EUROPEAN JOURNAL OF ENTOMOLOGY
ISSN (online): 1802-8829
http://www.eje.cz
Eur. J. Entomol. **123**: 14–23, 2026
doi: 10.14411/eje.2026.003
ORIGINAL ARTICLE

Ant assemblages (Hymenoptera: Formicidae) in rehabilitated areas of a coal mine in Cesar, Colombia

Danis HORMECHEA-GARCÍA, Rodian FONSECA-CAMPUZANO and Yamileth DOMÍNGUEZ-HAYDAR

Facultad de Ciencias Básicas, Universidad del Atlántico, Cra 30 # 8-49 Puerto Colombia, Colombia;
e-mails: danis_marcela@hotmail.com, rfonsecacampuzano@mail.uniatlantico.edu.co,
yamilethdominguez@mail.uniatlantico.edu.co

Key words. Tropical dry forest, open-pit mine, biodiversity, ecosystem degradation, bioindicators, reclamation

Abstract. Open-pit coal mine rehabilitation is essential to mitigate ecosystem degradation and biodiversity loss. Given that ants (Hymenoptera: Formicidae) are excellent bioindicators, we evaluated the response of their communities along a restoration gradient in a tropical dry forest ecosystem. Sampling was conducted in five sites: three areas with different rehabilitation ages (1.5, 4, and 7 years) and two ecosystems not affected by mining (a dry forest fragment and a natural regeneration area). A total of 65 species and morphospecies were recorded, belonging to 30 genera and seven subfamilies. A key finding was the asynchronous recovery of diversity: while species richness (q0) in the sites with longer rehabilitation times resembled that of the reference forest, community structure, measured by evenness (q1, q2), remained significantly lower, indicating a slower functional recovery. Composition analysis (NMDS) revealed a clear successional gradient, with the 7-year site representing an intermediate state in the trajectory toward reference forests. Notably, rehabilitation techniques such as mulch application in the youngest site (1.5 years) promoted the early colonization of specialist predatory ants, resulting in a more complex community than that of the 4-year site. We conclude that proactive rehabilitation, particularly measures focused on soil protection, accelerates the recovery of the ant community structure.

INTRODUCTION

Mining operations cause substantial alterations to ecosystems, leading to severe environmental damage and ecological degradation (Lei et al., 2016; Ličina et al., 2016). In particular, open-pit coal mining is a major driver of habitat disturbance, mainly through deforestation, extraction of the topsoil layer, and its subsequent deposition in landfills, causing spoilage in soil structure and density, loss of local biota, modifications to surface and underground water resources, large-scale landscape transformations, and environmental degradation (Holec & Frouz, 2005; Ribas et al., 2012; Yuan et al., 2017). Therefore, this activity has an impact on the structural dynamics of ecosystems and the degradation of biological diversity (Blinova & Dobrydina, 2017).

To mitigate the effects caused, it is necessary to carry out ecological restoration or rehabilitation in the affected areas (Tizado & Núñez-Pérez, 2016; Lima et al., 2016). A post-mining landscape necessarily implies the recovery of soil and vegetation cover as sources of organic matter and driver elements in biogeochemical processes, both as prerequisites for the rehabilitation and stabilization of biodiversity and ecosystem processes (Frouz et al., 2001; Gastauer et al., 2018). Assessments of these processes are necessary to provide evidence of recovery outcomes, however, monitoring in rehabilitated areas has been mainly directed towards vegetation, and despite the fundamental role played by fauna in these processes, there is little information available (Thompson & Thompson, 2004; Ruiz-Jaen & Aide, 2005; Cristescu et al., 2012).

Terrestrial invertebrates play an important role as drivers of ecosystem processes and functions (Majer et al., 2007), and they have been used for monitoring in rehabilitation sites, particularly ants (Hymenoptera: Formicidae). They are a group of insects that have been studied for their abundance, richness, sensitivity to environmental changes, ecological functionality, ease of sampling, habitat specificity, also, their assemblages can reflect responses to ecological changes because their disturbance requirements are well understood (Alonso, 2000; Andersen et al., 2003; Blinova & Dobrydina, 2017). For these reasons, ants are recognized as reliable indicators of terrestrial ecosystems (Andersen et al., 2003, Andersen, 2019, Yeo et al., 2019, Sithole & Tantsi, 2020).

Beyond bioindication, ants elucidate community reassembly mechanisms critical for restoration. Neotropical studies suggest that ant communities can exhibit remarkable resilience, with species richness recovering rapidly, while compositional similarity to old-growth forests may lag, taking decades to fully recover (Hoenle et al., 2022). Moreover, recent evidence indicates that for ants, dispersal is rarely the limiting factor; reproductive queens (alates) of old-growth forest species can reach even the earliest stages of regeneration. However, they often fail to establish colonies due to environmental constraints (Grella et al., 2025). Consequently, rehabilitation in open-pit mines must prioritize alleviating these abiotic constraints to enable the successful establishment of colonizing species.

In this specific context of mine rehabilitation, ants have been successfully employed to assess ecological integrity. In Brazil, ants have been successfully employed to assess the ecological integrity of rehabilitated bauxite mining areas (Fernandes et al., 2021), while in India, they have been used to monitor the presence of heavy metals of coal mine spoils (Khan et al., 2023). Furthermore, research in Europe demonstrates their effectiveness in evaluating post-mining landscape restoration in temperate forests (Holec & Frouz, 2005). Similarly, in Australia, ants have been extensively used as bioindicators in mining rehabilitation, given their high diversity and functional importance in Australian ecosystems (Andersen et al., 2003; Majer, 2009; Hoffmann & Andersen, 2003). However, studies using ants as bioindicators in rehabilitated areas of mines in tropical forests are still scarce (Majer, 2009; Domínguez-Haydar & Armbrecht, 2011; Fernandez et al., 2021).

The study site is located in an open-pit coal mine within a tropical dry forest, one of the most threatened and endangered ecosystems both globally and in Colombia (García et al., 2014). These rehabilitation efforts are intended to progressively recover biological characteristics and conserve the region's biodiversity. Therefore, understanding the outcomes of these efforts on the recovery of soil fauna is essential.

The objective of this study was to determine the variation in ant richness, abundance, and composition across a chronosequence of rehabilitated sites and undisturbed areas within the mining concession. Specifically, we aimed to answer the following questions: (1) How do ant richness and abundance change across different stages of rehabilitation compared to undisturbed reference forests? (2) Does the taxonomic composition of antassemblages in rehabilitated areas converge toward the composition of the original tropical dry forest over time? (3) To what extent can these ant assemblages serve as reliable bioindicators of restoration success in open-pit coal mining landscapes?

We hypothesized that rehabilitation measures, by improving the vegetation structure, would favor the reestablishment of ant communities. It is expected that the ant assemblage in sites with longer rehabilitation time would be more like reference sites compared to areas with shorter rehabilitation time.

MATERIAL AND METHODS

Study area

This study was conducted at the Calenturitas Mine, an open-pit coal mining operation in the Cesar Department of northern Colombia, South America, at an elevation of 70–75 m a.s.l. The predominant ecosystem is tropical dry forest. Precipitation follows a bimodal pattern (April–June and September–November), with an average annual rainfall between 1,600 and 2,000 mm and a mean annual temperature of 27.9°C. As of 2017, the mine's total disturbed area reached approximately 1,827.24 ha, of which 534.92 ha were undergoing active rehabilitation (Prodeco, 2017).

