

## RESEARCH ARTICLE

# Stratification and recovery time jointly shape ant functional reassembly in a neotropical forest

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**Handling Editor:** Tom Bishop**Abstract**

1. Microhabitat differentiation of species communities such as vertical stratification in tropical forests contributes to species coexistence and thus biodiversity. However, little is known about how the extent of stratification changes during forest recovery and influences community reassembly. Environmental filtering determines community reassembly in time (succession) and in space (stratification), hence functional and phylogenetic composition of species communities are highly dynamic. It is poorly understood if and how these two concurrent filters—forest recovery and stratification—interact.
2. In a tropical forest chronosequence in Ecuador spanning 34 years of natural recovery, we investigated the recovery trajectory of ant communities in three overlapping strata (ground, leaf litter, lower tree trunk) by quantifying 13 traits, as well as the functional and phylogenetic diversity of the ants. We expected that functional and phylogenetic diversity would increase with recovery time and that each ant community within each stratum would show a distinct functional reassembly. We predicted that traits related to ant diet would show divergent trajectories reflecting an increase in niche differentiation with recovery time. On the other hand, traits related to the abiotic environment were predicted to show convergent trajectories due to a more similar microclimate across strata with increasing recovery age.
3. Most of the functional traits and the phylogenetic diversity of the ants were clearly stratified, confirming previous findings. However, neither functional nor phylogenetic diversity increased with recovery time. Community-weighted trait means had complex relationships to recovery time and the majority were shaped by a statistical interaction between recovery time and stratum, confirming our expectations. However, most trait trajectories converged among strata with increasing recovery time regardless of whether they were related to ant diet or environmental conditions.
4. We confirm the hypothesized interaction among environmental filters during the functional reassembly in tropical forests. Communities in individual strata

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respond differently to recovery, and possible filter mechanisms likely arise from both abiotic (e.g. microclimate) and biotic (e.g. diet) conditions. Since vertical stratification is prevalent across animal and plant taxa, our results highlight the importance of stratum-specific analysis in dynamic ecosystems and may generalize beyond ants.

#### KEYWORDS

Chocó, chronosequence, community weighted means, Ecuador, environmental filters, forest regeneration, functional traits, phylogeny

## 1 | INTRODUCTION

Local species communities often represent a nonrandom subset of the regional species pool, and a plethora of ecological theories aim to describe the underlying assembly rules (e.g. Connor & Simberloff, 1979; Diamond, 1975; Hubbell, 2011; Keddy, 1992; MacArthur & Levins, 1967). A central concept in community assembly is the environmental filter hypothesis, which implies that the environment acts as a metaphorical 'filter' that selects potential species from the regional pool based on specific attributes of the species known as traits (Keddy, 1992). Traits mediate the interaction between species and their environment, and thus connect communities to their functional role in ecosystems (de Bello et al., 2021). As more closely related species are often more phenotypically similar, environmental filters are also reflected in the phylogenetic composition of a community (Kraft et al., 2007). Although environmental filtering is traditionally framed to relate to abiotic factors only (Kraft et al., 2015), we use it here in the broadest sense as any factor that can possibly select from the available species pool, such as predation or competition (Cadotte & Tucker, 2017).

A large fraction of tropical landscapes are now comprised of disturbed forests, often former agricultural areas, which are in recovery towards an old-growth forest state (Chazdon et al., 2009; Crouzeilles et al., 2016; Meli et al., 2017). A prominent application of the environmental filter concept is the reassembly of these communities (Davies et al., 2020; Edwards et al., 2014). When a forest recovers, environmental conditions change and lead to distinct species communities and functional turnover from agriculture to old-growth forests (Davies et al., 2020; Guariguata & Ostertag, 2001). Importantly, microclimatic conditions change in several dimensions. Daytime temperature rises by approximately 4°C through deforestation (Schultz et al., 2017). In a lowland Bornean rainforest, 20-m tall forests were on average 1.8°C cooler than deforested areas, and even 5.9°C cooler in their maximum temperature (Jucker et al., 2018). Further, the vapour-pressure deficit is about one fourth lower in forested areas (Jucker et al., 2018). Other successional changes relate to structural complexity such as biomass, canopy height, and gap frequency, which increase with older forest age (de Almeida et al., 2020; Kent et al., 2015). Forest recovery also results in changes in biological interactions, such as more complex foodwebs (Estes et al., 2011; Fraser et al., 2015; Jucker et al., 2020).

In tropical rainforest, vertical stratification from ground to canopy is pronounced and affects arthropod distribution, their functional traits and phylogenetic structure (Basset et al., 2015; Mena et al., 2020; Schulze et al., 2001). Even across small distances, for example above and within the litter layer and soil, communities are distinctly stratified, typically caused by environmental filters such as temperature and humidity (Giller, 1996; Widenfalk et al., 2016). With increasing vertical height, air temperature and solar insolation increase while relative humidity decreases (Scheffers et al., 2013). For instance, in Bornean rainforest, temperature increased by 0.13°C and relative humidity decreased by 1.4% every 10 m along a vertical transect (Xing et al., 2022). Resource limitations are different between strata, for instance, nitrogen availability is lower in the canopy than on the ground (Kaspari & Yanoviak, 2001). Finally, structural changes play an important role as communities become more isolated with vertical height. For instance, connectance through lianas is an important determinant of arboreal ant community assembly (Adams et al., 2019).

Thus, stratification and recovery can be understood as two overarching parallel environmental filters, ultimately determining community reassembly. Studies on trait and phylogenetic diversity therefore allow us to glimpse into the reassembly process, and enables us to analyse the consequences of environmental change for ecosystem functioning (Fornoff et al., 2021; Luck et al., 2012; Srivastava et al., 2012). Typically, ecological studies either focus on stratification within a habitat or along recovery of a single stratum but the role of stratification during recovery remains largely unknown (but see Neves et al., 2021). It is unclear whether recovery influences strata congruently or if processes are heavily stratum-specific.

Ants are one of the most abundant insect groups of tropical forests and play an important role in ecosystem functioning (Lach et al., 2010). They display a vast diversity of life histories, from minute subterranean dwellers to conspicuous canopy climbers, making them ideal to study both stratification and forest recovery (Sosiak & Barden, 2021). The functional traits of ants have been studied intensively and can be linked to ecosystem functions: for instance, the body size of scavenging ants has been linked to decomposition rate of their food (Nooten et al., 2022). Furthermore, ant communities have also been shown to be sensitive to environmental change in various traits, such as darker body coloration in brighter environments (Gibb et al., 2015; Law et al., 2020; Parr et al., 2017; Sosiak & Barden, 2021).

In the present study, we sampled ant communities along a 34-year tropical forest recovery chronosequence in the three microhabitats, leaf litter, ground, and tree trunk (hereafter 'strata'). We tested whether stratification and forest recovery jointly shape ant communities, traits, and phylogeny. In line with other studies, we expected that trait diversity and phylogenetic diversity would increase with recovery time (Edwards et al., 2017; Liu et al., 2016; Mo et al., 2013). Furthermore, we expected that taxonomic species overlap between the different strata would decrease with recovery because, for example, in agricultural areas there is only limited plant volume and ant colonies might thus need to forage on a wider range of strata.

