Decrease in $\beta$-diversity, but not in $\alpha$-diversity, of ants in intensively managed coffee plantations

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Abstract. 1. Local land-use intensity and surrounding landscape complexity affect the diversity of local species. Ants are an important biocontrol agent of the coffee berry borer (CBB), the main coffee pest worldwide. Although intensification of coffee production and deforestation in the surrounding landscape may reduce ant diversity, $\alpha$- and $\beta$-diversity patterns of ants in coffee landscapes remain poorly understood.

2. Ants foraging in coffee bushes were sampled, using tuna baits along an agricultural intensification gradient (forest, shaded coffee and sun coffee) in a Neotropical coffee landscape. We evaluated the differences in $\alpha$ and $\beta$ components of ant richness, community differentiation and habitat specificity of ant communities, in response to land-use type and the percentage of surrounding forest.

3. We found that ant $\beta$-diversity and community differentiation among plots were significantly reduced with coffee management intensity. The amount of forest border adjacent to coffee plantations did not affect $\alpha$- or $\beta$-diversity. Yet, ant habitat specificity in the forest increased with plots having greater amounts of forest border, although in sun coffee plantations, the opposite was found: plots with greater forest border decreased habitat specificity.

4. We found that conserving forest at landscape scales enhanced $\beta$-diversity, community differentiation and habitat specificity of ants in the forest. Loss of forest cover at landscape scales (i.e. predominance of sun coffee) may lead to biotic homogenisation of ant communities. In conclusion, landscape-wide ant richness is important in terms of biological CBB control by conservation.

Key words. Additive partitioning, diversity patterns, Hypothenemus hampei, multiplicative partitioning, natural enemies.

Introduction

Coffee is one of the most important cash crops worldwide as well as a vital source of income for 14–25 million families of smallholders (Jha et al., 2014; Valencia et al., 2014). Coffee landscapes under traditional crop management (i.e. with high diversity of shade trees) are important for biodiversity conservation and for the provision of ecosystem services such as natural pest control (Moguel & Toledo, 1999; Tscharntke et al., 2011; Jha et al., 2014), as they harbour a high diversity of natural enemies (De Beenhouwer et al., 2013; Aristizábal et al., 2016). Nevertheless, the transformation of traditionally managed coffee landscapes into simplified and intensively managed systems threatens their potential for natural pest control. Therefore, it is highly relevant to understand the mechanisms affecting the diversity of natural enemies in coffee landscapes and how they respond to management practices at different spatial scales (Karp et al., 2012; Tscharntke et al., 2012).

Ants are successful biocontrol agents of the coffee berry borer, Hypothenemus hampei (Coleoptera: Curculionidae: Scolytinae) (henceforth CBB), the most important coffee pest worldwide...
The abundance and diversity of ants in coffee agroecosystems respond to multiple practices, including habitat diversification (Armbrucht & Perfecto, 2003; Philpott et al., 2008a) and management intensity (Philpott et al., 2006, 2008a). Although ant diversity patterns in response to management intensity at the plot-scale (i.e. the farm) are well documented for coffee (Armbrucht et al., 2005; Philpott et al., 2006; Teodoro et al., 2010), patterns at multiple spatial scales and their relationship with crop management intensification and landscape heterogeneity are less clear (Escobar-Ramírez et al., 2019; but see de la Mora et al., 2013; Livingston et al., 2013).

Processes determining local assemblages and species richness of organisms driving ecosystem services operate at several spatial scales beyond the agricultural plot (Tscharntke et al., 2005). Thus, the coexistence of local species has been traditionally explained by species interactions and the physical and biological attributes of the environment they share (Ricklefs, 2004; Schmidt et al., 2017), while landscape structure may also affect local biodiversity due to species spillover across the crop/ non-crop interface (Tscharntke et al., 2007; Gámez-Virués et al., 2015; Schmidt et al., 2017). Diversity and distribution of natural enemies—such as ants—in the coffee landscape are also expected to respond to different spatial scales, management intensity and landscape heterogeneity. Yet, little is known about the spatial components of ant richness and community differentiation in coffee landscapes (but see de la Mora et al. 2013) for the main coffee-growing management practices.

