Received: 7 July 2022 | Accepted: 24 January 2023

DOI: 10.1111/icad.12632

ORIGINAL ARTICLE

Insect Conservation and Diversity

Royal Entomological Society

Land-use change in the Amazon decreases ant diversity but increases ant-mediated predation

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Funding information

Conselho Nacional de Desenvolvimento Científico e Tecnológico; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Number: Finance code: 001; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES/PROCAD), Grant/Award Number: 88887.200518/2018-00; Programa de Apoio à Publicação em Periódicos de Alto Impacto; Programa Institucional de Bolsas de Iniciação Científica (UFAC); Programa Nacional de Pós-Doutorado/CAPES

Editor: Raphael K. Didham and Associate Editor: Mark Wong

Abstract

1. Food production in Amazonian traditional societies often occurs through shifting cultivation that uses few pesticides and relies on ecosystem services provided by natural enemies. However, these sustainable agricultural practices are being threatened by increasing livestock and mechanised agriculture.
2. This study aimed to evaluate the effects of the conversion from Amazon Forest to anthropogenic land uses (shifting cultivation and pasture) on α- and β-diversity, functional groups, and ant-mediated predation.
3. Three types of habitats were sampled: forest (eight sites), shifting cultivation (five sites) and pasture (seven sites). The ant assembly of each site was sampled using pitfall traps in the epigeic and hypogeic strata. Beetle larvae were used to evaluate the predation function.
4. Negative effects on epigeic ants and functional groups were found to be greater in sites where anthropogenic land use was more intensive (pasture) than in those where it was less intensive (shifting cultivation). Furthermore, this change increased the predation of insects in shifting cultivation and pasture compared to that in forest. This increase in insect predation was due to high activity of *Ectatomma brunneum* Smith, 1858, an environmental indicator for shifting cultivation and pasture.
5. The increase in the number of predations in shifting cultivation and pasture may be beneficial from the perspective of biological pest control. However, this relationship needs to be better understood because the high presence and predatory activity of *Ectatomma brunneum* in these environments may be one mechanism by which α- and β-diversity decrease through antagonistic interactions and dominance.

KEYWORDS

biological control, ecosystem function, *Ectatomma brunneum*, pasture, richness, shifting cultivation, tropical forest, α-diversity, β-diversity

INTRODUCTION

Conversion from semi-natural habitats to anthropogenic land uses has led to decreases in population sizes and increases in species extinctions in terrestrial environments (Betts et al., 2017; Green et al., 2020; Newbold et al., 2015), and is the main driver of biodiversity loss over the last century, especially in tropical forests (Phillips et al., 2017; Sala et al., 2000). The conversion from semi-natural habitats to food production sites, such as for mechanised agriculture and livestock activities, is substantial (de Chazal & Rounsevell, 2009). Such conversions affect biodiversity worldwide, especially in tropical environments, such as the Amazon Forest, recognised as the most biodiverse region globally (Heckenberger et al., 2007; Sala et al., 2000). Currently, in Brazil, the Amazon Forest is most affected by pasture expansion (Parente & Ferreira, 2018). In response, there has been an increase in studies evaluating the conversion from semi-natural habitats to anthropogenic land uses to understand the effects. These studies seek to conserve biodiversity and mitigate anthropogenic impacts (Gardner et al., 2013; Newbold et al., 2015). The conversion from semi-natural habitats to anthropogenic land uses and other drivers can affect biodiversity differently (de Chazal & Rounsevell, 2009), with varied effects, from positive (e.g., higher butterfly species richness in forest-derived vanilla agroforests compared to forest fragment; Wurz et al., 2022) to negative (e.g., conversion of tropical savanna to pasture negatively affects ant species richness; Queiroz et al., 2020), or even neutral (e.g., conversion of Amazon Forest to shaded coffee does not affect ant species richness; Escobar-Ramírez et al., 2020). However, conversion from semi-natural habitats to anthropogenic land uses, such as mechanised production, usually generates negative effects, such as decreased species richness and biomass of most taxa, including invertebrates, birds, and plants (Barnes et al., 2017).

It is increasingly important to consider alternatives to mechanised production, such as agroforestry systems and traditional agriculture (Altieri, 2004). Among such systems is shifting cultivation, a traditional practice performed by small and medium producers, which creates a mosaic of different habitats and succession sites in tropical environments (Altieri, 2004). Accordingly, forests are cut down and burned to create planting sites (shifting cultivation), which are subsequently abandoned for forest growth (fallow) (Kleinman et al., 1995). The main crops in shifting cultivation in the Amazon are white rice, corn, beans, and cassava. After a fallow period, crop sites can be used for new agriculture (cutting and burning are performed again), for the formation of 'capoeira' (secondary forest), or even for pasture for livestock production (cattle), which is becoming the main local economic activity (Padoch & Pinedo-Vasquez, 2010; van Vliet et al., 2012). These practices turn shifting cultivation into a type of agriculture that harbours greater biodiversity in a landscape compared to that harboured by monocultures (Arroyo-Rodríguez et al., 2020; Mandal & Raman, 2016; Rerkasem et al., 2009). Such traditional practices, however, have been threatened by the intensification of agriculture and grazing (pastureland) in the Amazon in recent years (Padoch & Pinedo-Vasquez, 2010; van Vliet et al., 2012).

Many studies have used ants to understand the effects of conversion from semi-natural habitats to anthropogenic land uses on biodiversity (Escobar-Ramírez et al., 2020; Queiroz et al., 2020; Solar et al., 2016) because ants have high species richness and perform important ecosystem functions (Folgarait, 1998; Lach et al., 2010). Among these functions, ants are considered the largest resource removers in ecosystems (Griffiths et al., 2018) and are the predominant predators of arthropods in tropical environments (Seifert et al., 2016). Similarly, ants play important roles in the prevention and control of insect pests in agriculture (Morris et al., 2018; Perfecto & Vandermeer, 2015).

Substantial conversion from semi-natural habitats to anthropogenic land uses (such as from forest to agriculture) and intensive management (such as mechanised agriculture or pasture), tends to decrease ant α-diversity (species richness of a site) and β-diversity (difference in species or community composition between sites), causing the homogenisation of biotic communities (Ahuatzin et al., 2019; Costa & Schmidt, 2022; Escobar-Ramírez et al., 2020; Queiroz et al., 2020; Solar et al., 2015, 2016). These changes in species composition can be caused by species replacement in human-modified habitats (Costa & Schmidt, 2022; Solar et al., 2015), which, in addition to changes in species diversity, can also impact fundamental ecosystem functions (Bihn et al., 2010; Martins et al., 2022). In addition, conversion from semi-natural habitats to anthropogenic land uses decreases the diversity of specialist ant species while increasing the diversity of generalist ant species (Escobar-Ramírez et al., 2020; Martins et al., 2022; Solar et al., 2015). Decreases in the diversity of ant species that are specialist predators have been observed in shifting cultivation systems (Matsumoto et al., 2009). Species loss can lead to changes in the functions performed by ants due to a positive relationship between ant diversity and the diversity of ecosystem functions (Bihn et al., 2010; Menezes & Schmidt, 2020; but see Cadotte et al., 2011).

In tropical forests and agroforestry systems, a greater diversity of trees tends to harbour a greater abundance and richness (α-diversity) of ants (Armbrecht & Gallego, 2007; De la Mora et al., 2015; Escobar-Ramírez et al., 2020; Staab et al., 2014), generating a positive effect on predation (De la Mora et al., 2015; Pacheco et al., 2017). In this sense, a positive effect of β-diversity on predation would be expected. Although conversion from semi-natural habitats to anthropogenic land uses decreases ant α- and β-diversity, insect predation may not be affected by such conversions (De la Mora et al., 2015; Pacheco et al., 2017). This occurs because even though taxonomic diversity decreases in these environments, there is a greater abundance of some groups of medium and large-size omnivore/generalist predator ants in these environments (Escobar-Ramírez et al., 2020; Pacheco et al., 2017), which may be more important than greater diversity, per se, for predation (Penn et al., 2017). In addition, these generalist groups may perform the role of small specialist predators in disturbed ecosystems, which are negatively affected by ecosystem changes (Gibb et al., 2018; Rosenfeld, 2002), where local extinction causes niche expansion among the remaining species (Manlick & Newsome, 2021).

Some strategies can be used in human-modified landscapes to reconcile both the preservation of generalist and specialist species and food production (Arroyo-Rodríguez et al., 2020). Among these strategies and debates (e.g., land sharing vs. land sparing; Phalan et al., 2011), shifting cultivation systems are important alternatives to consider because they promote both food production and biodiversity conservation within a landscape (Padoch & Pinedo-Vasquez, 2010; Perfecto & Vandermeer, 2010). In addition to less intensive conversion from semi-natural habitats to anthropogenic land uses, shifting cultivation involves less use of fertilisers and pesticides, which together are considered the second largest driver of entomofauna loss (Sánchez-Bayo & Wyckhuys, 2019). Besides, species conservation can promote ecosystem functions that also benefit human communities, such as biological pest control, for example (Grass et al., 2019). However, most studies on conversion from semi-natural habitats to anthropogenic land uses address effects on community structure (e.g., species richness and composition), while the effects on ecosystem functions have been poorly studied (but see Tuma et al., 2019; Houadria et al., 2020). Filling this knowledge gap is even more important from the socioecological perspective of shifting cultivation because biodiversity loss can affect crucial ecosystem services for small farmers, such as pollination and pest control (Isaacs et al., 2009).

Therefore, we aimed to evaluate the effects of the conversion of Amazon Forest in a shifting cultivation system (conversion from forest to shifting cultivation and pasture) on the diversity of species and functional groups of ants and ant-mediated predation. We addressed the following hypotheses: (1) ant α- and β-diversities will decrease with increased intensity of anthropogenic land use (conversion from forest to shifting cultivation and pasture, respectively), mediated by species replacement (turnover); (2) forest sites will have more ant functional groups, including specialist ants, while shifting cultivation and pasture sites will have a predominance of ants belonging to functional groups of medium- and large-size epigeic and generalist predators; (3) the rate of insect predation by ants will be higher in sites with a higher α- and β-diversity of predatory ant species; and (4) ant-mediated predation will increase with increased intensity of anthropogenic land use (conversion from forest to shifting cultivation and pasture, respectively), caused specifically by the functional groups expected at these sites (medium- and large-size epigeic and generalist predators).