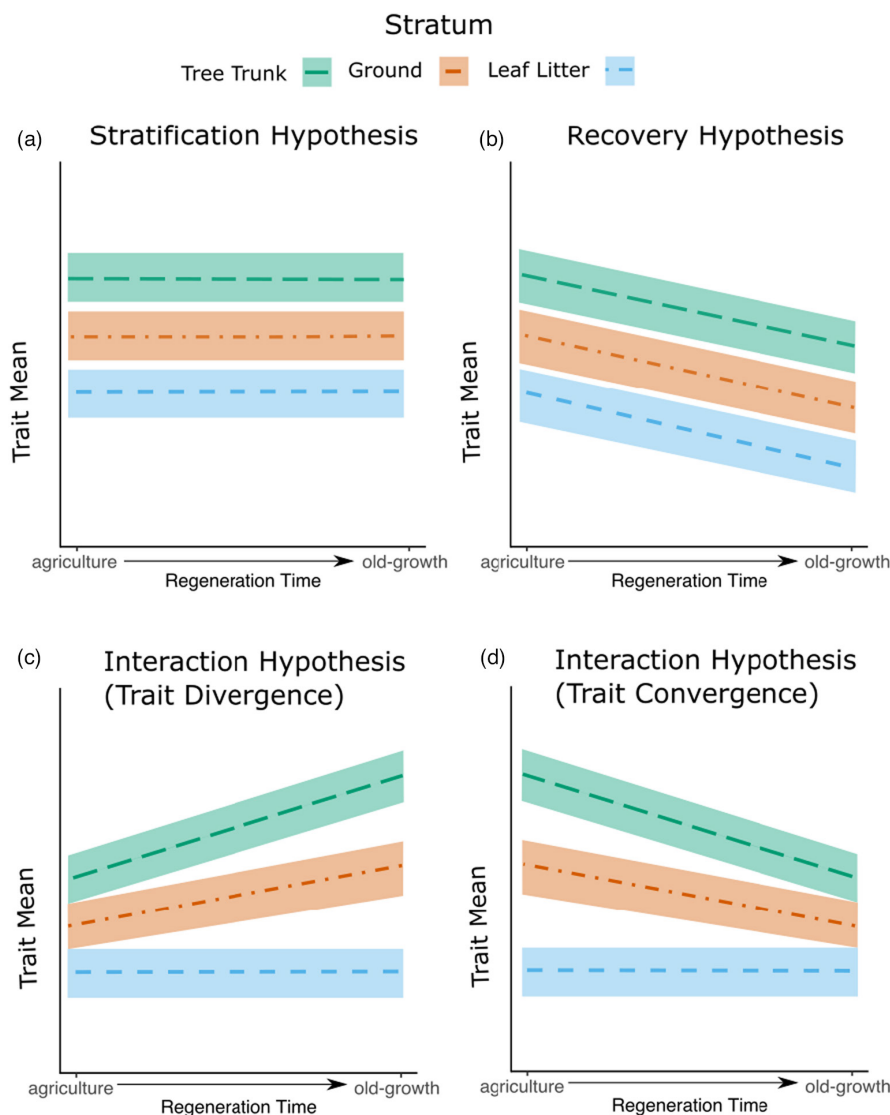
In the simplest scenario within a recovering forest, the functional traits of the ants will be filtered by stratification ('stratification hypothesis' Figure 1a) and/or recovery time ('recovery hypothesis', Figure 1b). If each stratum has a different response to recovery, the functional recovery could be stratum-specific, which would be evidenced by a statistical interaction ('interaction hypothesis'). For traits that adhere to the latter hypothesis, we expected two opposing trends: Different strata become either less similar (diverge, Figure 1d) or more similar (converge, Figure 1c) to each other during

recovery. Since closed canopy creates a more stable and homogeneous climate with less variation (de Frenne et al., 2019; del Pliego et al., 2016; Jucker et al., 2018), we expected traits that are more correlated with microclimate to converge. On the other hand, for diet-related traits we expected opposite trends, reflecting increased trophic diversity within and between strata in undisturbed habitats (Estes et al., 2011; Fraser et al., 2015; Gibb & Cunningham, 2013).

## 2 | MATERIALS AND METHODS

### 2.1 | Study site and plot design

Our study was conducted at the Reserva Río Canandé (0.5263N, 79.2129W) in Ecuador (Esmeraldas Province) in April–June 2018 and February–May 2019. The reserve and surrounding areas contain old-growth rainforests, recovering secondary forests on former pastures or cacao plantations ('recovery areas'), and currently used pastures and cacao plantations ('agricultural areas'). According to interviews with local farmers, land-use is mostly younger than



**FIGURE 1** The three main hypotheses for trait trajectories. On the y-axis, a community weighted mean (CWM) for a hypothetical trait is shown. The regression lines each depict the response of this trait to the recovery time on the x-axis. In (a), a trait is differentiated between strata, but does not change significantly with recovery time, which we refer to as the 'stratification hypothesis'. In (b), a trait is both differentiated among strata and changes with recovery time in a similar manner across the strata, which is the 'recovery hypothesis'. Finally, (c) and (d) depict two examples of a trait differentiation and a recovery time effect, which varies among the strata (indicated by a statistically significant interaction between recovery time and stratum), referred to as 'interaction hypothesis'. In (c), the trait means diverge to less similar values with recovery time, while in (d) traits converge. For simplicity, we assume that variation of the mean is stable over time.

50 years, and is comprised of small-scale farming in a forest mosaic landscape. We selected a total of 61 plots of 40 m × 40 m size in the following categories ('habitat types'): eight cacao plots, eight pasture plots, 12 cacao recovery plots, 17 pasture recovery plots, and 16 old-growth forest plots (as reference; Figure S1). All recovery plots were adjacent to forests. Spatial dependence was minimized by haphazardly selecting plots and keeping a minimum distance of at least 200 m among plots of the same habitat type. Plot elevation ranged between 127 and 615 m (Figure S1b). As elevation was weakly correlated with recovery time (Figure S1d), we account for the potential influence of elevation by incorporating elevation as a fixed effect in all analyses (see Statistical analysis).

We determined the recovery age by interviewing local park rangers and farmers and incorporated information on land purchase provided by the Fundación Jocotoco. We assigned each recovery plot the age as the number of years it has been in succession (year after abandonment, range 1–34 years). Two types of locally common agriculture (cacao plantations and pastures) were selected from nearby farms. Cacao plantations are typically monocultures, and cacao trees reached a height of approximately four meters. The pasture plots were extensively grazed by various livestock, mostly cattle, and typically some sparse trees provided shade. All old-growth forests have, to the best of our knowledge, not experienced logging in recent times. Further details on plot selection are described in Hoenle et al. (2022a, 2022b).

