

High species turnover but functional stability in tropical ground-dwelling ant assemblages over 12 years of monitoring in Central Amazonia

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Abstract

1. Understanding how assemblages change over time improves our ability to predict responses to local disturbances and global threats. Based on an extensive dataset collected across 25 km² in Reserva Ducke, Central Amazonia, we investigated the structure of taxonomical and functional-group ant assemblages over 12 years.
2. Ants were sampled in 30 permanent plots (250 m in length) spaced 1 km apart, using pitfall traps during four sampling events in 2006, 2012, 2014, and 2018. Each sampling event deployed 300 traps, totaling 1200 samples across the study.
3. Our results revealed significant taxonomic shifts over time, with a sharp decrease in species richness and abundance in 2014, followed by a recovery in 2018. Approximately 50% of species were re-sampled in subsequent years, suggesting a directional shift with no clear evidence of convergence or return to the composition observed in 2006. Species turnover was influenced by topographic factors, with flatter plots and valleys exhibiting higher turnover compared to steeper or well-drained higher areas.
4. Changes in functional groups at the plot level were also very high between sampling events, showing no clear pattern. However, all functional groups remained relatively stable at the site scale, with no clear sign of directional changes over time.
5. Despite climate change and the increase in the frequency of extreme weather events in the region, our results are consistent with the scarce information that indicates ant assemblages are relatively stable in tropical forests in the long term. These findings suggest that although ant species composition in tropical forests may fluctuate due to environmental changes, functional redundancy within the community may buffer ecosystem processes, ensuring long-term functional stability. However, our results also show large variations in univariate ant metrics (richness and abundance) between years that may obscure long-term patterns.

KEYWORDS

Formicidae, international long term ecological research, slope, spatiotemporal variability, topography

INTRODUCTION

Understanding assemblage dynamics in space and time is critical to predicting how climate change may affect biodiversity (Bewick et al., 2014) and ecosystem functions (Montoya & Raffaelli, 2010). Such knowledge can refine conservation models and improve decision-making processes regarding global biodiversity loss (Schiesari et al., 2019). The temporal variation of species composition, often called temporal beta diversity (Legendre & Gauthier, 2014), can result from natural movement, dispersal (Massol et al., 2017), local extinctions (Gonzalez et al., 2016) or changes in environmental conditions, whether gradual or abrupt (Shimadzu et al., 2015). As the climate continues to change, there has been a surge in interest in long-term assemblage dynamics (Blowes et al., 2019; Costa et al., 2020; Dornelas et al., 2018, 2014; Munyai & Foord, 2015), which are crucial for understanding the future of biodiversity.

Assemblages are often classified as stable when their composition remains constant over time, or they may exhibit directional change, where shifts accumulate (Fukami et al., 2005; Legendre, 2019). Directional changes may either diverge from or converge toward an initial state, often defined as the community composition at the first sampling point (Collins et al., 2000; Matthews et al., 2013). While many examples of stable assemblage composition exist (e.g., Magurran & Henderson, 2010), divergent directional changes are more frequently observed, particularly in natural ecosystems (Dornelas et al., 2014). However, the magnitude and nature of these changes often depend on the facet of biodiversity being investigated. Species compositional changes may not necessarily lead to corresponding functional changes, as species can be replaced from the same functional group (Fukami et al., 2005). Theory and evidence predict that functional changes should be slower than taxonomic changes, as species replacement tends to occur within functional groups (Holdaway & Sparrow, 2006; Silva & Brandão, 2010).

Despite growing knowledge of species dynamics, terrestrial biodiversity datasets are biased toward vascular plants, vertebrates, and temperate regions (Blowes et al., 2019; van Klink et al., 2020). Nevertheless, invertebrates are responsible for critical ecological processes, and most diversity is concentrated in the tropics (Prather et al., 2013). Invertebrates also have higher temporal turnover than long-lived taxa (Collins et al., 2018), making them more prone to changes related to climate or anthropogenic factors. As a result, the temporal diversity patterns in temperate domains differ from tropical areas (Blowes et al., 2019), making it hard to extrapolate patterns and processes among regions. For example, while temperature is frequently reported as the critical factor for seasonal dynamics and distribution changes in temperate regions (Parmesan, 2007; but see Uquillas et al., 2024), the effects of water availability and changes in precipitation are more intense in the tropics (Chaudhari et al., 2019; Rodrigues-Filho et al., 2024).

Ants (Hymenoptera: Formicidae) play a crucial role in ecological processes, influencing soil physical and chemical properties (Sousa-Souto et al., 2007), accelerating decomposition (McGlynn & Poirson, 2012) and interacting with other invertebrates, fungi, and

plants (Griffiths et al., 2018; Schultz & McGlynn, 2000). Ants are also sensitive to environmental changes (Gibb et al., 2015) and have relatively sessile colonies, making them an excellent model for studying temporal and spatial variation in species distributions (Andersen, 2019). For instance, in tropical forests, ant assemblages show high species turnover but no significant changes in species richness over time (Donoso, 2017). However, in open environments, moisture plays a key role in community stability, as wetter regions tend to exhibit greater stability compared to drier areas (Câmara et al., 2019).

Ant diversity and activity are higher in moister seasons and habitats, even in the tropics (Kaspari & Weiser, 2000; Vasconcelos et al., 2003). In general, ant species density (Munyai & Foord, 2015) and diversity (Queiroz et al., 2023) increase during wet seasons. However, the effects of precipitation on ant populations can vary depending on local conditions, as some species are capable of adapting to fluctuating moisture levels (Tozetto et al., 2023). In many tropical forests, microhabitat variability associated with topography plays a key role in shaping ground-dwelling ant assemblages. Better-drained areas at higher elevations contrast with the more humid conditions found in valleys, influencing species distribution patterns (Mezger & Pfeiffer, 2011; Oliveira et al., 2009). For instance, the richness of ground-dwelling ant species and the diversity of functional groups are closely linked to fluctuations in the water table, with generalist species being more diverse and active in humid areas (Baccaro et al., 2013; Souza Holanda et al., 2021). However, little is known about how topographic moisture gradients influence the taxonomic and functional diversity of ant assemblages over time.

Terrain slope is another facet of topography that may indirectly affect the occurrence of ant species. Sloping areas may suffer more erosion after heavy rains than flatter areas, decreasing litter density (Luizão et al., 2004) and increasing exposed soil (Rodrigues & Costa, 2012). Therefore, sloping areas may create a more heterogeneous and dynamic environment, fostering ant species turnover over time (Oberdorff et al., 2001). Reduced litter accumulation in these areas can differentially impact ant functional groups, particularly those that rely on leaf litter for nesting and foraging. Litter-nesting species, such as cryptobiotic attines and some specialist predators, may be more affected due to the loss of stable microhabitats and reduced prey availability (Silva & Brandão, 2014). In contrast, generalist ground-dwelling omnivores, which can exploit a broader range of nesting sites and food resources, may be less impacted by increased exposure to bare soil (Mezger & Pfeiffer, 2011). Consequently, the interplay between slope and species-specific ecological traits likely drives functional turnover within ant assemblages over time.