MATERIALS AND METHODS

Study area

Sampling was performed in the Reserva Extrativista Chico Mendes (RESEX Chico Mendes, created by Decree n° 99.144 of March 12, 1990) located in the state of Acre, southwestern Brazilian Amazon. Data were collected in Assis Brasil, along the road that connects this city to the Iaco River (10°54′42.50″ to 10°34′50.90″ south latitude, 69°33′55.10″ to 69°41′51.60″ west longitude). The climate in the region is humid tropical, with a mean annual temperature of approximately 27°C. The mean annual rainfall is between 1800 and 2200 mm, with the rainy season occurring between November and April and the dry season occurring during the months of June, July, and August (Costa & Schmidt, 2022). Ants were sampled in August 2019 during the dry season, since it is not possible to reach the sampled sites in the rainy season.

A total of 73% of the vegetation in the RESEX Chico Mendes is composed of open ombrophilous forest, with a large presence of bamboo (mainly *Guadua*), and the remaining 27% is composed of dense ombrophilous forest. In forest sites, residents extract Brazil nuts (*Bertholletia excelsa*), rubber latex (*Hevea brasiliensis*) and other plant products for trade and hunt animals for their own consumption. In addition, residents perform shifting cultivation in shifting cultivation systems that involve the cutting and burning of forests for the creation of short-term cultivation sites (4–5 years), subsequently followed by abandonment, leading to the formation of fallows, where forests regenerate by ecological succession (Padoch & Pinedo-Vasquez, 2010). Between 2000 and 2018, 14.4% of the semi-natural forest cover in the RESEX Chico Mendes was lost, with the main factor being conversion of forests to pasture establishments (Milien et al., 2021).

Experimental design

A total of 20 sites were sampled, eight forest sites ($n = 8$), five shifting cultivation sites ($n = 5$) and seven pasture sites ($n = 7$) (total $n = 20$, Figure 1). Different crops were planted in the shifting cultivation sites over the years of use. Thus, as standard methodology, collections were obtained from shifting cultivations that were growing the same crops at the time of collection, that is, the use period and type were the same (main crops: rice, beans, papaya, and pepper). A transect was established in each site consisting of five sampling points 20 m apart. Each treatment (same habitat category) was separated by at least two kilometres, seeking independence between samples. However, in most cases, more than one different habitat was sampled in the same region due to the distribution of habitats in the RESEX Chico Mendes. Thus, we avoided the effect of pseudoreplication in the statistical models and controlled the distance between sites (Bates et al., 2015).

Ant sampling

Ants were sampled at each of the five sampling points along transects using a pair of pitfall traps, one for the epigeic stratum and one for the hypogeic stratum. The traps consisted of plastic pots measuring 12 cm in diameter and 11 cm deep. Each trap received 200 mL of water in which detergent and salt were dissolved. The epigeic trap was buried at ground level for sampling epigeic ants (Bestelmeyer et al., 2000), while the hypogeic trap (openings on the sides) was buried 20 cm from ground level for sampling hypogeic ants (Schmidt & Solar, 2010). The traps were set for 48 h at

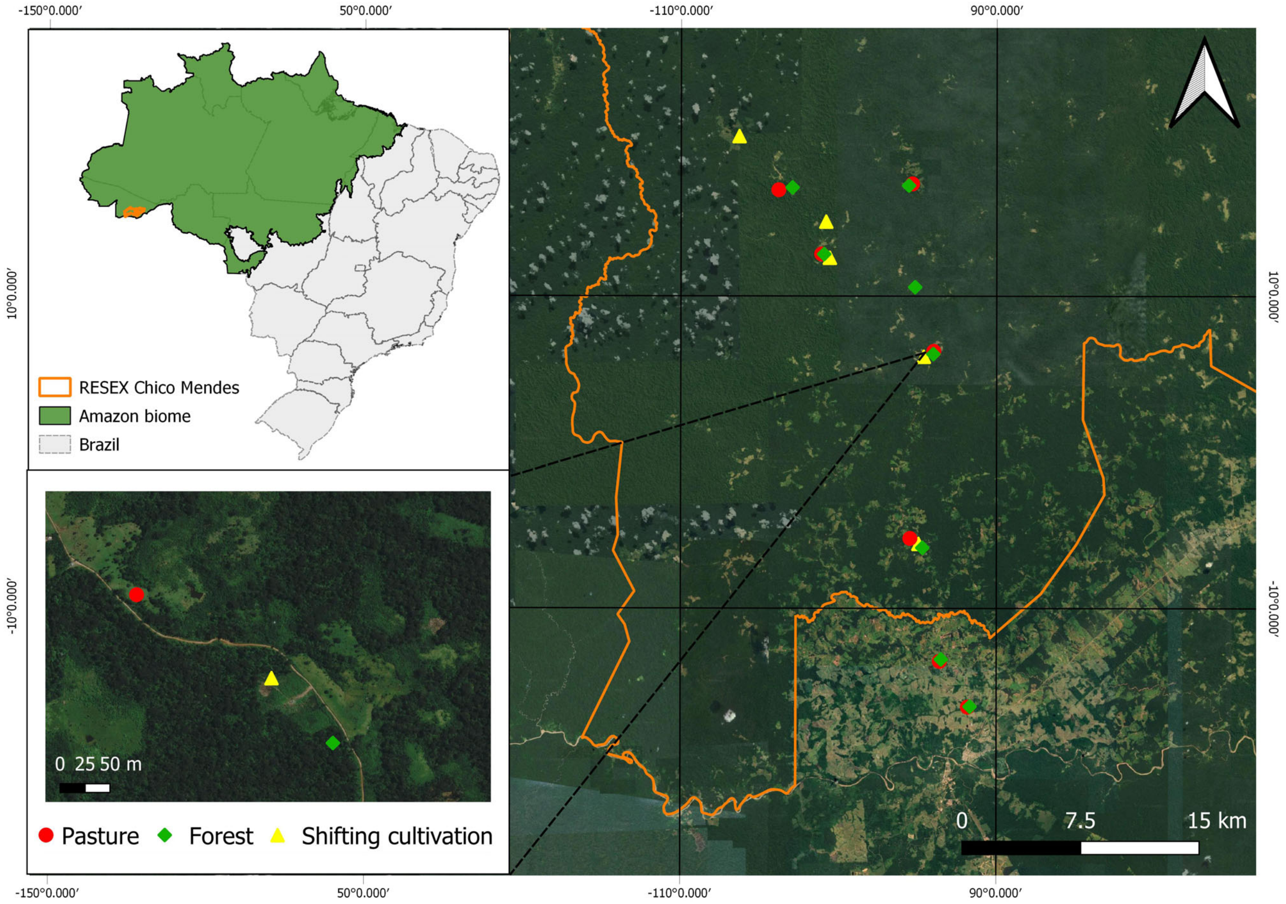

FIGURE 1 Distribution of sampling sites in the Reserva Extrativista Chico Mendes (RESEX Chico Mendes) in Assis Brasil, Acre, southwestern Brazilian Amazon. Land-uses: green square = forest, yellow triangle = shifting cultivation, and red circle = pasture.

the collection points. Collected ants were preserved and stored in 98% alcohol.

Insect predation

Ant-mediated predation was evaluated using two live Tenebrio beetle (*Tenebrio* sp.) larvae placed at each of the five sampling points along each transect. Each larva was tied with a piece of thread attached to a wooden toothpick fixed to the soil, preventing the larvae from leaving the sampling point. The larvae were exposed in the morning (between 7 am and 11 am). Four rounds of observations were performed, and each sampling point was observed for 5 min per round. Predation was considered an ant exhibiting attack behaviour towards the larvae, either by bite (using the mandible) or sting (using the stinger). Ants that showed attack behaviour were actively collected with entomological tweezers and stored in Eppendorf tubes containing 98% alcohol. Throughout the experiment, the larvae that died were replaced with live larvae. Metal cages were placed over the Tenebrio larvae as protection to prevent predation of the larvae by vertebrates. Sampling for the predation experiment was done before installing pitfall traps to avoid depleting the ant population by trapping (Lasmar et al., 2017).

Ant species identification

All collected ants (pitfall and predation) were transported to the Laboratório de Ecologia de Formigas at Universidade Federal do Acre (UFAC) and to the Laboratório de Ecologia de Formigas at Universidade Federal de Lavras (UFLA), where they were taxonomically identified to the genus level based on descriptions by Baccaro et al. (2015). Identification and confirmation of species and morphospecies was made by Mila F. O. Martins. For species and morphospecies, specific published descriptions were used to identify *Acromyrmex* (Gonçalves, 1961), *Acropyga* (LaPolla, 2004), *Apterostigma* (Lattke, 1997), *Atta* (Goncalves, 1942), *Brachymyrmex* (Ortiz-Sepulveda et al., 2019), *Camponotus* (Mackay, 1997), *Carebara* (Fernández, 2004), *Cephalotes* (Andrade & Urbani, 1999), *Crematogaster* (Blaimer, 2012; Longino, 2003), *Discothyrea* (Borgmeier, 1954), *Dolichoderus* (MacKay, 1993), *Dorymyrmex* (Cuezzo & Guerrero, 2012), *Ectatomma* (Kugler & Brown, 1982), *Gnamptogenys* (Camacho et al., 2020), *Holcoponera* (Camacho et al., 2020), *Leptogenys* (Lattke, 2011), *Linepthema* (Wild, 2007), *Megalomyrmex* (Brandão, 2003), *Mycetomoellerius* (Mayhe-Nunes & Brandão, 2002), *Ochetomyrmex* (Fernandez, 2003), *Octostruma* (Longino, 2013), *Odontomachus* (Brown Jr, 1976), *Pachycondyla* (Fernandes et al., 2014; Mackay & Mackay, 2010; Wild, 2005), *Pheidole* (Wilson, 2003), *Pogonomyrmex* (Johnson, 2021), *Solenopsis* (Pacheco et al., 2013; Pitts et al., 2018), *Trachymyrmex* (Solomon et al., 2019), and *Wasmannia* (Longino & Fernández, 2007). In addition, ant specimens from the Coleção Entomológica at Universidade Federal de Lavras (CEUFLA) and Antweb (www.antweb.org) were used for comparisons. Voucher specimens were deposited at UFAC and UFLA.

