




Up from the bottom: Consistent vertical distance-decay in arthropod assemblage similarity across native and exotic forests in Terceira island (Azores)

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ABSTRACT

This study compares the vertical stratification of arthropod assemblages in native and exotic forests on Terceira Island (Azores), focusing on how assemblage similarity decays with increasing vertical distance between strata. We tested three hypotheses: (H1) the overall arthropod assemblage similarity decays with vertical distance; (H2) exotic forests exhibit lower decay rates due to structural simplification; and (H3) the contribution of both indigenous and non-indigenous arthropod assemblages to vertical distance decay differs. Arthropods were sampled across four strata in ten native and ten exotic forest plots using pitfall and SLAM traps. We computed the beta diversity between each strata, partitioning turnover versus richness differences. We found a significant decay in the overall arthropod assemblage similarity with increasing vertical distance, driven primarily by species turnover rather than richness differences. Contrary to predictions, the rate of vertical decay did not differ significantly between native and exotic forests, suggesting that structural simplification in exotic forests does not necessarily reduce vertical stratification. However, the species origin of the arthropods had a significant effect on the vertical distribution patterns, with non indigenous species showing a restricted vertical ranges compared to indigenous species. These findings highlight the significance of incorporating vertical dimensions in biodiversity assessments and conservation strategies, emphasising the pivotal role of species biogeographical origin in shaping vertical community structure in island forest ecosystems.

1. Introduction

Distribution of organisms in forests is shaped by a combination of abiotic and biotic factors, including illumination, humidity, temperature, vegetation complexity, and resource partitioning (Brown, 1984; Jayasuriya and Pemasada, 1983). These factors undergo significant changes from the soil to the upper canopy, often giving rise to a wide range of habitats across a vertical gradient (Cooper et al., 2023; Xing et al., 2023) resulting in a high vertical distance-decay of similarity between strata as they harbour distinct assemblages (Basham et al., 2019, 2023; Camargo et al., 2018; Thiel et al., 2021).

Vertical stratification, i.e. the uneven distribution of species according to the canopy height, have been extensively studied across several taxa (Xing et al., 2023). In particular, arthropods, due to their

immense diversity and ecological roles stand as ideal model organisms (Basset et al., 2003, 2015). They respond sensitively to environmental gradients and habitat structure, occupying a variety of niches from the forest floor to the upper canopy (Basset et al., 2015; Camero Rubio et al., 2021; Ulyshen, 2011; Wardhaugh, 2014; Yoshida et al., 2021).

However, comparative studies examining their vertical distance-decay relationship in novel exotic forests relative to co-occurring native stands remain virtually absent. The degree of vertical differentiation (i.e. beta diversity between forest strata) is expected to vary significantly between forest types due to differences in species composition (Wilsey et al., 2009). As mature ecosystems, native forests tend to exhibit more complex vertical structure, offering a greater variety of microhabitats (Lopes et al., 2015). This ecosystem tends to host most of the indigenous taxa (Lhoumeau and Borges, 2023). In contrast, novel

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exotic-dominated forests are often characterized by uniformity in vegetation and simplified architecture (Balzotti and Asner, 2017), potentially reducing vertical environmental gradients and biotic homogenisation across layers. Studies in monoculture plantations, such as Japanese cedar (*Cryptomeria japonica*), have described within-stand vertical distribution (Yoshida et al., 2021), and work on soil invertebrate diversity has demonstrated declines under exotic *Pinus radiata* plantations (Cifuentes-Croquevielle et al., 2020) or *Eucalyptus* stands (Martello et al., 2024). Yet these studies do not evaluate how structural simplification in exotic stands influences vertical decay of arthropod similarity relative to native forests.

This contrast between forest types is particularly relevant in island ecosystems such as the Azores, where forest modification and the introduction of exotic tree species transformed large areas of native habitat (Cardoso et al., 2009; Pozsgai et al., 2023; Rull, 2023). On Terceira Island, fragments of native vegetation coexist with extensive novel exotic-dominated forests (Cardoso et al., 2009; Elias et al., 2016; Tsafack et al., 2021). These two forest types differ not only in plant composition but also in vertical structural complexity, microclimatic conditions, and ecological stability (Borges Silva et al., 2022). Native forests often support higher levels of endemism and are more resilient to ecological disturbances (Borges et al., 2006; Lhoumeau and Borges, 2023), whereas exotic forests may facilitate biological invasions and alter natural community dynamics (Borges Silva et al., 2023; Cardoso et al., 2009; Florencio et al., 2015, 2016).

In island ecosystems, the biogeographical provenance of species strongly affects assemblage organisation (Oyarzabal et al., 2024), but few studies have linked species origin (indigenous vs introduced) to vertical turnover in forest canopies (but see (Costa et al., 2023)). The extent to which exotic forests maintain comparable levels of vertical stratification, or whether they promote biotic homogenisation by favouring the widespread presence of a particular assemblage of species across all layers, remains unclear. Moreover, the role of indigenous and exotic species in shaping vertical assemblage structure is not well understood, especially in disturbed or novel habitats (Tsafack et al., 2021).