## 2.2 | Ant sampling and identification

We collected ants in each plot with three standardized methods to cover different strata: leaf litter, epigeal ('ground') and tree trunk (modified protocol from Agosti et al., 2000). Throughout the rest of the manuscript, we will address the methods as their representative stratum (tree trunk sampling: tree trunk; hand sampling: ground; Winkler: leaf litter). Each stratum was represented by five pooled subsamples per plot.

(1) To sample the leaf litter ant community, we used Winkler extraction. For this, we established a 20 m transect line parallel to one side of the plot. Leaf litter samples (including topsoil) were collected in an area of 20 cm × 20 cm every 5 m along the transect. Larger twigs and leaves were removed by sifting (1 cm mesh size). Because pastures had no leaf litter, we used a spade to cut out the first five centimetres of the grass turf with the same dimensions. The samples were subsequently pooled per plot and transferred to Winkler bags for 48 h.

(2) The ground ant community was assessed by standardized hand sampling. We used another transect parallel to the Winkler transect with the same length (20 m) and placed a 1 m<sup>2</sup> sampling subplot every 5 m, where we collected ants with forceps for 5 min. The subplots were pooled on plot level.

(3) To sample the tree trunk, we used the five largest trees in each plot. Using forceps, we collected ants in reachable heights (0–2 m) for 5 min per tree, also checking under epiphytes and bark.

If there were not enough trees within the limit of the pasture plot, we collected from adjacent trees in the same pasture. Nevertheless, three of the pastures had fewer than the required five trees, but at least one tree per plot was sampled ( $n = 10$  missing trees). Tree trunk samples were pooled at the plot level. In both tree trunk and ground sampling, we focused on maximizing species numbers by collecting only a few individuals per species (e.g. close to a nest). As the collection methods do not result in reliable abundance estimates, we calculated all analyses on incidence data only (Agosti et al., 2000; see statistical analysis).

To avoid a stratum-specific collector bias, the same person carried out all leaf litter sampling (AA), hand sampling (POH) and tree trunk sampling (POH). Inevitably, each collection method has certain limitations; for instance, Winkler samples may under-represent large-bodied ant species (Lee & Guénard, 2019). Stratum comparisons thus need to be interpreted with care, as each stratum-specific collection method may itself contribute to stratification patterns.

Specimens were first sorted into morphospecies and identified to species (or morphospecies). Due to the lack of identification literature on Ecuadorian ants (Salazar et al., 2015), we mainly relied on keys for Costa Rican and Colombian ants (e.g. Fernández et al., 2019; Longino, 2010). Taxonomic experts contributed to several identifications (see Acknowledgements). Voucher samples are deposited in the MEPN museum collection at the Escuela Politécnica Nacional in Quito. The Ministerio de Ambiente de Ecuador issued both the permits for collection (MAE-DNB-CM-2017-0068) and exportation (41-2018-EXPCM-FAU-DNB/MA and 144-2019-EXP-CM-FAU-DNB/MA).

## 2.3 | Species composition analysis

Altogether, we collected 183 ant subsamples (61 plots with 3 strata each). We used the species incidence, that is, presence/absence of ant species in each subsample for all analyses. All analyses were performed with the software R (R Core Team, 2018; Version 4.1.2). To analyse species composition, we used two-dimensional nonmetric multidimensional scaling (NMDS) with Jaccard similarity in the R package 'VEGAN' (Oksanen et al., 2010). The Jaccard index gives an overall similarity measure of communities and does not distinguish between turnover and nestedness components of beta diversity, which were not relevant to our study. The similarity matrix was tested for differences in species composition between the three strata and for correlations with recovery time and elevation in a PERMANOVA (function 'adonis' in VEGAN). We used the 'betadisper' function (VEGAN) to check the homogeneity dispersion assumption of the PERMANOVA (Anderson & Walsh, 2013), which was confirmed. Permutations were constrained by collection year. Using the same Jaccard similarity matrix, we also calculated species overlap among strata for each plot.

To visualize if the three strata follow similar trajectories across recovery time and elevation, we ran three separate NMDS on subsets of each stratum, and correlated the axes scores with 'recovery

time' and 'elevation' in a permutation test applying the function 'envfit'. Each stratum-specific matrix was finally analysed with a PERMANOVA (constrained by collection year) to test for correlations with elevation and recovery time. All permutation tests used 1000 replicates.

## 2.4 | Trait analysis

To test for influences of environmental filters on the ant community, we quantified 13 morphological traits (following Parr et al., 2017; Table 1) and investigated their response to stratification and forest recovery. The selected traits have been linked to the interaction of ant workers with their environments and represent classical functional traits (Gibb et al., 2015; Parr et al., 2017; Sosiak & Barden, 2021; Weiser & Kaspari, 2006). Using available ant literature, we broadly outlined their functional significance (Table 1).

We used a Keyence VHX-5000 (Keyence Deutschland GmbH) for trait measurements. We assessed traits of 653 specimens from 240 species (Table S1). Because of the high number of species, we measured for more common species (>10 occurrence) at least three individuals, and for rare species (>2 occurrences) at least one individual. Species with single occurrences were common, and traits could not be measured for all singletons (species without traits  $n = 36$ ; 2.5% of total occurrences; Table S1). This resulted in an average of  $2.7 \pm 1.6$  SD specimens per species/morphospecies (range 1–12). In polymorphic genera (*Azteca*, *Pheidole*, *Tranopelta*, *Camponotus*, and *Solenopsis*) we measured only minor workers. To assess the ants' colour lightness, we assigned each specimen a main colour, based on the colour wheel of Parr et al. (2017). GIMP Version 2.10.22 image software was subsequently used to extract the lightness value for each colour following Law et al. (2020).

We were interested in trait change independent of body size and therefore regressed each size-related trait with Weber's length (a proxy of body size) in linear models. We averaged the residuals of

**TABLE 1** List of ant traits that were quantified in this study. We present a proposed function for each trait, based on current literature knowledge. We highlight assumed environmental filters that could potentially influence these traits with regard to the proposed function.

