Diversity and co-occurrence patterns of wood inhabiting insects along a tropical forest regeneration gradient

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ABSTRACT

More than 90% of global carbon released during dead wood decomposition comes from the tropics, where insects contribute significantly to this process, especially in lowland rainforests. Understanding community assembly of dead wood-inhabiting insects is therefore important. We investigated diversity patterns between habitats and host trees, and co-occurrence of wood-inhabiting ants, termites, and beetles in the Chocó of northeastern Ecuador along a forest regeneration gradient spanning from agricultural land through regenerating forests (1–37 years) to old-growth forests. Using experimentally exposed dead wood from five locally occurring tree species, we quantified assemblages after six months of decomposition by rearing.

We found 174 insect species across 62 plots. Diversity was lowest in agricultural land and higher in regenerating and old-growth forests, indicating substantial recovery following tree regeneration. Differences among succession stages were strongest for rare species, whereas communities of dominant species were more similar across stages. Host tree identity further structured assemblages: *Trema micrantha, Theobroma cacao, and Inga spp.* supported higher diversity than *Triplaris cumingiana* and *Hieronyma alchorneoides*. These patterns could not be explained by wood density alone, and a comparison with tree availability suggests tree species abundance as a major driver. Co-occurrence analysis revealed predominantly neutral associations among insect species. A small number of positive associations occurred mainly among ambrosia beetles, suggesting facilitation, whereas negative associations including those between ants and termites were rare.

Our results demonstrate that diversity of wood-inhabiting insect communities is primarily shaped by coarse habitat filtering along the regeneration gradient and secondarily by fine scale filtering via the host tree, while biotic interactions leave only a limited signature in co-occurrence patterns. Our finding underlines that with return of trees in abandoned agriculture areas even the saproxylic insects, a cryptic but important functional group in the global carbon cycle from wood, rapidly recolonize, determined by local habitat conditions and resource availability, underscoring their conservation value alongside old growth forests.

1. INTRODUCTION

Dead wood is an important habitat for about 1/3 of forest arthropod species (Graf et al, 2022) and a critical carbon store in forest ecosystems, with tropical forests holding the largest share of global dead wood carbon (Pan et al., 2011). As dead wood decomposes, it releases nutrients back into the ecosystem and supports a diverse community of organisms dominated by insects and fungi. Among decomposers, the insects play a particularly important role, accounting for 10 to 20% of wood mass loss (Ulyshen, 2016), with termites being especially significant drivers of decomposition in the tropics (Griffiths et al., 2019; Njoroge et al., 2025; Seibold et al., 2021; Zanne et al., 2022). Organisms that depend on dead wood at any stage of their lifecycle are termed saproxylic (Speight, 1989; Stokland et al., 2012; Ulyshen, 2018), and understanding which species inhabit which dead wood, and why, is fundamental for understanding how these communities are assembled (Müller et al., 2020).

Community assembly theory provides a useful framework for understanding how species colonize dead wood. Species assembly is governed by processes operating across multiple spatial and ecological scales. The regional species pool determines which species are available for colonization (Cornell & Harrison, 2014), dispersal determines which of those species can reach a given habitat (Komonen & Müller, 2018; Leibold et al., 2004; Grella et al., 2026), and environmental filters determine whether arriving species can establish and persist based on their functional traits (Kraft et al., 2015; Mitesser et al., 2026). Within dead wood, these filters act sequentially and interactively together in shaping community composition.

Broad environmental conditions set the regional context in which saproxylic communities assemble (Seibold et al., 2016). As deforestation and land-use change are major threats to biodiversity in tropical forests (FAO, 2020), saproxylic insects are particularly sensitive to these changes because they depend on a continuous supply of dead wood. Studies of ants (Bihn et al., 2008; Karolak & Fiedler, 2024; Grella et al., 2026), termites (Luke et al., 2014; Castro et al., 2021; Duran-Bautista et al., 2024; Grella et al., 2026), and saproxylic beetles (Grove, 2002; Lachat et al., 2006) have shown that assemblages typically exhibit reduced diversity in anthropogenically disturbed habitats. Forest regeneration following agricultural abandonment can partially reverse these losses, but the speed and completeness of recovery remain poorly understood, especially for multiple saproxylic taxa within the same system. Along regeneration gradients, canopy closure increases with forest age and buffers temperature and humidity extremes (Newell et al., 2026), which may allow a greater diversity of thermally sensitive species to persist in older forests. At the same time, the availability and diversity of dead wood rise with succession, providing greater niche space for saproxylic communities (Seibold et al., 2016; Falconí-López et al., 2024).

Within a given habitat, the identity of the host tree species represents a second, finer-scale filter that shapes which saproxylic insects colonize and persist. Wood traits such as density and the relative proportions of carbon, nitrogen, phosphorus, lignin, and cellulose differ substantially among tree species, influencing the quality of dead wood as a resource (Guo et al., 2024). Among insects, three taxa are particularly prominent in tropical dead wood: termites, beetles, and ants, each using dead wood in distinct ways. Termites use dead wood both as food and nesting habitat, aided by symbiotic gut microbiota, and show strong trait-based preferences for wood of particular quality (Bignell, 2018; Guo et al., 2024). Beetles also use wood for food and shelter, with ambrosia beetles cultivating wood-decomposing fungi in their tunnels (Hulcr & Stelinski, 2017; Biedermann & Vega, 2020). Ants, in contrast, use dead wood primarily as nesting habitat rather than a food source, and their colonization preferences among tree species are less well understood. Despite its importance, few studies have examined how host tree identity mediates multi-taxon saproxylic assemblages in tropical forests (Jomura et al., 2022; Law et al., 2023; Ci et al., 2025).