Identification of functional groups

The classification of functional groups described by Silva and Brandão (2010, 2014) was used, which separates functional groups based on ant morphological characteristics. The 11 functional groups are: large-size epigeic predators; medium-size epigeic predators; medium-size hypogeic predators; small-size hypogeic predators; specialist predators; dacetine predators; generalists; small-size hypogeic generalists; fungus cultivators; army ants; and arboreal ants. All identified species and their functional groups are shown in Tables S1 and S2. For more details, refer to Table S1 or cited references.

Data analysis

First, we sought to address whether the levels of α-diversity as well as that of β-diversity and its components were affected by the conversion from forest to shifting cultivation and pasture. We considered mean species richness per transect (sum of the richness of the five pitfalls divided by five) as α-diversity. We calculated β-diversity per transect based on the differences between transect sampling points using the βsør index (Sørensen dissimilarity), obtained through the betapart R package (Baselga, 2010). The βsør index is a measure that varies from identical assemblages (0) to completely different assemblages (1). Thus, each of the sampled sites (represented by the transect) had an α-diversity value and a βsør-diversity value, totalling $n = 20$. We also partitioned βsør-diversity into turnover (βsim) and nesting (βsne) components, through the betapart R package, where βsim and βsne vary from 0 (0%) to 1 (100%), indicating their contribution to total βsør.

We then used the α and βsør values in two generalised linear mixed models (GLMMs) to evaluate the effects of conversion from forest to shifting cultivation and pasture on diversity. In the two models, we used habitat (forest, shifting cultivation, and pasture) as a predictor variable. For the response variable, we used α-diversity for the first model and βsør-diversity for the second model, with region as the random variable for the two models. In addition, the factors have different sample sizes (eight forests, seven pastures and five shifting cultivations) due to the limited presence of some habitats, mainly shifting cultivation, in the sampled RESEX Chico Mendes region. We used the Poisson family in the α-diversity model (counting of the number of species) and the quasibinomial family for βsør-diversity (diversity ratio between 0 and 1). Overdispersion was tested for all models with the Poisson family, and when overdispersion was identified, we replaced it with the negative binomial family. To test if the species turnover is the major component of the total βsør-diversity, we used two generalised linear mixed models (GLMMs), one for epigeic ants and another for hypogeic ants. We used the βsør-diversity components (turnover or nestedness) as a predictor variable for the two models. For the response variable, we used the value of β-diversity partitioning of epigeic ants in the first model and that of hypogeic ants in the second model. We used region as the random variable for the two models, and the quasibinomial family because βsør-diversity partitioning varies between 0 and 1.

We analysed indicator species to assess which functional groups and species of ants were most related to each habitat (Dufrêne & Legendre, 1997), and all species and their respective functional groups were identified. We considered species with IndVal > 0.7 (70% indication for the habitat in question) and $p < 0.05$ as indicator species (McGeoch et al., 2002).

We used a GLMM to evaluate whether ant-mediated predation changed with conversion from forest to shifting cultivation and pasture and whether it was influenced by α- and βsør-diversity of predatory ants. We considered habitat (forest, shifting cultivation, and pasture) and α- (richness) and βsør-diversity of predatory ants as predictor variables. The response variable was the number of predations per site, and the random variable was region. To obtain this value, mean predation at each sampling point was determined considering the four rounds of the predation experiment (sum of the four rounds at each sampling point divided by four). The mean of the five sampling points along each transect was then calculated (sum of the means for each sampling point divided by five). We considered only the ant species collected in the larvae predation experiments to be predatory ants. We also used a GLMM to evaluate whether the functional groups of medium-size and large-size generalist epigeic predators perform more predations; the predictor variable was the functional group that performed predation, and the response variable was the number of predations by each functional group per site. In this case, two random variables—region and habitat—were used because we wanted to evaluate only the effect of the functional groups. Some functional groups were rarely observed during the predation experiment; in this case, only the functional groups that predated insects in at least five different sites were considered in the analyses. Finally, a descriptive graph was generated for species of the functional groups with the highest predation values, indicating the contribution of these species to predation.

All analyses were performed using R 4.0.3 software (R Core Team, 2020). The lme4 package (Bates et al., 2015) was used to perform the GLMMs. The MASS package was used for the negative binomial family (Venables & Ripley, 2002). Post hoc analyses were performed using the postHoc package (Labouriau, 2020). Graphs were plotted with the ggplot2 package (Wickham, 2016). The analysis of indicator species (IndVal) was performed with the packages sjstats (Lüdecke, 2022) and indicspecies (Cáceres & Legendre, 2009).

RESULTS

A total of 255 species of ants were collected in pitfall traps; the species were separated into nine functional groups (Tables S1 and S3).

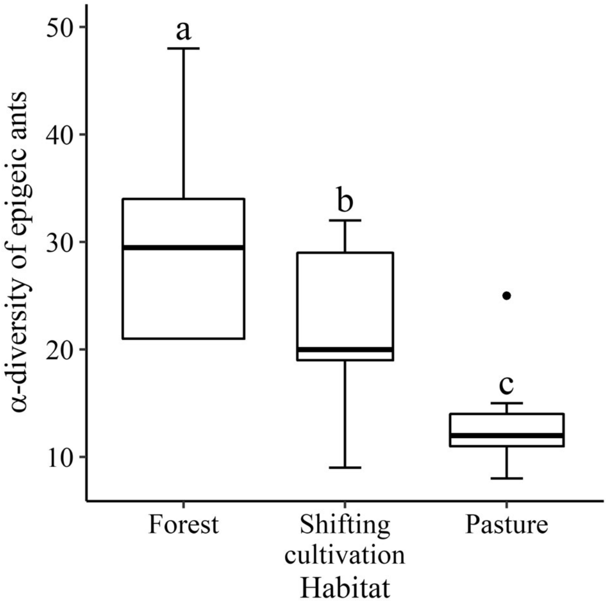

FIGURE 2 The α-diversity of epigeic ants is negatively affected by the conversion from forest to shifting cultivation and pasture. The *x*-axis shows the three habitats (forest, shifting cultivation, and pasture), and the *y*-axis represents α-diversity. The centreline of each boxplot indicates the central median of the data, and the boxes indicate the first percentile (mean of values greater than the central median) and third percentile (mean of values less than the central median). The vertical lines of each boxplot are Tukey-style whiskers (1.5× IQR). The points outside the boxes are outliers. Different letters on top of boxes indicate significant differences between habitats ($p < 0.05$).

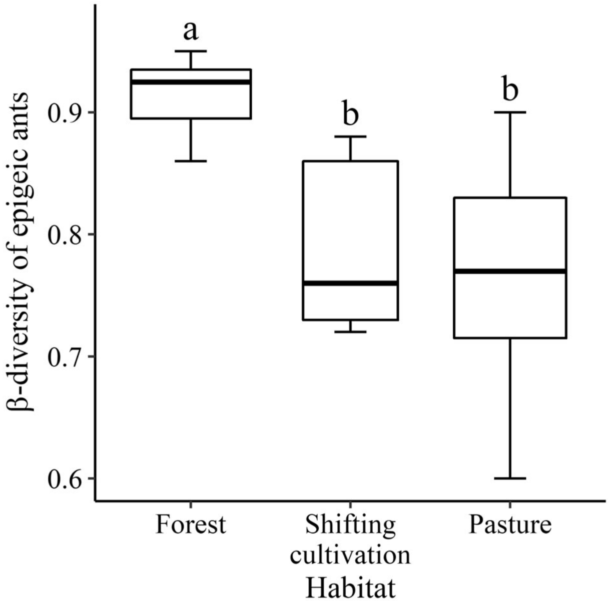

FIGURE 3 The β-diversity of epigeic ants is negatively affected by the conversion from forest to shifting cultivation and pasture, and these two anthropogenic land uses have communities that are more homogeneous and similar to each other. The *x*-axis shows the three habitats (forest, shifting cultivation, and pasture), and the *y*-axis represents βsør-diversity (βsør = Sørensen dissimilarity), which ranges from 0 (completely homogeneous communities) to 1 (completely different communities). The centreline of each boxplot indicates the central median of the data, and the boxes indicate the first percentile (mean of values greater than the central median) and third percentile (median of values less than the central median). Vertical lines in each boxplot are Tukey-style whiskers (1.5× IQR). Different letters on top of boxes indicate significant differences between habitats and the same letters indicate that there is no significant difference ($p < 0.05$).

Fifty species of ants engaged in insect predation; these species were separated into five functional groups (Table S2).

The α-diversity of epigeic ants decreased with an increase in anthropogenic land use (conversion from forest to shifting cultivation and pasture) (d.f. = 17; $\chi^2_3 = 43.602$; $p < 0.001$; Figure 2), and the βsør-diversity of epigeic ants decreased with the conversion from forest to shifting cultivation and pasture (d.f. = 17; $\chi^2_3 = 22.220$; $p < 0.001$; Figure 3), suggesting that these sites are more homogeneous than the forest sites in terms of species composition. However, no effect of conversion from forest to shifting cultivation and pasture was found on the α- (d.f. = 17; $\chi^2_3 = 5.836$; $p = 0.054$) and βsør-diversity (d.f. = 17; $\chi^2_3 = 3.835$; $p = 0.146$) of hypogeic ants. βsør-diversity partitioning revealed turnover as the main component of total βsør (Table S5), for epigeic (d.f. = 38; $\chi^2_3 = 229.342$; $p < 0.001$; Figure S1) and hypogeic ants (d.f. = 38; $\chi^2_3 = 24.195$; $p < 0.001$, Figure S2).

