



# Successional agroforestry systems as land use that promote the restoration and conservation of ant assemblages in the Amazon

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## Abstract

Land-use changes, driven by the expansion of agriculture and livestock farming, are one of the main drivers of biodiversity loss in the Amazon region. In this context, Successional Agroforestry Systems - SAFs, emerge as a potential alternative to reconcile agricultural production with biodiversity conservation and restoration. This study assessed the impact of different land-use types on ant diversity and the composition of habitat-use guilds in areas of primary forest, pastures, shifting cultivation, and SAFs at different ages. The results indicate that primary forests consistently exhibited the highest alpha, beta, and gamma diversity. The community composition also shifted along the land-use gradient, with disturbed areas showing a higher relative representation of generalist and open-area species, while forest specialists were proportionally more represented in primary forests. Old SAFs displayed diversity values and guild composition that were intermediate between primary forests and more intensively managed systems whereas young SAFs more closely resembled pastures and shifting cultivation areas. These findings highlight the importance of SAF age in shaping biodiversity recovery trajectories, suggesting that mature agroforestry systems have the potential to promote the recovery of biodiversity in human-modified landscapes. This study underscores the importance of long-term agroforestry management strategies to promote conservation and ecological restoration, especially in regions of high biodiversity value, such as the Amazon.

**Keywords** Habitat-use guild · Forest recovery · Human-modified landscapes · Land-use change

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## Introduction

In the Amazon, the main driver of land-use change is the conversion of forests into agricultural lands and pastures (Fearnside 2005). These transformations have led to the suppression and fragmentation of vast forest areas (Jaureguiberry et al. 2022), significantly altering the original habitat in terms of abiotic conditions and resource availability - such as temperature, humidity, and soil cover (Imazon 2012; Araújo et al. 2011) - as well as biodiversity (Menezes and Schmidt 2020; Costa and Schmidt 2022) and ecosystem functions (Fontenele and Schmidt 2021; Nunes et al. 2022). However, not all agricultural systems affect biodiversity in the same way. Depending on the intensity and management practices, different land-use types can have distinct impacts on species composition and ecological processes. Intensive systems often result in a low-quality matrix (Arroyo-Rodríguez et al. 2020), which may trigger unexpected ecosystem transitions and further amplify climate change (Flores et al. 2024).

Land-use alternatives that resemble natural habitats, reconciling economic income and biodiversity conservation, have been proposed (Tschardt et al. 2021). In this context, successional agroforestry systems (SAFs) emerge as a promising solution to address this issue (Franke et al. 2000; Arroyo-Rodríguez et al. 2020). SAFs are managed to promote natural secondary succession, aiming to mimic the structure, diversity, and ecological interactions of natural forests (Young 2024). Recent evidence shows that agroforestry systems can also act as important refuges for insects, including pollinators, across environmental gradients, thus reinforcing their potential role in biodiversity conservation (Kingazi et al. 2025).

Agroecology and agroforestry techniques are combined to the establishment of successional agroforestry systems, promoting a transition to forest restoration, which accelerates secondary succession and leads to the development of a vertically stratified forest. This structural stratification increases habitat heterogeneity and resource availability, while the producing crops in the initial phase to minimize restoration costs and actively involve farmers in restoration activities (Vieira et al. 2009). Additionally, they have the potential to slow down or reverse soil degradation, enhance fertility, capture carbon, and ensure livelihoods by providing both ecological and economic benefits (Braga et al. 2019).

In Acre, in the Reserva Extrativista Chico Mendes (RESEX-CM) covers the Acre River basin, which is considered the most deforested region in the southwestern Brazilian Amazon. Although the reserve acts as a protection against deforestation and preserves large areas of primary forests (Milien et al. 2021), deforestation still penetrates its boundaries (Mascarenhas et al. 2018), as much of the landscape is also composed of secondary forests, pastures, shifting cultivation (slash-and-burn), and successional agroforestry systems, which occur in smaller proportions compared to the other land uses. This heterogeneous landscape configuration creates a clear gradient of land-use intensity, making RESEX-CM an ideal setting to assess how different land uses and different successional stages affect species diversity and composition patterns.

To assess the effects of land-use changes on biodiversity, the use of bioindicators is necessary (McGeoch 1998; Newbold et al. 2015). Ants have been used as bioindicators (Underwood and Fisher 2006), as they perform key functions in ecosystems (Rocha et al. 2024) such as biological control, seed dispersal, ecosystem engineering, and nutrient cycling (Del Toro et al. 2012), and exhibit a predictable response of their community parameters to human impacts (Agosti et al. 2000; Philpott et al. 2010), specifically those that forage at

ground (Schmidt et al. 2013), reinforcing their value as indicators of ecosystem functioning and environmental change.