Trait	Proposed function	Potential environmental filter
Weber's length	Closely related to body size and related to metabolism (Gibb et al., 2018) and microclimate (Kaspari, 1993). Higher habitat complexity selects for smaller body size (Guilherme et al., 2019). It might predict ants' contribution to decomposition (Nooten et al., 2022)	Environmental complexity, microclimatic, resources
Head length	Indicator of diet, longer headlength in predators (Weiser & Kaspari, 2006)	Resources
Head width	Correlates positively with bite force (Rühr et al., 2022), can be indicative of feeding mode (Weiser & Kaspari, 2006)	Resources
Mandible length	Length of mandibles relates to diet, with predators typically having longer mandibles (Gibb & Cunningham, 2013; Sosiak & Barden, 2021)	Resources
Clypeus length	Larger clypeus likely linked to sucking ability and liquid-feeding behaviour (Davidson et al., 2004)	Resources
Scape length	Sensory abilities: longer scapes might facilitate following pheromone trails (Weiser & Kaspari, 2006); predators have, on average, shorter scapes (Sosiak & Barden, 2021); higher environmental complexity might select for shorter scapes (Kaspari & Weiser, 1999)	Environmental complexity, resources
Pronotum width	The pronotum accommodates the neck musculature, which is important for digging and feeding (Peeters et al., 2020)	Resources
Femur length	Larger femur is indicative of foraging speed (Feener et al., 1988); predators have often shorter legs (Sosiak & Barden, 2021); longer legs enable thermoregulatory strategy (Sommer & Wehner, 2012); higher environmental complexity might select for shorter legs (Kaspari & Weiser, 1999; but see Guilherme et al., 2019)	Environmental complexity, resources
Eye size	Eye size is indicative of food searching behaviour with omnivores often having largest eye size (Weiser & Kaspari, 2006); spatial niche, with larger eye size on arboreal ants (Sosiak & Barden, 2021); light availability drives to some degree eye size, with more light leading to larger eyes; higher habitat complexity might select for smaller eye size (Guilherme et al., 2019)	Environmental complexity, microclimate, resources
Eye position	Related to the hunting method (Fowler et al., 1991); eye size is related to the component of the habitat occupied (Gibb & Parr, 2013); eye position = residual of (Head width – Interocular width) with head length	Environmental complexity, resources
Colour lightness	Related to thermoregulation such as sunlight protection (Clusella-Trullas et al., 2007; Law et al., 2020); camouflage (Garcia et al., 2009)	Microclimate, predation
Number of spines	Spines are mostly defensive adaptations (Blanchard et al., 2020)	Predation
Sculpture	More sculptured cuticles might increase structural integrity and dehydration tolerance (Buxton et al., 2021)	Microclimate, predation

these regressions on species level. We used the package 'FD' to calculate community weighted means (CWMs) based on the averaged species traits and the species incidence matrix (Laliberté et al., 2014; Laliberté & Legendre, 2010; Villéger et al., 2008). CWMs are representative of trait structure and allow for detailed comparisons of single trait trajectories. Based on the same incidence matrix and averaged traits, we calculated the Rao Q standardized effect size index (SES) as an estimate of overall functional diversity in the package 'PICANTE' (Kembel et al., 2010), using a Gower distance matrix (function 'ses.mpd' with abundance weighted = T, resulting in Rao Q; de Bello et al., 2016). Rao Q expresses the average dissimilarity between species pairs in a community (de Bello et al., 2010). To test functional clustering and overdispersion, we compared the observed Rao Q to a null model using 'independent swap' (Tucker et al., 2017). Thus, the analysis of both CWMs and functional diversity results in complementary information on the overall multidimensional trait space, allowing a detailed assessment of trait filtering.

## 2.5 | Phylogenetic diversity analysis

Trait measurements will rarely capture the entire trait space of a species, as several traits may be elusive or not be quantifiable. Phylogenetic diversity can inform on functional reassembly processes, since environmental filters are expected to create phylogenetically clustered communities (Srivastava et al., 2012). Because our data set contained many ants that could only be assigned to morphospecies, we calculated phylogenetic diversity on the genus level, which is a suitable proxy for species level tips (Qian & Jin, 2021). We used the backbone phylogeny of Economo et al. (2018) as reference tree and pruned the full tree to all 58 ant genera present in our species occurrence data using the R-package 'PICANTE' (Kembel et al., 2010). We are not aware of polyphenies in our pruned genera subset. The resulting tree was then transformed into a cophenetic distance matrix, which was subsequently used to calculate the Rao Q as standard effect size of each subsample using the function 'ses.mpd' from 'picante' (with abundance weighted = T), with an independent swap as a null model (Tucker et al., 2017). This approach allowed us to directly compare functional and phylogenetic diversity.

## 2.6 | Stratification and recovery analysis

The main goal of the analysis was to test the possible interaction between the environmental filters of vertical stratification and forest recovery. We therefore tested each of the obtained community metrics (species richness, functional and phylogenetic diversity, CWMs) in linear mixed-effects models (LMEs) against an interaction between recovery time and stratum using the packages 'LME4' (Bates et al., 2015) and 'LMERTEST' (Kuznetsova et al., 2017). Further, to test if species composition overlap was related to recovery time, we regressed it in a LME against recovery time and elevation.

To allow the incorporation of old-growth forests and agricultural areas into the analysis (even though they do not have a formal recovery age), we rank-transformed the recovery time. Old-growth forests received the highest rank and agricultural areas the lowest. Rank transformation shifts the highest rank close to the oldest recovery plot (34 years). In a previous study based on the same dataset, we showed that the ant communities fully recovered within less than 30 years, supporting that these ranks depict a realistic monotonous trajectory without a huge step towards old growth (Hoenle et al., 2022a, 2022b).

Because the three collection methods are difficult to compare in terms of their relative collection effort, species richness differences among strata might influence some of the community metrics. To minimize this possible relationship, we added species richness to all LMEs as a fixed factor (except for the richness model itself). As species richness itself did not change with recovery time (see Figure S3a), differences in species richness could only possibly interfere with stratification results. Collection year and plot ID were used as crossed random intercepts. The plot ID is always associated with three strata collection events from the same day, while the collection year is unique for each plot (either 2018 or 2019).

Depending on the outcome of the LME, we applied further testing. If the fixed factor 'stratum' was significant in an Anova (type III analysis of variance) on the LME model, we assessed differences in a pairwise posthoc procedure (Bonferroni-Holm corrected; R-package 'EMMEANS'; Lenth, 2021). Trajectories with a statistically significant fixed factor 'stratum' (but without significant interaction or recovery term) were classified as supporting the stratification hypothesis (Figure 1a). If a community metric changed with recovery time (but without an interaction), we classified it as supporting the recovery hypothesis (Figure 1b,c). Note that the latter can also include metrics with a significant stratum term. If an interaction between recovery and stratum was significant in an Anova, we classified it as support for the 'interaction hypothesis' (Figure 1c,d).

The testing of legacy effects (i.e. different pasture or cacao recovery trajectories) required a separate procedure, because the rank-transformed recovery time included old-growth forests, which do not belong to a 'legacy' category. Therefore, we excluded old-growth forests and used a new LME with the same fixed and random-effects structure, but including the interaction term 'legacy × recovery time'. Residuals of all models met assumptions of normality and homogeneity of variances. For each variable, we also tested for positive spatial autocorrelation (Moran's *I* on model residuals; R-package 'APE4'), which was never found.

If a metric followed either the recovery or the interaction hypothesis, we created subsets of each stratum and generated new LMEs with fixed factors of recovery time, elevation, species richness and the random factor collection year to obtain slope estimates for stratum-specific recovery time. This allowed us to test whether the community metrics in each strata increased, decreased or did not change. Finally, we classified the CWM trajectories, which belonged to the 'interaction hypothesis', into two scenarios. Less overlap in

the 95% CI (from the LM) of the strata in old-growth forests compared to agriculture was classified as 'divergent', while more overlap was classified as 'convergent' (see also the concept in Figure 1).

