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ARTICLE

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Divergent temporal dynamics of native and non-native insular arthropods in fragmented forests

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Abstract

Non-native species introductions have caused biodiversity loss worldwide, yet it is unclear how temporal diversity patterns vary across native and non-native communities, and what mechanisms control their respective dynamics and assembly. Using a unique 12-year time series dataset of arthropods sampled in forest fragments on Terceira Island, we observed no systematic species losses but steady temporal β-diversity (Sørensen dissimilarity based on species presence–absence) for non-native, native endemic, and native non-endemic assemblages. However, native endemics and non-endemics showed an overall increasing trend in Bray–Curtis dissimilarity (incorporating species abundances), with many previously abundant native species becoming progressively rarer. By constructing neutral models, we accurately predicted temporal diversity patterns for non-natives but not for native endemics and non-endemics, displaying their divergent temporal dynamics. These results indicate that non-native assemblages are more consistent with stochastic source-sink mass effect dynamics, while neutral drift interacting with non-natives and/or environmental changes might drive native assemblage dynamics.

KEYWORDS
insular arthropods, native endemics and non-endemics, neutral model, non-native introduction, species abundance distribution, temporal β-diversity

INTRODUCTION

The introduction, spread, and establishment of non-native species are recognized as one of the major drivers of biodiversity loss worldwide (Delavaux et al., 2023; Vilà et al., 2011), often resulting in the extinction/extirpation of certain native species (Bellard et al., 2016; Storch et al., 2021) and substantial changes in the composition of native assemblages (Petsch et al., 2022; Villéger et al., 2011), and therefore greatly altering ecosystem functioning (Ehrenfeld, 2010; Hautier et al., 2018). Currently, anthropogenic activities are accelerating the introduction and spread of many non-native taxa in natural ecosystems (Kueffer, 2017; Seebens et al., 2017); thus, it is essential to accurately assess the impacts of non-natives on native communities, and particularly how the severity of impacts changes through time (Crystal-Ornelas & Lockwood, 2020).

Although some studies have analyzed the effects of non-natives on native communities over time (Moser et al., 2018), their findings are typically based on short-term observations or involve simple comparisons of differences in some ecological property before and after a single-species invasion (Kortz et al., 2023; Stricker et al., 2015). These short-term studies have identified the years subsequent to the introduction of a new non-native species as a fast-changing stage of the establishment process, often characterized by an evident decline in native species diversity (Flory et al., 2017; Strayer et al., 2006). The analysis of plant invasion over longer periods has found that the persistence of the invader over time can gradually alter plant community composition further, thereby leading to an irreversible detachment from the initial non-invaded natural state (so-called novel ecosystems which may be dominated by non-natives; Campbell et al., 2022; Marchante et al., 2015). At the same time, the introduction of non-natives may to some extent compensate for the loss of native species, potentially resulting in no systematic loss of α-diversity but a marked signal of compositional change in assemblages over time (temporal β-diversity; Dornelas et al., 2014; Winter et al., 2010). Therefore, there are three potential pathways for native communities following non-native introductions: they can either (1) be impacted in some way, resulting in the alteration of some community properties, but with an ultimate return to their pre-introduction structure and composition, indicating resilience; (2) progress toward alternative stable states, defined as the non-transitory change in community structure away from the initial state after disturbance; or (3) be resistant to introductions, indicated by a lack of response (Amor et al., 2020; Mawarda et al., 2022). Despite the perceived importance of non-native introductions in reorganizing native communities (Kortz & Magurran, 2019), the prevalence of these different pathways in empirical systems remains unclear (Strayer et al., 2006).

Islands are particular hotpots of non-native introductions, and their endemic biodiversity is often extremely vulnerable to non-native species (Whittaker et al., 2023). This vulnerability stems from the evolution of certain traits as part of the "island syndrome" (e.g., flightlessness), high levels of anthropogenic disturbance more broadly (e.g., habitat loss and degradation), and the restricted land area of islands reducing the amount of refugia and potential for escape via dispersal (Gillespie & Roderick, 2002; Matthews et al., 2019). Consequently, the rate of historical and contemporary anthropogenic extinction on islands surpasses that of the continents (Loehle & Eschenbach, 2012). While island species from various taxa are known to be experiencing population declines (Whittaker et al., 2023), few studies have tested for insular arthropod declines through time (Lhoumeau & Borges, 2023; Wagner, 2020), mostly because of the scarcity of systematic and standardized sampling of, and long-term databases on, insular arthropods. It is well known that arthropods are one of the fundamental elements in most ecosystems, displaying an astonishing diversity of species, adaptations and life forms and providing multiple ecosystem services (Marta et al., 2021). Due to ongoing global anthropogenic environmental change, however, studies of arthropods in various continental systems have found that they are undergoing dramatic biodiversity shifts and declines, which may lead to a deterioration of ecological functions provided by these organisms (Soroye et al., 2020), diminishing ecosystem services (e.g., pollination, regulation of pests, decomposition; Laliberté & Legendre, 2010) and, ultimately, leading to ecosystem collapse (Pecl et al., 2017). In addition, globalization in trade and transport has led to a breakdown of geographical barriers and subsequent colonization of islands by large numbers of non-native arthropod species (Sax et al., 2002). Nevertheless, studies focused on identifying variation in temporal diversity patterns across native and non-native arthropod communities and elucidating the respective driving mechanisms are still lacking.

So far, several potential drivers of temporal diversity patterns (including temporal change in α-diversity and temporal β-diversity) have been identified, including demographic stochasticity (i.e., neutral drift; Hubbell, 2001), intrinsic ecological interactions (e.g., competition; O'Sullivan et al., 2021) and external environmental forces (e.g., climate and land-use changes; Antão et al., 2020; Montràs-Janer et al., 2024; Newbold et al., 2015). To assess the relative contributions of these different drivers in real communities, the spatially implicit neutral model of Hubbell (2001)—in which all species are assumed to be functionally equivalent—has often been used as a null hypothesis (Gilbert et al., 2006; Kuczynski et al., 2023; Sgardeli et al., 2016). If the observed temporal diversity patterns are consistent with the neutral model predictions, we can conclude that they are primarily driven by neutral drift and dispersal (or at least, other mechanisms are not needed to explain these patterns). Otherwise, we conclude that additional processes, such as ecological interactions or/and environmental changes, are required to explain temporal diversity patterns in a given system.

By comparing predictions with observed temporal diversity patterns, we can also use the aforementioned neutral model to disentangle the mechanisms driving temporal dynamics between native and non-native arthropod assemblages. Previous work on island arthropods has theorized that non-native assemblages in native habitat patches are primarily driven by source-sink dynamics and mass effects, with more frequent colonization and extinction, and therefore much higher turnover than native assemblages (Lhoumeau & Borges, 2023; Matthews, 2021; Matthews et al., 2019). Thus, we hypothesize that the neutral model will accurately predict the temporal diversity patterns of non-natives, while other, more deterministic processes are necessary to explain the temporal diversity patterns of native arthropod assemblages, which are predicted to show relatively more stability.