In general, ant diversity is affected by the conversion of natural habitats into agricultural, forestry, and livestock areas (Philpott 2010). As a result, these anthropized areas exhibit fewer ant species, with a small number of species dominating the assemblages (Costa and Schmidt 2022). Additionally, the response of ant species varies according to their habitat-use guilds (i.e., open or forest habitat specialists and habitat generalists, which can live in both habitats) (Andersen 2019). Ant species grouped according to habitat-use guilds respond differently to human-driven environmental changes (Martins et al. 2022). Species associated with forest environments are generally the most vulnerable, often experiencing pronounced declines in richness, abundance, and biomass when native habitats are altered or converted (Sales and Schmidt 2023; Dutra et al. 2024). By contrast, taxa with broader ecological tolerances, including generalists and species typical of open habitats, frequently become more prevalent in modified landscapes, particularly where forest cover has been substantially reduced (Martins et al. 2022). Such opposing responses align with the “winner–loser” paradigm (McKinney and Lockwood 1999; Filgueiras et al. 2021), which posits that anthropogenic disturbance selectively filters communities, negatively affecting forest-dependent species while promoting a narrower group of disturbance-tolerant or open-area taxa (Paolucci et al. 2017).

In this study, we evaluated the potential contribution of successional agroforestry systems to biodiversity conservation in the southwestern Brazilian Amazon, using patterns of ant diversity as ecological indicators. Specifically, we hypothesize that young successional agroforestry systems will show lower gamma and alpha (number of species at different spatial scale) and beta diversity (differences in species composition), as well as the predominance of open-area specialist and generalist species, similar to pastures and shifting cultivation. In contrast, we hypothesize that old successional agroforestry systems will exhibit higher gamma, alpha, and beta diversity, and the predominance of forest specialist species, similar to primary forest areas. Our expectations are based on the fact that the greater structural complexity of the vegetation and heterogeneity of resources with advancing successional age will favor ant species associated with the forest and greater spatial rotation within the communities.

## Materials and methods

### Study area

We conducted the study in the Reserva Extrativista Chico Mendes (RESEX-CM), located in the state of Acre, southwestern Brazilian Amazon (10° 06' 11" 10° 58' 39" S and 67° 56' 13" 69° 48' 00" W). The RESEX-CM covers an area of approximately 970,550 ha, consisting of open ombrophilous forest (73%) and dense ombrophilous forest (27%), spanning parts of the municipalities of Assis Brasil, Brasiléia, Capixaba, Xapuri, Sena Madureira, Epitaciolândia, and Rio Branco (BRASIL 2006).

The climate of the region is tropical humid, with an annual average temperature of approximately 27 °C. The highest precipitation occurs between December and March, with January being the month with the highest average (297 mm). The dry season is long, span-

ning from May to August, with the driest period averaging 43 mm of precipitation (Alvares et al. 2013).

The ant samplings were carried out in the municipalities of Brasileia and Eptaciolândia (Fig. 1). The collections were carried out in September 2023, a transitional period between the dry and rainy seasons in the state of Acre (Duarte and Mascarenhas 2007).

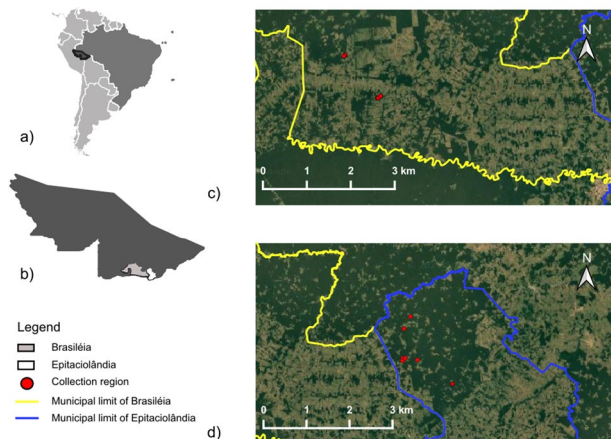
## Land-use types

To assess the effect of different land uses on ant assemblages, we conducted our samplings in pastures (i.e., areas with a history of deforestation and disturbance, characterized by open canopy and livestock use), shifting cultivation (i.e., open canopy, simplified vegetation structure, and recent or ongoing land-use activities), young successional agroforestry systems - young SAFs (i.e., systems with one year of implementation), and old successional agroforestry systems - old SAFs (i.e., systems between nine and 29 years of implementation) and primary forest areas (i.e., areas with no history of deforestation or agricultural use, characterized by well-developed vertical stratification and closed canopy) (Fig. 2).

Both successional agroforestry systems (young and old) at the initial phase have the same cropping design, which is the consortium of trees with several kinds of crops, such as banana, cassava, corn, pineapple, etc. The young SAFs were implemented in 2022 by the non-governmental organization - NGO SOS Amazônia, providing inputs and technical assistance for residents to implement the planting of half a hectare through the project “Faça Florescer Floresta” (SOS AMAZÔNIA 2022). The old SAFs were implemented through the initiative of the local residents between 1993 and 2014.

Finally, as we selected markedly distinct land-use types, and chose very similar replicates within each land-use types, we did not account vegetation parameters (e.g., canopy cover, tree density, etc.) along the land-use types and consequently did not consider them in the statistical models (see Statistical Analyses). We opted for that because there is a strong collinearity between land-use types and vegetation variables (Solar et al. 2015; Kuzevic et al. 2026).

