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Logging residues maintain ant functional diversity after clear-cutting of rubber plantations in Côte d'Ivoire

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ABSTRACT

Replanting rubber (*Hevea brasiliensis*) plantations involves canopy removal and major disturbance of the litter and soil surface. We tested whether retaining logging residues and sowing a legume cover (*Pueraria phaseoloides*) maintain the functional structure of ant assemblages after clear-cutting of 38-40-year-old stands at two sites with contrasting soils in Côte d'Ivoire. Ants were collected with pitfall traps before clear-cutting and 3 and 12 months thereafter across four residue-management treatments: bare soil, legumes only, legumes with leaves, branches and stumps, and legumes combined with all residues, including trunks. Weber's length, head width and mandible length were measured on 532 workers of 46 species (51 species and 4,389 workers collected in total). Intraspecific variation accounted for less than 3% of the variation in community-weighted traits; changes in functional composition were therefore primarily associated with species turnover. Residue retention increased species richness (+4.7 species), functional dispersion (+0.30), functional richness and community-weighted relative mandible length, and shifted functional composition (PERMANOVA R^2 = 0.18, p = 0.044). Without residues, Tetramorium sericeiventre, which was absent before clear-cutting, accounted for 52-85% of workers at 12 months, and functional dispersion fell below null-model expectations on bare soil (standardized effect size = -1.6, $p < 0.05$). In residue-retention plots, this species accounted for less than 2% of workers, while functional dispersion remained close to pre-disturbance levels. Legume cover alone did not prevent this functional homogenization. These results suggest that retaining logging residues can help maintain ant functional diversity during the first year of rubber replanting.

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INTRODUCTION

Natural rubber (*Hevea brasiliensis*) plantations have expanded rapidly across the humid tropics, with strong impacts on biodiversity (Ahrends *et al.*, 2015; Warren-Thomas *et al.*, 2015). Most plantations are now replanted after one or more 25-40-year cycles, and successive rotations degrade topsoil quality and soil biodiversity (Panklang *et al.*, 2022). The replanting phase is the most disruptive step of the cycle: the canopy is opened, trees are felled and uprooted with heavy machinery, and logging residues are usually exported or burned. In Côte d'Ivoire, retaining these residues after clear-cutting promotes the recovery of soil health (Perron *et al.*, 2022) and favours larger springtails with higher functional richness (Kouakou *et al.*, 2022). Whether residue retention also shapes the functional structure of soil-surface ant assemblages during rubber replanting remains unknown.

Ants are among the most abundant and functionally diverse arthropods of tropical soils and litter. They prey on other invertebrates, disperse seeds, tend hemipterans and move large amounts of soil (Folgarait, 1998; Philpott and Armbrecht, 2006). Because they respond quickly to changes in habitat structure, microclimate and resources, ants are widely used as indicators of disturbance (Andersen, 2019). Conversion of forest to rubber reorganizes the taxonomic, functional and phylogenetic diversity of ant assemblages (Liu *et al.*, 2016), and land-use change alters ant communities in Côte d'Ivoire (Yeo *et al.*, 2011; Vogel *et al.*, 2024). The response of ants to residue management within the replanting phase has not been examined.

Trait-based approaches link the morphology of organisms to the filters that act on them (Violle *et al.*, 2007; Pey *et al.*, 2014; Wong *et al.*, 2019). In ants, body size, head width and mandible length are standard traits related to resource use, foraging strategy and prey handling (Kaspari and Weiser, 1999; Weiser and Kaspari, 2006; Silva and Brandão, 2010; Parr *et al.*, 2017). Habitat structure filters these traits: simple, open habitats favour different sizes and shapes than complex litter-rich habitats (Kaspari and Weiser, 1999; Gibb and Parr, 2013). Multivariate indices such as functional richness and functional dispersion summarize how species occupy trait space (Villéger *et al.*, 2008; Laliberté and Legendre, 2010).

Compared with null models, low functional dispersion indicates trait convergence, a signature of environmental filtering (Mouchet *et al.*, 2010; Wiescher *et al.*, 2012).

Disturbance often reduces the functional diversity of ant assemblages even when species richness changes little (Bihn *et al.*, 2010). Finally, community-level trait shifts can arise from species turnover or from intraspecific trait variation, and both components can be separated (Lepš *et al.*, 2011).

This study used a replicated field experiment at two sites in Côte d'Ivoire to test how logging residues and a legume cover crop affect the functional structure of ant assemblages during the first year after clear-cutting of rubber plantations. We tested four hypotheses. (H1) On bare soil, the exposed conditions following clear-cutting filter ant assemblages, leading to lower functional dispersion and greater dominance by a few open-habitat species. (H2) Retaining logging residues maintains higher functional diversity and a greater representation of species with relatively long mandibles by increasing habitat structural complexity and resource availability. (H3) Legume cover alone has an intermediate effect on ant functional diversity between bare soil and residue-retention treatments. (H4) Community-level trait responses are driven by species turnover rather than by intraspecific trait variation.

MATERIALS AND METHODS

Study sites

The research was carried out at two industrial rubber plantations located in southern Côte d'Ivoire, as described in the studies by Perron *et al.* (2022) and Kouakou *et al.* (2023, 2025).

