Are tropical ant and termite assemblages along a forest recovery gradient habitat or dispersal limited?

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ABSTRACT

1. Regenerating forests comprise a significant proportion of forest ecosystems in the tropics. While we are beginning to understand assembly mechanisms of tree communities after anthropogenic disturbances, those of animal communities are still poorly understood. It has been shown that locally established ant communities clearly assemble along gradients of forest recovery with succession from active agriculture to old growth forests. However, if this is determined by dispersal limitation or habitat filtering is unclear.

2. To disentangle the two processes for ant as well as termite communities we compared community composition of dispersing and sessile life stages for both taxa based on OTUs, in a forest landscape of about 200 km^2 extend in the Chocó lowland tropical forest in Ecuador. Our chronosequence comprises a recovery gradient ranging from agricultural land to regenerating forests to old-growth forests.

3. Our results show that winged reproductives (alates) of both taxa disperse into all regeneration stages along the gradient, but communities were more similar in spatially closer plots suggesting that alates of both taxa have the potential to reach and colonize forests of all regeneration ages, but dispersal distances are smaller than the spatial extent of our study area.

4. Worker ant communities originating from sessile nests were driven by forest regeneration age and elevation, suggesting that ants can disperse into different regeneration stages, but not all species establish colonies in all regeneration stages and elevation. Termite worker communities were likewise more similar at similar elevation and less similar in spatially closer plots, which might be explained by species specific habitat preferences for certain elevations and by biotic interactions such as local competition for resources as termite workers were mainly found in dead wood.

5. These results suggest, that both taxa are only dispersal limited on the larger landscape scale, and while ant communities are more affected by the habitat filtering (abiotic and biotic conditions) of the forest structure along the chronosequence, termite communities seem to be more affected by intraspecific competition.

1. INTRODUCTION

Understanding species assembly rules in recovering forests is of particular importance as they cover large areas globally (Global Forest Resources Assessment 2020) and offer the potential to mitigate the effects of species loss during ongoing deforestation (Chazdon, 2009). However, unravelling the fundamental mechanisms that govern community assembly remains a central challenge in contemporary ecological theory (Vellend, 2010). Among the various proposed concepts, two key mechanisms are dispersal limitation and habitat filtering (Belyea & Lancaster, 1999). The dispersal limitation paradigm emphasizes the importance of dispersal between patches. Following this paradigm, differing species compositions in a landscape are explained by the species inability to reach suitable habitats due to limited dispersal mechanisms (Leibold et al., 2004). In contrast, the habitat filtering paradigm emphasizes the role of habitat heterogeneity caused by environmental gradients in structuring communities, where environmental conditions determine if species can establish and persist in a local patch (Kraft et al., 2015). It assumes a moderate dispersal rate which allows species to reach suitable patches but stresses the importance of niche separation caused by local biotic interactions and abiotic conditions (Leibold et al, 2004). The terms “environmental conditions” and “environmental filtering” often refer to abiotic factors such as temperature and humidity, hence in the following we use the term “habitat filter” to emphasize that besides abiotic conditions also biotic interactions such as mutualism or competition can have an influence on community assembly. While the two paradigms are not mutually exclusive (Livingston et al., 2013), their relative importance in structuring ecological communities continues to be debated and both mechanisms could potentially produce and explain the same observed pattern of local species distributions. By comparing dispersing stages with established communities the importance of the two factors in shaping local community structure can be disentangled.

Many (but not all) social insect species have two distinct life stages. In the first life stage winged reproductives (so-called alates) of many species leave their colony for nuptial flights to disperse into the surrounding for mating and the subsequent establishment of a new colony (Hartke & Baer, 2011; Hakala et al., 2019). Consequently, this mobile stage provides the opportunity to study dispersal abilities and possible dispersal limitations. In the second life stage following colony founding, social insects live in (quasi-)sessile colonies consisting of reproductive dealate queens (and males for some species) and a non-reproductive worker caste (and soldiers for some species). Workers of these colonies forage in the surroundings and exploit the available resources. As established colonies of many species usually do not move extensively, the distribution of colonies in a landscape provides information about the species' performance in different environmental conditions, but not of the species' ability to reach other potential habitats for the founding of new colonies. Hence this life stage is suitable to study the impact of habitat filters on social insect communities.

In this study, we aim to disentangle the effects of dispersal limitation and habitat filtering for the assembly of ant and termite communities in a tropical forest recovery gradient along a chronosequence ranging from agricultural land, regenerating forest of different ages and old-growth rainforest. This gradient represents an environmental gradient with differing biotic and abiotic conditions. As our study is situated in the Chocó-Darien Global Ecoregion (CGE), which is among the top 25 biodiversity hotspots for conservation worldwide (Myers et al., 2000), our study area provides a crucial context for evaluating the ecological consequences of land-use transformation (Escobar et al., 2015).

Former investigations in our study area have shown that community composition of ant workers emanating from sessile nests differs between agricultural land, regenerating forest and old-growth forest (Hoenle et al., 2022; Hoenle et al., 2023). Forest regeneration time, elevation and land-use legacy have been identified as drivers for species composition (Hoenle et al., 2022; Hoenle et al., 2023). Based on these outcomes environmental conditions appear to be central in shaping the distribution of ants in this region strengthening the habitat filtering paradigm as pivotal mechanism in explaining ant assemblages. But as described before, ant colonies do not disperse after colony founding and the study of sessile nests cannot indicate potential dispersal effects.