Finally, interactions between co-occurring species represent a third level of filtering that can further influence dead wood dwelling insect assemblages. Such interactions can take the form of facilitation, competition, or predation. Facilitation may occur when the activity of one species modifies the wood in ways that benefit others, for example through tunnel creation, frass deposition, or fungal inoculation (Brin & Bouget, 2018). Competition is often pronounced among social insects such as ants and termites, which live in large colonies and can monopolize entire wood pieces (Tuma et al., 2020). Predation is also relevant, as ants are major predators of termites (Tuma et al., 2020), suggesting that their presence could exclude termite colonization through priority effects. Whether such interactions leave a detectable signature in species co-occurrence patterns remains an open question that we address here.

To disentangle these three successive filters for saproxylic insect communities in different recovery stages of tropical forests we conducted an experiment in the highly threatened Chocó rainforest region of Ecuador, one of the top 25 global biodiversity hotspots (Myers et al., 2000), but under severe anthropogenic pressure from deforestation and land-use change (Fagua et al., 2019). Along a regeneration chronosequence spanning agricultural land, regenerating forests of 1 to 37 years old, and old-growth forests, we reared beetles, ants and termites from five locally occurring tree species.

Specifically, we investigate three key aspects of insect assembly in dead wood, namely habitat and host filtering, as well as species interactions: First, we assessed how dead wood dwelling insect diversity (ants, termites, and beetles) varies along the forest regeneration gradient, expecting diversity to increase from agricultural land through regenerating forests to old-growth forest due to recovery of forest complexity and integrity. Second, we examined whether host tree species identity influences the diversity of insect assemblages, expecting differences among tree species of different plant families to be mediated by wood density. Third, we investigated co-occurrence patterns among the three taxa within individual wood pieces, expecting predominantly neutral interactions with some negative associations between ants and termites given their predator-prey relationship, and possible positive associations among beetle species through facilitation.

2. METHODS

2.1 Study site and plot design

The study site is located in Esmeraldas province in northwest Ecuador in the two reserves Reserva Río Canandé and Reserva Tesoro Escondido (Figure 1). Research was carried out in a tropical lowland Chocó rainforest on 62 plots that were selected in the framework of the REASSEMBLY research unit (www.reassembly.de). The plots comprise a size of 50 x 50 m in forests (old-growth and regenerating forests) and 16 x 16 m in agricultural land. The study area encompasses a heterogeneous small-scale landscape of old-growth forests, regenerating forests of various successional stages, human settlements and agricultural land in close proximity to one another. The forest cover is generally high with an average of 74% (SD ± 2.8) within a 1-km radius of each plot (Escobar et al., 2025) and distances to the nearest old-growth forest are short with an average of 59 m (SD ± 46), which is typical for many tropical regions nowadays. The REASSEMBLY plots were selected to represent a spatially independent regeneration gradient (chronosequence) of naturally regrowing forest ranging from agriculture (pastures and cacao plantations) to regenerating forests (former pastures and cacao plantations) to old growth forests. The selection includes 12 plots on agricultural land (6 pastures and 6 cacao plantations), 22 in an early regeneration stage (1-20 years), 11 in a later regeneration stage (21-37 years) and 17 in old-growth forest. Detailed information on plot design and climatic conditions in the study area is described in Escobar et al. (2025) and Newell et al. (2026).