Here, we take advantage of the standardised sampling protocol used in a Brazilian Long Term Ecological Research – LTER site (Costa et al., 2015) to investigate the stability of ant species composition across four sampling periods (2006, 2012, 2014, and 2018) over an area of 25 km² in a typical terra-firme forest in Central Amazonia. By analysing such a large sampling area, we could examine the relationships between assemblage composition and environmental variables, such as slope and HAND (Height Above the Nearest Drainage). Furthermore, by adopting a functional-group approach (Groc et al., 2014),

we sought to provide a more comprehensive framework for understanding ant-assemblage dynamics. Our study addressed the following hypotheses: (i) Species richness remained stable over time; and (ii) ant assemblages exhibit directional changes, meaning species composition is expected to shift over time without returning to its initial state. (iii) Ant assemblages are consistently structured along the topographic moisture gradient, with species composition differing predictably between drier and more humid and steeper and flat areas. (iv) Taxonomic and functional temporal beta diversities differ along the topographic moisture gradient, with functional composition being more stable over time due to the redundancy of species within functional groups.

MATERIALS AND METHODS

Study site

The study was conducted at Reserva Ducke, 25 km North of Manaus (Headquarters at 2° 57.0' S, 59° 56.0' W), Amazonas State, Brazil. The reserve has topographic and edaphic variations typical of central Amazonian forests and has a total area of about 10,000 hectares. The terrain is undulating with elevation ranging from 30 to 180 m a.s.l. Soils are classified as Xanthic Hapludox on plateaus, Typic Epiaquods on slopes, and Typic Endoaquods associated with small streams in valleys

(Bravard & Righi, 1989). In recent years, the area around the Reserva Ducke has suffered a continuous loss of native forest due to real estate and agricultural expansion. However, parts of the north and northeast sides are still connected to continuous forest.

The vegetation is a typical dense rainforest with a closed canopy and abundant stemless palms in the understory (Costa et al., 2009). There are approximately 1200 known species of trees with a canopy height usually between 30 and 37 m, but some trees reach 40–45 m (Ribeiro et al., 1999). The mean annual temperature and rainfall in 2010–2011 were 25°C and 2763 mm, respectively, with a short, drier season between July and September (Coordination of Environmental Dynamics, INPA).

Sampling design

We sampled ants in 30 permanent 250 m-long plots covering 25 km² of tropical rainforest in 2006 and repeated the same sampling design in 2012, 2014, and 2018 (Figure 1). The plots were installed by the Program for Biodiversity Research of Western Amazônia (PPBio-AmOc) with support from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and the National Institute for Amazonian Biodiversity (INCT-CENBAM). Plots followed the terrain contours to minimise topographic and edaphic variation within plots and were regularly distributed across the landscape every 1 km (Magnusson et al., 2013).

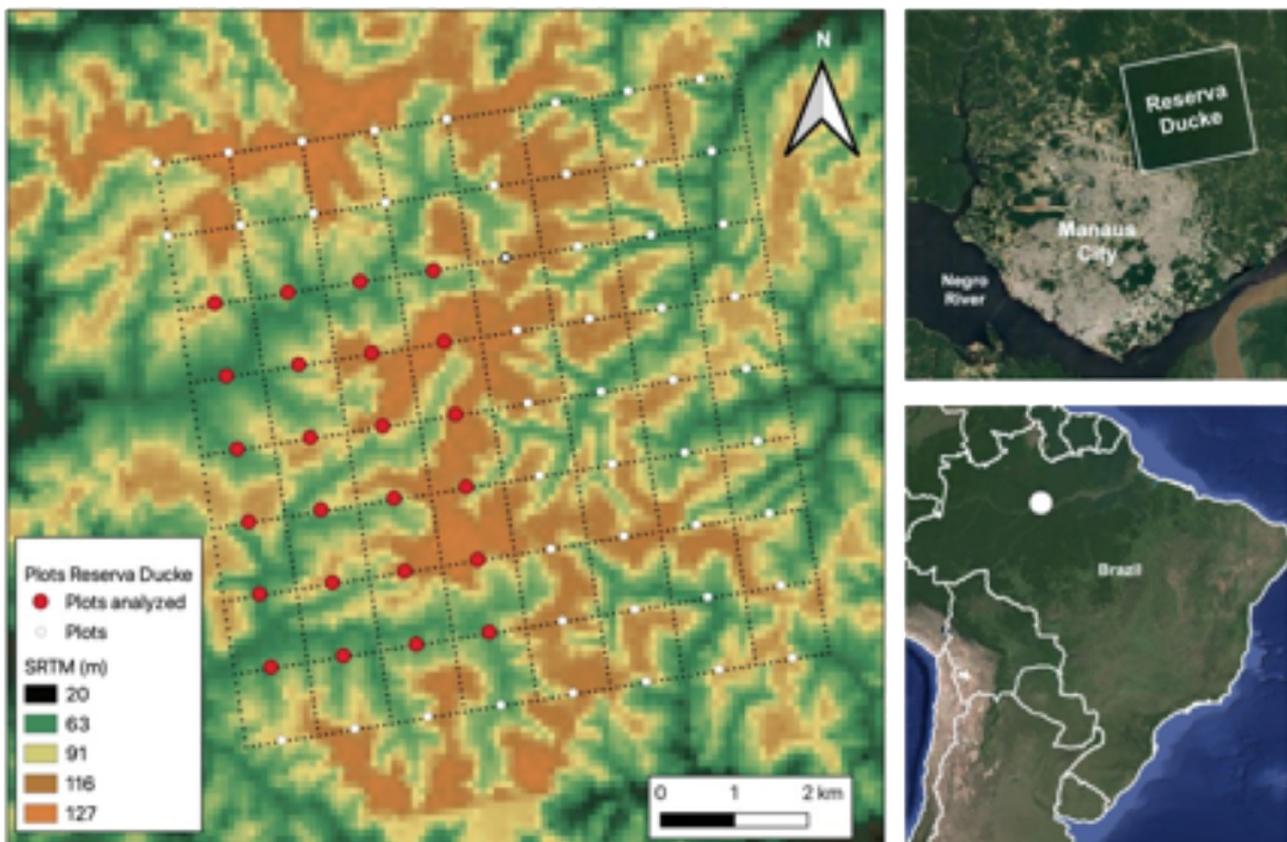


FIGURE 1 Map of study area, showing the spatial sampling design.

In each plot, pitfall traps (10 total) were placed at 25-m intervals to sample ants. The pitfalls consisted of 500-ml plastic cups with 95 mm diameter and 80 mm depth partially filled with alcohol and left open for 48 hours (see Souza et al., 2012 for more details). Overall, we used 1200 pitfalls, 300 per year. All sampling took place during the dry season (September and October).

We identified ground-dwelling ants first to the genus level using keys available in Baccaro et al. (2015), later to the species level whenever possible using available taxonomic keys, comparison with specimens in collections previously identified by experts, and vouchers sent to specialists (see acknowledgments). Where specific identifications were not possible, specimens were assigned to morphospecies. The morphospecies received unique codes and were consistent over the four sampling events. Vouchers are deposited in INPA's Entomological Collection.