Here, we investigate the community composition of ant and termite communities to test whether a potential dispersal limitation before colony founding already influences species distribution of social insects by comparing the communities of dispersing alates with the communities of workers deriving from sessile nests. We sampled worker ants with an extended sampling protocol in comparison to former studies and explored termite worker, and alate communities of both taxa for the first time in our study area. In addition to forest regeneration time, we control for elevation and space as factors potentially influencing community composition. As plots of different land use type, forest regeneration age and old-growth forests form a small scale mosaic in our study area (Escobar et al. 2025), dispersing alates should be able to reach different habitat types at short distances.

We analyse ant and termite community composition of both life stages separately via multiple regression models of Jaccard dissimilarity. In case ant and termite communities are dispersal limited along the recovery gradient we expect to find a high dissimilarity of dispersing alate community composition depending forest age. Additionally, if habitat filtering is an important mechanism in shaping ant and termite communities we expect to find high dissimilarities in worker communities depending on forest regeneration age and the entailing environmental gradient. This would imply that habitat characteristics determine the success of colonies to establish and persist, depending on the species performance in different habitat conditions. As these mechanisms are not mutually exclusive, a synthesis of both is also possible, where alate communities are dispersal limited and worker communities are driven by habitat filtering.

2. METHODS

2.1 Study sites and plot design

Our study area is located in the tropical lowland Chocó rainforest in north west Ecuador (province Esmeraldas) in the two reserves Reserva Río Canandé and Reserva Tesoro Escondido. 62 plots were selected in the framework of the REASSEMBLY research unit (www.reassembly.de). Plots are located across a 200-km^2 area and comprise each 50 x 50 m in forest plots (old-growth forest and regenerating forests) and 16 x 16 m in agricultural plots. The landscape in our study area is characterized by a small scale mosaic of heterogeneous environment encompassing old-growth forests, regenerating forests of various successional stages, human settlements and agricultural land with short distances among these land-use types. The distance of each plot to the nearest old-growth plot for example averages 59 m (SD

± 46) and 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). Our study sites consisted of a recovery gradient ranging from agriculture (pastures and cacao plantations) to regenerating forests (former pastures and cacao plantations) to old-growth forests. Time since abandonment (= age) of regenerating forests ranged from 1 to 37 years and plot elevations from 128 – 615 m. Further details on the study sites and the plot design of the Reassembly plots are described by Escobar et al. (2025) and climatic conditions along the recovery gradient by Newell et al. (2025). Some plots of our study are not in the final plot selection of the REASSEMBLY project because plot selection was finalized in 2022 (see details below).

2.2 Sampling

Our data consists of two data sets. The first data set comprises dispersing ant and termite alates that were collected during nuptial flights. The second data set comprises workers of both taxa, where specimens were collected directly from their nests or during foraging. All specimens of the latter data set belonged to sessile colonies and did not disperse for reproduction.

The first data set of dispersing ant and termite alates is a subset of data on flying insects which was published by Müller et al. (2023). The collection of all flying insects using light traps was conducted on 44 plots in October and November 2021. These plots comprise 10 agricultural plots (5 pastures, 5 cacao plantations), 13 regenerating pastures with regeneration times ranging from 4 to 34 years, 10 regenerating cacao plantations with regeneration times ranging from 4 to 25 years, and 11 old-growth forests. From 44 plots 38 were in the final Reassembly plot selection whereas 6 plots were sampled additionally. Although ants and termites are usually not the target taxa of light traps, studies have demonstrated that light traps are suitable for capturing flying ant and termite alates (Basset et al., 2020), hence we extracted the data of ants and termite alates for our analysis. The trapping methods and the metabarcoding approach for species identification are described in Müller et al. (2023). In short, an autonomous light trap was used for one night per plot for 8 hours avoiding full moon phase. It was installed at 2 m height in cleared vegetation free surrounding. To attract insects after dusk a LED light was used, which is optimized for insect sampling (LepiLED Mini Switch 0.65, UV-mode switched off, Brehm, Jena, Germany). The trap included a plexiglas roof and a funnel leading insects into chloroform. After collection, all insects were dry stored in a freezer and filtered by size. Laboratory and bioinformatic pipelines for species identification were followed as described in Hausmann (2020) to sequence the CO1-5P (mitochondrial cytochrome oxidase 1) gene of the collected insect bulk samples. This pipeline resulted in a list of taxa occurring on each plot. We did not assign species names to the taxa as many BINs (Barcode Index Numbers) were not clearly assigned to a species name in the BOLD database. We rather refer to the taxa of this data set and of the worker data set as OTUs (operational taxonomic units) to keep it consistent within our study.

Foraging and nest-dwelling workers were collected in three sampling seasons in 2022 and 2023. In the first season in February to April 2022 we sampled all 62 Reassembly plots and two additional plots (one regenerating pasture and one cacao plantation). The 64 plots comprise 12 agricultural plots (6 pastures, 6 cacao plantations), 17 regenerating pastures, 18 regenerating cacao plantations and 17 old-growth forests. Regeneration times of former pastures and cacao plantations range both from 1 to 37 years. We collected ants and termites with the use of Winkler traps, by hand sampling of foraging ants and termites on the ground and from tree trunks upon breast height and as described by Hoenle et al. (2022). In doing so we captured ant and termite communities of different strata including leaf litter dwelling (Winkler traps), epigeal (ground transects) and parts of tree dwelling (tree trunks) communities. In addition to the three methods used by Hoenle et al. (2022) we used methods to capture dead wood dwelling ants and termites. In the first field season, we opened five naturally occurring dead wood pieces per plot (mean per plot: 3.16 ± 1.24, n = 193, 61 plots) that were in contact with the ground (logs and stumps) and collected nesting ants and termites by opening the dead wood. In the second sampling season in August to October 2022 we used an additional baiting approach on the 62 Reassembly plots where we collected wood-dwelling ants and termites with dead wood baits from five different tree species. We placed one wood piece per plot from the tree species *Trema micrantha* (Sapanillo), *Theobroma cacao* (Cacao), *Inga sp*. (Guaba), *Triplaris cumingiana* (Fernán Sánchez) and *Hieronyma chocoensis* (Mascarey) each. Wood pieces had a diameter ranging from 7-10 cm and a length of 50 cm. In a third field season after 6 months (February-March 2023) we retrieved the five wood pieces from each plot and placed them in emergence chambers. These emergence chambers consisted of mesh tubes made of white fabric used for insect nets