The Bongo plantation, operated by the Société Africaine de Plantations d'Hévéas (SAPH), is situated

in the southeast of the country (5°30′32″ N, 3°32′52″ W), while the plantation belonging to the Société des Caoutchoucs de Grand-Béréby (SOGB) is in the southwest (4°43′10″ N, 7°06′42″ W). Both locations experience a subequatorial climate characterized by a major rainy season from May to July and a minor one from October to November, separated by a long dry season from December to April and a short dry period from August to September. The average annual rainfall is 1,640 mm at SAPH and 1,674 mm at SOGB, with monthly precipitation recorded during the study. The SAPH site is predominantly flat, with slopes less than 5%, and features a yellow ferralic Arenosol soil with a loamy sand texture in the top 0-10 cm layer (comprising 10% clay, 2% silt, and 87% sand). In contrast, the SOGB site is hilly, with slopes ranging from 10-25%, and has a red Ferralsol soil with a sandy clay loam texture (23% clay, 10% silt, and 67% sand). The topsoil (0-10 cm) at both locations is acidic, with a pH of 4.3 at SAPH and 4.7 at SOGB. SOGB exhibits higher total carbon (0.85% versus 1.28%) and total nitrogen (707 mg/kg versus 974 mg/kg) levels, whereas SAPH shows a greater availability of phosphorus (Bray II) at 7.2 mg/kg compared to 5.2 mg/kg at SOGB (Perron *et al.*, 2022). At both sites, the clear-cut areas represented the initial rubber cycle following the conversion of tropical rainforest, and the understory predominantly consisted of shrubs and grasses.

Experimental design

The 40-year-old (SAPH) and 38-year-old (SOGB) rubber stands (253 and 233 living trees ha^{-1}, respectively) were clear-cut using bulldozers in November 2017. Before clear-cutting, living trees were inventoried so that residue quantities would be similar among blocks. Branches and trunks were cut into 1-2 m sections with a chainsaw, and a bulldozer with a V-shaped blade built windrows so that logging residues were placed in the inter-rows.

Between November 2017 and January 2018, the same randomized complete block design was set up at both sites, with four treatments in each of four blocks, giving 16 plots per site (38.5 × 40 m, i.e. 1540 m^2, at SAPH and 40 × 40 m, i.e. 1600 m^2, at SOGB). At SOGB, one block was on a 10–20% slope and the others on slopes below 10%. The treatments formed a gradient of organic matter inputs (Perron *et al.*, 2022):

R0L0 (control): all logging residues exported and no legume sown; plots were kept bare by weekly mechanical weeding.
R0L1: all residues exported and the legume *Pueraria phaseoloides* sown.
R1L1: trunks and large branches exported, while leaves, fine branches (< 20 cm diameter) and stumps of the previous stand were left in the inter-rows, together with the legume. This treatment represents the conventional residue management in commercial rubber plantations in Africa.
R2L1: all residues retained, including trunks and large branches, together with the legume.

P. phaseoloides was broadcast-sown at 10 kg ha^{-1} in February 2018. From August 2018, the inter-rows were weeded twice a month until the legume outcompeted weeds; it eventually colonized the windrows and completely covered the residues. In early March 2018, all plots were subsoiled to 60 cm depth in the planting rows (not in the inter-rows) and received 200 kg ha^{-1} of dolomite. Young rubber trees were planted in May 2018 at SOGB (clone IRCA230, 8 × 2.5 m spacing) and in July 2018 at SAPH (clone IRCA41, 6 × 3 m spacing), with 40 g $tree^{-1}$ of a slow-release N-P-K-Mg fertilizer (15-8-9-3) in the planting hole (Perron *et al.*, 2022).

Ant sampling

Ants were sampled with pitfall traps (Agosti *et al.*, 2000): plastic cups 7 cm in diameter and 14 cm deep, a quarter filled with ethanol and glycerol, protected by a raised cover and left active for 48 h. In each plot, six traps were set in two lines of three within a central sampling area, to limit edge effects; in residue treatments the traps were placed in the windrows. Three campaigns were carried out: in the mature stands before clear-cutting (October 2017), about 3 months after clear-cutting (February 2018) and 12 months after clear-cutting. At 3 months, the R0L1

treatment was not sampled because the legume had just been sown and the plots did not yet differ from bare soil. Workers were counted, sorted and stored in 96% ethanol.

Identification and trait measurements

Specimens were mounted and identified to genus with Fisher and Bolton (2016), then to species with genus revisions and by comparison with a reference collection, with the help of a myrmecologist. Unnamed taxa were assigned to morphospecies.

Three morphological traits were measured on workers with a stereomicroscope (Motic SMZ-171) fitted with a camera (Table 1). In polymorphic species only minor workers were measured. Depending on availability, one to eight workers per species were measured in each assemblage, giving 532 workers of 46 species (median of four workers per species). Two size-corrected ratios were derived: relative head width (head width / Weber's length) and relative mandible length (mandible length / head width).

Table 1. Morphological traits measured on ant workers

Trait	Measurement	Ecological interpretation	Range among species
Weber's length (WL, mm)	Lateral view: anterodorsal margin of the pronotum to posteroventral margin of the propodeum	Body size; resource use, metabolic needs and movement through the litter (Kaspari and Weiser, 1999)	0.14-2.37
Head width (HW, mm)	Full-face view: maximum width of the head, eyes excluded	Size of prey handled and foraging strategy (Weiser and Kaspari, 2006)	0.13-1.62
Mandible length (ML, mm)	Full-face view: insertion at the clypeus to mandible apex	Diet breadth and degree of predatory specialization (Schofield *et al.*, 2016)	0.06-1.46
Relative head width (HW / WL)	Derived	Head shape independent of size	0.41-1.35
Relative mandible length (ML / HW)	Derived	Investment in mandibles independent of head size; associated with prey capture and dietary specialization	0.34-0.90

Ranges are species means across the 46 species measured.

