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Local and landscape habitat influences on bee diversity in agricultural landscapes in Anolaima, Colombia

Marcela Cely-Santos[1] · Stacy M. Philpott[1]

Abstract

Agricultural intensification drives biodiversity loss and is associated with bee declines. Bees are highly sensitive to environmental change, and while their diversity declines in simplified habitats distant from undisturbed areas, bees respond to agricultural practices and habitat configuration at different scales. Mountainous tropical agroecosystems are highly heterogeneous at local and landscape scales, and the responses of bee communities to environmental change in these regions are still underexplored. We examined the local and landscape habitat factors influencing bee abundance and diversity, and changes in bee generic and tribe composition in Anolaima, Colombia. We surveyed bees, measured local habitat features such as flower abundance, tree diversity, ground cover and vegetation structure, and evaluated land cover types and landscape characteristics in seventeen farms. We found that elevation, vertical structure of the vegetation and landscape structure influenced bee community structure. While local factors predicted the response of most individual bee groups, landscape factors influenced the abundance of *Apis* and *Trigona*, two genera with disproportionately high abundances across study sites. We also found that human constructions serve as refuges for several bee genera. Our paper suggests a process of biotic homogenization with the loss of bee diversity and concurrent spread of *Apis* and *Trigona* in landscapes dominated by pastures, unshaded crops or eroded soils. We also highlight the high sensitivity of native bees to habitat configuration and disturbance, and the importance of traditional farming systems for the conservation of bee communities in mountainous tropical agroecosystems.

Keywords Biotic homogenization · Land-use change · Tropical agroecosystems · Community composition · Hymenoptera

Introduction

Most land use change is associated with the expansion of croplands, habitat loss and fragmentation, and biodiversity declines (Grau et al. 2013; Green et al. 2005; Lambin et al. 2013; Tilman et al. 2011). Currently, agricultural land conversion is concentrated in the tropics (Gibbs et al. 2010; Meyfroidt et al. 2010), raising important global concerns for biodiversity in centers of biological diversification (Laurance et al. 2014). Agricultural intensification and changes in the management within farms may exacerbate the impacts of land use conversion for biodiversity (Flynn et al. 2009; Mogren et al. 2016; Tscharntke et al. 2005). Thus, factors acting at multiple spatial scales (within farm vs. across landscapes) may have strong impacts on diversity and alter processes structuring biotic communities (Tscharntke et al. 2005, 2012).

Yet, the effects of environmental change on community composition are not random (Gámez-Virués et al. 2015; McKinney and Lockwood 1999; Tylianakis et al. 2008). Changes in biotic communities depend on the responses of different species to the magnitude, frequency, and spatial patterns of disturbance (Betts et al. 2014; De Palma et al. 2015; Williams et al. 2010). With environmental change, communities can undergo biological homogenization whereby susceptible species experience range contraction or are lost from a regional pool of species, and tolerant species grow in abundance and range (Gámez-Virués et al. 2015; McKinney and Lockwood 1999; Olden et al. 2004). These non-random changes can affect ecosystem functioning, with

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important implications for the provisioning of ecosystem services (Suding et al. 2008; Zavaleta et al. 2009).

Bees provide pollination services to crops and perpetuate wild plant communities, but are highly sensitive to environmental change. Most tropical crop (> 85%) and wild (> 95%) plant species require or benefit from visits by bees for successful reproduction, and receive greater benefits from diverse bee communities (Hoehn et al. 2008; Klein et al. 2003; Martins 2013; Motzke et al. 2016; Rosso-Londoño 2008; Roubik 1995). Composition of bee communities is affected by land use modifications at both local and landscape scales (Brosi et al. 2007a, b; Kennedy et al. 2013; Kremen et al. 2002; Mandelik et al. 2012). Bee diversity increases with flowering plant diversity and nest site availability (i.e., bare soils, mature wood) (Kennedy et al. 2013; Quistberg et al. 2016; Torné-Noguera et al. 2014), while agricultural practices such as tillage, sowing and pesticide use diminish resources and negatively affect bees (Kohler and Triebskorn 2013; Potts et al. 2010; van der Sluijs et al. 2013). At the landscape scale, land use diversity, connectivity and proximity to undisturbed forest fragments benefits bees (Basu et al. 2016; Brosi et al. 2007; Carré et al. 2009; Klein 2009; Quistberg et al. 2016). Local factors impact bee community composition more in simple landscapes, compared with highly diverse landscapes (Kremen et al. 2002; Steffan-Dewenter et al. 2002; Tscharntke et al. 2005). Furthermore, impacts differ with bee identity, with specialist and low-dispersal ability species being more strongly affected by intensification and fragmentation compared with generalist, social, and high-dispersal ability species such as *Apis mellifera* (Brosi et al. 2007a, b; Jha and Vandermeer 2009; Rader et al. 2014).

