







## RESEARCH ARTICLE

# Shade-growing practices lessen the impact of coffee plantations on multiple dimensions of ant diversity

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## Abstract

1. Land use management influence changes in biodiversity beyond the targeted species. Management practices in coffee plantations have shifted from coffee growing below accompanying (shade) trees, to intensified monocultures in which coffee grows fully exposed to the sun. Anthropogenic disturbance causes changes in species composition relative to adjacent natural patches and reduces their biotic heterogeneity. Here, we assessed the impact of coffee plantation management practices on the taxonomical, phylogenetic and functional composition of ant communities, an ecologically dominant group and crucial biological pest controller in these agroecosystems. We hypothesized that shade-grown coffee plantations would harbour ant communities similar to those of nearby forest patches, but dissimilar to those of intensified monocultures.
2. We surveyed ant diversity in eight shade-grown coffee farms, eight intensive coffee monocultures and eight forest patches. We used a combination of active and passive sampling methods over two field campaigns spanning 6 months.
3. Our results support our hypothesis for all diversity dimensions. Additionally, ant communities in intensified monocultures were taxonomically and functionally, but not phylogenetically, more homogeneous than those found in forest patches and shade-grown plantations.
4. *Synthesis and applications.* Our findings support the idea that practices in shade-grown coffee plantations buffer the impoverishment of multiple diversity dimensions after forest conversion. Additionally, we identified that leaf-litter depth and number of twigs mitigate ant diversity loss which, in turn, can favour the presence of potential biocontrol agents. By assessing and integrating multiple biodiversity dimensions into management strategies, farmers and interested parties can minimize future biodiversity and ecosystem service loss.

## KEYWORDS

agricultural management strategies, beta diversity, biotic homogenization, coffee plantation, Formicidae, functional diversity, phylogenetic diversity

## 1 | INTRODUCTION

The conversion of natural forests to croplands degrades natural ecosystems and increases the rate of biodiversity loss, increasingly threatening biodiversity world-wide (Beckmann et al., 2019; Newbold et al., 2015). Pervasive land conversion results from the increasing demand for food production that is causing farmers to transition from traditional, sustainable practices to more intensive ones (Rudel et al., 2009). These habitat shifts cause biodiversity decline mainly through the loss of forest cover (Koh et al., 2004), especially in tropical regions (Vergara & Badano, 2009). Coffee production, which is concentrated in the most biodiverse regions of the world, is an important cause of natural habitat loss. Between 1994 and 2017, ~10 million ha/year of tropical forests were transformed to coffee crops (FAO, 2019). Nevertheless, the choice of management practices can affect biodiversity and associated ecosystem services.

Coffee producers use various management strategies for its cultivation. Farmers traditionally grow coffee in the understory of indigenous shade trees, providing refuges for accompanying biodiversity (Moguel & Toledo, 1999; Perfecto et al., 1996). This management practice (hereby shade-grown) increases the sustainability of landscape and livelihoods of farmers (Toledo & Moguel, 2012). However, many farmers transition to unshaded monocultures (hereby sun-grown) to improve the yield (Rappole et al., 2003). The removal of accompanying vegetation increases erosion, chemical runoff and consolidation, combined with a lower long-term sustainability of the ecosystem (Perfecto et al., 1996; Rappole et al., 2003). Moreover, the lack of accompanying vegetation changes the resources (e.g. nesting sites, prey) available for other taxa, causing a decline in species richness when compared to shaded systems (Philpott et al., 2008). This decline could translate to changes in the community structure of keystone taxa, altering ecological processes that regulate ecosystem functions (Naeem et al., 1994; Symstad et al., 1998). Thus, studies focusing on the changes of keystone taxa become essential for predicting the influence of management approaches on ecosystem services provided by local biodiversity (Power et al., 1996).

In coffee agroecosystems, such keystone species include ants, which are abundant and important biological control agents (Morris et al., 2018; Philpott & Armbrrecht, 2006). Agricultural systems harbour low species richness of ants, particularly of twig-nesting and litter-dwelling ants (Armbrrecht & Perfecto, 2003; De la Mora et al., 2013; Perfecto & Vandermeer, 2002). Moreover, management strategies influence ant behaviour and their potential for providing ecosystem services, such as pest control (Aristizábal & Metzger, 2019; Armbrrecht & Gallego, 2007; Jiménez-Soto et al., 2019). Ant diversity loss in coffee plantations may exacerbate declines in ecosystem functioning due to already low levels of functional redundancy in these systems (Bihn et al., 2010). However, studies rarely address ant functional diversity in agroecosystems and could be a better proxy for ecosystem service loss.