(1mm double-thread netting, bioform.de; Model A110e) and a 50 ml sampling tube filled with ethanol attached at the bottom. Insects emerging from the wood pieces and falling into the ethanol were collected for the following six months (February-August).

Sampled worker ants and termites were identified with a combination of a morphological analyses and a DNA barcoding approach. First, we identified samples to genus level if possible using taxonomic literature (Bolton, 1994; Constantino, 2002) and subsequently separated them into morphospecies. For every sampling method from every plot we prepared one specimen of each morphospecies for the barcoding of the CO1-5P gene by cutting off one leg of ants and the heads of termites. The dissected tissues were sent to the Canadian Centre for DNA Barcoding (University of Guelph, Canada) for DNA isolation and sequencing. DNA sequences were uploaded to the BOLD (Barcode of Life Data System) database. BOLD creates BIN clusters of sequences that have been shown to be in high concordance with species and can be used for species identification (Ratnasingham & Hebert, 2013). Based on these BINs, phylogenetic trees and additional morphological analyses based on taxonomic literature (as cited in Hoenle et al., 2022) we made our final species identifications. These resulted in a list of taxa for each plot.

2.3 Statistical analyses

We performed statistical analyses separately for both taxa and both data sets using R version 4.4.1 (R core team, 2024). Considering diversity analyses, it is often criticized that species richness does not consider abundance and sampling effort (Gotelli & Colwell, 2001). For our data a standardization considering sampling effort was not possible due to the difficulties of estimating social insect abundance (as discussed by Basset et al., 2015), especially when using a metabarcoding approach where specimens are homogenized after collection. Hence, we used incidence data for the first Hill number q0 (Hill, 1973), which is the number of observed species to quantify OTU diversity. We calculated the number of observed OTUs, using the ‘specnumber’ function from the *vegan* package (Oksanen et al., 2022).

For exploring the relation of the number of observed OTUs with forest age and elevation, we performed generalized linear models (GLM) choosing a negative binomial distribution with the ’glm.nb` function of the MASS package (Ripley et al., 2002). We checked the distribution of residuals using the DHARMa package (Hartig, 2024). For this and the following analyses, we set the age of old-growth forests to 55 years to enable inclusion of old growth forest data as predictions have shown that tree species richness recovers to 90% in comparison to old growth already after 55 years (Escobar et al., 2025).

For the identification of the factors influencing community composition between plots we used a multiple regression model (MRM) using the ‘MRM’ function of the *ecodist* package. We made one model for each taxon and caste combination (ant alates, ant workers, termite alates, termite workers) resulting in four multiple regression models. As input we computed a distance matrix of the Jaccard dissimilarity index with the ‘vegdist’ function of the *vegan* package based on the OTU incidence data on the plots as well as Euclidian distance matrices between plots for regeneration age, elevation, and space (coordinates of longitude and latitude) with the ‘dist’ function. Afterwards, all matrices were standardized using the ‘decostand’ function. The predictors of these models can indicate towards the presence of dispersal limitation and habitat filtering. When community composition of alates differs depending on regeneration age, elevation and/or space we expect a dispersal limitation between plots caused by parameters associated with regeneration age, elevation and/or space (plot location). If none of these community composition does not differ depending on these predictors, then we expect that alates are not dispersal limited among plots. The same applies to the habitat filtering mechanism for the worker models. When community composition of workers differs depending on regeneration age, elevation and/or space we expect a habitat filtering for certain OTUs induced by parameters associated with regeneration age, elevation and/or space, while no effect would suggest there is no strong habitat filter resulting in similar communities between plots. In addition to these models, we used NMDS (Non-metric multidimensional scaling) for the visualization of OTU composition along the recovery gradient with the ‘metaMDS’ function of the *vegan* package by grouping all plots into four categories representing the different land-uses with differing habitat conditions in our study area (agricultural land, early regenerating forests (1-20 years), late regenerating forests (21-37 years) and old growth forest).

3. RESULTS

3.1 General results and diversity

Using the light trap approach for capturing alates, we successfully identified 188 ant OTUs and 17 termite OTUs Alate diversity of both taxa was not influenced by forest age or elevation (Figure 1a,b; Table 2). In comparison, we identified 300 ant OTUs and 29 termite OTUs from the worker caste (Table 2). The diversity of worker ants and termites increased along the recovery gradient and was predicted by forest age. (Figure 1c,d; Table 2). Worker ants were found in all strata (leaf litter, forest floor, tree trunks, dead wood), and common genera such as *Pheidole*, *Wasmannia*, *Crematogaster* and *Solenopsis* were found in more than 50 of the 64 sampled plot (Appendix Fig. A1). In contrast, termite workers were observed infrequently on the forest floor and tree trunks, with only three occurrences documented in each of these environments. The majority of termite worker specimens were collected from large pieces of naturally occurring dead wood or in experimental wood baits. The most frequently observed termite genera by plot were *Cylindrotermes* and *Nasutitermes* (Appendix Fig. A2), while other genera were found in less than 18% of plots.