Studying the spatial organisation of biodiversity might contribute to understanding the processes that maintain species diversity in a landscape (Socolar et al., 2016). A widely used approach for comparing spatial biodiversity patterns in a landscape is the partitioning of \( \gamma \)-diversity (regional diversity) into its \( \alpha \) and \( \beta \) components, where \( \alpha \) is the diversity of the communities at a given spatial scale, and \( \beta \) the extent of change in community composition at that spatial scale. Thus, high \( \beta \)-diversity means large differences in species diversity between communities (Wagner et al., 2000; Tylianakis et al., 2005; Schmidt et al., 2017), where the spatial heterogeneity in species distributions may result from habitat heterogeneity, dispersal limitation or stochastic effects (Crist & Veech, 2006). The contribution of \( \alpha \)- and \( \beta \)-diversity to \( \gamma \)-diversity can be quantified using additive partitioning (\( \gamma = \alpha + \beta \) (Lande, 1996), while the level of community differentiation at multiple spatial scales can be estimated using a multiplicative approach (Jost, 2007). Traditionally, diversity partitioning has been a helpful approach in analysing spatial patterns of biodiversity and identifying the appropriate spatial scale for species conservation (Gering et al., 2003). By comparing spatial ant biodiversity patterns for different coffee management intensities, the agricultural practices and the spatial scale that are more favourable in preserving the regional diversity of these natural enemies can be identified (Tylianakis et al., 2005; Clough et al., 2007).

Landscape heterogeneity and the proximity to near-natural habitat patches might increase the natural enemies diversity at the farm-level (Duelli, 1997; Tscharntke et al., 2007; Clough et al., 2007) and affect the specific species composition (Tylianakis et al., 2005). Nevertheless, the response of natural enemies to habitat heterogeneity may vary according to their degree of habitat specialisation and the spatial scale considered. For instance, generalist enemy response to natural habitat tends to occur at larger spatial scales than for specialist enemies (Chaplin-Kramer et al., 2011). Likewise, the magnitude of natural enemy spillover into crops by habitat generalists that use non-crop habitats will depend greatly on the quality, quantity and proximity of non-crop habitats in the landscape (Bianchi et al., 2006). A study conducted by de la Mora et al. (2013) found that the number of leaf-litter ant colonies in coffee plantations tended to be higher with more forest area within 200 m, while the richness of twig-nesting species was higher at a greater distance from the forest fragment. To our knowledge, there are no studies assessing the relationship between spatial components of ant diversity, habitat specialisation and the quantity of non-crop area surrounding coffee plantations.

This study simultaneously analyses the relative contributions of spatial scale, habitat management and landscape heterogeneity on the diversity of ants with potential as biocontrol agents of the CBB in a Neotropical coffee landscape. Specifically, this study examines diurnal omnivore/predatory ant species foraging in coffee branches for: (i) the contribution of \( \alpha \)- and \( \beta \)-diversity to \( \gamma \)-diversity of understory foraging ants in forest, shaded coffee and sun coffee; (ii) the effective community differentiation at different scales; (iii) the main drivers of \( \beta \)-diversity (species replacement or species loss/gain); and (iv) whether diversity patterns and habitat specificity are affected by the proportion of the crop perimeter in contact with forest in the surrounding landscape.

First, we hypothesised that ant diversity and community differentiation occur from fine to broader spatial scales due to the ants’ sensitivity to changes at the microscale as well as to differences due to management practices among land uses. Secondly, we hypothesised that ant species richness increases with the proportion of crop perimeter that is in contact with forest vegetation, as a result of a higher species spillover from forest to cropped areas.

**Methods**

**Study area**

The study was carried out in the Popayán Plateau (Department of Cauca, Colombia) in altitudes ranging from 1574 to 1779 masl in the southwestern Colombian Andes, located between the western and central mountain ranges (Ayerbe-Quinones & Johnston-Gonzalez, 2010) (Supporting Information Fig. S1). The municipalities sampled, La Rejoya and La Venta, display an agricultural mosaic dominated by small-farm holders (1–2 ha) combining mainly shaded and sun coffee plantations, cattle pastures, sugar cane, cassava, pine plantations and forest vegetation in fragmented patches, riparian forest or strips dividing or crossing the farms.