**Fig. 1** Location of the sampling areas in the municipalities of Brasileia and Eptaciolândia, Acre state, southwestern Brazilian Amazon. **(a)** Location of Brazil in relation to South America. **(b)** State of Acre; the municipality colored in gray is Brasileia, and the one colored in white is Eptaciolândia. **(c)** Red dots show the project collection regions in the municipality of Brasileia; yellow lines show the municipal boundaries. **(d)** Red dots show the project collection regions in the municipality of Eptaciolândia; blue lines show the municipal boundaries





**Fig. 2** Land-use types where ant samplings were carried out in the municipalities of Brasileia and Epitaciolândia, Acre state, southwestern Brazilian Amazon. **A** - pasture area; **B** - shifting cultivation; **C** - primary forest; **D** - old successional agroforestry systems; **E** - young successional agroforestry systems

### Sampling design

Ant collections were carried out in six replicates of each land use, resulting in a total of 30 sampling units. Replicates were spatially independent and separated by distances sufficient to ensure independence, varying according to land-use configuration. In each replicate, a 250 m transect was established, with 10 sampling points spaced 25 m apart. At each sampling point, ants were collected using pitfall traps placed on the soil surface (Bestelmeyer et al. 2000). The pitfall traps consisted of 200 ml plastic containers filled with 150 ml of a killing solution made of water, glycerol (5%), and salt (0.9%) (Schmidt and Solar 2010), which killed and preserved the ants. The traps were left in the field for 48 h. The ants collected in the traps were preserved in 90% alcohol for later sorting and mounting in the Laboratório de Ecologia de Formigas da Universidade Federal do Acre (UFAC).

Pitfall traps efficiently sample epigeic ant assemblages actively foraging on the soil surface and across the litter–soil interface, including both ground-nesting and arboreal species during foraging activity, and are widely used for comparative diversity studies across land-use gradients (Bestelmeyer et al. 2000; Schmidt and Solar 2010). This method has proven particularly effective for detecting changes in community composition, dominance patterns, and habitat-use guilds across land-use gradients (Agosti et al. 2000; Philpott et al. 2010).

## Ant species identification

We identified the ants to the genus level using identification keys from Feitosa and Dias (2024) and Baccaro et al. (2015). Species identification was initially conducted by comparing the morphospecies with specimens from the ant collection at the Laboratório de Ecologia de Insetos da Universidade Federal do Acre (UFAC).

Unidentified morphospecies were transported to the Laboratório de Sistemática e Biologia de Formigas da Universidade Federal do Paraná (UFPR) for species identification and confirmation by ant taxonomists. The reference specimens for this study were deposited in the collections of UFAC and UFPR.

## Habitat-use guilds

All ants identified to the species level were classified into three habitat-use guilds (i.e., forest specialists, generalists, and open-area specialists) (Dutra et al. 2024). To determine the guild of each species, we used the Brazilian Ant Habitat-use Guilds (BAH) (BAH 2023) application, which provides the classification of approximately 80% of the Brazilian ant fauna into habitat-use guilds. The BAH uses a database of habitat-use guilds based on the methodology contained in Dutra et al. (2024) that calculate the habitat preference of ants through an online database.

## Statistics analysis

First, to assess the effects of which land uses on ant species diversity, we employed gamma diversity ( $\gamma$ ), which is the total number of ant species sampled in each replicate of land uses. Alpha diversity ( $\alpha$ ) was obtained as the mean number of species present across the ten points of each transect in a replicate. Beta diversity ( $\beta$ ) between the sampling points of each transect was calculated using a presence-absence matrix, which allowed the computation of the *Sørensen* dissimilarity index. This index considers the number of species shared between the samples and the number of species exclusive to each one. The *Sørensen* dissimilarity index ranges from 0 to 1, with values close to 0 indicating that the samples share many species, and values close to 1 indicating that the samples represent distinct set of species. The index was obtained using the *beta.multi* function from the *betapart* package (Baselga et al. 2013).

To test our hypothesis, we constructed three Generalized Linear Models (GLMs), each with land-use type as the predictor variable and the response variable for the first model was  $\gamma$  diversity, modeled with a Poisson error distribution. The response variable for the second model was  $\alpha$  diversity, modeled with a normal error distribution. Finally, the third model used  $\beta$  diversity as the response variable, applying a binomial error distribution adjusted with a quasibinomial distribution (Crawley 2013). Finally, in all tests described above, we applied ANOVA to access the significance of differences among land use types. The significance of land-use means that at least one land-use type has alpha, gamma or beta diversity significantly different to the others land-use types. The R packages used to run the analyses described above were *lme4* (Bates et al. 2007; Douglas et al. 2015), *car* (Fox and Weisberg 2019) and *ggplot2* (Wickham 2016) to construct the graphics.

Thus, we proceeded a model simplification to verify each land-uses could be joined in a single levels. We did it sorting the land-use types by average of gamma, alpha, and beta diversity and joined the levels with similar average of these metrics. Thus, we created a new model with less levels (land-use types) and then compare with the initial model (with all land-use types), if there is non-significant difference, we opted to the simplest model (with less types of land-use) (Crawley 2013). We proceeded it until to arrive in the simplest model for each diversity metric (i.e. alpha, beta and gamma).

To identify the predominant ant habitat-use guild in each land-use type, we calculated the percentage of each guild relative to the total species richness in each land-use replicate. Thus, we used GLM, where the percentage was the response variable and land-use types (primary forest, old SAFs, young SAFs, shifting cultivation, and pasture) and habitat-use guilds (forest specialists, generalists, and open-area specialists) were the explanatory variables. Finally, we included the interaction between land-use type and habitat-use guild. We assumed a binomial error distribution due to the percentage nature of the response variable and if necessary we adjusted to quasibinomial error distribution (Crawley 2013) and applied to ANOVA to access the significance of the explanatoies variables.