In this study, we investigate how arthropod assemblages are stratified within island forest ecosystems, comparing patterns between native and exotic forests on Terceira Island in the Azores. By sampling arthropods across multiple forest strata we assess how assemblage similarity change with height within each forest type. Building on earlier arthropod surveys conducted in the region (e.g., Matthews et al., 2019, Borges et al., 2020, Lhoumeau and Borges, 2023), our approach offers a novel perspective by explicitly focusing on vertical beta diversity as a measure of spatial assemblage dissimilarity. Specifically, we test whether vertical patterns in assemblage structure differ between native and exotic forests, addressing the following hypotheses:

H1. The overall arthropod assemblage similarity decays with increasing vertical distance between forest strata, independently to the forest type.

H2. : The vertical decay in the overall arthropod assemblage similarity is stronger in native forests than in exotic forests because of biotic homogenisation in exotic forests.

H3. The contribution of each arthropod assemblage to the vertical stratification differs in native and exotic forests.

Based on previous insight of invasion dynamics in Azorean forests (Borges et al., 2020; Lhoumeau and Borges, 2023; Matthews et al., 2019), we predict the following:

(i) Arthropods are vertically stratified, with turnover being the main cause of dissimilarity between strata, resulting from a combination of species adaptation and environmental filtering.

Also, (ii) we expect native forest, being more a mature and complex ecosystem, to support pronounced vertical stratification, due to indigenous species adapted to specific forest strata.

Finally, (iii) we expect introduced arthropod assemblages to be

predominant in the lower strata, especially in exotic forests.

By testing forest type and species origin interactions within a vertical distance-decay framework, our study seeks to improve our understanding of the ecological consequences of forest changes in island systems. This is ultimately a necessary step in assessing the ecological integrity of different forest types, and in informing conservation strategies aimed at preserving arthropod diversity and ecosystem function.

2. Material and methods

2.1. Study area

This study was conducted on Terceira Island, part of the Azores Archipelago in the North Atlantic Ocean, approximately 1400 km west of mainland Portugal. The archipelago comprises nine volcanic islands formed along the Mid-Atlantic Ridge, known for their steep topography, diverse microclimates, and levels of endemism (Ferreira et al., 2019; Triantis et al., 2012a). The third biggest one, Terceira, retains the best-preserved fragments representative of the native vegetations (Borges et al., 2020; Dias et al., 2004; Fattorini et al., 2012; Henriques et al., 2017).

Twenty forest plots (20 m × 20 m each, Fig. 1) were established: ten in core native forests (Fig. 2, Left) dominated by endemic tree species (*Juniperus brevifolia*, *Erica azorica*, *Laurus azorica*, and *Ilex azorica*), and ten in secondary exotic forests (Fig. 2, right) dominated by *Pittosporum undulatum* and *Hedychium gardnerianum*. While native plots exhibited high canopy cover and an important vertical complexity, exotic plots were comparatively structurally simpler with some native ferns (*Dryopteris azorica*, *Diplazium caudatum*) persisted in the understory.

Because of historical alterations in land use the sites varied in altitude. Exotic plots were situated at lower elevations (256–461 m), while native plots ranged from 590 to 927 m. Based on the classification from (Elias et al., 2016), native forests consist in three different types: Laurus Submontane Forests (n = 3 plots), Juniperus-Ilex Montane Forests (n = 2 plots), Juniperus Montane Woodlands (n = 5 plots).

2.2. Sampling design and vertical stratification

Sampling took place between mid-June and mid-September 2024. In each of the 20 plots, up to three SLAM traps (Sea, Land and Air Malaise traps) were deployed to capture arthropods across vertical forest strata (SuppInfo 1, left). These passive flight interception traps measured 110 × 110 × 110 cm and were placed at approximately 0 % (ground level; GRD), 50 % (understory; UND), and 75 % (canopy; CAN) of the maximum canopy height. For two sites (namely TER-NFBF-T-02 and TER-NFSB-TE49) the understory traps could not be positioned at least 1 m vertically apart from other traps due to reduced canopy height and were excluded to ensure independent sampling between strata. SLAM traps intercept flying arthropods that enter the mesh and fall into a central collection container. Each trap was filled with pure 1,2-propanediol (propylene glycol), which serves both as a killing agent and DNA-preserving medium. Traps remained in the field for the entire 90-day period and were collected at the end of the season. Although originally designed for flying insects, these traps also sample non-flying taxa such as spiders due to their structural integration with the surrounding vegetation (Fig. 2). The successful use of this trap for long term monitoring of arthropods within the Azorean forests leads to numerous findings about this ecosystem (see for example (Borges et al., 2017; Lhoumeau and Borges, 2023; Tsafack et al., 2021)).