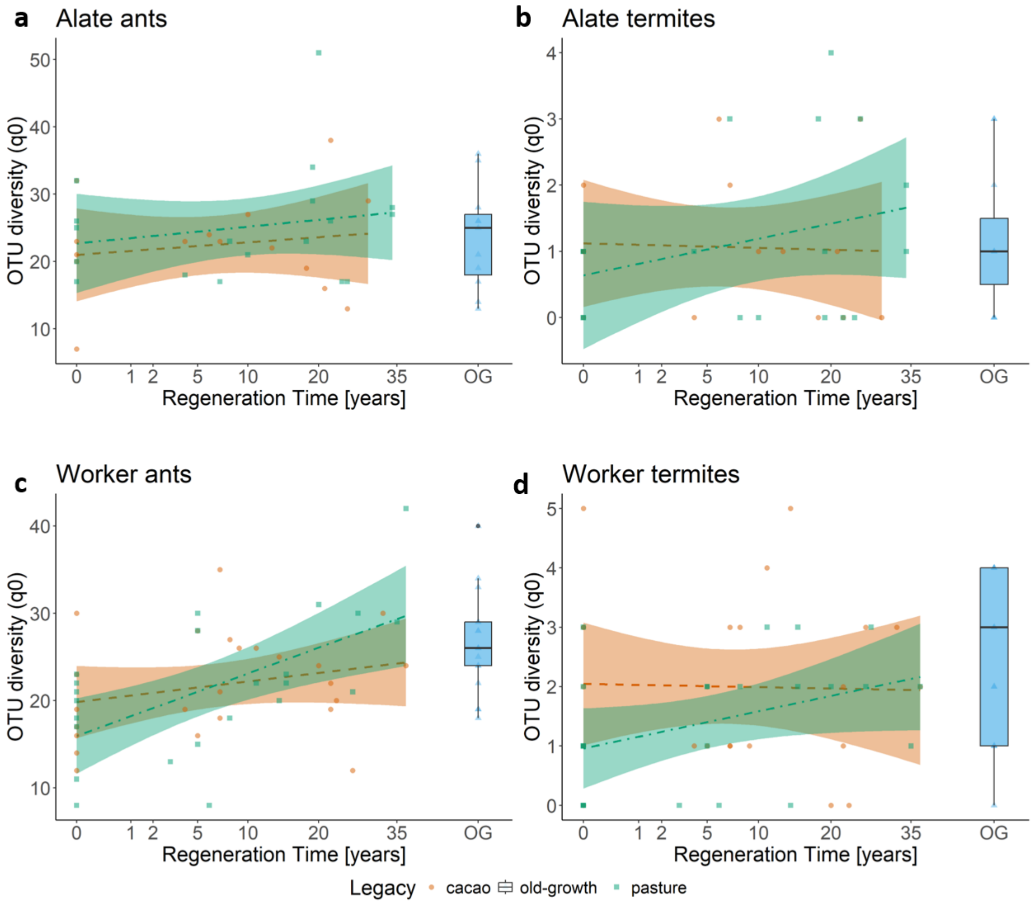

Figure 1: Recovery trajectories of ant (a,c) and termite (b,d) diversity (number of observed OTUs q0) along a tropical forest recovery gradient. Workers (c,d) originate from manual sampling of nest-dwelling or foraging specimen while alates (a, b) were captured during nuptial flights using light traps. Land-use legacy of active and former pastures and cacao plantations are highlighted by colour and shape. Their trajectories are predicted by a linear model with 95% confidence interval. Old-growth forest (OG) is plotted without forest age for comparison with the regenerating plots.

Table 1 Generalized linear models (GLM) of alate and worker ant and termite diversity (number of observed species q0) with forest age and elevation as predictors. Significant p-values are highlighted in bold.

	Estimate	**95 % CI**	**p-value**
Alate ants			
Intercept	3.03	0.14	**$<2e^{-15}$**
Age	0.0002	0.002	0.93
Elevation	0.0004	0.0004	0.3
Worker ants			
Intercept	2.98	0.11	**$<2e^{-16}$**
Age	0.006	0.002	**$7e^{-5}$**
Elevation	$8e^{-6}$	0.0003	0.98
Alate termites			
Intercept	0.29	0.42	0.49
Age	0.006	0.008	0.46
Elevation	-0.0009	0.001	0.49
Worker termites			
Intercept	0.68	0.3	**0.02**
Age	0.009	0.004	**0.03**
Elevation	-0.0007	0.0008	0.38

3.2 Community composition

While the diversity can only give information about the number of OTUs in the plots, community composition considers the identities of observed taxa. Our results from the analysis of alate community composition of both taxa showed a strong overlap between agricultural land, regenerating forests and old-growth forests (Figure 2a,b) and the multiple regression models likewise showed that community composition (Jaccard dissimilarity index) is independent of forest regeneration age or elevation (Table 2). However, alate communities of both taxa were driven by space where communities were more similar in spatially closer plots (Table 2).

Ant worker communities were best predicted by forest age and elevation with more similar communities on plots with similar regeneration ages and similar elevations (Figure 2c, Table 2). Termite worker community composition was not influenced by forest age but by space and elevation with communities being more similar on similar elevation and more dissimilar when plots were spatially closer (Figure 2d, Table 2).

