The importance of forest floor connectivity on saproxylic arthropod succession in a lowland tropical rainforest.

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ABSTRACT

Tropical saproxylic arthropods form a high proportion of diversity on earth yet are significantly understudied compared to their temperate counterparts. Litter provides habitat space, a stable microclimate and nutrients for arthropods. However, the influence of the forest floor on saproxylic arthropods remains relatively unknown. This study investigates the effects of long-term litter removal and its interactions with tree-size (diameter at breast height (DBH), wood density and deadwood age on saproxylic arthropods in a neotropical forest. Complementary sampling methods, namely emergence traps and wood samples were used to collect arthropods from deadwood. In wood samples, arthropod abundance and richness increased with deadwood age in control plots and declined in litter removal plots. Furthermore, community composition showed a clear trajectory in the control plots that was disrupted by litter removal. This suggests that forest floor connectivity is important for saproxylic succession with isolated deadwood fragments acting as refuges between the hostile bare soil. Wood density and DBH did not influence arthropod succession. Non-significant findings for emergence traps are attributed to the collection of flying taxa, which are less susceptible to the challenges posed by the bare soil in the litter removal plots. Comparison with the results of a previous studies on soil and litter fauna in the same litter manipulation experiment found distinct communities between habitats: a high proportion of fauna were forest floor generalists, some were specialists of a particular habitat, and others appeared to migrate between. I conclude that forest floor connectivity plays a vital role in the succession of arthropods in deadwood.

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AUTHOR DECLARATION

I declare that this thesis is my own work and has not been submitted in substantially the same form for the award of a higher degree elsewhere.

Isabel Sharpe

INTRODUCTION

The majority of terrestrial flora and fauna diversity on earth are arthropods in tropical rainforests (Basset *et al*., 2015). There are an estimated seven million terrestrial arthropod species on earth, approximately 6.1 million of which are insects (Kitching *et al*., 2020). Despite their numerical dominance, arthropods receive less attention than more charismatic mega-fauna (Kimber and Eggleton 2017), leaving tropical arthropods significantly understudied compared to their temperate counterparts (Basset *et al*., 2015). This knowledge gap limits our understanding of their diversity and ecological roles.

Forest floor arthropods are some of the most abundant and diverse communities in forests (Sayer, 2010; Tennakoon *et al* 2021) They provide a myriad of ecosystem services including decomposition, nutrient cycling, pollination, and predation (Sayer, 2010; Tennakoon *et al* 2021). Notably, the significance of forest floor fauna in decomposition and nutrient cycling appears to be disproportionately higher in tropical forests compared to temperate ones, primarily due to the less constraining climatic conditions on the activity of soil and litter organisms (Lavelle *et al*. 1993; Yang *et al.,* 2007).

Saproxylic species form a high proportion of tropical arthropod fauna and are a vital part of the forest floor community (Grove and Stork, 1999). These arthropods are associated with deadwood or with the fungi and micro-organisms that decompose it (Grove and Stork, 1999). The term 'saproxylic' encompasses a range of species, from wood-feeders and fungus-feeders (primary saproxylics) to predators, parasitoids (secondary saproxylics), and commensals (tertiary saproxylics) (Grove and Stork, 1999). In the context of this study, 'saproxylic arthropods' refers to any arthropod species found within or on deadwood for ease of analysis and communication. In tropical regions, deadwood is predominantly influenced by termites, while major insect orders such as Coleoptera and Diptera also make substantial contributions (Grove and Stork, 1999).

The importance of deadwood is widely recognised and serves as a crucial component of forest ecosystems. Deadwood not only provides a multitude of microhabitats for saproxylic insects but also enhances structural diversity, influences microclimates, and plays a pivotal role in organic matter and nutrient cycling (Law *et al.,* 2019). It stores approximately 8% of the world's forest carbon, with tropical forests holding the highest proportions (Pan *et al.,* 2011). Recent research has shown that deadwood exerts a significant influence on soil and litter arthropods, impacting species as far as five meters away and even on relatively small trunks as small as 14 cm in diameter (Castro and Wise, 2010; Evans *et al.,* 2003; Varadi-Szabo and

Buddle; Jabin *et al.,* 2004). Notably, the majority of arthropods demonstrate higher densities, greater abundance, and increased diversity in the vicinity of deadwood within the soil and litter (Castro and Wise, 2010; Evans *et al.,* 2003; Varadi-Szabo and Buddle; Jabin *et al.,* 2004), underscoring the vital role deadwood plays in supporting these arthropod communities.

The importance of the forest floor is similarly well studied. Extensive research has highlighted its pivotal role in ecosystems, providing habitat for a diverse range of arthropods, fostering favourable microclimates, acting as a shield against soil erosion and substantially contributing to organic matter and nutrient cycling (Sayer, 2006; Sayer, 2010; Eaton *et al*., 2004; Krishna and Mohan, 2017). Plant litter encompasses any material that naturally accumulates on the forest floor and includes seeds, flowers and woody debri as well as fallen leaves, all of which subsequently enter decomposition. During decomposition, nutrients are recycled and carbon dioxide is released into the atmosphere (Krishna and Mohan, 2017). The accumulation of litter can be regarded as natural complete fertiliser (Sayer *et al*., 2012), serving as the primary source of organic material and nutrients containing all the elements for plant growth for the hummus layer (Sayer *et al*., 2020; Berg and McClaugherty 2008). It is also crucial for nutrient retention by effectively mitigating soil erosion and compaction. Litter accumulation alters the surrounding environment by intercepting light, retaining moisture and maintaining soil temperature by evapotranspiration (Sayer, 2006; Facelli and Pickett 1991). This in turn creates a microclimate favourable for fungal growth and faunal activity (Sayer, 2006; Eaton *et al*., 2004). Furthermore, enhanced structural complexity due to litter accumulation augments niche availability (Law *et al*., 2019; Sayer, 2010). Thus, litter provides habitat space as well as essential nutrients and substrate. Collectively, these factors lead to an astounding diversity of fauna inhabiting the forest floor, ranging from bacteria to fungi to macro-arthropods (e.g. insects, earthworms and spiders). Furthermore, litter provides nesting materials for birds (Nickell, 1958) and small mammals (Dickman, 1991) However, it is important to note that litter accumulation influences trophic and taxonomic groups in distinct ways; prey for example grapple with nutrient limitations (Milton and Kaspari, 2007), whereas predators tend to respond to prey density and shifts in habitat structure (Uetz 1979). Moreover, while the benefits of litter accumulation are undeniable, it may also have adverse effects on arthropod populations, as compaction can restrict habitat space and make the forest floor unsuitable for many taxa (Levings & Windsor, 1984). Furthermore, the presence of phenolic compounds from decomposing litter can act as deterrents to arthropods (Sayer, 2006).

Despite the well-documented importance of the forest floor, its significance for deadwood arthropods remains relatively unknown. To address this gap, our study employs a long-term litter removal experiment in a lowland tropical forest in Panama, shedding light on the forest floor's role in supporting deadwood arthropods. The removal or disturbance of leaf litter, whether due to natural processes or anthropogenic activities, may have cascading effects on arthropod communities within dead trees. The Gigante Litter Manipulation Project (GliMP) in Panama stands as one of the few experimental investigations into the connection between arthropod assemblages and organic matter quantity on the forest floor, particularly in tropical regions (Sayer, 2010). This study focuses on litter removal rather than addition, as previous on-site studies found that the abundance and biomass of soil fauna significantly declined with litter removal but remained unaffected by litter addition (Ashford *et al*., 2013). Furthermore, the response of litter fauna was more pronounced to litter removal than addition (Sayer, 2006). Changes were attributed to different parameters: a reduction in total carbon and litter depth for the soil community, and a reduction in sodium and calcium for the litter community, although phosphorus was important in both environments (Ashford *et al*., 2013; Gora *et al*, 2017; Sayer, 2006).

The natural succession of saproxylic arthropods in tropical forests remains mostly unknown. Existing tropical studies are limited in scope, with a predominant focus on beetle communities (Ramírez-Hernández *et al*., 2019; Muñoz-López *et al*., 2016). Additionally, these studies tend to emphasize successional changes with forest age rather than presenting a chronological sequence of wood decay within the same forest. In contrast, research from temperate regions reveals a more comprehensive understanding of saproxylic arthropod dynamics. These studies indicate that species diversity of saproxylic arthropods tends to increase with the progression of decomposition stages (Sky, 2011; Mlynarek *et al*., 2018; Irmler *et al*., 1996; Dennis *et al*., 2018; Hammond *et al*., 2004). Notably, shifts in community composition are observed, with specialist colonizers dominating the early stages of wood decay when the wood is relatively intact, often represented by wood-burrowing beetles (Sky, 2011; Ramírez-Hernández *et al.,* 2019; Muñoz-López *et al.,* 2016; Ulshen and Hanula, 2010; Lee *et al.,* 2014; Savely, 1939). These specialists facilitate the presence of more generalist arthropods, including fungal feeders and predators, as decomposition progresses to mid-stages and more nutrients become available. (Sky, 2011; Ramírez-Hernández *et al.,* 2019; Muñoz-López *et al.,* 2016; Ulshen and Hanula, 2010; Lee *et al.,* 2014; Savely, 1939). In the late stages of succession, moisture levels decrease, shelter from predators becomes scarcer, and only specific compounds remain, which are exploited by specialized arthropods (Sky, 2011; Ramírez-Hernández *et al.,* 2019; Muñoz-López *et al.,* 2016; Ulshen and Hanula, 2010; Lee *et al.,* 2014; Savely, 1939). In order to bridge this knowledge gap, this study employs a space-for-time approach, utilizing time-since tree death (TSD) as a proxy for decomposition stage. This approach enables us to gain valuable insights into the natural succession of saproxylic arthropods and how it is influenced by litter removal, thereby elucidating the significance of the forest floor.

This study also investigated the potential influence of initial wood density and diameter at breast height (DBH) on saproxylic arthropods. Initial wood density and tree size have been demonstrated to play a critical role in wood decomposition (e.g. Mori *et al*., 2014; Van Geffen *et al*., 2010), thereby affecting the dynamics of saproxylic arthropods during deadwood succession. Trees with a lower initial density may offer more habitat space and readily available nutrients during the early decay stages, thus potentially supporting a greater diversity of arthropods. Conversely, denser wood, due to its slower decomposition rate and reduced accessibility for wood-boring insects, provides fewer niches for arthropods. Additionally, wood density influences microclimate, with low wood density characterised by a high water holding capacity and reduced insulation against temperature fluctuations and high wood density characterised by low water holding capacity and greater insulation against temperature fluctuations. Furthermore, high wood density provides greater protection against predators than low density wood. Larger logs often possess thicker bark and greater number of crevices and hollows. This structural complexity provides a broader range of habitats than smaller logs. Additionally, larger logs often take longer to decompose, potentially accumulating greater faunal diversity overtime. Greater species richness of saproxylic insects in larger logs has been shown in an Australian tropical forest for example (Grove, 2002).

In this study, factors such as tree species, sunlight exposure, and wood moisture were not accounted for or measured, despite their potential impact on natural saproxylic succession. Existing literature suggests that these factors, while influential to some extent, generally have less pronounced effects compared to other key factors, such as wood age. Limited replicates for tree species, which exhibit variations in wood density and chemical compounds, posed a constraint on their inclusion. Moreover wood type tends to have diminishing influence as wood ages and decomposition progresses (Irmler *et al*., 1996; Szabo and Buddle, 2005). Sunlight exposure, found to impact arthropod assemblages in temperate forests (Vintstad *et al.,* 2020), has reduced significance in tropical environments due to less constraining climatic conditions. Wood moisture, can affect microclimate, resource availability, and decay processes, subsequently shaping arthropod habitat suitability. However, arthropod responses are likely to vary widely and its effect is difficult to measure due to the influence of precipitation and topography.