For all models, we used diagnostic functions such as *rldiagnostic* from the RT4Bio package (Junior et al. 2015), which checks the distribution of residuals and other fit indicators. We conducted all analyses using R 2024.04.2 (<https://www.r-project.org/>). Specific packages and functions relevant to the statistical analyses described above were used accordingly.

## Results

### Ant fauna

A total of 265 ants records were obtained, of which 176 (66.41%) were identified to the species level, and 89 (33.58%) were classified as morphospecies or grouped into broader taxonomic categories. The ants were distributed across 56 genera, belonging to ten subfamilies. The subfamily Myrmicinae had the highest number of genera (24 genera), followed by Ponerinae and Dorylinae, each with seven genera. Formicinae had six genera, Dolichoderinae had five, Ectatomminae had four, and Amblyoponinae, Paraponerinae, Proceratiinae, and Pseudomyrmecinae each one had one genus (Supplementary Material, Table S1).

Of the 176 ants identified to the species level, 166 species were classified according to their habitat-use guild using the BAH application, while six species were classified using the methodology reported by Dutra et al. (2024). The classification of only two species (*Camponotus compositor* Santschi, 1922 and *Hylomyrma dolichops* Kempf, 1973) was not possible, as there was insufficient data to apply the method reported in Dutra et al. (2024).

A total of 21 new ant species records were found for the state of Acre (Table 1, occurring across the different land-use types).

### Gamma, alpha, and beta diversity

Gamma diversity differed among the land-use types ( $F_{4, 25} = 183.22; p < 0.001$ ). The gamma diversity of primary forest (mean 68.00) was higher than the other land-use types. The old (mean 40.50) and young (mean 32.00) SAFs showed respectively the second and third larg-

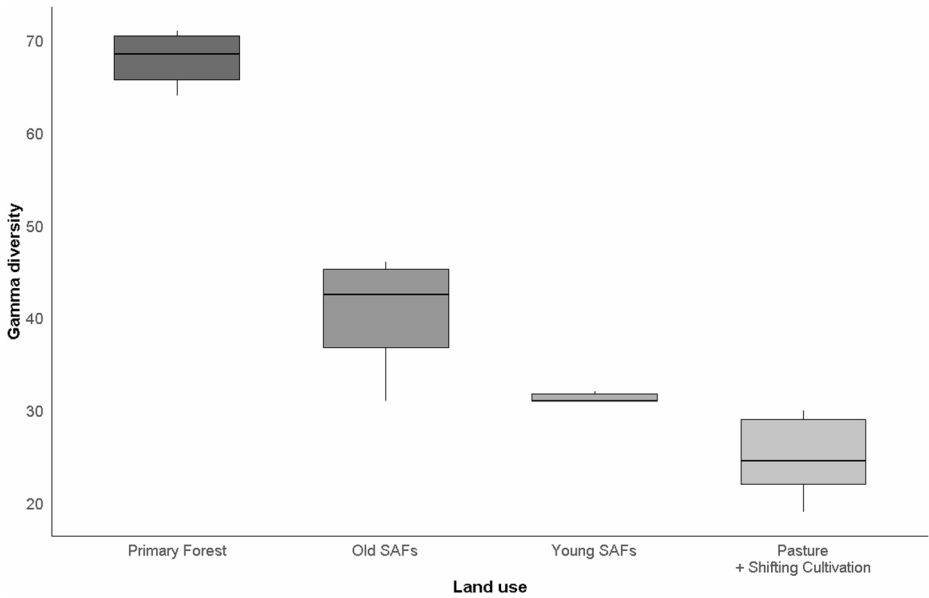
**Table 1** Ant species with new occurrence records for the state of Acre. Land uses: F - Primary Forest, OS - Old successional agroforestry system, YS - young successional agroforestry system, P - Pasture, R - Shifting cultivation. NF - Not found. Habitats-use guilds: for.spe - forest specialists, generalist - generalists, open-habitat - open-area specialists

Taxon	Land-use					Habitat-use guilds
	F	OS	YS	P	R	
<i>Dolichoderus rufescens</i> Mann, 1912	1	0	1	0	0	for.spe
<i>Dolichoderus abruptus</i> (Smith, 1858)	0	1	0	0	0	open-habitat
<i>Cylindromyrmex striatus</i> Mayr, 1870	0	1	0	0	0	for.spe
<i>Brachymyrmex cordemoyi</i> Forel, 1895	1	1	1	1	1	generalist
<i>Brachymyrmex termitophilus</i> Forel, 1895	0	0	1	1	0	open-habitat
<i>Brachymyrmex pictus</i> Mayr, 1887	1	1	1	0	0	for.spe
<i>Brachymyrmex degener</i> Emery, 1906	1	0	0	0	0	generalist
<i>Camponotus sanctaefidei convexinodis</i> Wheeler, 1934	1	0	0	0	0	NF
<i>Camponotus substitutus</i> Forel, 1899	1	0	1	1	1	generalist
<i>Camponotus excisus</i> Mayr, 1870	1	0	0	0	0	for.spe
<i>Camponotus burtoni</i> Mann, 1916	1	0	0	0	0	for.spe
<i>Camponotus compositor</i> Santschi, 1922	1	0	1	1	1	NF
<i>Acromyrmex rugosus</i> (Smith, 1858)	0	1	0	0	0	generalist
<i>Carebara anophthalma</i> (Emery, 1906)	1	0	0	0	0	for.spe
<i>Mycetarotes acutus</i> Mayh�-Nunes, 1995	1	0	0	0	0	open-habitat
<i>Mycetophylax lectus</i> (Forel, 1911)	1	0	0	0	1	open-habitat
<i>Strumigenys urrhobia</i> (Bolton, 2000)	1	0	0	0	0	for.spe
<i>Anochetus neglectus</i> Emery, 1894	0	1	0	0	0	generalist
<i>Platythyrea punctata</i> (Smith, 1858)	0	1	0	0	0	for.spe
<i>Probolomyrmex brujitae</i> Agosti, 1995	0	1	0	0	0	for.spe
<i>Pseudomyrmex tenuissimus</i> (Emery, 1906)	0	1	0	0	0	generalist

