 observations of 403 arthropod species (of which 91 or ~23% are archipelagic endemics and 153 or ~38% introduced).

To assess the yearly changes in overall arthropod abundances between the sampling events, we first calculated the average differences for the years between consecutive sampling events. Using Cohen's d and bootstrapped confidence intervals, we determined whether standardized effect sizes of transect-wise changes significantly diverged from zero.

Our findings indicated no significant overall change in arthropod abundance (i.e. when endemics, natives, and exotics, were all included), between the initial (B1) and final (B3) sampling campaigns conducted from 1999 to 2023, in either ground- or canopy-dwelling communities. However, notable differences were observed between B1 and B2, and B2 and B3. A minor decrease from B1 to B2 was seen for non-endemic native species, which was somewhat offset by increases between B2 and B3. (Supplementary Table S1). However, ground-dwelling species exhibited slight reductions in abundance, with Cohen's d values of -0.47 (CI: [-0.81, -0.12]) for endemics and -0.48 (CI: [-0.82, -

0.35]) for natives. The abundance of arboreal native species also declined, with a Cohen's d of -0.32 (CI: [-0.57, -0.1]). (Fig 2 A-B). The proportions of endemics and exotics relative to overall number of individuals remained unchanged between B1 and B2. (Supplementary Table S1).

Changes in biomass

Since body mass is a disproportionately important trait driving ecosystem functions and it is often regarded as a superior currency in terrestrial invertebrate community analysis[28], we also analysed changes in arthropod biomass. Despite estimating biomass using taxon-specific indices and individual counts (see Methods), the correlation between overall biomass and abundance was not very strong (Pearson's ρ = 0.82 for ground-dwellers, 0.68 for canopy-dwellers; $p < 0.001$). Yet, biomass trends closely mirrored abundance patterns, with small-magnitude losses between B1 and B2 offset by gains from B2 to B3, resulting in no net changes in overall biomass across the 25 years. However, when the groups of different biogeographic origin were examined separately, the biomass of both endemic and native ground fauna showed a decline between B1 and B3 (d = -0.32, CI: [-0.71, -0.07] and d = -0.67, CI: [-1.31, -0.50], respectively), whilst there was an increase in the biomass of arboreal exotics (d = 0.41, CI: [0.21, 0.64]) (Fig 2 C-D, Supplementary Table S1). This increase also significantly elevated the biomass-proportion of exotics in the canopy-dwelling community from B1 to B3 (Supplementary Table S1).

Changes in species richness

Moderate declines in species richness were noted for both epigeal and arboreal arthropods between B1 and B2, with Cohen's d values of -0.75 (CI: [-1.25, -0.35]) and -0.59 (CI: [-1.32, -0.17]), respectively (Fig 2 E-F, Supplementary Table S1). This was followed by a substantial increase in canopy-dwelling species from B2 to B3 (d = 1.27, CI: [0.86, 2.07]), resulting in no net change in arboreal species richness between B1 and B3. Conversely, ground-dwelling species showed no significant increases between B2 and B3, leading to declines in species richness from B1 to B3 (d = -0.80, CI: [-1.28, -0.47]).

When species groups of different biogeographic origins were analysed separately, ground-dwelling exotics and natives experienced greater losses from B1 to B3 (d = -0.68, CI: [-1.23, -0.35]) compared to Azorean endemics. Arboreal native species showed the largest increase between B2 and B3. Species-richness proportions of endemics and natives relative to total richness remained unchanged throughout the study (Supplementary Table S1, Figure S1).