Functional diversity

Since ant samples were combined across blocks for each treatment × site × date combination, the experimental blocks cannot be regarded as independent replicates in the functional analyses. Consequently, the treatment effects discussed here should be understood at the assemblage level, rather than as estimates for individual plots. Each species was given its mean trait values over all measured workers. Functional analyses used three weakly correlated traits: log-transformed Weber's length, relative head width and relative mandible length (Spearman $|\rho| \leq 0.59$), each standardized to zero mean and unit variance. Head width and mandible length were not used directly because they were almost collinear with Weber's length ($r = 0.94$-0.97 on log scale).

Because pitfall counts of social insects are inflated by recruitment, species were weighted by $\log(n + 1)$ workers. For each assemblage we computed community-weighted means (CWM) of each trait, functional dispersion (FDis; Laliberté and Legendre, 2010), Rao's quadratic entropy and functional richness (FRic, the convex-hull volume occupied by the species; Villéger *et al.*, 2008). Five species without measurements accounted for less than 0.3% of workers and were excluded from trait analyses.

To assess whether observed functional dispersion differed from that expected given species richness and abundance, we used a null model in which trait values were shuffled among the 46 species of the regional pool while species abundances were kept unchanged (999 randomizations; Gotelli and Graves, 1996). Standardized effect sizes (SES = [observed - mean of null] / standard deviation of null) below zero indicate trait convergence and above zero trait divergence (Mouchet *et al.*, 2010).

Statistical analyses

Treatment effects were tested on the 14 post-clear-cutting assemblages using linear models with site and sampling date included as fixed effects. The main predictor was residue retention, contrasting the residue-retention treatments (R1L1 and R2L1) with the treatments without retained residues (R0L0 and R0L1). We also fitted the organic matter gradient as an ordinal predictor (R0L0 = 0, R0L1 = 1, R1L1 = 2, and R2L1 = 3). To assess the sensitivity of the results to abundance weighting, FDis and community-weighted means (CWM) were recalculated using both presence–absence and raw abundance data.

Functional diversity metrics, including functional dispersion (FDis), functional richness (FRic) and Rao's quadratic entropy (RaoQ), were calculated using the FD package (Laliberté *et al.*, 2014). Functional composition was described using a principal component analysis (PCA) of standardized community-weighted trait values. Differences in functional composition were tested using permutational multivariate analysis of variance (PERMANOVA) based on Euclidean distances, implemented with the vegan package (Oksanen *et al.*, 2025). For PERMANOVA, 9999 permutations were used, with permutations restricted within each site × sampling-date stratum for the residue-retention effect and within sampling dates for the site effect.

Intraspecific trait responses were evaluated using linear mixed-effects models fitted with the lme4 package (Bates *et al.*, 2015), with significance testing performed using lmerTest (Kuznetsova *et al.*, 2017). Models with and without treatment effects were compared using likelihood-ratio tests. Variation in community-weighted traits was partitioned into species turnover, intraspecific trait variability and their covariation following Lepš *et al.* (2011), using assemblage-specific species means where available.

To examine whether species responses to residue retention were related to morphological traits, we calculated the log response ratio of abundance in residue-retention plots relative to plots without retained residues for the 29 species represented by at least three workers at 12 months. Response ratios were averaged across the two sites and related to morphological traits using Spearman rank correlations and weighted multiple regression.

Mean trait values among treatments were also compared within each site at 12 months using one-way ANOVA or Kruskal–Wallis tests, as appropriate. All statistical analyses were conducted in R (R Core Team, 2025). Statistical significance was assessed at $\alpha = 0.05$.

RESULTS

Ant assemblages

In total, 4,389 workers of 51 species, 21 genera and five subfamilies were collected: Myrmicinae (25 species), Formicinae (12), Ponerinae (10), Dolichoderinae (3) and Dorylinae (1). The richest genera were *Strumigenys* (6 species), *Lepisiota* and *Tetramorium* (5 each). A total of 43 species were found at SAPH and 37 at SOGB (Table 2). Species richness was 17 (SAPH) and 14 (SOGB) before clear-cutting. At 12 months it ranged from 12-13 species on bare soil to 18-25 species in residue plots.

Trait space

The first two axes of the species-level PCA explained 85.1% of trait variation (Fig. 1). The first axis (58.4%) opposed large species with relatively narrow heads, such as *Camponotus maculatus* and the ponerines *Paltothyreus tarsatus* and *Odontomachus troglodytes*, to small species with relatively broad heads, such as *Tetramorium anxium* and *Pheidole megacephala*.

The second axis (26.7%) was driven by relative mandible length, highest in *Paltothyreus tarsatus*, *O. troglodytes* and some *Strumigenys* species. *Tetramorium sericeiventre*, the species that colonized bare soil, was of intermediate size with relatively short mandibles.

Trait values within species did not respond to treatments

At 12 months, mean trait values per species did not differ detectably among treatments at either site (one-way ANOVA: SAPH $F \leq 0.52$, $p \geq 0.67$; SOGB $F \leq 0.35$, $p \geq 0.79$; Kruskal-Wallis $p \geq 0.55$). In mixed models, treatment did not affect any trait within species (likelihood-ratio tests, $p = 0.15$-0.81). Species identity accounted for 96-98% of the variance in Weber's length, head width and mandible length, 69%

in relative head width and 47% in relative mandible length. Species turnover explained 94% (Weber's length), 97% (head width) and more than 99% (mandible length) of the variation in community-weighted traits among assemblages, against at most 2.7% for intraspecific variability.