The Calenturitas mining concession has 6677 ha and has two types of zones: natural biosensor areas (forests) and areas under rehabilitation process. The biosensor areas are characterized by forest cover at different stages of vegetation succession, whereas the dumps are areas that were used for the accumulation of rock, soil, and sterile material and are now undergoing vegetation cover rehabilitation, where pastures and planted trees at various developmental stages predominate (Calenturitas, 2018).

Five sites were selected, comprising three rehabilitated areas (1.5, 4, and 7 years post-rehabilitation) and two undisturbed reference forest sites (Fig. 1), each of which is described below.

• 1.5 years: At the time of the investigation, this site had been under rehabilitation for 1.5 years, covering an area of 2.6 ha. A distinct soil preparation methodology was applied here, consisting of depositing mulch (vegetative material from grass leaves and stems) to prevent water erosion and retain soil moisture. The site is located on a slope and supports a high cover of shrubs and herbaceous plants. No trees were planted.

• 4 years: Physical modifications were made to the terrain to accommodate the removed topsoil, followed by the planting of native tree species. The site is located on a slope with gullies and unstable, erosion-prone soil, leaving some areas uncovered. Grasses are present, along with sparsely distributed shrubs and trees. Vegetation cover ranges from 0% to 11%. This is the largest site, covering approximately 118 ha.

• 7 years: Located on the western spoil pile, this site covers an area of 90 ha. It has been under rehabilitation for approximately seven years, following the same method as the previous site (4 years). It is situated on a slope with some gullies, and in certain areas, the soil is very compact. There is greater tree coverage, some thorny shrubs, overgrown grasses, and scarce leaf litter. Vegetation cover ranges between 86% and 94%.

• Natural Regeneration (NR): This area (8.57 ha) is in the mine's advancing zone and has had no intervention for over 10 years, allowing for natural regeneration. Trees exceed eight meters in height, with the presence of native species and *Leucaena leucocephala* (Lam.) de Wit. The soil is partially covered with leaf litter and herbaceous plants. Average vegetation cover was 97%.

• Forest: This area, referred to as "biosensor zones", serves to facilitate the coexistence of native flora and fauna, functioning as a representative sample of the dominant ecosystems within the mining project. The sampled zone, covering approximately 9 ha, is characterized by native species, with trees over ten meters tall, an irregular canopy, and the occasional presence of shrubs, palms, and lianas, as well as high leaf litter coverage and regenerating seedlings. Some areas include a matrix of scattered trees with grassy undergrowth. Average vegetation cover was 98%.

Sampling design

Sampling was conducted three times during 2018 (May, September, and December). In each of the five sites, a 150 m transect was established in the interior of the habitat patch to minimize edge effects. We acknowledge that our study design represents a limited sample size for broad generalization. To address this, we employed statistical approaches that maximize the utility of the data collected and account for the repeated measures structure.

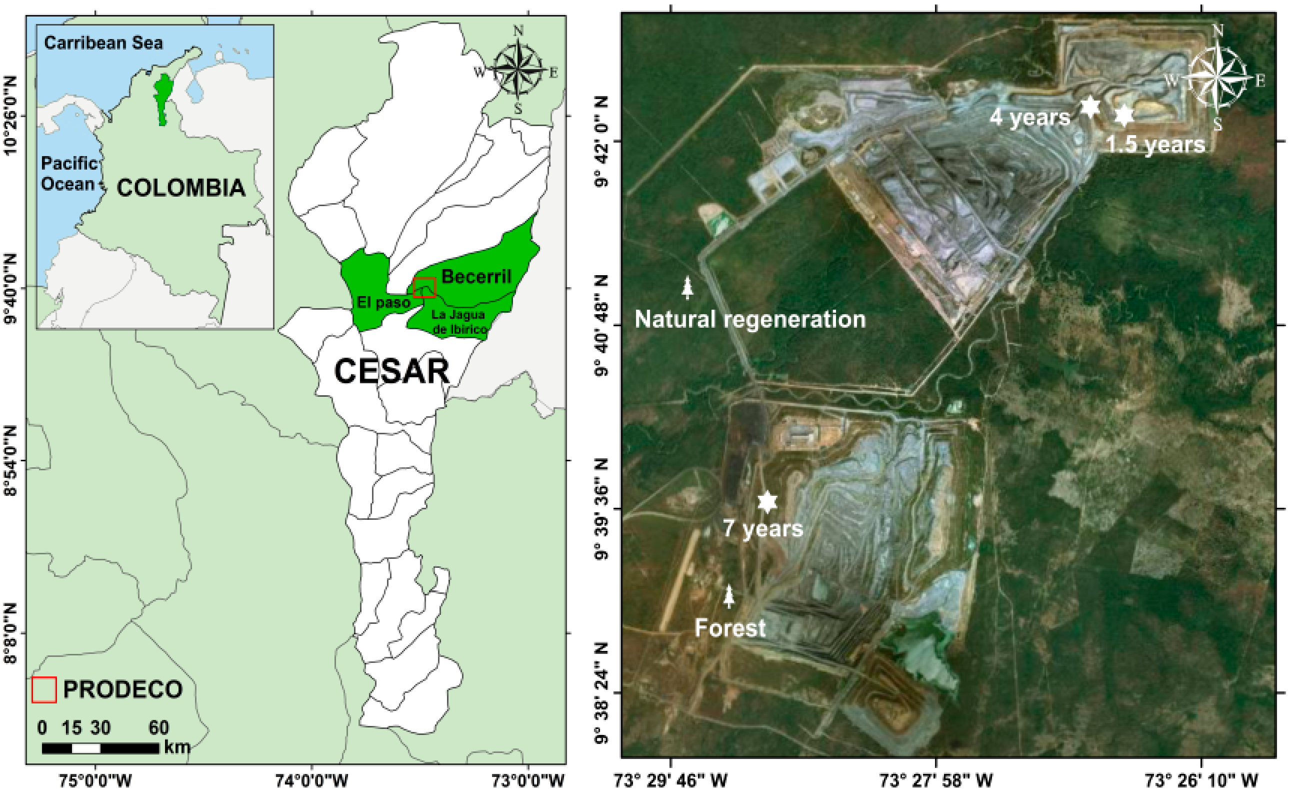

Fig. 1. Schematic map of the study area at the Calenturitas mine, showing the location of the three rehabilitated sites (1.5, 4, and 7 years) and two reference forests (one natural regeneration site, and one older successional forest).

A total of 12 sampling stations were installed along each transect, arranged in two distinct clusters. The first cluster of six stations was placed within the first 50 m of the transect (from the 0 m to the 50 m mark). The second cluster of six stations was placed within the final 50 m of the transect (from the 100 m to the 150 m mark). This design left a 50-meter gap in the center of the transect. Ants were collected were measured at each of these 12 stations. Two complementary sampling methods were employed at each station:

• Pitfall Traps: A 10-oz (approx. 295 ml) plastic container was installed buried flush with the ground. Each trap was partially filled with a solution of salt water and liquid soap and remained active in the field for approximately 48 h.

• Manual Sampling: A 10-minute per-person sampling effort was conducted at each station, focused between 08:00 and 10:00. This active search targeted ants found on the ground, in the leaf litter, within decomposing logs, under rocks, and on the surrounding vegetation.