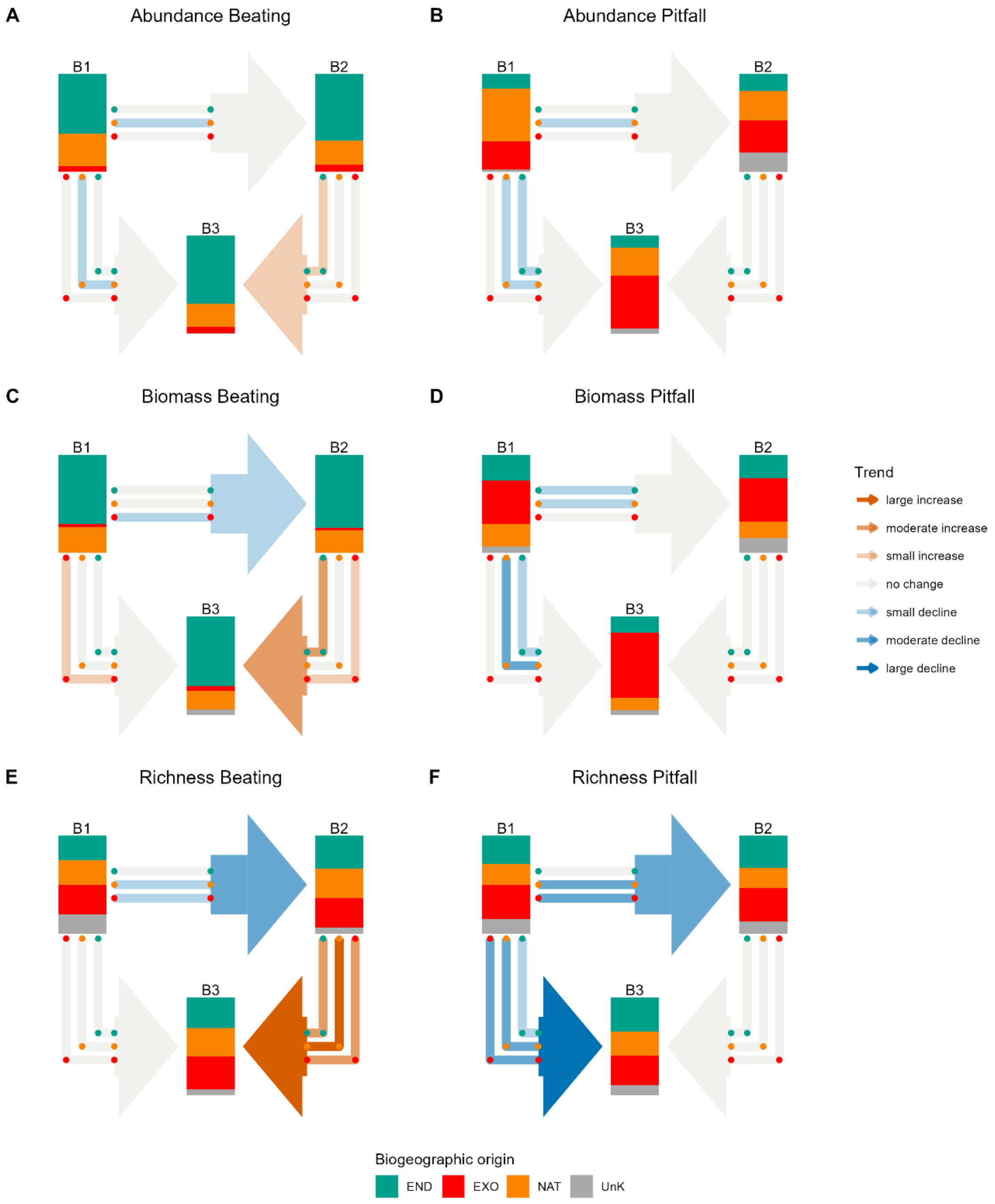

Figure 2. Summary of changes in abundance (A-B), biomass (C-D), and richness (E-F) between BALA sampling campaigns (B1-B3) in arboreal (A, C, E) and epigeal (B, D, F) communities. The proportion (from top to bottom) of endemic (END), non-endemic native (NAT), introduced (EXO) species, and those with unknown biogeographic origin (UnK) in the communities are shown in the barplots. The colours in the barplots, representing biogeographic origins (refer to legend), also correspond to the dots along the thin lines that indicate changes for each group (excluding unknown origins). The arrows indicate the direction of comparison and their colour indicates the overall changes. Changes are standardised to time unit (year) and compared to a 'zero change' null model. Change was considered statistically not significant when confidence intervals crossed zero. The magnitude of change is indicated with colour depth, increasing from small (representing a Cohan's d value between 0.2 and 0.5), through medium (Cohan's d value between 0.5-0.7) to a large change (Cohan's d > 0.7).

Changes in individual species abundances

Our second approach focused on the abundance changes of individual species, particularly those of high conservation concern, namely single-island endemics and strict forest-dependent endemics[20,24]. Of the 403 species present in our dataset, 84 (~21%) were sufficiently abundant to comply with our criteria for formal analysis (see Methods). For these, we used the same methodology as above to investigate how the abundances of individual species changed from B1 to B2 and B3, and from B2 to B3. Of these, 22 species declined significantly from B1 to B3, including 3 with small declines (Cohen's d between 0.2 and 0.5), 13 with moderate declines (Cohen's d between 0.5 and 0.7), and 6 with large declines (Cohen's d > 0.7). The mean Cohen's d for declines was -0.74 (range: -1.23 to -0.41). In contrast, 5, 7, and 1 species showed small, moderate, and large increases, respectively, with magnitude comparable to that of the declines (mean Cohen's d = 0.67, range: [0.36, 2.20]).

For endemic species, the mean effect size for overall decline (between B1 and B3) was -0.67 (range: [-0.71, -0.62]), while the increase was recorded at 0.53 (range: [0.36, 0.66]). Introduced species showed a decline with a mean effect size of -0.76 (range: [-1.14, -0.50]) and an increase of 1.09 (range: [0.46, 2.20]) (Fig 3.).

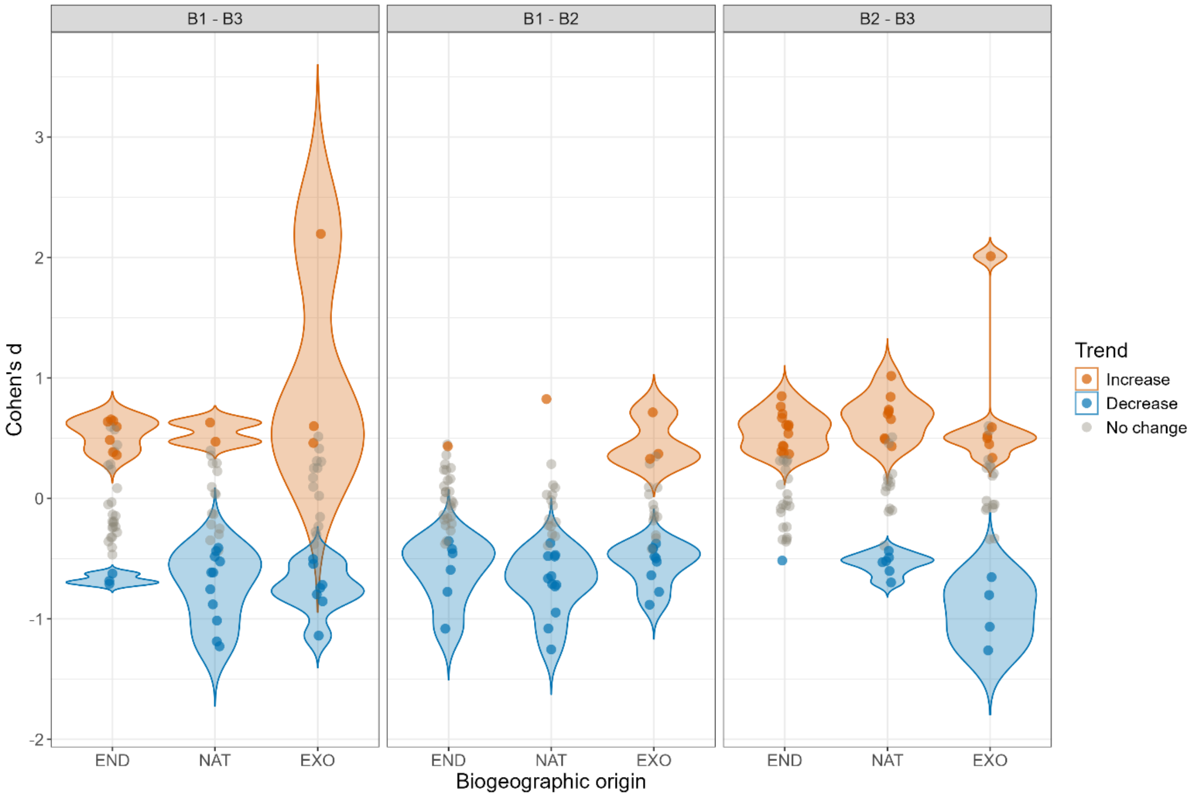

Figure 3. Mean change across transects in the abundances of Azorean native forest arthropod species between sampling campaigns. Changes are standardised to time unit (year) and compared to a ‘zero change’ null model. Species experiencing no significant changes (i.e. confidence intervals cross zero) are marked in grey. Violin plots indicate the first quartile, the median, and the third quartile of the data, as well as the frequency distribution of data points (each dot represents a species). END stands for endemic species, NAT for native but non-endemic, and EXO for introduced species. Only species whose abundance reached the requirements for the statistical analysis are included in the figure.