To complement vertical sampling, ground-dwelling arthropods were collected using 14 passive pitfall traps following original sampling design from (Borges, 1992) (SuppInfo 1, right). They were distributed evenly and randomly within each plot (epigeal layer; EPI). Pitfall traps consisted of plastic cups (5 cm diameter) partially filled with ethylene glycol and left open for 14 consecutive nights between July and August 2024. Traps were placed away from paths and dense vegetation to avoid

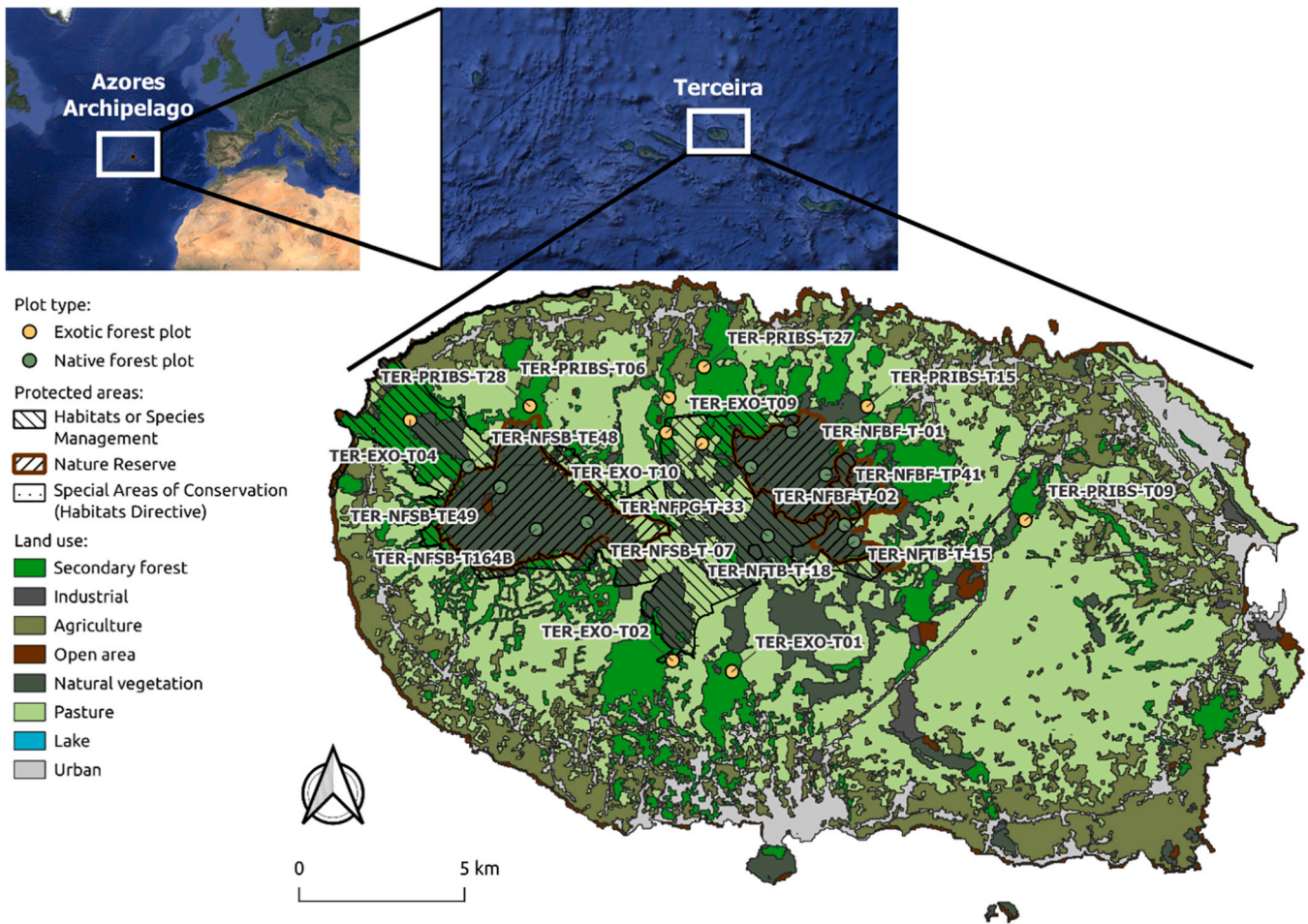


Fig. 1. Map of Terceira Island (Azores Archipelago), sourced from Lhoumeau et al. (2025) showing the location of the 20 sampling plots. Ten plots were established in native forest (green markers) and ten in exotic forest (yellow markers). The native plots are situated in remnants of native vegetation, while the exotic plots are in secondary woodlands dominated by introduced species. The background map includes land use (sourced from the Azorean government, <https://ot.azores.gov.pt/>) and protected areas boundaries (UNEP-WCMC, 2025) for geographic context.



Fig. 2. Representative views of the two forest types sampled on Terceira Island. Native forest (Left, Laurus Submontane Forests) dominated by endemic tree species such as *Laurus azorica*, *Juniperus brevifolia*, *Erica azorica*, and *Ilex azorica*, characterized by a closed canopy and complex vertical structure. Exotic forest (Right) dominated by *Pittosporum undulatum* and *Hedychium gardnerianum*, showing a more open canopy and simplified understory.

edge effects and microhabitat biases.

2.3. Identification and taxonomic scope

Arthropods were sorted and identified to the lowest possible taxonomic level, typically species or subspecies, using curated reference collections (DTP – Dalberto Teixeira Pombo Insect Collection at University of Azores). We focused on target groups for which reliable identification was possible: Diplopoda (Chordeumatida, Julida), Chilopoda (Geophilomorpha, Lithobiomorpha, Scolopendromorpha), Arachnida (Araneae, Opiliones, Pseudoscorpiones), and Insecta (Blattaria,

Coleoptera, Hemiptera, Microcoryphia, Neuroptera, Psocoda, Thysanoptera, Trichoptera, Hymenoptera Formicidae). Species nomenclature and colonization status (endemic, native non-endemic, or exotic) followed the recent classification system established in (Borges, Lamelas-Lopez, et al., 2022). Only arthropod taxa reliably identified at least at order level were included in the analyses, ensuring consistency across forest types and strata. All specimens were preserved in alcohol to allow for future morphological or molecular analysis. Data are available in (Lhoumeau et al., 2025).