The captured specimens were preserved in vials containing 70% ethanol. The ants were identified to the lowest possible taxonomic level using the keys for subfamilies and genera by Fernández et al. (2019) and the AntWeb page (https://www.antweb.org/). Those that could not be identified at this level were assigned a code (morphospecies). The specimens are deposited in the entomological collection of the Museum of the Universidad del Atlántico, Barranquilla, Colombia.

Data analysis

To account for the colonial nature of ants, we quantified abundance as a frequency of occurrence rather than by counting individuals (Domínguez-Haydar & Armbrecht, 2011). For each specific species, we evaluated its presence or absence separately for both the pitfall trap and the hand collection at each of the 12 sampling stations. The total abundance for that species was then calculated as the sum of these occurrences. Therefore, with 12 stations and 2 distinct methods, the maximum possible abundance score for any single species was 24.

Given the logistical constraints that prevented spatial replication, we treated the three sampling events conducted in 2018 as temporal repeated measures to assess differences in ant communities among the study sites. Ant diversity in each area was estimated using Hill's effective number of species. The diversity orders considered were q0 (species richness or zero-order diversity), q1 (the exponential of Shannon's index), and q2 (the inverse of Simpson's index), following Hill (1973). Expected richness at each site was calculated as the mean of observed and estimated q0 numbers, along with sample coverage (Hsieh et al., 2024).

Linear Mixed Models (LMMs) were used to examine the effect of habitat type on Hill's diversity estimators. Area was included as a fixed, nominal factor, with Forest set as the reference level. Random intercepts for sampling event were incorporated to account for the hierarchical structure of the data (Zuur et al., 2009). Post-hoc Tukey's multiple comparison tests were performed to identify significant differences among areas in each Hill's diversity estimator, with a 95% confidence level (Lenth, 2025).

A Venn diagram comparing unique and shared ant species among areas was generated using the *ggVennDiagram* R package (Gao et al., 2024). Non-metric Multidimensional Scaling (NMDS) was performed using the Bray-Curtis distance to visualize species composition patterns among different areas. The ordination stress value was reported to assess the goodness of fit (Legendre & Legendre, 2012).

To assess differences in species composition among sampling sites, a Permutational Multivariate Analysis of Variance (PERMANOVA) was performed based on Bray-Curtis distance matrices using 999 permutations. Prior to this, the assumption of homogeneity of multivariate dispersions was verified using the PERMDISP test (Betadisper). Pairwise comparisons (pairwise

PERMANOVA) were conducted with a False Discovery Rate (FDR) correction for multiple testing. Due to the balanced design with three replicates per site (n = 3), the mathematical constraint on possible permutations often limited the resolution of P-values in pairwise tests. Consequently, the interpretation of differences was primarily based on the effect size (R2) and the F-statistic, rather than the statistical significance of the P-value (Martinez, 2017; Oksanen et al., 2025).

All data processing, analysis, and visualization were performed with R (R Core Team, 2025).

RESULTS

Richness and abundance patterns

A total of 10824 individuals belonging to 65 species and morphospecies, 30 genera, and seven subfamilies were recorded (see Table S1 for a complete list). Of these, 40% were identified to the level of species, while the remaining were sorted as distinct morphospecies (e.g., *Pheidole* sp. 1). These morphospecies represent groups for which comprehensive taxonomic keys are not available for the region, or where major workers are required for identification but were not collected. The subfamily that contributed the most to total richness was Myrmicinae, with 32 species, followed by Formicinae (13), Ponerinae (6), Pseudomyrmicinae (6), and Dolichoderinae (4), while the subfamilies with the lowest richness were Dorylinae and Ectatomminae with two species respectively. Regarding the genera, *Pheidole* Westwood, 1839 (11), *Camponotus* Mayr, 1861 (6), *Pseudomyrmex* Lund, 1831 (6), and *Solenopsis* Westwood, 1840 (5) were the most species rich. The highest richness by sites was observed in areas not affected by mining activity, especially in Forest, while in rehabilitated areas, the highest richness was for the 7-year site and the lowest was for the 1.5-year site. *Acropyga* Roger, 1862 (Formicinae), *Leptogenys* Roger, 1861 (Poneriane) and *Gnamptogenys* Roger, 1863 (Ectatomminae) were the rarest genera, since only one species was found for each of them and with one or two workers.

Sample coverage for all study sites ranged from 88% in the Natural Regeneration area to 94% in the 1.5-year rehabilitated site (Table S2). Ant diversity, quantified using Hill's effective number of species, varied among different habitat types. Boxplots visually revealed clear patterns in the diversity distribution for each habitat type (Fig. 2).

Linear mixed models confirmed the visual evidence, revealing a significant overall effect of habitat type on ant diversity for all Hill numbers ($p < 0.001$) (Table S3). For species richness estimates (q0), post-hoc comparisons (Tukey test) revealed that the 7-year rehabilitation site reached levels statistically indistinguishable from the reference ecosystems (Forest and Natural Regeneration); in contrast, the younger rehabilitation stages (1.5-year and 4-year) formed a distinct statistical group with significantly lower species richness, showing median species counts below 20 and narrower interquartile ranges. Observed richness values (red points) were consistent with these estimates.

Regarding community structure, Shannon (q1) and Simpson (q2) diversity displayed a distinct, non-linear pattern. Forest sites exhibited the significantly highest values for

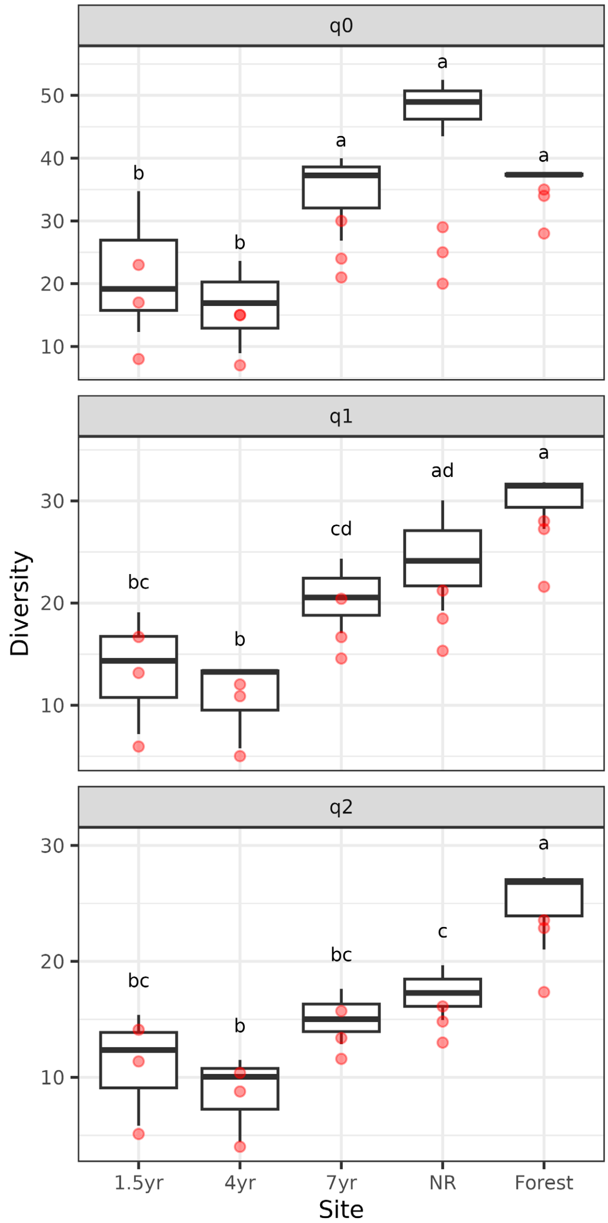

Fig. 2. Comparison of estimated and observed ant diversity (Hill numbers) across a rehabilitation chronosequence (1.5, 4, and 7 years) and reference forests (Natural Regeneration, Forest) in a coal mine. The panels display diversity orders q = 0 (Richness), q = 1 (Shannon), and q = 2 (Simpson). Boxplots visualize the median (solid line) distribution of estimated diversity values, and overlaid red dots show the raw observed values. letters indicate significant differences between habitats (LMM followed by Tukey's post-hoc test, alpha = 0.05).