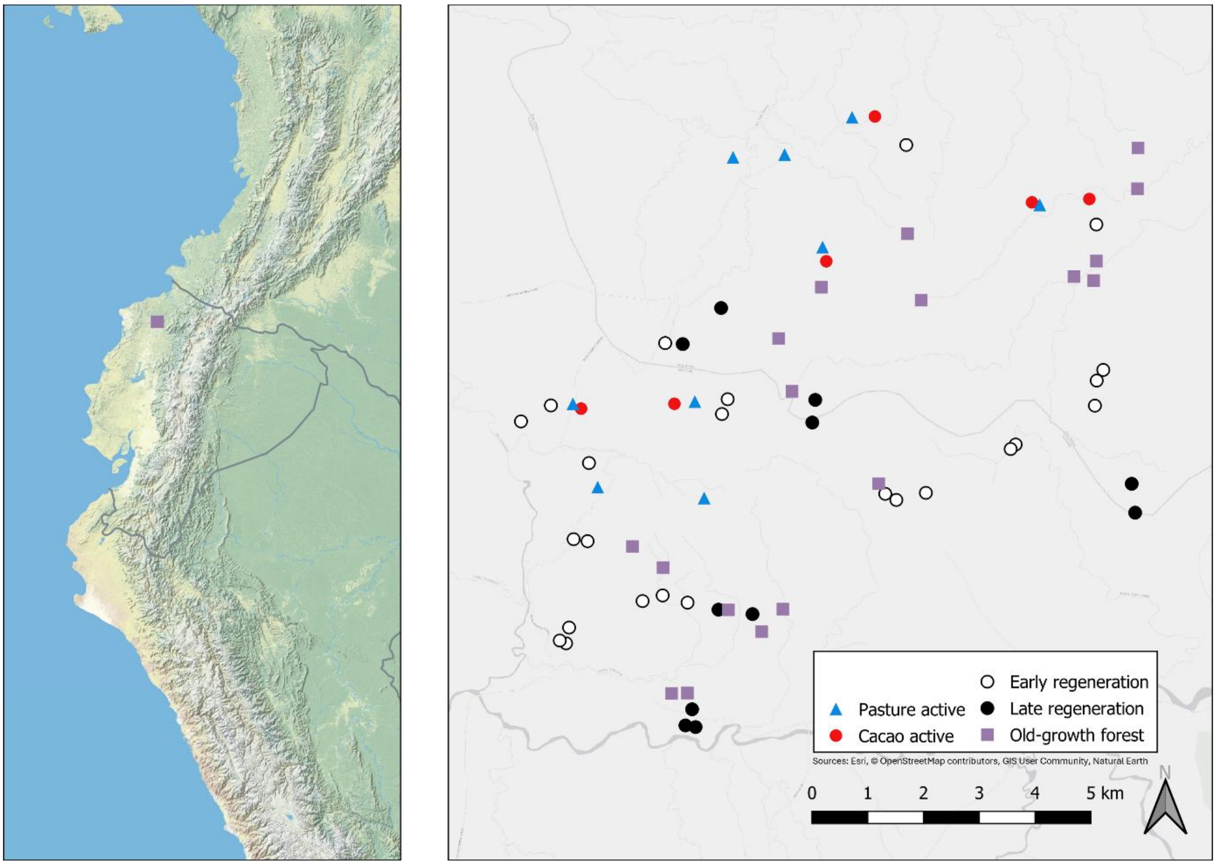

Figure 1: Distribution of the study plots in the Chocó rainforest in north-western Ecuador. Symbols indicate different forest regeneration categories of the study plots.

2.2 Insect sampling

The collected data consisted of the ants, termites and beetles emerging from dead wood from five different tree species that was experimentally exposed on the ground in all 62 plots. On each plot one wood piece each of the locally occurring tree species *Trema micrantha* (Sapanillo, Cannabaceae), *Theobroma cacao* (Cacao, Malvaceae), *Inga spp*. (Guaba, Fabaceae), *Triplaris cumingiana* (Fernán Sánchez, Polygonaceae) and *Hieronyma alchorneoides* (Mascarey, Phyllanthaceae) was placed. The wood pieces had a length of 50 cm and a diameter ranging from 7-10 cm and were laid out in August to October 2022. After six months on the plots, they were retrieved in February-March 2023 and placed into emergence chambers. These consisted of mesh tubes made of white fabric used for insect nets (1 mm double-thread netting, bioform.de; Model A110e) and a 50 ml sampling tube filled with ethanol attached at the bottom. In the following six months (February-August 2023) insects emerging from the woods were frequently collected from the ethanol (see also Grella et al. 2026 and Falconí-López et al. 2025 for a detailed description of the experimental setup).

2.3 Species identification

The collected insects were identified with a combination of a morphological and a DNA barcoding approach as described in Grella et al. (2026) and Falconí-López et al. (2025). In short, ants, termites and beetles were identified to genus or family level using taxonomic literature (Bolton, 1994; Constantino, 2002; Pérez-Silva et al., 2021; Wood, 2007) and separated into morphospecies. Subsequently, one specimen per morphospecies and wood piece was prepared for DNA barcoding of the cytochrome c oxidase I (COI) gene (658 bp). Insect tissues were sent to the Canadian Centre for DNA Barcoding (University of Guelph, Canada) for DNA isolation and sequencing. The resulting DNA sequences were uploaded to the BOLD (Barcode of Life Data System, www.boldsystems.org) database. For species identification we used the classification into BINs (Barcode Index Numbers) and phylogenetic trees (Neighbour-Joining trees with Kimura Two-Parameter distances) from BOLD. BOLD groups sequences into BIN clusters which are in high concordance with species (Ratnasingham & Hebert, 2013). Many ant, beetle and termite species in the tropics are not described yet. Hence, when reference species names of the BINs were missing, we used a provisional name consisting of the family or genus name together with the BIN for some specimens. In addition to the species identification, we also counted the individuals of each species in each wood for abundance-based sampling standardizations.

2.4 Statistical analyses

We conducted statistical analyses in R version 4.5.1 (R Core Team, 2025). All analyses are based on species incidences per log. For comparing species diversity along the forest regeneration gradient and in the five different host tree species, we analysed the species incidences via rarefaction-extrapolation functions of the *iNEXT* package (Chao et al., 2014). *iNEXT* estimates diversity indices along the three Hill numbers $q = 0$, $q = 1$ and $q = 2$ (Hill, 1973), which give different weight to infrequent to highly frequent species. The Hill number $q = 0$ is the species richness, which gives equal weight to all species. The Hill number $q = 1$ represents the effective number of species with focus on frequent species, calculated as the exponential function of Shannon's entropy index (exp(Shannon)), which focus on common species. The Hill number $q = 2$ is calculated as the inverse of Simpson's concentration index, which focus on highly frequent, dominant species.

For the analysis of diversity along the forest regeneration gradient, we grouped the plots into four categories: agricultural land, early regenerating forests (1-20 years), late regenerating forests (21-38 years), and old-growth forest.

For exploring co-occurrence patterns in single dead wood pieces, we used the ‘cooccur’ function of the *cooccur* package (Griffith et al., 2016). This method compares the observed with expected co-occurrences of species pair combinations and estimates if they are neutral, positive, or negative associated in the dead wood pieces. We set the option to filter out species pairs that are expected to have fewer than one co-occurrence from the analyses, which resulted in an exclusion of 15111 pairs from 15225 pairs.