Land conversion not only alters the composition of communities, but also the level of redundancy (Olden et al., 2004; Rodrigues et al., 2013). Biotic homogenization is the increase in the similarity of two or more species assemblages caused by the extinction or introduction of species (McKinney & Lockwood, 1999). Although the causes and consequences of taxonomic homogenization have received much attention, fewer studies have focused on either the functional or phylogenetic dimensions of this process (Olden et al., 2018). Novel selective pressures deriving from land conversion and agricultural intensification may act differentially at the taxonomic, phylogenetic and functional levels (Devictor et al., 2008; Olden, 2006), and have a different impact on ecosystem function, thus making integrative approaches crucial for biodiversity assessments. Both functional and phylogenetic homogenization occur when species invasions and extinctions are related to intrinsic life-history traits of closely related species (Blackburn & Jeschke, 2009; Devictor et al., 2008). However, the degree of homogenization will depend on the type and intensity of disturbance, the ecology of the organism, and the surrounding landscape matrix (Gámez-Virués et al., 2015; Rousseau et al., 2019; Sonnier et al., 2014; Villéger et al., 2014). The increase in phylogenetic and functional similarity may lead to less stable, less productive and extinction-prone ecosystems which can translate to a decrease in the provision of ecosystem services (van der Plas et al., 2016).

In this study, we assessed the effects of two different coffee plantation management practices on the taxonomic, phylogenetic and functional diversity of ant communities. We asked whether shade-grown coffee practices could buffer the effect of land conversion on ant community structure. Specifically, we tested the hypotheses that ant communities in shade-grown coffee plantations (a) do not differ significantly in composition from forest patches but differ significantly from sun-grown coffee plantations; and (b) are as heterogeneous as in forest patches, but less homogeneous than in sun-grown coffee plantations. In addition, we examined which environmental variables underlie changes in ant communities within and between habitats.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

We conducted our study in Cauca, Colombia, between 2°49'44"–2°51'32"N and 76°34'8"–76°33'25"W; with an altitude range of 1,336–1,538 m, with mean annual temperature and precipitation of 21.5°C and 2,191 mm, respectively. This region has two precipitation peaks during the year April–May and October–November (Instituto de Hidrología Meteorología y Estudios Ambientales (IDEAM), 2019). This is an area dominated primarily by shade-grown coffee (commercial polycultures, and shaded monocultures sensu Moguel & Toledo, 1999). We selected eight shade-grown and eight sun-grown coffee plantations with areas between 0.5 and 8 ha, and where owners reported a low number of agrochemicals used and similar management practices (see Appendix S2: Table S2a in supporting

information). In shade-grown coffee plantations, farmers planted shade trees (*Inga spectabilis* and/or *I. edulis*, Fabaceae) interspersed with rows of coffee bushes. In sun-grown coffee plantations, farmers planted *Musa paradisiaca* (Musaceae), *Manihot esculenta* (Euphorbiaceae) or *Citrus sinensis* (Rutaceae) on the edge of the plots, providing no shade to coffee bushes. To establish a comparison with residual forests, we collected samples from eight neighbouring forest patches no bigger than 2 ha (Figure 1).

## 2.2 | Local and landscape environmental characteristics

To evaluate the effect of environmental variables that could contribute to biodiversity differences between management practices, we measured environmental variables at local and landscape scales. At local (plot-level) scale, we measured soil temperature and humidity, canopy cover and litter depth in all our sampled sites. Additionally, in sampled coffee plantations we measured number of twigs and litter volume below coffee bushes, coffee bush height, distance among coffee bushes and among rows as an estimate of crop density in each plantation. We characterized the landscape surrounding each site using geographic information system (GIS) approaches. We computed the maximum Normalized Difference Vegetation Index (NDVI) value from available Landsat images available in Google Earth Engine (Gorelick et al., 2017) for our sampling region. Using QGIS 3.14.15-Pi (QGIS.org, 2020), we calculated the mean NDVI and its coefficient of variation within 50-, 100-, 250- and 500-m buffers for each site. We chose these buffer sizes following others who have studied landscape effects on ants (e.g. De la Mora et al., 2013; Iverson et al., 2019). See Appendix S2 for details on how we measured and processed these variables, and subsequently used them for supplementary analyses.