In this study, we utilize a unique time series dataset of arthropods sampled over 12 years in the native forest fragments of Terceira Island in the Azores (i.e., the SLAM Project; Borges, 2025), Portugal, to undertake a comprehensive analysis of temporal diversity patterns for non-natives, native endemics and native non-endemics (herein termed “chorotypes”), respectively. This dataset is ideal for examining temporal diversity patterns (i.e., temporal β-diversity and temporal change in α-diversity) in these chorotypes, as the regular census interval (four seasons every year from 2013 to 2024 inclusive) allows us to accurately describe temporal turnover, and the Azorean arthropod fauna contains a high proportion of non-natives (Borges et al., 2022). Firstly, we investigated variation in temporal diversity patterns across the non-native, native endemic, and native non-endemic assemblages, as well as changes in the species abundance distribution (SAD) of the different chorotypes through time. Second, we constructed a neutral model based on the empirical data, to assess whether neutral dynamics alone can produce similar temporal diversity patterns to the empirical patterns, and whether the relative performance of the neutral model varies across the three chorotypes. Our aim is to identify variation in temporal diversity patterns across native and non-native assemblages and provide insights into the mechanisms controlling their respective community dynamics and assembly.

METHODS

Empirical data

The Azorean archipelago is located in the North Atlantic (Figure 1A). Since human occupation of the islands in the 15th century, there have been substantial changes in the size and quality of native forest habitat, with the loss of about 95% of the original native forest cover, mostly due to the creation of urban areas, agricultural fields, pastures, and non-native plantations (Borges et al., 2006). Terceira Island (Figure 1B), a roughly circular island of 402-km^2 area, contains the largest remaining area of native pristine forests in the Azores (Borges et al., 2006).

Arthropods were sampled using ten 50 × 50 m plots located in four fragments of pristine forest on Terceira Island in the Azores (Figure 1B). Sampling was standardized, with the number of plots proportional to fragment size: 1347 ha Caldeira Santa Bárbara e Mistérios Negros (NFSB) with four plots, 557 ha Biscoito da Ferraria (NFBF) with three plots, 180 ha Terra Brava (NFTB) with two plots, and 38 ha Pico Galhardo (NFPG) with one plot. We sampled arthropods using a passive flight interception trap called a SLAM (sea, land, and air malaise) trap. The SLAM traps are approximately 110 × 110 × 110 cm and work by intercepting arthropods on an area of black mesh and funneling them into a sampling bottle filled with a killing liquid. Propylene-glycol was used as it persists for a long time without evaporating and enables the collection of good quality specimens for posterior DNA extraction. Normally, the collecting bottles were collected and changed every three months (in March, June, September and December); thus, each sample covers one season of the year (winter, spring, summer and autumn). However, due to logistical challenges and problems with the traps, in a small number of cases certain 3-month samples were excluded (see dataset in Borges & Lhoumeau, 2025). Samples were sorted and individuals identified to species level by experienced taxonomists and to morpho species where specific determinations were not possible. The following main arthropod groups were considered: Diplopoda, Chilopoda, Pseudoscorpiones, Opiliones, Araneae and most of the insect orders (excluding Diptera, Lepidoptera, and Hymenoptera). Based on the last checklist of Azorean arthropods (Borges et al., 2022), the arthropods were then grouped into three chorotypes: non-native, native endemic, and native non-endemic. A very small number

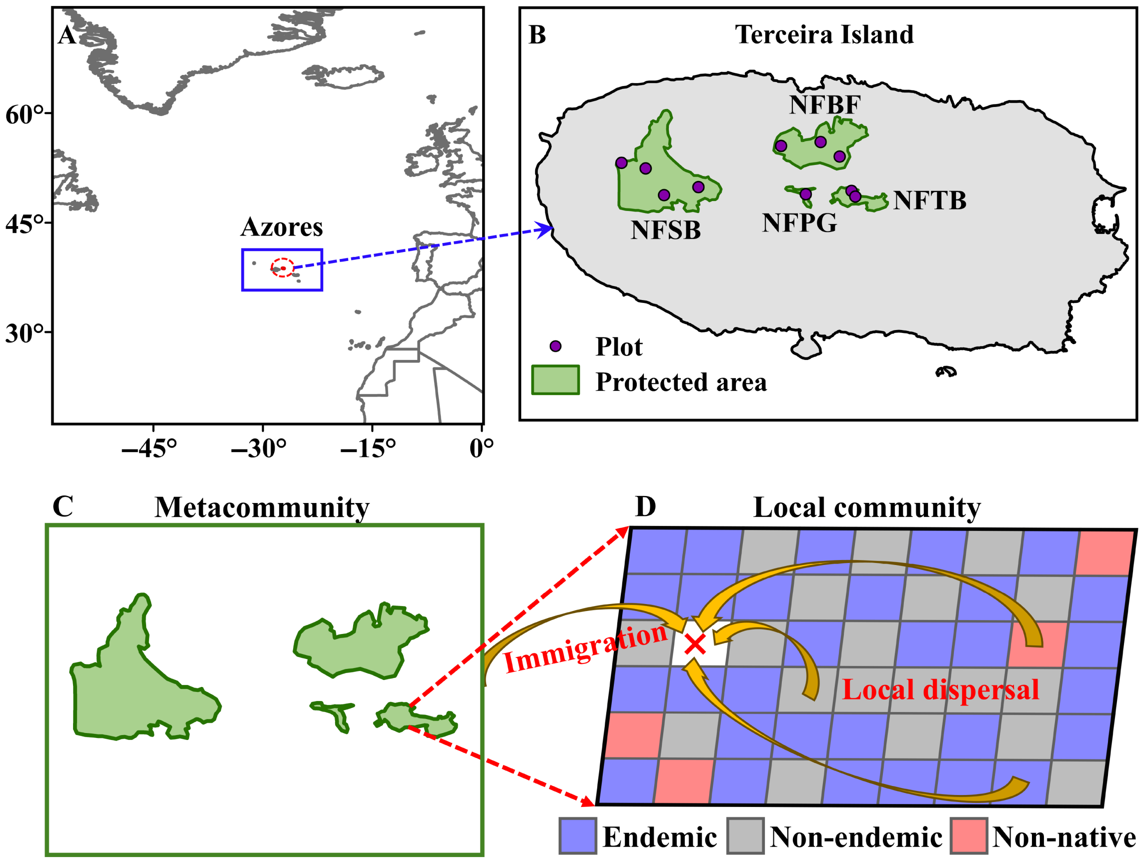

FIGURE 1 (A, B) A map of the 10 sampled 50 × 50 m plots, uniformly distributed in four fragments (NFSB with four plots, NFBF with three plots, NFTB with two plots, and NFPG with one plot) of native forest on Terceira Island, Azores. (C, D) The neutral modeling framework, with the metacommunity defined as the sampling pool across spatiotemporal scales, containing non-native, native endemic, and native non-endemic species. The local community dynamics include species mortality, colonization via local dispersal, and immigration from the metacommunity. NFBF, Biscoito da Ferraria; NFPG, Pico Galhardo; NFSB, Caldeira Santa Bárbara e Mistérios Negros; NFTB, Terra Brava.

of indeterminate species (2.78%—possibly introduced but status not definitively known) were ignored in our analyses (see dataset in Borges & Lhoumeau, 2025). In this study, we used data sampled consecutively over the years 2013 ~ 2024 (inclusive), with 12 years in total. A more comprehensive overview of the sampling methodology can be found in Lhoumeau and Borges (2023) and Matthews et al. (2019).