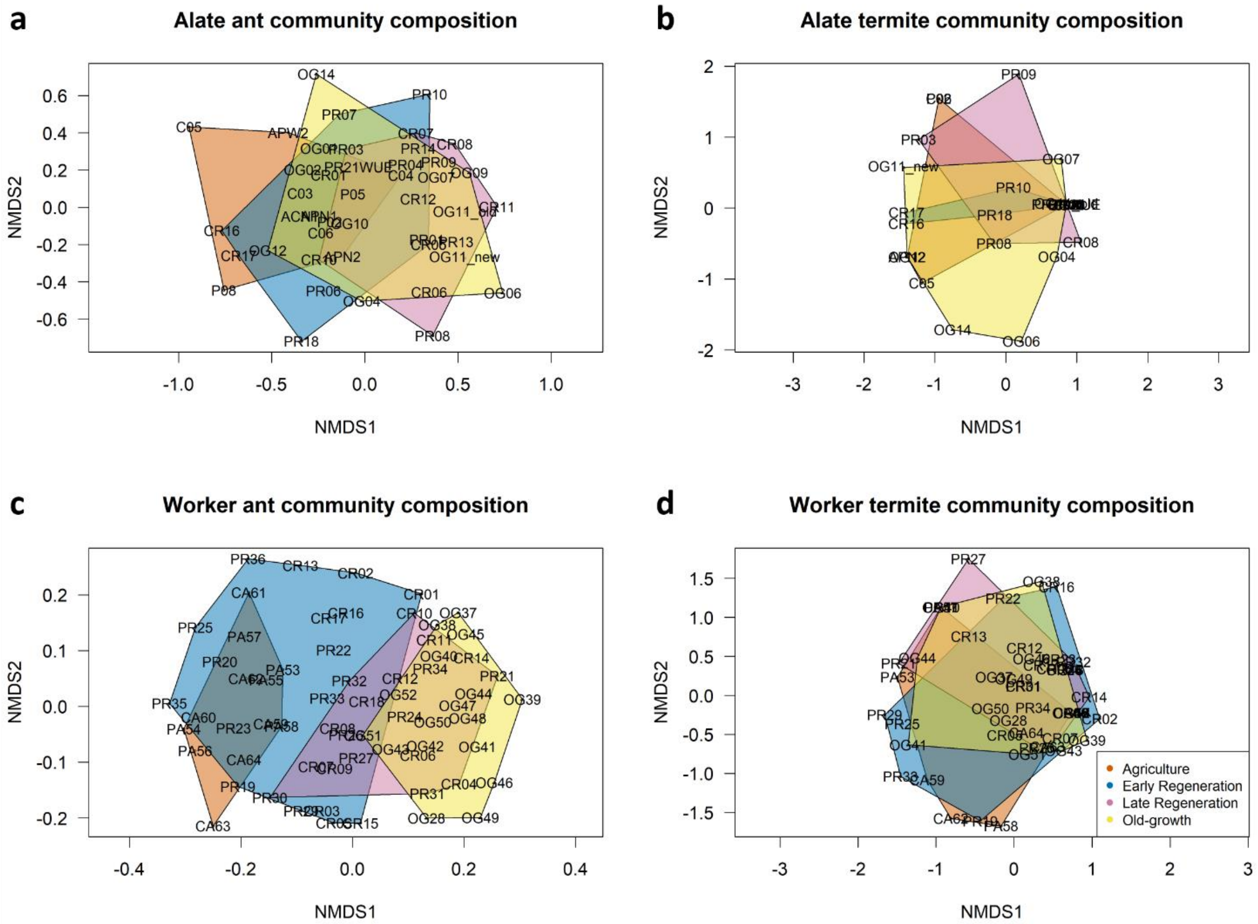

Figure 2: Non-metric multidimensional scaling (NMDS) of alate (a,b) and worker (c,d) community composition of ants (a,c) and termites (b,d) in agricultural land, early regenerating forests (1-20 years), late regenerating forests (21-37 years) and old-growth forests.

Table 2: Multiple regression model of alate and worker community composition (Jaccard dissimilarity index) of ants and termites with Jaccard dissimilarity, forest age, elevation and space (longitude and latitude) as input dissimilarity matrices. Significant p-values are highlighted in bold.

	Estimate	**p-value**
Ant alates		
Intercept	0.14	**0.001**
Age	0.03	0.14
Elevation	-0.03	0.18
Space	0.25	**0.001**
Ant workers		
Intercept	0.1	**0.001**
Age	0.14	**0.001**
Elevation	0.07	**0.001**
Space	0.002	0.82
Termite alates		
Intercept	0.09	0.9
Age	0.01	0.8
Elevation	-0.03	0.48
Space	0.15	**0.005**
Termite workers		
Intercept	0.11	0.36
Age	0.02	0.45
Elevation	0.12	**0.003**
Space	-0.06	**0.03**