Of the 255 species identified, 25 were selected as environmental indicator species (Table S1). Out of the nine functional groups that were identified, only two were environmental indicators (Table S3). Specialist predators and dacetine predators are functional groups found only in forest sites and were excluded with the conversion from forest to shifting cultivation and pasture. Out of these species, only four presented high IndVal values (>0.7): *Brachymyrmex* cf. *bruchi* Forel, 1912 (generalist) with 73% indication for shifting cultivation; and *Brachymyrmex* cf. *australis* Forel, 1901 (generalist) with 76% indication for pasture and shifting cultivation, *Ectatomma brunneum* Smith, 1858 (large-size epigeic predators) with 73% indication for pasture and shifting cultivation, and *Pheidole* cf. *capillata* Emery, 1906 (generalist) with 71% indication for pasture and shifting cultivation.

Finally, 51 species of ants presented predatory behaviour. Insect predation was positively affected by the α-diversity of predatory ants (d.f. = 16; $\chi^2_4 = 28.303$; $p < 0.001$; Figure 4) but decreased with an increase in the βsør-diversity of predatory ants (d.f. = 15; $\chi^2_5 = 19.982$; $p < 0.001$; Figure 5). Insect predation was positively affected by conversion from forest to shifting cultivation and pasture while shifting cultivation and pasture had higher insect predation than forest (d.f. = 17; $\chi^2_3 = 7.501$; $p = 0.020$; Figure 6). Large-size epigeic predators exhibited high insect predation (d.f. = 80; $\chi^2_5 = 35.525$; $p < 0.001$; Figure 7). *Ectatomma brunneum*, which is an indicator of shifting cultivation and pasture, was responsible for 56% of the total predation and was the main predator in shifting cultivation and pasture (Figure 8). The mean values, sample sizes, and standard deviations of the study data are provided in Table S4.

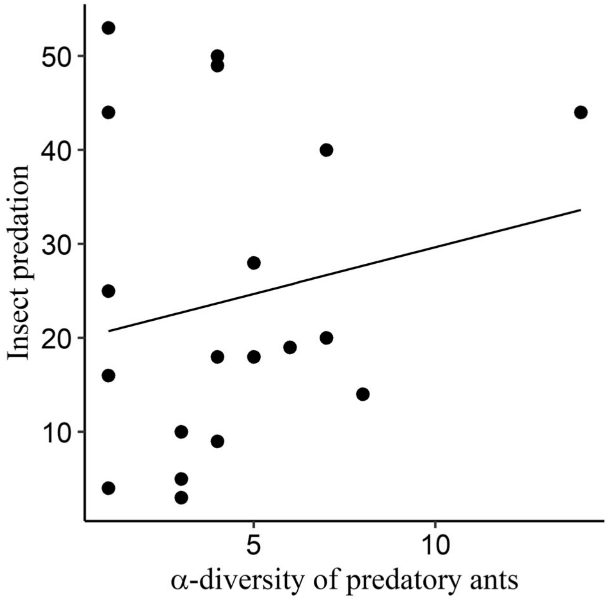

FIGURE 4 Insect predation by epigeic ants is positively affected by an increase in the α-diversity of predatory ants. The *x*-axis represents the α-diversity of predatory ants (richness = number of species collected in the predation experiment), and the *y*-axis represents the number of insect predations (number of predations). Larvae were used as bait in the experiments and biting and/or stinging by ants was considered as predation.

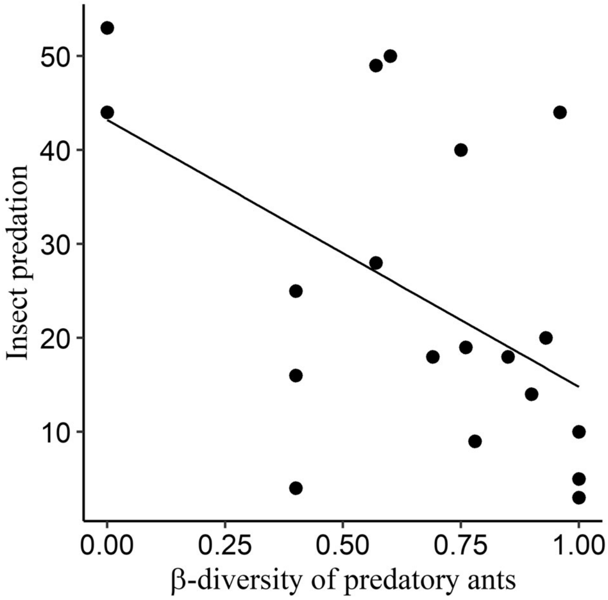

FIGURE 5 Insect predation by epigeic ants is negatively affected by an increase in the β-diversity of predatory ants. The *x*-axis represents the general βsør-diversity (βsør = Sørensen dissimilarity), which ranges from 0 (completely homogeneous communities) to 1 (completely different communities). We consider here only the diversity of predatory ants (species collected in the predation experiment). The *y*-axis represents the number of insect predations (number of predations). Larvae were used as bait in the experiments and biting and/or stinging by ants was considered as predation.

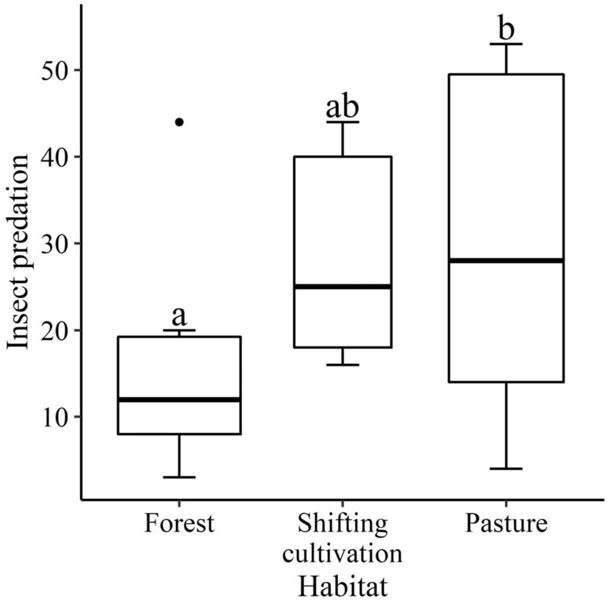

FIGURE 6 Insect predation by epigeic ants is positively affected by the conversion from forest to shifting cultivation and pasture; there is less predation in forest; more predation in pasture; and an intermediate amount of predation in shifting cultivation, similar to that in the forest and in the pasture. The *x*-axis shows the three habitats (forest, shifting cultivation, and pasture), and the *y*-axis represents the number of predations. The centreline of each boxplot indicates the central median of the data, and the boxes indicate the first percentile (mean of values greater than the central median) and third percentile (mean of values less than the central median). Vertical lines in each boxplot are Tukey-style whiskers (1.5× IQR). Different letters on top of boxes indicate significant differences between habitats and the same letters indicate that there is no significant difference ($p < 0.05$).

DISCUSSION

We found that the conversion of Amazon Forest to shifting cultivation and pasture was associated with the loss of ant species from communities, a decrease in the overall diversity of ant functional groups (through the loss of specialist predators and dacetine predators), a decrease in the level of heterogeneity among ant communities, and a surprising increase in the rate of ant-mediated insect predation. This predation was caused mainly by ants from the large-size epigeic predators functional group, more specifically by the large amount of predatory activity of *Ectatomma brunneum*. Thus, our results highlight that there may be benefits for biodiversity in maintaining shifting cultivation in the Amazon biome compared to more intensive anthropogenic land uses. Moreover, our results show that *E. brunneum* can play an important role in biological control in these sites.

Our study revealed that the greater the intensity of conversion from semi-natural habitats to anthropogenic land uses (forest into shifting cultivation or pasture), the greater the loss of epigeic ant species (α-diversity), but similar βsør-diversity for shifting cultivation and pasture; in both cases, diversity decreased compared to forest, making the ant communities more homogeneous. According to the

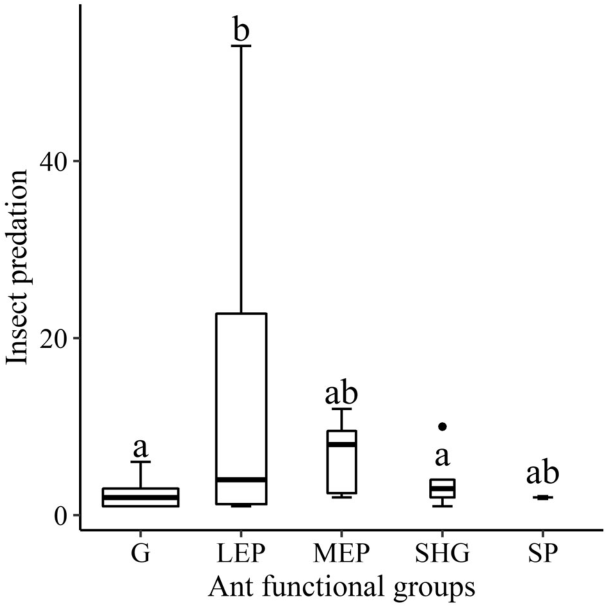

FIGURE 7 The functional groups of large- and medium-size epigeic predator ants engage in more insect predation than do generalist ants. The *x*-axis shows the functional groups (G = generalists, LEP = large-size epigeic predators, MEP = medium-size epigeic predators, SHG = small-size hypogeic predators, SP = specialist predators), and the *y*-axis represents the number of predations. The centreline of each boxplot indicates the central median of the data, and the boxes indicate the first percentile (mean of values greater than the central median) and third percentile (mean of values less than the central median). Vertical lines in each boxplot are Tukey-style whiskers (1.5× IQR). Different letters on top of boxes indicate significant differences between habitats and the same letters indicate that there is no significant difference ($p < 0.05$).