Temporal diversity patterns

In each fragment, we pooled the sampling plots within each year to create yearly datasets for each local community. Where the same species had been observed in multiple samples within a single year, we combined records and summed the abundances. Converting these data into 12 presence–absence matrices (one for each of the 12 sampling years from 2013 to 2024), we calculated α-diversity (species richness and Hill numbers) for each year and temporal β-diversity across years, respectively, for non-natives, native endemics, and native non-endemics in each fragment. We calculated temporal β-diversity using two approaches. First, we used Sørensen dissimilarity (based on species presence–absence data), which can be partitioned into its temporal species replacement and richness difference components (Carvalho et al., 2012), using the "BAT" package in R (Cardoso et al., 2015). Specifically, the species replacement component measures the dissimilarity between the two sampling years which arises from one set of species being replaced by another different set, independent of any difference in the total number of species. In contrast, the richness difference component measures the dissimilarity due solely to a difference in the total number of species between the two sampling years, irrespective of which specific species are present. This partitioning aids in identifying the underlying ecological assembly processes, such as dispersal limitation versus habitat filtering (Magurran et al., 2019). Second, we calculated Bray–Curtis dissimilarity over time (i.e., considering temporal variation in species abundance) to describe temporal β-diversity using the "beta.multi.abund" function in the "betapart" R package (Baselga, 2017). Specifically, we used 2013 as the base year and calculated temporal β-diversity between each local community (from 2014 to 2024) and the first local community (in 2013) in the time series. Although there are a few 3-month samples missing in our data for various logistical reasons (38 out of 480 total samples across 2013 ~ 2024; note all winter samples in 2024 are not available), this is unlikely to affect our estimation of temporal diversity patterns given the missing number is small (≈7.9%) and spread across the time periods and fragments.

To assess the temporal trends in these diversity metrics respectively for the three chorotypes in each fragment, we adopted a simple linear regression model $Y = a_0 + a_1 \times \Delta t + \varepsilon$ (Y—diversity metrics, Δt—duration, i.e., the interval between each sampling year and the first sampling year in the time series, a_0—the intercept, a_1—the slope, and $\varepsilon \sim N(0, \sigma^2)$—the error term following a normal distribution with a variance σ^2 around the mean 0), based on the ordinary least squares method. Model diagnostics included examining the residuals versus fitted values to verify linearity and homoscedasticity, and testing the normality of the residuals and the temporal autocorrelation. All these diagnostics indicated that these modeling assumptions are well satisfied.

We also tested the sensitivity of species diversity to the spacing of sampling locations within fragments, as there are more sampled plots in larger fragments, sampled plots are typically further apart in larger fragments, and the total sampled species richness at the fragment level can be significantly influenced by fragment size (i.e., species pool). As recommended previously (see details in Gonçalves-Souza et al., 2025; Marion et al., 2017), we estimated the average "pairwise sample diversity" by controlling for differences in the number of plots between fragments. We found that species dissimilarity between plots increases significantly with increasing mean distance between plots within fragments (i.e., with increasing fragment size), whereas species richness surprisingly decreased at both the plot and fragment levels (Appendix S1: Figure S1; cf. Matthews et al., 2019). However, while interesting, these results do not bias our main analyses, as these are focused on the analysis of temporal diversity patterns within fragments, and it is not our objective to make comparisons between fragments.

Temporal trends in SADs

We investigated temporal changes in the SAD respectively for non-natives, native endemics, and native non-endemics in each fragment. On a per-fragment (local assemblage) basis, we firstly defined the SAD intervals and counted the number of species falling into them following van Klink et al. (2024). For each chorotype (i.e., non-native, native endemic, and non-endemic), we created five equally sized intervals of $\log_{10}$(abundances) relative to the highest abundance (<20%: rare species with low abundance; 20%–40%: moderately low-abundant species; 40%–60%: intermediate abundant species; 60%–80%: moderately high-abundant species; and 80%–100%: common species with high abundance), which ranged between zero and the maximum abundance (100%: the most abundant species) observed in that fragment over the course of the time series. In other words, the baseline for "locally abundant" in a given fragment is the highest abundance of any species recorded from the fragment over the course of the entire time series. Here, we were only interested in changes in the number of species in different SAD intervals through time, disregarding the precise shape of the SAD. Using this approach allows us to precisely assess how and to what extent native species with different relative abundances respond to non-native introductions and establishment, in order to better understand temporal trends in rare and abundant species. Within each year, we calculated the number of species whose $\log_{10}$(abundances) fell in each interval. Then, we used a Bayesian mixed-effects model $Y_i = a_0 + a_1 \times \Delta t_i + b_{\text{fragment}[i]} + \varepsilon_i$ to evaluate an overall temporal trend for change in the number of species for each SAD interval (i.e., Y_i—the response variable) across all fragments, by taking Δt_i as the only fixed effect and fragment as a random effect, with random intercepts $b_{\text{fragment}} \sim N\left(0, \sigma^2_{\text{fragment}}\right)$ and the error term $\varepsilon_i \sim N(0, \sigma^2)$ (see code in Zhang et al., 2025). In this model, the error family of Y_i followed a Poisson distribution (counts of species per bin), and the fixed-effect coefficient a_1 of Δt_i was a flat prior, indicating no preconceived assumption about the direction of the effect. We set the SD of the random effect $\sigma_{\text{fragment}} \sim \text{student\_}t(3, 0, 2.5)$, the residual SD $\sigma \sim \text{student\_}t(3, 0, 2.5)$, and the intercept $a_0 \sim \text{student\_}t(3, \text{location}, 2.5)$, where the location was determined by the range of Y_i (i.e., a standard adaptive prior setting). The model coefficients and posterior estimates were obtained using the "brms" package in R (Bürkner, 2021). Convergence of these models was evaluated via the R-hat diagnostic (always ~1) and bulk effective sample size (typically >1000). Thus, temporal changes in the number of species in different SAD intervals were described by the probability density of the trend slope estimates from the Bayesian mixed-effects models. Any 95% credible interval that did not overlap zero was interpreted as strong evidence for a directional trend, a credible interval overlapping zero between 90% and 95% levels as moderate evidence, an overlap between 80% and 90% levels as weak evidence, and an overlap <80% as no evidence (van Klink et al., 2024).