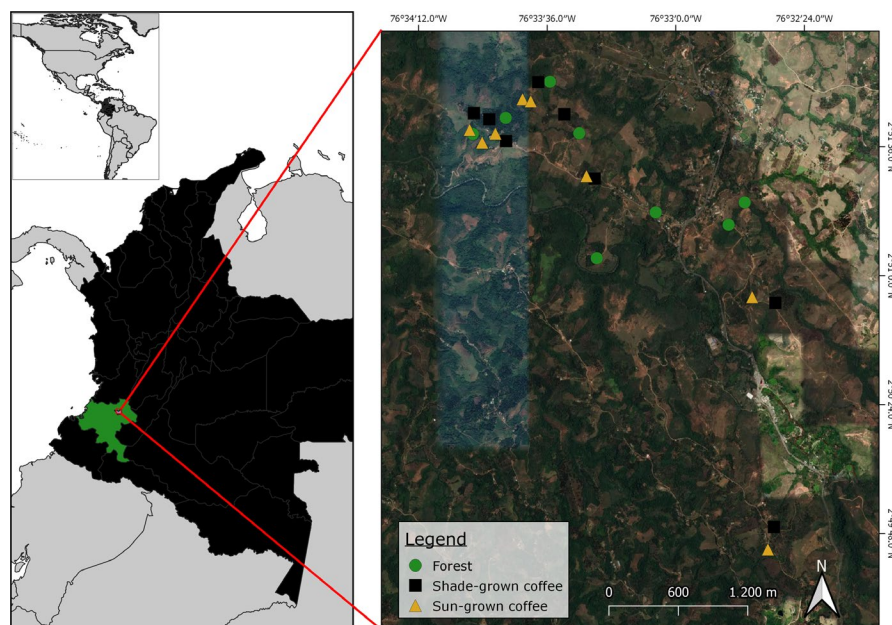
## 2.3 | Ant community sampling

At each sampling site, we used five pitfall traps and five 1-m<sup>2</sup> leaf-litter extractions, each located 10-m apart, following a 50-m transect into the farm that started at least 10 m away from the edge of the plantation. Each pitfall trap consisted of a 266-ml cup filled with 90 ml of 70% ethanol, collected after 48 hr. We hung five Winkler Extractors to air-dry for 48 hr, inducing ants to fall to an ethanol-filled vial. Additionally, two researchers systematically examined coffee bushes, tree branches at and below eye-level, leaf-litter, under rocks and logs at each site for 30 min/researcher (adapted from Bestelmeyer et al. 2000). We sampled all sites twice, in August 2015 and between December 2015 and January 2016. We pooled these data for our main analyses. We conducted secondary analyses using data from each sampling campaign separately to account for any seasonal differences. All samples were transported to the Laboratorio de Ecología y Comportamiento de Insectos at Universidad del Valle in Cali, Colombia, for identification and permanent storage.

## 2.4 | Community phylogenetics

To assess the phylogenetic structure of ant communities, we grafted current subfamily-level trees (Blaimer et al., 2015; Schmidt & Shattuck, 2014; Ward et al., 2015) onto a backbone, genus-level phylogeny (Moreau & Bell, 2013), maximizing genera coverage. We pruned this tree to only include genera found in our samples. We excluded the genus *Rasopone* from our analyses because its phylogenetic placement remains unknown (Schmidt & Shattuck, 2014). Based on our species list, we simulated 1,000 species-level trees to account for phylogenetic uncertainty in later analyses (Fowler et al., 2014). We obtained species phylogenetic relationships from

**FIGURE 1** Distribution of sampling sites in the department of Cauca, Colombia



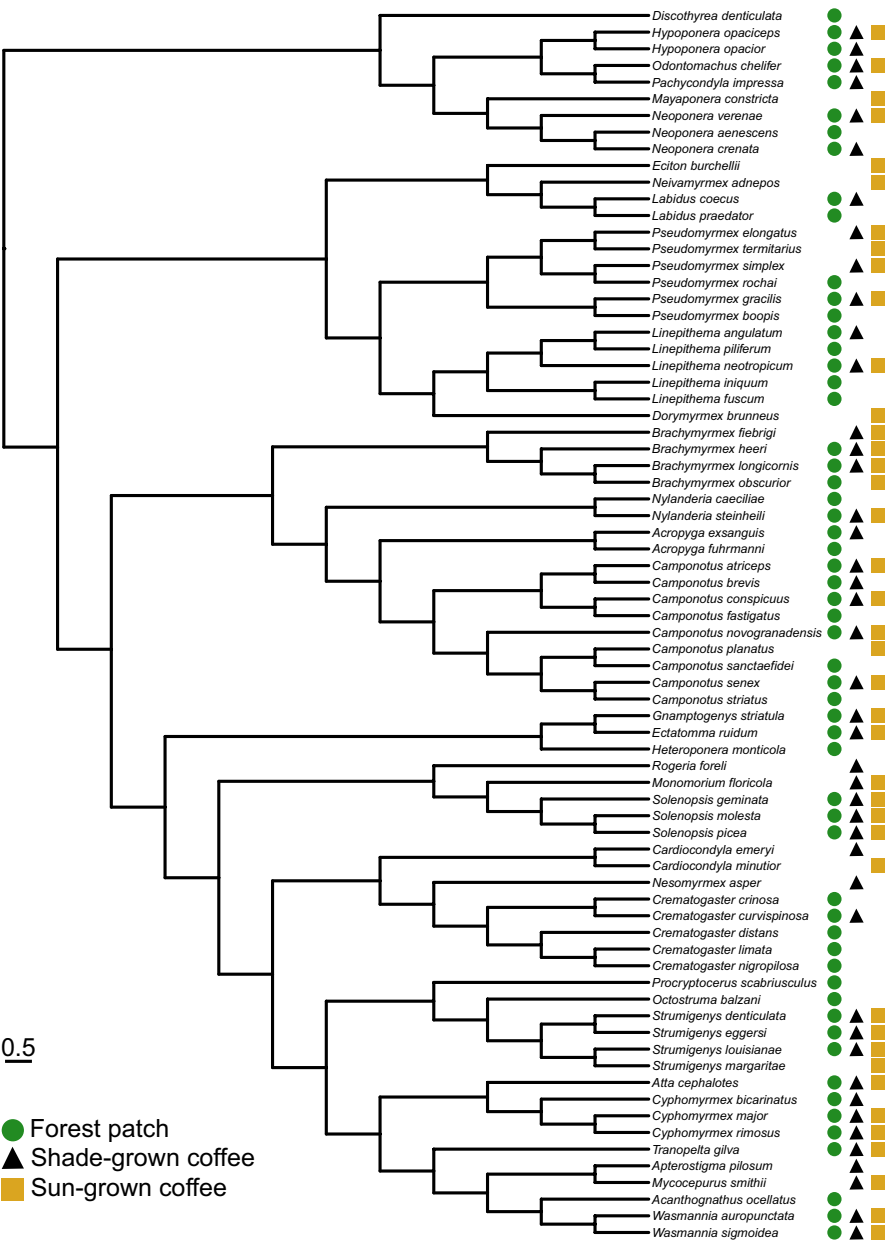
a Yule (pure-birth) process using the *genus.to.species.tree* function in the *PHYTOOLS* package for *R* (Revell, 2012). We calculated a consensus tree using maximum clade credibility (Heled & Bouckaert, 2013) using the *mcc* function in the *PHANGORN* package (Schliep, 2011). This method tallies the support of clades across the 1,000-tree set and then selects the tree (Figure 2) with the highest overall clade support (i.e. highest posterior probability).