2.4. Diversity metrics and statistical analyses

Only adult arthropod specimens were retained to ensure consistency in ecological interpretation, as juvenile stages can be more difficult to identify reliably across all taxa and may not reflect stable habitat associations. Due to the temporal difference of the sampling methods, the relative abundance of each taxonomic unit was computed for a given stratum, allowing the comparison of samples.

Vertical distance between strata was modelled as an ordinal variable, with values assigned as 1 for adjacent layers (e.g., GRD–UND), 2 for intermediate distances (e.g., GRD–CAN), and 3 for the largest vertical separation (e.g., EPI–CAN). They reflect increasing spatial and potential environmental differentiation. For the two sites where it was not possible to install traps in the understory, the canopy and ground layers were considered to be adjacent and thus a distance value of 1 was attributed.

To quantify vertical differences in arthropod assemblage, pairwise beta diversity (B_{Total}) was calculated between forest strata within each plot using the Sørensen dissimilarity index (Equation 1 from Sørensen, 1948).

$$B_{Total} = \frac{b + c}{2a + b + c}$$

Equation 1: Sørensen dissimilarity index which a is the number of shared species between two strata, b and c are the numbers of exclusive species of either stratum.

We selected the analytical framework from Carvalho et al. (2012) rather than Baselga partitioning (Baselga, 2010) because it explicitly decomposes beta-diversity into two ecologically interpretable components: species replacement (B_{Repl} , beta diversity due to species replacement only) and richness differences (B_{Rich} , beta diversity due to gain or loss species only). Unlike Baselga's method, Carvalho's partitioning provides a clearer distinction between processes of species substitution and variation in species richness, which is particularly useful in disentangling the ecological mechanisms underlying community assembly in structurally diverse environments, such as the vertical strata of forests. Computation of the beta diversity and its decomposition was performed with BAT package (Cardoso et al., 2015) using R version 4.4.1 (R Core Team, 2024).

As Sørensen dissimilarity values and their components are continuous and bounded between 0 and 1, all values were transformed to fall strictly within this interval, with the extremes excluded, using the bias-reducing formula (Equation 2).

$$B'_{Total} = \frac{B_{Total}(n - 1) + 0.5}{n}$$

Equation 2: Bias-reducing transformation to ensure data compatibility with beta regression. The formula rescales values bounded between 0 and 1 to fall strictly within the interval (0, 1), where B_{Total} is the original value, B'_{Total} the transformed value and n is a constant (set to 1000 in this study).

Hypothesis 1. Vertical distance-decay of assemblage similarity

To test whether the overall arthropod assemblage similarity decayed with increasing vertical distance, a beta regression model was fitted using the glmmTMB package in R (Brooks et al., 2017), with B'_{Total} as the response variable and vertical distance as the sole fixed effect. Site identity was included as a random intercept to account for repeated measures within sampling plots. This model tested for a general pattern of decay in similarity as vertical distance increased, regardless of forest type or assemblage origin. Additionally, to explore the ecological processes underpinning observed patterns in vertical assemblage dissimilarity, we employed paired Wilcoxon rank sum tests to assess differences in the relative contributions B_{Repl} and B_{Rich} across the vertical gradient. This complementary analysis provided further insight into the dominant mechanisms, i.e. species replacement or variation in species richness

driving changes in arthropod community composition between different forest strata.

Hypothesis 2. Stronger vertical decay in native forests

To evaluate whether the vertical decay in similarity was more pronounced in native forests than in exotic forests, a second beta regression model was built with vertical distance, forest type (native vs. exotic) as fixed effects and site as a random intercept. The same B'_{Total} values were used as the response variable.

Hypothesis 3. Assemblage-specific contributions to vertical stratification

To investigate whether the relative abundance of different assemblage types (endemic, native non-endemic and introduced) varied across forest strata and forest types, a third beta regression model was constructed. The response variable was the relative abundance of each assemblage in each stratum within each plot. Fixed effects included assemblage category, stratum, and forest type, while site identity was included as a random effect.

3. Results

3.1. Sampling description

We collected a total of 32,797 terrestrial arthropod specimens using SLAM and pitfall traps deployed across four vertical forest strata in both native and exotic forest plots on Terceira Island. Of the total collected, 18,372 individuals (56 %) were identified to species or subspecies level. Adult specimens with reliable identification ($n = 12,822$) were retained for analysis of assemblage composition and vertical beta diversity patterns.

H1. Vertical distance-decay of similarity

The beta regression model showed that B'_{Total} increased significantly with vertical distance between strata (Table 1, hypothesis H1), indicating a strong spatial signal in arthropod community composition along the vertical axis of the forest. Heatmaps of pairwise B'_{Total} (Fig. 3) reinforced these findings, showing consistently high dissimilarity values between vertically distant strata for all arthropod assemblages in the two forest types.