For species whose abundance is too low to allow individual temporal trends to be analysed, we merely compared the sum of collected individuals from each sampling campaign and no statistical tests were conducted to compare the sampling campaigns. Here, 186 (~58%) showed declines, 37 (~12%) showed no change (i.e. no more than 20% difference between the first and last sampling events), and 96 (~30%) increased. Endemics and natives accounted for only ~36% of declines, while exotics made up ~38%. No significant differences were found when the proportion of increasing and decreasing species based on biogeographic origin was compared (two-sided Fisher test p = 0.204). There were also no differences among the different biogeographic origin in the number of species increasing, being stable, or decreasing in the number of occupied sites (see Methods and Supplementary Table S8).

Changes in individual FDE and SIE species abundances

In our samples, 30 SIEs and 34 FDEs were found (Supplementary Table S2), and of these, the trends of 14 FDEs meet our criteria for the calculation of reliable effect sizes and estimation of trends (see Methods). The only SIE with sufficient data for testing, *Cixius azoterceirae*, also appears as an FDE. The abundance patterns for FDE species mirrored overall abundance trends: marked declines between B1 and B2 were followed by increases between B2 and B3. Indeed, while three FDE species declined moderately from B1 to B2 and one increased, seven species showed small to large increases between B2 and B3 without declines. Overall, only two species of FDE, the bug *Aphrodes hamiltoni* and the spider *Minicia floresensis*, showed moderate declines between B1 and B3, whereas four experienced small to large increases in abundance. (Fig. 4, Supplementary Table S2).

Of those FDE and SIE species that did not meet our criteria for statistical analysis (see Methods), 25 became less numerous (by more than 20% of the original abundance) from B1 to B3, 4 showed no change, and 12 increased (Supplementary Tables S4-S7). The proportions of these outcomes did not significantly differ from non-SIE or non-FDE species (two-sided Fisher test > 0.05). However, the proportion of species decreasing in the number of occupied sites was significantly lower for FDE/SIE species compared to non-FDE/SIE species and exotics (one-sided Fisher tests, p = 0.015 and p = 0.048, respectively, Supplementary Table S8).

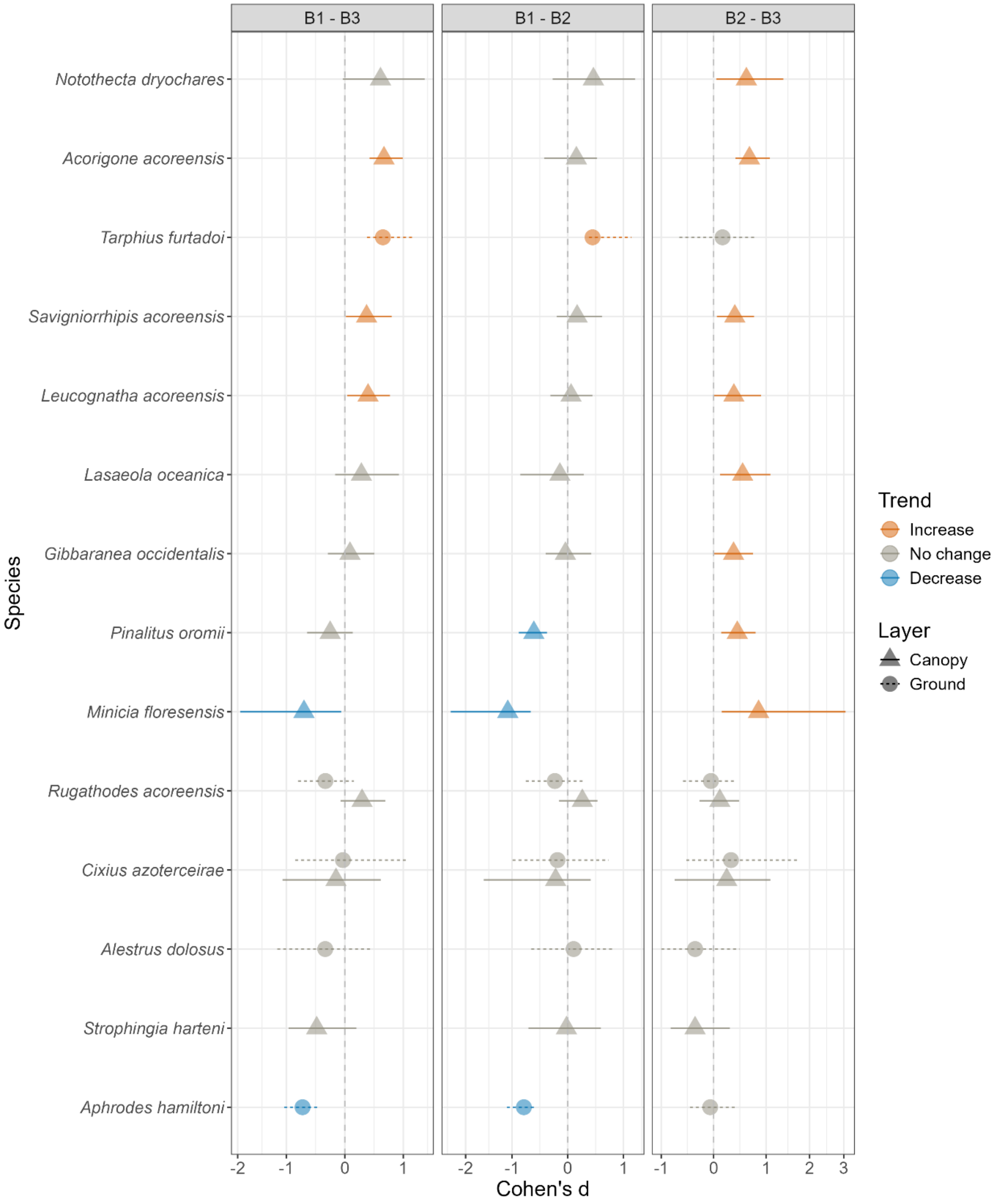

Figure 4. Abundance changes for strict forest-dependent endemics (FDE) from BALA 1 to BALA 3 (first panel), BALA 1 to BALA 2, and BALA 2 to BALA 3 sampling campaigns. Symbols indicate the mean log-transformed Cohen d-value and horizontal lines the corresponding confidence intervals. Statistically not significant (i.e. confidence intervals cross zero) changes indicated with grey colour. Labels on the x-axis are back-transformed and show mean annual changes in the number of individuals.