Functional groups

To explore the dynamics of ground-dwelling ant assemblages, ant species were assigned to functional groups, following Groc et al. (2014) classification (see their supplementary material for additional sources). The species were placed in two groups of fungus-grower ants: (1) Cryptobiotic attines and (2) Leaf-cutters; three groups of omnivores: (3) Arboreal omnivores, (4) Generalist omnivores (generalist nesting) and (5) Ground-dwelling omnivores (ground nesting); and three groups of predators: (6) Ground-dwelling generalist predators, (7) Ground-dwelling specialist predators, and (8) Raid-hunting predators. This classification accounts for foraging behaviour, food choice, and nesting site, grouping species with potentially similar lifestyles. Arboreal omnivores species were included because they often forage on the ground and, therefore, were relatively well sampled. The remaining omnivore groups were categorised based on their nesting behaviour, with generalist omnivores showing flexible nesting strategies across various substrates (such as soil, litter, and dead wood), while ground-dwelling omnivores specifically nest in the soil. Due to the significant variation in natural history information, some genera with well-studied species were classified into several functional groups, while those with less-studied species were assigned to one group based on the most prevalent syndrome within the genus. Arboreal predators (mainly *Pseudomyrmex*) and truly subterranean species (i.e., *Acropyga*) were removed from the analysis, as the sampling method underestimated their occurrence and abundance (both groups represented ~2% of sampled species). Table S1 shows the species membership of each functional group.

Environmental variables

We used HAND and terrain slope as predictors of ant-assemblage composition. HAND represents the vertical relative draining potential, reflecting the amount of water in the soil (Schietti et al., 2014). The HAND algorithm uses the vertical distance between the terrain and

the closest drainage points based on SRTM images (Rennó et al., 2008). The algorithm measures the water net capacity to drain from an elevated position to the nearest drainage channel (Nobre et al., 2011). High HAND values mean greater draining potential, and low HAND values indicate proximity to the water table. Areas with shallow water tables are more prone to short-term waterlogging, especially after heavy rains, which can affect ant diversity (Baccaro et al., 2013; Souza Holanda et al., 2021). More details on HAND calculation can be found in Nobre et al. (2011), for the Amazon in Rennó et al. (2008), and Schietti et al. (2014) validation in Ducke Reserve. Slope measures were taken every 50 m perpendicularly to the central axis of the plot with clinometers and summarised as plot averages. Both variables are available from the Brazilian Biodiversity Program (PPBio—www.ppbio.inpa.gov.br), where the data and metadata for each variable are described in detail. Both environmental predictors were stable during this study (8 years) and were sampled in 2005. In our plots at Ducke Reserve, HAND and terrain slope are not correlated and together are good edaphic descriptors related to elevation, soil granulometry, and soil nutrients (Figure S1).

Data analysis

Ants live in colonies, so we used occurrence data within the plot as a measure of ant abundance. Occurrence data corresponds to the number of traps in each plot where a species was captured, varying from zero (no detection of a given species) to 10 (the species was detected in all pitfalls in a given plot). Given the distance between subsamples (25 m), the number of occurrences is a good proxy for the number of colonies per plot.

Using the occurrence data per plot, we constructed rarefaction and extrapolation curves based on Hill numbers (Hill number qD , where $q = 0$) for each year (Chao et al., 2014). We used 999 bootstrap samples to construct confidence intervals around Hill numbers (species number in our case), facilitating the comparison of multiple assemblages of rarefied and extrapolated samples. Based on Hill's numbers, these estimations are accurate for rarefaction and short-range extrapolation (Chao et al., 2014). We then created sample-based and coverage-based rarefaction curves to assess the representativeness of the sampling between years (Chao & Jost, 2012).

We construct two matrixes, one with plots in rows and species in columns and the other with plots in rows and functional groups in columns. Both matrixes were filled with occurrence data. We calculated the Bray–Curtis distance between the sampling rounds (2006–2012, 2006–2014, and 2006–2018) per plot for species and functional-group matrixes (Legendre, 2019). We then partitioned each Bray–Curtis dissimilarity matrix into two scaled components, losses and gains, for each plot. These metrics represent the abundance per species and functional group changes per plot. Then, a permutational procedure was used to test the overall tendency to change (difference between gains and losses) over all plots in both periods (Legendre, 2019). These analyses provide a general picture of taxonomic and functional changes at the site scale.

We also compared the species-assemblage and functional-group composition in 2006, 2012, 2014, and 2018 using a Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson, 2001), followed by pairwise comparisons between years. *P*-values were adjusted following Holm's method for multiple testing (Holm, 1979). Both analyses were based on the Bray–Curtis distance measure after Hellinger standardisation (Legendre & Gallagher, 2001). For plotting, we reduced the dimensionality of the assemblages (species and functional groups) sampled each year using Non-Metric Multi-Dimensional Scaling (NMDS) based on Bray–Curtis dissimilarity matrices. These analyses provide an overall view of taxonomic and functional changes at the plot scale.

We also compared the abundance variation of each functional group between the three sampling years. Given the marked difference in occurrence numbers from 2014, we converted the occurrence numbers to proportions. The number of species in each functional group was divided by the total number of species present in a given plot and year. We then used the proportion of each functional group per plot as the dependent variable against the sampling round in beta-regression models. Beta-regression models are less prone to distortions caused by the lower and upper bounds of proportions (Ferrari & Cribari-Neto, 2004).

We used distance-based redundancy analysis (dbRDA) to determine the extent to which environmental variables account for variation in species and guild composition (response variables) in each sampling year. Distance-based redundancy analysis (dbRDA) is an ordination method similar to Redundancy Analysis (RDA) but allows non-Euclidean dissimilarity indices (Legendre & Anderson, 1999). The distance matrices were based on the Bray–Curtis measure. The dissimilarity matrices of ant-assemblage composition and functional-group composition from each year were used as dependent variables, and HAND and slope were the predictor variables in the dbRDA models.

To investigate the role of environmental variables in the dynamics of ant assemblages over time, we used the Bray–Curtis distance between the four sampling rounds (2006–2012, 2006–2014 and 2006–2018) as the dependent variable against HAND and slope as predictor variables in GLM models. The statistical analyses were undertaken in the R statistical environment (R Core Team, 2021), using *vegan* (Oksanen et al., 2021), *iNEXT* (Hsieh et al., 2016), *betareg* (Cribari-Neto & Zeileis, 2010), and graphed using *ggplot* (Wickham, 2016) packages.

RESULTS

We registered 5827 occurrences (~17,850 ants) from 340 species and morphospecies distributed in 60 genera and 10 subfamilies over the study period (Table S1). The number of species observed per plot ranged between 26 and 43 in 2006, 19 to 51 in 2012, 7 to 36 in 2014, and from 13 to 39 in 2018.

The rank order of species demonstrated significant changes over the four sampling rounds. *Crematogaster tenuicula* Forel, 1904, which

was the most abundant species in 2006 and 2012, suffered a sharp decline and was not detected in our 2014 sampling (Figure 2). Similarly, *Crematogaster brasiliensis* Mayr, 1878, one of the three most abundant species in 2012, was absent in 2014 but rebounded in 2018. Some species displayed contrasting trends. *Pheidole biconstricta* Mayr, 1870, *Solenopsis clytemnestra* Emery, 1896, and *Solenopsis castor* Forel, 1893, which were not dominant in earlier rounds, were the three most abundant species in 2014. Further shifts were observed in 2018, with *Pheidole radoszkowskii* Mayr, 1884 rising in abundance, and previously dominant species, such as *Pheidole biconstricta*, declining.