both indices (medians around 27 for q1 and 19 for q2), reflecting greater evenness and reduced species dominance. The NR and 7-year rehabilitation areas tended to display intermediate diversity; however, post-hoc tests showed no significant differences among themselves, nor with the 1.5-year site. Notably, the Natural Regeneration (NR) area showed a broad range of statistical overlap, suggesting high variability in its community structure. Unlike the pattern observed for richness, the observed values (red points) for both Shannon and Simpson indices closely aligned with the estimated medians across all sites.

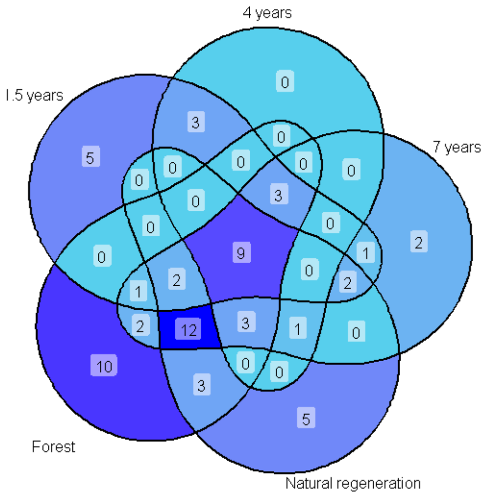

Fig. 3. Venn diagram illustrating the exclusive and shared ant species across the rehabilitation chronosequence (1.5, 4, and 7 years) and reference forests (Natural Regeneration, Forest) in a coal mine in Cesar, Colombia. Color intensity is proportional to the number of species within each intersection.

Compositional convergence

The Forest site hosted the highest number of exclusive species (11), followed by the Natural Regeneration and 1.5-year sites (five species), and the 7-year site (two species). The 4-year site contained no exclusive species. A total of 11 species were found to be shared across all five sites (Fig. 3).

Non-metric Multidimensional Scaling (NMDS) (Fig. 4) ordination visualized distinct ant assemblage compositions across the chronosequence. The Stress value of 0.09 is considered good, indicating that the two-dimensional ordination reliably represents community similarities in a reduced-dimensional space. A global PERMANOVA confirmed that habitat type structured species composition ($F = 8.2$; $R^2 = 0.77$; $p < 0.001$).

Pairwise comparisons revealed distinct compositional clusters. The early rehabilitation stages, 1.5-year (blue points) and 4-year (red) were compositionally similar to each other ($F = 1.6$, $R^2 = 0.28$, $p = 0.2$). This group was characterized by *Solenopsis geminata*, *Dorymyrmex tuberosus*, and *Forelius damiani*. Samples from the 7-year rehabilitation area (orange) occupied an intermediate position but tended to shift toward the Forest and NR clusters, particularly toward NR. Strong compositional shifts were confirmed between this 7-year site and the 4-year stage ($F = 14.04$, $R^2 = 0.77$)

In contrast, samples from undisturbed vegetation, Forest (purple) and NR (green), occupied the upper-right portion of the ordination space, remaining separated from the early rehabilitation stages. While pairwise comparisons indicated some variation between these two reference habitats ($F = 3.21$, $R^2 = 0.44$), they were clearly distinct from the younger sites and associated with a diverse assemblage including *Pachycondyla harpax*, *Labidus coecus*, *Strumigenys marginiventris*, and multiple species of Cephalotes, Pseudomyrmex, and Camponotus.

Although these pairwise comparisons yielded p-values of 0.1, which corresponds to the lowest possible probability value achievable with the permutation limits of our sample size ($n = 3$), the high coefficients of determination R^2 0.60

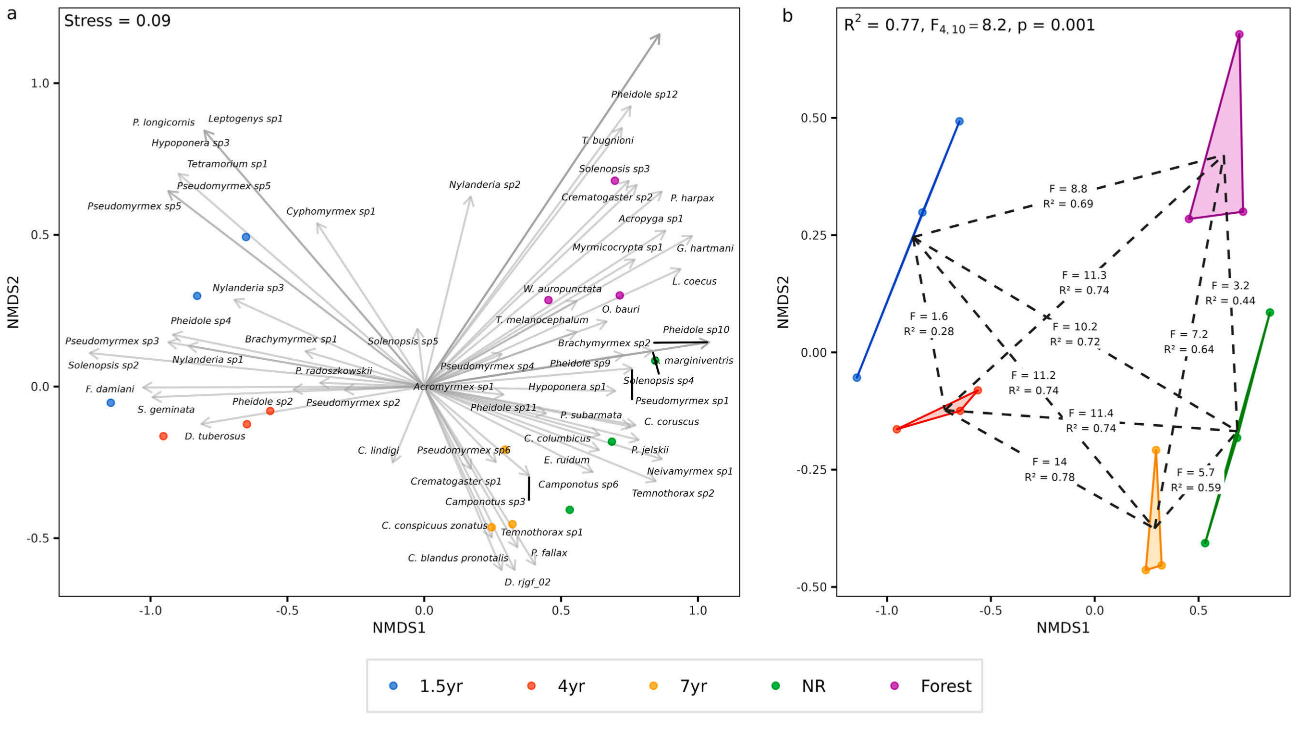

Fig. 4. (a) Non-metric Multidimensional Scaling (NMDS) of ant community composition based on Bray-Curtis dissimilarities. Biplot displaying species vectors driving the ordination patterns. (b) Habitat differentiation visualized with convex hulls grouping site replicates (n = 3). Dashed lines connect centroids of compared groups, indicating the F-statistic and effect size (R2) from pairwise PERMANOVA tests to highlight the magnitude of species turnover. Global stress value = 0.091. NR: Natural regeneration.