To explore how individual islands contributed to overall trends in abundance, biomass, and richness, we used a simulation approach, removing one island at a time from the dataset or omitting combinations of two or three islands, and recalculating differences between B1 and B3 (see Methods).

These analyses showed that Terceira positively contributed to changes in overall abundance and richness of arboreal species, particularly endemics, while negatively contributing to trends in arboreal exotic species. Other islands had varying effects; for example, São Jorge positively contributed to endemic species in epigeal communities but added to declines in canopy arthropods and Santa Maria samples generally made a positive contribution to exotic abundances and richness (Supplementary Figures S2-S10).

Discussion

Understanding population trends of arthropods in insular biotas is essential for effective protection and the preservation of the ecosystem services that they provide as well as to fully answer the challenges of global insect declines. In this study, we found minimal evidence of large-scale depletion in the arthropod fauna of Azorean native forests since the start of sampling (in 1999/2000) and neither did we observe significant declines in either endemic or non-endemic but native arthropod populations. Instead, we found highly variable abundances, biomasses, and species richness between sampling events in both epigeal and arboreal communities, with a balance of gains and losses over time. This finding contrasts with the prevailing narrative of dramatic insect decline worldwide and aligns with other large-scale analyses reporting natural fluctuations or stable insect populations[29,30]. Since endemics dominate in abundance over natives and exotics in the arboreal communities in the Azores[15,31], this unchanging trend was driven by the relative stability of endemic species abundances. Similarly stable populations of endemic flying insects have been reported from Terceira Island over 6 and 10 year study periods[16,32]. In our study, even the species predicted to decline the most—such as single island endemics and forest-dependent endemics—generally remained stable, with some canopy-specialised endemic species, like the spider *Acorigone acoreensis*, even experiencing population increases between the first and last sampling campaigns. Moreover, site occupancy for both forest-dependent (FDE) and single island endemics (SIE) did not significantly change and even showed slight increases, indicating at least some degree of habitat stability.

Although the current protected remnants of Azorean native forests face some disturbances, including the aggressive spread of the invasive ginger lily (*Hedychium gardnerianum*)[33], which alters the edaphic conditions and microclimate of the forest understorey and inhibits the regeneration of indigenous flora[34], these factors do not appear to significantly impact overall native ground or canopy fauna trends. Yet, the invasion by ginger lily may still be linked to negative trends we observed in epigeous species richness and declines in specialist herbivorous species like *Aphrodes hamiltoni*. However, excluding São Miguel from our analysis, the largest island where tourism pressure is high and the ginger lily is abundant, did not change the population trends of either the native ground or canopy fauna. Indeed, studies suggest that land use adjacent to native forest remnants has a greater influence on the spread of invasive plants than outdoor activities, such as hiking[35,36]. Nonetheless, the number of SIE and FDE species decreased only on this island. This discrepancy could be due to the presence of already degraded and small habitat patches that cannot sustain viable populations of specialised species like FDEs and SIEs. Thus, some arthropod species may have already gone extinct due to historical events[24] rather than current pressures.

Intensive conservation measures implemented over the past three decades in the Azores appear to have mitigated significant direct threats to native habitats and our results allow for cautious optimism regarding the resilience of endemic arthropods to indirect anthropogenic effects. Native forest patches on Terceira Island, which are among the largest in the Azores, seem to exhibit resilience against invasive species, further supporting the idea that habitat protection is crucial for the survival of endemic species. On the other hand, secondary forests of exotic tree species may serve as refuges for some forest specialist endemics, allowing for population stability[37,38]. However, there is no evidence of spatial rescue effects for isolated populations of rare endemic species[39] and no protection fully excludes long-term disturbances from invasive plant encroachment and occasional human or livestock disturbances, nor does it mitigate the ongoing effects of climate change. Indeed, some endemics continue to show declines, with three FDEs—*Eupteryx azorica*, *Cixius azoricus azoricus* leafhoppers, and the *Atlantocis gillerforsi* beetle—not found in recent samples, and others, such as the spider *Minicia floresensis*, becoming increasingly rare.

Yet, while Triantis et al.[20] predicted that 55-99% of FDEs would eventually face extinction, we found strong statistical evidence of decline in only two species, with untestable indications of decline in 25 additional species out of a total of 55 species (SIEs and FDEs combined). Of the 34 FDE species analysed by Triantis et al., only 14 (~41%) showed any signs of decline—far below the predicted range. Moreover, 11 FDE species exhibited population increases, challenging the prevailing narrative of impending biodiversity loss.

The limited information on the original arthropod fauna prevents us from ruling out the possibility that the lack of widespread decline among SIE and FDE species indicates that the Azorean fauna had already been impoverished by the time biodiversity research began in this archipelago, with many rare habitat specialists potentially extirpated[2] or only persisting within relictual sites[38]. Nonetheless, based on our current knowledge, protecting native habitats appears key to the long-term survival of prospering species, while declining species may benefit from additional focused protection programs[40].

As introduced species often drive endemic extinctions[41], simultaneous increases in exotics and declines in endemics can be anticipated. However, despite reports of a clear increase in non-native species in other studies on Azorean arthropods[16,32], we found little evidence that exotics are rapidly outcompeting natives or endemics. On the contrary, declines of comparable magnitudes were noted in the abundances of both endemics and exotics, with slightly (but not significantly) higher increases in exotics. While it is particularly reassuring that neither the abundance nor the species richness proportion of exotics changed in communities over this ca. 25-year timespan, their biomass and biomass-based proportions did increase between the first and last sampling campaigns. While this solely impacted canopy-dwelling communities, the gains exotics exhibited indicate unfavourable changes for indigenous species. Nevertheless, exotics decreased more in site occupancy than SIE and FDE species, suggesting a continuous influx of exotics with low colonization success from disturbed edges of the forest patches[42]. Although these pioneer individuals have the potential to get established and trigger processes that rewire island ecosystems[43], in previous studies, neither Whittaker et al.[44] nor Pozsgai et al.[43] found clear evidence for functionally matching exotics outcompeting indigenous species in the Azores. Furthermore, within healthy forest remnants, like those on Terceira Island, the increase of exotics appears limited, while endemic arthropod populations have persisted well. It thus seems possible that long-term environmental shifts, including climate change, provide a greater threat than invasive non-native species.