Most research evaluating how local and landscape factors influence patterns of bee diversity in agricultural landscapes focuses on temperate latitudes, where farms tend to be large (> 10 ha) and homogeneous (Holzschuh et al. 2008; Kremen et al. 2004; Steffan-Dewenter et al. 2002). However, agricultural fields in tropical mountains are heterogeneous over short distances and are nested within a matrix of high levels of plant endemism, which influences insect distribution and diversity. Effects of habitat configuration on the composition of bee communities have been explored in Central America (Garibaldi et al. 2016; Klein et al. 2002; Brosi et al. 2007a, b; Badano and Vergara 2011), yet are underexplored in the Andes (but see Gutiérrez-Chacón et al. 2018). Crop fields in this region are mainly visited by wild native bees but some of these bee species have narrow home ranges or are restricted to use certain habitat types, making them additionally susceptible to local land use change (Molau 2004; Larsen et al. 2018; Gill et al. 2016; Zhang et al. 2016). Therefore, understanding how local and landscape factors affect bees in tropical montane agroecosystems is important for designing conservation strategies in

areas with high dependence on wild bees. In this study, we ask how differences in local habitat structure and landscape configuration affect bee communities across an Andean agricultural landscape in Anolaima, Colombia. We asked (1) Which local and landscape factors influence bee abundance and diversity (generic richness, evenness and dominance)? (2) Which local and landscape factors drive dissimilarities in generic and tribe abundance and composition across farms? and (3) Is the availability of different land use types associated with generic richness and abundance of different bee tribes? We predicted that (1) both local and landscape factors would influence bee abundance and diversity; (2) local factors would have greater influence on dissimilarity of bee community composition, compared with landscape factors; and (3) bee generic richness and abundance of specific tribes would vary depending on the availability of different land use types.

Methods

Study site

We conducted this study in Anolaima, in the eastern slope of Andes mountains in Colombia (Fig. 1). This municipality extends between 900 and 2800 m.a.s.l., with an average elevation of 1650 m.a.s.l. Most lands in the municipality have steep slopes (50% or higher). The traditional precipitation regime is bimodal, with marked dry seasons between Dec–Mar and Jul–Sept, mean annual precipitation of 1232 mm, and average relative humidity between 70% (dry seasons) and 80% (rainy seasons). Life zones in the municipality transition between cloud-submontane forest and tropical dry forest, but most land cover is in cattle ranching (41.6% of total area) and cropland (19.3%). Coffee is the most extensive crop covering 10% of the total area. Small farms (< 5 ha) represent 92.6% of private landholdings in the area and cover 53% of land area in the municipality (EOT 2016).