Species richness through time

The rarefaction curves for 2006 and 2012 exhibited similar shapes (Figure 3a), with large overlapping confidence intervals, indicating consistent species richness during these periods. However, the number of ant species dropped significantly in 2014, from approximately 190 species in 2006 and 2012 to just 118 in 2014, marking an apparent deviation from the earlier sampling rounds. This decline remained evident when extrapolated species richness was considered at 2000 occurrences per sampling event. The 2018 data showed a recovery in species richness, with the number of species approaching those observed in 2006 and 2012, suggesting potential recolonization or environmental changes favouring species return. The coverage-based curves (Figure 3b) indicated that sample coverage remained relatively stable across the years, varying only slightly: 93.8% in 2006, 93.6% in 2012 and 2014, and a slight decrease to 88% in 2018.

Taxonomic and functional temporal turnover

Across the entire reserve, temporal taxonomic beta diversity consistently remained much higher than functional beta diversity (Figure 4a,b), likely due to the larger number of species than functional groups. Between 2006 and 2012, gains (C) and losses (B) were relatively balanced for both taxonomic (mean [C-B] = 0.030, Stat = 0.864, *p*.perm = 0.381) and functional turnover (mean [C-B] = 0.029, Stat = 1.021, *p*.perm = 0.329). From 2006 to 2014, the losses far exceeded the gains for both taxonomic (mean [C-B] = -0.306, Stat = -6.911, *p*.perm = 0.001) and functional diversity (mean [C-B] = -0.246, Stat = -7.028, *p*.perm = 0.001). In 2018, there was a slight reduction in the disparity between gains and losses, but a difference between 2006 and 2018 was still there for both taxonomic (mean [C-B] = -0.064, Stat = -2.206, *p*.perm = 0.035) and functional turnover (mean [C-B] = -0.102, Stat = -4.314, *p*.perm = 0.001).

The species composition changed markedly over the years (PERMANOVA, $R^2 = 0.19$, $F = 9.159$, $p = 0.001$), with only 46 species consistently recorded in all four sampling events. There was considerable variation in species composition among plots each year, resulting in different assemblage compositions between years (Table S2). Despite this variation, the direction of change in multivariate space for most plots was similar, with lines connecting plots across

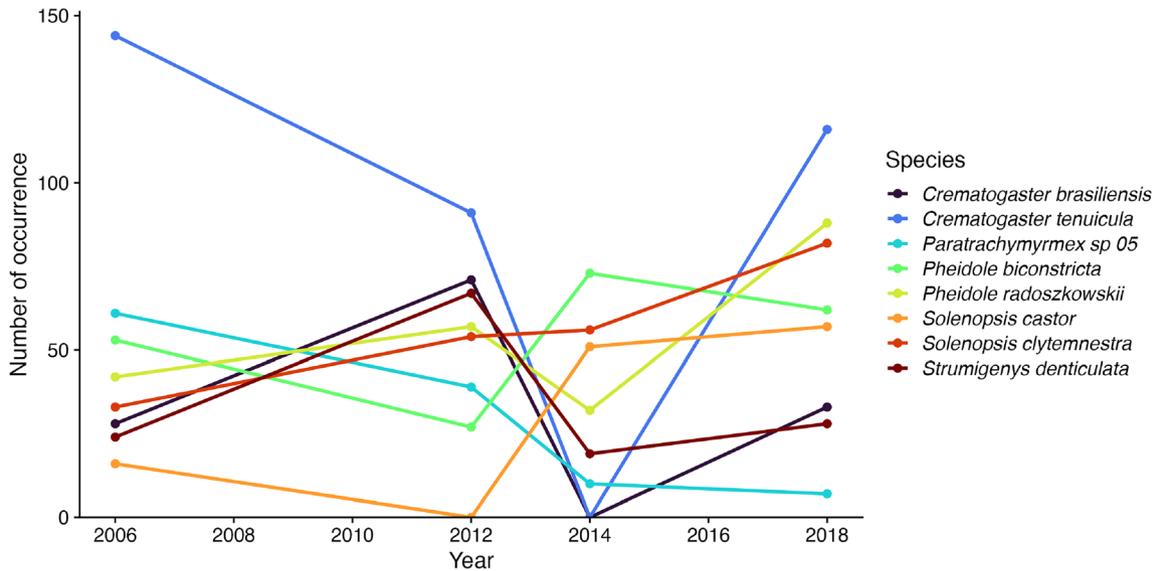


FIGURE 2 The three most frequent ant species sampled in 2006, 2012, 2014, and 2018. There are 8 instead of 12 species because *Crematogaster tenuicula* was among the top three in 2006, 2012, and 2018, *Pheidole biconstricta* was among the top three in 2006 and 2014, and *Solenopsis clytemnestra* was among the top three in 2014 and 2018.

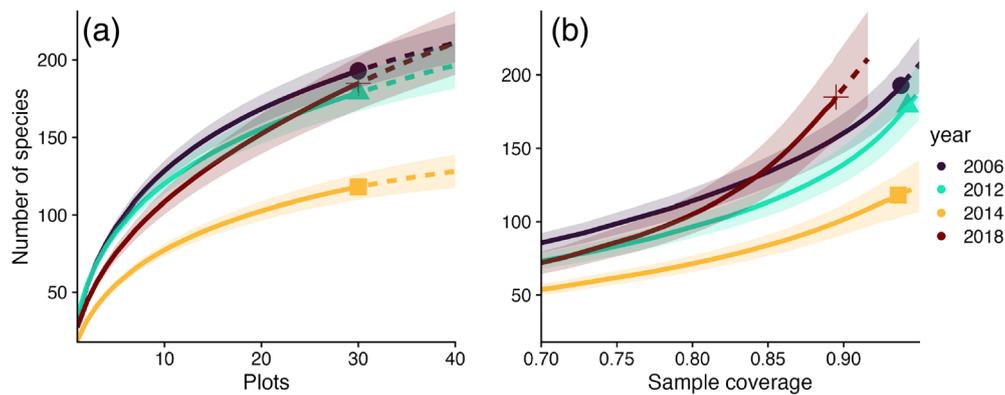


FIGURE 3 Sample-based (a) and sample coverage (b) curves for Pitfall trapping in 2006, 2012, 2014, and 2018 in the Brazilian Amazon (Reserva Ducke). Solid lines represent the rarefaction, and the dashed lines represent the extrapolation curves. Shaded areas represent the 95% confidence intervals.