4. DISCUSSION

Ant and termite alates

The results of our community composition analysis of alates and workers deliver insights into the species assembly of ants and termites in regenerating forests. We found evidence that alates of both taxa are dispersal limited at landscape scale with more similar communities in spatially closer plots. However, alate communities were not influenced by forest regeneration age and thus habitat type of the plots. The observed results may be attributable to limited dispersal ranges for many ant and termite species, which potentially do not extend to the full spatial scale of our study area. Studies on flight ecology of these social insects are scarce and dispersal distances are only known for a selected number of species. Ants have been shown to have a broad range of dispersal distances (see overview in Helms, 2018). For example, for *Pheidole minutula* a maximum dispersal distance of 30 m has been estimated (Bruna et al., 2011), for *Azteca* species up to 400 m (Bruna et al. 2011), *Atta sexdens* is estimated to disperse up to 11 km (Jutsum & Quinlan, 1978), and *Solenopsis invicta* between 5.4 km and 32 km depending on the study (Helms, 2018). For termites, that are typically regarded as poor fliers, there has been remarkably little research on flight distances and most studies focused on pest species. The globally significant pest species *Coptotermes formosanus*, for example, has been shown to disperse mainly in a 250 m radius from the nest with some individuals dispersing as far as 1.3 km (Mullins et al., 2015), while another pest species, *Odontotermes formosanus*, has been shown to fly on average 146 m from its nest (Hu et al., 2010). Although our study area spans over 200 km^2, distances between plots are comparatively short. The Reassembly plots of different habitat type (pastures, cacao plantations, regenerating pastures and cacao plantations of different regeneration age, and old-growth forest) are evenly distributed across the landscape and distances between plots of the same type range from 184 m minimum to 14 km (average between 4.6 km and 5.5 km), while the minimum distance between plots of different type was 250 m (Escobar et al., 2025). Due to this small scale landscape heterogeneity ants and termites are likely able to disperse into plots of all regeneration ages where they could potentially found new colonies, but are dispersal limited on the larger scale with communities being spatially more similar as most species are likely not dispersing the whole study area.

Ant workers

The results of the ant worker diversity analysis support previous findings where ant richness or diversity increase with forest regeneration age (Bihn et al., 2008; Rocha-Ortega et al, 2018; Karolak & Fiedler, 2024). In contrast to ant alates, regeneration age and elevation have been identified as factors influencing community composition with more similar OTUs in similar regeneration ages and elevation. Although our elevation gradient only comprises 487 m, effects of elevation that are probably correlated with environmental conditions already affected community composition. This has been shown for ants globally (Smith, 2015; Szewczyk et al., 2016) but also in tropical and subtropical elevational gradients (Staab et al., 2014; Hethcoat et al., 2019; Leahy et al., 2024) and in our study area (Hönle et al., 2022). Shifts in ant community composition with recovery time have also been extensively documented across multiple studies elsewhere (Dunn, 2004; Bihn et al., 2008; Neves et al., 2010; Schmidt et al., 2013; Staab et al., 2014; Gomes et al., 2014; Hethcoat et al., 2019) and in the study region; (Hoenle et al., 2022). Different regeneration ages represent different environments as environmental parameters change over time with succession. Two important abiotic parameters are temperature and humidity, which are linked to canopy openness. Logging and habitat conversion can alter the canopy openness resulting in hotter and drier below-canopy microclimate in comparison to forests. The maximum temperature in our study area has been shown to be 6.2° C lower in old-growth forests than in agriculture (Newell et al., 2025). For ants, canopy openness has been identified as a key driver of community dynamics in disturbed habitats (Andersen, 2019). In Borneo for example, Boyle et al. (2021) have shown that ants with higher thermal tolerance were more abundant in more disturbed and warmer habitats. Klimes et al. (2012) additionally identified tree density, tree size and taxonomic diversity of trees as parameters explaining differences in ant communities during succession. As tree species richness and many structural variables such as light availability, maximum tree height, number of stems, vertical vegetation heterogeneity, aboveground biomass, diversity of coarse woody debris, and availability of fine woody debris have been shown to change with forest regeneration age in our study area (Falconí-López et al., 2024, Escobar et al., 2025), we argue that habitat filters associated with regeneration age might explain the observed distribution of ant workers. A previous analysis of recovery mechanisms of our worker ant data set has shown that after perturbation ant recovery is driven by resistance of the species community rather than resilience (Metz et al., under review.). This suggests that community composition along the recovery gradient is rather driven by the persistence of ants remaining on or close to disturbed or previously disturbed land rather than by recolonization of arriving alates. While we demonstrated that ant alates disperse into all forest regeneration ages, it remains uncertain whether the observed pattern of ant workers results from alates choosing or rejecting certain habitats for colony founding by the mated queens, or from failure of the establishment of colonies that subsequently cannot persist in these environments. Additional research examining nesting site selection and post-establishment colony success rates would be valuable for further understanding the mechanisms of ant community reassembly.

Termite workers

Although termites are considered to be sensitive to land-use changes in the Neotropics (Ackerman et al., 2009; Luke et al., 2014, de Paula et al., 2016; Duran-Bautista et al., 2020; Duran-Bautista et al., 2024; Castro et al., 2021), only the diversity but not the community composition of termite workers was influenced by forest age in our study. Though, community composition was influenced by space and elevation, which might be explained by our sampling method. Our approach of sampling leaf litter, forest floor and tree trunks as different microhabitats has been shown to detect differing vertically stratified ant communities (Hoenle et al., 2023). In our study, however, termite workers were mostly found in the additionally sampled naturally occurring dead wood or in dead wood baits. As naturally occurring dead wood is equally distributed in volume across the recovery gradient (Falconí-López et al, 2024), we assume that there are no confounding effects of dead wood amount across the regeneration gradient influencing community composition. As dead wood inhabiting insects might be protected from disturbance associated conditions such as increased heat exposure, termite communities in dead wood might not be influenced by environmental filters associated with regeneration age. However, termite communities were more dissimilar in spatially close plots, which might be caused by competition for dead wood as food or nesting resource. In general termites have a specialized dietary niche comprising predominantly of dead plant material at various stages of decomposition (Donovan et al., 2001). With 6 from 11 collected genera, most of our collected termites belonged to wood-feeding guilds, compared to four soil-feeding genera and one litter-feeding genus based on the trophic classifications by Donovan et al. (2001). Competition for food or resources is expressed in agonistic behavior, which is a common behavior in termites (Prestwich, 1984; Thorne & Haverty, 1991; Shelton & Grace, 1996; Šobotník et al., 2010). Especially termites from the frequently observed genus *Nasutitermes* have been shown to exhibit intra- and interspecific agonistic behavior by defending foraging areas in natural inter-colony encounters (Levings & Adams, 1984), in field manipulation induced intraspecific encounters or in laboratory experiments (Thorne, 1982; Leponce et al., 1996). Another study of the termite *Anoplotermes banksi* has shown to that nest distribution is driven by intraspecific behavior resulting in overdispersion of nests of the same species (Bourguignon et al., 2011). In addition to the effect of space we also found an effect of elevation on community composition which has also frequently observed to influence termite communities (Gathorne-Hardy et al., 2001; Palin et al., 2011; Nunes et al., 2017) probably driven by elevation associated environmental filters similar as described for ants. Hence, we conclude that our sampled worker termite communities were not influenced by environmental filters associated with regeneration age, but competition and environmental filters associated with elevation shaped the community composition.