Two distinct sampling methods, namely emergence traps and wood samples, were employed in this study. This approach aligns with the literature, which suggests that employing complementary techniques yields more reliable data on saproxylic communities (Quinto *et al*., 2013; Alinvi *et al*., 2007). Many saproxylic arthropods exhibit limited dispersal capabilities (Thomas, 2000; Ewers and Didham, 2006), with some being small and cryptic in nature (Bouget *et al*., 2008). The choice of sampling techniques is pivotal in ensuring accurate and comprehensive inventories (Quinto *et al*., 2013). Therefore, this study adopted a log-focused sampling approach. Unlike the more commonly used flight-interception traps in other studies, emergence traps and wood samples offer a more specific and detailed representation of individual logs (Alinvi *et al*., 2007). It is worth noting that while emergence traps may not be entirely sealed due to irregularities in bark or drying-induced cracks (Hagge *et al*., 2019), the likelihood of non-saproxylic insects gaining entry is minimal, as they would need to actively search for and access the traps. Thus, it can be assumed that species captured in trunk emergence traps are either obligate or facultative saproxylic arthropods, without assessing individual life history traits (Graf *et al*., 2022). Wood samples, while less commonly employed due to their destructive nature, have proven effective in collecting arthropods in other studies (Floren *et al*., 2015; Macagno *et al*., 2015).

To summarise, this study investigates whether the forest floor, wood density or tree size (DBH) affects saproxylic arthropod succession in a lowland tropical forest. Time-since tree death was used as a proxy for wood decomposition stage. Arthropod abundance, richness and community composition were measured in deadwood from litter removal and control plots using a dual sampling approach: emergence traps and wood samples. Higher abundance and richness is expected in older and larger trees of a lower wood density in control plots, with a succession of the arthropod community. Litter removal is expected to negatively affect this natural succession.

MATERIALS AND METHODS

Study Site

The study was conducted within an ongoing long-term, large-scale litter manipulation experiment, the Gigante Litter Manipulation Project (GLiMP; Figure 1). The site under study is an old growth lowland tropical rainforest, located on the Gigante Peninsula (91060 N, 791540 W) in the Barro Colorado Nature Monument (BCNM) in Panama, Central America. Nearby Barro Colorado Island (C. 5 km from the study site) has an average temperature of 27°C and receives 2600 mm of mean annual rainfall with a strong dry season from January to April (Leigh, 1999).

Fifteen 45 x 45 m plots were established within a 38.1 ha area of old growth forest in 2000. Starting in January 2003, the five litter removal plots have been raked every four to six weeks to remove the litter and the five control plots were left undisturbed (Figure 2). Five litter addition plots received the litter from the litter removal plots, but the litter addition treatment is not considered in this study. In this study litter removal refers to the removal of anything that a single person can comfortably carry and therefore includes coarse woody debri (CWD) and small branches in addition to leaf litter. The experimental design of the GLiMP is described in detail in Sayer and Tanner (2010).

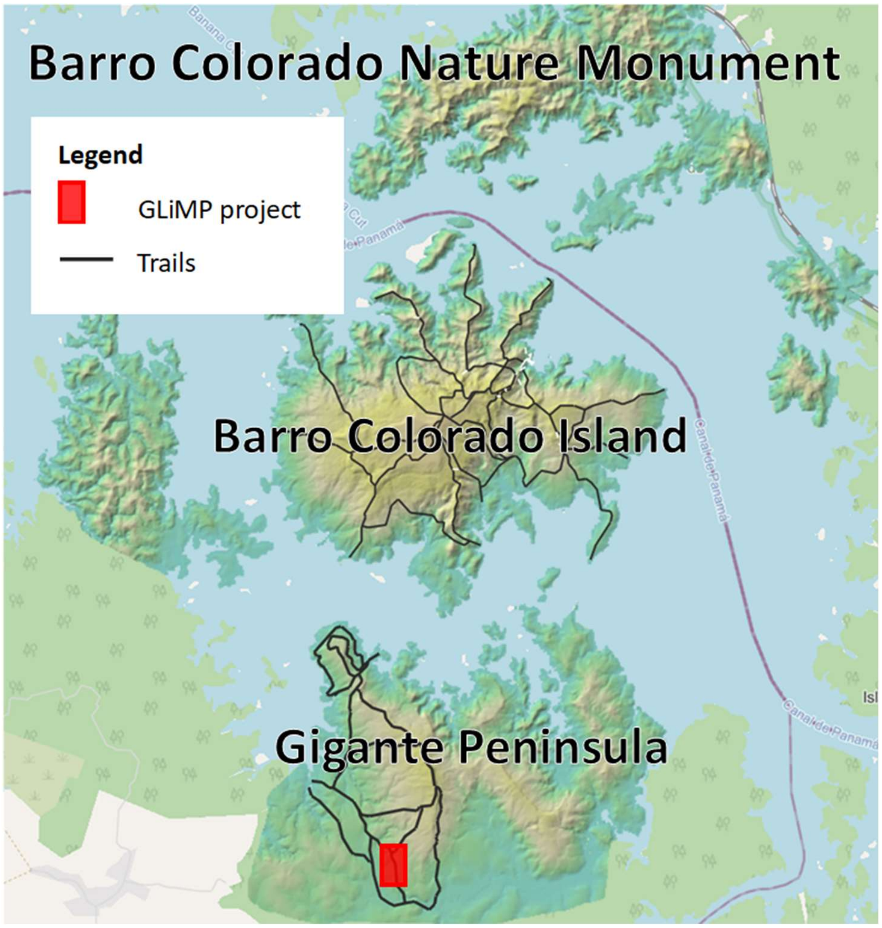

Figure 1. Barro Colorado Nature Monument topographic map (Solano, 2022) with the location of the Gigante Litter Manipulation Project (GLiMP) on Gigante Peninsula.

Figure 2. The Gigante Litter Manipulation Project (GLiMP), showing adjacent litter removal The Gigante Litter Manipulation Project (GLiMP), showing adjacent litter removal and control plots separated by plastic-lined trenches (A) during the first year of treatments in 2003; (B) the soil surface after the first application of treatments in February 2003; and (C) the soil surface after 5 years of treatments in 2000. Figure and caption replicated from Sayer *et al.,* (2020).

Sampling

All trees in the plots with a diameter at breast height (DBH) > 10 cm were identified to species, tagged, measured and mapped between 2000 and 2001 and have been remeasured at least every other year since. The tree census data from the plots thus indicates the year in which a given tree has died, the size of the tree at death, the species of tree, and its location in the plot (Sayer *et al.,* unpublished data). Using this information, we were able to locate trees that had died between 2003 and 2023 but had not completely decomposed. Only fallen trees (non-standing) and non-palm trees were considered for this study as these factors can affect arthropod diversity and community composition due to differences in microhabitats available, shade and moisture conditions (Stockland *et al*., 2012).

In total, 11 trees from four control plots and 14 trees from five litter removal plots were sampled (Figure 2). The tree census also provided data for predictors of arthropod fauna, specifically diameter at breast height (DBH) and time-since death (TSD). Trees belonged to 16 species and their DBH ranged from 10 cm to 76 cm. Given that the census was not yearly, TSD was calculated from 2023 using the midpoint between when a tree was recorded as alive and when a tree was recorded as dead. This approach aimed to provide a more gradual range of tree deaths. Wood density data were based on tree species and taken from Wright *et al.* (2011) via the databases TRY (Boenisch and Kattge, 2019) and FAO (Brown, 1997). Traits for each individual tree are displayed in Table 1.

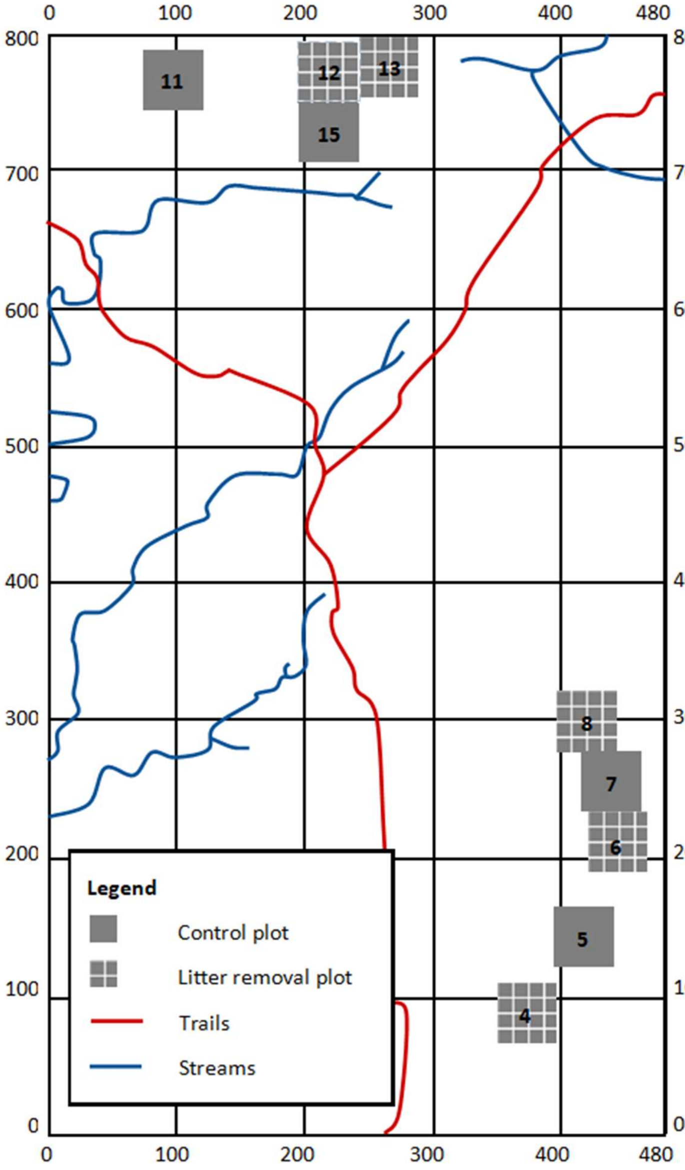

Figure 3. Approximate representation of plots used within the 38.1 ha Gigante Litter Manipulation Project (GLiMP) site. Distance in meters are given on the x and y axes.

Table 1. Tree traits. Diameter at Breast Height (CBH). Time-since-death (TSD). Control (C) and litter removal (L-).

Tree	Treatment	Plot	Tree species	DBH (cm)	TSD (years)	Wood density (g/cm³)
1	C	5	Casearia commersioniana	19	3	0.617
2	C	5	Phoebe cinnamomifolia	45	17.5	0.524
3	C	7	Pourouma bicolor	44	3	0.357
4	C	7	Cassipourea elliptica	24	2	0.660
5	C	7	Simarouba amara	25	7.5	0.390
6	C	7	Nectrandra purpurascens	23	2.5	0.513
7	C	11	Inga sapindoides	18	5.5	0.612
8	C	11	Prioria copaifera	76	7.5	0.391
9	C	11	Tetragastris panamensis	22	7.5	0.589
10	C	15	Protium panamense	24	0.5	0.447
11	C	15	Simarouba amara	10	9	0.390
1	L-	4	Jacaranda copaia	61	3	0.374
2	L-	4	Simarouba amara	44	9	0.390
3	L-	4	Inga cocleensis	27	0.5	0.666
4	L-	4	Amaioua corymbosa	13	0.5	0.678
5	L-	4	Trichospermum galeottii	16	0.5	0.296
6	L-	6	Jacaranda copaia	53	18	0.374
7	L-	6	Tetragastris panamensis	42	3	0.590
8	L-	8	Pourouma bicolor	28	7	0.357
9	L-	8	Pourouma bicolor	30	7	0.357
10	L-	12	Prioria copaifera	24	0.5	0.391
11	L-	13	Cassipourea elliptica	28	16	0.660
12	L-	13	Tachigalia versicolor	75	13	0.582
13	L-	13	Prioria copaifera	75	16	0.391
14	L-	13	Dialium guianense	37	0.5	0.547

Arthropod collection

Arthropods were collected using emergence traps and wood samples. All field work was conducted at the start of the wet season from April to June as several studies suggest that in areas with a pronounced dry season, such as most of Panama, the abundance of insects increases during the wet season (Wolda, 1992, Wolda, 1978; Kishimoto-Yamada and Itioka, 2015; Wiwatwitava and Taskeda, 2005).