and Pseudo-F values indicate differentiation between these stages, confirming that community composition changes with rehabilitation age.

DISCUSSION

Ants responded to rehabilitation measures in the Calenturitas mine. After seven years of rehabilitation, the assemblage already differs from those found in areas at earlier successional stages. Moreover, the composition and structure of these communities reflect the history of transformations that the region has experienced due to various anthropogenic activities. This is evidenced by the lower number of ant species recorded in this study compared with previous research conducted in other rehabilitated mining areas (Fontalvo-Rodríguez & Solís-Medina, 2009; Domínguez-Haydar & Armbrecht, 2011) and in dry forests of the same region, where species richness typically ranges between 60 and 70 in mature forest and natural regeneration areas (Marquez-Peña & Domínguez-Haydar, 2023).

This lower recorded richness, however, must be interpreted within the context of our sampling methodology. The high sample coverage values indicate that our sampling effort was sufficient to thoroughly characterize the epigeic ant community. Our focus on this stratum, using pitfall traps and manual collecting, means that other important guilds, such as arboreal, hypogeic, and cryptic species, were likely underrepresented (Andersen, 1991; Bestelmeyer et al., 2000). Therefore, the actual species richness in these areas is probably higher than what we report.

Consistent with patterns frequently reported in ant restoration ecology, where species richness exhibits rapid resilience (Ottonetti et al., 2006; Majer et al., 2007; Domínguez-Haydar & Armbrecht, 2011), species richness (q0) in the 7-year rehabilitation site successfully reached levels statistically indistinguishable from the undisturbed forest. However, the results expose a decoupling between the recovery of species richness and community structure. While richness rebounded quickly, evenness and dominance (q1and q2) followed a slower trajectory; the forest maintained significantly higher values than all rehabilitation stages. This confirms that while the rehabilitation strategy effectively removes colonization barriers, allowing diverse species to arrive, the complex structural balance of the undisturbed ecosystem requires more time to reassemble (Hoenle et al., 2022).

Although NR possesses high species richness, its community structure (q1 and q2) is very similar to that of the 7-year site. This suggests that targeted rehabilitation measures (such as planting and soil management) contribute to the recovery of community structure (Andersen et al., 2003), achieving in 7 years what passive regeneration takes a decade or more to accomplish. This finding highlights the effectiveness of active rehabilitation over simply abandoning areas for natural recovery (Meli et al., 2017).

In terms of species composition, the results of this study show that rehabilitation measures at the Calenturitas mine promote the recovery of ant communities, showing a clear successional gradient. The NMDS ordination (Fig. 4) shows this trend into three groups: the early rehabilitation areas (1.5 and 4 years), the advanced rehabilitation area (7 years) in an intermediate position, and areas with greater vegetation complexity (Forest and NaturalRegeneration) as a more advanced state. This pattern confirms that species composition is a sensitive indicator of ecological restoration progress in this tropical dry forest ecosystem. This pattern can be associated with variations in the composition and structure of vegetation (structural heterogeneity) that influence the maintenance of suitable microclimatic conditions and the supply of nesting and food resources (Schmidt et al., 2013; Andersen, 2019).

The transition in the composition of ant communities, visible in the NMDS and in the number of shared species in the Venn diagram, can be related to habitat complexity. Early rehabilitation areas (1.5 and 4 years) are dominated by generalist and pioneer species such as *Dorymyrmex tuberosus* Cuezzo & Guerrero, 2012, *Solenopsis geminata* (Fabricius, 1804), and *Nylanderia* Emery, 1906, known for their preference for open and disturbed habitats (Cuezzo & Guerrero, 2012; Carval et al., 2016). However, these species with minor abundance were also found in undisturbed areas, indicating some degree of intervention in these zones, either due to proximity to human settlements or previous land use. On the other hand, the reference forest harbors the greatest number of exclusive species (11 species), including leaf-litter specialists like *Strumigenys marginiventris*, Santschi, 1931 and *Gnamptogenys hartmani* (Wheeler, 1915) (Andersen, 2000; Fernández et al., 2019) which underscores the forest's role as a reservoir of unique biodiversity that is lost with disturbance.

The hunter ant *Ectatomma ruidum* dominated in the Forest and the 7-year rehabilitation site. While this species is often associated with open, disturbed habitats in other regions of the country (Santamaría et al., 2009a), our findings show it prefers sites with greater tree cover. This pattern is consistent with observations from other Colombian coal mines (Santamaría et al., 2009b; Gutiérrez-Rapalino & Domínguez-Haydar, 2017). This aligns with recent research suggesting that the dominance of *E. ruidum* in tropical dry forests is not necessarily an indicator of disturbance or low species richness. Instead, its presence is strongly shaped by habitat characteristics, particularly vegetation cover and temperature (Ramos & Guerrero, 2023). Thus, its dominance in our mature reference sites likely reflects its preference for the specific microclimatic and structural conditions found there, rather than a response to disturbance.

The success of the rehabilitation techniques is evidenced by comparing the 1.5- and 4-year sites. Despite having less than half the recovery time, the 1.5-year site exhibited almost twice as many species as the 4-year site and a more complex composition. We attribute this remarkable success to the implementation of soil protection techniques such as mulching at the younger site. This practice improves moisture retention and facilitates the establishment of an herbaceous cover, creating favorable microclimates and refuges that enable rapid colonization (Dawes, 2010; Williams et al., 2012).

A clear indicator of the success of this methodology is the exclusive presence of the specialist predatory ant *Leptogenys pubiceps* Emery, 1890, at this 1.5-year site. The early occurrence of a specialist predator, usually a late colonizer (Hoffmann & Andersen, 2003), signals the effectiveness of the rehabilitation strategy. This finding aligns with the habitat filtering hypothesis. A study from the Ecuadorian Chocó shows that although reproductive queens disperse successfully across the entire regeneration gradient, their successful establishment is strictly constrained by harsh abiotic conditions (Grella et al., 2024). In the mine, the application of mulch likely mitigated this environmental filter by improving thermal stability and humidity retention, thus allowing specialized propagules to survive and establish functional colonies in an environment that would otherwise have been hostile.

We acknowledge the limitations imposed by our sample size. While the number of site replicates is low, the intensive sampling effort within each site (12 stations, two complementary capture methods, and three temporal events) allowed for a detailed characterization of the local ant assemblages. Our results should therefore be interpreted as a case study of chronological recovery trajectories within this specific mining complex, providing a necessary baseline for future, large-scale monitoring programs in the region.