Limitations and future perspectives

While the discontinuous time series presents a limitation, the extensive temporal and spatial scale, combined with significant sampling efforts, make the BALA data a uniquely well-specified basis for uncovering changing diversity patterns. Our sensitivity analysis, which showed minimal divergences in results with up to 20% random sample removal (see Methods and Supplementary Figures S11-S13) confirms the robustness of these patterns. However, the relatively low number of species whose temporal trends could be statistically tested underscores the urgency of establishing a large-scale and continuous monitoring system to assess long-term impacts on arthropod communities.

Several key questions remain unanswered. For instance, we know little about nuanced community changes, such as species replacement, or how species traits influence population trends. Future research should delve into the details driving these trends, considering species' traits, environmental constraints, and biotic interactions. Additionally, understanding whether secondary or semi-natural habitats can mitigate biodiversity losses will be essential.

Concluding remarks

Our findings challenge several studies on global insect declines and the predictions surrounding the demise of insular biotas. They foster moderate optimism for the future of island biotas where habitats remain intact and highlight the importance of long-term monitoring and effective conservation strategies and the need for habitat protection to preserve obscure biodiversity.

However, one unfortunate conclusion from our work is that declines may still occur within protected areas, indicating that the quality or size of these preserves may not be sufficient to buffer all negative anthropogenic impacts and prevent biodiversity losses. Thus, our study has some significant implications. First, although habitat protection appears to be effective in at least the short run, some species require additional support from specific protection programs, such as ongoing LIFE Beetles[40,45] and LIFE Snails[46] projects. Second, the presence of introduced arthropods does not seem generally to adversely impact indigenous species within Azorean native forest remnants but, instead, the structural health of habitats is crucial for the persistence of indigenous arthropod communities. Therefore, plant invasions may pose a more serious threat than competition from other arthropods.

Last but not least, if the natural capital of oceanic islands and the dependent ecosystem services are to be protected, monitoring both indigenous and introduced species, and regularly re-assessing community changes should be a priority[47]. Even simplified, regular monitoring systems utilising advanced technologies and focusing on selected indicator species would be adequate for establishing early warning systems to detect the establishment of potentially competitive species or significant declines in species of high conservation importance. This proactive approach, combined with targeted removal of invasive habitat-structuring plants and competing arthropod exotics, will be key to the success of conservation efforts in the Azores and other insular ecosystems.

Methods

Study sites and sampling methods

We used arthropod data collected from the Azorean archipelago (Fig. 1), using standardised sampling protocols under the umbrella of the ‘Biodiversity of Arthropods the Laurisilva of Azores’ (BALA) project[23,26,27]. In the course of the project, 30 sites of native Azorean humid forests[48] were chosen for standardised arthropod sampling, repeated in three sampling campaigns: B1 (1999-2002), B2 (2010-2011), and B3 (2021-2023). The sites were spread across 15 native forest remnants, on seven out of the nine Azorean islands (from west to east: Flores, Faial, Pico, São Jorge, Terceira, São Miguel, and Santa Maria), those with remaining native vegetation. Summary data on the transects and remnants are available in Pozsgai et al.[23]. All samples were collected between July and September when arthropod activity is at its peak in the Azores.

To encompass a broad range of micro-habitats, we employed two primary sampling techniques. The first involved pitfall trapping, to effectively capture soil- and ground-dwelling (epigeal) arthropods. At each site, across a 150 m transect, 30 pitfall traps were evenly distributed, maintaining a separation of 5 m between each. Alternating preservative/attractive solutions of ethylene-glycol and Turquin’s solution[49] were employed in these traps, maximising catch. Pitfall traps were active for one week in each sampling campaign.

The second technique, canopy beating, was employed to target canopy-dwelling (arboreal) arthropods. At each selected site, the beating was performed on the three, locally most abundant tree species, primarily focusing on native *Juniperus brevifolia* (Cupressaceae), *Erica azorica* (Ericaceae), *Ilex azorica* (Aquifoliaceae), *Laurus azorica* (Lauraceae), and *Vaccinium cylindraceum* (Ericaceae). For each of the three species, ten individual trees were randomly selected along the transect and the branches were beaten five times at the height of 1.5–2 m. All visually observable arthropods, except for mites (Acari) and springtails (Collembola), were sampled. Specimens were sorted into morphospecies and, where possible, identified to the biological species. Due to difficulties in their identification, Diptera and Hymenoptera (with the exception of Formicidae, which were included) were excluded from the dataset. Biogeographic origin, categorised as endemic to the Azores, native but not endemic to the Azores (termed as native for brevity), introduced (non-native, also termed as exotic), and of unknown origin, was assigned to each species (Ref.[23,25] and references therein). Single-island endemics (SIE) were identified based on the dataset described in Ref.[23] and the species list in the Supplementary Material of Ref. [20] was used as the basis to identify strict forest-dependent endemics (FDE).

We also estimated the species-specific body mass for each non-lepidopteran species in our database. The body length of 3-10 individuals of each (morpho)species in an adult stage was measured and species-specific body mass was calculated based on published body length – body mass equations of the higher taxa (data available from Ref.[50]). Since adult and larval biomasses of Lepidoptera differ significantly, we excluded this group from the biomass-based analysis. Lepidoptera, however, were included in species counts and abundance data. To calculate sample-based biomass, we multiplied the number of collected individuals of each species occurring in the samples by their corresponding species-specific body mass value.

Data analysis

We took two different approaches to explore potential arthropod declines in Azorean native forests.

First, we compared the changes at a community level and investigated whether there was a change between the first (B1) and second (B2), second and third/last (B3), and the first and third sampling events in any of three calculated measures: abundances, biomasses, and species richness. We used Spearman's correlation test to estimate the interdependence of biomass and abundance values.