## 2.5 | Functional traits

We used a combination of 12 morphological and life-history traits relevant to resource use and microhabitat preference (see Appendix S1). Due to the social structure of ants, we focused on traits at three levels: colony, worker and queens. We hypothesized

trait-specific responses to a reduction in canopy cover as a result of agricultural intensification (Andersen, 2019; Brousseau et al., 2018). We assumed traits had no intra-specific trait variation. This omission likely results in a bias towards weaker trait-environment relationships (Hulshof & Swenson, 2010; Jung et al., 2010). Thus, future work should include intra-specific variation in their analyses (Siefert et al., 2015).

We obtained species-specific trait values from taxonomic descriptions and specimen photographs from databases such as Antweb ([www.antweb.org](http://www.antweb.org)) and AntWiki ([www.antwiki.org](http://www.antwiki.org); see full reference list in Appendix S1). We complemented life-history information from observations made in the field by our research group. To measure morphological traits from photographs, we used the software ImageJ v1.51j8 (Schneider et al., 2012) following the protocol described by Parr et al. (2017).



**FIGURE 2** Dendrogram depicting the hypothesized phylogenetic relationships between species present in sampled sites. Calculated using Maximum Credibility Clade (MCC). Symbols represent the habitat in which a species occurred

## 2.6 | Statistical analyses

### 2.6.1 | Functional traits

To quantify the functional structure of ant communities, we relied on a trait dendrogram. We first log-transformed and scaled our trait data. We then used these data in a Principal Coordinate Analysis (PCoA) to produce orthogonal axes of function. From these, we selected the first six axes that explained ~90% (Villéger et al., 2008). These calculations were done using the *dbFD* function of the *FD* package for R (Laliberté et al., 2014). We converted these trait axes into a Euclidean distance matrix (*dist* function) that we used to produce a dendrogram representing the functional relationship among species using the *UPGMA* (*hclust* function) method (Mouchet et al., 2010).

### 2.6.2 | Compositional dissimilarity between habitats

To investigate the compositional differences between nearby forest patches and coffee plantation management strategies, we calculated a dissimilarity matrix based on the Simpson pair-wise index (Lennon et al., 2001; Simpson, 1943). This metric generally reflects the compositional differences due to species turnover (replacement), while accounting for differences in species richness between sites (Baselga, 2010). To calculate this index for all diversity

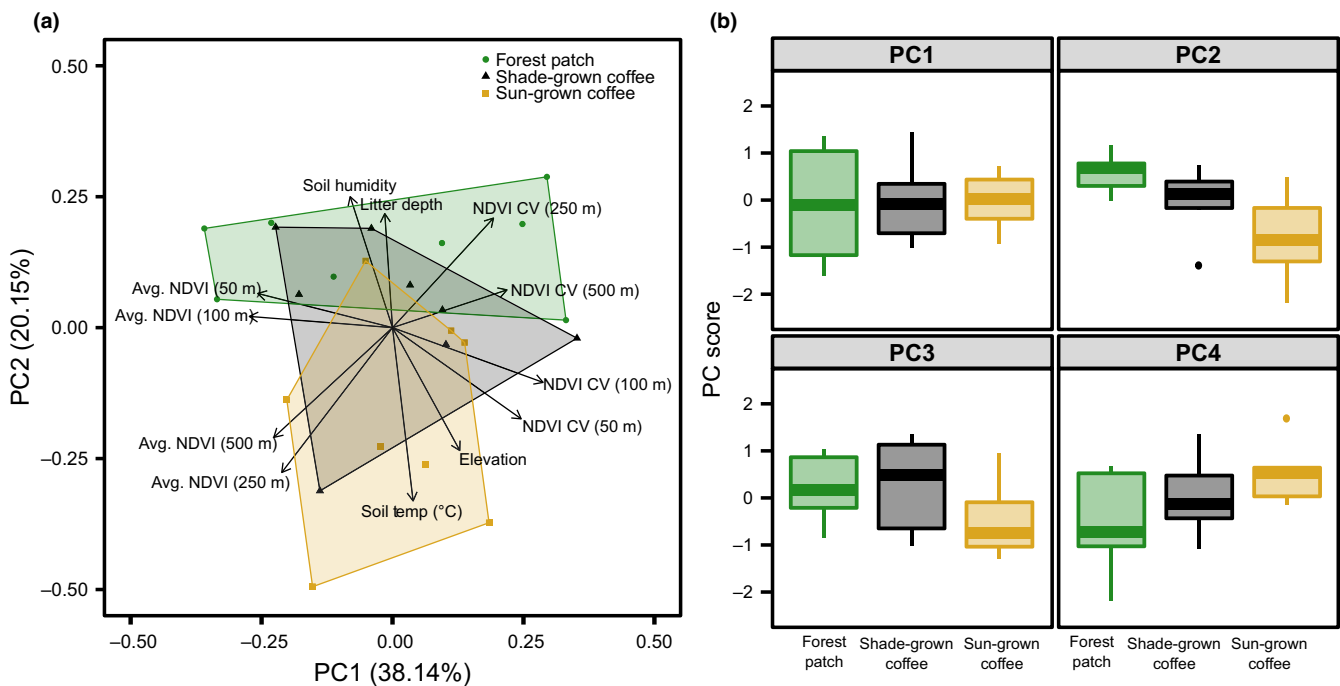
components of interest, we used the functions *beta.pair* and *phylo.beta.pair* from the *BETAPART* package (Baselga & Orme, 2012). To visualize dissimilarities, we generated nonparametric multidimensional scaling (NMDS) plots via the *metaMDS* function in the *VEGAN* package for R (Oksanen et al., 2019). We tested the differences in the taxonomic, phylogenetic and functional position of the community centroids (multivariate location) between forest and both coffee plantation management practices via 'Permutational Multivariate Analysis of Variance' (PERMANOVA) using the *adonis2* function in the *VEGAN* package.