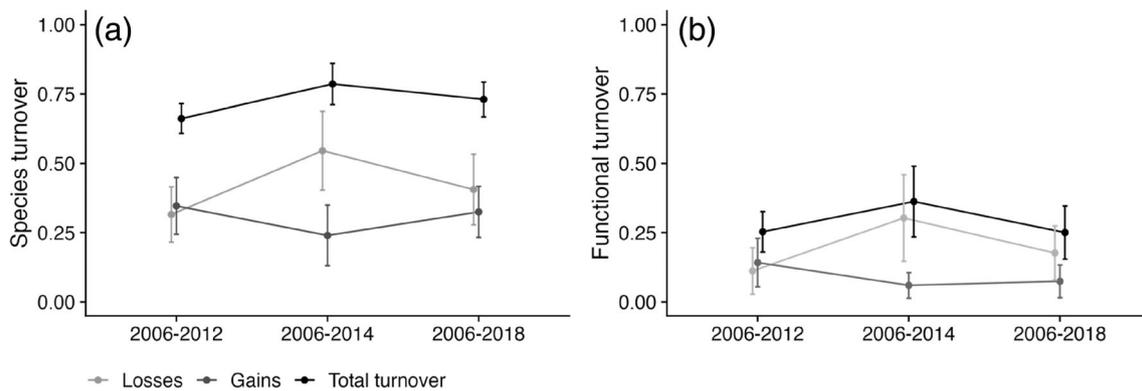


FIGURE 4 The mean and standard deviation of the partitioned turnover of species (a) and functional groups (b) in losses and gains per plot.

years showing nearly parallel trajectories, especially from 2006 to 2012 and 2012 to 2014 (Figure 5a). This suggests that the factors driving these changes had similar effects on most plots, though the trajectories began to diverge more notably in the 2014–2018 comparisons. The pattern was somewhat mirrored in the functional-group composition (PERMANOVA, $R^2 = 0.28$, $F = 15.192$, $p = 0.001$), but

the trajectories of change were less parallel, indicating less consistent effects on functional composition than on species composition (Figure 5b).

At the site scale, the relative abundance of ground-dwelling omnivores increased, particularly in 2012, 2014, and 2018, when it was significantly higher than in 2006 (Figure 6). On the other hand,

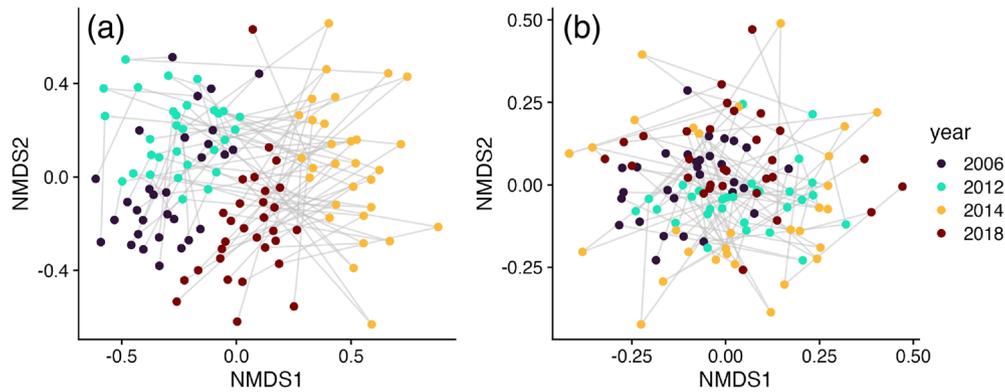


FIGURE 5 Non-Metric Multi-dimensional Scaling solution of the plots sampled in 2006, 2012, 2014 and 2018 according to ant species (a) and functional-group composition (b). In both cases, ordinations were based on species occurrence data. Lines link the same plot among years.

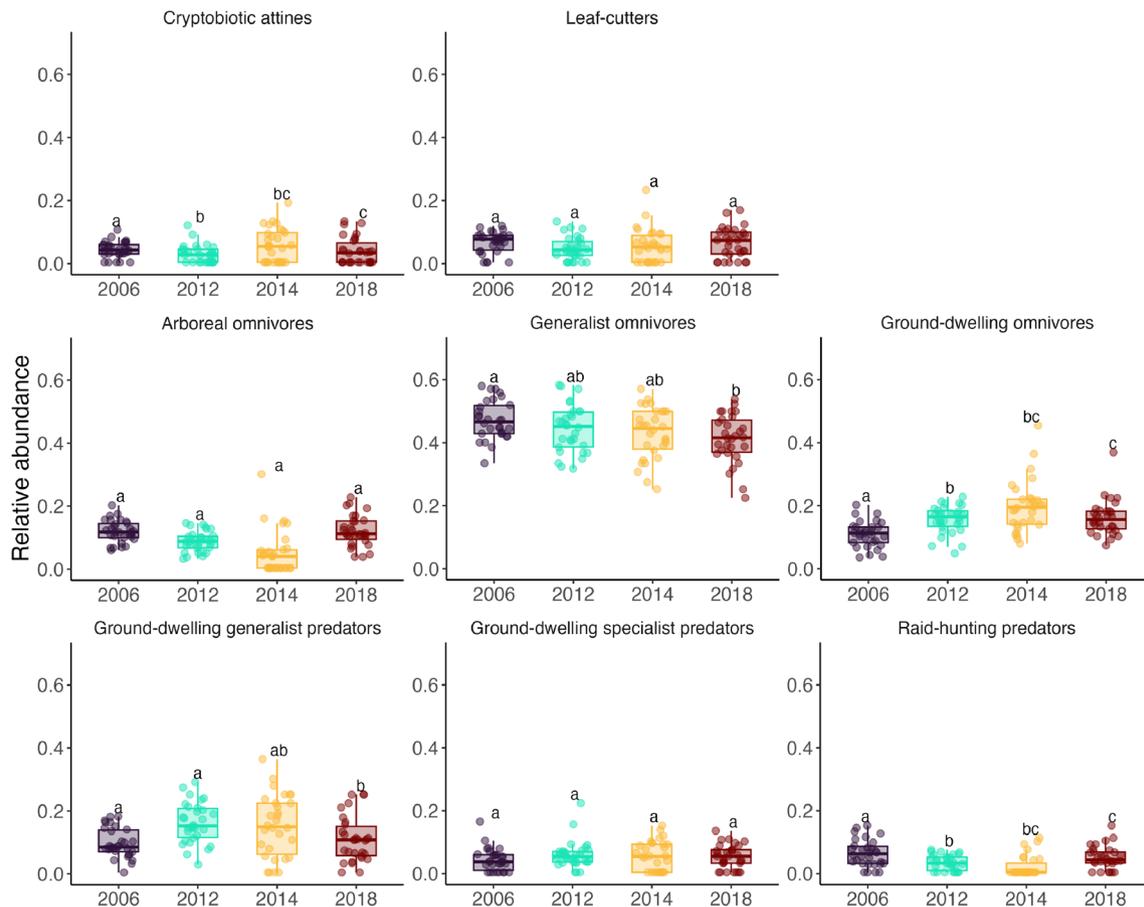


FIGURE 6 Relative abundance per plot for each functional group over the four sampling years at Ducke Reserve. Different letters indicate differences between pairwise comparisons between sampling rounds after Holm adjustment for multiple tests.

generalist omnivores and raid-hunting predators decreased in abundance in 2014, with a rebound in 2018, while ground-dwelling generalist predators slightly reduced in 2018. Despite these changes, the seven functional groups showed no directional changes in relative abundance across the four sampling periods, maintaining consistent levels throughout (Figure 6).