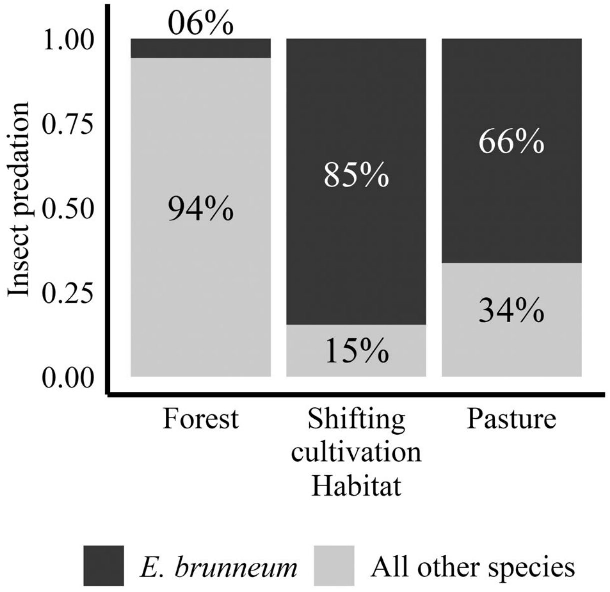

FIGURE 8 Contribution of *Ectatomma brunneum* to insect predation in the three different habitats. The *x*-axis indicates the habitats (forest, shifting cultivation, and pasture), and the *y*-axis indicates the proportion of contribution (contribution = *E. brunneum* predation/total predation). The dark grey portion indicates the contribution of *E. brunneum*, and the light grey portion indicates the contribution of all other species by habitat.

environmental filter hypothesis, local changes associated by different habitats promote a filter that selects species able to establish and survive in those sites (Clavel et al., 2011; Martins et al., 2022; McKinney & Lockwood, 1999; Olden, 2006; Olden et al., 2016). More heterogeneous and complex habitats, such as the Amazon Forest, tend to harbour a greater species diversity (Costa & Schmidt, 2022; Tews et al., 2004). However, the conversion from Amazon Forest to shifting cultivation (limited to some crops) and pasture (grassland monoculture) was associated with habitat homogenisation, due to the decrease of plant species and more homogenous environmental conditions in these anthropogenic land uses. Moreover, shifting cultivation is more environmentally heterogeneous and resource-diverse than pasture, which may allow shifting cultivation to harbour more ant species. In this sense, the habitat homogenisation was associated with the conversion from forest to shifting cultivation or pasture may be responsible for the decrease in the diversity parameters studied here, where such habitat homogenisation is probably higher in pasture than in shifting cultivation.

Here, the conversion from forest to shifting cultivation and pasture had no effect on α- and βsør-diversity of hypogeic ants. This pattern was also found in other studies and indicates that the resources and environmental conditions in the subterranean stratum may be little affected by conversion from semi-natural habitats to anthropogenic land uses, with little to no effect on ant assemblages (Schmidt et al., 2013; Queiroz et al., 2020; but see Luke et al., 2014). The conversion from forest to simplified habitats (e.g., pasture) can alter environmental factors, such as soil compaction, texture, organic matter, and microporosity, which may affect the local invertebrate community (Jacquemin et al., 2012; Schmidt, Ribas, et al., 2017; Schmidt, Schoereder, & Caetano, 2017). This, in turn, may decrease food resources for ants and select specific ant traits (e.g., small-size ants), however, it imposes low or no impact on ant diversity (Jacquemin et al., 2012; Schmidt, Ribas, et al., 2017; Schmidt, Schoereder, & Caetano, 2017), as observed in this study. Therefore, we think that hypogeic ants are more resistant to the conversion from Amazon Forest to shifting cultivation and pasture, or these changes may have little impact on the hypogeic microhabitat.

We found a greater contribution of turnover to βsør-diversity, indicating large species replacement between sites. Species turnover has been reported as the main component of βsør-diversity (Soininen et al., 2018). This species replacement may be due to greater heterogeneity in forest environments, which is positively related to taxonomic diversity (Ribas et al., 2003; Stein et al., 2014), in addition to anthropogenic disturbances favouring generalist and more resistant species (Costa & Schmidt, 2022; Solar et al., 2015). In the same context, as taxonomic diversity is directly related to functional diversity (Bihn et al., 2010), this conversion from forest to shifting cultivation and pasture, with replacement by generalist species, might alter ecosystem functions in these sites.

The conversion from forest to shifting cultivation and pasture was associated with the loss of two functional groups, dacetine predators (e.g., *Strumigenys*) and specialist predators (e.g., *Gnamptogenys*). The species in these groups live and forage in leaf litter and rotten trunks, specialise in foraging and nesting in this type of habitat, and are sensitive to environmental changes (Baccaro et al., 2013, 2015; Bolton, 1999). Local environmental characteristics change with the conversion from semi-natural habitats to anthropogenic land uses (shifting cultivation and pasture), affecting resources and conditions of the local semi-natural habitat, resulting in an environmental filter for functional groups (Manlick & Newsome, 2021; Martins et al., 2022); these changes may be responsible for the loss of specialist predators and dacetine predators. Thus, as also occurs for α- and βsør-diversity of epigeic ants, conversion from forest to shifting cultivation and pasture likely led to a decrease in ant functional groups. This greater number of species and functional groups in forests may indicate high resilience in these assemblages, due to functional redundancy, as the chances are also high for the trophic functions of lost species to be replaced by other species (Bihn et al., 2010). Thus, the loss of functional groups was associated with by the conversion of Amazon Forest to shifting cultivation and pasture probably makes these novel ecosystems more vulnerable.

In contrast, four species (*Brachymyrmex* cf. *bruchi*, *Brachymyrmex* cf. *australis*, *Ectatomma brunneum*, *Pheidole* cf. *capillata*) benefited from conversion from forest to shifting cultivation and pasture and were considered habitat indicators of shifting cultivation and pasture. This is likely because these generalist species are open habitat specialists, and the characteristics of shifting cultivation and pasture are more similar to those of open habitats than are those of forest (Fontenele & Schmidt, 2021; Vasconcelos et al., 2018). In addition to being an environmental indicator for anthropogenic land uses, large-size epigeic predators accounted for most of the predation in this study. As expected, this functional group is less affected by changes due to conversion from forest to anthropogenic land uses (Gibb et al., 2018), and some species even benefit from anthropic impacts, because they are more generalist in terms of the usage of habitat and resources, and can be considered more resistant to anthropic impacts or habitat changes, such as *Ectatomma brunneum* (Gomes et al., 2009; Tschinkel & King, 2017). Moreover, *E. brunneum* is probably an ecologically dominant ant (in terms of numerical and functional dominance) in these shifting cultivation and pasture sites (Cerda et al., 2013). Numerical dominance (large presence of *E. brunneum* in shifting cultivation and pasture) associated with functional dominance (strong competitor) can make this ant species a stronger competitor than the few other species filtered with open anthropogenic land uses, excluding other possible species that could also be present and intensifying their roles as insect predators. Consequently, despite increasing insect predation, the possible dominance of *E. brunneum* may also reduce ant diversity locally in shifting cultivation and pasture. However, our sampling was performed in the morning (between 7:00 h and 11:00 h) because the sunlight in open environments (shifting cultivation and pasture) was very high in the afternoon, killing the Tenebrio larvae and decreasing ant foraging because of high solar incidence. However, due to the high canopy cover and low solar incidence within the forests, the ants probably continue to forage and prey on insects in the afternoon, which increases the amount of predation in these locations and may generate results different from those found in this study. Thus, we suggest new studies that use methodologies to evaluate predation throughout the day and, if possible, also during the night.

In conclusion, we revealed important effects of conversion from Amazon Forest to shifting cultivation and pasture. For epigeic ants, pastures had negative effects on ant α- and βsør-diversity. Conversion from forest to shifting cultivation was associated with the community to be more homogeneous and decreased βsør-diversity; however, the impact of conversion from forest to pastures on ant richness was greater, which may indicate benefits for maintaining shifting cultivation, compared to more intensive anthropogenic land uses, from the perspective of biodiversity. The conversion from forest to shifting cultivation and pasture increased insect predation, primarily by large-size epigeic predators, more specifically by *E. brunneum*, an indicator of these anthropogenic land uses and present in many environments modified by humans. These ants can play an important role in biological control in these sites, assisting residents in food production without the need to use insecticides and avoiding losses due to pests. However, these generalist predatory ants are dominant at these sites, and they may exclude other ant species and prey on other animals important for these sites, such as other predators (intraguild predation) and pollinators. Therefore, we suggest new studies to evaluate the effect of insect predation by *E. brunneum* and other generalist ants in agricultural and livestock sites (e.g., do generalist ants from modified environments only prey on 'pests', or do they prey on other organisms such as pollinators and detritivores?).

AUTHOR CONTRIBUTIONS

Icaro Wilker: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); supervision (lead); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Chaim José Lasmar:** Conceptualization (supporting); formal analysis (supporting); methodology (supporting); supervision (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Fernando Schmidt:** Conceptualization (lead); data curation (supporting); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead); resources (lead); supervision (lead); writing – original draft (supporting); writing – review and editing (supporting). **Marília Maria Silva da Costa:** Conceptualization (supporting); data curation (supporting); methodology (supporting); writing – original draft (supporting). **Daniely da Frota Almeida:** Data curation (supporting). **Dhâmyla Bruna de Souza Dutra:** Data curation (supporting). **Adriana de Lima Alves:** Data curation (supporting). **Lucas Lima da Silva:** Data curation (supporting). **Carla Ribas:** Conceptualization (lead); investigation (supporting); methodology (supporting); project administration (lead); supervision (lead); writing – original draft (supporting); writing – review and editing (supporting).