**Plot selection and characterisation**

A total of 12 plots were selected: four forest plots, four shaded coffee plantations and four sun coffee plantations. The plots...
were similar in age (coffee plants about 3–4 years old), area (Mean = 1.8; SD = ±1.1 ha), coffee variety (var. Colombia) and management practices, but differed in the percentage of forest surrounding the plots (Supporting Information Table S1). The percentage of bordering forest was estimated for each plot as the amount of the total perimeter of the coffee plantation that bordered forest vegetation, using ArcGIS software (10.2) over orthophotos provided by the Colombian Coffee Growers Federation. Additionally, for each plot, we estimated plant structure variables distributed in three vertical strata, following Mas and Dietsch (2003) and Armbrecht (2003): (i) Arboreal strata (canopy cover, canopy height, tree richness and tree density), (ii) Coffee bush strata (coffee bush density, coffee bush height, epiphyte richness and epiphyte density) and (iii) Soil stratum (litter depth) (Supporting Information Fig. S2).

Ant sampling

The ants able to forage on coffee shrubs may directly reduce CBB attacks on fruit (Morris et al., 2018). We specifically sampled a subset of diurnal ants foraging on coffee shrubs, using tuna baits. Ant species attracted to tuna baits (henceforth, ants) might be omnivorous or predators and eventually might prey on CBB (Philpott et al., 2008b). Between July and September 2014, in each of the 12 plots, we baited a total of 49 coffee bushes separated 10 m from each other, in a 7 × 7 grid arrangement (Fig. 1) similar to Perfecto et al. (2003). At each coffee bush, we set a bait consisting of approximately 3 g of tuna (in oil) in a piece of bond paper (14 × 13 cm), folded and fixed to the main stem of the coffee bush (trees with a DBH > 8 cm in forest plots), at breast height (Fig. 1). The baits were offered for 2 h in each plot, either between 08:00 and 10:00 h or between 14:00 and 16:00 h. The baiting hours were carefully assigned so that the different land-uses had both morning and afternoon baiting hours. After 2 h, all ants visiting the baits were collected in ethanol (96%) for later quantification and identification in the laboratory. Ants were identified to species level with the help of taxonomic keys (Palacio & Fernández, 2003; AntWeb, 2017). An ant reference collection was deposited at the Entomology Museum at Universidad del Valle (Cali, Colombia). Ant individuals that could not be identified to species level were sorted in morphospecies according to their morphological traits. Details on these ant captures are published in the studies by Jiménez et al. (2016).

Statistical analysis

In order to assess sampling efficiency, species accumulation curves were constructed for each habitat type using the function ‘specaccum’ (random method, 1000 permutations) in the vegan package in R (Oksanen et al., 2011). Sample coverage was calculated for each habitat type based on incidence data using the ‘iNEXT’ R package (Hsieh et al., 2016).

For each land-use type, hierarchical spatial components were established to reflect diversity variation at the level of baits (α<sub>bait</sub>), between baits (β<sub>bait</sub>), at plot level (α<sub>plot</sub>), between plots of the same land-use type (β<sub>plot</sub>), and total diversity per land-use type (γ). The following diversity partitions were all based on species richness (S) and carried out with species presence/absence data.

### Contribution of α- and β-diversity to γ-diversity

In order to analyse the relative contribution of α- and β-diversity to ants’ γ-diversity in all land-use types, we performed an additive diversity partitioning (Lande, 1996, Anderson et al., 2011). The α<sub>bait</sub> was defined as the mean number of species per bait in each plot. The β<sub>bait</sub> was calculated for each plot as the total species richness per plot, minus the mean number of species per bait for that plot. The α-diversity at plot level (α<sub>plot</sub>) was the mean number of species per plot in each land-use type. The β<sub>plot</sub> was calculated as the total species richness of that land-use type (sampled over all four replicates) minus the number of species per plot of that land-use type. The sum of α<sub>bait</sub>, β<sub>bait</sub> and β<sub>plot</sub> gives the γ-diversity (γ = α<sub>bait</sub> + β<sub>bait</sub> + β<sub>plot</sub>), quantifying the relative contribution of each diversity component to total diversity in each land-use type. In the additive partition, α, β and γ values are expressed in the same units (mean number of species) and thus directly comparable (Veech et al., 2002).