### 2.6.3 | Compositional dispersion within habitats

To evaluate the degree of biotic homogenization in each habitat type, we quantified the distance to centroid (multivariate dispersion) of ant communities residing in forests and both types of coffee plantations through a 'Permutational Analysis of Multivariate Dispersion' (PERMDISP) using the *betadisper* function in the *VEGAN* package.

### 2.6.4 | Standardized effect size

To allow for comparisons between habitat types, we calculated a standardized effect size (SES) of multivariate dispersion



**FIGURE 3** PCA of environmental variables measured in all habitat types. (a) PCA biplot depicting the Euclidean distances between the sampled sites and the eigenvectors of environmental variables measured in all habitat types. Different coloured symbols represent different habitat types with green circles, black triangles and golden squares representing nearby forest patches, shade-grown coffee plantations and sun-grown coffee plantations, respectively. (b) Boxplots depicting the scores of sampled sites for each significant PC axis. The box encloses the 25–75th percentiles of the values, bold lines represent median and the whiskers extend to 1.5 times the interquartile range. See Table S2b in Appendix S2 for contributions to each PC axis for each environmental variable



( $D_{\text{centroid}}$ ) for each community and diversity dimension using the following equation:

$$\text{SES } D_{\text{centroid}} = \frac{\text{Mean}_{\text{obs}} - \text{Mean}_{\text{null}}}{\text{SD}_{\text{null}}}$$

We calculated 1,000 null  $D_{\text{centroid}}$  values for each observed  $D_{\text{centroid}}$  value (Swenson, 2014). For this, we generated 1,000 null communities using the 'Independent swap' algorithm found in the *randomizeMatrix* function of the *PICANTE* package (Kembel et al., 2010). We then calculated the taxonomic, phylogenetic and functional multivariate dispersion on each of these null communities using the method described in the previous paragraph and used them to calculate the null  $D_{\text{centroid}}$  values. Finally, we used a one-sample *t*-test (*t.test* function) to investigate whether average SES  $D_{\text{centroid}}$  for each habitat differed from zero (null expectation). All analyses were performed using R (R Core Team, 2020).