B'_{Total} between forest strata was predominantly explained B_{Repl} , with significantly higher values than B_{Rich} across all vertical distances (Paired Wilcoxon rank sum test; Fig. 4). This pattern was consistent from the smallest to the greatest vertical separation suggesting that stratification in the overall arthropod assemblage is largely due to species replacement rather than differential richness.

Table 1

Summary of beta regression models testing the effects of vertical distance (hypothesis H1) and a combination of vertical distance and forest types (hypothesis H2) on B'_{Total} between forest strata. Fixed effect estimates are shown with standard errors, z-values and significance levels. All models used the logit link and included site identity as a random intercept (variance shown). Significant predictors for each hypothesis are highlighted in bold (***) $p < 0.001$, ns $p < 0.1$.

Hypothesis	Fixed Effect	Estimate	Std. Error	z value	Significance
H1	(Intercept)	0,09005	0,25456	0354	ns
H1	Distance	0,57207	0,14251	4014	***
H2	(Intercept)	-0,04311	0,27254	-0158	ns
H2	Distance	0,57472	0,14216	4043	***
H2	Habitat (Native forest)	0,27577	0,20711	1332	ns

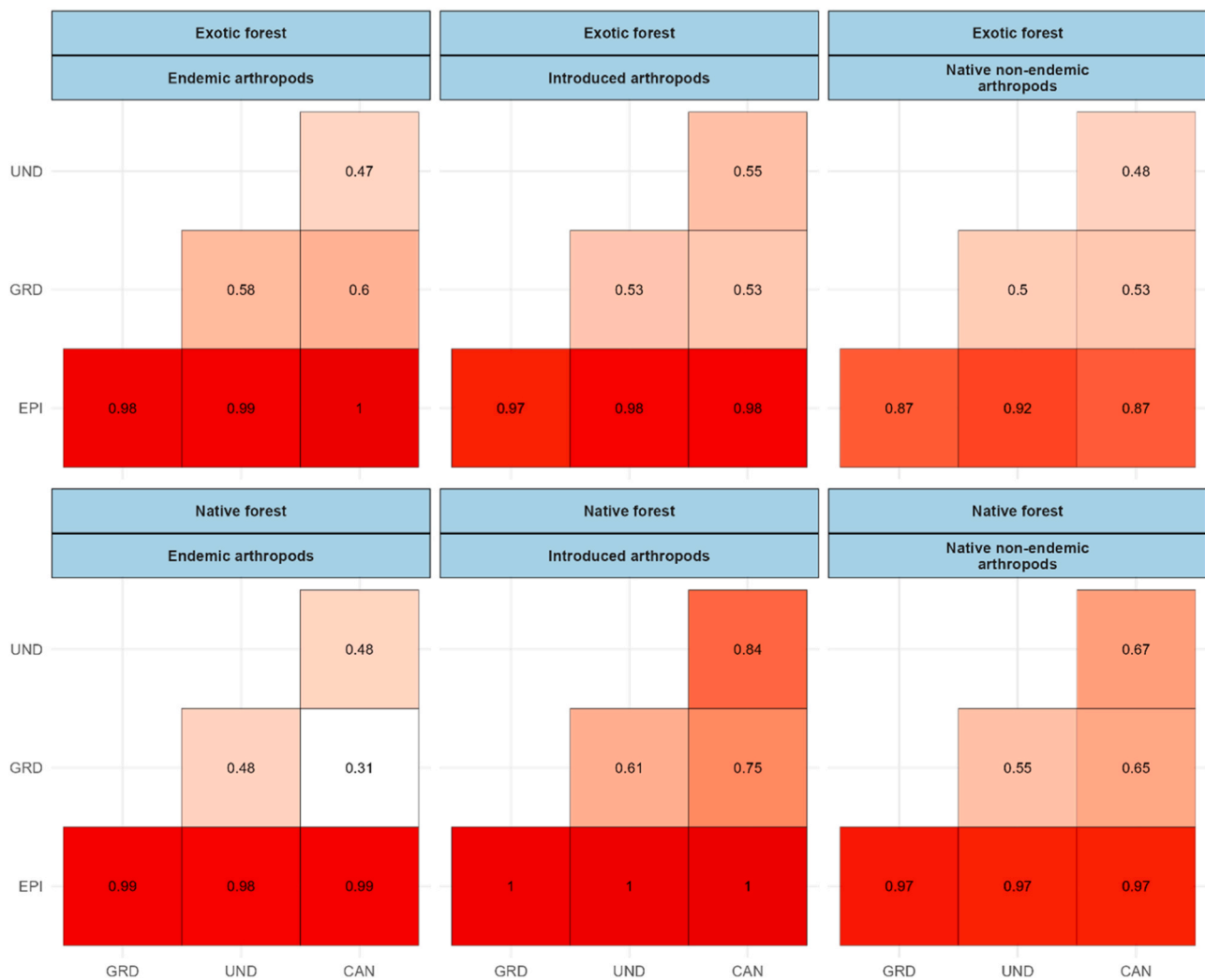


Fig. 3. Heatmap of B'_{Total} across vertical strata for terrestrial arthropod assemblages on Terceira Island. Darker colors indicate higher values (i.e., lower community similarity) between strata. Panels are organized by forest type (native vs. exotic) and assemblage origin (endemic, native non-endemic and introduced). Assemblages in native forests and exotic forest exhibit similar vertical stratification, as reflected in close dissimilarity values between all strata. Introduced arthropods show more differentiated distributions across vertical strata, especially in native forests.