For the visualization of the species occurrences in the five host tree species of taxa with non-random co-occurrences we used the ‘bipartite’ package (Dormann et al., 2008).

3. RESULTS

3.1 Species diversity along the forest regeneration gradient

We obtained a total of 174 saproxylic insect species across all plots and host tree species, comprising 73 ant, 10 termite, and 91 beetle species (Table 1). Of the 310 pieces of dead wood, 248 were colonized by insects. In total we counted 22260 specimens that emerged from the wood pieces (4234 ants, 7510 termites, 10516 beetles). When ants were encountered in single dead wood pieces their mean number of individuals (±SD) was 18.57 (± 2.32), termites had an average number of individuals of 96.28 (± 2.76), and beetles of 25.1 (± 16.12).

The overall diversity of all three insect groups differed with regeneration categories (Figure 1) and between Hill numbers (Figure 2). The analysis of diversity by sampling units (Figure 2a) showed that the number of observed species ($q = 0$) was highest in late regenerating forests (Regeneration II) and in old-growth forest followed by early regenerating forests (Regeneration I) and was lowest in agriculture (Figure 2a). With increasing emphasis on dominant species ($q = 1$ and $q = 2$), the diversity in the forest habitats (regenerating forests and old-growth forest) becomes more similar, while agriculture remains lowest in diversity. The coverage-based analysis (Figure 2b) followed a similar pattern but with greater overlap among categories. Notably, agriculture showed lower sample coverage at equivalent sample sizes compared to forest habitats, meaning part of the steeper diversity decline observed in the size-based analysis reflects incomplete sampling.

Table 1: Number of ant, termite, and beetle species in different habitat categories along the recovery gradient and in different host tree species. Early regenerating forests (Regeneration I) range from 0 to 20 years, while late regenerating forests (Regeneration II) range from 21 to 37 years.

	Ants	**Termites**	**Beetles**	**All**
Habitat category				
Agriculture	20	1	21	42
Regeneration I	40	6	44	90
Regeneration II	29	4	43	76
Old-growth forest	26	5	51	82
All habitats	73	10	91	174
Host tree species				
Trema micrantha	30	9	36	75
Theobroma cacao	31	4	42	77
Triplaris cumingiana	29	4	40	73
Inga spp.	28	4	24	56
Hieronyma alchorneoides	23	3	31	57
All host trees	73	10	91	174