### Community differentiation

We performed a multiplicative partitioning of γ-diversity to assess the level of differentiation among ant communities at different spatial scales, for all land-uses. In the multiplicative approach, β-diversity corresponds to the effective number of different communities at a given spatial scale (Veech et al., 2002). For each land-use type, we estimated β<sub>mult/bait</sub>, which corresponds to the effective number of completely distinct communities in terms of species composition at plot scale, and can range from 1 to 49 (i.e. when β = 1, all communities are identical in species composition); and β<sub>mult/plot</sub>, meaning the community differentiation at the land-use type scale, which can range from 1 to 4. We used the ‘multpart’ function from the vegan package. The β values were obtained by the γ-diversity of each spatial scale (Oksanen et al., 2011). Alpha and beta estimates were then compared with a null distribution to test the null hypothesis that the observed α- and β-diversity is obtained by a random distribution of individuals among samples at all hierarchical levels (Schmidt et al., 2017).

### Partitioning the components of β-diversity

Overall, β-diversity was additively portioned into two components explaining community differentiation. This approach allowed us to estimate whether community differentiation is related to similar driving factors for the different land-uses. Following Baselga (2010), we estimated overall β-diversity as Sørensen dissimilarity (β<sub>mult</sub>) and partitioned it into the two components

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components driving variation in species composition: spatial turnover (as Simpson dissimilarity – $\beta_{\text{sim}}$) and species loss/gain (as nestedness-driven dissimilarity – $\beta_{\text{nes}}$). We partitioned the overall $\beta$-diversity only for spatial scales where $\beta$-diversity was higher than expected from a null model (Schmidt et al., 2017).

Species habitat specificity

We assessed habitat specificity using the index introduced by Tylianakis et al. (2005). This index compares the observed distribution of species among study plots, with an expected distribution if species distribute themselves randomly among all habitats proportionally to the relative abundance of all species in each land-use type (Tylianakis et al., 2005). The expected number of ants per species $i$ for plot $j$ was calculated as $E_{ij} = N_i \times P_j$, where $N_i$ is the total number of ants of species $i$ across all land-uses, and $P_j$ is the proportion of all ants of all sampled species (across all land-uses) that were found in plot $j$. For each species, we compared $E_{ij}$ to the observed number of ants of species $i$ in plot $j$ ($O_{ij}$) to calculate its habitat specificity as $\text{specificity} = \log_{10} \left( \frac{O_{ij}}{E_{ij}} + 1 \right)$. Mean habitat specificity was calculated per study plot and modelled in response to land-use type.

Effect of forest presence in the surrounding landscape

In order to assess whether diversity components are affected by the presence of forest in the surrounding landscape, we used linear regression to model the additively partitioned diversity components ($\alpha_{\text{bait}}$ and $\beta_{\text{bait}}$, $\beta_{\text{plot}}$) in response to land-use type and the percentage of plot perimeter bordering forest vegetation, as well as the interaction between the two predictors. We validated the assumptions of normality using the Shapiro–Wilk test and of homocedasticity using the Breush–Pagan test. Outlier values and influencers were identified through studentised residuals and the Cook distance. The interaction term was dropped from the model if not significant for model parsimony. Mean habitat specificity was also modelled in response to the percentage of plot perimeter bordering forest vegetation. The models in this
section were built using the ‘lm’ function in R (R Development Core Team, 2017).

Results

In total, we sampled 17 288 ants from 40 species (including morphospecies) in 17 genera (Supporting Information Fig. S3). Species accumulation curves showed high sample coverage (above 90%) for each habitat type (Supporting Information Figs. S4 and S5). Linepithema was the most abundant genus (38.1% of ant workers), followed by Solenopsis (26.6%) and Pheidole (21.1%) (Fig. S6). The forest showed the highest number of total species, followed by shaded and sun coffee plots (Fig. 2). The forest registered the highest number of exclusive species (14 out of 40) compared to shaded and sun coffee plots (five and six species, respectively). Additionally, shaded and sun coffee plots shared more ant species (seven species) among each other than with the forest.