Emergence traps were constructed from black cotton and metal mesh (Figure 4). Traps were installed at approximately 1.3 m from the base of the fallen tree trunks in April and May and left for 40 days. Sampling bottles were half-filled with a solution of approximately 75% ethanol and 5% water to kill and preserve the specimens, and 20% glycerol to help specimens remain supple and better preserve some colours (Gibbs and Oesto, 2006; Schauff, 2001). Sampling bottles were emptied a minimum of two times with the last collection occuring on day 40. Emergence trap sampling bottles were stored in a refrigerator until identification. A photo and details of emergence trap construction can be found in Appendix A.

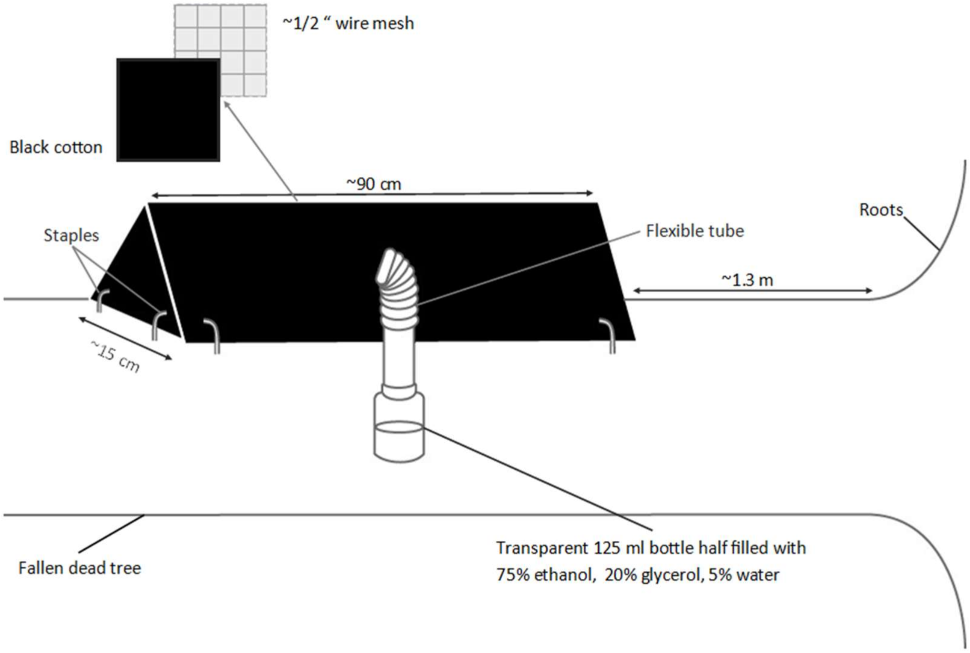

Figure 4. Diagram of emergence trap used on fallen dead trees.

Wood sample collection depended on the decomposition state of the dead tree: for largely intact trunks, wedges approximately 25 cm long and two inches in diameter were cut with a saw, whereas for heavily decomposed trunks a one litre plastic bag was filled with pieces broken off by hand. White cotton was placed on the ground around the fallen tree to collect fallen wood debris that fell whilst sawing or breaking apart the wood. The debris was added to the wood samples. All wood samples were placed into plastic bags for transport.

In the laboratory, wood samples were manually searched prior to being placed into Berlese-Tullgren funnels (Figure 5) to maximise arthropod sampling. A few wedges remained intact and were immediately placed in the funnels. Manual searching found larger arthropods (> 5 mm) that would not fit through the mesh gauze. Additionally, some arthropod groups are easier to identify alive than dead. Soft-bodied arthropods for example, are subject to breakages when decomposing (Gibbs and Oesto, 2006; Schauff, 2001). Wood samples were left in Berlese-Tullgren funnels for a minimum of 48 hours or until no more arthropods had emerged. The collecting jar contained 95% ethanol to preserve the arthropod samples until identification. After extracting the arthropods, wood samples were dried in an oven at 105 ± 5 °C for 72 hours and then weighed (to ± 0.1 g) to calculate wood dry mass.

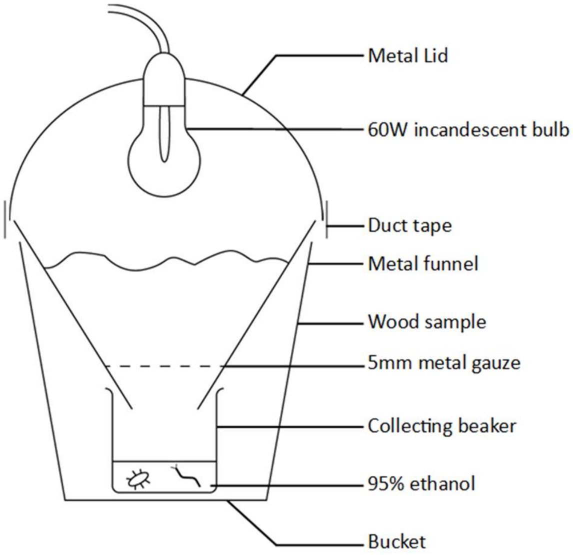

Figure 5. Diagram of Berlese-Tullgren funnel used to extract arthropods from wood samples.

Identification

Specimens from both sampling methods were initially identified to class or order level using a stereoscope following Gibb and Oseto (2006). Later, most animals were grouped to order level, but in some cases higher and lower taxonomic levels were used. The animals collected also included a Gastropod, but as this was only one individual the term arthropod is used throughout in the interests of succinctness.

Data Analysis

Data for wood samples and emergence traps were analysed separately. Arthropod abundance, richness and community composition data collected in wood samples were standardised per 300g of dry wood rounded to the nearest integer as wood sample mass ranged between 154 g and 754 g with a mean of 317 g. Although treatments were applied at the plot level, analyses were based on individual trees because each tree has unique characteristics including the environmental variables (wood density, TSD and DBH) which are subject to comparison in this study. For this reason, individual trees can be considered replicates within the control (n = 11) and litter removal plots (n = 14).

Generalised linear models (GLMs) were used to analyse the influence of treatment (control and litter removal plots) and its interaction with the environmental variables (wood density, TSD and DBH) on the response variables abundance and species richness. Treatment was a fixed categorical variable and the environmental variables were numerical random effects in the model. The most adequate models were GLMs fitted using Gaussian distribution on logged abundance and species richness data. Both statistical and graphical diagnosis from the performance package (Lüdecke *et al.*, 2023) were used to check assumptions and model fit. Specifically, different models were ranked based on the indices R2, Akaike Information Criterion (AIC) weights, Bayesian Information Criterion weights, Root-Mean-Square Error (RMSE) and sigma and graphs were analysed visually for posterior predictive check, linearity, homogeneity of variance, influential observations and normality of residuals.

Where continuous variables or interactions were significant, simple linear models were used to determine their correlation with the response variable. For significant interactions between treatment (a fixed factor), post hoc pairwise comparison were implemented using non-parametric Mann-Whitney U tests ($p < 0.05$) as the data were resistant to transformation.

To assess the influence of treatment on the most common arthropod taxa, I reran the abundance and richness analyses including only arthropod groups with more than 20 individuals or species across treatments. To assess the influence of sampling method on the most common arthropod taxa, differences in abundance and richness of arthropod groups with more than 20 individuals or species across sampling methods were tested using Mann-Whitney U pairwise contrasts ($p < 0.05$). The differences in species richness for the most common arthropod groups across treatments and sampling methods were illustrated using boxplots.

To test for differences in community composition, I used permutational multivariate analysis of variance (PERMANOVA; *adonis2* function) based on Jaccard similarity in the vegan package (Oksanen *et al.,* 2022). The influence of treatment, environmental variables (wood density, TSD and DBH) and their interactions on community composition was tested at species and order level using 9999 permutations to generate significance values. To visualise differences in community composition for each treatment and their development with TSD, I used non-metric multidimensional scaling (NMDS) ordinations based on the Jaccard dissimilarity matrix. To show this development process, only centroids were plotted with links by a straight line representing time. Two dimensions of NMDS with stress less than 0.15 was considered satisfactory.

Statistical analyses were performed using R version 4.2.1 (R Core Team, 2023). The ggplot2 package (Wickham *et al*., 2023) was used to produce the NMDS and boxplots.

RESULTS

A total of 4239 individuals from 154 taxa were identified (101 orders, 46 families and 7 species; Table 2). Images of each taxa can be found in Appendix B: Table S1. Springtails (*Collembola: Entomobryomorpha*) were the most abundant order with 56% of total individuals. Termites (*Blattodea: Termitidae*) were the second most abundant order (27% of all individuals). Of the Hymenoptera (7% of all individuals), 87% of identified individuals were ants (*Formicidae*). Larvae and unidentified individuals made up less than one percent of all individuals collected. Termites were the only arthropod group that displayed significant variation ($p < 0.05$) in abundance between treatment in wood samples (Table 2).

Table 2. Summary of arthropod taxa identified in fallen dead tree trunks in control (C) and litter removal (L-) plots using two sampling methods: emergence traps and wood samples, in a lowland tropical forest in Panama, Central America. Taxa with more than 20 in total across treatment or sampling methods were tested for significance using Mann-Whitney U pairwise contrasts *($p < 0.05$)*. Asterisks indicate significant differences between C and L- plots. The letter 'A' denotes a significant difference in taxon abundance between emergence traps and wood samples in C plots; 'B' denotes a significant difference in taxon abundance between emergence traps and wood samples in L- plots.

Taxon		**Emergence Traps**			**Wood Samples**			
		Control	**Litter Removal**		**Control**	**Litter Removal**		
Arachnida	Acari	2	2		1	13		
	Aranea	1	4		4	7		
	Opiliones	4	4		0	0		
	Psuedoscorpiones	0	0		4	1		
Coleoptera		4	3		2	9		
	Carabididae	0	0		0	13		
	Ciidae	1	6		1	7		
	Curculionidae	30	85	*	1	1		AB
	Endomychidae	1	3		0	0		
	Nitidulidae	5	1		0	2		
	Passalidae	0	0		1	0		
	Scarabidiae	0	0		2	0		
	Staphylinidae	9	29		4	16		
Blattodea		0	0		1	0		
	Termitidae	4	6		168	966	*	AB
Collembola		1616	759		0	4		A
Diptera		46	30		0	1		AB
Gastropoda		1	0		0	0		
Hemiptera		1	0		0	0		
Hymenoptera	Apocrita	4	6		9	17		
	Formicidae	25	46		37	140		
Isopoda		0	0		0	3		
Leipidoptera		0	3		0	0		
Myriapoda	Chilopoda	0	0		3	1		
	Diplopoda	1	1		1	11		
Orthoptera		2	5		0	0		
Pscoptera		7	8		0	1		
Larvae		1	0		8	7		
Unidentified		0	2		1	3		
Total		1765	1003		248	1223		
Grand total 4239								

The GLMs and PERMANOVA identified significant differences in arthropod species richness and abundance across treatments and time-since tree death for the wood sample data but not for the emergence trap data. Consequently, the following results pertain only to wood samples, and the results from emergence traps are shown in Appendix C.

The GLMs identified the interaction between treatment and time-since tree death as the most significant predictor of arthropod abundance and richness (Table 3). Similarly, PERMANOVA revealed that both order and species composition were significantly influenced by the interaction between treatment and time-since tree death (Table 4). While both treatment and time-since tree death contribute individually to explaining variation in the response, their combined effect demonstrates that treatment influenced the relationship between time-since tree death and abundance, richness and community composition. There was no influence of wood density, DBH or their interactions with treatment on abundance, richness or community composition.