We worked in seventeen farms between 1230 and 1870 m.a.s.l. Farms were separated by a minimum of 2 km and were chosen to represent the full range of agricultural management types present in Anolaima. Land uses included secondary forests; agroforests (e.g., shaded coffee and cacao intercropped with native and fruit trees); shaded crops with simplified shade (coffee intercropped with plantain); unshaded staple crops (e.g., sugar cane, and diversified crops grown for self-consumption); conventional unshaded short-cycle cash crops; fallow lands or unmanaged areas undergoing natural regeneration; and pastures. Permanent shaded crops (e.g., coffee, cacao) and unshaded staple crops grown for self-consumption are managed in traditional diversified systems seldom treated with synthetic biocides. In contrast,
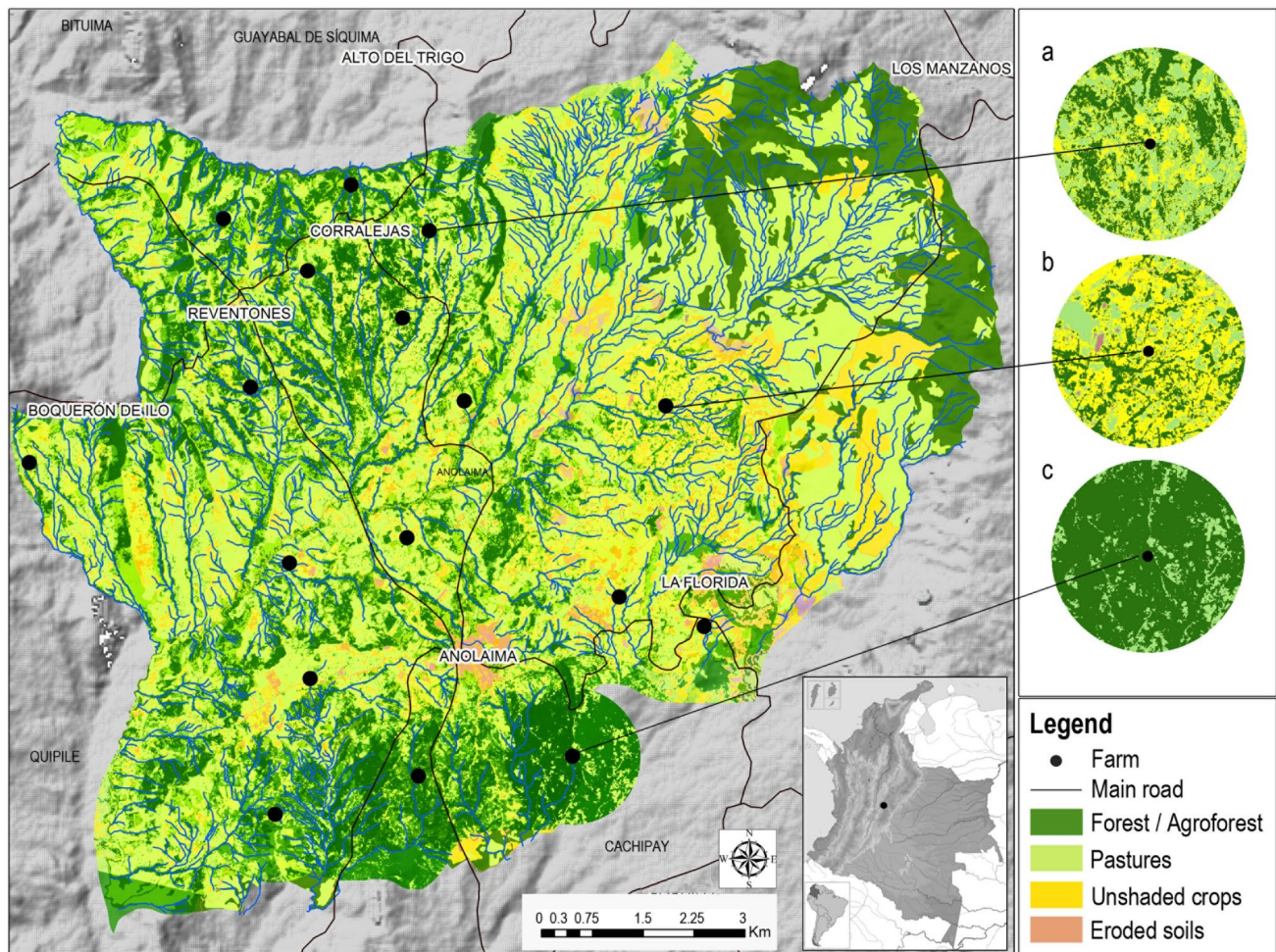
Fig. 1 Map of Anolaima showing the seventeen study sites and land cover types in the study region. Panels show farms surrounded primarily by pastures (a), unshaded crops (b) and forest or agroforests (c)

conventional unshaded cash crops are monocultures or polycultures intensively managed with synthetic biocides and with short fallow periods. Because of the average farm size (1.5 ha), monocropping seldom extends over large areas (Alcaldía Municipal de Anolaima 2016).

Experimental design

We sampled bees and measured local and landscape habitat features for each study farm. To survey bees and vegetation, we established a 1-ha plot centered on a random point within each farm and divided it into sixteen 25 m × 25 m quadrants (Fig. 2). We classified land use types and measured canopy cover in each 25 m × 25 m quadrant. Within each quadrant, we established four random 2 m × 2 m sub-plots, 64 in total per farm, in which we measured ground cover and flower abundance. In addition, we established a 200 m-radius circle around the center of the 1-ha plot and divided it into six wedges. In each wedge we randomly established a

15 m × 15 m plot in which we measured arboreal vegetation. We conducted landscape analyses within circles of 200 m, 500 m and 1 km radii around the 1-ha plot.