Plot characterisation

As expected, forest vegetation exhibited the most complex plant structure in terms of higher litter depth, tree density, canopy cover, tree richness, epiphyte richness and epiphyte density (Supporting Information Fig. S7). On one hand, the shaded coffee plantations resembled some structural characteristics found in the forest, such as the presence of epiphytes and high values of canopy cover, height and litter depth. Shaded coffee also presented a lower density of coffee bushes and significantly higher richness and density of epiphytes than sun coffee. On the other hand, sun coffee showed the most intensified and simplified system – almost deprived of arboreal stratum and epiphytes – as well as a higher coffee density than in shaded coffee plots and the lowest litter depth.

Contribution of α- and β-diversity to γ-diversity

Regarding species richness, additive partitioning showed that α-diversity at the local scale contributed with 2–4% of γ-diversity all land-uses. The contribution of β-diversity to γ-diversity was 30–40% among baits (βbaits) and 54–66% among plots of a given land-use type (βplots). Mean α-diversity at bait level was 0.40 ± 0.06 (mean ± 1SE throughout) ant species in forest, values not significantly different than those for shaded coffee (0.48 ± 0.25) or sun coffee plantations (0.79 ± 0.12) (Table 1). Similarly, neither β-diversity between baits (forest: 7.10 ± 1.27; shaded coffee: 6.27 ± 0.96; sun coffee: 7.21 ± 1.27) nor α-diversity at plot level (forest: 7.50 ± 1.32; shaded coffee: 6.75 ± 1.18; sun coffee: 8.00 ± 1.23) significantly differed among land-use type (Fig. 3a; Table 1). Only β-diversity of ant species richness between plots within each land-use type (βplots) was significantly higher in forest vegetation (14.50 ± 1.32) than in sun coffee plantations (10.00 ± 1.23) (Fig. 3a, b; Table 1).

Community differentiation

In the multiplicative diversity partitioning, values of α-diversity at the local scale (αmult/baits) fell within the expected interval in null models, while β-diversity values of community differentiation were different from the expected intervals (Table 2). The number of completely distinct communities among baits (βbaits) was lower than expected in null models, while a higher level of community differentiation was found among plots of the same land-use type (βplots) (Table 2). Regarding land-use, sun coffee presented the lowest community differentiation among plots (βplots = 1.81) compared to forest vegetation (βplots = 2.88) and shade coffee (βplots = 2.34) (Table 2).

Partitioning the components of β-diversity

β-diversity among plots (βmult/plot) was higher than expected in the null models, showing community differentiation only at this scale. Partitioning of this component showed that overall beta diversities (βact) were similar among land-uses with values over 97% (Table 3). Spatial turnover in species composition (Simpson dissimilarity; βsim) was the predominant component (over species loss/gain), explaining more than 99% of ants’ β-diversity among plots, for all land-uses in our coffee landscape (Table 3).

Habitat specificity of ant species

Overall, the ants’ average habitat specificity was always lower than expected from an index value at which the observed ant species distributions match those of the expected distribution,
i.e. under the assumption that ants are distributed among land-uses in proportion to sample sizes (the index value when observed = expected distribution: log10 (1 + 1) = 0.30; dashed line in Fig. 4). Although higher in the forest than in coffee plots, the specificity index values were not different among land-uses (Table 4).

Effect of forest presence in the surrounding landscape

The proportion of the plots’ perimeter bordering the forest did not affect α- or β-diversity in any of the land-uses (Fig. 3a; Table 1). The interaction between land-use type and forest perimeter was not significant in any of the models and thus omitted from these analyses.

Table 1. Additively partitioned diversity of ants in response to land-use type (forest, shaded coffee, sun coffee) and the amount of forest bordering the plantation edges. Ant species richness was partitioned into spatial scales: (a) the mean number of species per bait within each plot; (b) the mean β-diversity between baits; (c) α-diversity at plot level (n = 4 per land-use type); and (d) β-diversity between plots within land-uses. The interaction between land-use type and forest border was not significant in any of the models and thus omitted from these analyses.