3.1.1. H2: Higher vertical gradient in native forest

The beta regression model revealed a significant effect of vertical distance between strata on B'_{Total} (Table 1, hypothesis H2), confirming that similarity in arthropod assemblages decays with increasing vertical separation. However, the effect of habitat type (native vs. exotic forest) was not statistically significant. This indicates that the rate of vertical distance-decay in assemblage similarity does not differ between native and exotic forests, contrary to our hypothesis that biotic homogenization in exotic forests would reduce vertical differentiation. Visual inspection of the heatmap (Fig. 3) supports this conclusion: the degree of vertical stratification appeared similar between native and exotic forest plots. These findings suggest that while vertical distance is a strong driver of compositional turnover, its effect is not mediated by forest type in this system.

3.1.2. H3 – The contribution of each assemblage to the vertical stratification differs in native and exotic forests

The beta regression model revealed a strong and highly significant effect of the origin of the assemblage on vertical distribution patterns (Table 2). Specifically, introduced assemblages were significantly less represented along the forest profile compared to other assemblages, suggesting a more restricted vertical distribution for introduced taxa. By contrast, native non-endemic and endemic assemblages exhibited a

comparable vertical distribution across strata.

Strata themselves did not exhibit strong effects overall, though the epigeal layer showed a trend toward lower relative abundance. Also, forest type (native vs. exotic) did not significantly influence assemblage vertical contributions. These results indicate that while species origin shapes their vertical distribution of their abundance, this pattern is consistent across forest types. Thus, our third hypothesis is partially supported: the contribution of assemblage to the overall vertical stratification of arthropod differ but native and exotic forests harbour a similar pattern.

4. Discussion

We investigated how arthropod assemblages are structured across vertical strata in both native and exotic forests on Terceira Island in the Azores. By focusing on beta diversity and its components, we explored the variability of the vertical distance-decay of similarity among habitat type and species origin. Our findings provide new insights into the vertical distribution of arthropod diversity within oceanic island forests, with implications for biogeography, invasion ecology, and conservation.

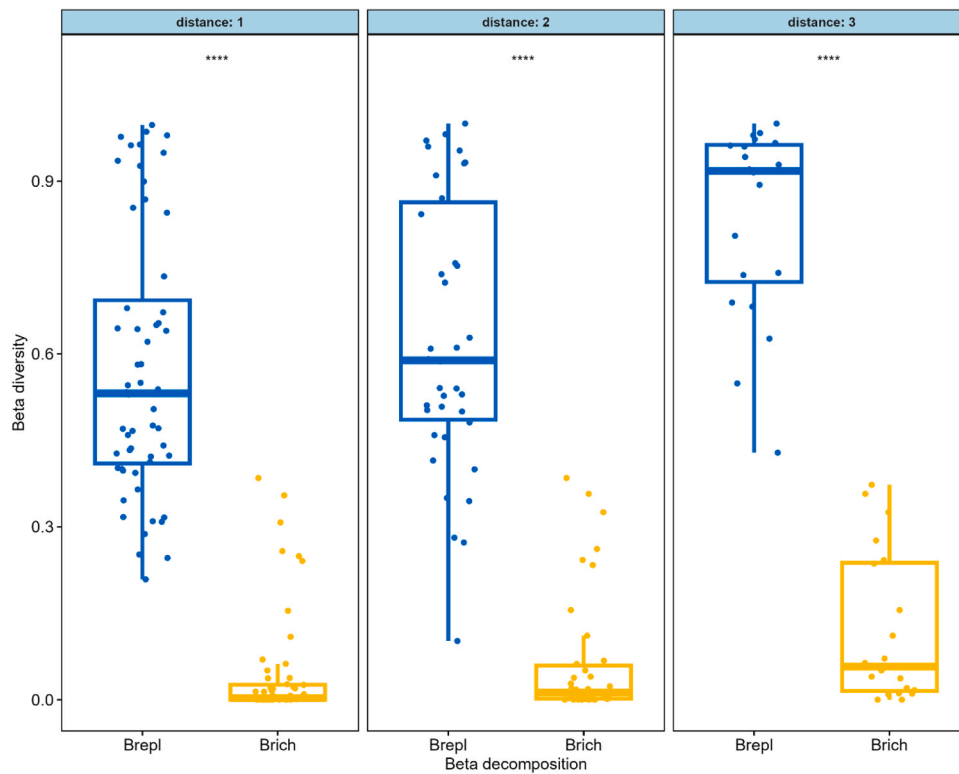


Fig. 4. Decomposition of B'_{Total} into B_{repl} (blue) and B_{rich} (yellow) across increasing vertical distances between forest strata. Each panel corresponds to a specific vertical separation (distance 1, $n = 58$; distance 2, $n = 38$; distance 3, $n = 18$). Asterisks denote statistically significant differences between B_{repl} and B_{rich} at each distance level based on Paired Wilcoxon rank sum tests ($*** = p < 0.001$). Species turnover consistently dominates beta diversity across all vertical distances, while the contribution of richness differences remains low but increase with distance between strata.