### 3 | RESULTS

#### 3.1 | Species composition

We reported 284 ant morphospecies belonging to 58 genera in all habitats (Table S1). Three of the species were not native but overall rare (*Cardiocondyla emeryi*,  $n = 1$  occurrence; *Cardiocondyla minor*,  $n = 2$ ; *Monomorium floricola*,  $n = 7$ ) and therefore unlikely to affect results of functional or phylogenetic analyses. Per stratum subsample 2–23 ant species co-occurred in each plot (Figure 4a), with the fewest species found in leaf litter (Figure 2a). Species richness was neither related to recovery time ( $p = 0.12$ ) nor land-use legacy ( $p = 0.40$ ) but increased with elevation (elevation estimate  $0.80 \pm 0.27$  species per 100m,  $p = 0.004$ ; Table S2). The three collection methods resulted in three well-separated communities (PERMANOVA,  $F = 6.06$ ,  $R^2 = 0.06$ ,  $p < 0.001$ , Figure 2). There was clear vertical stratification, with leaf litter being most distinct from

tree trunks, and ground being intermediate. Species turnover with recovery time was pronounced across all strata (PERMANOVA, all  $p < 0.001$  and  $R^2 > 0.036$ ; Table S2; Figure 2). Similarly, elevation influenced turnover, except in leaf litter (PERMANOVA,  $F = 1.32$ ,  $R^2 = 0.021$ ,  $p = 0.10$ ; Table S2). Ant communities on the tree trunk and ground became more dissimilar with increasing forest recovery time and elevation (LME recovery time  $p = 0.005$ , elevation  $p = 0.03$ ; Table S2). However, the overlap of ground and tree trunk subsamples with the leaf litter subsamples was not influenced by recovery (all  $p > 0.38$ ; Table S2).

#### 3.2 | Functional traits

Functional diversity was consistent with the 'stratification hypothesis' and community trait diversity (SES Rao Q) was stable during recovery. The tree trunk subsamples had slightly higher diversity (overdispersion) compared to the ground and leaf litter. We detected no influence of land use legacy (Table S3).

Among the 13 traits analysed as community-weighted means (CWMs), only the number of spines and femur length were unrelated to both stratum and recovery time (Figure S3, Table S4; correlations

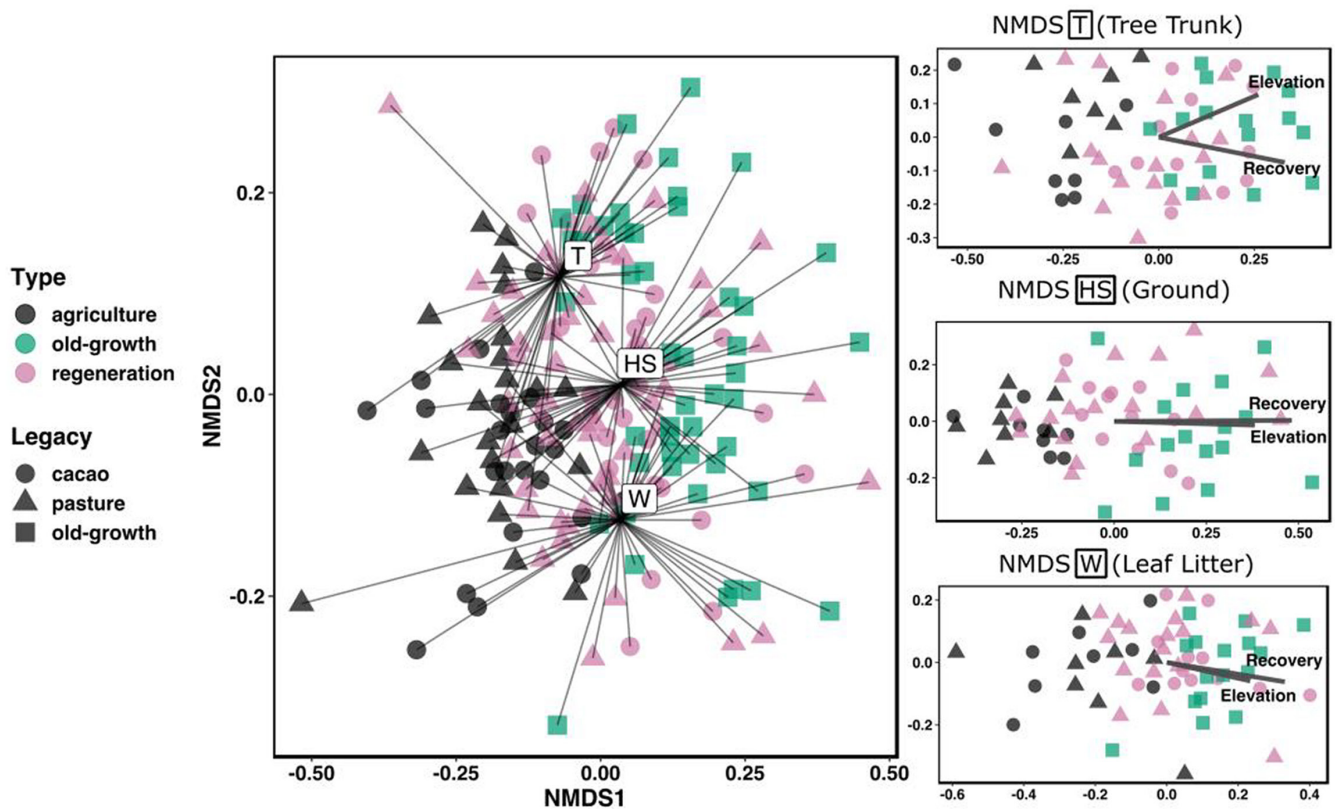


FIGURE 2 Nonmetric multidimensional scaling (NMDS) of species composition for tree trunk (T), ground (HS), and leaf litter (W). The type 'agriculture' consists of currently used cacao plantations and pastures. The left NMDS ordination (stress = 0.21) shows all strata (subsamples) combined depicting the vertical stratification, while on the right each of the three strata is plotted separately (stress: T = 0.23; HS = 0.19; W = 0.17). The influences of recovery time and elevation on species composition are indicated as grey vectors (all  $p < 0.001$ ; for detailed statistics see Table S2). One tree subsample ('T APN01') contained a very dissimilar community that would skew the ordination, which is why it is not shown (but included in statistical analyses).

among raw traits shown in Figure S2). The CWMs of head width had a trajectory consistent with the stratification hypothesis; sculpture and eye position with the recovery hypothesis; and the remaining eight traits with the interaction hypothesis (Figure 4; Table S4). Trait CWMs were not correlated with elevation (all  $p > 0.07$ ; Table S4). Legacy only influenced mandible length, however, without a significant pairwise contrast (Table S4).

Two traits, scape length and Weber's length (Figure 4a,d; Table S4), diverged with recovery time (i.e. strata became more dissimilar), while colour lightness, pronotum width, mandible length, clypeus length and eye size converged (Figure 4b,f,e,g,j; Table S4). A special case was head length, because its interaction term was significant, but neither the intercept nor stratum differences were (Table S4). Thus, it was neither converging nor diverging. A schematic overview of trait changes with vertical stratification and recovery is depicted in Figure 5.