ACKNOWLEDGEMENTS

We thank the residents of the Rio Branco (Acre) and Comunidade Divisão (RESEX Chico Mendes) for helping with the collection and housing during the field activities, especially, Ketlen Bona, Zequinha, Fabiane, Wendel, Sandrey, Ilmar, Sebastiana, Sebastião, Valdeci, Chagas, Michael, and Barrote. We thank Antonio C. M. Queiroz and Cássio A. Nunes for their help with statistics and discussions regarding the study. We thank Gabriela B. Nascimento for help during the morphospecies identification of the ants and Mila F. O. Martins for the identification and confirmation of the species. We thank Paulo S. Pompeu and José H. Schoereder for participating in the qualification panel for this project and Paulo S. Pompeu and Tatiana G. Cornelissen for their contributions to the MSc. thesis associated with this study. We thank the Editor Raphael Didham, the Associate Editor Mark Wong and the anonymous reviewers of Insect Conservation and Diversity for their contributions and criticisms of the manuscript. This study was part of Icaro Wilker's MSc. thesis at the Universidade Federal de Lavras that was supported by Coordenação de Aperfeiçoamento Pessoal de Nível Superior (CAPES, Finance code: 001). Chaim J. Lasmar received a postdoctoral fellowship from Programa Nacional de Pós Doutorado da CAPES (PNPD/CAPES, Finance code: 001). Marília M. S. Costa was supported by Coordenação de Aperfeiçoamento Pessoal de Nível Superior (CAPES, Finance code: 001). Daniely F. Almeida was supported by Conselho Nacional de Desenvolvimento Científco e Tecnológico and Adriana L. Alves was supported by Programa Institucional de Bolsas de Iniciação Científica (UFAC). We are grateful to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES/PROCAD—Amazônia 2018. Proc. Núm.: 88887.200518/2018-00) for financial support. We also thank ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade) and all landowners and farmers for giving us permission and support to collect data on RESEX Chico Mendes and on their properties. The document was edited for proper English language, grammar, punctuation, spelling, and overall style by one or more of the highly qualified native English-speaking editors at AJE (verification code: 578D-8634-8ABB-7D7A-8D6P) supported by Programa de Apoio à Publicação em Periódicos de Alto Impacto.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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REFERENCES

Ahuatzin, D.A., Corro, E.J., Jaimes, A.A., Valenzuela González, J.E., Feitosa, R.M., Ribeiro, M.C. et al. (2019) Forest cover drives leaf litter ant diversity in primary rainforest remnants within human-modified tropical landscapes. *Biodiversity and Conservation*, 28, 1091–1107.

Altieri, M.A. (2004) Linking ecologists and traditional farmers in the search for sustainable agriculture. *Frontiers in Ecology and the Environment*, 2, 35–42.

Andrade, M.L. & Urbani, C.B. (1999) Diversity and adaptation in the ant genus *Cephalotes*, past and present. *Staatliches Museum für Naturkunde*, 271, 1–889.

Armbrecht, I. & Gallego, M.C. (2007) Testing ant predation on the coffee berry borer in shaded and sun coffee plantations in Colombia. *Entomologia Experimentalis et Applicata*, 124, 261–267.

Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J.I., Tischendorf, L., Benchimol, M. et al. (2020) Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecology Letters*, 23, 1404–1420.

Baccaro, F.B., Feitosa, R.M., Fernandez, F., Fernandes, I.O., Izzo, T.J., Souza, J.L.P. et al. (2015) *Guia para os gêneros de formigas do Brasil*. Manaus, Brazil: Editora INPA.

Baccaro, F.B., Rocha, I.F., Del Aguila, B.E.G., Schietti, J., Emilio, T., Pinto, J. L.P.V. et al. (2013) Changes in ground-dwelling ant functional diversity are correlated with water-table level in an Amazonian terra firme forest. *Biotropica*, 45, 755–763.

Barnes, A.D., Allen, K., Kreft, H., Corre, M.D., Jochum, M., Veldkamp, E. et al. (2017) Direct and cascading impacts of tropical land-use change on multi-trophic biodiversity. *Nature Ecology and Evolution*, 1, 1511–1519.

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global ecology and biogeography*, 19, 134–143.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.

Bestelmeyer, B.T., Agosti, D., Alonso, L.E., Brandão, C.R.F., Brown, W.L., Jr., Delabie, J.H. et al. (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*. Washington, USA: Smithsonian Institution Press, pp. 122–144.

Betts, M.G., Wolf, C., Ripple, W.J., Phalan, B., Millers, K.A., Duarte, A. et al. (2017) Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature*, 547, 441–444.

Bihn, J.H., Gebauer, G. & Brandl, R. (2010) Loss of functional diversity of ant assemblages in secondary tropical forests published by: ecological Society of America content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms los. *Ecology*, 91, 782–792.

Blaimer, B.B. (2012) A subgeneric revision of *Crematogaster* and discussion of regional species-groups (Hymenoptera: Formicidae). *Zootaxa*, 3482, 47–67.

Bolton, B. (1999) Ant genera of the tribe Dacetonini (Hymenoptera: Formicidae). *Journal of Natural History*, 33, 1639–1689.

Borgmeier, T. (1954) Uma nova *Discothyrea* com seis articulos antenais (Hymenoptera, Formicidae). *Revista Brasileira de Entomologia*, 1, 191–194.

Brandão, C.R.F. (2003) Further revisionary studies on the ant genus *Megalomyrmex* Forel (Hymenoptera: Formicidae: Myrmicinae: Solenopsidini). *Papéis Avulsos de Zoologia*, 43, 145–159.

Brown, W.L., Jr. (1976) Contributions toward a reclassification of the Formicidae. Part VI. Ponerinae, tribe Ponerini, subtribe Odontomachiti. Section A. Introduction, subtribal characters. Genus *Odontomachus*. *Studia Entomologica*, 19, 67–171.

Cáceres, M.D. & Legendre, P. (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology*, 90, 3566–3574.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48, 1079–1087.

Camacho, G.P., Franco, W. & Feitosa, R.M. (2020) Additions to the taxonomy of *Gnamptogenys* Roger (Hymenoptera: Formicidae:

Ectatomminae) with an updated key to the New World species. *Zootaxa*, 4747, 450–476.

Cerda, X., Arnan, X. & Retana, J. (2013) Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology. *Myrmecological News*, 18, 131–147.

Clavel, J., Julliard, R. & Devictor, V. (2011) Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment*, 9, 222–228.

Costa, M.M.S.D. & Schmidt, F.A. (2022) Gamma, alpha, and beta diversity of ant assemblages response to a gradient of forest cover in human-modified landscape in Brazilian Amazon. *Biotropica*, 54, 515–524.

Cuezzo, F. & Guerrero, R.J. (2012) The ant genus *Dorymyrmex* Mayr (Hymenoptera: Formicidae: Dolichoderinae) in Colombia. *Psyche*, 2012, 1–24.

de Chazal, J. & Rounsevell, M.D.A. (2009) Land-use and climate change within assessments of biodiversity change: a review. *Global Environmental Change*, 19, 306–315.

De la Mora, A., García-Ballinas, J.A. & Philpott, S.M. (2015) Local, landscape, and diversity drivers of predation services provided by ants in a coffee landscape in Chiapas, Mexico. *Agriculture, Ecosystems and Environment*, 201, 83–91.

Dufrêne, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67, 345–366.

Escobar-Ramírez, S., Tscharntke, T., Armbrecht, I., Torres, W. & Grass, I. (2020) Decrease in β-diversity, but not in α-diversity, of ants in intensively managed coffee plantations. *Insect Conservation and Diversity*, 13, 445–455.

Fernandez, C.F. (2003) Myrmicine ants of the genera *Ochetomyrmex* and *Tranopelta* (Hymenoptera: Formicidae). *Sociobiology*, 41, 633–662.

Fernández, C.F. (2004) The American species of the myrmicine ant genus *Carebara* westwood (hymenoptera: formicidae). *Caldasia*, 26, 191–238.

Fernandes, I.O., Oliveira, M.L.D. & Delabie, J.H.C. (2014) Description of two new species in the Neotropical Pachycondyla foetida complex (Hymenoptera: Formicidae: Ponerinae) and taxonomic notes on the genus. *Myrmecological News*, 19, 133–163.

Folgarait, P.J. (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation*, 7, 1221–1244.

Fontenele, L.K. & Schmidt, F.A. (2021) Forest-pasture shifting alters the assemblages of seed-removing ants in southwestern Brazilian Amazon. *Journal of Insect Conservation*, 25, 213–220.

Gardner, T.A., Ferreira, J., Barlow, J., Lees, A.C., Parry, L., Vieira, I.C.G. et al. (2013) A social and ecological assessment of tropical land-uses at multiple scales: the sustainable Amazon network. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368, 1–11.

Gibb, H., Sanders, N.J., Dunn, R.R., Arnan, X., Vasconcelos, H.L., Donoso, D.A. et al. (2018) Habitat disturbance selects against both small and large species across varying climates. *Ecography*, 41, 1184–1193.

Gomes, L., Desuo, I.C., Gomes, G. & Giannotti, E. (2009) Behavior of *Ectatomma brunneum* (Formicidae: Ectatomminae) preying on dipterans in field conditions. *Sociobiology*, 53, 913–926.

Goncalves, C.R. (1942) Contribuição para o conhecimento do gênero *Atta* Fabr., das formigas saúvas. *Boletim da Sociedade Brasileira de Agronomia*, 5, 333–358.

Gonçalves, C.R. (1961) O gênero *Acromyrmex* no Brasil (Hym. Formicidae). *Studia Entomologica*, 4, 113–180.

Grass, I., Loos, J., Baensch, S., Batáry, P., Librán-Embid, F., Ficiciyan, A. et al. (2019) Land-sharing/-sparing connectivity landscapes for ecosystem services and biodiversity conservation. *People and Nature*, 1, 262–272.

Green, E.J., McRae, L., Freeman, R., Harfoot, M.B., Hill, S.L., Baldwin-Cantello, W. et al. (2020) Below the canopy: global trends in forest vertebrate populations and their drivers: drivers and trends of forest vertebrates. *Proceedings of the Royal Society B: Biological Sciences*, 287, 1–9.

Griffiths, H.M., Ashton, L.A., Walker, A.E., Hasan, F., Evans, T.A., Eggleton, P. et al. (2018) Ants are the major agents of resource removal from tropical rainforests. *Journal of Animal Ecology*, 87, 293–300.