Table 2

Summary of beta regression models testing the effects of assemblage, forest type, and strata on arthropod relative abundance. Fixed effect estimates are shown with standard errors, z-values, and significance levels. All models used the logit link and included site identity as a random intercept. Significant predictor is highlighted in bold ($*** p < 0.001$, ns $p < 0.1$).

Hypothesis	Fixed Effect	Estimate	Std. Error	z value	Significance
H3	Assemblage (Introduced)	-1.13646	0.16474	-6.898	***
H3	Assemblage (Native)	0.14402	0.14747	0.977	ns
H3	Habitat (Native forest)	0.06906	0.12617	0.547	ns
H3	Strata (EPI)	-0.31989	0.18034	-1.774	ns
H3	Strata (GRD)	0.00520	0.17218	0.030	ns
H3	Strata (UND)	-0.01817	0.17662	-0.103	ns

4.1. The vertical distribution of arthropods is characterised by aggregation within forest strata

A marked decay in the similarity of the overall arthropod assemblage was evident as a function of vertical distance along the forest profile.

This pattern was expected regarding the well-documented relationship between decreasing arthropod assemblage similarity with an increase of vertical distance observed in both tropical and temperate forests (Basham et al., 2019; Basset et al., 2003; Chapin and Smith, 2019). Canopy-dwelling species often exhibit low overlap with ground-level communities due to differences in biotic and abiotic conditions (Ashton et al., 2016; Basset et al., 2003; Dial et al., 2006). For instance, in tropical rainforests, Basset et al. (2003) demonstrated that moths (Lepidoptera) exhibit strong vertical stratification, with species composition changing significantly between understory and canopy layers. Weiss et al. (2019) documented distinct vertical turnover in saproxylic beetle assemblages (Coleoptera) between three forest types of varying altitude and latitude, including a tropical lowland forest in Panama, a temperate lowland forest and a temperate montane forest in the eastern Czech Republic. They highlighted that stratification patterns

varies markedly between tropical and temperate forests. In temperate forests, Pinzon et al. (2011) also described that spider (Araneae) communities show pronounced stratification, with guild structure differing among layers. Finally in part of the Macaronesia, Costa et al. (2023) found that spiders (Araneae) exhibited a differentiation in the vertical distribution.

The decomposition of total beta diversity revealed that species turnover, rather than differences in species richness, was the main driver of vertical distance-decay in the overall arthropod assemblage. This suggests that as one moves from the forest floor to the canopy, changes in assemblage composition occur primarily through species replacement rather than through net species gains or losses.

Regional species richness can influence local turnover, potentially through interspecific competition that narrows realized ecological niches (Olivares and Kessler, 2020). Environmental conditions and dispersal limitations also contribute differently to community assembly across forest layers (Griffin et al., 2009). For example, Wang et al. (2013) showed that herbs and shrubs respond more strongly to environmental factors, while canopy layers are more shaped by spatial processes. Elevation gradients are also known to influence plant

community assembly mechanisms across vertical layers (Luo et al., 2019). Together, these findings highlight the complexity of ecological mechanisms driving species turnover across forest strata and spatial scales.

As vegetation forms the basis of arthropod food webs, arthropod distributions are expected to reflect the vertical structuring of vegetation and been indirectly influenced by similar processes (Bolu and Varga, 2021; Rodrigues et al., 2015; Tsafack et al., 2022). The availability of primary resources affects species richness, with more heterogeneous strata supporting greater species numbers (Griffin et al. 2009). Therefore, the turnover component likely results from faunal specialization driven by competitive exclusion, where ecologically similar species are restricted from co-occurring in resource-limited environments (Segre et al., 2014). Nonetheless, recent research on spiders by Costa et al. (2023) found that the Azores exhibit lower vertical stratification compared to other Macaronesian archipelagos, possibly due to their shorter forest canopies and younger geological age. Because specialization is an evolutionary process requiring time, the relatively young age of the Azorean islands may explain the broader vertical distribution of many taxa. Similar conclusions were drawn by (Triantis et al., 2012b), who linked widespread distribution of indigenous species in the Azores to island age among other factors (Borges and Brown, 1999a; Borges and Hortal, 2009)

Beyond eco-evolutionary considerations, the predominance of turnover across strata likely reflects the aggregation of species within particular layers, shaped by both deterministic and stochastic processes. At local scales, habitat availability and biotic interactions are important drivers (Fattorini and Baselga, 2012; Münzbergová, 2004; Sexton and Dickman, 2016; Veech et al., 2003), while dispersal limitation affects species distributions at fine scales, especially for understory assemblages (Lin et al., 2013). Soil properties and topography contribute at broader spatial scales (Eiserhardt et al., 2011), and historical processes also leave lasting legacies on current patterns (Münzbergová, 2004). Temporal dynamics are another key factor: arthropod assemblages in the Azores show clear seasonal variation (Borges et al., 2017; Lhoumeau and Borges, 2023), and our late-summer sampling coincided with the known peak in species richness and abundance, particularly in native forests (Lhoumeau and Borges, 2023). Although this likely ensured a representative snapshot of vertical diversity, extending the sampling throughout an entire year would greatly improve our understanding of seasonal vertical dynamics, species aggregation, and their vulnerability to environmental changes, since exotic species tend to have lower diversity and abundance in cold seasons (Tsafack et al., 2023).