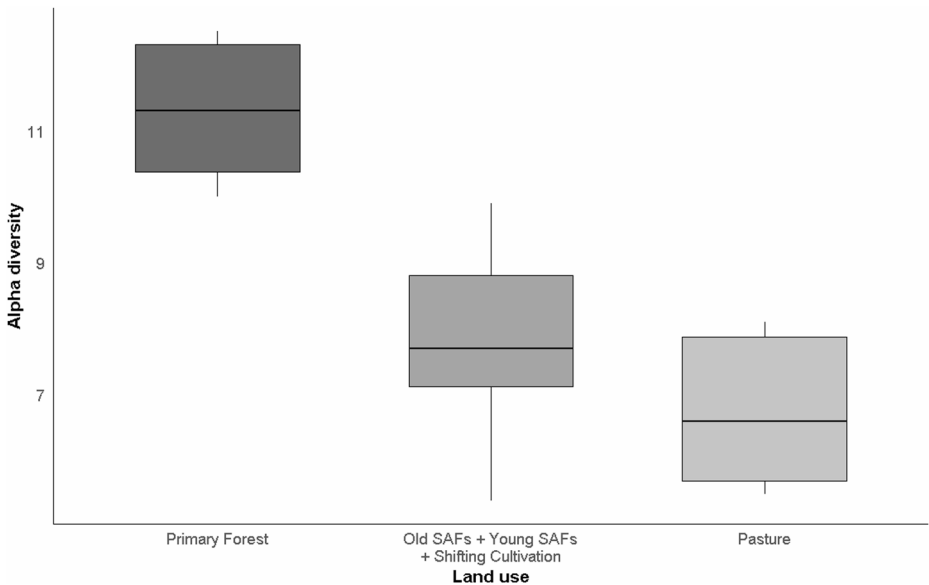
est gamma diversity. The most intensive land-use types (i.e. pasture and shifting cultivation) presented the smallest gamma diversity (mean-pasture: 23.33; mean-shifting cultivation: 26.83), which were similar and were joined in a single level by model simplification (Fig. 3).

Alpha diversity differed among the various land-use types ( $F_{4, 25} = 13.34$ ;  $p < 0.001$ ) (Fig. 4). Differences among land-use types were identified through model simplification, in which land-use levels with statistically similar mean values were progressively grouped based on non-significant model comparisons. Primary forest presented the higher alpha diversity (mean 11.30) (Fig. 4). The alpha diversity of old SAFs (mean 7.55), young SAFs (mean 8.21) and shifting cultivation (mean 7.75) presented similar values. Thus, these land-uses were joined at a single level (Fig. 4) by model simplification. Finally, pastures exhibited the lowest alpha diversity (mean 6.75) (Fig. 4).

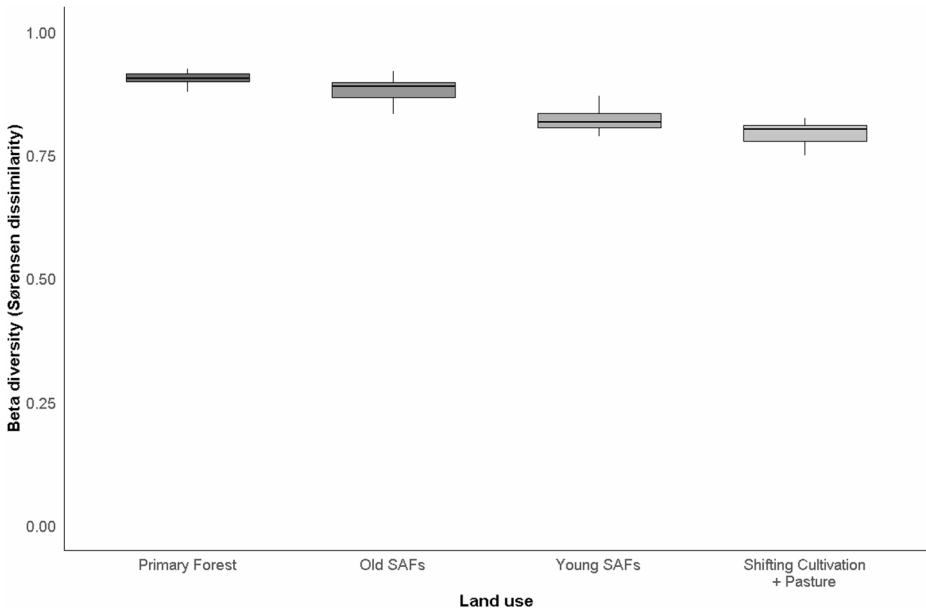
Consistent with our expectations, beta diversity also varied across land-use types ( $\chi^2_{(4,25)} = 16.11$ ,  $p < 0.01$ ). More intensive land use types (pasture and shifting cultivation) showed lower  $\beta$  diversity (i.e., higher similarity among ant assemblages across sampling points) compared to less intensive use-types (primary forest and old SAFs) (Fig. 5). The beta diversity of pastures (mean 0.79) and shifting cultivation (mean 0.79) presented similar values, then, was possible joined them in a single level by model simplification (Fig. 5). Both SAFs presented higher beta diversity (mean-old: 0.882; mean-young: 0.82) than more intensive land-use types (i.e. pasture and shifting cultivation), but still lower than primary forest (mean 0.90) (Fig. 5).