Taxonomic and functional composition along the topographical gradient

Despite the high species turnover across years, the variation constrained by the environmental predictors was similar in each sampling round, except for a slight decrease in 2018 (dbRDA 2006 = 0.096, $p \leq 0.001$; dbRDA 2012 = 0.106, $p \leq 0.001$; dbRDA 2014 = 0.093, $p \leq 0.001$; dbRDA 2018 = 0.076, $p = 0.02$). However, the magnitude of the influence of each environmental predictor shifted over time. Species assemblages were significantly constrained by slope in the first three sampling rounds, while HAND had a significant impact in 2006, 2012, and 2018 (Table 1).

Functional-group composition was less environmentally structured. The environment explained around 8% of the functional-group composition sampled in 2006 (dbRDA = 0.086, $p = 0.148$), 2012 (dbRDA = 0.099; $p = 0.072$), 2014 (dbRDA = 0.117; $p = 0.013$) and 2018 (dbRDA = 0.100; $p = 0.035$). In contrast to species composition, slope was the only environmental variable consistently associated with functional-group composition throughout the earlier sampling years. By 2018, HAND emerged as a significant predictor for functional-group composition ($p = 0.013$), whereas slope did not show a significant effect ($p = 0.232$). (Table 1).

Taxonomic and functional temporal turnover along the topographical gradient

The species turnover, measured here as the difference in the Bray-Curtis distance of each plot between years, was inconsistent over time. The GLM model explained ~20% of the species composition

turnover between 2006 and 2012 ($R^2_{adj} = 0.201$, $p = 0.018$) and ~16% of species composition turnover between 2006 and 2018 ($R^2_{adj} = 0.164$, $p = 0.033$). In both models, the terrain slope was correlated with species composition turnover ($b = -0.004$; $p = 0.005$ for 2006–2012; and $b = -0.002$; $p = 0.045$ for the 2006–2018 comparison). Plots with more temporal turnover in species composition were at the beginning of the slope gradient, which are flat areas, while most similar plots were on more inclined terrain (Figure 7). HAND values were only related to species composition turnover in the 2006–2018 comparison ($b = -0.001$; $p = 0.036$), with relatively higher species turnover in areas closer to the streams (Figure 7). The spatiotemporal turnover of species composition between 2006 and 2014 was not related to any environmental predictor ($R^2_{adj} = -0.027$, $p = 0.553$).

The composition of functional groups over time followed a similar pattern, but the responses were more variable. The multiple regressions explained ~17% of the functional composition turnover between 2006 and 2012 ($R^2_{adj} = 0.175$, $p = 0.028$), ~10% ($R^2_{adj} = 0.103$, $p = 0.045$) between 2006 and 2014, and ~20% ($R^2_{adj} = 0.202$, $p = 0.017$) between 2006 and 2018. The slope was related to the Bray-Curtis distance of plots in the first two comparisons (2006–2012: $b = -0.005$; $p = 0.009$ and 2006–2014: $b = 0.007$; $p = 0.029$) but in opposite directions (Figure 8). However, functional composition turnover between 2006 and 2018 was related only to HAND values ($b = -0.003$; $p = 0.005$), with more functional turnover in areas closer to streams (Figure 8).

DISCUSSION

This study reveals complex taxonomic and functional composition patterns of ant assemblages across four sampling periods (2006, 2012, 2014, and 2018) in a Central Amazonian terra-firme forest. The sharp declines in ant richness and abundance in 2014 were reversed in 2018, ruling out the possibility of an ant collapse during the monitoring period. However, the results also highlight substantial temporal turnover (around 50% between sampling events), with significant differences in species composition between the sampling periods, particularly between 2006 and 2018. These strong taxonomic shifts were

TABLE 1 Summary of dbRDA statistics for species and functional-group composition in the 3 years studied.

	Year	HAND		Slope	
		F	p	F	p
Species composition	2006	1.546	0.002	1.330	0.009
	2012	1.797	0.001	1.550	0.001
	2014	1.134	0.185	1.652	0.001
	2018	1.293	0.042	1.028	0.384
Functional-group composition	2006	1.078	0.363	1.587	0.049
	2012	1.096	0.340	1.956	0.034
	2014	0.904	0.535	2.441	0.003
	2018	1.882	0.013	1.233	0.232

Note: Significant results ($p \leq 0.05$) are in bold.

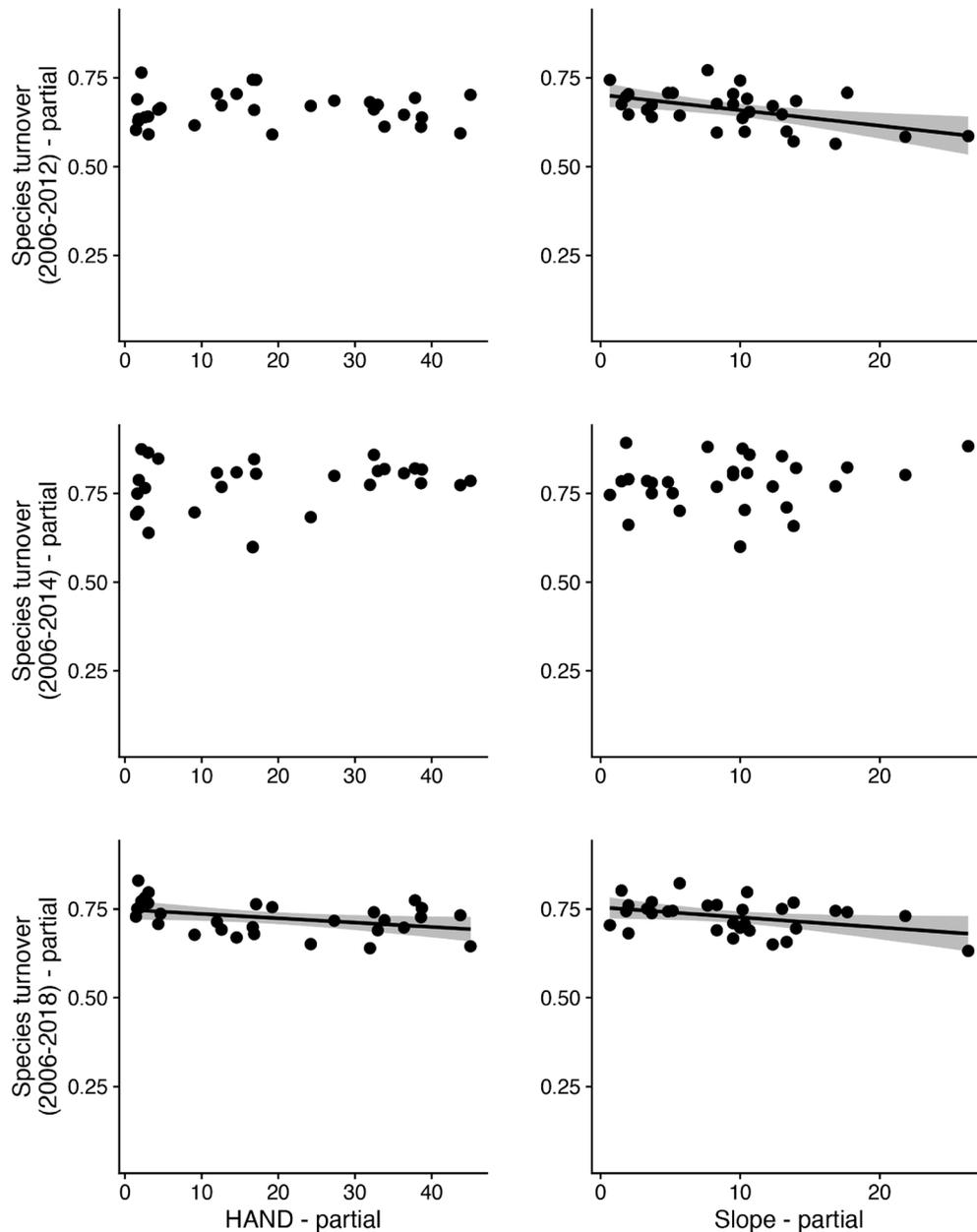


FIGURE 7 Partial regression plots showing the taxonomic temporal turnover between 2006–2012, 2006–2014, and 2006–2018 samples. Please note that the y-axis is on the same scale as Figure 8.