4.2. The overall arthropod assemblages have similar vertical distance-decay pattern between forest types

Contrary to our expectations, we did not detect a significant difference in the rate of vertical beta diversity decay between forest types. Regardless the biogeographic origin of the species, the vertical stratification of species are consistent between the native and exotic forest of Terceira. Although native forests are generally more structurally complex (Willim et al., 2019), with higher diversity in canopy (Basset et al., 2003), this did not translate into greater vertical differentiation of the overall arthropod assemblage. One possible explanation is that exotic forests, while floristically simplified, still maintain enough vertical structure, such as distinct foliage layers and vertical microclimatic gradients to support stratified arthropod communities.

Therefore, the type of forest does not impact the existence of the vertical distance-decay of similarity of the overall arthropod assemblage within a given forest type. However, the species included in the assemblages are likely not to be identical between forest types as exotic forests usually exhibit more disturbed arthropod assemblages with a dominance of exotic and invasive species (Borges et al., 2006, 2020; Borges, Lamelas-López, et al., 2022; Tsafack et al., 2021). Notwithstanding the uniformity in the pattern of species distribution across the

various layers of forest types, there is a high probability of disparate ecosystem functioning, consequent to the replacement of indigenous species with exotic species that fulfil divergent ecological roles (Borges et al., 2006; Matthews et al., 2019; Rigal et al., 2018).

This finding suggests that structural simplification does not always result in compositional flattening in the overall arthropod assemblages. Despite the potential for differences in the composition of arthropod assemblages, these organisms demonstrate a uniform response to the factors that determine their vertical distribution within the Azorean forests.

Ground dwelling introduced arthropod species are fundamental components of the vertical distance-decay of similarity in both native and exotic forests.

Our third hypothesis, that the contribution of each assemblage to vertical stratification differs between native and exotic forests, received partial support. We found that species origin significantly influenced vertical distribution, with introduced arthropods displaying a more restricted vertical range compared to endemic species. Contrary to expectations of faunal homogenization, exotic arthropods do not simplify assemblage composition; instead, they create distinct assemblage. Florencio et al. (2015) showed that these new introduced species are likely to increased beta-diversity across habitats as a result of an uneven invasion pattern.

While exotic arthropods contribute significantly to vertical distance-decay patterns, their restricted vertical range compared to indigenous taxa suggests underlying ecological constraints. Indeed, our results highlight that ground-dwelling introduced species are successful in both of the forest types. This may reflect narrower ecological tolerances or dispersal limitations among introduced taxa many of which may be ground-associated or unable to effectively colonize aerial strata. In Azorean native forests, the specific abiotic conditions are likely to be the primary factor responsible for the significant environmental filtration that hinders the propagation of exotic arthropods (Borges et al., 2006; Lhoumeau and Borges, 2023). Supporting this, (Florencio et al., 2016) demonstrated that native forests act as dispersal barriers for exotic canopy spiders, while habitat and plant structure have strong effects on indigenous species richness. However, the mechanisms explaining why exotic species are not effectively spreading up from the bottom remain to be investigated in the Azorean exotic forest. Study by (Borges et al., 2006) highlighted the importance of past disturbance in shaping the spatial distribution of exotic arthropods.

Consequently, it was hypothesised that exotic forests would harbour a consistent arthropod assemblage through the different forest strata. Contrary to expectations, the abundance of introduced arthropods has been observed to decrease with height in both forest types, thus indicating a degree of resilience in the upper strata. Indigenous species appeared more vertically integrated, likely due to longer evolutionary histories (Borges and Brown, 1999b) and adaptation to vertically structured forest environments (Costa et al., 2023). From an ecological perspective, the restricted vertical range of introduced species may lead to disproportionate impacts at specific strata, particularly at the epigeal level, where they may compete with or displace native taxa. This vertical niche compression has potential implications for community assembly, trophic interactions, and ecosystem functioning.

5. Conclusion

We demonstrated that vertical stratification of arthropod communities was a robust feature of both native and exotic forests on Terceira Island. However, species origin, not forest type, emerged as the strongest predictor of vertical community structure.

Taken together, our results highlight the importance of integrating vertical structure into biodiversity monitoring and ecological research. Vertical sampling reveals patterns that would remain undetected in single-layer or ground-based surveys, particularly in systems like oceanic island forests where spatial constraints magnify the significance

of local interactions. The observed vertical beta diversity patterns can also inform conservation priorities by identifying forest strata that are particularly sensitive to invasion. Future studies should consider incorporating functional traits or ecological roles, such as trophic guilds or body size, to better understand the mechanisms driving vertical stratification. Additionally, integrating microclimatic data would provide valuable insight into how environmental gradients along the vertical axis influence species distributions and interactions.

Authors contributions

Both authors contributed equally to the study conception and data management. Data were analysed by Sébastien Lhoumeau. Paulo A. V. Borges oversaw the project's funding.

Sébastien Lhoumeau wrote the first draft and all authors contributed significantly to the final version.

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Declaration of Competing Interest

All authors agree with the contents of the manuscript and approved the submitted version of the manuscript. No conflict of interest is to be declared.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2025.123059](https://doi.org/10.1016/j.foreco.2025.123059).

Data availability

Data are available from GBIF Repository: Lhoumeau S, Borges P A V (2025). Stratified sampling of Azorean forest arthropods. Version 1.6. Universidade dos Açores. Sampling event dataset

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