### 3.3 | Phylogenetic diversity

Phylogenetic SES Rao Q values remained similar across the entire chronosequence but exhibited consistent differences among strata, thus supporting the stratification hypothesis (Figure 3d; Table S5). Communities were predominantly random in their phylogenetic structure; however, the tree trunk subsample was slightly more overdispersed compared to ground and leaf litter.

## 4 | DISCUSSION

Our results from a naturally recovering tropical rainforest revealed that the reassembly of a tropical ant community was dynamic and shaped by stratification within the forest. All three strata (leaf litter, ground, tree trunk) differed in their reassembly trajectories, particularly when functional traits were considered. As expected, stratification and recovery filters influenced the mean trait values for most of the assessed traits (10 out of 13), and lead to stratum-specific trajectories (interaction hypothesis) for eight out of 13 traits. Contrary to our expectation, for most traits the differences between strata became smaller with increasing recovery time, including traits related to diet. This highlights an unexpected decrease in functional differentiation with recovery time, possibly reflecting an increased functional redundancy of the ants' contribution to ecosystem function. Moreover, functional and phylogenetic diversity were unexpectedly consistent over recovery time, but were distinctly stratified. Previous research on the role of stratification during forest recovery has been limited (Neves et al., 2021; Whitworth et al., 2019), and our results highlight the importance of stratification in shaping dynamic communities, in particular when interpreting species functional contributions in recovering ecosystems.

Stratification had a large influence on ant communities. Lower tree trunks had comparatively higher phylogenetic diversity in our study, although it typically is the leaf litter which contains evolutionary older lineages (Lucky et al., 2013; Sosiak & Barden, 2021).

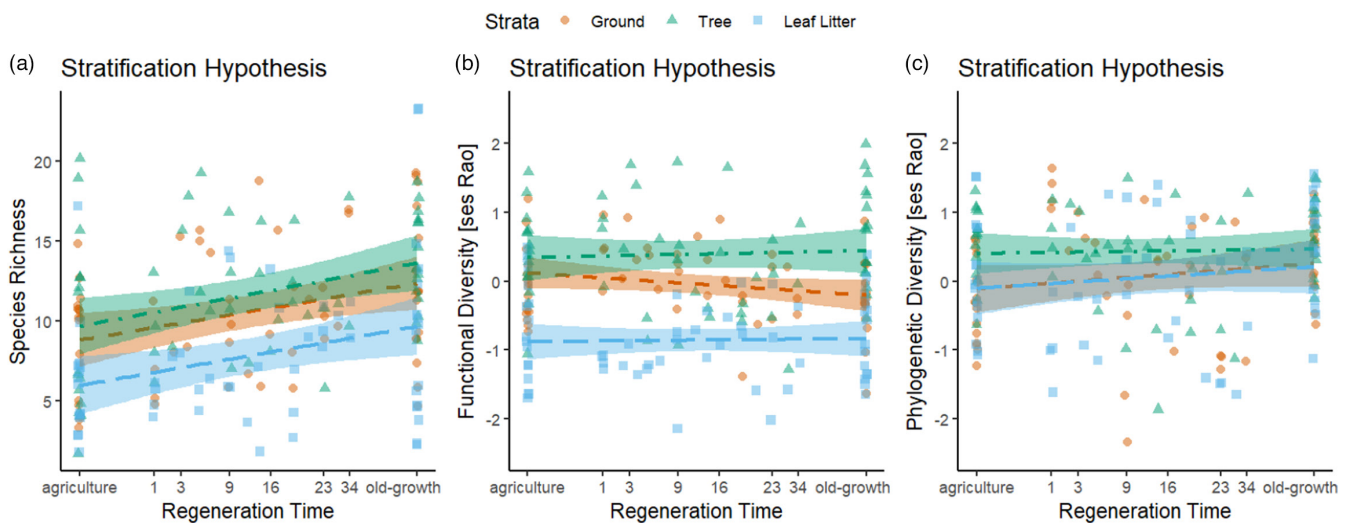
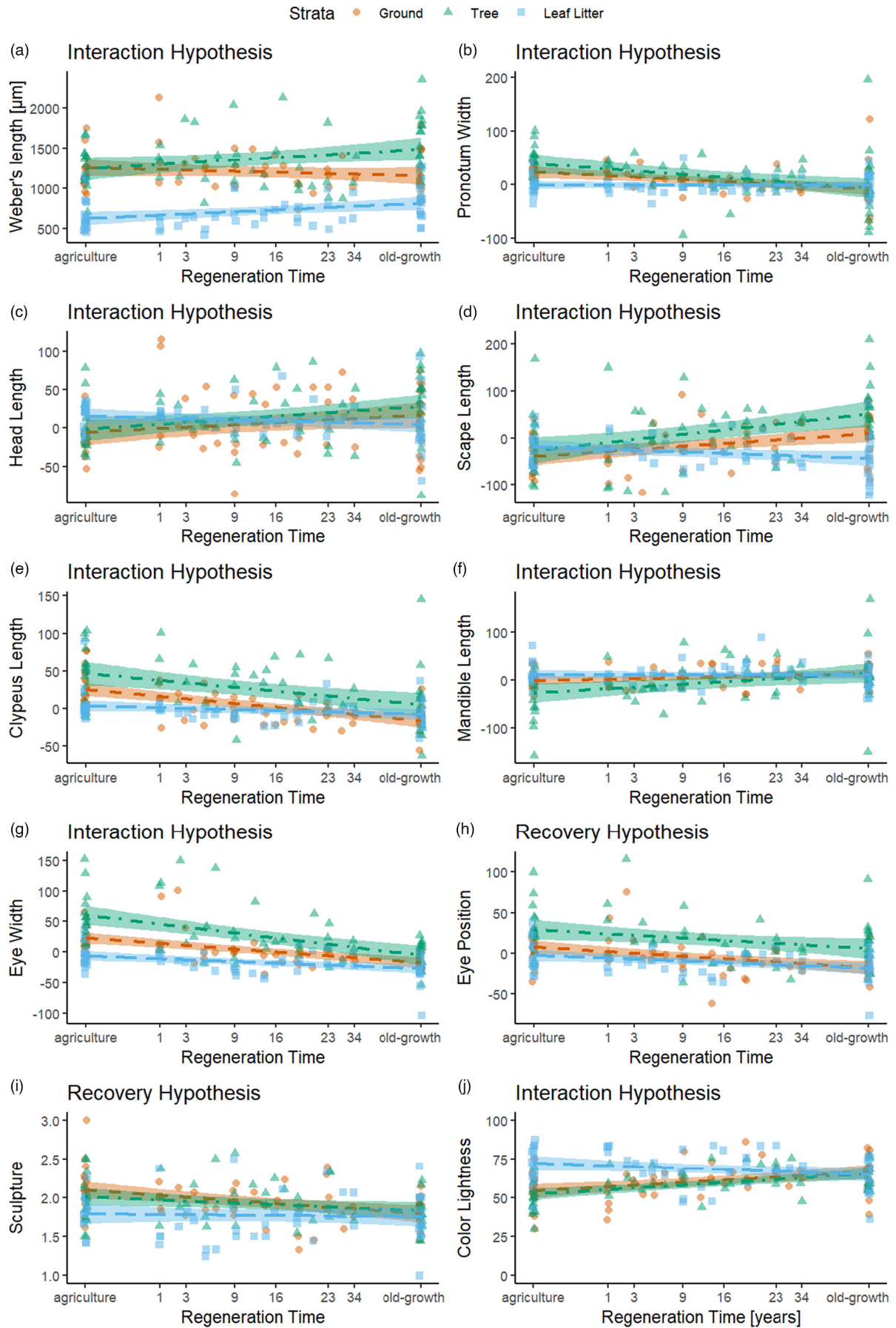
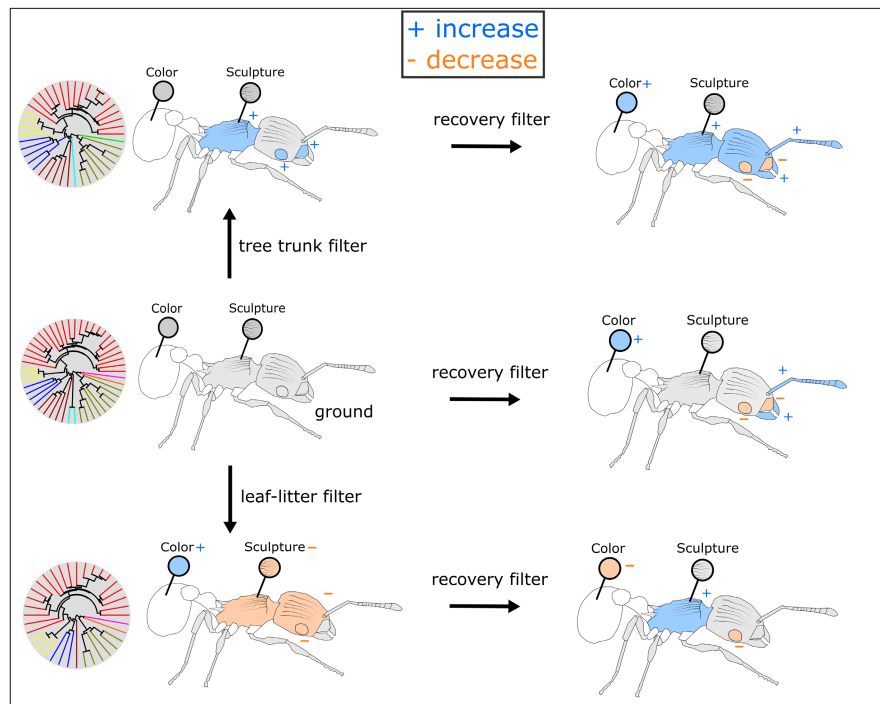