not entirely mirrored by functional-group composition, indicating that functional redundancy may buffer ecosystem processes against species loss. These findings align with other long-term studies of tropical invertebrates, where community shifts often occur without significant losses in functional roles (Blowes et al., 2019; Donoso, 2017).

Is there evidence of changes in the number of species with time?

The Amazonian hydrological cycle has intensified since the 1980s, with dry seasons becoming drier and wet seasons becoming wetter (Gloor et al., 2015), concomitant with an increase in the frequency of

extreme floods and droughts (Marengo & Espinoza, 2016). For instance, Central Amazonian forests have experienced significant increases in extreme climatic events over the last 30 years, with a higher relative frequency of water excess than water-deficit anomalies (Costa et al., 2020). It rained more than expected in 2014 (2 SD higher than the 50-year monthly average) for eight consecutive months (Marengo & Espinoza, 2016). While we always sampled ants during the peak of the dry season and did not record any heavy rain during sampling, excess rainfall may interfere with ant movement (Porter, 2005), lowering the number of species captured, or may lead to local extinction of some species. Interestingly, despite an extremely dry season in 2016 (2 SD lower than the 50-year monthly average—Costa et al., 2020), the ant assemblages seemed to recover. The 2018

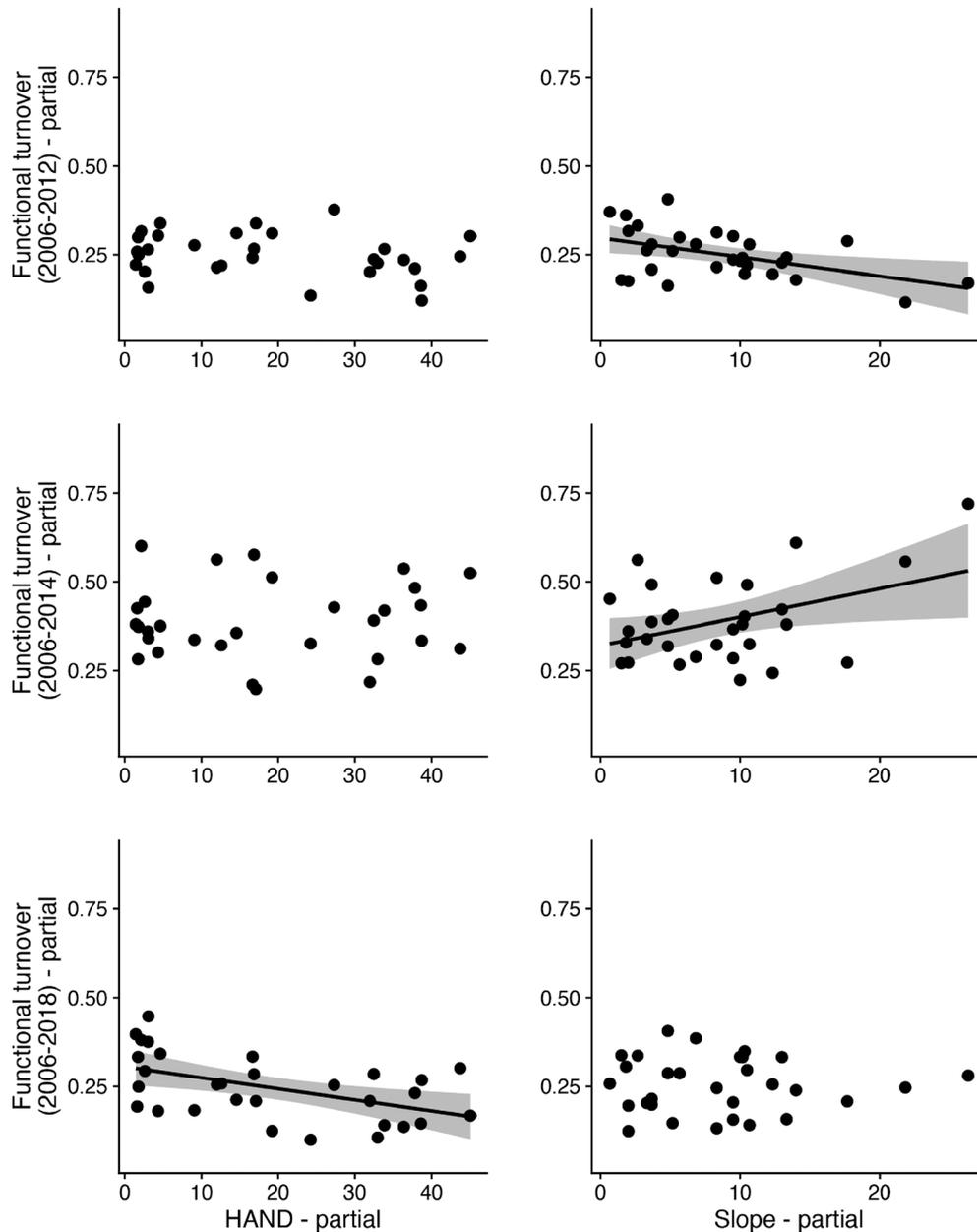


FIGURE 8 Partial regression plots showing the functional temporal turnover between 2006–2012, 2006–2014, and 2006–2018 samples. Please note that the y-axis is on the same scale as Figure 7.

data showed signs of recolonization, with species richness rebounding toward levels observed in 2006 and 2012. This recovery in species richness could reflect either a response to favourable environmental conditions for two consecutive years or natural successional dynamics within the ant assemblage. Given these observations, we do not have strong evidence to attribute the sharp decline in ant richness in 2014 to either methodological bias or climatic variation alone. The observed fluctuations in species richness suggest that ant assemblages in tropical forests undergo natural cycles of decline and recovery, reinforcing the idea that these systems exhibit long-term resilience rather than a unidirectional decline. Future monitoring rounds closer to extreme climatic events may help better understand the dynamics of ant assemblages.

Is there evidence of directional or stable trajectories in ant assemblages with time?