The GLMs revealed a significant difference in arthropod abundance but not richness between treatments (Table 3). Median abundance was significantly higher in litter removal plots (Mann Whitney U = 36, $p < 0.05$) with 19 ± 51 individuals per sample (n = 14), compared to control plots, which had 6.5 ± 28 individuals (n = 10).

Table 3. Results of statistical tests from generalised linear models (GLM) testing the influence of litter treatment and time since tree death (TSD) on the abundance and species richness of arthropods in decaying tree trunks in a lowland tropical forest. Results are shown for wood samples; non-significant results for emergence traps are shown in appendix C. Data for abundance and species richness were logged before conducting the GLM.

Variables and Effects	**df**	**F or Chisq**	**P**
Arthropod abundance			
Treatment	1	5.15	**0.034**
TSD	1	208	0.782
Treatment X TSD	1	12.13	**0.023**
Arthropod richness			
Treatment	1	2.2	0.154
TSD	1	0.42	0.523
Treatment X TSD	1	7.98	**0.01**

Table 4. Results of PERMANOVA (vegan::adonis2) based on Jaccard similarity testing the influence of litter treatment, time since tree death (TSD) and diameter at breast height (DBH) on the community composition of arthropods at order and species level in decaying tree trunks in a lowland tropical forest. Results are shown for wood samples; non-significant results for emergence traps are shown in appendix C. Data were standardised per 300g of dry wood.

Variables and Effects	**df**	**F**	**P**
Order			
Treatment	1	0.6634	0.8051
TSD	1	1.2023	0.2543
Treatment X TSD	1	2.8096	**0.0015**
Species			
Treatment	1	0.9994	0.4613
TSD	1	1.0559	0.3398
Treatment X TSD	1	1.4207	**0.0081**

In control plots, the simple linear model revealed a statistically significant increase in arthropod abundance with TSD ($R^2 = .56$, $F_{1,9} = 11.31$, $t = 3.36$, $p < 0.05$; Figure 6a). Conversely, in litter removal plots, arthropod abundance declined significantly with time since tree death ($R^2 = .22$, $F_{1,13} = 3.56$, $t = -1.88$, $p < 0.05$; Figure 6a). Similar patterns were found for arthropod species richness. In control plots, the linear model indicated a statistically significant increase in arthropod richness with TSD ($R^2 = .41$, $F_{1,9} = 6.34$, $t = 2.52$, $p < 0.05$; Figure 6b). In contrast, although richness also appeared to decline with TSD in the litter removal plots, the relationship was not significant (Figure 6b).

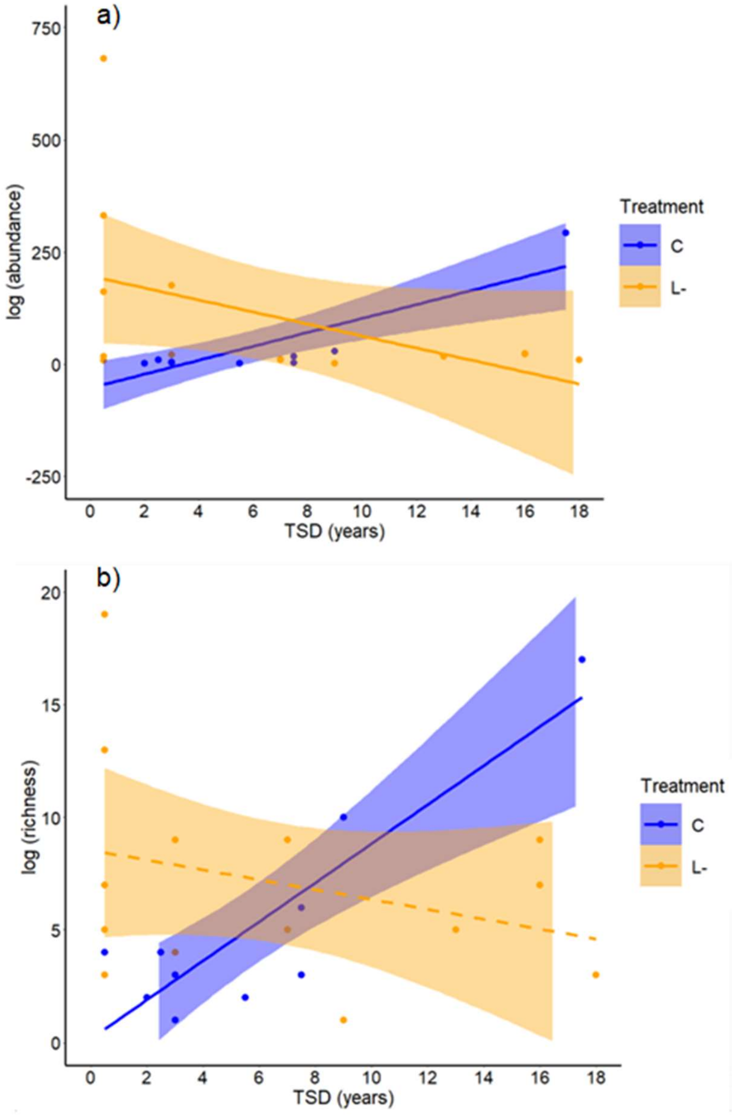

Figure 6. The relationship between log-transformed arthropod a) abundance and b) species richness and Time-Since-Death (TSD) in years of fallen dead trees in control (C) and litter removal (L-) plots in a lowland tropical forest in Panama, Central America. Data shown are for wood samples, where solid lines

indicate significant relationships ($p < 0.05$) determined by linear models, and shading denotes 95% confidence intervals.

The GLMs for the most common arthropod groups identified the interaction between treatment and time-since tree death as the most significant predictor of both Hymenoptera and Formicidae abundance and richness (Table 5). Further analysis using simple linear models revealed that only Formicidae abundance in litter removal plots was significantly correlated, with a decline as time-since tree death increased (Estimate = - 0.12, SE = 0.04, $p < 0.05$). Termite abundance but not richness was also predicted by the interaction between treatment and time-since tree death by a GLM (Table 5). However, simple linear models found no significant correlations for either treatment between time-since tree death and termite abundance or richness. There was no influence of wood density, DBH or their interactions with treatment on abundance or richness of the most common arthropod groups.

Table 5. Significant results for Generalised Linear Models (GLMs) conducted for arthropod groups with at least 20 individuals or species across treatments. The GLMs test the influence of litter treatment and time since tree death (TSD) on the abundance and species richness of each arthropod group in decaying tree trunks in a lowland tropical forest. Note that the order Hymenoptera includes the family Formicidae. Results are shown for wood samples; non-significant results for emergence traps are shown in appendix C. Data for abundance and species richness were logged before conducting the GLM.

Variables and Effects	**df**	**F or Chisq**	**P**
Termite Abundance			
Treatment	1	1.5967	0.22856
TSD	1	0.385	0.54569
Treatment X TSD	1	5.0228	**0.04311**
Termite Richness			
Treatment	1	1.7365	0.20874
TSD	1	0.6557	0.43162
Treatment X TSD	1	4.3051	0.05691
Hymenoptera Abundance			
Treatment	1	6.3073	**0.02491**
TSD	1	0.3992	0.53768
Treatment X TSD	1	7.1255	**0.01832**
Hymenoptera Richness			
Treatment	1	2.935	0.10873
TSD	1	0.0625	0.80628
Treatment X TSD	1	5.3121	**0.03701**
Formicidae Abundance			
Treatment	1	1.1293	0.35907
TSD	1	8.1886	**0.01256**
Treatment X TSD	1	11.131	**0.004896**
Formicidae Richness			
Treatment	1	0.2816	0.60396
TSD	1	3.8529	0.06985
Treatment X TSD	1	8.1226	**0.01285**

The NMDS ordination (Figure 7) illustrated distinct trajectories in arthropod composition with time-since tree death between treatments. In the control plots, the arthropod groups show a clear direction with time-since tree death (Figure 7a), whereas the direction is unclear in the litter removal plots (Figure 7b). Differences in community composition between treatments could not be attributed to specific taxa due to similarity in trajectories between the arthropod groups.

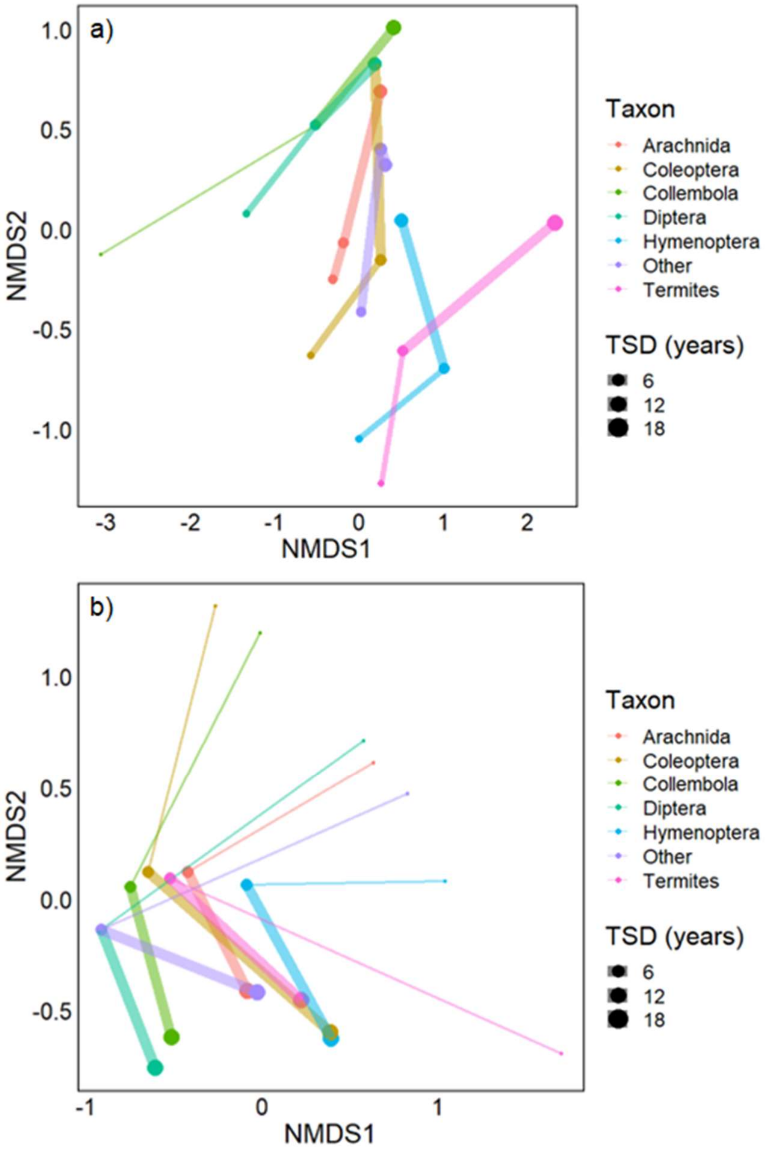

Figure 7. Non-metric multidimensional scaling (NMDS) plots of arthropod abundance by taxonomic groups for a) control plots and b) litter removal plots illustrating compositional variation in trajectories with Time-Since-Death (TSD) depending on treatment.

The arthropod community was also notably influenced by the sampling method employed (Table 2: Figure 8). Across treatments wood samples detected fewer taxa than emergence traps and had a different composition. Coleoptera and Diptera median richness were significantly higher in emergence traps compared to wood samples (Figure 8). Similarly, the median abundance of Curculionidae and Diptera were also significantly higher in abundance in emergence traps compared to wood samples (Table 2). Median termite abundance, however, was significantly higher in wood samples compared to emergence traps (Table 2).