Developing a neutral model based on the empirical data

We used a spatially implicit neutral model of biodiversity to approximate the drift of the sampling plots from the empirical data. The sampling plots within each fragment were pooled to form a local community, where all species, including non-native, native endemic, and non-endemic, were assumed to be ecologically equivalent (i.e., identical fecundity, mortality, and immigration per capita rates for all species; Hubbell, 2001) when competing for empty sites. Each local community was linked to a metacommunity via immigration (illustrated in Figure 1C,D).

Following Jabot et al. (2008), we identified the metacommunity by pooling all plots together (containing non-natives, native endemics, and non-endemics) from four fragments across all sampling years (2013 ~ 2024) in Terceira Island, so as to estimate the relative abundance of each species in the metacommunity. As our constructed metacommunity is much larger than the sampling pool observed annually, this would underestimate immigration rates (m) for local communities in a given year (Sgardeli et al., 2016). Thus, we estimated the immigration rates for each local community independently based on the sampling pool every year in Terceira Island, using the sampling formula (maximum likelihood estimation) of Etienne (2005), as applied by Jabot et al. (2008) via the freeware tetame. Finally, we took the average of the estimated immigration rates over 12 years as m_i for each local community i.

To simulate the local dynamics for a given community i, we firstly estimated the local community size J_i (i.e., the number of habitat sites, with each only accommodating one individual of a species) as the number of individuals averaged over 12 sampling years. Initially, each habitat site was occupied randomly by an individual of a species from the metacommunity, and the identity and chorotype of the individual (i.e., non-native, native endemic, or non-endemic) were recorded. After all habitat sites were fully occupied, we started simulating local community dynamics: We randomly selected an individual to die in the local community and consequently left an empty site (illustrated by Figure 1D), which was then immediately occupied either by an immigrant from the metacommunity or by an offspring of the existing species in the local community. More specifically, (1) an individual from the metacommunity occupied this empty site with probability m_i (estimated immigration rate), and the probability that this immigrant was an offspring of a specific species is proportional to its relative abundance in the metacommunity constructed above; or (2) the probability of this empty site being occupied by a new recruit from the local community is $1 - m_i$, and the probability of this new recruit being an offspring of existing species is proportional to their relative abundances in the local community. The local community dynamics were iterated until a dynamic equilibrium was achieved. Here, the dynamic equilibrium is defined as the stable species richness with fluctuations around the mean in a local community, since numerous empirical observations have shown no systematic biodiversity loss in local assemblages over time (Dornelas et al., 2014). From preliminary analysis, all local communities in our simulations achieved dynamic equilibria after 500 generations (i.e., repeating $500 \times J_i$ iterations). Thus, we additionally simulated 500 generations (i.e., 1000 generations in total) for all local communities, each with 100 replicates (see code in Zhang et al., 2025).

As many arthropod species can produce multiple generations per year and each generation can produce numerous individuals, here we roughly estimated one year as 10 simulation generations. Thus, we randomly selected a starting point at the dynamic equilibrium and recorded community structure and composition at every interval of 10 generations to mirror the actual sampling time (12 years from 2013 to 2024). Using this recorded community information, we calculated the α-diversity (species richness and Hill Numbers) of each local community and temporal β-diversity (Sørensen and Bray–Curtis dissimilarities) and identified any temporal trends in the number of species in different abundance intervals for all three chorotypes in order to determine whether these simulated communities are similar to the empirically observed patterns.

RESULTS

Temporal change in α-diversity

For all four fragments (NFTB, NFPG, NFSB, and NFBF), both native endemic and non-endemic assemblages showed almost equal richness, with both having much higher species richness than non-native assemblages (about 2:1) across 12 sampling years (Figure 2). Moreover, the slopes of a linear model fitted to the richness–time relationships for the native endemic, native non-endemic, and non-native chorotypes were all statistically indistinguishable from zero (95% confidence