**Fig. 3** Gamma diversity across the land-use types in the municipalities of Brasileia and Epitaciolândia, Acre state, southwestern Brazilian Amazon. Land use types: Primary Forest areas; Old SAFs - old successional agroforestry systems; Young SAFs - young successional agroforestry systems; Pasture+Shifting Cultivation - merging group composed by pasture areas and shifting cultivation



**Fig. 4** Alpha diversity across the land-use types in the municipalities of Brasileia and Epitaciolândia, Acre state, southwestern Brazilian Amazon. Land use types: prim\_for - primary forest areas; Old SAFs + Young SAFs + Shifting cultivation - merging group composed by old successional agroforestry systems and young successional agroforestry systems and shifting cultivation; pasture - pasture areas



**Fig. 5** Beta diversity across the land use types in the municipalities of Brasileia and Epitaciolândia, Acre state, southwestern Brazilian Amazon. Land use types: Primary Forest areas; Old SAFs - old successional agroforestry systems; Young SAFs - young successional agroforestry systems; Shifting Cultivation + Pasture - merging group composed by pasture areas and shifting cultivation

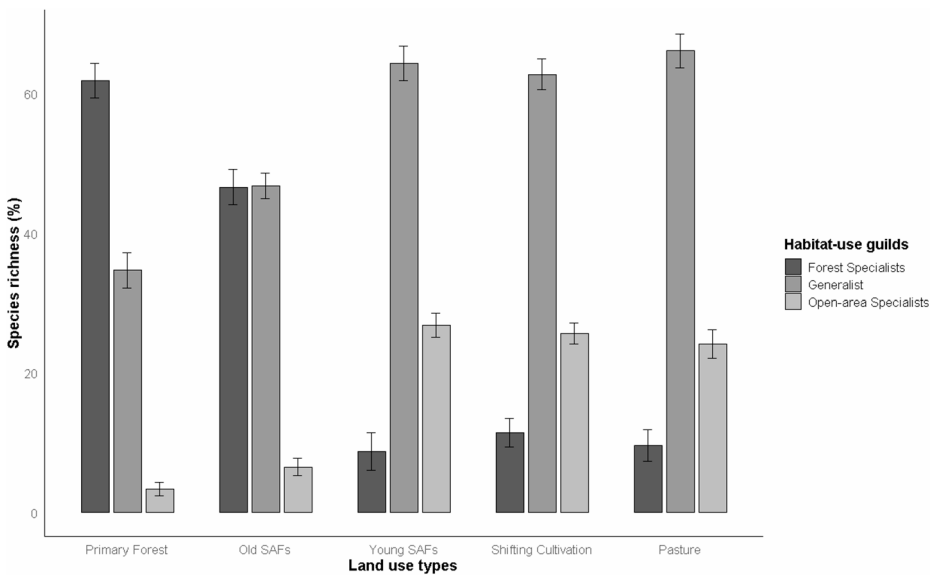
## Habitat-use guilds

Corroborating our expectation, the percentage of species richness in habitat-use guilds did not vary across land use types ( $\chi^2_{(85,4)}=23.63$ ;  $p=1$ ), but this was different among habitat-use guilds ( $\chi^2_{(83,2)}=13.43$ ;  $p<0.001$ ) and the interaction between land-use types and habitat-use guilds was significant ( $\chi^2_{(75,8)}=1.58$ ;  $p<0.001$ ). This means that ant assemblages in areas of more intensive land use (i.e., pastures and shifting cultivation) were relatively composed of more generalist ants and open-area specialists, whereas primary forest (less intensive land use) was relatively more composed of forest specialists (Fig. 6).

The ant assemblages of young SAFs were more relatively composed by generalist ants and open-areas specialists, similar to the ant assemblages from more intensive land uses (i.e., pastures and shifting cultivation) (Fig. 6). In turn, the ant assemblages of old SAFs, although presented a higher proportion of forest specialist than open-area specialists, it was followed closed by generalist (Fig. 6).