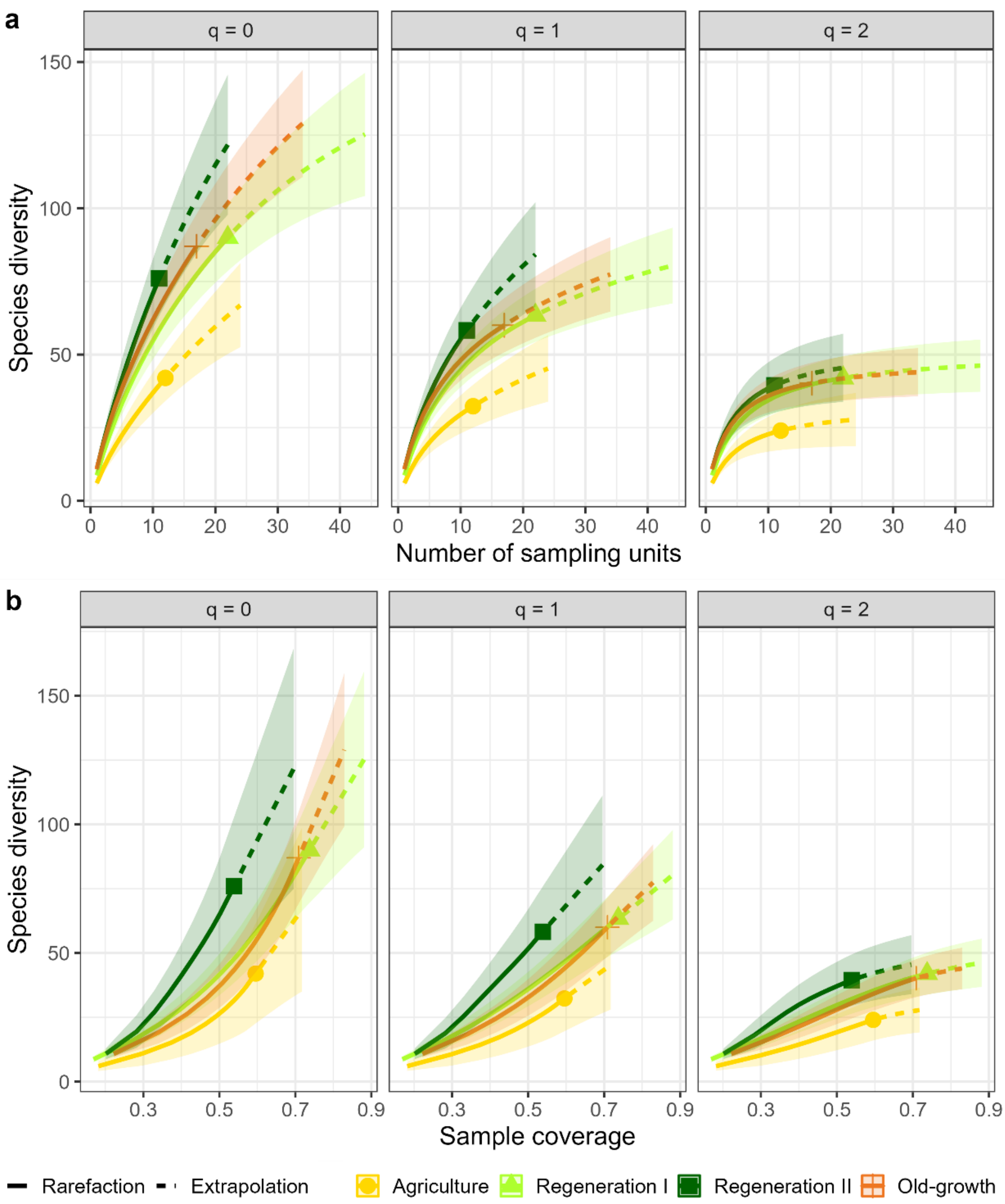

Fig 2: Rarefaction (solid lines) and extrapolation (dashed lines) curves of observed species (q = 0), the effective species number (q = 1) and the inverse of Simpson concentration (q = 2) of dead wood-dwelling insect diversity (ants, termites, beetles). Different colours represent the different forest regeneration categories ranging from agriculture, early and late regenerating forest (Regeneration I, Regeneration II) and old-growth forest. Shaded bands depict 95% confidence intervals. Differences in species diversity are significant when confidence intervals do not overlap.

3.2 Diversity in host tree species

The diversity of all three taxa also showed differences depending on host tree species (Figure 3). The sample-based and the coverage-based analysis show two clusters of host tree species. *T. cacao*, *T. micrantha* and *Inga spp*. host a higher species diversity while *H. alchorneoides* and *T. cumingiana* host less species. This pattern becomes more pronounced with increasing weight on dominant species (q = 1 and q = 2).

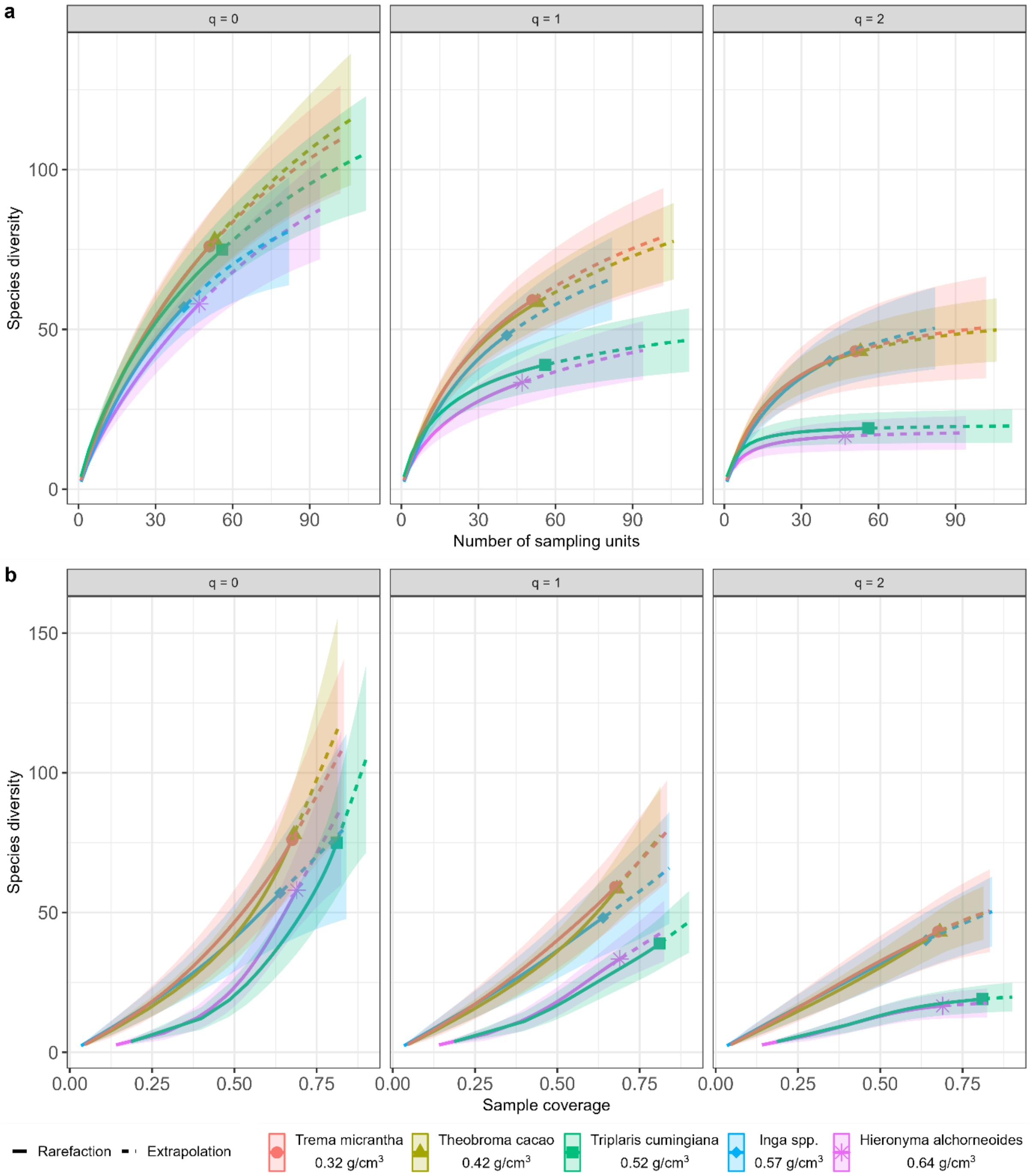

Figure 3: Rarefaction (solid lines) and extrapolation (dashed lines) curves of observed species (q = 0), the effective species number (q = 1) and the inverse of Simpson concentration (q = 2) of wood-dwelling insect diversity (ants, termites, beetles). Different colours represent different host tree species. Wood densities are given after the tree species. Differences in species diversity are significant when confidence intervals do not overlap.