Median richness of each arthropod group (Collembola, Termites, Hymenoptera, Diptera, Arachnida, Coleoptera and Other) did not differ significantly between treatments (Figure 8). However, treatment influenced the arthropod groups captured by the two sampling methods. In control plots, Collembola abundance and richness were significantly higher in emergence traps compared to wood samples (Figure 8). However, no differences in Collembola abundance or richness were found between methods in litter removal plots. By contrast, in control plots, termite richness did not differ between methods, whereas in litter removal plots, termite richness was significantly higher in wood samples than in emergence traps (Figure 8).

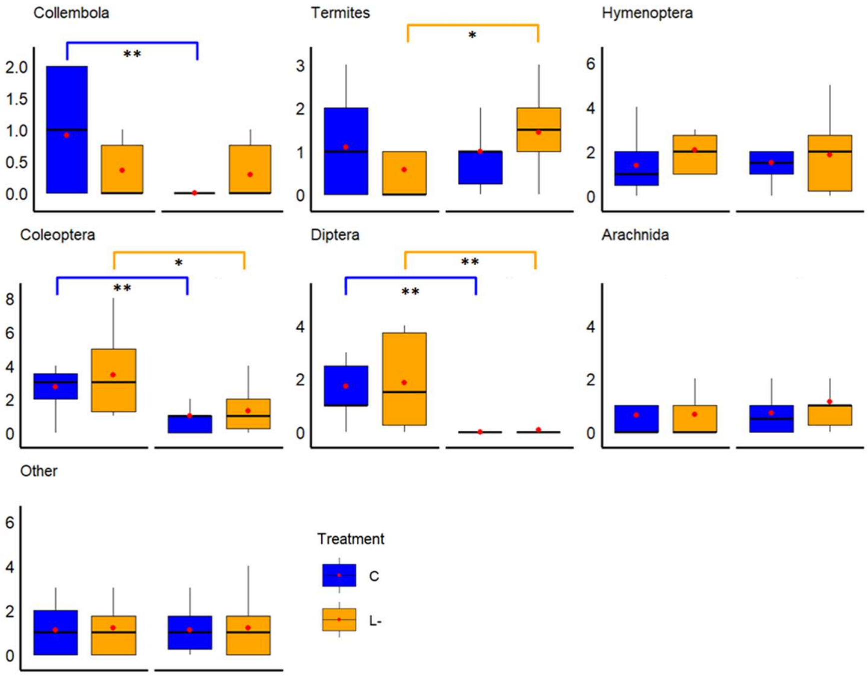

Figure 8. Arthropod species richness in fallen dead tree trunks in control (C) and litter removal (L-) plots using two sampling methods: emergence traps and wood samples, in a lowland tropical forest in Panama, Central America. Separate panels show data for different arthropod groups. Horizontal bars indicate significant differences in median species richness between sampling methods (Mann-Whitney U pairwise contrasts). Level of significance is coded as *$p < 0.05$*, **$p < 0.01$*. Note that the scale of the y-axis varies among panels. The boxplots represent the distribution of data. The central bold line is the median (50th quantile), inferior boxline is the 25th quantile, superior boxline is the 75th quantile, and whiskers represent minimum and maximum values. The red point is the mean.

DISCUSSION

The findings of this study offer valuable insights into the succession of saproxylic arthropods in a lowland tropical rainforest. While previous research has revealed successional changes in relation to forest age, this study examines a chronosequence of wood within the same forest using a space-for-time approach. To my knowledge this is the first study to address the role of forest floor litter in saproxylic arthropod succession. It is important to note that, although treatments were applied at the plot level, the analyses were performed on individual trees, which are treated as replicates. Given the limited understanding of saproxylic arthropod succession in tropical ecosystems, the discussion will initially place our findings in the context of temperate studies, while highlighting key distinctions between tropical and temperate forests. Then I will delve into the specific effects of the litter removal treatment.

Natural saproxylic arthropod succession

In the control plots, the significant increase in both arthropod abundance and richness with increasing time-since tree death (TSD; Figure 6a; Table 3), suggests that a natural succession process occurs during wood decomposition. Notably, this trend is primarily driven by termites and ants, which were the most abundant taxa found in wood samples (Table 2). In control plots, ants and termites exhibited particularly high abundance levels in the later stages of decay and generalized linear models (GLMs) identified treatment interacting with TSD as a significant predictor of their abundance (Table 5). Moreover, the non-metric multidimensional scaling (NMDS) ordination for the control plots, illustrated in Figure 7a, reveals a clear and consistent trajectory across all arthropod groups with increasing time-since tree death. This observation is reinforced by the significant interaction between treatment and time-since tree death for both order and species composition (Table 4). These conclusive results regarding order and species diversity provide compelling evidence that responses occur even at high taxonomic levels.

It is well-documented that species diversity typically increases with succession and has been observed across various ecosystems (Gibb *et al.,* 2013; Dennis *et al.,* 2018). There are two reasons for this in decaying trees. First, it is plausible that trees that have been dead for longer create more habitat space due to their structural complexity, leading to greater species abundance and richness. Second, there is more time for colonisation of the decomposer community to occur. As this study only assessed logs up to 18 years after death, we did not witness the levelling off and decline of the decomposer community that presumably occurs when the resource (wood) becomes scarcer.

My findings are supported by previous temperate studies. For instance, Sky (2011) observed an increase in saproxylic invertebrate richness in a plantation forests with TSD. Additionally, Mynarek *et al.* (2018) noted an increase in Diptera abundance in deciduous forests as time-since tree death progressed. Furthermore, considering that time-since tree death serves as an indicator of wood decay stage, my study aligns with research investigating the effect of wood decay stage on arthropod assemblages. Several studies reinforce my findings, showing increased abundance and richness with decay stage for broadleaved trees (Irmler *et al.,* 1996; Dennis *et al.,* 2018; Hammond *et al.,* 2004). Wu *et al*.'s (2008) study in a subtropical forest, where beetle species density decreased with decay stage in broadleaved dead trees, stands as the sole exception of this trend, to my knowledge. For coniferous trees, responses appear more diverse, with some reporting higher diversity in early (Saint-Germain *et al.,* 2007; Ulyshen and Hanula, 2010; Wu *et al.,* 2008) or mid successional stages (Ferro *et al.,* 2012) as well as late successional stages (Irmler *et al.,* 1996; Dennis *et al.,* 2018). Given that all the dead trees in this study were broad-leaved, the prevailing evidence in decay stage literature backs my findings of an increase in saproxylic abundance and richness with deadwood age. Tropical literature on arthropod succession with deadwood age or decay stage was absent with the only studies on saproxylic succession in the tropics found to be at the forest rather than individual log level.

Changes in saproxylic composition with decay stage are well documented with studies showing changes in beetles in tropical deciduous forests (Muñoz-López *et al*., 2016), beetles in cloud forests (Ramírez-Hernández *et al*., 2019), beetles in white-spruce boreal forests (Lee *et al*., 2014), spiders in oak-maple forests (Ulyshen and Hanula, 2010), fauna in Oak and Pine logs (Savely, 1939) and invertebrates in a New Zealand plantation (Sky, 2011).

Changes in saproxylic assemblage are expected during the decomposition process (Dennis *et al.,* 2018). As wood decomposes its physical and chemical properties change (Grove, 2002; Songvorawit *et al.,* 2017) affecting the habitat and resources available to arthropods. Different species often depend on resources that peak at different points in succession (Gibb *et al.,* 2013). Thus, species typically have distinct responses to succession depending on their ecological role. However, my study found a relatively uniform response of arthropod groups to increasing deadwood age, as visually represented in the NMDS ordination (Figure 7a). This uniform pattern can be attributed to the pronounced prevalence of the most abundant taxa, termites and ants, in the later stages of decay. While it's conceivable that other arthropod groups exhibit varying responses to increasing deadwood age, their abundances were either too limited to discern an observable effect or too minimal for robust statistical analysis. For instance, beetle abundance displayed a declining trend with deadwood age, but their numbers were significantly lower compared to the prominence of termites and ants within the wood samples. The shifts in termite and beetle abundance observed in my study align with findings from Muñoz-López *et al*.'s (2016) study in the tropics, where Coleopterans were gradually replaced by organisms more closely associated with soil and leaf litter, including termites. In contrast, this study observed a lack of response to deadwood age among arachnids, Dipterans and Collembola unlike temperate studies that commonly link both taxa to late decay stages (Sky, 2011; Mlynarek *et al*., 2018).

The different responses of Collembola, Arachnida and Diptera in my study can be attributed to three potential factors: (1) the limited number of older trees (Table 1), (2) the study's assessment of logs up to 18 years after death may not suffice to reveal these compositional changes, and (3) the challenge of deadwood age accurately representing late decay stages, as wood of the same age can decay at different rates due to various factors, including tree species, trunk size, or sunlight exposure. For a comprehensive analysis of arthropod taxa's varied responses, it is advisable to measure both decay stage and deadwood age, ensure that trees are of the same species and similar size, and sample a larger number of trees across various decay stages.

Differences in Coleoptera composition also varied with deadwood age, contingent upon functional groups, although statistical testing was precluded due to small sample sizes and limited representation of trees in late decay stages. Beetles, being among the most extensively studied saproxylic arthropods have a multitude of studies that support my observation that beetle community composition differs between age classes (Sky, 2011; Ramírez-Hernández *et al*.,. 2019; Muñoz-López *et al.,* 2016; Ulshen and Hanula, 2010; Lee *et al.,* 2014; Savely, 1939). These studies identified a transition from primarily wood feeding species to predators and fungal feeders as deadwood age increases (Ramírez-Hernández *et al.,* 2019; Muñoz-López *et al.,* 2016; Ulshen and Hanula, 2010; Lee *et al.,* 2014; Savely, 1939). In line with these findings, my observations also reveal distinctions between wood-feeders and predators. Wood-feeders, primarily from the subfamily Scotlytinae, were more abundant in younger logs, while Staphylinidae beetles, predominantly predators, exhibited a peak in abundance at mid-aged deadwood and sustained higher numbers in late decay stages compared to most beetle taxa. However, I did not find fungus-feeding beetles in older trees, and those in the subfamily Platypodinae were solely present in young deadwood, which deviates from other studies. This discrepancy might be attributed to the limited number of fungus-feeding individuals found in my study. Additionally, it's worth noting that the majority of previous studies are from temperate regions where fungi play a more prominent role in decomposition compared to the tropics, largely due to the absence of termites.

The presence of fungal-feeders and predators within deadwood highlights that wood is not the sole resource available to arthropods during wood decomposition. Wood decay influences fungal succession as well as arthropod succession with more fungi typically present at intermediate decay stages. As a result, fungi play a crucial role in shaping arthropod succession, (Persiani *et al.,* 2010; Weslien *et al.,* 2011) and vice versa (Strid *et al.,* 2014; Lunde *et al.,* 2022; Vindstad *et al.,* 2020). As well as being an important food source for many arthropod species, fungi changes the wood resources available to wood-feeding arthropods (Weslien *et al.,* 2011). In turn, arthropods affect fungi colonisation and succession by bringing fungal material including spores to recently cut logs and facilitating the spread of fungi by tunnelling (Jacobsen, 2017). A limited number of studies have investigated both fungi and arthropods in decaying wood. For example, part of the variance in beetle communities on aspen tree stumps in a boreal forest in Norway was explained by fungal community composition and development over four years (Vindstad *et al.,* 2020).

DBH

While log size (DBH) did not affect arthropod assemblages in this study, the effects may have been obscured by multiple species of tree at different deadwood ages being used. A larger log is expected to contain greater diversity than smaller logs, primarily due to the assumption that they offer more niches and resources. Grove (2002) for instance found a positive correlation between the volume of coarse woody debris and tree basal area with the species richness of saproxylic insects in an Australian tropical forest. However, an older but smaller log could harbour a greater diversity of arthropods than a smaller but larger log, as supported by my own findings that arthropod abundance and richness increases with wood age. Furthermore, larger trees are expected to take longer to decompose than smaller trees, potentially affecting how arthropod assemblages respond to time-since tree death. Therefore, to analyse the effects of log size on arthropod abundance with wood age, future study should have replicates within tree species and replicates of tree size classes across wood ages.