Individual samples (i.e. one pitfall trap or the material from beating one tree) were pooled within each sampling transect, for each year when sampling was conducted, and the three measures were calculated for each of these pooled samples. Since the length between two sampling campaigns at the same place varied slightly, we did not directly compare the summarised measures from each sampling round but calculated a standardised yearly change in all three measures. To do so, at each site and for each measure, we subtracted the value of the later sampling from the earlier one and divided it by the number of years that passed between the two sampling events. This gave us the absolute yearly change in species richness, abundance, and biomass for each transect. Although this absolute value was used for further analysis, we also calculated the change as a percentage by dividing the absolute yearly change by the corresponding value (i.e. abundance, biomass, or species richness) of the previous sampling event. To estimate the magnitude of changes between sampling events and to test whether they were significant, we calculated Cohen D-s, using the cohens_d() function from the rstatix R package[51]. In-text categorisation of effect sizes (i.e. "negligible", "small", "moderate", and "large") followed that of Cohen[52]. We estimated the confidence intervals (CI) through a bootstrapping process with 10,000 iterations with the help of the BootES R package[53] and compared the resulting values to a hypothetical zero change (a 'zero change' null model). We ran this analysis by including all data, and separately for subsets including species of each different biogeographic origin. Moreover, data for this analysis were separated by the sampling method. Thus, each of the three measures resulted in eight trend estimations (pitfall trap – all species, pitfall trap –

endemic species, pitfall trap – native species, pitfall trap – introduced species, beating – all species, beating – endemic species, beating – native species, beating – introduced species) between two sampling events.

As our second approach, we compared the changes at a species level, paying particular attention to the single-island endemics and strict forest-dependent endemics that may carry an extinction debt[20]. For this, we separated the species in our samples into two major groups: those represented in at least five samples with four individuals and which were present in at least two sampling campaigns, and those that did not fulfil these criteria. For the first group, we used the same analysis as above to estimate whether abundance differences between two sampling events significantly differed from zero. We considered a species unsuitable for including in the analysis (‘rare species’ henceforth) if they were represented with fewer than 30 individuals across all samples (i.e. fewer than the median number of individuals per species across all samples, when singletons and doubletons are removed), present in less than 1% of samples, or exhibiting scarcity or low presence (less than four individuals) in two entire sampling rounds. Whilst these values are inherently somewhat arbitrary, lower thresholds resulted in comparisons between extremely low abundances (1-2 individuals), or mean values calculated from unreasonably low sample sizes (three individuals) and lowered the power of our analysis. As these ‘rare species’ were not abundant nor widespread enough to conduct a fully-fledged analysis, we only categorised the differences between sampling events as “no change”, “declines”, and “increases” based on how summary abundances differed between samplings. Since we wanted to avoid considering very little variability in abundances as changes, unless at least 20% change between two sampling events was observed, we considered the differences as “no change”. We conducted a sensitivity analysis to assess how altering this threshold influences our conclusions but, despite some numerical differences, they held until we reached 30%, and even after minor differences were present only in native species SIE/FDE species and (Supplementary Figure S14). Although we did not conduct formal tests on the differences here, we compared whether the occurrence probability of categories (i.e., no change, declines and increases) differs significantly by undertaking a series of Fisher tests.

Fisher tests were also used to compare whether the site occupancy of species groups with a different biogeographic origin or conservation status (as defined by IUCN categorisation), has changed. For this, we recorded at how many sites each species occurred in each sampling event and compared them between sampling events. Changes were only considered when they reached a 20% difference. They then were categorised as “no change”, “declines”, and “increases” and Fisher tests were used to assess if site occupancy changes could be predicted from the biogeographic origin or SIE/FDE categorisation.

To assess the impact of island identity on the observed changes we removed one, two, and three islands in every combination from the original dataset and recalculated the changes in community measures (i.e., abundance, biomass, and richness) using the Cohen d calculation above.

For the sensitivity analysis, we randomly removed 1, 3, 5, 10, and 15 sites from the analysis and recalculated all community-level changes, using Cohen’s d, as above. We repeated each removal round 1000 times and compared the d values visually. All analyses were conducted in an R environment[54], with the dplyr[55], ggplot2[56], and reshape[57] packages used for data manipulation and plotting.

Data availability

The BALA dataset is available on the Global Biodiversity Facility’s (GBIF) website under the https://doi.org/10.15468/rpdkx9 identifier. Basic information on the sampling sites and summary datasets used in the analysis are available on GP’s GitHub repository (https://github.com/pozsgaig/BALA_diversity).

Code availability

All code and data needed to reproduce the results presented in the article and supplementary material are available on the https://github.com/pozsgaig/BALA_diversity GitHub repository.

References

1. Fernández-Palacios, J. M. *et al.* Scientists' warning – The outstanding biodiversity of islands is in peril. *Glob. Ecol. Conserv.* **31**, e01847 (2021).
2. Terzopoulou, S., Rigal, F., Whittaker, R. J., Borges, P. A. V. & Triantis, K. A. Drivers of extinction: the case of Azorean beetles. *Biol. Lett.* **11**, 20150273 (2015).
3. Matthews, T. J. & Triantis, K. Island biogeography. *Curr. Biol.* **31**, R1201–R1207 (2021).
4. Whittaker, R. J., (role)aut, Fernández-Palacios, J. M. (role)aut & Matthews, T. J. (role)aut. *Island Biogeography : Geo-Environmental Dynamics, Ecology, Evolution, Human Impact, and Conservation*. (Oxford University Press, Oxford, UK, 2023).
5. Gillespie, R. G. & Roderick, G. K. Arthropods on islands: colonization, speciation, and conservation. *Annu. Rev. Entomol.* **47**, 595–632 (2002).
6. Loehle, C. & Eschenbach, W. Historical bird and terrestrial mammal extinction rates and causes. *Divers. Distrib.* **18**, 84–91 (2012).
7. Hallmann, C. A. *et al.* More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLOS ONE* **12**, e0185809 (2017).
8. Wagner, D. L. Insect declines in the Anthropocene. *Annu. Rev. Entomol.* **65**, 457–480 (2020).
9. Noriega, J. A. *et al.* Research trends in ecosystem services provided by insects. *Basic Appl. Ecol.* **26**, 8–23 (2018).
10. Cardoso, P. *et al.* Scientists' warning to humanity on insect extinctions. *Biol. Conserv.* **242**, 108426 (2020).
11. Sánchez-Bayo, F. & Wyckhuys, K. A. G. Worldwide decline of the entomofauna: A review of its drivers. *Biol. Conserv.* **232**, 8–27 (2019).
12. van Klink, R. *et al.* Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science* **368**, 417–420 (2020).
13. Dornelas, M. *et al.* A balance of winners and losers in the Anthropocene. *Ecol. Lett.* **22**, 847–854 (2019).