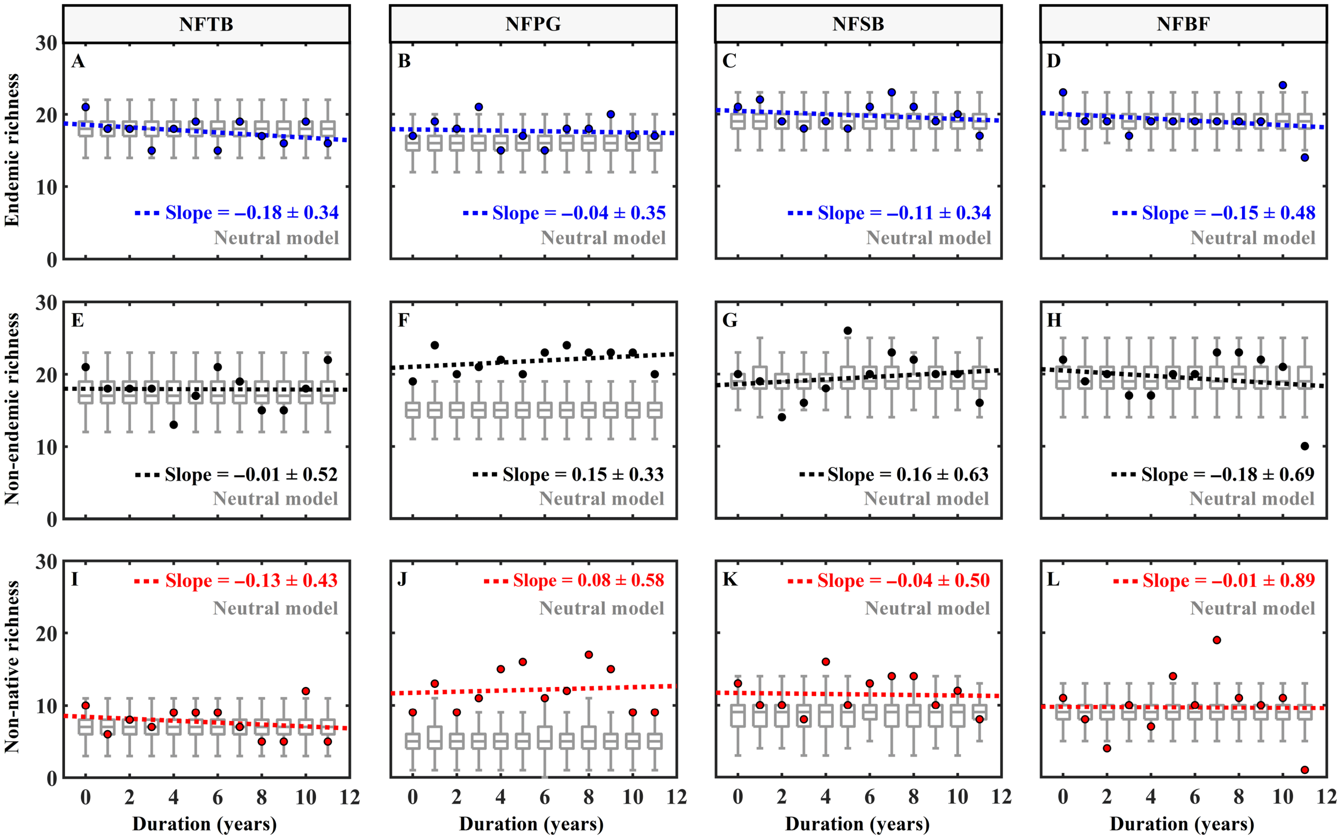

FIGURE 2 Temporal change in species richness respectively for native endemics (blue points), native non-endemics (black points), and non-natives (red points) in each fragment (NFTB, NFPG, NFSB, and NFBF) of Terceira Island from 2013 to 2024 (2013 as the base year), with a simple linear model fitted to each time series (slope ± 95% CI). The dotted lines represent that these slopes are not significantly different from zero. Box-plots show the corresponding values generated by the neutral models in the four fragments at the dynamic equilibrium, each with 100 replicates. The bottom and top limits of each box are the lower and upper quartiles, respectively; the horizontal band within each box is the median; and error bars equal ±1.5 times the interquartile range. NFBF, Biscoito da Ferraria; NFPG, Pico Galhardo; NFSB, Caldeira Santa Bárbara e Mistérios Negros; NFTB, Terra Brava.

intervals [CIs] of all slopes including zero; Figure 2). Thus, from analysis of species richness patterns alone, it would seem that the different empirical assemblages have reached a form of dynamic equilibrium. Using the neutral model with 100 replicates for each observed local assemblage, we found that most observed richness values for native endemics, non-endemics, and non-natives fall within the 1.5 times interquartile range in three of the four fragments (NFSB, NFBF, and NFTB in Figure 2), with several observed points being outliers. In the NFPG fragment, our neutral model generally predicted well species richness of the native endemics (as almost all observed richness values fell within the 1.5 times interquartile range of the box-plots; Figure 2B), while species richness of both native non-endemics and non-natives was underestimated (as all their richness values were outliers and much higher than the values generated by the neutral model; Figure 2F,J). This is likely because the NFPG fragment is the smallest of the four studied fragments and thus might suffer the most from anthropogenic disturbance, resulting in increased non-native immigration rates. However, when considering variation in species abundance via the use of Hill numbers (see details in Appendix S1: Figures S2 and S3), we found significant decreasing trends in both the exponential Shannon index and the inverse Simpson index for native endemics and non-endemics over time in both the NFTB and NFSB fragments, though again our neutral model generally predicted them well with only several outliers. This indicates that using raw species richness alone might not tell the full story of temporal trends in α-diversity.

Temporal β-diversity

For all four fragments, temporal β-diversity in the time series, characterized by Sørensen dissimilarity between each local community and the first local community (2013 as the base year), was generally lowest for native endemics (Figure 3A–D), intermediate for

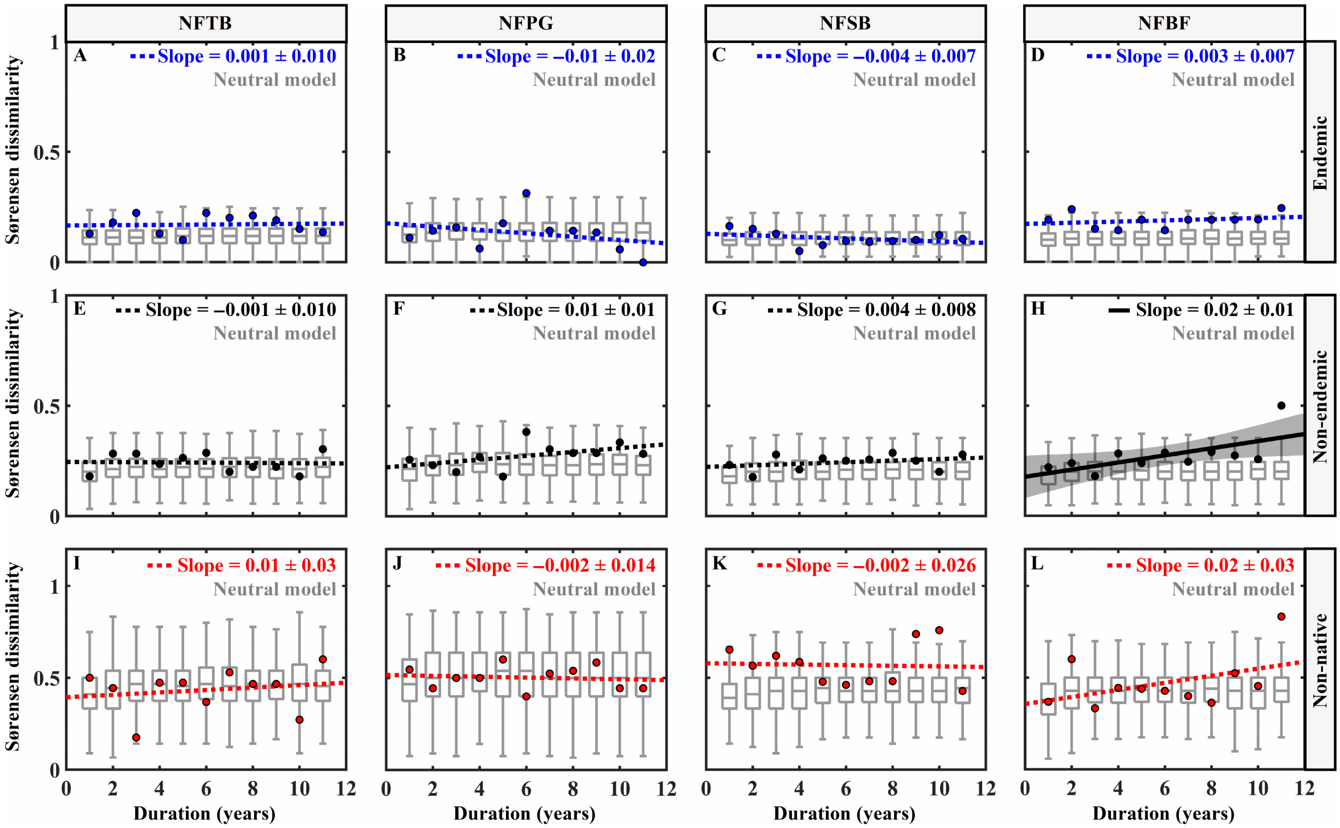

FIGURE 3 Temporal β-diversity, characterized by Sørensen dissimilarity between each local community (from 2014 to 2024) and the first local community (in 2013 as the base year) in the time series, respectively, for native endemics (blue points), non-endemics (black points), and non-natives (red points) in the four fragments (NFTB, NFPG, NFSB, and NFBF) of Terceira Island. A simple linear model (slope ± 95% CI) has been fitted to these empirical data (dotted lines: nonsignificant slope; solid lines with shaded area: significant slope). Box-plots show the corresponding values generated by the neutral model in the four fragments at the dynamic equilibrium, each with 100 replicates. NFBF, Biscoito da Ferraria; NFPG, Pico Galhardo; NFSB, Caldeira Santa Bárbara e Mistérios Negros; NFTB, Terra Brava.