On average, around half of the ant species caught in one sampling round were recovered in the following sampling period, and only 13.5% of the species were sampled in the four censuses. In some cases, variation in species composition over time can be attributed to unpredictable occurrences of rarer species (Magurran & Henderson, 2003). Rare species are less likely to be detected and may also represent species with higher dispersal abilities (van Schalkwyk et al., 2019). Thus, the most abundant species are usually more adapted to local environmental conditions and are subject to smaller abundance fluctuations over time (Magurran & Henderson, 2010). However, that does not seem to be

the case in Reserva Ducke. Only *Crematogaster tenuicula* was recorded three times among the three most frequent species per year, and only two other species (*Pheidole biconstricta* and *Solenopsis clytemnestra*) figured among the top three in two sampling rounds. These results strongly suggest that the ant assemblages in this tropical forest are highly dynamic over time, even among the most common species.

Taxonomic beta diversity was consistently higher than functional beta diversity across all sampling rounds, supporting that species replacements tend to occur within functional groups (Silva & Brandão, 2010). This is evident in the fact that despite the considerable taxonomic turnover, the overall functional structure of the ant community remained relatively stable over the 12-year monitoring period. For instance, although some species, such as *C. tenuicula* and *C. brasiliensis* displayed marked declines, and *P. radoszkowskii* became more abundant in 2018, these changes did not result in significant shifts in the functional groups relative abundance in each sampling event. Thus, no functional group showed a strong trend to increase or decrease over time. This suggests that functional redundancy within the functional groups may buffer ecosystem processes from taxonomic changes, a pattern commonly observed in diverse tropical systems (Blowes et al., 2019).

Are the assemblages consistently structured along the topographic gradient?

Although the composition of ant assemblages sampled in 2006, 2012, 2014, and 2018 strongly differed, the responses to terrain variables were remarkably stable over the topographic gradient and correlated with HAND or slope in all sampling periods. The contrasting roles of HAND and slope over time suggest a dynamic interplay between topographical and hydrological factors. In central Amazonia, topography is a good predictor of environmental and microclimate changes. Higher sites are usually drier and well-drained, have more clayey soils, and higher litter productivity. On the other hand, the lowlands have sandy and poorly drained soils, with greater water availability and greater tree mortality (Chauvel et al., 1987; Luizão et al., 2004; Toledo et al., 2012). Unpredictable and frequent flooding after heavy rains in the valleys may also be a recurring disturbance for part of the ant assemblage (Souza Holanda et al., 2021). These factors result in different environmental and microclimatic conditions, favouring the consistent replacement of ant species along the topographic gradient. The exception was in 2014, the wettest year in our sampling period. Although we did not sample ants during the rainy season, the excess rainfall in 2014 may weaken the relationship between ant species composition and HAND detected in other years.

Terrain slope was also an important predictor of spatial taxonomic and functional ant composition changes. In steeper areas, there is less accumulation of leaf litter and greater spacing between plants due to the high mortality rate of trees and larger gap formation (Toledo et al., 2012). Consequently, plant species' composition differs from that of the flat areas (Oliveira et al., 2009). Areas with steep slopes also have less leaf litter (Luizão et al., 2004) and more exposed soil than flatter

areas (Rodrigues & Costa, 2012), resulting in a more heterogeneous environment. Thus, the smaller amount of litter in the steeper areas can limit species occurrence (Sabu et al., 2008), selecting only species more adapted to these conditions. The lower species turnover at one end of the gradient (steeper slopes) may explain the stable correlation of taxonomic and functional composition in the three sampling events.

Topography is a consistent predictor of the local distributions of other taxonomic groups, such as plants (Schietti et al., 2014), pseudoscorpions (Aguar et al., 2006), oribatid mites (Moraes et al., 2011), frogs (Menin et al., 2007), snakes (Fraga et al., 2011), birds (Bueno et al., 2012), bats (Pereira et al., 2019), and monkeys (Kinap et al., 2021). In these studies, topographic and edaphic factors, such as elevation, HAND, slope, and soil granulometry, explained part of the variation in species composition in space. However, these studies have yet to investigate whether these patterns are stable. Our results showed that, regardless of the species identity (more than 50% of the ant species composition changed between years), topography remained a good predictor of ant assemblage composition over time.

Is temporal beta diversity similar along the topographic gradient?

Terrain slope was the best predictor of species composition changes between years. We hypothesized that steeper areas would be more susceptible to species substitutions due to more recurrent disturbances. However, our data indicated the opposite trend. While this was not a strong pattern, the ant assemblage turnover between 2006 and 2012 and 2006 and 2018 was higher in flat than inclined plots. This result, together with the spatial pattern (within sampling periods), also suggests that steeper slopes may act more as an environmental filter than a recurrent disturbance source for the ground-dwelling ants. The environmental conditions in areas with steep slopes may select or limit species establishment, favouring some species over others. In this case, the reduced number of species capable of establishing and persisting in these conditions may lower the species turnover over time.

For many organisms, including ants, the valleys are often cited as dynamic environments because of the water-level fluctuations in areas closest to the streams (Souza Holanda et al., 2021; Toledo et al., 2012). Valleys also have fewer species and differ from higher and better-drained areas (Landeiro et al., 2018). These two characteristics led us to predict that the topo-edaphic gradient would explain at least some variation in taxonomic and functional composition change over time. The most frequent disturbances in the valleys would act as a continuous source for the reorganisation of the species in each sampling year. Thus, the valleys would concentrate most of the species turnover. Our results confirm this hypothesis. However, the pattern was relatively weak and inconsistent, detected only between 2006 and 2018. These results make it clear that our understanding of the effects of environmental variables on ant diversity is still limited and that predicting temporal patterns based on ant diversity spatial patterns needs to be done with caution.

In tropical forests, ants are locally highly diverse, and patterns reported for one stratum may not hold for the entire assemblage (Torres et al., 2020; Wilkie et al., 2010). The leaf-litter ant fauna, typically sampled with Winkler extractors, is composed of more cryptic and smaller species, many of them with specialised habitat requirements, while ground-dwelling ant assemblages, often sampled with pitfall traps, are dominated by larger and more mobile species (Olson, 1991; Wiezik et al., 2015). Although both strata are highly dynamic, leaf-litter ant assemblage composition seems more stable over time than ground-dwelling-ant assemblages (Castro et al., 2012; Donoso, 2017). Despite ground-dwelling ants showing desirable characteristics to indicate ecological disturbance (larger species with higher dispersal abilities), more studies are needed to understand if patterns gathered from pitfall traps apply to other strata or the entire ant community.

AUTHOR CONTRIBUTIONS

Ana Cristina da Silva Utta: Investigation; writing – original draft; methodology; validation; visualization; writing – review and editing. **Adriano Henrique Cruz de Oliveira:** Investigation; methodology; validation; visualization; writing – review and editing. **Jorge Luiz Pereira de Souza:** Investigation; methodology; validation; visualization; writing – review and editing. **Itanna Oliveira Fernandes:** Investigation; methodology; validation; visualization; writing – review and editing. **William Ernest Magnusson:** Investigation; methodology; validation; visualization; writing – review and editing. **Fabricio Beggiato Baccaro:** Conceptualization; investigation; validation; visualization; writing – review and editing; software; methodology; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at https://github.com/Fabricera/Utta_etal/.

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SUPPORTING INFORMATION

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

Data S1. Supporting Information.

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