14. Sax, D. F., Gaines, S. D. & Brown, J. H. Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *Am. Nat.* **160**, 766–783 (2002).
15. Gaspar, C., Borges, P. A. V. & Gaston, K. J. Diversity and distribution of arthropods in native forests of the Azores archipelago. *Arquipelago Life Mar. Sci.* **25**, 1–30 (2008).
16. Borges, P. A. V., Rigal, F., Ros-Prieto, A. & Cardoso, P. Increase of insular exotic arthropod diversity is a fundamental dimension of the current biodiversity crisis. *Insect Conserv. Divers.* **13**, 508–518 (2020).
17. Ferreira, M. T. *et al.* Effects of climate change on the distribution of indigenous species in oceanic islands (Azores). *Clim. Change* **138**, 603–615 (2016).
18. Ferreira, M. T. *et al.* Implications of climate change to the design of protected areas: The case study of small islands (Azores). *PLOS ONE* **14**, e0218168 (2019).
19. Wallon, S. *et al.* Effects of a short-term temperature increase on arthropod communities associated with pastures. *Biodivers. Data J.* **11**, e107385 (2023).
20. Triantis, K. A. *et al.* Extinction debt on oceanic islands. *Ecography* **33**, 285–294 (2010).
21. Hortal, J. *et al.* Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **46**, 523–549 (2015).
22. Cardoso, P., Erwin, T. L., Borges, P. A. V. & New, T. R. The seven impediments in invertebrate conservation and how to overcome them. *Biol. Conserv.* **144**, 2647–2655 (2011).
23. Pozsgai, G. *et al.* The BALA project: A pioneering monitoring of Azorean forest invertebrates over two decades (1999–2022). *Sci. Data* **11**, 1–9 (2024).
24. Borges, P. *et al.* Conservation status of the forest beetles (Insecta, Coleoptera) from Azores, Portugal. *Biodivers. Data J.* **5**, e14557 (2017).
25. Borges, P. *et al.* An updated checklist of Azorean arthropods (Arthropoda). *Biodivers. Data J.* **10**, e97682 (2022).
26. Borges, P. A. V. *et al.* Ranking protected areas in the Azores using standardised sampling of soil epigean arthropods. *Biodivers. Conserv.* **14**, 2029–2060 (2005).

27. Ribeiro, S. P. *et al.* Canopy insect herbivores in the Azorean Laurisilva forests: key host plant species in a highly generalist insect community. *Ecography* **28**, 315–330 (2005).

28. Saint-Germain, M. *et al.* Should biomass be considered more frequently as a currency in terrestrial arthropod community analyses? *J. Appl. Ecol.* **44**, 330–339 (2007).

29. Crossley, M. S. *et al.* No net insect abundance and diversity declines across US Long Term Ecological Research sites. *Nat. Ecol. Evol.* **4**, 1368–1376 (2020).

30. Dornelas, M. *et al.* Assemblage time series reveal biodiversity Change but not systematic loss. *Science* **344**, 296–299 (2014).

31. Tsafack, N. *et al.* Edge effects constraint endemic but not introduced arthropod species in a pristine forest on Terceira (Azores, Portugal). *For. Ecol. Manag.* **528**, 120646 (2023).

32. Lhoumeau, S. & Borges, P. A. V. 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 (2023).

33. Pereira, M. J., Eleutério, T., Meirelles, M. G. & Vasconcelos, H. C. Hedychium gardnerianum Sheph. ex Ker Gawl. from its discovery to its invasive status: a review. *Bot. Stud.* **62**, 11 (2021).

34. Minden, V., Jacobi, J. D., Porembski, S. & Boehmer, H. J. Effects of invasive alien kahili ginger (Hedychium gardnerianum) on native plant species regeneration in a Hawaiian rainforest. *Appl. Veg. Sci.* **13**, 5–14 (2010).

35. Pavão, D. C. *et al.* Land cover along hiking trails in a nature tourism destination: the Azores as a case study. *Environ. Dev. Sustain.* **23**, 16504–16528 (2021).

36. Queiroz, R. E., Ventura, M. A. & Silva, L. Plant diversity in hiking trails crossing Natura 2000 areas in the Azores: implications for tourism and nature conservation. *Biodivers. Conserv.* **23**, 1347–1365 (2014).

37. Meijer, S. S., Whittaker, R. J. & Borges, P. A. V. 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 (2011).

38. Tsafack, N. *et al.* The role of small lowland patches of exotic forests as refuges of rare endemic Azorean arthropods. *Diversity* **13**, 443 (2021).

39. Aparício, B. A. *et al.* Assessing the landscape functional connectivity using movement maps: a case study with endemic Azorean insects. *J. Insect Conserv.* **22**, 257–265 (2018).

40. Lhoumeau, S. *et al.* Monitoring arthropods under the scope of the LIFE-BEETLES project: I - Baseline data with implementation of the Index of Biotic Integrity. *Biodivers. Data J.* **12**, e124799 (2024).

41. Bellard, C., Rysman, J.-F., Leroy, B., Claud, C. & Mace, G. M. A global picture of biological invasion threat on islands. *Nat. Ecol. Evol.* **1**, 1862–1869 (2017).

42. Borges, P. A. V. *et al.* Invasibility and species richness of island endemic arthropods: a general model of endemic vs. exotic species. *J. Biogeogr.* **33**, 169–187 (2006).

43. Pozsgai, G. *et al.* Arthropod co-occurrence networks indicate environmental differences between islands and signal introduced species in Azorean native forest remnants. *Front. Ecol. Evol.* **11**, 1139285 (2023).

44. Whittaker, R. J. *et al.* Functional biogeography of oceanic islands and the scaling of functional diversity in the Azores. *Proc. Natl. Acad. Sci.* **111**, 13709–13714 (2014).

45. Tsafack, N. *et al.* Arthropod-based biotic integrity indices: A novel tool for evaluating the ecological condition of native forests in the Azores archipelago. *Ecol. Indic.* **154**, 110592 (2023).

46. Borges, P. *et al.* Monitoring arthropods under the scope of LIFE-SNAILS project: I - Santa Maria Island baseline data with implementation of the Index of Biotic Integrity. *Biodivers. Data J.* **12**, e116829 (2024).