Table 2. Ant species collected before and after clear-cutting at SAPH and SOGB, with species mean Weber's length (WL), head width (HW) and mandible length (ML), number of workers measured and number of workers collected per site (all treatments and dates pooled)

Subfamily	Species	WL (mm)	HW (mm)	ML (mm)	Workers measured	Workers SAPH	Workers SOGB
Dolichoderinae	*Tapinoma lugubre*	0.20	0.17	0.10	20	67	45
Dolichoderinae	*Tapinoma luteum*	0.22	0.15	0.08	1	18	1
Dolichoderinae	*Technomyrmex andrei*	—	—	—	0	1	0
Dorylinae	*Parasyscia* sp.1	—	—	—	0	0	1
Formicinae	*Camponotus acvapimensis*	0.80	0.61	0.31	11	12	7
Formicinae	*Camponotus cinctellus*	0.96	0.57	0.32	19	37	1
Formicinae	*Camponotus maculatus*	1.51	0.62	0.38	11	14	1
Formicinae	*Lepisiota capensis*	0.29	0.22	0.11	2	2	0
Formicinae	*Lepisiota* sp.1	0.32	0.25	0.13	1	0	1
Formicinae	*Lepisiota* sp.2	0.33	0.23	0.10	2	1	3
Formicinae	*Lepisiota* sp.3	0.20	0.18	0.09	4	6	3
Formicinae	*Lepisiota* sp.4	0.21	0.18	0.09	6	5	7
Formicinae	*Nylanderia boltoni*	0.21	0.19	0.11	31	89	58
Formicinae	*Nylanderia scintilla*	0.21	0.19	0.10	17	59	24
Formicinae	*Oecophylla longinoda*	1.06	0.72	0.47	4	4	2
Formicinae	*Polyrhachis viscosa*	0.57	0.56	0.19	1	1	0
Myrmicinae	*Cardiocondyla emeryi*	0.16	0.14	0.07	2	2	0
Myrmicinae	*Cardiocondyla neferka*	—	—	—	0	1	0
Myrmicinae	*Cardiocondyla shuckardi*	0.22	0.19	0.11	26	148	18
Myrmicinae	*Carebara* sp.1	—	—	—	0	0	7
Myrmicinae	*Monomorium bicolor*	0.31	0.24	0.11	1	0	0
Myrmicinae	*Monomorium inquietum*	0.18	0.14	0.08	5	2	6
Myrmicinae	*Monomorium invidium*	0.20	0.17	0.10	6	0	8
Myrmicinae	*Monomorium rosae*	0.15	0.12	0.09	6	5	8
Myrmicinae	*Monomorium trake*	0.14	0.12	0.07	8	16	1
Myrmicinae	*Pheidole buchholzi*	0.49	0.36	0.25	11	74	69
Myrmicinae	*Pheidole megacephala*	0.28	0.26	0.15	63	365	635
Myrmicinae	*Pheidole* sp.4	0.24	0.22	0.15	4	11	47
Myrmicinae	*Pheidole* sp.5	0.22	0.20	0.13	48	102	315
Myrmicinae	*Solenopsis* sp.1	0.15	0.13	0.06	5	12	0
Myrmicinae	*Strumigenys bernardi*	0.15	0.15	0.10	2	0	4
Myrmicinae	*Strumigenys ludovici*	0.23	0.18	0.10	2	13	0
Myrmicinae	*Strumigenys ninda*	—	—	—	0	0	1
Myrmicinae	*Strumigenys rogeri*	0.18	0.18	0.12	4	1	4
Myrmicinae	*Strumigenys rufobrunea*	0.16	0.15	0.09	7	6	6
Myrmicinae	*Strumigenys serrula*	0.20	0.16	0.09	1	1	2
Myrmicinae	*Tetramorium anxium*	0.21	0.22	0.11	29	169	63
Myrmicinae	*Tetramorium ataxium*	0.23	0.31	0.15	1	2	0
Myrmicinae	*Tetramorium intonsum*	0.25	0.24	0.13	1	2	0
Myrmicinae	*Tetramorium sericeiventre*	0.42	0.33	0.19	57	481	794
Myrmicinae	*Tetramorium zapyrum*	0.27	0.30	0.15	1	11	0
Ponerinae	*Euponera brunoi*	0.44	0.34	0.22	3	0	3
Ponerinae	*Hypoponera dulcis*	0.25	0.19	0.11	3	3	0
Ponerinae	*Hypoponera lepida*	0.23	0.16	0.09	1	0	2
Ponerinae	*Hypoponera punctatissima*	0.31	0.19	0.13	1	1	1
Ponerinae	*Hypoponera venusta*	0.22	0.16	0.10	1	3	0
Ponerinae	*Leptogenys nussera*	0.41	0.24	0.12	1	1	0
Ponerinae	*Mesoponera ambigua*	0.49	0.37	0.28	2	0	3
Ponerinae	*Mesoponera caffraria*	0.83	0.60	0.34	14	9	9
Ponerinae	*Odontomachus troglodytes*	1.14	0.80	0.59	50	88	233
Ponerinae	*Paltothyreus tarsatus*	2.37	1.62	1.46	36	140	11

Monomorium bicolor was recorded only among the measured specimens (one worker at SAPH). —, no measurement.

Table 3. Mean functional metrics of ant assemblages by treatment, and effect of residue retention (R1L1 and R2L1 versus R0L0 and R0L1) on the 14 after clear-cutting assemblages, from linear models with site and date as blocking factors (coefficient ± SE).