Heckenberger, M.J., Russell, J.C., Toney, J.R. & Schmidt, M.J. (2007) The legacy of cultural landscapes in the Brazilian Amazon: implications for biodiversity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362, 197–208.

Houadria, M.Y., Feldhaar, H., Fiala, B., Lestina, D., Chung, A., Salleh, A. et al. (2020) Reduced benefits of ant occupation for ant-trees in oil palm compared with heavily logged forest. *Symbiosis*, 81, 79–91.

Isaacs, R., Tuell, J., Fiedler, A., Gardiner, M. & Landis, D. (2009) Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Frontiers in Ecology and the Environment*, 7, 196–203.

Jacquemin, J., Drouet, T., Delsinne, T., Roisin, Y. & Leponce, M. (2012) Soil properties only weakly affect subterranean ant distribution at small spatial scales. *Applied Soil Ecology*, 62, 163–169.

Johnson, R.A. (2021) A taxonomic revision of south American species of the seed-harvester ant genus *Pogonomyrmex* (Hymenoptera: Formicidae). Part II. *Zootaxa*, 5033, 1–230.

Kleinman, P.J.A., Pimentel, D. & Bryant, R.B. (1995) The ecological sustainability of slash-and-burn agriculture. *Agriculture, Ecosystems & Environment*, 52, 235–249.

Kugler, C. & Brown, W.L. (1982) Revisionary and other studies on the ant genus *Ectatomma*, including the descriptions of two new species. Estudios de revisión y de otros tipos en el género de hormigas *Ectatomma*, incluyendo las descripciones de dos nuevas especies. *Agriculture*, 24, 1–7.

Labouriau, R. (2020) postHoc: Tools for Post-Hoc Analysis. R package version 0.1.3. https://CRAN.R-project.org/package=postHoc

Lach, I., Parr, C. & Abbott, K. (2010) *Ant ecology*. UK: Oxford University Press.

LaPolla, J.S. (2004) *Acropyga* (Hymenoptera: Formicidae) of the world. *Acropyga* (Hymenoptera: Formicidae) del mundo. *Contributions of the American Entomological Institute*, 33, 1–130.

Lasmar, C.J., Queiroz, A.C.M., Rabello, A.M., Feitosa, R.M., Canedo-Júnior, E.O., Schmidt, F.A. et al. (2017) Testing the effect of pitfall-trap installation on ant sampling. *Insectes Sociaux*, 64, 445–451.

Lattke, J.E. (1997) Revisión del género *Apterostigma* mayr: (hymenoptera: formicidae). *Arquivos de Zoologia*, 34, 121–221.

Lattke, J.E. (2011) Revision of the new world species of the genus *Leptogenys* Roger (Insecta: Hymenoptera: Formicidae: Ponerinae). *Arthropod Systematics and Phylogeny*, 69, 127–264.

Longino, J.T. (2003) The *Crematogaster* (Hymenoptera, Formicidae, Myrmicinae) of Costa Rica. *Zootaxa*, 151, 1–150.

Longino, J.T. (2013) A revision of the ant genus *Octostruma* Forel 1912 (Hymenoptera, Formicidae). *Zootaxa*, 3699, 1–61.

Longino, J.T. & Fernández, F. (2007) Taxonomic review of the genus *Wasmannia*. *Memoirs of the American Entomological Institute*, 80, 271–289.

Lüdecke, D. (2022) sjstats: Statistical Functions for Regression Models. R package version 0.18.2. https://CRAN.R-project.org/package=sjstats

Luke, S.H., Fayle, T.M., Eggleton, P., Turner, E.C. & Davies, R.G. (2014) Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. *Biodiversity and Conservation*, 23, 2817–2832.

Mackay, W. & Mackay, E. (2010) *Systematics and biology of the New World ants of the genus Pachycondyla (Hymenoptera: Formicidae)*. UK: Edwin Mellen Press.

MacKay, W.P. (1993) A review of the New World ants of the genus *Dolichoderus* (Hymenoptera: Formicidae). Revisión de las hormigas del nuevo Mundo del género *Dolichoderus* (Hymenoptera: Formicidae). *Sociobiology*, 22, 1–148.

Mackay, W.P. (1997) A revision of the neotropical ants of the genus *Camponotus*, subgenus *Myrmostenus* (Hymenoptera: Formicidae). *Proceedings-Entomological Society of Washington*, 99, 94–203.

Mandal, J. & Raman, T.R.S. (2016) Shifting agriculture supports more tropical forest birds than oil palm or teak plantations in Mizoram, Northeast India. *Condor*, 118, 345–359.

Manlick, P.J. & Newsome, S.D. (2021) Adaptive foraging in the Anthropocene: can individual diet specialization compensate for biotic homogenization? *Frontiers in Ecology and the Environment*, 19, 510–518.

Martins, I.S., Ortega, J.C.G., Guerra, V., Costa, M.M.S., Martello, F. & Schmidt, F.A. (2022) Ant taxonomic and functional beta-diversity respond differently to changes in forest cover and spatial distance. *Basic and Applied Ecology*, 60, 89–102.

Matsumoto, T., Itioka, T., Yamane, S. & Momose, K. (2009) Traditional land-use associated with swidden agriculture changes encounter rates of the top predator, the army ant, in southeast Asian tropical rain forests. *Biodiversity and Conservation*, 18, 3139–3151.

Mayhe-Nunes, A.J. & Brandão, C.R.F. (2002) Revisionary studies on the attine ant genus *Trachymyrmex* Forel. Part 1: Definition of the genus and the Opulentus group (Hymenoptera: Formicidae). *Sociobiology*, 40, 667–698.

McGeoch, M.A., Van Rensburg, B.J. & Botes, A. (2002) The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. *Journal of Applied Ecology*, 39, 661–672.

McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, 14, 450–453.

Menezes, A.S.O. & Schmidt, F.A. (2020) Mechanisms of species coexistence and functional diversity of ant assemblages in forest and pasture habitats in southwestern Brazilian Amazon. *Sociobiology*, 67, 33–40.

Milien, E.J., da Silva Rocha, K., Brown, I.F. & Perz, S.G. (2021) Roads, deforestation and the mitigating effect of the Chico Mendes extractive reserve in the southwestern Amazon. *Trees, Forests and People*, 3, 100056.

Morris, J.R., Jiménez-Soto, E., Philpott, S.M. & Perfecto, I. (2018) Ant-mediated (Hymenoptera: Formicidae) biological control of the coffee berry borer: diversity, ecological complexity, and conservation biocontrol. *Myrmecological News*, 26, 1–17.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A. et al. (2015) Global effects of land-use on local terrestrial biodiversity. *Nature*, 520, 45–50.

Olden, J.D. (2006) Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography*, 33, 2027–2039.

Olden, J.D., Comte, L., & Giam, X. (2016) *Biotic Homogenisation. In: Encyclopedia of Life Sciences*. Chichester, UK: John Wiley & Sons Ltd.

Ortiz-Sepulveda, C.M., Van Bocxlaer, B., Meneses, A.D. & Fernández, F. (2019) Molecular and morphological recognition of species boundaries in the neglected ant genus *Brachymyrmex* (Hymenoptera: Formicidae): toward a taxonomic revision. *Organisms Diversity & Evolution*, 19, 447–542.

Pacheco, J.A., Mackay, W.P. & Lattke, J. (2013) *The systematics and biology of the New World thief ants of the genus Solenopsis (Hymenoptera: Formicidae)*. UK: Edwin Mellen Press.

Pacheco, R., Camacho, G.P., Frizzo, T.L.M. & Vasconcelos, H.L. (2017) Effects of land-use changes on ecosystem services: decrease in ant predation in human-dominated landscapes in central Brazil. *Entomologia Experimentalis et Applicata*, 162, 302–308.

Padoch, C. & Pinedo-Vasquez, M. (2010) Saving slash-and-burn to save biodiversity. *Biotropica*, 42, 550–552.

Parente, L. & Ferreira, L. (2018) Assessing the spatial and occupation dynamics of the Brazilian pasturelands based on the automated classification of MODIS images from 2000 to 2016. *Remote Sensing*, 10, 606.

Penn, H.J., Athey, K.J. & Lee, B.D. (2017) Land cover diversity increases predator aggregation and consumption of prey. *Ecology Letters*, 20, 609–618.

Perfecto, I. & Vandermeer, J. (2010) The agroecological matrix as alternative to the land-sparing/agriculture intensification model. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 5786–5791.

Perfecto, I. & Vandermeer, J. (2015) *Coffee agroecology: a new approach to understanding agricultural biodiversity, ecosystem services and sustainable development*. London, UK: Routledge.

Phalan, B., Onial, M., Balmford, A. & Green, R.E. (2011) Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science*, 333, 1289–1291.

Phillips, H.R.P., Newbold, T. & Purvis, A. (2017) Land-use effects on local biodiversity in tropical forests vary between continents. *Biodiversity and Conservation*, 26, 2251–2270.

Pitts, J.P., Camacho, G.P., Gotzek, D., Mchugh, J.V. & Ross, K.G. (2018) Revision of the fire ants of the *Solenopsis* saevissima species-group (Hymenoptera: Formicidae). *Proceedings of the Entomological Society of Washington*, 120, 308–411.

Queiroz, A.C.M., Rabello, A.M., Braga, D.L., Santiago, G.S., Zurlo, L.F., Philpott, S.M. et al. (2020) Cerrado vegetation types determine how land-use impacts ant biodiversity. *Biodiversity and Conservation*, 29, 2017–2034.

R Core Team. (2020) *R: a language and environment for statistical computing*. Vienna, Austria: R foundation for statistical computing.

Rerkasem, K., Lawrence, D., Padoch, C., Schmidt-Vogt, D., Ziegler, A.D. & Bruun, T.B. (2009) Consequences of swidden transitions for crop and fallow biodiversity in southeast Asia. *Human Ecology*, 37, 347–360.