native non-endemics (Figure 3E–H), and highest for non-natives (Figure 3I–L). For each chorotype (i.e., native endemic, non-endemic, and non-native), there was little variation in Sørensen dissimilarity among the four fragments through time. When fitting a linear model to the time series, we found that none of the slopes (all the 95% CIs including zero) were significantly different from zero, though there was a significantly increasing trend for the native non-endemics in NFBF (slope = 0.02 ± 0.01 in Figure 3H due to the contribution of the last observed point, as the slope = 0.006 ± 0.008 if it was removed). For each chorotype, we also constructed the corresponding neutral models, each with 100 replicates. It was found that almost all observed temporal β-diversity values fall into the 1.5 times interquartile range of the box-plots created by the neutral model predictions (Figure 3), with the exception of a small number of outliers.

When partitioning temporal β-diversity (Sørensen dissimilarity) into its temporal species replacement and richness difference components (Appendix S1: Figures S4–S6), we observed that both native non-endemics and non-natives generally display larger temporal species replacement than richness differences, whereas both components contribute approximately equally to temporal β-diversity in native endemic assemblages. Comparing patterns across the three chorotypes indicates that temporal replacement was the highest for non-natives but the lowest for native endemics, while all the chorotypes displayed roughly similar low levels of temporal richness difference. Similarly, all the slopes from linear models fitted to the observed temporal replacement and richness difference time series were statistically indistinguishable from zero (Appendix S1: Figures S4–S6 with all the 95% CIs including zero). The neutral models generally predicted these temporal replacement and richness differences, as almost all the observed data fell into the 1.5 times interquartile range of the box-plots of neutral modeling predictions, occasionally with a few outliers (Appendix S1: Figures S4–S6).

When using Bray–Curtis dissimilarity to characterize temporal β-diversity, a measure that incorporates data on species abundances (Figure 4), we again observed the highest temporal β-diversity for non-natives and the

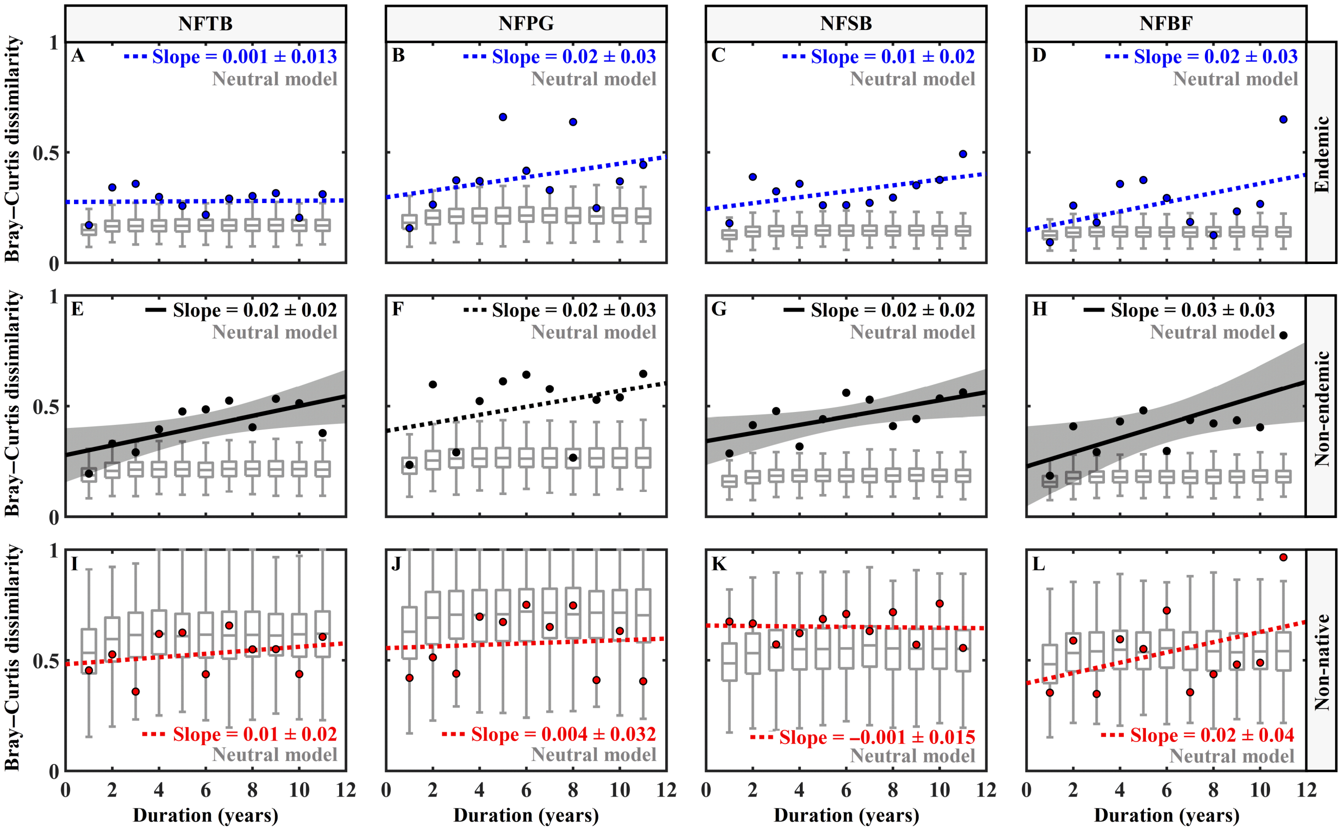

FIGURE 4 Temporal β-diversity, characterized by Bray–Curtis dissimilarity (i.e., considering temporal variation in species abundances) between each local community (from 2014 to 2024) and the first local community (2013 as the base year) in the time series, respectively, for native endemic (blue points), native non-endemic (black points), and non-native assemblages (red points) in the four fragments (NFTB, NFPG, NFSB, and NFBF) on Terceira Island. A simple linear model (slope ± 95% CI) has been fitted to these empirical data (dotted lines: non-significant slope; solid lines with shaded area: significant slope). Box-plots show the corresponding values generated by the neutral model in the four fragments at the dynamic equilibrium, each with 100 replicates. NFBF, Biscoito da Ferraria; NFPG, Pico Galhardo; NFSB, Caldeira Santa Bárbara e Mistérios Negros; NFTB, Terra Brava.

lowest for native endemics in general. Furthermore, we found no significant trend in temporal Bray–Curtis dissimilarity for either native endemics or non-natives (all the 95% CIs including zero in Figure 4A–D,I–L), but native non-endemics generally showed a significantly increasing trend (all the 95% CIs excluding zero in Figure 4E,G,H), except in NFPG (slope = 0.02 ± 0.03 in Figure 4F). The neutral model generally underestimated temporal changes in Bray–Curtis dissimilarity for both native endemics and non-endemics (Figure 4A–H), with almost all the observed data being outliers. For non-natives (Figure 4I–L), almost all observed data fell into the 1.5 times interquartile range of the box-plots of neutral model predictions.