CONCLUSION

Consistent with our hypothesis, ant communities became progressively more complex with increasing rehabilitation age at mining sites. Techniques such as mulching enhance soil moisture and facilitate the establishment of grasses and herbs, creating favorable microclimates, nesting substrates, and food resources that promote ant colonization. We recommend that future monitoring programs evaluate not only species richness butalso multiple dimensions of diversity and functional composition to provide a more comprehensive assessment of restoration success.

CONFLICT OF INTEREST STATEMENTS. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

AUTHOR CONTRIBUTION. D. Hormechea García: Conceptualization, methodology, data collection, formal analysis, investigation, data curation, writing – original draft; R. Fonseca Campuzano: Formal analysis, statistical modeling, writing – review and editing. Y. Domínguez Haydar: Conceptualization, validation, resources, writing – review and editing, supervision, funding acquisition.

ACKNOWLEDGEMENTS. The authors would like to thank the C.I. Prodeco S.A. for providing logistical and financial support to this research, as well as the "Vicerrectoría de Investigaciones y Proyección Social" at the Universidad del Atlántico for the grant "Séptima Convocatoria para Fortalecimiento de Equipos" grant code CB03-FGI2016. We also thank A. Velez for the elaboration of the map.

REFERENCES

ALONSO L.E. 2000: Ants as indicators of diversity. In Agosti D., Majer J.D., Alonso L.E. & Schultz T.R. (eds): *Ants: Standard Methods for Measuring and Monitoring Biodiversity.* Smithsonian Institution Press, Washington, D.C., pp. 80–88.

ANDERSEN A.N. 1991: Sampling communities of ground-foraging ants: Pitfall traps versus quadrat counts. — *Aust. J. Ecol.* **16**: 273–279.

ANDERSEN A.N. 2000: *The Use of Ants as Bioindicators: A Review and Prospects for the Future.* CRC Press, Boca Raton, 241 pp.

ANDERSEN A. 2019: Responses of ant communities to disturbance: Five principles for understanding the disturbance dynamics of a globally dominant faunal group. — *J. Anim. Ecol.* **88**: 350–362.

ANDERSEN A.N., HOFFMANN B.D. & SOMES J. 2003: Ants as indicators of mine site restoration: community recovery at one of eight rehabilitation sites in central Queensland. — *Ecol. Manag. Restor.* **4**: 12–19.

BESTELMEYER J.P., AGOSTI D., ALONSO L.E., BRANDÃO C.R.F., BROWN W.L. JR., DELABIE J.H.C. & SILVESTRE R. 2000: Field techniques for the study of ground-dwelling ants: An overview, description, and evaluation. In Agosti D., Majer J.D., Alonso L.E. & Schultz T.R. (eds): *Ants: Standard Methods for Measuring and Monitoring Biodiversity.* Smithsonian Institution Press, Washington, D.C., pp. 122–144.

BLINOVA S. & DOBRYDINA T. 2017: Influence of coal industry enterprises on biodiversity (on the example of Formicidae). — *E3S Web Conf.* **21**: 02011, 6 pp.

CARVAL D., COTTÉ V., RESMOND R., PERRIN B. & TIXIER P. 2016: Dominance in a ground-dwelling ant community of banana agroecosystem. — *Ecol. Evol.* **6**: 8617–8631.

CRISTESCU R.H., FRÈRE C. & BANKS P.B. 2012: A review of fauna in mine rehabilitation in Australia: Current state and future directions. — *Biol. Conserv.* **149**: 60–72.

CUEZZO F. & GUERRERO R.J. 2012: The ant genus *Dorymyrmex* Mayr (Hymenoptera: Formicidae: Dolichoderinae) in Colombia. — *Psyche* **2012**: 516058, 24 pp.

DAWES T. 2010: Reestablishment of ecological functioning by mulching and termite invasion in a degraded soil in an Australian savanna. — *Soil Biol. Biochem.* **42**: 1825–1834.

DOMÍNGUEZ-HAYDAR Y. & ARMBRECHT I. 2011: Response of ants and their seed removal in rehabilitation areas and forests at El Cerrejón coal mine in Colombia. — *Restor. Ecol.* **19**: 178–184.

FERNANDES G.W., LANA T.C., RIBAS C.R., SCHOEREDER J.H., SOLAR R., MAJER J.D., CORDEIRO E.G., DELABIE J.H.C. & VILELA E.F. 2021: Changes in epigaeic ant assemblage structure in the Amazon during successional processes after bauxite mining. — *Sociobiology* **68**: 4973, 11 pp.

FERNÁNDEZ F., GUERRERO R.J. & DELSINNE T. 2019: *Hormigas de Colombia.* Universidad Nacional de Colombia, Bogotá D.C., 1198 pp.

FONTALVO-RODRÍGUEZ L. & SOLÍS-MEDINA C. 2009: Ant assemblage (Hymenoptera: Formicidae) in dry forest fragments in the Cerrejón coal complex (La Guajira, Colombia). — *Rev. Intropica* **4**: 5–15 [in Spanish].

FROUZ J., KEPLIN B., PIŽL V., TAJOVSKÝ K., STARÝ J., LUKEŠOVÁ A., NOVÁKOVÁ A., BALÍK V., HÁNĚL L., MATERNA J., DÜKER C., CHALUPSKÝ J., RUSEK J. & HEINKELE T. 2001: Soil biota and upper soil layer development in two contrasting post-mining chronosequences. — *Ecol. Eng.* **17**: 275–284.

GAO C.-H., CHEN C., AKYOL T., DUŞA A., YU G., CAO B. & CAI P. 2024: ggVennDiagram: Intuitive Venn diagram software extended. — *iMeta* **3**: e177, 4 pp.

García H., Corzo G., Isaacs P. & Etter A. 2014: Distribution and current status of the remnants of the tropical dry forest biome in Colombia: Inputs for its management. In Pizano C. & García H. (eds): *El bosque seco tropical en Colombia.* Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH), Bogotá, pp. 229–249 [in Spanish].

Gastauer M., Silva J.R., Caldeira C.F., Ramos S.J., Souza P.W.M., Furtini A.E. & Siqueira J.O. 2018: Mine land rehabilitation: Modern ecological approaches for more sustainable mining. — *J. Clean. Prod.* **172**: 1409–1422.

Grella N., Donoso D.A., Müller J., Falconí-López A. & Feldhaar H. 2025: Habitat filtering, not dispersal limitation, drives ant and termite community assembly along a tropical forest regeneration gradient. — *EcoEvoRxiv* preprint, https://doi.org/10.32942/X2N92C

Gutiérrez-Rapalino B.P. & Domínguez-Haydar Y. 2017: Contribution of *Pheidole fallax* and *Ectatomma ruidum* (Hymenoptera: Formicidae) to seed dispersal and germination in rehabilitated areas of the Cerrejón coal mine, Colombia. — *Biol. Trop.* **65**: 575–587 [in Spanish, English abstract].

Hill M.O. 1973: Diversity and evenness: a unifying notation and its consequences. — *Ecology* **54**: 427–432.