Metric	Before clear-cutting	R0L0	R0L1	R1L1	R2L1	Residue effect	p
Species richness	15.5	13.3	16.5	18.0	18.5	+4.65 ± 1.52	0.012
Functional dispersion (FDis)	1.49	1.09	1.31	1.48	1.46	+0.30 ± 0.09	0.005
Rao's quadratic entropy	1.94	1.48	1.79	1.96	1.95	+0.38 ± 0.11	0.005
Functional richness (FRic)	8.89	4.02	7.49	7.92	9.23	+3.96 ± 1.41	0.018
SES of FDis	0.31	-1.12	-0.51	0.19	0.24	+1.14 ± 0.35	0.009
SES of FRic	0.13	-0.89	-0.50	-0.62	-0.43	+0.27 ± 0.15	0.102
CWM Weber's length (mm)	0.54	0.42	0.48	0.53	0.52	+0.075 ± 0.036	0.062
CWM relative head width	0.82	0.84	0.83	0.83	0.84	−0.003 ± 0.013	0.840
CWM relative mandible length	0.632	0.599	0.597	0.620	0.614	+0.016 ± 0.005	0.010
FDis, presence-absence weights	1.56	1.30	1.60	1.51	1.46	+0.08 ± 0.08	0.293
FDis, raw abundance weights	1.28	0.53	0.73	1.27	1.42	+0.72 ± 0.17	0.002

Means are over sites and dates (before clear-cutting n = 2; R0L0, R1L1, R2L1 n = 4; R0L1 n = 2, 12 months only). SES, standardized effect size against the null model; CWM, community-weighted mean.

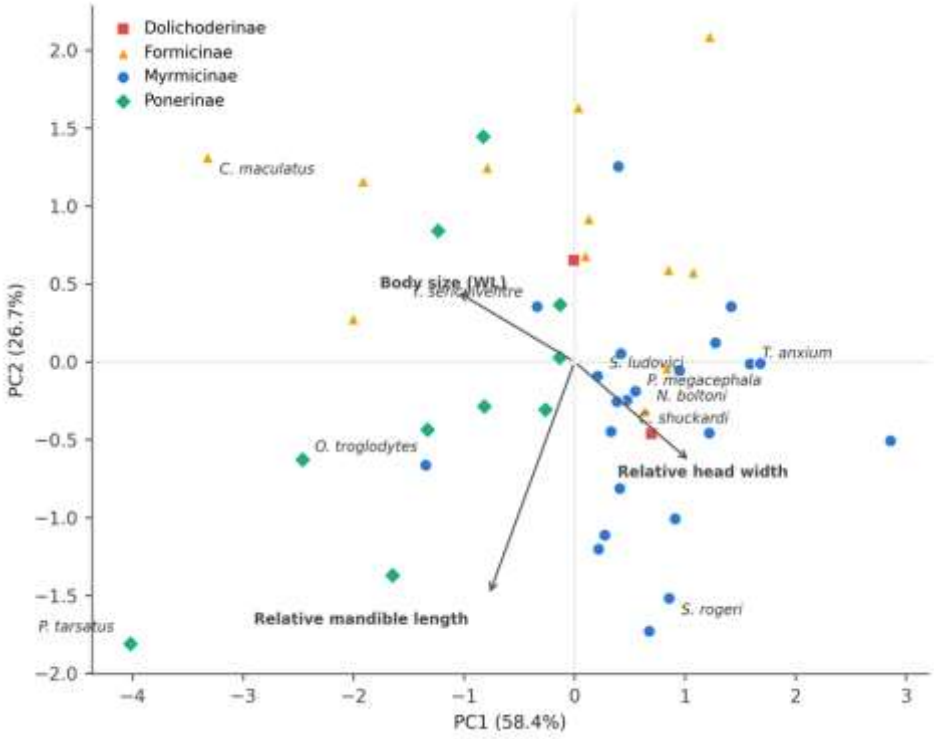


Fig. 1. Functional trait space of the ant species measured: principal component analysis of log Weber's length, relative head width and relative mandible length (standardized species means). Arrows show trait loadings; labelled species are the most abundant or most extreme.

Residues maintained functional diversity

Retaining residues increased species richness, functional dispersion, Rao's entropy and functional richness, and shifted community-weighted relative mandible length upwards (Table 3). The same metrics increased along the organic matter gradient ($p \leq 0.027$). After clear-cutting, functional dispersion fell sharply on bare soil, from 1.72 to 1.05 at SAPH after 3 months and from 1.27 to 0.88 at SOGB after 12 months, whereas residue plots stayed within 12% of pre-felling values (Fig. 2C, D). Bare-soil assemblages had lower functional dispersion than expected from their richness and abundances (SES = -1.62, p = 0.037 at SAPH after 3 months; SES = -1.58, p = 0.023

at SOGB after 12 months; Fig. 2E, F). The standardized effect size of functional dispersion increased with residue retention (+1.14; Table 3). By contrast, the standardized effect size of functional richness did not change with residues ($p = 0.10$), showing that the gain in functional richness followed the gain in species. The legume-only treatment was intermediate for all metrics.