|                  | Estimate | SE  | t     | P     |
|------------------|----------|-----|-------|-------|
| (a) α-diversity at bait level |           |     |       |       |
| Intercept = Forest | 0.25     | 0.201 | 1.248 | 0.247 |
| Shaded coffee    | 0.04     | 0.227 | 0.174 | 0.866 |
| Sun coffee       | 0.325    | 0.231 | 1.403 | 0.198 |
| Forest border    | 0.803    | 0.668 | 1.202 | 0.264 |
| (b) β-diversity between baits within plots |     |       |       |       |
| Intercept = Forest | 7.321    | 1.572 | 4.657 | 0.002 |
| Shaded coffee    | −0.769   | 1.779 | −0.432 | 0.677 |
| Sun coffee       | 0.208    | 1.813 | 0.115 | 0.911 |
| Forest border    | −1.192   | 5.236 | −0.228 | 0.826 |
| (c) α-diversity at plot level |           |     |       |       |
| Intercept = Forest | 7.572    | 1.669 | 4.536 | 0.002 |
| Shaded coffee    | −0.730   | 1.889 | −0.386 | 0.709 |
| Sun coffee       | 0.533    | 1.925 | 0.277 | 0.789 |
| Forest border    | −0.389   | 5.559 | −0.070 | 0.946 |
| (d) β-diversity between plots within land-uses |     |       |       |       |
| Intercept = Forest | 14.429   | 1.669 | 8.644 | <0.001 |
| Shaded coffee    | −2.270   | 1.889 | −1.202 | 0.264 |
| Sun coffee       | −4.533   | 1.925 | −2.355 | 0.046 |
| Forest border    | 0.389    | 5.559 | 0.07  | 0.946 |

*Indicates P values between 1% and 5% (statistically significant).

Fig. 3. Additive diversity partitioning of (a) ant species richness from bait to plot scale for each land-use type (means ± 1SE); (b) beta diversity between study plots, which is highest in the forest and significantly (p < 0.05) reduced in sun coffee plantations.

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Discussion

Diversity patterns of diurnal omnivore/predator ant species foraging in coffee branches responded to spatial scale, land-use type and the presence of forest in the surrounding landscape. Additive and multiplicative partitioning of γ-diversity showed similar diversity patterns for the ant communities in all land-use types across the landscape. Different than expected, local species diversity at the bait scale remained as expected from null models, while β-diversity between baits inside plots was lower than expected from null models. β-diversity showed community differentiation only between plots. Ant communities in sun coffee presented the lowest species turnover among plots and were taxonomically more similar throughout the landscape. For all land-uses, the most important driver of β-diversity among plots was species replacement. The presence of forest in the surrounding landscape did not affect any spatial component of diversity but negatively affected habitat specificity of ant species in sun coffee plots.
Table 2. Multiplicative partitioning of $\gamma$-diversity. We considered the average number of species per bait as the local $\alpha$-diversity. $\beta_{\text{mult/baits}}$ and $\beta_{\text{mult/plots}}$ represented the community differentiation at the local scale and habitat-type scale, respectively.

| Diversity | Observed | Expected values | $P$-value |
|-----------|----------|----------------|-----------|
| **Forest** |          |                |           |
| $\alpha_{\text{mult/baits}}$ | 1.13 | 1.0928–1.1304 | 1         |
| $\beta_{\text{mult/baits}}$ | 5.21 | 8.4962–10.4145 | 0.01**    |
| $\beta_{\text{mult/plots}}$ | 2.88 | 1.4462–1.7838 | 0.01**    |
| $\gamma$ | 16.97 | 1              | 1         |
| **Shade coffee** |          |                |           |
| $\alpha_{\text{mult/baits}}$ | 1.28 | 1.2181–1.3108 | 0.33      |
| $\beta_{\text{mult/baits}}$ | 4.89 | 6.2079–8.1311 | 0.01**    |
| $\beta_{\text{mult/plots}}$ | 2.34 | 1.3983–1.7478 | 0.01**    |
| $\gamma$ | 12.81 | 1              | 1         |
| **Sun coffee** |          |                |           |
| $\alpha_{\text{mult/baits}}$ | 1.12 | 1.0781–1.1159 | 0.19      |
| $\beta_{\text{mult/baits}}$ | 5.20 | 7.6643–8.4968 | 0.01**    |
| $\beta_{\text{mult/plots}}$ | 1.81 | 1.1383–1.2593 | 0.01**    |
| $\gamma$ | 10.58 | 1              | 1         |