3.3 Co-occurrence analysis

The co-occurrence analysis determined whether species co-occur randomly in the wood pieces, or whether they co-occurred significantly more frequently (positive association) or less frequently (negative association) than predicted by a null model. The analyses revealed that most species pair combinations (99.25%) from the possible total number of 15225 combinations have an expected co-occurrence below 1. When removing these 15111 combinations, our results showed that from the remaining 114 species pairings 21 (13.2%) were non-random with 12 positive and 3 negative pairings. These non-random co-occurrences were distributed among 12 of the 174 identified insect species (Figure 4). Positive co-occurrences were found exclusively among beetles. Beetles that could be determined to genus level (*Xyleborus, Xyleborinus, Hypothenemus*) belonged to the subfamily Scolytinae which are commonly called ambrosia beetles. *Xyleborus ferrugineus* showed the highest number of positive associations (n = 7) and also a negative co-occurrence with the ant *Nylanderia steinheili*, followed by *Xyleborinus exiguus* with the second most positive co-occurrences (n = 4).

From the ten termite species in our study area, only a *Cylindrotermes* species showed non-random co-occurrences with other species. It was negatively associated with the ants *Strumigenys alberti* and *Wasmannia auropunctata*. It was also the most encountered species with 40 encounters and a total of 4051 individuals.

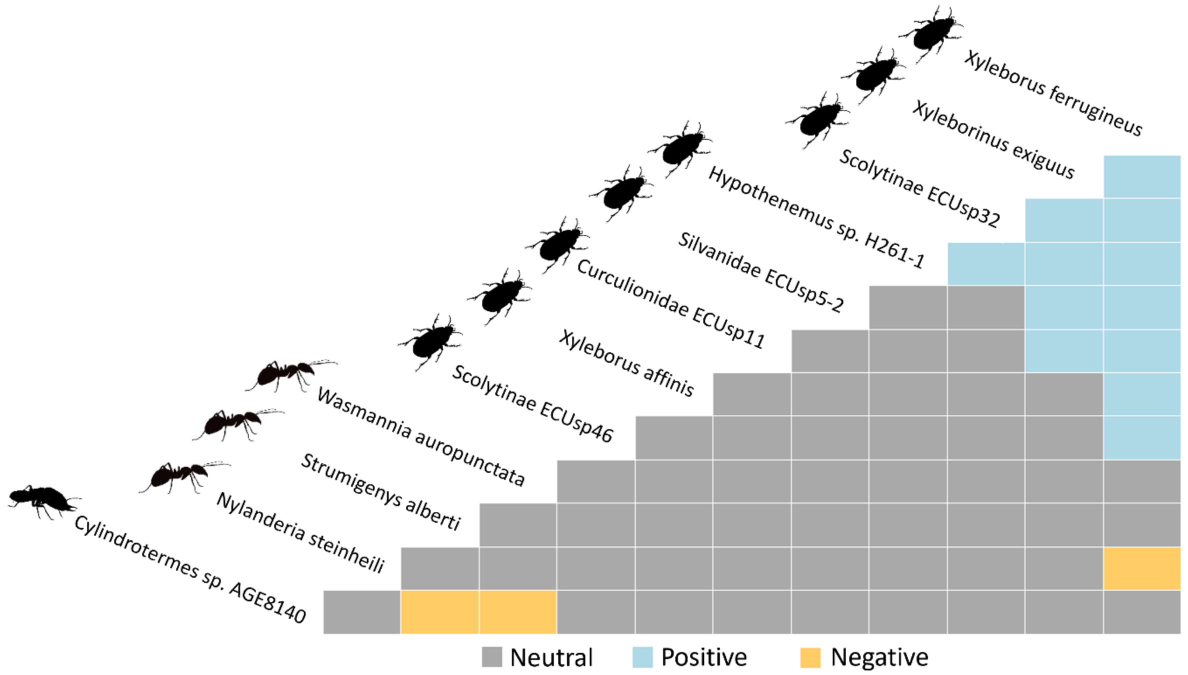

Figure 4: Co-occurrence patterns of ant, termite, and beetle species with non-random associations. The taxa were identified as positively associated when intersecting boxes are blue, negatively when boxes are yellow, and neutral when boxes are grey.

4. DISCUSSION

Our results demonstrate that diversity of dead wood dwelling insect communities in the Chocó rain forest is shaped by different filters, with forests hosting a high diversity compared to agriculture, followed by host tree identity as a driver of diversity, while biotic interactions between taxa played a comparatively minor role. Below we discuss each filter and consider their relative importance in this threatened tropical forest system.

Diversity of saproxylic insects along the forest regeneration gradient

Insect diversity in dead wood was higher in regenerating and old-growth forest, demonstrating the importance of forest habitats for dead wood dwelling insect diversity. We propose that this pattern results from the combined effects of climate and increasing dead wood diversity with forest age, which together promote niche differentiation and species diversity.