Bee sampling

We surveyed bees with aerial nets and observations. We enumerated and consecutively walked each 25 m × 25 m quadrant during 10 min., and we netted bees seen flying or on flowers between 0 and 3 m above ground. We surveyed all quadrants four times during the same day to account for potential variation in the time of activity of different bee species, for a total of 40 min. per quadrant and 10.6 h of sampling per farm. Thus, sample effort was equal for each farm. We netted all bees except *Apis*, *Trigona* (cf. *amalthea* and *fulviventris*), *Tetragonisca* and *Eulaema* that we identified and counted in the field. To account for the influence of floral availability and land use types on bee abundance and diversity, we counted flowers within four random 2 m × 2 m

Fig. 2 Diagram of the experimental design of the study. We analyzed land cover types at the landscape scale sampled at 200 m, 500 m, and 1000 m scales surrounding the center of the 1-ha plot (a). Local factors included arboreal vegetation sampled within 15 m × 15 m plots in 200 m circles centered on the 1-ha plot (b); ground cover sampled within 25 m × 25 m quadrants in the 1-ha plot (c); and herbaceous vegetation sampled within four 2 m × 2 m mini-plots on each 25 m × 25 m quadrant (d). We surveyed bees within each of the 25 m × 25 m quadrants, and bee data was aggregated at the 1-ha plot (c)
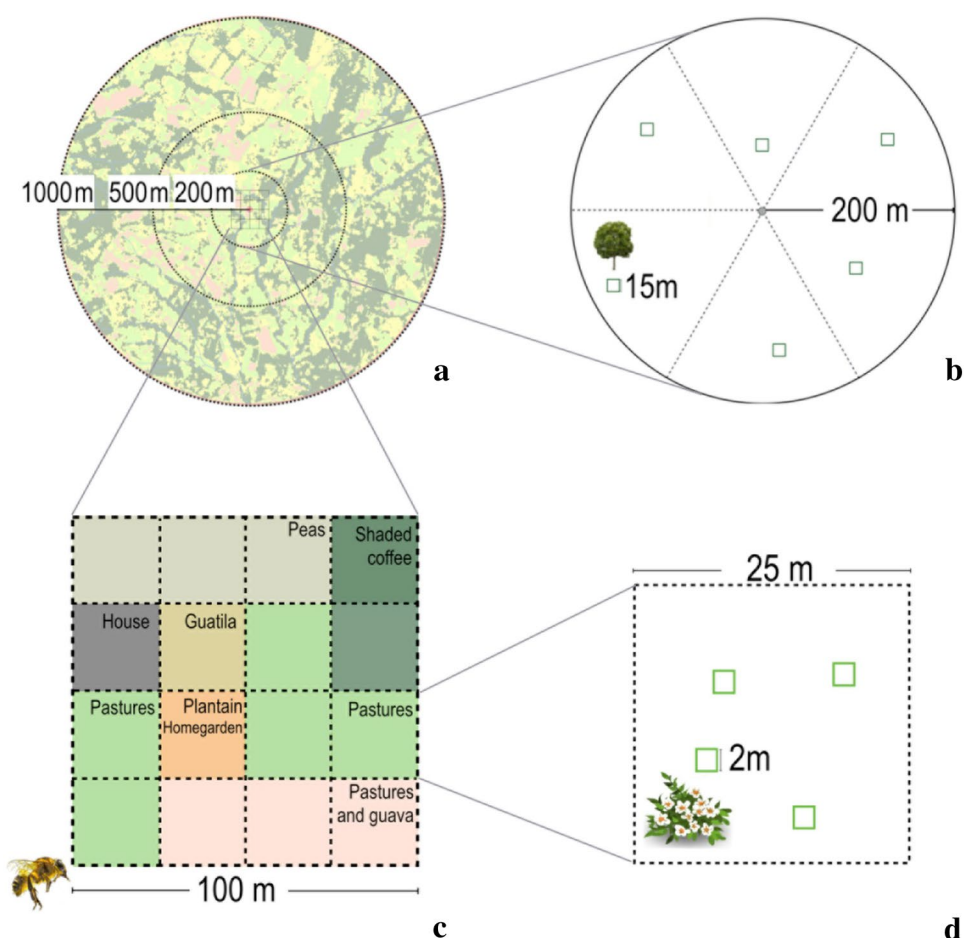
sub-plots established within each 25 m × 25 m quadrant and registered the type of land use in which we sampled each bee. Collected bees were pinned and deposited at the Laboratorio de Abejas in Universidad Nacional de Colombia. We determined bees using identification keys for bees in Colombia, Panama and Brazil (Camargo et al. 2007; Michener 2000; Moure 2008; Nates-Parra 2001); some bees were identified only to genus (Meliponini, Halictidae, Megachilidae) due to problematic keys for species level identification. We sampled bees in the dry (Feb–March) and wet seasons (Jul–Aug) of 2016. Bee sampling took place between 7 AM and 2 PM on sunny days with low wind speed and no rain.