Spatial partitioning of ant diversity

The low species diversity at the bait scale plus low $\beta$-diversity between baits inside the plots suggest that ant species from the regional pool are exposed to weak environmental filtering, resource limitation and species interactions (Crist et al., 2003; Schmidt et al., 2017). Similar results were reported for ant communities in rainforests and savannas of Brazil and Indonesia, using pitfall traps (Schmidt et al., 2017). Regarding $\beta$-diversity, it contributed to the largest part of overall species richness (>95%) in the coffee landscape. Community differentiation and higher species turnover occurred only between plots. Our results support the hypothesis that natural enemies distribution in agricultural landscapes is determined mainly by heterogeneity at the landscape scale (Tscharntke et al., 2007) and less at the local scale – as supported for multiple taxa in agricultural landscapes – including arable weeds, surface-dwelling arthropods, butterflies and bees (Wagner et al., 2000; Roschewitz et al., 2005; Clough et al., 2007; Ribeiro et al., 2008). High values of $\beta$-diversity are expected in heterogeneous and highly fragmented landscapes like ours, where the overall species richness may be the result of dissimilarity in the composition of the species assemblages on the different patches that make up this landscape (Lande, 1996; Harrison, 1997; Pineda & Halffter, 2004). Furthermore, the predominant contribution of species replacement in explaining $\beta_{\text{plot}}$ diversity for all land-uses supports the hypothesis that dispersal limitation is also contributing to ant richness and community differentiation in the coffee landscape (Schmidt et al., 2017).

Sampling artefacts (i.e. absence of replicates) may also have affected our estimations for $\beta$-diversity (Chandy et al., 2006; Crist & Veech, 2006; Clough et al., 2007). Species accumulation curves showed a satisfactory sampling efficacy at the land-use type level (over 90%), but in two specific plots, we achieved less than 80% of sampling coverage, which might have affected the estimation of diversity components. Furthermore, the diversity captured by the baits might reflect the diversity of highly competitive omnivores/dominant ant species, which are expected to be less susceptible to local environmental filtering, resource limitation and species interactions. Nevertheless, diversity patterns in our study are consistent with studies assessing ant richness variation along tropical landscapes (rainforest and savannas) in different continents, using more comprehensive sampling methods (i.e. pitfall traps, where $\beta$-diversity greatly contributed to $\gamma$-diversity at intermediate and larger spatial scales (Campos et al., 2011; Pacheco & Vasconcelos, 2012; Marques & Schoereder, 2013, Schmidt et al., 2017).

Effects of land-use type on ant diversity

Despite the strong structural differences found among forest, shaded and sun coffee plots, our target ant community was hardly affected by local habitat characteristics. Similar results were found by Perfecto and Snelling (1995) for ants foraging on coffee bushes in Mexico and may be related to the generalist habits of ants attracted to baits. Yet, the reduction in ant species richness and community differentiation between plots in sun coffee plantations indicates a negative effect of crop management intensity on species turnover of ant species with a high potential as CBB biocontrol agents at this scale (Duelli, 1997; Wagner et al., 2000; Tscharntke et al., 2007). Forest fragments supported the highest overall species richness, number of exclusive species and community differentiation, highlighting the importance of better-preserved habitats to sustain $\gamma$-diversity in the coffee landscape. Whether ant species preying on CBB might spill into coffee plantations from the forest and reduce fruit attacks was not tested in this study.

Habitat specificity of ant species

Overall, we found lower ant habitat specificity, which further decreased in response to the degree of habitat disturbance. The same pattern was found by Tylianakis et al. (2005) for

Table 3. Additive partitioning of $\beta$-diversity. $\beta$-diversity ($\beta_{\text{add}}$) partitioning in its spatial turnover ($\beta_{\text{num}}$) and nestedness ($\beta_{\text{res}}$) components at the plot scale for forest, shade coffee and sun coffee, in a Colombian coffee landscape.