Our study plots experienced different microclimatic conditions depending on forest age. Canopy cover increased with forest age, leading to climatic conditions with lower daily extremes of temperatures and humidity as well as lower daily fluctuations of these (Newell et al., 2026). Therefore, older regenerating forests and old-growth forests might offer more stable and less extreme climatic conditions that can harbour more diverse assemblages of dead wood dwelling insects.

Additionally, dead wood diversity and availability may also shift across the regeneration gradient. While coarse woody debris (diameter > 7 cm) remains relatively constant in volume and features (wood position, diameter class, and decay stages) across the gradient, fine woody debris (< 7 cm) increases substantially in amount with forest age in our study area (Falconí-López et al., 2024). This pattern parallels increases in tree species richness, forest structural complexity (Escobar et al., 2025), and tree related microhabitats such as tree rot-holes and dead lianas (Hausmann et al., 2026). This increased availability and diversity of dead wood structures should provide greater niche space and resource heterogeneity, promoting overall saproxylic species diversity and functional differentiation (Seibold et al., 2016; Heidrich et al., 2020). These results align with previous research in the study area showing that forest regeneration drives diversity increases across multiple taxa (Metz et al. 2026), including trees (Escobar et al., 2025) and vertebrates (Grella et al., 2025) and insects (Grella et al., 2026).

Our results meet our expectations and are in line with many other studies demonstrating that ant (Bihn et al., 2008; Rocha-Ortega et al, 2018; Karolak & Fiedler, 2024; Grella et al., 2026), termite (Ackerman et al., 2009; Luke et al., 2014, de Paula et al., 2016; Duran-Bautista et al., 2020; Castro et al., 2021; Duran-Bautista et al., 2024, Grella et al., 2026) and saproxylic beetle (Grove, 2002; Lachat et al., 2006; Lachat & Müller, 2008) assemblages can react sensitively to land-use change.

The low numbers of dead wood dwelling insect species in agricultural land underline the threat of deforestation and land conversion to biodiversity. However, we showed that after abandonment diversity has the potential to recover naturally. Hence, we argue that recovering forests can also be valuable habitat for harbouring saproxylic species diversity, when given enough time to recover. This conservation value of naturally regenerating forests has also been proposed in other studies (Chazdon et al., 2009; Chazdon & Guariguata., 2016; Poorter et al., 2021; Chazdon et al., 2025).

Diversity of saproxylic insects in host tree species

The host-tree diversity analysis revealed that host-tree identity acts as an additional filter on saproxylic insect diversity. The highest diversity of common and dominant species ($q = 1$ and $q = 2$) was found in *Trema micrantha*, *Theobroma cacao*, and *Inga spp.*

Contrary to our expectations, wood density did not explain differences in insect diversity among host trees. Instead, the pattern appears to reflect the local abundance of each tree species across the plots. A tree inventory by Escobar et al. (2025) showed that among all plots *Theobroma cacao* was the most frequent tree (n = 590), followed by *Inga sp*. (n = 327), and by *Trema micrantha* (n = 239). The host tree species with the lowest diversity of dead wood dwelling species were also rarely found on the plots (*Hieronyma alchorneoides*: n = 43, *Triplaris cumingiana*: n =1). The genus Inga represented 37 different species/morphotypes while there was only one tree of another *Trema* species (*T. integerrima*), two trees of another and *Hieronyma* species (*H. macrocarpa*), 20 trees of other *Theobroma* species (*Th. chocoensis*, *Th. gileri*) and no other *Triplaris* species.

These results suggest that the insect communities are adapted to the local abundances of tree species, with higher insect species richness found in host trees that are also more abundant in the landscape. This is consistent with studies in European forests where the diversity of scolytid beetles in a host tree correlated with the resource availability of the tree species

(Bussler et al., 2011) and where phytophagous insect and mite diversity correlated with tree abundance (Brändle & Brandl, 2001). However, a key limitation of studies such as Brändle & Brandl (2001) is that they rely on compiled literature data, making it impossible to disentangle whether certain tree species harbour high insect diversity because they are frequently sampled, or because they are genuinely abundant and thereby promote insect diversity. Our study overcomes this limitation through a standardized design in which insects could actively choose from wood among co-occurring host tree species, and in which the occurrence of each tree species was recorded from the same plots. This allows for direct, unconfounded comparisons between insect diversity in host trees and the local availability of those trees. Crucially, to our knowledge, this is one of the first studies that demonstrates this relationship under such controlled conditions in a tropical forest, showing that tree species which are more abundant in a tropical forest also support higher insect diversity.

Other studies have shown ambiguous results concerning the specialization of saproxylic insects on host tree species. For instance, Hulcr et al. (2007) showed that most bark and ambrosia beetles in a New Guinean rainforest were broad generalists in their selection of host trees. In contrast, Müller et al. (2015) showed that saproxylic beetles prefer certain host tree species while avoiding others in temperate forests in Germany. A further study in Germany found no effect of host tree species on community composition (Vogelfänger et al., 2025).

Species co-occurrences

After initial habitat filtering by the surrounding habitat and by the host tree species, interactions between species colonizing the dead wood can also play a role during dead wood assembly. The results of our co-occurrence analysis, which identified positive, negative, or neutral species-pair combinations, have shown that most species combinations have a very low likelihood of co-occurrence in the dead wood pieces due to the low frequency of co-occurrence of most species pair combinations. Nonetheless, the analysis identified some positive and negative co-occurrences.