## Discussion

Our results show that ant assemblages of Old SAFs, although with lower diversity metrics (i.e. alpha, gamma and beta), show guild compositions approaching those of primary forests, but at this stage, forest specialist and generalist presented almost the same percentage of species richness. In it turns, young SAFs resemble the more intensive land uses



**Fig. 6** Percentage of ant species richness in habitat-use guilds through out different land-use types in the municipalities of Brasília and Epitaciolândia, Acre state, southwestern Brazilian Amazon. Habitat-uses guilds: Forest Specialists, Generalists, and Open-area Specialists. Land use types: Primary Forest, Old SAFs - Old Successional Agroforestry Systems, Young SAFs - Young Successional Agroforestry Systems, Shifting Cultivation, and Pasture areas

(i.e., pastures and shifting cultivation). In the sections below, we provide explanations for these results and present implications for biodiversity conservation in human-modified landscapes.

## Ant fauna

In our study, the new records for the state of Acre are particularly interesting because they appear in even in intensive land-use types (i.e. pasture, shifting cultivation, young successional agroforestry systems) such as *Brachymyrmex cordemoyi* Forel, 1895, a generalist species, was recorded in all land-use types in this study and *Brachymyrmex termitophilus* Forel, 1895 and *Camponotus substitutus* Forel, 1899, only in intensive land-use types. This reinforce the lack of ant sampling in the southwestern Amazon (Schmidt et al. 2025).

In addition to foraging strategies, the presence of these species can be explained by the type of habitat they occupy, whether as generalists or specialists of open habitats. Species from these guilds are able to withstand different ecological filters. The fact that our study resulted in 21 new records is highly expressive and improve the ant species record to Acre for 455, highlighting the southwestern Amazon as a frontier on ant sampling in the Neotropical region (Schmidt et al. 2025; Dias and Feitosa 2024). This discovery further emphasizes the region's importance for biodiversity and underscores its potential to yield more insights into the richness of ant species in this part of the world.

The conversion to more intensive land-uses resulted in the loss of certain functional groups of ants. For example, predatory species such as those from the genera *Strumigenys* and *Gnamptogenys* were predominantly found in areas with lower land-use intensity (e.g.,

primary forest and old SAFs). These species typically forage in the leaf litter and build their nests in these habitats (Baccaro et al. 2015), which may explain the decline in their populations in pasture and shifting cultivation areas due to environmental changes.

In contrast, species from the genera *Brachymyrmex*, *Pheidole* and *Solenopsis* benefitted from the conversion of forests to pasture and shifting cultivation. This is evidenced by the characteristics of these intensive land-uses, which resemble open habitats (Vasconcelos et al. 2018; Fontenele and Schmidt 2021). These species are largely considered generalists and/or adapted to open habitats (Dutra et al. 2024).

### Gamma, alpha and beta diversity

Regarding gamma diversity, our results show that primary forest harbors the highest values followed by old SAFs. This indicates that, beyond maintaining high local diversity (alpha diversity) and species turnover (beta diversity) (Costa and Schmidt 2022), these environments support a broader regional species pool. In contrast, more intensive land-use types (i.e. pasture and shifting cultivation), exhibited significantly lower gamma diversity, highlighting their selective ecological role on the regional ant fauna, which only species adapted to open habitat are more prompt to survive (Dutra et al. 2024) (see also our Fig. 6). Old SAFs presented the second highest gamma diversity, which allow it to be a friendly land-use for ant diversity conservation in tropical human-modified landscapes (Hoenle et al. 2022), but the fact that forest specialists and generalist presented almost the same percentage of species richness indicates that more time of forest recover is necessary to the successional agroforestry systems sampled achieved similar level biotic complexity and biodiversity than primary forests.

These patterns are consistent with what has been observed across the Neotropics. According to Wilker et al. (2024), the conversion of forest to pasture, an example of an intensive land-use change leads to strong declines in ant diversity due to the simplification of vegetation structure and environmental conditions. Andersen (2019) further explains that such disturbances act as strong environmental filters, excluding disturbance-sensitive and specialist species while favoring disturbance-tolerant generalists. As a result, habitat homogenization leads to the exclusion of unique species and reduced regional richness (gamma diversity).

We found out that all human-induced land-uses presented a lower alpha diversity than primary forest (Fig. 4) which corroborates the findings of Wilker et al. (2023). However, considering only alpha diversity is not possible differentiate the ant assemblages among the human-induced land-uses (i.e., old and young successional agroforestry systems and shifting cultivation), reinforcing the necessity of the use of other diversity metrics, such as beta diversity (Costa and Schmidt 2022) and the use of habitat-use guilds (Dutra et al. 2024).

Beta diversity, on the other hand, seems to be more sensitive to land-use changes. Even with a more subtle change (Escobar-Ramírez et al. 2020) or with an intense change, we can find differences in  $\beta$  values in ant assemblages, which become evident according to the type of land-use. In our study, areas with more intensive land use (i.e., pasture) exhibited low beta diversity values. On the other hand, in areas with less intensive land use (i.e., primary forest), the high beta diversity values are intrinsically linked to a more restricted distribution of species in these environments and to environmental heterogeneity (Ribas et al. 2003).

The biotic and abiotic constraints of a habitat determine the functional traits that will be useful for ant species survival (Hoffmann and Andersen 2003; Philpott et al. 2010; Oliveira

et al. 2017, 2019; Ribeiro-Neto et al. 2023) and ultimately their distribution (Heino et al. 2015). Thus, the homogeneity of resources and conditions in more intensive land-use (Fearnside 2005; Imazon 2012; Araújo et al. 2011) could favor ant species overdispersion within these habitats leading to low beta diversity among the assemblages. In turn, in less intensive land-use, the heterogeneity of resource and conditions could impose more restriction to ant species distribution, leading to high values of beta diversity (Costa and Schmidt 2022).