47. Borges, P. A. V. *et al.* Global Island Monitoring Scheme (GIMS): a proposal for the long-term coordinated survey and monitoring of native island forest biota. *Biodivers. Conserv.* **27**, 2567–2586 (2018).

48. Elias, R. B. *et al.* Natural zonal vegetation of the Azores Islands: characterization and potential distribution. *Phytocoenologia* **46**, 107–123 (2016).

49. Turquin, M. J. Une biocenose cavernicole originale pour le Bugey: le puits de Rappe. in *Comptes Rendus 96e Congresse Naturel Societes Savantes* vol. 3 235–256 (Sciences, Toulouse, France, 1973).
50. Brush, M., Matthews, T. J., Borges, P. A. V. & Harte, J. Land use change through the lens of macroecology: insights from Azorean arthropods and the maximum entropy theory of ecology. *Ecography* **2022**, e06141.
51. Kassambara, A. *Rstatix: Pipe-Friendly Framework for Basic Statistical Tests*. https://CRAN.R-project.org/package=rstatix (2023).
52. Cohen, J. A power primer. *Psychol. Bull.* **112**, 155–159 (1992).
53. Kirby, K. N. & Gerlanc, D. BootES: An R package for bootstrap confidence intervals on effect sizes. *Behav. Res. Methods* **45**, 905–927 (2013).
54. R Core Team. R: A language and environment for statistical computing. (2012). https://CRAN.R-project.org
55. Wickham, H., François, R., Henry, L., Müller, K. & Vaughan, D. *Dplyr: A Grammar of Data Manipulation*. https://CRAN.R-project.org/package=dplyr (2023).
56. Wickham, H. *Ggplot2: Elegant Graphics for Data Analysis*. (Springer-Verlag New York, 2016).
57. Wickham, H. Reshaping Data with the reshape Package. *J. Stat. Softw.* **21**, 1–20 (2007).

Acknowledgements

We are grateful to all researchers who collaborated in the field and lab work: Álvaro Vitorino, Anabela Arraiol, Annabella Borges, Ana Rodrigues, Carlos Aguiar, Clara Gaspar, Emanuel Barcelos, Francisco Dinis, Genage André, Hugo Mas, João Amaral, Joaquin Hortal, João Moniz, Lara Dinis, Lucas Lamelas López, Luís Vieira, Paula Gonçalves, Sandra Jarroca. Several taxonomists identified morphospecies from BALA 1, which were fundamental for the success of the project, namely, António Bivar de Sousa, Arturo Baz, Fernando Ilharco, Henrik Enghoff, Jordi Ribes, Jörg Wunderlich, Margarida T. Pitta, Ole Karsholt, Richard zur Strassen, Virgílio Vieira, Volker Assing, Volker Mahnert and Wolfgang Rücker. The Azorean Forest Services provided logistic support on each island during BALA 1. This work was funded by the Azorean Direcção Regional dos Recursos Florestais (Azorean Government / project 17.01-080203) during BALA 1; FCT- project PTDC/BIA-BEC/100182/2008 – “Predicting extinctions on islands: a multi-scale assessment” during BALA 2; and (FCT) - MACRISK-Trait-based prediction of extinction risk and invasiveness for Northern Macaronesian arthropods

(FCT-PTDC/BIA-CBI/0625/2021), FCT - Fundação para a Ciência e a Tecnologia in the frame of the projects FCT-UIDB/00329/2020–2024 DOI 10.54499/UIDB/00329/2020 (Thematic Line 1 – integrated ecological assessment of environmental change on biodiversity) and Project LIFE BEETLES (LIFE 18NAT/PT/000864) in BALA 3. Data curation and open Access of this manuscript were supported by the project MACRISK-Trait-based prediction of extinction risk and invasiveness for Northern Macaronesian arthropods (FCT-PTDC/BIA-CBI/0625/2021). G.P. was funded by the project FCT-UIDP/00329/2020; G.O. was funded by the project FCT - PTDC/BIA-CBI/0625/2021; S.L. was funded by the Ph.D. project M3.1.a/F/012/2022; R.C. was funded by the Ph.D. project in the frame of the projects FCT-UIDB/00329/2020–2024. M.T.F. was funded by Project LIFE BEETLES (LIFE 18NAT/PT/000864). A.M.C.S. was supported by a Spanish Ramón y Cajal fellowship RYC2020-029407-I, funded by MICIN/ AEI/10.13039/501100011033, and by “ESF Investing in your future”. I.R.A. and M.B. were funded by Portuguese funds through FCT – Fundação para a Ciência e a Tecnologia, I.P., under the Norma Transitória – https://doi.org/10.54499/DL57/2016/CP1375/CT0003 and DL57/2016/CP1375//CT0001, respectively. S.R. was funded by the SPR Research Grant (CNPq-306572-2019-2). P.A.V.B., R.G., I.R.A. and M.B. were also funded by the project Azores DRCT Pluriannual Funding (M1.1.A/FUNC.UI&D/010/2021–2024). A.R.M.S. and J.A.Q. are currently funded by FCT - Fundação para a Ciência e a Tecnologia in the frame of the projects FCT-UIDB/00329/2020–2024 DOI 10.54499/UIDB/00329/2020.

Author contributions

G.P. and P.A.V.B. conceived the ideas presented in the paper. P.A.V.B. designed the experimental design, conceived the sampling protocol, led the data collection and early data management. The arthropods were collected by A.M.C.S., A.L., A.R-P., C.M., C.R., G.P., F.P., F.R., I.R.A., J.A.Q., K.A.T., M.B., M.T.F., P.A.V.B., P.C., R.C., R.G., and S.R. The specimens were sorted and identified by A.L., A.R.M. S., A.R-P., C.M., J.A.Q., L.C.C., P.A.V.B. and S.R. G.P. drafted the first manuscript with the active involvement of G.O., J.M.O., K.A.T., L.B.D.Á., P.C., P.A.V.B., R.J.W., S.F. and T.J.M. G.P. conducted the statistical analysis and data visualisation with contributions from F.R., G.O., P.A.V.B., P.C., R.G., S.F., and S.L. P.A.V.B. supervised the work and acquired the necessary funding with the collaboration of J.A.Q and A.R.M.S. (BALA 1), K.A.T. and F.R. (BALA 2) and P.C., F.R and R.G (BALA 3). All authors reviewed the final version of the manuscript.

Competing interests

The authors declare no competing interests.