Hoenle P.O., Donoso D.A., Argoti A., Staab M., von Beeren C. & Blüthgen N. 2022: Rapid ant community reassembly in a Neotropical forest: Recovery dynamics and land-use legacy. — *Ecol. Appl*. **32**(4): e2559., 15 pp.

Hoffmann B.D. & Andersen A. 2003: Responses of ants to disturbance in Australia, with particular reference to functional groups. — *Austral Ecol.* **28**: 444–464.

Holec M. & Frouz J. 2005: Ant (Hymenoptera: Formicidae) communities in reclaimed and unreclaimed brown coal mining spoil dumps in the Czech Republic. — *Pedobiologia* **49**: 345–357.

Hsieh T.C., Ma K. & Chao A. 2016: iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). — *Meth. Ecol. Evol.* **7**: 1451–1456.

Hsieh T.C., Ma K.H. & Chao A. 2024: iNEXT: *iNterpolation and EXTrapolation for Species Diversity. R Package Version 3.0.1.* URL: http://chao.stat.nthu.edu.tw/wordpress/software-download/.

Khan S.R., Rastogi N. & Singh S.K. 2023: Bio-transfer and bioaccumulation patterns of heavy metals in mine site-inhabiting ants and grasshoppers across a mine site restoration chronosequence. — *Ecotoxicology* **32**: 683–698.

Legendre P. & Legendre L. 2012: *Numerical Ecology (3rd ed.).* Elsevier, Amsterdam, 990 pp.

Lei K., Pan H. & Lin C. 2016: A landscape approach towards ecological restoration and sustainable development of mining areas. — *Ecol. Eng.* **90**: 320–325.

Lenth R. 2025: *emmeans: Estimated Marginal Means, aka Least-Squares Means*. *R Package Version 1.11.1.* https://CRAN.R-project.org/package=emmeans

Ličina V., Fotirić M., Tomić Z., Trajković I., Antić Mladenović S., Marjanović M. & Rinklebe J. 2017: Bioassessment of heavy metals in the surface soil layer of an opencast mine aimed for its rehabilitation. — *J. Environ. Manag.* **186**: 240–252.

Lima A.T., Mitchell K., O'Connell D.W., Verhoeven J. & Van Cappellen P. 2016: The legacy of surface mining: remediation, restoration, reclamation, and rehabilitation. — *Environ. Sci. Policy* **66**: 227–233.

Majer J.D. 2009: Animals in the restoration process – progressing the trends. — *Restor. Ecol.* **17**: 315–319.

Majer J.D., Brennan K.E.C. & Moir M.L. 2007: Invertebrates and the restoration of a forest ecosystem: 30 years of research following bauxite mining in Western Australia. — *Restor. Ecol.* **15**: 104–115.

Marquez-Peña J. & Domínguez-Haydar Y. 2023: Riqueza y diversidad de hormigas (Hymenoptera: Formicidae) según uso de suelo en dos paisajes agroforestales de Colombia. — *Rev. Biol. Trop.* **71**: e52087, 15 pp.

Martinez P. 2017: *pairwiseAdonis: Pairwise Multilevel Comparison Using Adonis*. *R Package Version 0.4.1.* URL: https://github.com/pmartinezarbizu/pairwiseAdonis

Meli P., Holl K.D., Rey Benayas J.M., Jones H.P., Jones P.C., Montoya D. & Moreno Mateos D. 2017: A global review of past land use, climate, and active vs. passive restoration effects on forest recovery. — *PLoS ONE* **12**(2): e0171368, 17 pp.

Oksanen J., Simpson G., Blanchet F., Kindt R., Legendre P., Minchin P., O'Hara R., Solymos P., Stevens M., Szoecs E. et al. 2025: *vegan: Community Ecology Package. R Package Version 2.7-2.* URL: https://CRAN.R-project.org/package=vegan

Ottonetti L., Tucci L. & Santini G. 2006: Recolonization patterns of ants in a rehabilitated lignite mine in central Italy: potential for the use of Mediterranean ants as indicators of restoration processes. — *Restor. Ecol.* **14**: 60–66.

Prodeco 2017: *Reporte de sostenibilidad.* URL: https://www.grupoprodeco.com.co/.rest/api/v1/documents/3e75afa9f9d2fa1b15de8815cc4d1393/Reporte+de+Sostenibilidad+2017+Espanol.pdf (accessed 22 Jan. 2019).

R Core Team 2025: *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna URL: https://www.R-project.org/

Ramos Ortega L.M. & Guerrero R.J. 2023: Spatial turnover and functional redundancy in the ants of urban fragments of tropical dry forest. — *Diversity* **15**: 880, 16 pp.

Ribas C.R., Schmidt F.A., Solar R.R.C., Campos R.B.F., Valentim C.L. & Schoereder J.H. 2012: Ants as indicators of the success of rehabilitation efforts in deposits of gold mining tailings. — *Restor. Ecol.* **20**: 712–720.

Ruiz-Jaen M.C. & Aide T.M. 2005: Restoration success: how is it being measured? — *Restor. Ecol.* **13**: 569–577.

Santamaría C., Armbrecht I. & Lachaud J. 2009a: Nest distribution and food preferences of *Ectatomma ruidum* (Hymenoptera: Formicidae) in shaded and open cattle pastures of Colombia. — *Sociobiology* **53**: 517–540.

Santamaría C., Domínguez-Haydar Y. & Armbrecht I. 2009b: Changes in nest distribution and abundance of the ant *Ectatomma ruidum* (Roger, 1861) in two regions of Colombia. — *Bol. Mus. Entomol. Univ. Valle* **10**: 10–18 [in Spanish].

Schmidt F.A., Ribas C.R. & Schoereder J.H. 2013: How predictable is the response of ant assemblages to natural forest recovery? Implications for their use as bioindicators. — *Ecol. Indic.* **24**: 158–166.

Sithole H. & Tantsi N. 2021: Ants as indicators of terrestrial ecosystem rehabilitation processes. In Rebolledo Ranz R.E. (ed.): *Arthropods: Are They Beneficial for Mankind?* IntechOpen, London, 24 pp.

Thompson S.A. & Thompson G.G. 2004: Adequacy of rehabilitation monitoring practices in the Western Australian mining industry. — *Ecol. Manag. Restor.* **5**: 30–33.

Tizado E. & Núñez-Pérez E. 2016: Terrestrial arthropods in the initial restoration stages of anthracite coal mine spoil heaps in northwestern Spain: Potential usefulness of higher taxa as restoration indicators. — *Land Degrad. Dev*. **27**: 1131–1140.

Williams E.R., Mulligan D.R., Erskine P.D. & Plowman K.P. 2012: Using insect diversity for determining land restoration development: examining the influence of grazing history on ant assemblages in rehabilitated pasture. — *Agric. Ecosyst. Environ.* **163**: 54–60.

Yeo K., Kouakou L.M.M., Touao M.K., Gauze E., Ouattara K. & Soro A.N. 2019: Ants response to mining prospection disturbances across vegetation zones in tropical mountain chains of Mount Nimba, Guinea, West Africa. — *Int. J. Biol. Chem. Sci.* **13**: 899–913.

Yuan Y., Zhao Z., Zhang P., Chen L., Hu T. & Niu S. 2017: Soil organic carbon and nitrogen pools in reclaimed mine soils under forest and cropland ecosystems in the Loess Plateau, China. — *Ecol. Eng.* **102**: 137–144.