## Habitat-use guilds

The use of habitat-use guilds have provided more clarity on ant composition change (Dutra et al. 2024), bearing in mind that ant species within these guilds respond differently according to their various tolerances to habitat openness (Andersen 2019) and consequently according to the winner–loser framework (McKinney and Lockwood 1999; Filgueiras et al. 2021), anthropogenic disturbances disproportionately disadvantage forest specialists, while favoring a limited subset of generalist and open-habitat species (Paolucci et al. 2017; Martins et al. 2022). Furthermore, these guilds often exhibit specialized aspects of morphology, ecology, or behavior (Gibb et al. 2015), and their richness throughout secondary succession tends to change differently (Schmidt et al. 2013; Marques et al. 2017; Neves et al. 2021; Sousa-Souto et al. 2016; Bombi-Haedo et al. 2025).

Dutra et al. (2024) has reported that ant assemblages of forest habitat are predominantly made up by forest specialist and in turn, ant assemblage of pasture generalists and open-habitat specialist are dominant. This highlights that canopy cover has a direct effect on the selection of habitat-use ant guilds and thus the response of ants to human-induced disturbances is essentially indirect because they respond to changes on vegetation structure that was affected by these disturbance (Andersen 2019).

Studies have documented multiple relationships between ants and agroforestry systems, including how ant communities influence ecosystem services and disservices, how ant species richness and community composition correlate with vegetation structure (Bisseleua et al. 2009, 2017) and how ant assemblages recover during secondary succession following agricultural disturbance (Bombi-Haedo et al. 2025). According to Khoo and Ho (1992), ant species can yet act as biological control agents in agroecosystems, reducing the presence of undesirable pests. Furthermore, studies highlight the importance of ants in agroecosystems due to their roles in regulating arthropod populations, influencing plant performance, and contributing to key ecosystem processes such as pest suppression and trophic interactions (de la Fuente and Marquis 1999; Roberts et al. 2000; Klein et al. 2003). In addition, ants provide intermediate ecosystem services, such as the natural control of pests and plant diseases through predation, competition, and interactions (Philpott and Armbrrecht 2006; Zovi et al. 2008). These studies have demonstrated the contribution of SAFs to conservation (Brown et al. 2006) and their importance in conservation and reforestation plans aimed to protect ant diversity. Agricultural areas that are vegetatively complex, with high diversity, density, and height, are able to maintain biodiversity levels similar to those of native forests (Moguel and Toledo 1999), and regenerating forests become taxonomically, functionally, and phylogenetically similar to mature forests (Barros et al. 2021).

In our study, even considering its limitations (i.e. single-stratum, single-method design) the ant habitat-use guilds in areas of old SAFs are approaching those of primary forest areas, which suggests that this similarity between the areas is due to shared habitat characteristics.

However, the fact that generalist has a similar percentage than forest specialists in old SAFs shows that this land-use is not equivalent to a forest in biodiversity, but is a much better land-use than pasture and shifting cultivation for Amazon biome. On the other hand, young SAFs resembled pasture and shifting cultivation areas.

Finally, our findings instigate a key question: which point during SAFs development the replacement among the ant habitat-use guilds occur? Although there are studies that track the recovery of ant assemblages and changes in vegetation along chronosequences (Lawes et al. 2017; Hoenle et al. 2022), there is a lack of studies on SAFs context regarding to track the vegetation recovery where this guild replacement occurs and the necessary time for that. The investigation of that (theoretically or/and empirically) is extremely useful for the use of ant assemblages as clear and predictable indicator on monitoring programs (Dale and Beyeler 2001).

## Conclusion

Our study showed that the time of succession of the SAFs has a direct impact on ant composition, with areas of Old SAFs supported ground-foraging ant assemblages and guild compositions approaching those of primary forests, dominated by forest specialists. In contrast, young SAFs displayed a pattern more similar to that of intensively used land areas, such as pastures and shifting cultivation, with a predominance of generalist ants and open-areas specialists. These results suggest that ecological succession in SAFs may be a gradual process, where system maturity is key to achieving a species diversity closer to that observed in native forests.

The SAFs is a key factor for biodiversity and composition of ant habitat-use guilds. This raises important questions about the time needed for SAFs to develop and become effective in restoring the diversity of forest ant specialists. Further studies are needed to more accurately assess the temporal aspects of this process, investigating how long it takes for an SAFs to achieve vegetation cover that favors the predominance of specialized forest species. Such studies could provide valuable information for the management of SAFs as tools for ecological restoration, highlighting the importance of considering the age, development stage and management history of successional agroforestry systems in biodiversity conservation strategies.

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**Data availability** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Consent for publication** All authors approve the publication of this manuscript.

**Competing interests** The authors declare no competing interests.

**Conflict of interest** All the authors declare that don't have known financial interests or personal relationships that could have to influence the work reported in this paper.

**Ethics approval** Not applicable.

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**Consent from the authors** All persons who meet in this manuscript authorship are listed as authors, and all authors certify that they have participated sufficiently in this work to assume public responsibility for the content, including participation in the list, analysis, writing and proofreading.

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