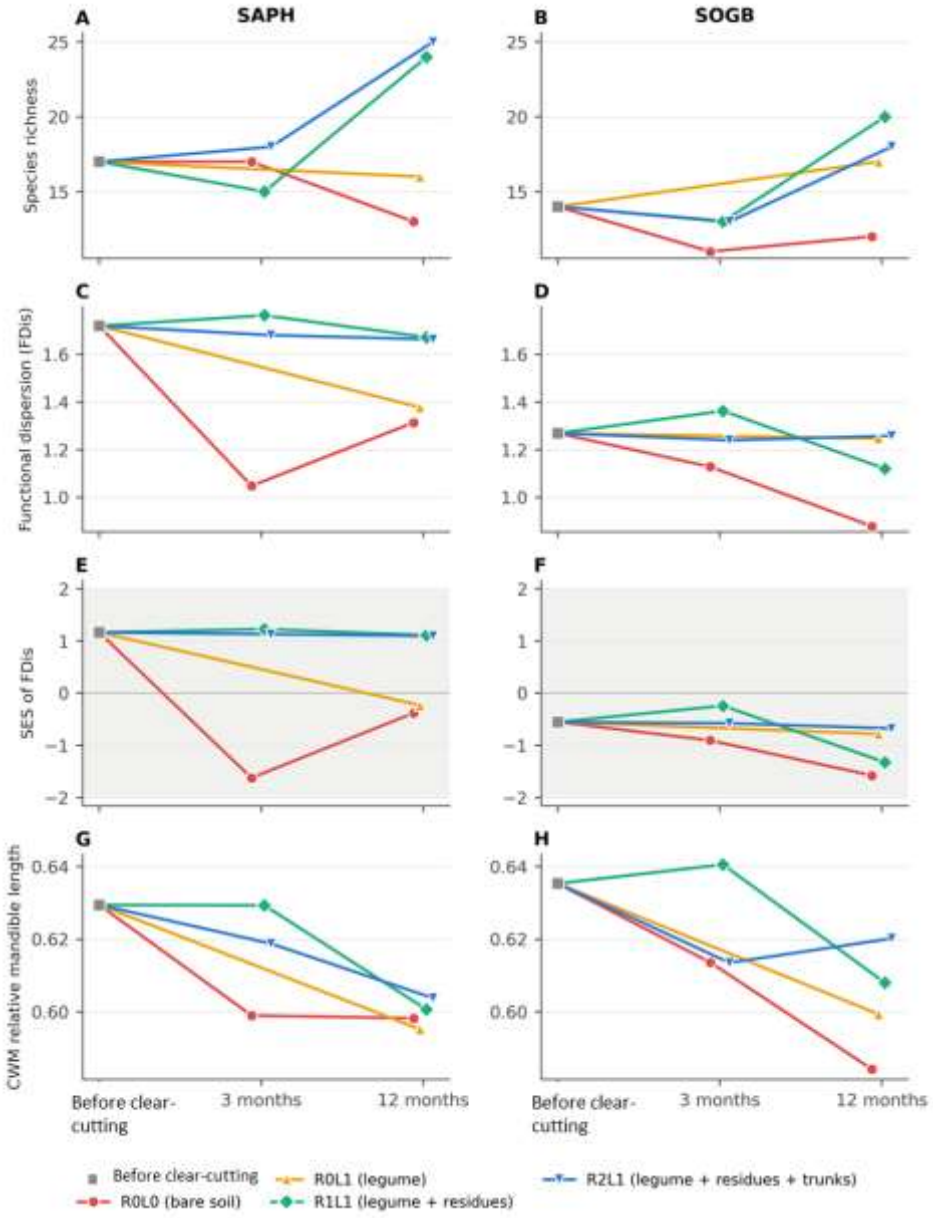


Fig. 2. Species richness (A, B), functional dispersion (C, D), standardized effect size of functional dispersion (E, F) and community-weighted relative mandible length (G, H) of ant assemblages before clear-cutting and 3 and 12 months after felling at SAPH and SOGB. The shaded band in E-F (-1.96 to 1.96) shows the range expected under the null model. R0L1 was not sampled at 3 months.

Dominance by an open-habitat species on bare soil

The weighting test in Table 3 shows where the functional signal came from: with presence-absence weights, functional dispersion no longer differed between treatments, whereas with raw abundances the residue effect was stronger. The effect therefore came from changes in dominance. *Tetramorium sericeiventre* was absent from both sites before clear-cutting. At 12 months it made up 85% (SAPH) and

79% (SOGB) of workers on bare soil and 58% and 52% in legume-only plots, but less than 2% in residue plots at both sites (Fig. 3). Residue plots were shared among several species, including *P. megacephala*, *T. anxium*, *O. troglodytes* and *Nylanderia boltoni*. At SOGB, *P. megacephala* nevertheless made up 48-58% of workers in residue plots at 12 months, and functional dispersion in R1L1 was then lower than expected by chance, though not significantly (SES = -1.32, p = 0.087).

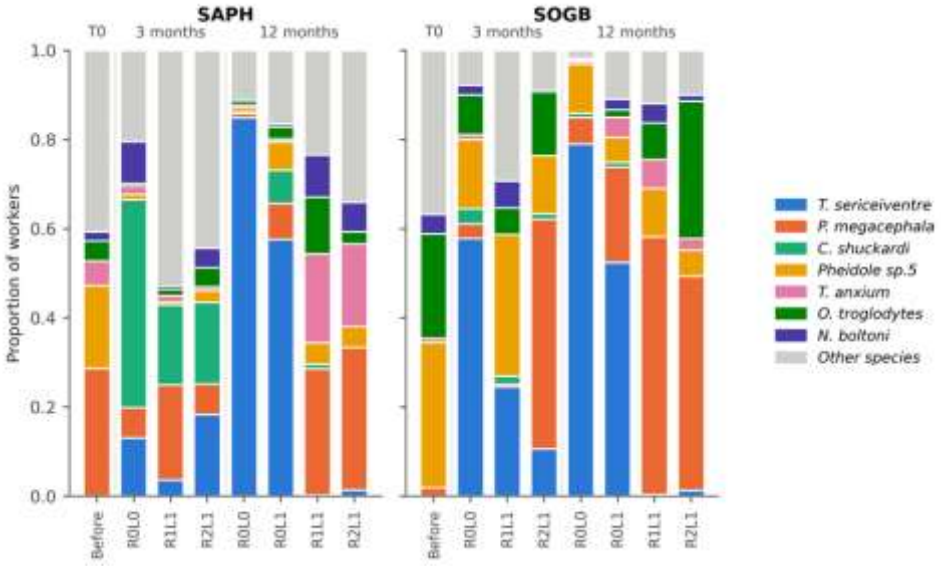


Fig. 3. Proportion of workers belonging to the seven most abundant ant species in each treatment before clear-cutting (T0) and 3 and 12 months after clear-cutting at SAPH and SOGB.