Zuur A.F., Ieno E.N., Walker N., Saveliev A.A. & Smith G.M. 2009: *Mixed Effects Models and Extensions in Ecology with R.* Springer, New York, 574 pp.

Received March 4, 2025; revised and accepted January 7, 2026
Published online January 27, 2026

Table S1. Composition of ants and capture frequency of species in the five sites of the Calenturitas mine.

Subfamily	Species or morphospecies	1.5 year			4 year			7 year			Natural regeneration			Forest			Total
		S1	S2	S3	S1	S2	S3	S1	S2	S3	S1	S2	S3	S1	S2	S3	
Dolichoderinae	*Dorymyrmex rjgf_02*								1	1							2
	Dorymyrmex tuberosus	7	11	12	12	12	12	3	5	3	3	4	1	3	3	2	93
	Forelius damiani	8	12	12	4	5	11	1		2						1	56
	Tapinoma melanocephalum		1					1			1		3	2		4	12
Dorylinae	*Labidus coecus*										1				2		3
	Neivamyrmex iridescens										2	1	1				4
Ectatomminae	*Ectatomma ruidum*							10	12	11	10	10	12	12	11	12	100
	Gnamptogenys hartmani															1	1
Formicinae	*Acropyga sp1*														1		1
	Brachymyrmex sp1	1	5	11		2	3	2	2	1	3	1		2	1	1	35
	Brachymyrmex sp2										1						1
	Camponotus blandus pronotalis					1		6	6	5	1	1					20
	Camponotus coruscus							1			2	5	7	2	4	4	25
	Camponotus lindigi		4	10	3	6	9	12	11	12	5	6	8	6	3		95
	Camponotus sp3			1		1	3	7	7	5	4	5	4	7	4	2	50
	Camponotus sp6							3	2			1	1		5		12
	Camponotus zonatus					1	3	8	7	11	1	2	3			1	37
	Nylanderia sp1	2	11	8		4	7		1					1	1		35
	Nylanderia sp2		2	2						1				6	1	5	17
	Nylanderia sp3		5	1					1	1							8
	Paratrechina longicornis			5													5
Myrmicinae	*Acromyrmex santschii*						3	1	3	2		1		5	4	3	22
	Cephalotes columbicus							2	4	5	3	5	3	5	4	6	37
	Cephalotes femoralis															2	2
	Cephalotes minutus															4	4
	Cyphomyrmex rimosus		4	8			1			1	1			4		2	21
	Temnothorax sp1								1	2							3
	Temnothorax sp2												1				1
	Megalomyrmex sp1															1	1
	Myrmicocrypta sp1									1	1			1	1	2	6
	Paratrachymyrmex bugnioni													2		3	5
	Pheidole fallax			3				12	8	10	1	8	1				43
	Pheidole jelskii							1	1	1	9	5	5	3	1	2	28
	Pheidole radoszkowskii	1	11	11	2	6	6	3	4	7	1	3	3	6	4	7	75
	Pheidole sp10										1						1
	Pheidole sp11								1					2			3
	Pheidole sp12													3		7	10
	Pheidole sp2	1		3			1	2		1				3			11
	Pheidole sp4		5			2											7
	Pheidole sp6															5	5
	Pheidole sp9										3	4		9	2	3	21
	Pheidole subarmata							1		2	6	10	5	5	7	4	40
	Solenopsis geminata	8	12	9	7	6	8			2	2		1	3	1		59
	Solenopsis sp2	4	7	2		1											14
	Solenopsis sp3									1			1	4	1	10	17
	Solenopsis sp4									1	4	1	6	2	1	6	21
	Solenopsis sp5		3		1	1			1		2		2	5	3	5	23
	Strumigenys marginiventris										2						2
	Strumigenys sp2															1	1
	Tetramorium sp1		2	4													6
	Wasmannia auropunctata									2				1		2	5
	Crematogaster sp1					5	5	6	9	8	3	4	6	4	2	8	60
	Crematogaster sp2													2	2	2	6
Ponerinae	*Hypoponera sp1*							1					1	1	2		5
	Hypoponera sp2															3	3
	Hypoponera sp3			1													1
	Leptogenys pubiceps			1													1
	Odontomachus bauri							2	2	4	1		2	8	7	9	35
	Pachycondyla harpax										1			1	4	4	10
Pseudomyrmicinae	*Pseudomyrmex sp1*								1				4	1	1	3	10
	Pseudomyrmex sp2			4		1	3		1	2	38	1		3			15
	Pseudomyrmex sp3		1	5	1		2										9
	Pseudomyrmex sp4			1						1			1	1			4
	Pseudomyrmex sp5		1	1													2
	Pseudomyrmex sp6			1					1	2			1				5
Total relative abundance		32	97	116	30	54	77	85	92	108	75	78	83	125	83	137	1272
Richness			26			19			38			37			46		

Table S2. Mean values and standard deviations (in brackets) of observed and estimated Hill's effective species numbers, and sample coverage.

Area	Sample coverage	q0		q1		q2	
		Observed	Estimated	Observed	Estimated	Observed	Estimated
1.5 yr	94% (3.1%)	16 (7.5)	22.1 (11.5)	11.9 (5.5)	13.5 (6)	10.2 (4.6)	11.2 (4.9)
4 yr	93.4% (4.2%)	12.3 (4.6)	16.5 (7.4)	9.3 (3.8)	10.8 (4.4)	7.7 (3.3)	8.7 (3.7)
7 yr	90.7% (1.4%)	25 (4.6)	34.7 (6.9)	17.2 (3)	20.6 (3.6)	13.6 (2.1)	15.2 (2.4)
NR	88% (3.3%)	24.3 (4)	44.7 (3.7)	18.2 (2.8)	23.7 (4.3)	14.6 (1.5)	17.3 (2.3)
Forest	93.1% (4.1%)	32.3 (3.8)	37.4 (0.2)	25.6 (3.5)	30.2 (2.5)	21.3 (3.4)	25 (3.5)

Table S3. Estimates of the fixed effects parameters of the linear mixed model of Hill's species diversity by habitat type.

Hill's species diversity	Area	Estimate	Confidence interval	p value
	(Intercept)	37.36	27.55 – 47.18	<0.001
q0 n = 15,	1.5 yr	−15.30	−25.75 – −4.84	0.010
logLik = –35.48,	4 yr	−20.88	−31.34 – −10.42	0.002
df = 8	7 yr	−2.67	−13.13 – 7.79	0.573
	NR	7.38	−3.08 – 17.84	0.142
	(Intercept)	30.19	24.56 – 35.82	<0.001
q1 n = 15,	1.5 yr	−16.65	−24.17 – −9.13	<0.001
logLik = –31.41,	4 yr	−19.34	−26.86 – −11.82	<0.001
df = 8	7 yr	−9.55	−17.07 – −2.03	0.019
	NR	−6.46	−13.98 – 1.06	0.083
	(Intercept)	25.04	20.46 – 29.61	<0.001
q2 n = 15,	1.5 yr	−13.84	−19.75 – −7.94	<0.001
logLik = –29.14,	4 yr	−16.37	−22.28 – −10.47	<0.001
df = 8	7 yr	−9.86	−15.77 – −3.96	0.005
	NR	−7.78	−13.69 – −1.88	0.016