| $\beta$-diversity | Absolute value | Percentage of overall $\beta$ |
|-------------------|----------------|-----------------------------|
| **Forest**        |                |                             |
| $\beta_{\text{num}}$ | 0.978          | 100                         |
| $\beta_{\text{res}}$ | 0.975          | 99.72                       |
| $\beta_{\text{res}}$ | 0.003          | 0.28                        |
| **Shade coffee**  |                |                             |
| $\beta_{\text{num}}$ | 0.976          | 100                         |
| $\beta_{\text{res}}$ | 0.969          | 99.31                       |
| $\beta_{\text{res}}$ | 0.007          | 0.69                        |
| **Sun coffee**    |                |                             |
| $\beta_{\text{num}}$ | 0.985          | 100                         |
| $\beta_{\text{res}}$ | 0.984          | 99.82                       |
| $\beta_{\text{res}}$ | 0.002          | 0.18                        |
Hymenoptera in a coffee landscape in Ecuador, where low community differentiation found inside plots (\(\beta_{\text{plots}}\)) suggested a considerable overlap in community composition at this scale, rather than high complementarity. The lack of habitat specificity might be enhanced by the fact that we used tuna baits to specifically capture omnivore/predator ants foraging on coffee branches. Tuna attracted several competitively dominant ants (i.e. Linepithema spp., Pheidole spp, Solenopsis spp, Wasmannia auropunctata) that might have been able to displace specialised predator species foraging on the bait after 2 h of exposure (Perfecto & Vandermeer, 1996; Philpott et al., 2006; Ramírez et al., 2010). Although in sun coffee plots, species-specificity decreased as the proportion of forest border increased (read below).

**Effect of forest vegetation in the surrounding landscape**

Contrary to our second hypothesis, the proportion of plot perimeter bordering forest vegetation affected neither \(\alpha\) nor \(\beta\)-diversity, suggesting that ants foraging in coffee branches might not have been spilling over from the forest to the coffee plots. Nevertheless, species-specificity decreased in sun coffee plots as the proportion of forest border increased. Furthermore, a higher amount of forested area around sun coffee was related to a reduction in the abundance of some habitat specialist species (like the very abundant Linepithema neotropicum and Linepithema sp1), while other species (i.e. Solenopsis sp.1) showed the opposite trend. These results suggest a role of the surrounding landscape in determining the identity and the local assemblage of ant species in coffee plots (Tscharntke et al., 2005), rather than augmenting the number of species. Increasing the amount of forested areas bordering sun coffee plantations might help to reduce the dominance of sun-coffee specialists, stressing the importance of natural habitat for functional diversification of natural enemies into coffee plantations. Nevertheless, in order to better understand the role of landscape on CBB biocontrol, sampling artefacts need to be discarded, and other relevant variables describing configurational (i.e. average patch size) and compositional heterogeneity (i.e. diversity of land cover types) of the surrounding landscape could be assessed.

| Table 4. Mean habitat specificity of ant species in the study plots in response to land-use type and the amount of forest bordering the study plots. |
|---------------------------------|-------|-------|-------|
|                                | Estimate | SE    | t     | P     |
| (Intercept = Forest)           | 0.141   | 0.036 | 3.901 | 0.008*** |
| Forest border                   | 0.395   | 0.161 | 2.452 | 0.05*  |
| Shaded coffee                   | −0.056  | 0.064 | −0.878| 0.414  |
| Sun coffee                      | −0.007  | 0.052 | −0.136| 0.896  |
| Forest border × Shaded coffee   | −0.141  | 0.261 | −0.543| 0.607  |
| Forest border × Sun coffee      | −0.547  | 0.2   | −2.738| 0.034* |

The \(P\) values are presented, with those between 1% and 5% highlighted by an asterisk (statistically significant) and those less than 1% highlighted by three asterisks (highly statistically significant).
Species diversity and community differentiation of omnivore/predator ants foraging on coffee foliage did respond above the mesoscale (i.e. above plot-level). The diversity needed for conservation biocontrol in coffee landscapes might occur where patch heterogeneity at larger spatial scales is high, as suggested by Tscharntke et al. (2007). Loss of forest and tree cover at landscape scales leads to biotic homogenisation (Karp et al., 2012; Gámez-Virués et al., 2015) of the regional pool of ants, potential CBB biocots. Keeping landscape heterogeneity, preserving forest fragments and reforesting coffee farms would help to preserve regional taxonomic and functional ant diversity and – eventually – CBB biocontrol services. To understand how bordering forest affects – and might help to enhance – CBB biocontrol by ants in coffee plots, we need to experiment and investigate further. In conclusion, landscape-wide ant richness, associated with higher potential response diversity, is important in terms of biological CBB biocontrol.

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Conflict of interest
The authors confirm that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications or opinions stated.

Data Availability Statement
The data sets used and/or analysed during the current study are available from the corresponding author on reasonable request.

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

Appendix S1. Supporting Information.

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