The positive co-occurrences occurred mostly among ambrosia beetles (*Xyleborus*, *Xyleborinus, Hypothenemus*). These beetles live in facultatively social groups of parents and their offspring in dead wood (Hulcr & Stelinski, 2017). They cultivate an ambrosia fungus in their wood tunnels which they feed on (Hulcr & Stelinski, 2017; Biedermann & Vega., 2020). The positive co-occurrences among these beetles might be explained by facilitation effects among them. Brin & Bouget (2018) suggest several mechanisms how saproxylics can facilitate the colonization of other saproxylic species: aiding in the localization of suitable host substrate by the release of kairomones, increasing habitat quality by enriching wood mold with nutrient rich frass or by creating entering holes, and the swamping of predators by group colonization in high abundances. For example, an experiment conducted in north America has shown that ambrosia species are attracted to volatiles released by their fungal symbionts or the symbiont fungi by other ambrosia species (Hulcr et al., 2011). Thus, the occurrence of one ambrosia species and its fungal symbiont might attract other species to the same wood. Interestingly, many species had positive co-occurrences in *Triplaris cumingiana*. This host tree species shows a low diversity when given more weight on common species (q = 1, q = 2) but a higher diversity when giving more weight to rare species (q = 0). Hence, our results suggest that the high effective number of species (q = 0) in *T. cumingiana* might be driven by rare species that also have many co-occurrences in this host tree species. One possible explanation is that *T. cumingiana*, which harbours lower diversity of abundant species, may offer a less colonized and therefore more accessible substrate for rare specialists.

In contrast to our expectations, we did not detect many negative co-occurrences between ants and termites. Since ants are important predators of termites (Tuma et al., 2020), we expected them to exclude the colonization of termite colonies in the same wood pieces. However, there were only two negative co-occurrences between these two groups. Hence, we suggest that negative interactions between the captured saproxylics play a minor role for dead wood colonization.

A study conducted in a subtropical forest in southeastern United States had a similar outcome when comparing co-occurrence patterns of ant, termite and beetles when investigating the impacts of fire on saproxylics in pine trees (Ulyshen et al., 2020). Their results likewise showed that most interactions were neutral, while 6.2% of interactions were positive and 2.4% negative. Similarly, also a high proportion of interactions were excluded from analysis (85.45%) as the expected co-occurrence was smaller than one. Our study yielded a higher proportion of non-random interactions (13.2% of the 114 retained pairs), which may reflect differences in species diversity (and here especially the presence of many rare species), community composition, substrate diversity, or the higher decay rates in tropical forests (Seibold et al., 2021) enforcing the interactions of species within logs. Even in the temperate zone a higher number of species and individuals per unit of wood, increasing the potential of interactions has been shown with increasing temperature (Müller et al., 2015). Despite this difference, the predominance of neutral interactions in both studies supports the conclusion that biotic interactions might not be the primary drivers of saproxylic community assembly in dead wood.

Limitations and outlook

While our study provides insights into diversity, host tree specialization and species co-occurrences of three saproxylic taxa in dead wood along a tropical forest regeneration gradient, some open questions and constraints remain. The first affects the understanding of assembly mechanisms in dead wood. As discussed before, our study comprises a snapshot of the diversity and co-occurrences that had been established after six months. However, priority effects taking the assembly history into account could also have influenced the species community and diversity and were only indirectly measured by co-occurrence analysis. In dead wood, decomposers can change wood properties during the different stages of decomposition leading to niche modification and a succession of different decomposer communities adapted to each decomposition stage (Fukami, 2015; Ulyshen, 2016). For understanding priority effects, repeated measurements would be necessary, which are difficult to conduct in dead wood.

Additionally, our co-occurrence analysis only compared observed co-occurrences with those expected under a probabilistic null model. This means that our predominantly neutral result may underestimate the role of biotic interactions: aggressive encounters during the initial colonization phase could have excluded certain taxa from a wood piece entirely, leaving no detectable trace in the final assemblage. Future research using staged colonization experiments or direct behavioural observations is needed to assess whether such early exclusion events shape the communities we observe.

Furthermore, positive co-occurrences do not necessarily reflect direct facilitation between species. They could equally result from independent specialization on shared wood traits, with multiple species converging on the same wood piece because it offers particular chemical or structural properties rather than because one species facilitates another. This has been demonstrated in a study by Azeria et al. (2012) where significant aggregations in saproxylic beetle species co-occurrences were mainly explained by habitat effects such as tree size, diameter at breast height, tree species and burn severity after fire. However, even after accounting for habitat effects more than a quarter of co-occurrences remained significant indicating the effects of species interactions.

Because our study design does not allow us to directly distinguish whether co-occurrences arise from shared habitat requirements or from interspecific interactions, disentangling these mechanisms would require experimental approaches that examine wood chemistry and colonization sequences independently, which would substantially advance our understanding of the processes driving deadwood community assembly and diversity.

Conclusion

Our study delivers valuable insights into the ecology of dead wood dwelling insects in regenerating tropical forests. We have shown that insect diversity can recover in regenerating forests which highlights the resilience of dead wood dwelling communities in the tropics to recover in regrowing forests but also the importance of old-growth forests. The low diversity of saproxylic insects in agricultural land underlines the threat that deforestation poses to these communities.

Aside from forest age, also host tree species and thus wood traits determine the diversity in dead wood, but with no clear pattern with wood density. The insect diversity in the different host tree species rather corresponded with the tree abundance of the same species in the landscape.

The results of our co-occurrence analysis revealed possible facilitation effects among ambrosia beetles and some exclusion effects among ants and termites as well as for a single ambrosia beetle species. However, as most species interactions were neutral, these results suggest that interaction between the observed species might not play a major role during assembly.

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