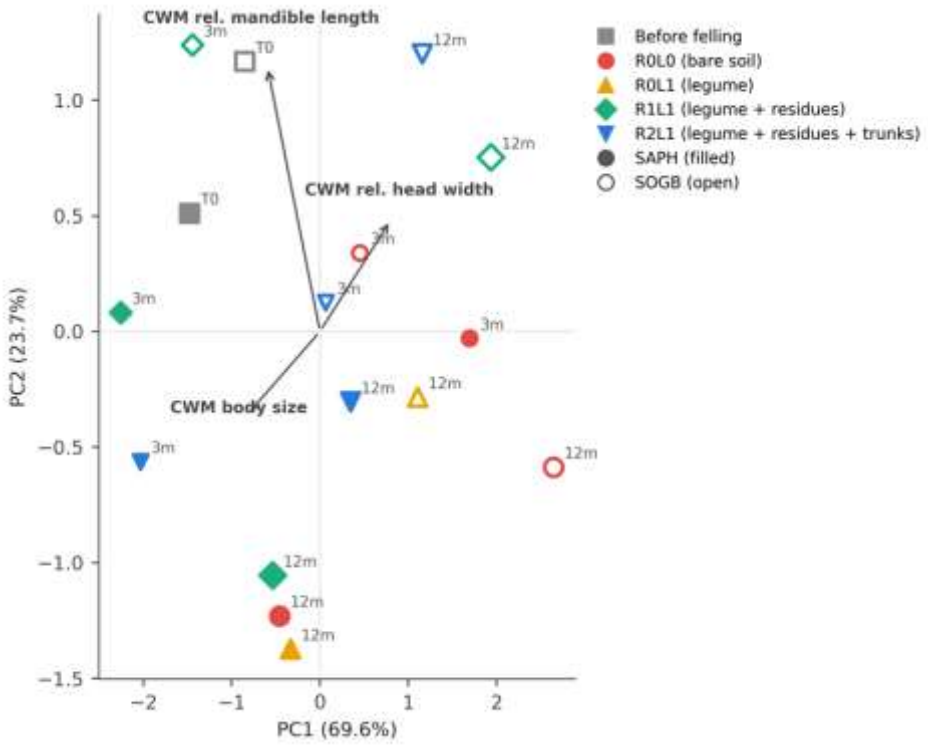


Fig. 4. Principal component analysis of community-weighted mean traits of the ant assemblages. Filled symbols, SAPH; open symbols, SOGB; labels give the sampling date (T0, before; 3months and 12months after clear-cutting).

No single trait predicted how species responded to residues at 12 months (29 species; Spearman $|\rho| \leq 0.32$, $p \geq 0.09$; weighted multiple regression $R^2 = 0.10$, $p = 0.43$). No significant relationship was detected between the measured traits and species responses to residue retention, suggesting that the response cannot be explained by any single trait measured here.

Functional composition of ant community

The first two PCA axes of community-weighted traits explained 93.3% of the variation (Fig. 4). The first axis (69.6%) ran from assemblages of larger workers (before clear-cutting and residue plots at 3 months) to assemblages dominated by small, broad-headed species: bare soil at SAPH after 3 months and at SOGB after 12 months, and SOGB residue plots at 12 months, where *P. megacephala* dominated. The second axis (23.7%) mainly reflected relative mandible length, which was lowest at SAPH after 12 months. Functional composition differed with residue retention (PERMANOVA, pseudo-$F = 2.64$, $R^2 = 0.18$, $p = 0.044$) and between sites (pseudo-$F = 4.37$, $R^2 = 0.24$, $p = 0.014$).

DISCUSSION

Bare soil filters ant traits through dominance

On bare soil, functional dispersion fell below null-model expectations, consistent with trait convergence under environmental filtering (Mouchet *et al.*, 2010; Wiescher *et al.*, 2012). This filtering appeared to act mainly through dominance rather than through the loss of species: with presence-absence weights, functional dispersion did not differ between treatments, whereas with abundance weights the difference was large. *Tetramorium sericeiventre*, absent from the mature stands, colonized the bare plots and made up to 85% of workers after one year. This open-habitat species appears well suited to the exposed and mechanically disturbed soil surface created after clear-cutting. The spread of a few stress-tolerant or opportunistic species after disturbance is a general feature of ant communities (Andersen, 2019), and disturbance often erodes functional diversity before species richness (Bihn *et al.*, 2010). Our results suggest that such erosion can occur within the first year after clear-cutting. Its timing differed between sites: the deficit in functional dispersion was significant at SAPH after 3 months and at SOGB after 12 months (Fig. 2E, F), which may reflect the contrasting soils and topography of the two sites.

The legume-only treatment did not prevent this shift: *T. sericeiventre* still made up more than half of workers there at 12 months. During the first year after clear-cutting, the young *Pueraria* cover, sown in February 2018, may have provided a less structurally complex habitat and fewer physical refuges than woody residues. This agrees with the response of the soil macrofauna in the same experiment, in which legume cover alone restored density but not diversity (authors' unpublished data), and with the faster recovery of soil health in residue plots (Perron *et al.*, 2022).