Wood density

Tree species with low density wood could provide more initial habitat space and more readily available nutrients during early decay stages and therefore harbour a greater arthropod diversity. While wood density did not affect arthropod assemblages in this study, the effects may have been obscured by deadwood age varying from zero to 18 years as older wood decomposition is less likley to be affected by initial wood density. Hence study on the effects of wood density using only early decay or young wood may reveal the effects of initial wood density on arthropod assemblages. Previous research has already shown wood density to affect arthropod preferences in dead wood (Liu *et al.,* 2015, Songvorawit *et al.,* 2017; Lanuza-Garay and Barrios, 2018). For instance, research on tropical trees in China found that termites prefer dead wood with a lower initial density (Liu *et al.,* 2015).

Furthermore, changes in wood density with deadwood age can also affect arthropod abundance. Late decay logs tend to have a low wood density, offering more accessible nutrients (wood and fungi) and higher moisture level but at a higher risk from natural enemies due to the soft wood (Songvorawit *et al.,* 2017). Early decay logs tend to have a high wood density, offering improved saftey due to the hard structure of the wood but reduced nutrient availability and a lower moisture level (Songvorawit *et al.,* 2017). Therefore, wood of a lower to intermediate density provides balance between nutrient availability and risk from natural enemies (Songvorawit *et al.,* 2017). Songvorawit *et al.* (2017) for example observed that stag beetles in a temperate forest in Thailand preferred ovipositing in moderately decaying wood with a low density because of this balance between risk and reward. Wood density measurements for this study were ex-situ, species based and from living trees. Consequently, future study would benefit from measuring log wood density in-situ overtime or using a space-for-time approach to provide insights into how arthropod abundance is affected by wood density changes with deadwood age.

Litter removal impacts natural arthropod succession.

The natural succession of arthropod communities in deadwood appears to be disrupted by litter removal, as evidenced by a decrease in total arthropod abundance with TSD, along with a declining trend in richness that, while not statistically significant, is notable (Figure 6b; Table 3). This trend is primarily attributable to termites and ants, which were the most abundant taxa found in wood samples (Table 2). In litter removal plots ants exhibited a significant decline with deadwood age and termites were notably higher more abundant in younger wood (Table 5). Furthermore, the NMDS ordination for the litter removal plots does not display a clear pattern in relation to TSD, in contrast to the control plot ordination (Figure 7). This discrepancy indicates that the disruption of community composition can be attributed to litter removal. This observation is also supported by the significant interaction between treatment and TSD, for both order and species composition (Table 4). In light of these findings, it becomes apparent that litter removal significantly impacts the connectivity of the forest floor between the soil, litter, and deadwood, underscoring the pivotal role of the forest floor in saproxylic arthropod succession.

The importance of the forest floor in the decomposition of coarse woody debri (CWD) has already been well-documented in prior research and experiments conducted at the same project study site. Gora *et al.* (2017) revealed that soil nutrient availability affects long-term CWD decomposition as litter removal decreased long-term CWD decomposition rates by reducing nutrient availability. With the absence of litter inputs, soil concentrations of phosphorus (P) and potassium (K) were diminished (Gora *et al.,* 2017). Notably, these elements were identified as the limiting factors in cellulose decomposition, as demonstrated in NPK addition experiments (Kaspari *et al.,* 2008). Cellulose, a primary component of leaf litter, provides energy-rich nutrients for decomposers (Kaspari *et al.,* 2008). Consequently, the diminished availability of cellulose in the litter removal plots, owing to limited P and K accessibility, has a direct impact on the activity of wood decomposers (Gora *et al.,* 2017; Kaspari *et al.,* 2008). Cumulatively, these findings strongly suggest that the influence of litter removal on saproxylic arthropod succession can be largely attributed to alterations in nutrient availability within the forest floor. This decline in forest floor nutrients also offers a plausible explanation for the reduction in arthropod abundance associated with deadwood age in the litter removal plots.

Moreover, the diminished nutrient availability in the litter removal plots may have imposed limitations on fungal growth (Gora *et al.,* 2017). While this study did not specifically examine variations in fungal-feeders in response to treatments, with insufficient nutrients or substrates, it is reasonable to assume that fungal feeder diversity would be curtailed. In such conditions, the community may adapt towards alternative strategies, such as scavenging for soil nutrients or forming symbiotic relationships with plants (Gora *et al.,* 2017). Furthermore, prior research conducted on-site has already established significant alterations in arbuscular mycorrhizal fungal communities within the litter removal plots (Sheldrake, Rosenstock, Revillini, Olsson, Mangan *et al.,* 2017 in Gora *et al.,* 2017).

The observation of reduced wood decomposition rates within the litter removal plots implies that a dead tree of the same age in the litter removal plot is, in fact, at an earlier stage of decomposition compared to a similar-aged tree in the control plots. Consequently, the arthropods found in the litter removal plots may correspond to an earlier decomposition stage, which is not in line with what would be expected in natural succession. Nevertheless, it is important to note that the results do not indicate a delay in succession. This observation underscores the intricacies of the forest floor's role in the overall process.

In this study, litter removal refers to the removal of anything that a single person can comfortably carry and therefore encompasses CWD and small branches in addition to leaf litter. This practice, by its nature, tends to target wood in more advanced stages of succession. Additionally, it results in the removal of any arthropods residing within smaller woody material. As a result, litter removal may exert a more pronounced impact on early and late successional species inhabiting deadwood than on those found in intermediate decomposition stages. While my results do not allow for a definitive confirmation of this effect, it is plausible that such an impact contributed to the observed differences in arthropod assemblages between treatments.

Furthermore, the presence of CWD and smaller branches decomposing on the forest floor plays a critical role in improving the connectivity of larger logs. Consequently, the removal of CWD in the litter removal plots disrupts this connectivity, impacting saproxylic arthropod assemblages. Recent research has established that deadwood is important for soil and litter arthropods by comparing the arthropods in litter and soil immediately adjacent to CWD with those in sites further away from CWD. The majority of studies report higher arthropod densities and diversity in litter near CWD. This pattern is evident across various arthropod taxa in different ecosystems, such as oak beech forests in Germany (Jabin *et al.*, 2004), loblolly pine forests in the United States (Ulyshen and Hannula, 2009b), oak-maple forests in the United States (Castro and Wise, 2010), and sugar maple forests in Canada (Varady-Szabo and Buddle, 2006).

However, a few studies have documented higher abundances of certain arthropod taxa in litter further from CWD. For instance, Evans et al. (2003) found that Diptera and Thysanura significantly increased in abundance with distance from logs. The diverse responses of various arthropod groups have led to changes in community composition with increasing distance from deadwood in many studies (Castro and Wise, 2010; Evans *et al.,* 2003; Varadi-Szabo and Buddle; Jabin *et al.,* 2004). The distance effect acts on trunks as small as 14 cm in diameter and starts to decline between 0.5 and 1.5 m (Castro and Wise, 2010).

These studies collectively emphasize that arthropods do not necessarily have to be saproxylic to benefit from the presence of deadwood. Moreover, the advantages of deadwood are likely more pronounced in the litter removal plots due to the less hospitable conditions of the forest floor. Additionally, the distance effect between soil arthropod abundance and deadwood may have influenced the results in the litter removal plots. Distances between individual dead trees in this study varied, ranging from isolated to those close to other dead trees. Deadwood situated close to other deadwood may have mitigated some of the effects of litter removal on saproxylic arthropods, while completely isolated dead trees are more exposed. Although this study did not yield discernible patterns in this regard, the distance between deadwood should be considered in future studies exploring the interplay between the forest floor and deadwood.

The distance effects associated with deadwood have been attributed to various factors, including increased structural complexity, a higher abundance of potential prey, and more favourable microclimatic conditions in the vicinity of deadwood (Castro and Wise, 2010; Evans et al., 2003; Jabin et al., 2004; Varadi-Szabo and Buddle, 2006). These principles can also be extended to the importance of litter and soil for arthropods inhabiting deadwood.

Both litter and deadwood contribute to the structural complexity of the forest floor, offering additional habitat space and niches for arthropods. Numerous studies have demonstrated the influence of litter depth on arthropod communities (Ashford *et al.,* 2013). For example, research has shown that hunting spiders tend to exhibit increased diversity in environments with greater litter depth and complexity (Uetz 1991). Litter removal considerably reduces structural complexity and the only places for prey to hide are near the remaining deadwood; the bare soil of the litter removal plots is highlighted in Figure 2. However, the removal of litter significantly diminishes structural complexity. In these conditions, the limited hiding places for prey are predominantly confined to the vicinity of the remaining deadwood, as vividly depicted in Figure 2.

Litter removal has the effect of increasing the visibility and vulnerability of prey species. Consequently, predators in litter removal plots may have reduced encounters with prey due to the reluctance of prey species to traverse the hostile forest floor, even when resources within logs are reduced. However, predators may also find it easier to capture prey that does venture across the forest floor due to the heightened conspicuousness of prey in the absence of litter. In this study, distinguishing the responses of predator and prey species to the treatment was challenging due to limitations in identification capabilities and the low number of replicates for known prey and predator groups. However, taxa primarily consisting of predators, such as arachnids, displayed less variation between treatments and sampling methods compared to taxa that are typically prey species. A more detailed examination of beetle families provides additional support for these observations. For instance, Staphylinidae or rove beetles, known as predators of other invertebrates, maintained relatively consistent abundance between treatments and sampling techniques (Table 2). On the other hand, other beetle families, which are typically prey species, exhibited greater variability in abundance between treatments and sampling techniques. These findings suggest that litter removal exerts a more pronounced impact on prey species compared to predatory species, highlighting the greater reliance of prey species on the forest floor. Further studies, encompassing a larger number of tree replicates for statistical analysis, could provide validation for these observations.

In the absence of leaf litter, the soil tends to become drier and warmer (Sayer, 2006). Litter removal might also slightly alter the microclimate of deadwood, as it loses the shade and moisture provided by the leaf litter. It's important to note that many arthropods favour higher moisture conditions (Levings and Windsor, 1984), as well as cooler and shaded environments (Nakamura et al., 2009). For instance, numerous spider species exhibit a preference for higher moisture levels and lower temperatures (Huhta, 1971). Soft-bodied arthropods like termites are particularly susceptible to desiccation and tend to thrive in moister conditions. Consequently, in the hotter and drier conditions of the litter removal plots, these arthropods may be less inclined to migrate between logs due to the risk of desiccation.

Collectively, these factors underscore the vital role of leaf litter in enhancing structural complexity, offering a secure passage for arthropod migration, and creating favourable microclimatic conditions. These factors help explain the significantly higher median abundance in litter removal plots compared to control plots, which can be attributed to two potential reasons. Firstly, litter removal establishes a hostile environment that restricts arthropod movement as illustrated by Figure 2 and secondly, isolated deadwood fragments function as refuges for the remaining forest floor species. Consequently, litter removal exhibits effects on the forest floor similar to how fragmentation impacts a forest; hedgerows provide connectivity between forests, and litter provides connectivity between deadwood. Additionally, the decline in total abundance and Formicidae abundance with decay stage, along with the marked reduction in termite abundance in litter removal plots, may be linked to the increasing impact of dis-connectivity over time. Furthermore, the diverse environmental conditions generated by litter removal contribute to the unclear trajectory of community composition with time-since tree death.

Comparison of deadwood, litter and soil fauna

Comparing this study with previous onsite study demonstrates that soil, litter and deadwood have distinct arthropod communities (Ashford et al., 2013; Sayer et al., 2010). However, there are notable similarities in the abundance of certain taxa across these different forest floor habitats. Notably, the relative proportions of Coleoptera, Diptera, Collembola, and Hymenoptera in relation to other taxa exhibited consistency among these forest floor habitats.