Temporal trends in SADs

Finally, we explored the temporal trend of yearly changes in the number of species within five different equally sized abundance intervals for native endemics, native non-endemics, and non-natives, respectively (Figure 5). For the native endemic chorotype (Figure 5A), we observed strong declines in species richness in the 60%–80% abundance interval (i.e., moderately high-abundant species) and weak evidence for an increasing trend in the interval of 20%–40%, while other intervals (<20%, 40%–60%, and 80%–100%) displayed little evidence of any trend. For the native non-endemic chorotype (Figure 5B), we found strong evidence for increasing trends in the interval of 20%–40% and decreasing trends in the 40%–60% interval, weak evidence for an increase in rare species (0%–20%) and a decline in the 60%–80% interval, and little evidence for any trend in common species (80%–100%). When combining native endemics and non-endemics as natives (Figure 5C), we found strong declines in native species richness in both the intervals of 40%–60% and 60%–80%, while the 20%–40% interval showed strong evidence for an increasing trend. There were also little or weak evidence for increasing trends in rare (0%–20%) and common

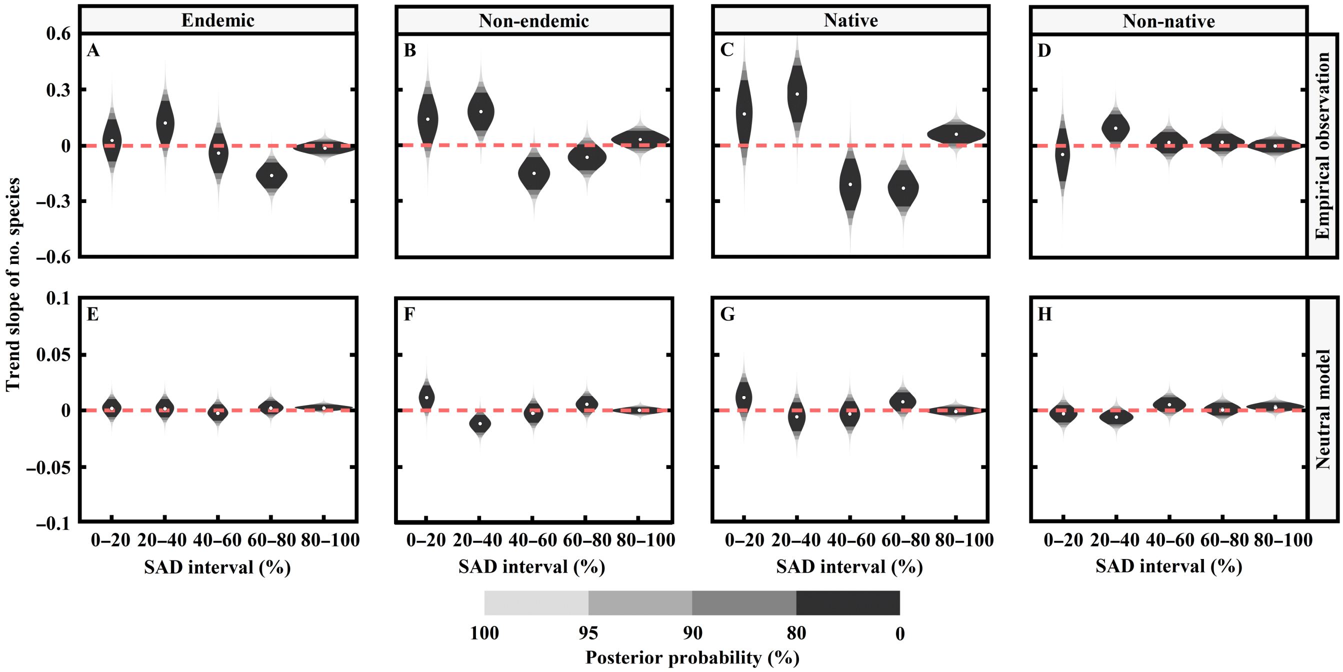

FIGURE 5 Probability density of the posterior trend slope estimates of the changes in the number of native (including endemic and non-endemic) and non-native species in five equally sized ($\log_{10}$-tranformed) species abundance distribution (SAD) intervals over time for both the empirical observations and neutral modeling predictions. Shading represents the posterior probability of the mean slope estimate, corresponding to the 80%, 90%, and 95% credible intervals from the Bayesian mixed-effects models. The five SAD intervals were assigned separately from each time series in each fragment for each chorotype (non-natives, native endemics, and non-endemics), scaled to the highest abundance of any species observed in any year. The red dashed lines indicate the slope estimate equal to zero.

(80%–100%) species. For the non-native chorotype (Figure 5D), we did not detect a significant change in any abundance interval. In our neutral models, however, all chorotypes displayed little or weak evidence for any trend in different abundance intervals, and all the mean trend slopes were close to zero (Figure 5E–H). This indicates that the neutral model is unable to replicate empirical temporal changes in the SAD of native endemics and/or non-endemics, though the SAD of non-natives is more accurately predicted.

DISCUSSION

This study builds on 12 years of ecological monitoring within the SLAM project on Terceira Island (Borges, 2025). We have integrated multiple analytical frameworks, including community turnover, SAD patterns, and neutral simulations, to provide a more comprehensive mechanistic understanding of how native endemic, native non-endemic, and non-native arthropod assemblages respond to long-term environmental pressures through time. While previous work demonstrated compositional changes and β-diversity trends in arthropods across native forest fragments in the Azores (Lhoumeau & Borges, 2023; Matthews et al., 2019), here we extend those findings by quantifying variation in abundance structure (via Bray–Curtis dissimilarity and SADs) and linking all patterns explicitly to temporal community dynamics. Furthermore, by comparing the empirical temporal diversity patterns to predictions from a neutral model (Gilbert et al., 2006; Kuczynski et al., 2023; Sgardeli et al., 2016), we were able to critically assess the role of stochastic versus deterministic processes in shaping the observed patterns. To this end, we found that, while non-native assemblage patterns are more consistent with those generated via stochastic processes (neutral drift and dispersal), native communities (i.e., native endemic and non-endemic assemblages) are seemingly shaped by both stochastic and deterministic processes.