Outlook and conservation implications

By analyzing community composition of dispersing alates and workers from sessile nests of ants and termites, we successfully disentangled assembly mechanisms and explored the relevance of dispersal and environmental filters along a recovery gradient of a lowland tropical rainforest. In comparison to other animal groups, social insects show a distinct morphology for their dispersing caste characterized by winged reproductives that are easily recognizable. Hence we propose that these organisms represent a promising model system to further understand assembly mechanisms in future studies. However, the present study encompasses some limitations that need to be considered when evaluating the results of such approaches. For instance, we assume that our data sets of flying alates and workers did not capture the same species communities. As our methods for capturing flying alates and workers differ, we assume that both sampling schemes have different constrains of capturing different vertical forest strata. While light traps might attract species nesting in many strata such as soil, leaf litter, dead wood and tree canopy; our sampling methods for workers did not cover canopy dwelling species. Hence, especially the results for termite workers are influenced by the sampling method. Additionally, some open questions and limitations remain that need to be addressed in future studies. We also expect other spatial scales or landscape configurations with larger and more homogeneous or more isolated forest patches to produce other results and suggest that our observed community compositions along the recovery gradient might be influenced by the landscape configuration of our study area where plots of different recovery ages are close and thus easier to reach. Given the increasing importance of secondary forests (Chazdon et al., 2009; Chazdon & Guariguata, 2016) for mitigating the loss of old-growth forests and the complexity of recovery processes (Poorter et al., 2021), our approach provides an initial insight into the assembly processes of tropical ant and termite communities, which is crucial for developing evidence-based management and conservation strategies.

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Author contributions

HF, NG, JM and DAD conceived the ideas and designed methodology; NG, AF-L, HF, JM, AB, PK, MP, DR, and SS collected the data; NG analysed the data; NG led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability Statement

Annotated R code, including the data needed to reproduce the statistical analyses and figures, is publicly available from figshare: ttps://doi.org/10.6084/m9.figshare.28650614.v1