In contrast, while Acari were highly prevalent in both soil and litter, comprising 35% and 14% of all individuals collected respectively (Ashford *et al*., 2013; Sayer *et al*., 2010), the Acari population in deadwood were less than one percent of total individuals. This aligns with findings from temperate regions where Acari are recognized as significant components of soil and litter fauna (Behan-Pelletier, 2002). In deadwood, their presence is considered an extension of the soil ecosystem (Bluhm et al., 2015) or a habitat for more specialized species (Skubala and Duras, 2008).

Conversely, termites were more abundant in deadwood, constituting 27% of all individuals, compared to only 8% in litter (Sayer et al., 2010) and less than 1% in the soil (Ashford et al., 2013). This observation is consistent with the well-established understanding that termites are prolific in decaying wood in tropical ecosystems (Law et al., 2019; Barca et al., 2018). It suggests that termites likely migrate from the soil, passing through the leaf litter, to reach their preferred deadwood habitat.

In summary, these findings collectively indicate that a substantial portion of the arthropod fauna comprises generalists that inhabit the forest floor, while others specialize in a particular habitat. Some arthropods demonstrate the ability to migrate between these habitats, and any arthropod that can migrate between soil and deadwood can benefit from the logs, especially in the litter removal plots. Therefore, this study advances our understanding of the various arthropod groups associated with soil, litter, and decaying wood and their behaviours.

A comparative study of arthropods in soil, litter, and deadwood over different stages of succession could provide insights into connectivity and the colonization of deadwood. For instance, in a beech forest in Germany, Irmler and colleagues (1996) found that the number of species immigrating from the adjacent litter layer into the dead wood increased over the course of succession, eventually resembling the fauna dwelling in the litter layer.

Moreover, arthropods in deadwood displayed distinct responses to litter removal compared to soil and litter-dwelling organisms. Litter removal significantly reduced the abundance and biomass of soil arthropods (Ashford et al., 2013; Sayer, 2006), whereas it had the opposite effect in deadwood. This further supports the notion that deadwood serves as a refuge in the absence of litter.

Emergence Traps

The lack of significant findings for emergence traps could be attributed to the isolation and connectivity of logs within the study area. Most flying arthropod taxa were predominantly captured in emergence traps rather than in wood samples. This group includes Diptera, the majority of beetles, Hemiptera, Lepidoptera, and Psocoptera (as shown in Table 2). Arthropods capable of flight may be less affected by the absence of leaf litter, as they do not need to traverse the bare soil to move between habitats. For instance, only one Diptera individual was found in wood samples, whereas emergence traps yielded 76 individuals and a diverse range of species. Furthermore, a significant proportion of termite alates (flying adults) were primarily captured in emergence traps rather than wood samples. Additionally, carabidae beetles, found exclusively in wood samples, are typically flightless due to fused elytra (wing cases) or are reluctant fliers if they possess the physical capability. The Apocrita order represented the only flying taxa where more individuals were found in wood samples. However, it's essential to note that in this study, most Apocrita taxa were parasitoid wasps, which are typically idiobionts and live in close association with their host organisms, such as beetle larvae that are often found within the wood. This explains why emergence traps yielded a richer diversity of flying arthropods as compared to wood samples, and how the connectivity or isolation of logs may have influenced the distribution of these flying taxa in the study.

Conclusion

Overall, this study provides significant insight into the dynamics of saproxylic arthropods succession in a lowland tropical rainforest. Termites and ants emerged as the primary drivers of observed changes between treatments with deadwood age with notably higher abundance and richness in older logs during natural succession compared to notably higher abundance and richness in younger logs in litter-removal disrupted plots.

One of the key findings of this study is the significance of forest floor connectivity in saproxylic succession. The forest floor provides structural complexity, a safe space to migrate and a favourable microclimate. In contrast, the removal of litter introduces a hostile environment that impedes arthropod movement. In this altered landscape, isolated deadwood fragments emerge as refuges for the remaining forest floor species. Over time, the disruptive effects of dis-connectivity become increasingly pronounced.

The lack of significant findings for emergence traps are attributed to the collection of flying taxa. These arthropods are less susceptible to the challenges posed by the bare soil in the litter removal plots due to their flight capability.

Additionally, this study offers the first, to our knowledge, comprehensive comparison of arthropod communities in deadwood, litter, and soil within a tropical forest context, leveraging insights from prior onsite research. The community compositions observed across these forest floor habitats emphasize the capacity of some arthropod groups to migrate from the soil to deadwood, thereby benefiting from the presence of logs in the litter removal plots.

In conclusion, our research provides a deeper understanding of saproxylic arthropod succession in tropical ecosystems, underlining the intricate interplay between deadwood, litter, and soil. Furthermore, we recommend future investigations to explore deadwood colonization and migration, particularly focusing on how these processes relate to leaf litter.

Additionally, studies considering tree size and wood density variations across deadwood age would contribute to a more comprehensive understanding of these factors in the context of succession.

APPENDIX A

Figure A1. Photo of an emergence trap installed on a decaying tree trunk in a control plot.

Emergence traps were constructed from approximately half-inch metal mesh to create structure and give a standard size. Black cotton was draped over the mesh to achieve dark conditions and allow air circulation. Staples were then used along the borders of the trap to secure the fabric to the trunk. A hole was made in the mesh and fabric on one side of the trap for a flexible plastic tube which held a translucent collecting bottle (volume 125 ml). The translucent bottle was the only source of light for the trap, thus arthropods attracted to the light such as those emerging from the wood, migrated towards the bottle and fell into a mixture of with 75% ethanol, 20% glycerol and 5% water which killed and preserved the specimens.

APPENDIX B

Supplementary Material

The supplementary material contains Table S1, a record of every species found in this study, complete with images for the majority of species. Taxa were assigned a morphospecies and identified at minimum to order level.

APPENDIX C

The GLMs (Table C1) and PERMANOVA (Table C2) identified non-significant differences in arthropod species richness and abundance across treatments and time-since tree death for the wood sample data but not for the emergence trap data. Staphylinidae beetles were the only common arthropod group to have significant GLM findings, the interaction between treatment and TSD was the most significant predictor of Staphilinidae abundance. However, simple linear models found no significant correlations for either treatment between time-since tree death and Staphilindae abundance. The NMDS ordination (Figure C1) illustrates different trajectories in arthropod composition with time-since tree death between treatments. The NMDS for emergence traps show different patterns to the NMDS ordination for wood samples.

Table C1. Non-significant results for emergence traps of generalised linear models (GLM) testing the influence of litter treatment, time since tree death (TSD), diameter at breast height (DBH) and wood density on the abundance and species richness of arthropods in decaying tree trunks in a lowland tropical forest. Data for abundance and species richness were logged before conducting the GLM.

Variables and Effects	**df**	**F or Chisq**	**P**
Arthropod abundance			
Treatment	1	1.2053	0.2876
TSD	1	0.3813	0.5451
DBH	1	0.1097	0.7446
Wood density	1	0.1413	0.7116
Treatment X TSD	1	0.0001	0.9922
Treatment X DBH	1	0.7096	0.4113
Treatment X wood density	1	0.8477	0.3701
Arthropod richness			
Treatment	1	0.0107	0.91867
TSD	1	0.0042	0.94934
DBH	1	0.1805	0.6763
Wood density	1	1.6927	0.21061
Treatment X TSD	1	0.3437	0.56541
Treatment X DBH	1	0.0723	0.79121
Treatment X wood density	1	3.2173	0.9067

Table C2. Non-significant emergence trap results of PERMANOVA (vegan::adonis2) based on Jaccard similarity testing the influence of litter treatment, time since tree death (TSD) , diameter at breast height (DBH) and wood density on the community composition of arthropods at order and species level in decaying tree trunks in a lowland tropical forest.

Variables and Effects	**df**	**F**	**P**
Order			
Treatment	1	1.4922	0.1953
TSD	1	0.7026	0.5205
DBH	1	0.7961	0.4593
Wood density	1	0.1947	0.9511
Treatment X TSD	1	0.9371	0.3996
Treatment X DBH	1	0.7184	0.5264
Treatment X Wood density	1	0.4711	0.6993
Species			
Treatment	1	0.9649	0.4075
TSD	1	0.5064	0.6586
DBH	1	1.0915	0.3397
Wood density	1	0.2991	0.8777
Treatment X TSD	1	0.3007	0.8858
Treatment X DBH	1	0.5646	0.6723
Treatment X Wood density	1	1.3475	0.2474

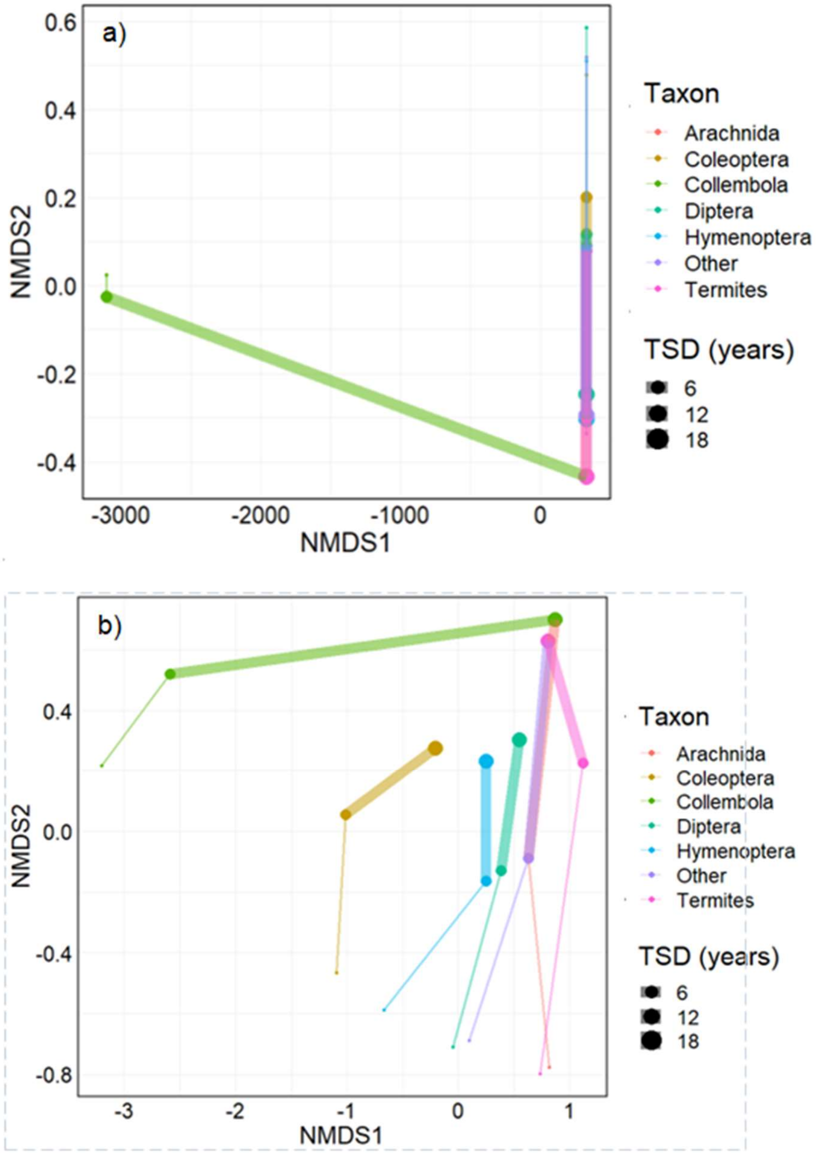

Figure C1. Non-metric multidimensional scaling (NMDS) plots of arthropod abundance by taxonomic groups for a) control plots and b) litter removal plots illustrating compositional variation in trajectories with Time-Since-Death (TSD) depending on treatment. Results for emergence traps shown.