### 2.6.5 | Influence of spatial and environmental factors on ant communities

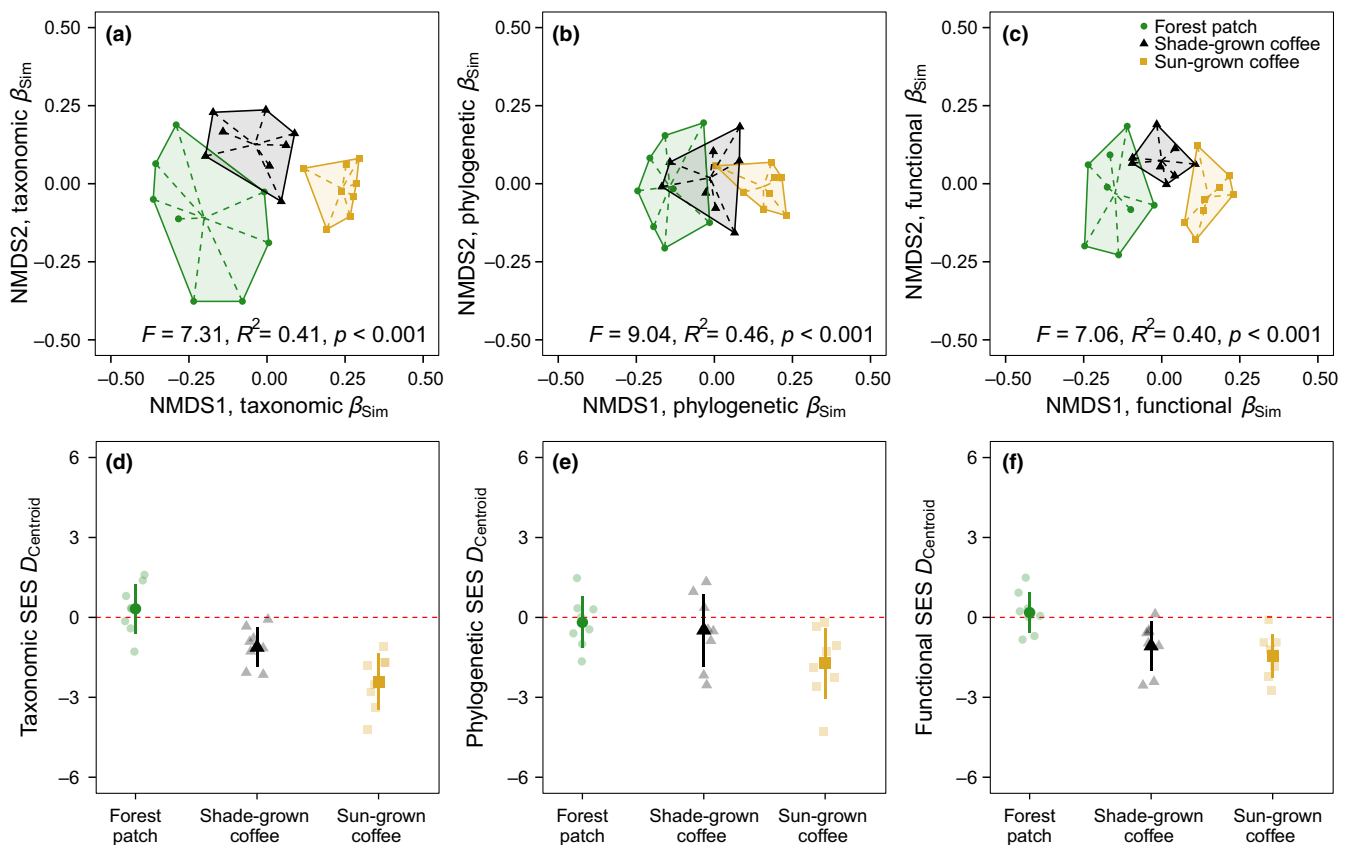
To test for spatial autocorrelation of our sampling sites, we performed a Mantel test with the *mantel.test* function of the *ADE4* package for R (Dray & Dufour, 2007). We found that spatial distance and land use

type were not correlated ( $r = -0.04$ ,  $p = 0.70$ , 9,999 replicates). This result allowed us to reject the spatial distribution of the sampled farms and forest patches as a confounding factor for our interpretation.

To analyse the effect of environmental variables on the compositional differences of ant assemblages, we performed a PERMANOVA as described above. To account for the multicollinearity among our measured environmental variables, we performed PCAs using the *prcomp* function in R (R Core Team, 2020) and produced a biplot to visualize the summarized information (Figure 3a). We then used these orthogonal axes that describe local and landscape environmental variables as independent variables in the PERMANOVA (see Table S3a in Appendix S3).

## 3 | RESULTS

We collected a total of 25,865 individual workers belonging to 75 ant species from nine subfamilies and 36 genera across the 24 sites. Of these, 28% species were found exclusively in forest patches, ~7% exclusively in shade-grown coffee plantations, and ~11% exclusively in sun-grown coffee plantations. There was some overlap in species occurrence; however, only 35% species occurred in all three land-use types (see Figure S3a in Appendix S3). Species accumulation curves confirmed the adequacy of our species sampling (see Figure S3b in Appendix S3).



**FIGURE 4** Ant community composition analyses between pairs of local communities in each environment. (a–c) NMDS ordination of sites within forest and coffee plantations based on taxonomic, phylogenetic and functional Simpson's dissimilarity index. (d–f) Scatterplot of mean  $\pm$  SD of standardized effect size of the distance to multivariate space centroid (SES  $D_{\text{centroid}}$ ) of each site. Red dashed line represents null expectation

### 3.1 | Local and landscape environmental differences between habitats

While we found significant differences in the local environmental factors between habitats, we found no significant differences at the landscape scale (Figure 3; see, Figure S2b in Appendix S2). More specifically, we found that soil humidity ( $F = 35.73$ ,  $df = 2$ ,  $p < 0.001$ ) and litter depth ( $F = 18.23$ ,  $df = 2$ ,  $p < 0.001$ ) are higher in forest patches and shade-grown plantations. Additionally, shade-grown plantations had higher crop density (distance between planted rows;  $F = 5.99$ ,  $df = 1$ ,  $p = 0.02$ ), number of twigs ( $F = 21.54$ ,  $df = 1$ ,  $p < 0.001$ ) and leaf-litter volume ( $F = 9.04$ ,  $df = 1$ ,  $p < 0.01$ ).

### 3.2 | Compositional differences between forest patches and management strategies

The taxonomic ( $F = 7.31$ ,  $p < 0.001$ ,  $R^2 = 0.41$ ), phylogenetic ( $F = 9.04$ ,  $p < 0.01$ ,  $R^2 = 0.46$ ) and functional trait composition ( $F = 7.06$ ,  $p < 0.001$ ,  $R^2 = 0.41$ ) differed between habitat types (Figure 4a–c; Table 1). When analysing the data separately, we observed significant differences in ant composition across biodiversity dimensions in both seasons (Table 1). Specifically, pairwise analyses for each sampling campaign revealed that there were no significant differences between the taxonomic, phylogenetic and functional compositions of shade-grown plantations and that of nearby forest patches (Table 1).