FIGURE 3 Trajectories of species richness (a), functional diversity (b) and phylogenetic diversity (c), all of which were consistent with the stratification hypothesis. The prediction and 95% confidence intervals of each stratum taken from a linear model are plotted. Colours indicate strata (green = tree trunk; red = ground; blue = leaf litter). For the full statistical models see Tables S2, S3 and S5.

FIGURE 4 Changes in trait means across recovery time and strata, which are consistent with the recovery or interaction hypothesis (indicated on top). Weber's Length (A) and Scape Length (D) show diverging patterns, while the rest which are in line with the interaction hypothesis have converging patterns. All morphological traits are community weighted means of residuals from a regression with Weber's Length, except for Weber's Length (A; in  $\mu\text{m}$ ), sculpture (I; 0–3, 0 = smooth and shiny and 3 = heavy sculpturing), and colour lightness (J; 0–100 scale, with 0 = darkest). Strata differences are highlighted with green (tree trunk), red (ground) and leaf litter (blue), and their trajectories to recovery time are shown as predictions from a linear model with 95% CI (Table S4).







**FIGURE 5** Morphological and phylogenetic differences between the three strata and induced morphological changes with recovery time. The middle ant on the left side represents the ground assemblage, which serves as comparison baseline for the tree and leaf-litter community. Phylogenetic trees show all genera found per stratum, with colours indicating subfamily affiliation (same colour = same subfamily). On the ants' body, grey areas indicate traits that were measured, but did not change (either between stratum: upper left & lower left; or induced by recovery, all ants at to the right; For statistical model values see [Table S4](#)). Blue-coloured traits indicate a significant increase, while orange indicates a significant decrease. Three body parts are represented by two different trait measurements (mesosoma: Weber's length and pronotum width; Head: head length and head width; Eye: Eye size and Eye positioning). If any of these traits changed significantly, we coloured the respective body part. Legs indicate changes in femur length, spines the number of spines, mandibles the mandible length, clypeus the clypeus length, and the antenna the scape length. Note that on the left side, only significant differences between either tree trunk and ground or leaf-litter and ground are highlighted, that is, not those between tree and leaf-litter. The sketch drawing shows a simplistic depiction of *Wasmannia auropunctata*, which was the most common ant across all strata.

Consistent with an unexpected lower phylogenetic diversity, leaf litter ants also showed a lower functional diversity than the other strata. These patterns suggest that species can be filtered towards the few combinations of traits that are well adapted to living in the leaf litter layer (e.g. pale body coloration, relatively short scapes and legs), a prominent finding that has previously been described for the diversity of traits in stratified soil macroinvertebrate communities (Ellers et al., 2018). Possibly, there is a stochastic component, as smaller body size could limit the degree of possible variation in other traits. Stratification had pronounced effects on several key functional traits, which are largely in agreement with previous ant studies (Gibb et al., 2015; Sosiak & Barden, 2021; Weiser & Kaspari, 2006). Forest microclimate probably represents one of the most important abiotic environmental filters for ants. Temperature is known to have a strong influence on ant vertical stratification, as arboreal ant communities are well adapted to temperature extremes and ants live close to their thermal limits (Kaspari et al., 2015). In our study, this is reflected in several traits, such as colour lightness which is influenced by insolation which increases with height (Law et al., 2020), eye size becomes larger as more light is available (Schofield et al., 2016) and body size as

well as leg size increase, possibly reflecting larger thermal tolerance of the warmer environment (Silva & Brandão, 2010; Sosiak & Barden, 2021). Some of the potentially resource-related traits were also strongly stratified, hinting at underlying trophic differentiation: For example, tree-living ants often belong to relatively lower trophic levels, as they rely more on plant-based resources than ground dwellers (Blüthgen et al., 2003), which in our data is evident in the larger clypeus (associated with liquid feeding) in tree stem communities. Competition for limited nesting resources on trees is likely an important driver of community structure (Blüthgen & Stork, 2007; Mottl et al., 2021; Plowman et al., 2020; Wittman et al., 2010). However, we did not analyse traits related to competition, as these are difficult to measure (such as colony size and behavioural dominance), and thus, the influence of competition was likely not captured by our methods. It is possible that findings related to stratification are potentially introduced by our different collection methods, acting as an artificial filter on the community (Lee & Guénard, 2019). Since our results are based on incidence data, are largely comparable to other studies and match general expectations, we believe that this methodological bias is not strong.