Appendix

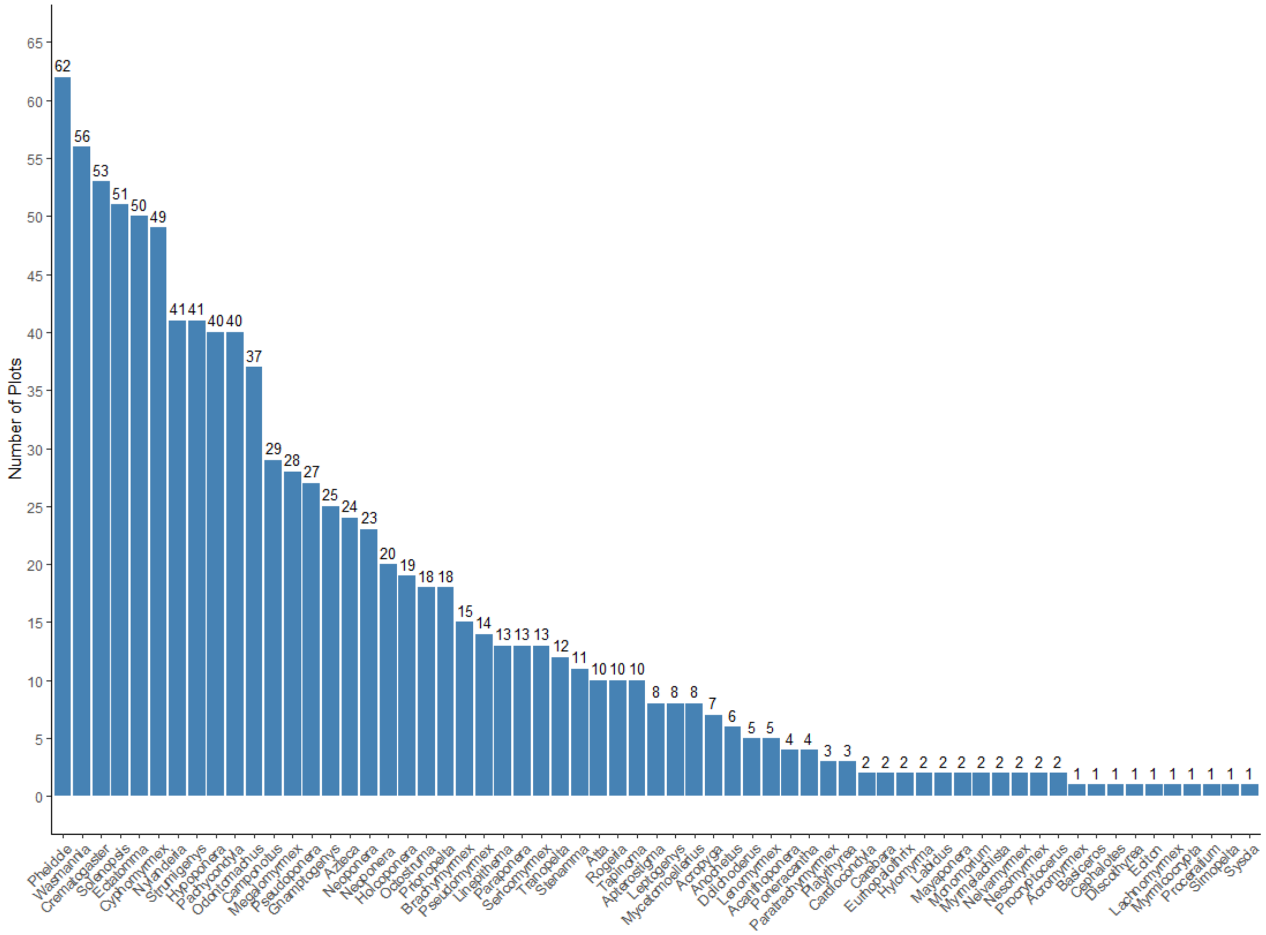

Figure A1: Number of sampling plots where each ant genus was detected. Only data from the collection of workers are included. The values above each bar represent the total count of plots where specimens from each genus were collected.

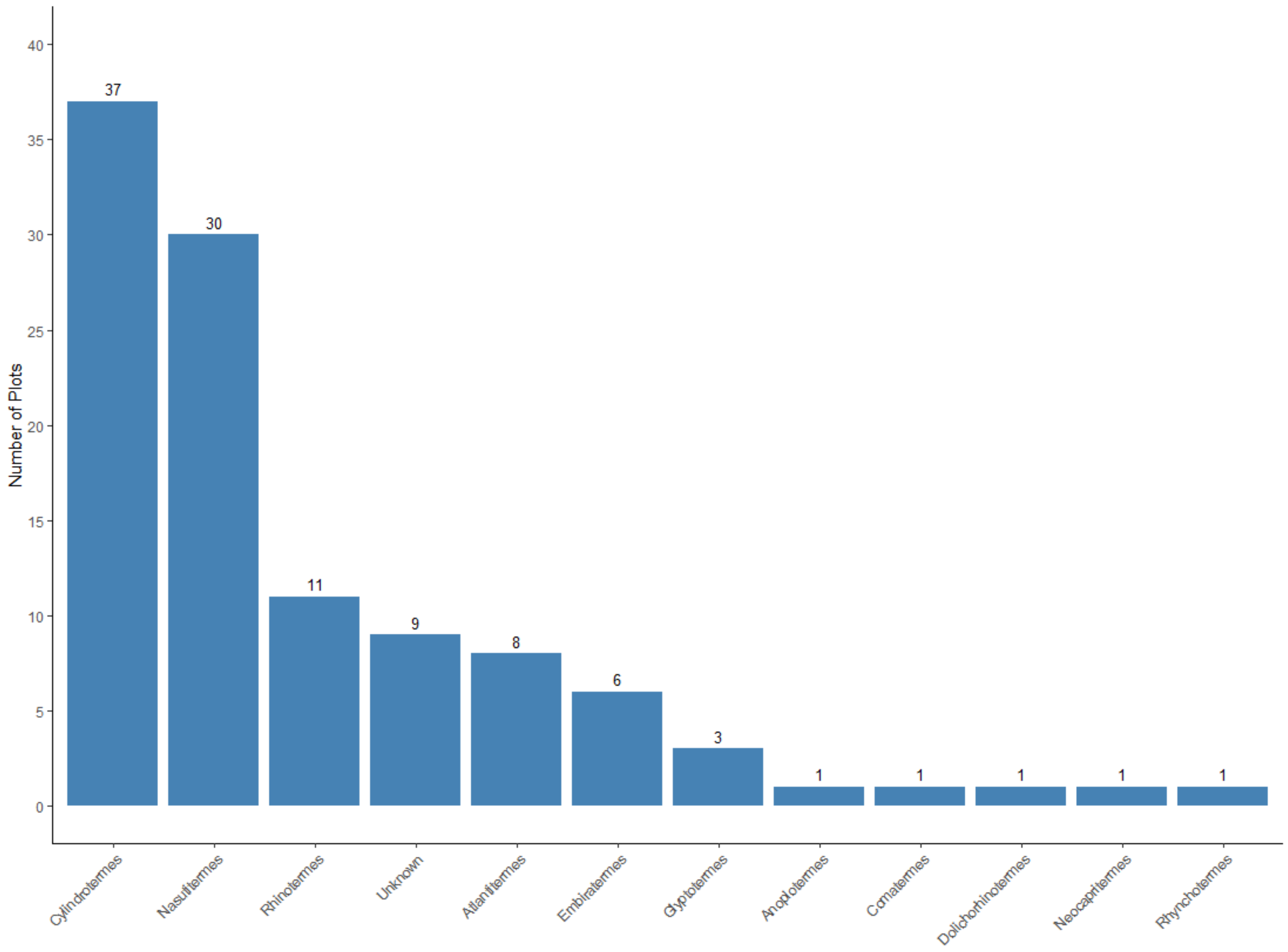

Figure A2: Number of sampling plots where each termite genus was detected. Only data from the collection of workers are included. The values above each bar represent the total count of plots where specimens from each genus were collected.