These 12-year samples of insular arthropods generally show consistent temporal diversity patterns (i.e., temporal Sørensen dissimilarity and change in species richness through time) for all chorotypes based on species presence–absence data. These results seemingly indicate that the system has achieved a dynamic equilibrium, with no systematic change in species richness (Dornelas et al., 2014) and a steady and consistent change in species composition. Most likely, this is because: (1) many arthropod species undergo rapid generational turnover and can produce multiple generations per year, with each producing numerous individuals; and (2) many non-native arthropod species are less adapted to local microhabitat conditions and thus may simply be ephemeral members of the community with a higher risk of local extinction, as they are likely driven by consistent stochastic source-sink mass effect dynamics involving immigration from surrounding human land use (Matthews, 2021). In contrast to the incidence-based metric trends, when considering temporal variation in species abundance, we find an overall increasing trend in Bray–Curtis dissimilarity for both native endemics and non-endemics. Among them, many moderately high-abundant species, which may be particularly sensitive to non-native introductions and other human disturbances, are gradually becoming low-abundant species. In a separate study, Lhoumeau and Borges (2023) observed that in these assemblages, there is also a decrease in the biomass of native non-endemics. Currently, these changes only involve abundance declines rather than extirpations/extinctions, thereby leading to no net decline in native species richness across the 12 sampling years (similar to Dornelas et al., 2019). Our neutral model fails to reproduce these temporal diversity patterns in the native species chorotypes, indicating that besides stochastic drift, other deterministic assembly processes are likely important. These processes might include interactions between natives and non-natives (e.g., competition; O'Sullivan et al., 2021) or/and environmental change (e.g., land-use and climate change; Antão et al., 2020; Montràs-Janer et al., 2024; Newbold et al., 2015), leading to a significant temporal change in native species composition. In this sense, the findings of previous studies that reported stable native arthropod populations in the Azores (Lhoumeau & Borges, 2023; Matthews et al., 2019; Pozsgai et al., 2025) might not hold long term.

It has often been reported that, as introductions proceed and non-natives become established, which can facilitate the establishment of further non-native species (i.e., invasional meltdown; Simberloff & Von Holle, 1999), more profound temporal changes in non-native species composition would emerge (Kortz et al., 2023). However, in our 12-year sample data, non-natives show no systematic increase in species richness, and steady and consistent temporal β-diversity (including both Sørensen and Bray–Curtis dissimilarities) and changes to the SAD. This confirms the previous finding of Pozsgai et al. (2025), using a different dataset, that neither the abundance patterns nor the species richness of non-natives has changed substantially in local assemblages on Terceira Island over the last ca. 25-years. However, this does not mean that these measures have remained unchanged at larger regional scales (e.g., island or archipelago). Interestingly, our neutral model generally predicts well the empirical temporal diversity patterns of non-natives, implying that stochastic drift might be a primary driver shaping non-native assemblages in this system. In Azorean native forest fragments, non-native arthropods are often rare relative to native endemics and non-endemics, and they have a much higher rate of species replacement/turnover (Lhoumeau & Borges, 2023; Matthews et al., 2019). In addition, all native forest fragments on Terceira are surrounded by anthropogenic land-use types, primarily pastures, which support large numbers of non-native arthropod species. Thus, most likely, there are large mass effects and a constant supply of non-native individuals permeating into the native habitats where they frequently undergo stochastic local extinction and re-colonization, thereby leading to higher temporal β-diversity (Matthews, 2021; Matthews et al., 2019) and temporal diversity patterns more consistent with the neutral model predictions. In other words, many non-natives present in a fragment may simply be ephemeral members, indicating that they should be less adapted to the conditions within local habitats and should have a higher risk of extinction and turnover. Therefore, our conclusion that neutral drift likely shapes non-native community dynamics, in combination with previous work in the Azores (Borges et al., 2006), supports the view that the presence of non-native arthropods within native habitats in Terceira Island is primarily driven by stochastic source-sink mass effect dynamics linked to immigration from surrounding disturbed land use (Sgarbi & Melo, 2018).

Our findings have important implications for the conservation of native endemic arthropods in the Azores, and island ecosystems more broadly. Despite consistent temporal β-diversity (Sørensen dissimilarity) and α-diversity for native endemics within the 12-year sampling period, many native endemics with originally moderately high abundance are declining and gradually becoming rarer. In this sense, the use of temporal diversity metrics based solely on species presence–absence data (e.g., species richness and Sørensen dissimilarity) might result in misleading conclusions. By extension, our results highlight the importance of focusing on temporal variation in species abundance (Magurran & Henderson, 2010; van Klink et al., 2024), such as temporal trends in the SAD, which is more sensitive to anthropogenic disturbance than richness (Matthews & Whittaker, 2015) and thus gives us important early-warning signals of temporal structural changes in native assemblages (MacLachlan et al., 2021). Another important finding with conservation implications is our observation that human-driven stochastic source-sink mass effect dynamics are a likely driver of non-native species assembly and persistence. This knowledge offers new insights into native endemic biodiversity management. For example, the realization that native habitat is likely just a sink for many non-natives, and their constant influx from anthropogenic source habitats in close proximity to the native habitats (i.e., mass effects) means that the local extinction (e.g., due to conservation and management actions in the fragments) of many non-natives within native habitats is unlikely to be permanent. Thus, simply reducing and removing non-native populations within native habitats may not be successful for endemic biodiversity conservation. Instead, a more efficient future management strategy and land-use policy will be to interrupt these source-sink dynamics by improving the harsh boundaries between native habitats and adjacent anthropogenic habitats (Fahrig, 2017; Ries et al., 2004).

CONCLUSION

This study demonstrates that insular arthropod assemblages, when observed through the lens of long-term monitoring, reveal complex and often divergent temporal trajectories between natives and non-natives. Our integration of temporal variation in species abundance (SADs) and neutral model simulations uncovers critical shifts in native community structure, pointing to potential regime changes that may be invisible through traditional diversity metrics alone. In contrast, non-native species appear to follow dynamics more consistent with neutral expectations, likely suggesting stochastic colonization and high turnover as key drivers of their success. These findings support the growing recognition that native biodiversity change on islands is not only about species loss but also about compositional transformation—a "silent reshuffling" that may precede more visible ecosystem disruption. The take-home messages are that: (1) we should not solely focus on temporal diversity metrics based on species presence–absence data as an indicator of ecosystem status, but must also consider temporal variation in the SAD; and (2) long-term, standardized monitoring, instead of short time series observations, remains indispensable for detecting nuanced temporal changes in community structure. Overall, our results highlight that it is necessary to understand the long-term population trends of both native and non-native arthropods together in island systems if we are to prevent the further spread of non-natives and protect native island endemic biodiversity.

AUTHOR CONTRIBUTIONS

Yiheng Zhang performed data analyses and simulations. Paulo A. V. Borges and Sébastien Lhoumeau collected data and contributed revisions. Jinbao Liao conceived the study and wrote the first draft; all authors discussed the study and contributed substantially to revising and editing the draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Zhang et al., 2025) are available in Zenodo at https://doi.org/10.5281/zenodo.17384545.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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