In a previous study based on the same data, Hoenle et al. (2022a, 2022b) showed that the ant community recovers quickly and that species turnover during recovery is pronounced. Here, we confirm that this turnover occurs consistently across strata. Although we sampled only a fraction of all available microhabitats—higher strata represent a difficult challenge across multiple sites in tropical forests (Basset et al., 2015)—it is conceivable that the documented changes are representative for other strata. Indeed, similar studies in the tropics that employed chronosequences found pronounced species turnover in different strata (Bihn et al., 2010; Schmidt et al., 2013; Staab et al., 2014). We expected that due to larger and more diversified microhabitats, species community stratification would increase with recovery time, and this was indeed the case in the comparison between ground and tree communities. On the contrary, comparisons with leaf litter communities did not reflect this change, possibly because they were already made up of very distinct communities in the early stages of recovery and agriculture.

We expected more evolutionary-preserved lineages in old-growth forests compared to agricultural areas (Edwards et al., 2017; Liu et al., 2016; Mo et al., 2013). However, phylogenetic diversity was not related to recovery, indicating that during taxonomic turnover with recovery time individual species are replaced by phylogenetically similar species (such as turnover of species in the same genus) or higher clades were replaced by similarly distant lineages. Therefore, ant phylogenetic diversity was only structured by stratification and not by recovery.

With the potential to assess environmental effects on the community beyond species identity, the functional trait perspective used by us provides detailed information on the outcome of environmental filters on the average community bauplan (de Bello et al., 2021; Kraft et al., 2007; Sosiak & Barden, 2021; Wong et al., 2019). Our finding of largely stable ant functional diversity contrasts with some previous studies along disturbance gradients (Rocha-Ortega et al., 2018; Santoandré et al., 2019) but is supported by others (e.g. Skarbek et al., 2020). Possibly, the close proximity of all plots to old-growth forests facilitated a comparable level of functional diversity by reducing environmental filters imposed by dispersal limitation in more fragmented landscapes (Chazdon et al., 2009; Dent & Wright, 2009; Lennox et al., 2018).

The relatively stable functional and phylogenetic diversity contrasts with the dynamic patterns in functional traits, most of which changed with recovery time. The observed trends in traits were mostly consistent with the expected environmental changes during forest recovery. Ants in the cooler, darker forest environment were brighter, had a less sculptured cuticle and reduced average eye size, but the trends were weak. However, other than expected in structurally more complex forest, we did not find a trend towards shorter appendages (antennae and legs) among ants.

Introduced through the interplay of different environmental filters across recovery and stratification, trait trajectories were complex and stratum-specific. We sorted trait trajectories into two

categories: community means (CWMs) in different strata either became more or less similar with increased recovery time, that is, they converged or diverged. Contrary to our expectations, the majority of traits converged, regardless whether traits were linked to diet or represented possible microclimate adaptations. Our results on morphological traits (but not dietary measurements *per se*) therefore suggest that trophic niche diversity of ants is not promoted by stratification.

An important caveat of our study is that we did not measure any environmental variables (such as microclimate) directly, but use general trends from the literature to formulate the initial hypothesis. Thus, we can only approximate several potential underlying environmental filters, for instance, we are currently unaware in which quantity resources (e.g. sugar availability through plants and trophobionts) or competition pressure change with recovery. Finally, we want to stress that many traits are related to more than one ecological function, are often context dependent (e.g. species use the same trait for different functions), and are shaped by complex evolutionary trade-offs, thus complicating their interpretation (Luck et al., 2012). Our analysis is based on the assumption that the set of commonly measured morphological traits can be linked to ecosystem function, however there are few studies that go beyond the correlation of traits with their environment (Gibb et al., 2015; Lach et al., 2010; Parr et al., 2017). Fortunately, several recent research studies address this persistent gap, and future experimental studies further exploring the link between will certainly make the foundation of trait-based approaches in ant ecology stronger (e.g. Buxton et al., 2021; Law et al., 2020; Nooten et al., 2022).

Mechanisms of community assembly are central to understanding ecosystem recovery. Here, we show for the first time how stratification is intertwined with reassembly. While we focus on ant communities, vertical stratification is prevalent across animal and plant taxa (e.g. Basset et al., 2015; Chmel et al., 2016; Floren et al., 2014; Laurans et al., 2014; Schulze et al., 2001). Our study shows how community (re)assembly can be driven by a complex interplay of environmental filters that lead to unexpected outcomes in the functional structure. Strata becoming more similar during recovery might be a common functional pattern that warrants confirmation across different biomes and taxa. Stratum-dependent recovery is not only interesting from the perspective of functional reassembly, but also has conservation implications, for instance, if one stratum is more heavily affected by human disturbance (Klimes et al., 2012; Whitworth et al., 2016, 2019).

## AUTHOR CONTRIBUTIONS

Nico Blüthgen, Philipp Otto Hoenle and Michael Staab conceived the ideas and designed the methodology; Philipp Otto Hoenle and Adriana Argoti conducted the field work; Philipp Otto Hoenle and David Donoso identified the ant species; Philipp Otto Hoenle and Michael Staab analysed the data; Philipp Otto Hoenle led the writing of the manuscript; Nico Blüthgen supervised the study. All authors critically contributed to the drafts and gave their final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

None declared.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.jsxksn0fc> (Hoenle et al., 2023).

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## SUPPORTING INFORMATION

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

**Figure S1:** (a) Map of all plots superimposed on an elevation heatmap of the study area, made with the R-package ‘RASTER’ (Hijman, 2011: <http://raster.r-forge.r-project.org/>). (b) Elevational distribution of each plot category. (c) Distances among each plot within each category. The y-axis is log-transformed. Mean  $\pm$  SD distance is  $5799 \pm 3373$  m. The shortest inter-category distance is 170 m, the longest is 13,403 m. (d) Relationship between elevation and recovery time. The two variables are significantly correlated (linear model;  $F = 4.80$ ,  $R^2 = 0.18$ ,  $p = 0.003$ ), and there is no difference between cacao and pasture land-use legacy (same model,  $p = 0.95$ ).

**Figure S2:** Correlation plot of all measured ant traits.

**Figure S3:** Community weighted means of head width and along the recovery sequence.

**Figure S4:** Pairwise comparison of species overlap (as Bray-Curtis Dissimilarity) along recovery time in (a) ground vs. leaf litter communities, (b) ground vs. tree trunk communities and (c) tree trunk vs. leaf litter communities.

**Table S1:** Species list of the ants collected during this study.

**Table S2:** Statistical results for analysis on species richness from Figure 3a and species composition from Figure 2 and Figure S4.

**Table S3:** Model results for functional diversity, as SES Rao Q.

**Table S4:** Model results for the trait community weighted mean trajectories which are shown in Figures 4 and 5.

**Table S5:** Model results for the phylogenetic diversity trajectory from Figure 3D, which was consistent with the stratification hypothesis.

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