Residues maintain functional dispersion and species with relatively long mandibles

Residue plots kept functional dispersion within 12% of pre-clear-cutting values and had slightly longer relative mandibles on average (+0.016). Species with relatively long mandibles include predatory taxa such as *Odontomachus troglodytes*, *Paltothyreus tarsatus* and *Strumigenys* spp. (Weiser and Kaspari, 2006; Schofield *et al.*, 2016). Woody residues provide moist microsites, nesting sites in decaying wood and abundant prey: in the same experiment, springtails were more abundant and larger where residues were retained (Kouakou *et al.*, 2022). The maintenance of species with relatively long mandibles may therefore reflect differences in habitat structure and resource availability between residue-retention and bare-soil treatments. Body size tended to be larger in residue plots ($p = 0.062$), but our data do not allow a firm test of the size-grain hypothesis, which predicts that small ants are favoured in complex litter (Kaspari and Weiser, 1999; Gibb and Parr, 2013). The direction of this trend is opposite to that prediction. Windrows of logs and branches may form a coarser-grained structure than the fine litter for which the hypothesis was formulated, but this remains to be tested. Leg length, the trait most directly linked to that hypothesis, was not measured.

During the first year after clear-cutting, retaining trunks in addition to leaves, branches and stumps (R2L1 versus R1L1) provided no detectable additional benefit for the functional metrics measured, despite more than doubling the carbon input. The same pattern was found for the soil macrofauna in this experiment (authors' unpublished data). With four assemblages per treatment, however, the absence of a detectable difference does not show that the two treatments are equivalent, and trunks, which decompose slowly, may influence ant assemblages over a longer period.

Residue retention did not consistently prevent dominance by a single species. At SOGB, the big-headed ant *Pheidole megacephala*, already present before clear-cutting, made up about half of workers in residue plots after one year, and functional dispersion there tended to be lower than expected (SES = -1.32, p = 0.087). *Pheidole megacephala* is a widespread species frequently associated with disturbed tropical habitats and can form highly dominant populations (Holway *et al.*, 2002; Wetterer, 2012). This site-specific pattern is consistent with the stronger effect of site than of residue retention on functional composition (PERMANOVA R^2= 0.24 versus 0.18), and suggests that residue retention reduces, but does not remove, the risk of dominance by a single species. Its dynamics, and its possible effects on other ants, should be monitored during the immature phase of the plantations.

Species turnover drives the functional response

Within species, trait values did not differ detectably among treatments, and intraspecific variability accounted for less than 3% of community-level trait variation. Over the first year after clear-cutting, the observed functional response was therefore primarily associated with changes in species composition and, particularly, species dominance (Lepš *et al.*, 2011). This may also explain why simple comparisons of mean trait values among treatments, which give each species the same weight, did not detect any effect. Abundance-weighted indices compared with null models were needed to reveal the filtering of bare soil. No single trait predicted species responses to residue retention (Spearman $|\rho| \leq 0.32$), which suggests that the response combines several traits or depends on traits not measured here, such as thermal tolerance, diet or nesting habits (Parr *et al.*, 2017; Wong *et al.*, 2019).

Limitations

Pitfall traps primarily sample epigaeic foragers and may underrepresent cryptic species associated with litter and soil habitats (Agosti *et al.*, 2000). Because worker abundance in social insects can be strongly influenced by recruitment, raw worker counts may not accurately reflect colony-level or species-level abundance. We therefore used log-transformed weights to reduce the influence of highly recruited species and tested alternative weighting schemes: the residue effect on functional dispersion was stronger with raw abundances and was not detected with presence-absence weights. Our conclusions on functional dispersion therefore concern changes in dominance rather than in species occurrence. In residue treatments, traps were placed in the windrows, so that the comparison with bare soil partly reflects differences in microhabitat at the trap location rather than at the scale of the whole plot.

Trait data were available for treatment-level assemblages rather than individual blocks, preventing block-level analyses of functional composition. Consequently, the statistical tests were based on 14 post-clear-cutting assemblages, with site and sampling date included as blocking factors. This design limits the statistical resolution at the assemblage level and calls for cautious interpretation of treatment effects.

The study covered only the first year following clear-cutting. Longer-term monitoring is therefore needed to determine whether the observed functional differences persist as vegetation recovers and the rubber canopy develops. In addition, the three morphological traits measured here represent only a subset of the functional dimensions of ant communities. Incorporating additional traits, such as

leg length and eye size, together with ecological traits related to habitat use, foraging strategy or trophic position, would provide a more comprehensive assessment of functional responses and their potential consequences for ecosystem functioning.

Finally, morphological measurements were based on a limited number of workers per species, with a median of four individuals. Although species-level mean trait values captured most of the variation in community-weighted traits, this sampling intensity may have reduced our ability to detect subtle intraspecific variation. Increasing the number of measured workers per species would therefore improve estimates of within-species trait variability and provide a stronger basis for partitioning functional responses into interspecific turnover and intraspecific variation.

CONCLUSION

One year after clear-cutting, bare-soil treatments were associated with reduced functional dispersion and a strong dominance of *Tetramorium sericeiventre*, whereas retaining logging residues maintained ant functional diversity closer to that of mature stands at both sites.

Legume cover alone did not prevent this functional shift, while retaining trunks provided no detectable additional benefit over retaining leaves, branches and stumps during the first year.

Because trait values did not differ detectably within species over this period, changes in functional structure primarily reflected species turnover and shifts in species dominance, as indicated by abundance-weighted indices and null-model analyses. Overall, our results suggest that retaining fine logging residues and stumps, together with legume cover, can help maintain ant functional diversity during the first year of rubber replanting.

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