ABBREVIATIONS

CWD – coarse woody debris

DBH – Diameter at Breast Height

GLM – generalised linear model

GLiMP – Gigante Litter Manipulation Project

NMDS - non-metric dimensional scaling

TSD – time-since tree death

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Table S1. Arthropod species found in deadwood in a lowland tropical forest, Panama. Taxa were assigned a morphospecies and at minimum identified to order level.

Order	Identification	Photos	Additional information
Blattodea	Isoptera/ Termite		Soldier is 5– 8 mm. Workers are smaller and translucent
Blattodea	Isoptera/ Termite		
Blattodea	Isoptera/ Termite		8 mm

Blattodea	Isoptera/ Termite		4 mm
Blattodea	Isoptera/ Termite (possibly Nasutitermes costalis)	 	

Blattodea	Isoptera/ Termite		
Blattodea	Isoptera/ Termite		3 mm

Blattodea	Isoptera/ Termite	
Blattodea	Isoptera/ Termite	

Blattodea	Isoptera/ Termite	
Blattodea	Isoptera/ Termite	
Blattodea	Isoptera/ Termite	
Entomobryomorpha (subclass: SPRINGTAIL/COLLEMBOLA)	Possibly isotomidae Collembola	

Entomobryomorpha (subclass: SPRINGTAIL/COLLEMBOLA)	Isotomidae Collembola		< 1mm
Hymenoptera	Psuedonponera stigma (family: ANTS/ FORMICIDAE)		Forest-dwelling ant, nests under the bark of rotting logs, forages solo in leaf litter. (Ant Wiiki, NA)
Hymenoptera	Odontomachus bauri (family: ANTS/ FORMICIDAE)		Abundant in the neotropics, has trap-jaws, forages individually, found in leaf litter, frequently forages on other ants and termites (Ehmer and Hölldobler, 1996).

Hymenoptera	Neoponera (family: ANTS/ FORMICIDAE)		Common neotropical genus (dos Santos *et al.* 2017). Generalists: as well as forage in deadwood and moss on deadwood, they will forage on fruit debri and vertebrate carcases. (Fresneau, 1985)
Hymenoptera	Crematogaster (family: ANTS/ FORMICIDAE		High diversity and abundance in tropical and subtropical regions. Found in forest, woodland and shrub. Most tropical Crematogaster nest arboreally, some nest in the ground. (Ant Wiiki, NA)
Hymenoptera	Ectatomma tuberculatum (family: ANTS/ FORMICIDAE		Preys primarily on small invertebrates, foraging at night (Wheeler, 1986)

Hymenoptera)	Myrmicinae (family: ANTS/ FORMICIDAE		
Hymenoptera)	Aphaenogasrter araneoides (family: ANTS/ FORMICIDAE		
Hymenoptera	Ponerinae (family: ANTS/ FORMICIDAE		

Hymenoptera	Ponerinae (family: ANTS/ FORMICIDAE		1 mm
Hymenoptera	Solenopsis (family: ANTS/ FORMICIDAE		<1mm
Hymenoptera	Brachmyrmex pictus (family: ANTS/ FORMICIDAE		<1mm

Hymenoptera	Tapinoma melanocephalum (ghost ant) (family: ANTS/ FORMICIDAE		1 mm
Hymenoptera	Wasmannia auropunctata (little fire-ant) (family: ANTS/ FORMICIDAE		
Hymenoptera	(family: ANTS/ FORMICIDAE		15 – 20 mm

Hymenoptera	Myrmicinae (family: ANTS/ FORMICIDAE		
Hymenoptera	(family: ANTS/ FORMICIDAE		Flying Queen Ant
Hymenoptera	Pheidole (family: ANTS/ FORMICIDAE		2 – 4 mm

Hymenoptera	Pheidole (family: ANTS/ FORMICIDAE		1-2 mm
Hymenoptera	Azteca (family: ANTS/ FORMICIDAE		
Hymenoptera	Pseudomyrmex boopis (family: ANTS/ FORMICIDAE		

Hymenoptera	Narrow waisted wasps/ APOCRITA (suborder)	No photos of wasp species A as only remains	6 mm
Hymenoptera	Narrow waisted wasps/ APOCRITA (suborder)		1mm
Hymenoptera	Narrow waisted wasps/ APOCRITA (suborder)	No photos of wasp species C as only remains	2 mm
Hymenoptera	Diapriidae (family of parasitoid wasps) Narrow waisted wasps/ APOCRITA (suborder)		

Hymenoptera	Platygastridae family Potentially Trissolcus Narrow waisted wasps/ APOCRITA (suborder)		1mm Parasitic wasp Idiobiont – lives in close association with host – attacks larvae of beetles, hemiptera
Hymenoptera	Narrow waisted wasps/ APOCRITA (suborder)		1 mm

Hymenoptera	Narrow waisted wasps/ APOCRITA (suborder)		
Hymenoptera	Narrow waisted wasps/ APOCRITA (suborder)		1 mm

Coleoptera	Pselaphinae Staphylinidae / Rove beetle family		
Coleoptera	Pselaphinae Staphylinidae / Rove beetle family		2 + species
Coleoptera	Pselaphinae Staphylinidae / Rove beetle family		1 mm
Coleoptera	Staphylinidae / Rove beetle family		15 mm

Coleoptera	Staphylinidae / Rove beetle family		2 mm
Coleoptera	Staphylinidae / Rove beetle family		7 mm
Coleoptera	Pselaphinae Staphylinidae / Rove beetle family		
Coleoptera	Staphylinidae / Rove beetle family		2 mm

Coleoptera	Staphylinidae / Rove beetle family		1.5 mm
Coleoptera	Staphylinidae / Rove beetle family		5 mm
Coleoptera	Staphylinidae / Rove beetle family		4 mm
Coleoptera	Staphylinidae / Rove beetle family		3 mm
Coleoptera	Staphylinidae / Rove beetle family		

Coleoptera	Staphylinidae / Rove beetle family		
Coleoptera	Ciidae/ minute tree-fungus beetle family) Staphylinidae / Rove beetle family		
Coleoptera	Ciidae/ minute tree-fungus beetle family) Staphylinidae / Rove beetle family		2 mm
Coleoptera	Canthon vidris Scarabaeidae / Scarab beetle family		

Coleoptera	Scolytinae/ Bark beetles (sub-family) Xyleborini most likely Curculionidae / True weevils and bark beetle family		4mm
Coleoptera	Curculionidae / True weevils and bark beetle family Scolytinae (sub-family)		4mm
Coleoptera	Curculionidae / True weevils and bark beetle family Scolytinae (sub-family)		3mm
Coleoptera	Curculionidae / True weevils and bark beetle family Platypodinae Most likely melandryidae		4 mm

Coleoptera	Curculionidae / True weevils and bark beetle family Platypodinae	 	
Coleoptera	Curculionidae / True weevils and bark beetle family Molytinae?		20 mm
Coleoptera	Carabidae/ ground beetles family		< 2mmm
Coleoptera	Carabidae/ ground beetles family		< 2mm

Coleoptera	Nitidulidae / sap beetle family	 	
Coleoptera	Nitidulidae / sap beetle family		10 – 15 mm
Coleoptera	Nitidulidae / sap beetle family		2 mm

Coleoptera	Passalidae family		
Coleoptera	Endomychidae family		10 mm
Coleoptera	Possibly a silvanid		3mm
Coleoptera	Maybe colydiinae		7 mm

Coleoptera			
Coleoptera	Possibly Phalacridae		2.5 mm
Coleoptera	Cleridae?		8 mm
Coleoptera			> 5 mm

Coleoptera			2.5 mm
Coleoptera			30 mm
Coleoptera	Possibly cerambycidae/ longhorn beetle family		15mm
Diptera			2MM

Diptera	Sciaridae/ gnat family?		3 mm
Diptera			
Diptera			

Diptera		10 mm
Diptera		3 mm

Diptera	Sciaridae/ gnat family?		< 1mm
Diptera			
Diptera			

Diptera		1 mm
Diptera		4 mm
Diptera		

Diptera	Sciaridae/ gnat family?		3 mm
Diptera	Sciaridae/ gnat family?		2mm
Diptera	Sciaridae/ gnat family?		3 mm
Diptera	Sciaridae/ gnat family?		3 mm
Diptera	Sciaridae/ gnat family?		4 mm

Diptera	Sciaridae/ gnat family?		
Diptera			5 mm
Diptera	Sciaridae/ gnat family?		2 mm

Diptera	 
Diptera	

Arachnida	Spiders/ Aranea order		5 mm
Arachnida	Spiders/ Aranea order		15 mm Pattern along abdomen
Arachnida	Spiders/ Aranea order		20 mm

Arachnida	Spiders/ Aranea order		5 mm
Arachnida	Spiders/ Aranea order		Body 20 mm legs 50 mm
Arachnida	Spiders/ Aranea order		2 mm
Arachnida	Spiders/ Aranea order		2 mm

Arachnida	Spiders/ Aranea order		3 mm
Arachnida	Harvestmen/ Opiliones (order)		Body 7mm, legs 20-25 mm Black body with two yellow lines of small dots on either side, dark brown legs
Arachnida	Harvestmen/ Opiliones (order)		
Arachnida	Harvestmen/ Opiliones (order)		

Arachnida	Harvestmen/ Opiliones (order)		
Arachnida	Harvestmen/ Opiliones (order)		
Arachnida	Acariformes/ Mites (superorder) Oribatida mite		< 1 mm
Arachnida	Acariformes/ Mites (superorder) Oribatida mite		

Arachnida	Acariformes/ Mites (superorder) Oribatida mite		1 mm
Arachnida	Acariformes/ Mites (superorder) Oribatida mite		2 mm
Arachnida	Acariformes/ Mites (superorder)		
Arachnida	Acariformes/ Mites (superorder) Trombidiformes		

Arachnida	Acariformes/ Mites (superorder) Trombidiformes		1mm body, 2mm legs
Arachnida	Psuedoscorpiones (order)		
Subphylum myriapoda	Class: Diplopoda/ millipedes Julida order		
Subphylum myriapoda	Class: Diplopoda/ millipedes Siphonophorida order?		2mm width, 20 mm length

Subphylum myriapoda	Class: Diplopoda/ millipedes Siphonophorida order			35 mm
Subphylum myriapoda	Class: Diplopoda/ millipedes Aphelidesmidae family Polydesmida order			10 mm diameter, 80 mm long
Subphylum myriapoda	Class: Diplopoda/ millipedes Trigoniulus family Spirobolida order			10 mm diameter, 95 mm length

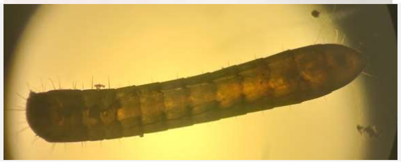
Subphylum myriapoda	Chilopoda/ centipedes class Scolopendromorpha		30 mm length, 7 mm width
Subphylum myriapoda	Chilopoda/ centipedes class Geophilomorpha	 	20 mm, 1.5 mm width

Lepidoptera	 	10 mm
Lepidoptera		10 mm
Lepidoptera		6 mm

Isopoda		10 mm
Isopoda		4 mm
Orthoptera		
Orthoptera		4mm

Orthoptera		Body 7mm, legs and antenna much longer
Orthoptera		2.5 mm
Psocoptera		

Psocoptera			
Psocoptera			
Psocoptera			4 mm
Blattodea	Blaberidae/ giant coachroach		

Gastropoda (class)			
Hemiptera			< 2mm
Larvae	Beetle larvae?		25 mm
Larvae	Rootworm beetle larvae?		

Larvae		 	
Larvae	Lepidoptera MOTH larvae?		
Larvae	Beetle larvae		
Larvae			

Larvae		
Larvae		8 mm

Larvae		4 mm
Other		4mm

Other			2mm long
Other			1mm
Other	Possibly a juvenile coachroach/ blattodea