### 3.3 | Biotic homogenization of ant communities in coffee plantations

The taxonomic ( $F = 11.47$ ,  $df = 2$ ,  $p < 0.01$ ), phylogenetic ( $F = 4.44$ ,  $df = 2$ ,  $p = 0.02$ ) and functional ( $F = 5.71$ ,  $df = 2$ ,  $p = 0.01$ )

multivariate dispersion (i.e. homogenization) differed significantly between the habitat types (Figure 4d–f). We found that homogenization patterns were consistent with null expectations across diversity dimensions in forest patches ( $p > 0.05$ , one-sample  $t$  test). Our analysis detected ant communities found in shade-grown plantations were taxonomically ( $t = -4.3$ ,  $df = 7$ ,  $p = 0.03$ ) and functionally ( $t = -3.26$ ,  $df = 7$ ,  $p = 0.01$ ) less homogeneous than expected, but not phylogenetically ( $t = -0.99$ ,  $df = 7$ ,  $p = 0.35$ ). In contrast, ant communities found in sun-grown coffee plantations were more homogenous than null expectations across diversity dimensions ( $p < 0.05$ ).

## 4 | DISCUSSION

Our results indicate that management practices of shade-grown coffee plantations can lessen the effects of anthropogenic disturbance on ant diversity when compared to intensified unshaded monocultures. As hypothesized, ant communities found in shade-grown coffee plantations neighbouring forest patches were more similar across diversity dimensions but differed from those found in sun-grown coffee plantations. Additionally, we observed high levels of redundancy in ant composition in unshaded monocultures. Finally, we discuss the environmental factors by which land management practices alter ant diversity.

### 4.1 | Compositional dissimilarity of ant communities

Shade-grown coffee practices appear to buffer the effect of coffee growing on ant communities. The taxonomic composition of ant communities in shade-growing plantations was more similar to those in nearby forest patches than to those in sun-grown coffee

**TABLE 1** Summary of statistics for PERMANOVAs of the effect of habitat type on taxonomic, phylogenetic and taxonomic compositional turnover of ant communities. Significant values ( $p < 0.05$ ) are highlighted in bold

	Pooled			August			December-January		
	<i>F</i>	<i>R</i> <sup>2</sup>	<i>p</i> -value	<i>F</i>	<i>R</i> <sup>2</sup>	<i>p</i> -value	<i>F</i>	<i>R</i> <sup>2</sup>	<i>p</i> -value
Taxonomic	7.301	0.411	<0.001	6.251	0.373	<0.001	5.139	0.328	<0.001
Forest/Shade-grown	3.422	0.196	0.003	2.068	0.129	0.044	2.881	0.171	0.012
Forest/sun-grown	9.095	0.394	<0.001	8.598	0.381	<0.001	6.416	0.314	<0.001
Shade-grown/Sun-grown	11.821	0.458	<0.001	10.111	0.419	<0.001	7.015	0.334	<0.001
Phylogenetic	9.037	0.463	<0.001	6.312	0.375	<0.001	5.812	0.356	<0.001
Forest/shade-grown	4.279	0.234	0.002	2.379	0.145	0.061	1.829	0.116	0.175
Forest/sun-grown	14.081	0.501	<0.001	10.351	0.425	<0.001	8.321	0.373	<0.001
Shade-grown/sun-grown	10.235	0.422	<0.001	8.002	0.364	<0.001	8.338	0.373	<0.001
Functional	7.061	0.402	<0.001	4.981	0.322	<0.001	4.354	0.293	<0.001
Forest/shade-grown	3.581	0.204	0.002	1.319	0.086	0.332	1.859	0.117	0.192
Forest/sun-grown	9.302	0.399	<0.001	6.221	0.308	<0.001	4.561	0.246	0.004
Shade-grown/sun-grown	9.349	0.401	<0.001	9.115	0.394	<0.001	8.879	0.388	<0.001

plantations. One might expect these compositional differences to be driven by the presence of arboreal ants typical of natural forest patches in shade-grown but not in sun-grown coffee plantations. However, we observed a similar pattern when excluding arboreal species from our analyses (see Figure S4a; Tables S4a–b in Appendix S4). Furthermore, we found habitat generalists occurring ubiquitously in all environments, matching previous studies (Armbrrecht et al., 2005; Vergara & Badano, 2016; Gallego Roper, 2005; Urrutia-Escobar & Armbrrecht, 2013). We found nine species occurring in both forest patches and shade-grown plantations, and only one species occurring in both forest patches and sun-grown plantations. Ant communities found in sun-grown plantations were also phylogenetically distinct from both shade-grown plantations and forest patches. While arboreal genera (e.g. *Camponotus*, *Crematogaster*) occurred mostly in shade-grown plantations and forest patches, sun-grown plantations mainly harboured soil-dwelling ants (Figure 2). This pattern indicates that ants occurring in these habitats have distinct evolutionary histories and relationships (Lucky et al., 2013). Most ant lineages present in forest patches and shade-grown plantations were associated with more humid and closed canopy environments, pointing to their convergent habitat of origins and evolutionary history (Economo et al., 2018; Lessard et al., 2012; Vasconcelos et al., 2018).