Rosenfeld, J.S. (2002) Functional redundancy in ecology and conservation. *Oikos*, 98, 156–162.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R. et al. (2000) Global biodiversity scenarios for the year 2100. *Science*, 287, 1770–1774.

Sánchez-Bayo, F. & Wyckhuys, K.A. (2019) Worldwide decline of the entomofauna: a review of its drivers. *Biological Conservation*, 232, 8–27.

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. *Ecological Indicators*, 24, 158–166.

Schmidt, F.A., Ribas, C.R., Sobrinho, T.G., Ubaidillah, R., Schoereder, J.H., Clough, Y. et al. (2017) Similar alpha and beta diversity changes in tropical ant communities, comparing savannas and rainforests in Brazil and Indonesia. *Oecologia*, 185, 487–498.

Schmidt, F.A., Schoereder, J.H. & Caetano, M.D.N. (2017) Ant assemblage and morphological traits differ in response to soil compaction. *Insectes Sociaux*, 64, 219–225.

Schmidt, F.A. & Solar, R.R.C. (2010) Hypogeic pitfall traps: methodological advances and remarks to improve the sampling of a hidden ant fauna. *Insectes Sociaux*, 57, 261–266.

Seifert, C.L., Schulze, C.H., Dreschke, T.C.T., Frötscher, H. & Fiedler, K. (2016) Day vs. night predation on artificial caterpillars in primary rainforest habitats – an experimental approach. *Entomologia Experimentalis et Applicata*, 158, 54–59.

Silva, R.R. & Brandão, C.R.F. (2010) Morphological patterns and community organization in leaf-litter ant assemblages. *Ecological Monographs*, 80, 107–124.

Silva, R.R. & Brandão, C.R.F. (2014) Ecosystem-wide morphological structure of leaf-litter ant communities along a tropical latitudinal gradient. *PLoS One*, 9, e93049.

Soininen, J., Heino, J. & Wang, J. (2018) A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography*, 27, 96–109.

Solar, R.R.C., Barlow, J., Andersen, A.N., Schoereder, J.H., Berenguer, E., Ferreira, J.N. et al. (2016) Biodiversity consequences of land-use change and forest disturbance in the Amazon: a multi-scale assessment using ant communities. *Biological Conservation*, 197, 98–107.

Solar, R.R.C., Barlow, J., Ferreira, J., Berenguer, E., Lees, A.C., Thomson, J. R. et al. (2015) How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecology Letters*, 18, 108–1118.

Solomon, S.E., Rabeling, C., Sosa-Calvo, J., Lopes, C.T., Rodrigues, A., Vasconcelos, H.L. et al. (2019) The molecular phylogenetics of *Trachymyrmex* Forel ants and their fungal cultivars provide insights into the origin and coevolutionary history of 'higher-attine' ant agriculture. *Systematic Entomology*, 44, 939–956.

Staab, M., Schuldt, A., Assmann, T. & Klein, A.M. (2014) Tree diversity promotes predator but not omnivore ants in a subtropical Chinese forest. *Ecological Entomology*, 39, 637–647.

Stein, A., Gerstner, K. & Kreft, H. (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17, 866–880.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. et al. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, 31, 79–92.

Tuma, J., Fleiss, S., Eggleton, P., Frouz, J., Klimes, P., Lewis, O.T. et al. (2019) Logging of rainforest and conversion to oil palm reduces bioturbator diversity but not levels of bioturbation. *Applied Soil Ecology*, 144, 123–133.

van Vliet, N., Mertz, O., Heinimann, A., Langanke, T., Pascual, U., Schmook, B. et al. (2012) Trends, drivers and impacts of changes in swidden cultivation in tropical forest-agriculture frontiers: a global assessment. *Global Environmental Change*, 22, 418–429.

Vasconcelos, H.L., Maravalhas, J.B., Feitosa, R.M., Pacheco, R., Neves, K.C. & Andersen, A.N. (2018) Neotropical savanna ants show a reversed latitudinal gradient of species richness, with climatic drivers reflecting the forest origin of the fauna. *Journal of Biogeography*, 45, 248–258.

Venables, W.N. & Ripley, B.D. (2002) *Modern applied statistics with S-PLUS*. New York, USA: Springer Science & Business Media.

Wickham, H. (2016) *ggplot2: elegant graphics for data analysis*, Vol. 10. New York: Springer-Verlag. 978-0.

Wild, A.L. (2005) Taxonomic revision of the *Pachycondyla apicalis* species complex (Hymenoptera: Formicidae). *Zootaxa*, 834, 1–25.

Wild, A.L. (2007) *Taxonomic revision of the ant genus Linepithema (Hymenoptera: Formicidae)*. California, USA: Univ of California Press.

Wilson, E.O. (2003) *Pheidole in the New World: a dominant, hyperdiverse ant genus*, Vol. 1. USA: Harvard University Press.

Wurz, A., Grass, I., Lees, D.C., Rakotomalala, A.A.N.A., Sáfián, S., Martin, D. A., Osen, K., Loos, J., Benasoavina, E., Alexis, T., & Tscharntke, T. (2022) Land-use change differentially affects endemic, forest and open-land butterflies in Madagascar. *Insect Conservation and Diversity*, 15, 606–620.

SUPPORTING INFORMATION

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

Table S1. We used the classification of functional groups described by Silva and Brandão (2010, 2014); this classification separates the functional groups based on the morphological characteristics of the ants. The 11 functional groups are: large-size epigeic predators (LEP—epigeic generalist predator of large body size; e.g., *Ectatomma edentatum*); medium-size epigeic predators (MEP—epigeic generalist predator of medium body size; e.g., *Gnamptogenys rastrata*); medium-size hypogeic predators (MHP—hypogeic generalist predator of medium body size; e.g., *Heteroponera inermis*); small-size hypogeic predators (SHP—hypogeic generalist predator of small body size; e.g., *Hypoponera*); specialist predators (SP—small- to medium-size specialist predators living in the soil superficial layers; e.g., *Prionopelta antillana*); dacetine predators (DP—small- to medium-size hypogeic specialist predators; e.g., *Acanthognathus ocellatus*); generalists (G—small- to medium-size epigeic generalists—omnivorous, saprophagous and granivorous; e.g., *Camponotus canescens*); small-size hypogeic generalists (SHG—very small-size hypogeic ants probably omnivorous—very little studies; e.g., *Discothyrea neotropica*); fungus cultivators (FG—cultivate a symbiotic fungus on organic material like carcasses and/or dead or live plant; e.g., *Atta sexdens*); army ants (N—predator ants without permanent nests; e.g., *Eciton burchelli*); arboreal ants (A—ants with nests and foraging in the arboreal stratum; e.g., *Procryptocerus convergens*). The columns 'Forest', 'Pasture' and 'Swidden' indicate whether the morphospecies occurred in (1) or were absent from (0) a given land-use type. The 'index' column indicates the land-uses or combinations of land-uses to which the ants were associated. The 'stat' column shows the environmental indication values, and the '*p*.value' column shows the *p* values.

Table S2. Number of insect predations by each morphospecies. The 'Species' column indicates the species of ants that engaged in predation. The 'Functional group' column shows the five functional groups to which the ant species that underwent predation are classified: large-size epigeic predators (LEP); medium-size epigeic predators (MEP); specialist predators (SP); generalists (G); and small-size hypogeic generalist (SHG). The 'Land-use' column shows whether the morphospecies that engaged in predation is classified as an environmental indicator. The 'Predation' column indicates the number of predations per species.

Table S3. Nine functional groups of identified ants and their respective environmental indication values. The 'Functional groups' column shows the nine functional groups identified: large epigeic predators (LEPs); medium-size epigeic predators (MPEs); small-size hypogeic predators (SHPs); specialist predators (SPs); dacetine predators (DPs); generalists (Gs); small-size hypogeic generalists (SHGs); fungal cultivators (FCs); and army ants (Ns). The columns 'Forest', 'Pasture' and 'Swidden' indicate whether the morphospecies occurred in (1) or were absent from (0) a given land-use. The 'index' column indicates the land-uses or combinations of land-uses to which the ants were associated. The 'stat' column shows the environmental indication values, and the '*p*.value' column shows the *p* values (NA indicates that *p* values were not calculated).

Table S4. Mean values, standard deviations and sample sizes of ant diversity and insect predation

Table S5. The βsør-diversity (Sørensen dissimilarity) partitioning in βsim (turnover) and βsne (nestdeness). The 'Region' shows the areas where ants were sampled in 'Land-uses' (forest, pasture and shifting cultivation), in the strata epigeic (epi) and hypogeic (hip).

Figure S1. The turnover is the main component of the total βsør for epigeic ants. The *x*-axis shows the β-diversity components (turnover and nestedness), and the *y*-axis shows the Epigeic ants β-diversity portioning, which vary from 0 (0%) and 1 (100%). The centreline of each boxplot indicates the central median of the data, and the boxes indicate the first percentile (mean of the values greater than the central median) and third percentile (mean of the values less than the central median). The vertical lines on each boxplot are the Tukey-style whiskers (1.5× IQR). The points outside the boxes are outliers. The letters on the boxes indicate significant differences between land-uses (p < 0.05).

Figure S2. The turnover is the main component of the total βsør for hypogeic ants. The *x*-axis shows the β-diveristy components (turnover and nestedness), and the *y*-axis shows the Epigeic ants β-diversity portioning, which vary from 0 (0%) and 1 (100%). The centreline of each boxplot indicates the central median of the data, and the boxes indicate the first percentile (mean of the values greater than the central median) and third percentile (mean of the values less than the central median). The vertical lines on each boxplot are the Tukey-style whiskers (1.5× IQR). The points outside the boxes are outliers. The letters on the boxes indicate significant differences between land-uses (p < 0.05).

How to cite this article: Wilker, I., Lasmar, C.J., Schmidt, F.A., da Costa, M.M.S., Almeida, D.F., Dutra, D.B.d.S. et al. (2023) Land-use change in the Amazon decreases ant diversity but increases ant-mediated predation. *Insect Conservation and Diversity*, 1–14. Available from: https://doi.org/10.1111/icad.12632