Consistent with previous studies, we showed that land conversion and agricultural intensification can alter ant functional diversity and composition (Armbrrecht et al., 2005; Liu et al., 2016; Urrutia-Escobar & Armbrrecht, 2013). Specifically, we found that ants are smaller in shade-grown coffee plantations and are lighter-coloured in both shade-grown and sun-grown coffee plantations compared to those found in forest patches (see Appendix S5). Smaller workers are able to navigate more complex habitats (Kaspari & Weiser, 1999) such as the leaf litter layer present in shade-grown plantations (Armbrrecht et al., 2005). On the other hand, a light-coloured cuticle absorbs heat more slowly than dark-coloured cuticles (Trullas et al., 2007). Cuticle lightness has been linked to the ability of species to adapt to altered thermal conditions (Bishop et al., 2016; Law et al., 2019), potentially allowing workers to forage closer to their maximum thermal limits (Cerdá et al., 2013).

## 4.2 | The effect of management on environmental conditions and compositional dissimilarity

While local environmental conditions differ between habitat and management types, the landscape matrix surrounding farms does not vary significantly (see Figure S2b in Appendix S2). Shade-grown plantations share more environmental similarities with forest patches than with sun-grown plantations. Besides having trees providing shade to the forest floor, shade-grown plantations have similarly deep and damp leaf-litter relative to sun-grown plantations (Figure 3; Figure S2b in Appendix S2). These differences in soil characteristics drive compositional differences between habitat types (see Table S3a in Appendix S3), which corroborate results from

previous studies in Colombian coffee plantations (e.g. Armbrrecht et al., 2006).

Management-related variables differ significantly between shade-grown and sun-grown coffee plantations. Shade-grown plantations have a higher crop density (see Figure S2b–c in Appendix S2), number of twigs and leaf-litter volume than sun-grown plantations, which was associated with distinct ant communities (see Table S3a in Appendix S3). The more dense and diverse vegetation found in shade-grown plantations may enhance resource (e.g. nesting sites, prey) availability and diversity, and in turn, increase ant diversity (Ashraf et al., 2018). Previous work with ants conducted in similar systems also showed that high leaf-litter volume and number of twigs could increase the richness of native ants (Armbrrecht & Perfecto, 2003; De la Mora et al., 2013).

## 4.3 | Biotic homogenization of ant communities

We found low compositional dispersion (i.e. high redundancy) between sun-grown coffee plantations and across diversity dimensions. Besides increasing habitat openness, intensive management practices limit the types of habitat and feeding resources needed by specialist ants (Philpott & Foster, 2005). Sun-grown plantations contained more taxonomically, phylogenetically and functionally homogenous ant communities. These communities were mainly comprised of a subset of generalist species found in forest patches or shade-grown plantations. Additionally, we found at least twice as many unique species exclusive to forest habitats compared to both types of management practices (Figure S3a in Appendix S3). In ant communities, rare species are often cryptic specialized predators nesting in the leaf litter (Lessard et al., 2007; Philpott & Armbrrecht, 2006) and therefore providing unique and targeted services.

Agricultural intensification produces more homogeneous habitat, which favours subsets of closely related and morphologically similar species (Armbrrecht et al., 2005; Morelli et al., 2016). The loss of closely related specialized ant predators in response to various forms of disturbance could be a general pattern (Lessard et al., 2009). Therefore, these ecosystems could be less stable, less resilient and vulnerable to extinction and should be properly evaluated to avoid the loss of ecosystem functions (Naeem et al., 1994; Oliver et al., 2015). Currently, our knowledge of the role of ants in agroecosystems is still limited to pest control and subsequent increased yield (De la Mora et al., 2015; Morris et al., 2018; Philpott & Armbrrecht, 2006). However, their role as seed dispersers and nutrient cyclers (Del Toro et al., 2012 and references therein) points to a potential greater importance in agroecosystems (Wielgoss et al., 2014).

## 5 | CONCLUSIONS

Improving our understanding of the effects of agricultural activities on biodiversity is a critical subject of agroecology and conservation.



Our results highlight how polyculture management practices lessen the negative effects of intensive practices across multiple biodiversity dimensions. Furthermore, our environmental analyses allowed us to identify that shade-grown plantations maintain similar environmental conditions to forest patches. Thus, farm managers should strive for forest-like leaf-litter conditions to help mitigate loss across diversity dimensions. Additionally, maintaining, or augmenting leaf-litter depth and twig number below coffee bushes could be used as a strategy to conserve ant predation services by favouring the persistence of specialized arboreal predators that can act as bio-control agents. These practices would not only benefit ant diversity, but numerous additional benefits may come indirectly from ant conservation-oriented practices.

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## AUTHORS' CONTRIBUTIONS

J.I.-I., I.T.H., J.-P.L. conceived the ideas and statistical analyses; I.A., S.E.-R., A.A.-C. conceived the methodology, collected data and identified specimens; J.I.-I. analysed data and led manuscript writing. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.0zpc866wp> (Ibarra-Isassi et al. 2020).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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