Local and landscape vegetation sampling

We measured local vegetation features within 2 m × 2 m subplots, 25 m × 25 m quadrants and 15 m × 15 m plots on each farm. Within each 2 m × 2 m sub-plot we estimated ground cover (percent of pasture, herbs, rocks, leaf-litter, mulch, and bare soil), measured height of the tallest herbaceous vegetation, and counted flowers on herbs and shrubs. Within 25 m × 25 m quadrants we counted flowering trees, and measured canopy cover with a concave spherical

densitometer by averaging measurements at the center, and 10 m to the east, west, north and south of the quadrant center. We observed and registered the land use of each 25 m × 25 m quadrant and then grouped them in one of seven categories: (1) forest/agroforest; (2) crops with simplified shade; (3) unshaded crops with traditional management; (4) fallowed lands; (5) pastures; (6) unshaded crops with conventional management; (7) constructions (e.g., buildings, sheds); and (8) border of roads. We registered the intensity of agricultural management as an index ranging from 1 to 10 (10 representing low-impact management) based on the percent of 25 m × 25 m quadrants with unshaded crops managed conventionally on each farm, the frequency at which farmers sprayed agrochemicals, and soil-preparation practices. We collected site data on the same days we collected bees in each site. Within each 15 m × 15 m plot, we estimated the vertical structure of the vegetation (percent of the vegetation reaching 1 m, 1–3 m, 3–5 m, > 5 m height), counted trees (> 5 cm DBH), and registered tree morpho-species, tree height, and tree diameter at breast height (DBH). We measured trees and the vertical structure of the canopy between Jun–Aug 2015.

We analyzed landscape configuration and composition with SPOT satellite images and digitalized aerial photographs from Instituto Geográfico Agustín Codazzi. To estimate landscape composition, we classified images and created four land cover categories: (1) complex habitat (agroforest, secondary and primary forest); (2) unshaded crops; (3) pastures; and (4) eroded soils. Land cover category percentages were calculated within 200 m, 500 m and 1000 m of the center of each farm. We also calculated the nearest distance from the center of the bee survey plot to complex habitat, unshaded crops, and to water. We conducted these analyses in ArcGis 10.3.

Data analysis

We selected 13 response variables for inclusion in model analysis: five bee abundance variables, six bee diversity variables, and two community similarity variables. Although our initial intent was to sample in two seasons, weather during the survey year was erratic making this logistically difficult. Nonetheless, separate analysis by season revealed that similar factors influenced bee richness and abundance in the two seasons, thus we aggregated bee data from both seasons at the farm scale (e.g., 1-ha plot) for all analyses. For abundance, we used total bee abundance, partial abundance after excluding the two most common genera, and abundance of the three most common tribes (Apini, Meliponini and Augochlorini). For bee diversity we used estimators of bee richness, evenness and dominance including and excluding the two most common genera. We calculated these estimators using rarefied Hill numbers, which convert basic diversity measures to "effective number of species" numbers that obey a duplication principle. We calculated Hill numbers at three different orders (q) of diversity. Order q = 0 (^0D) is equal to species richness, giving more weight to rare species; when q = 1 (^1D) the weight of each species is based on its relative abundance; and when q = 2 (^2D) abundant species have a higher weight in the community (Chao and Jost 2012). We used ^0D numbers as estimators of richness, the Hill estimator of evenness (q1:0 = $^0D/^1D$), and the Hill inequality factor (q2:0 = $^0D/^2D$) as estimator of dominance (Jost 2010). Because sample size differed across farms, we rarefied Hill numbers at q = 0, q = 1 and q = 2 to assemblages of 72 individuals with all genera, and to 31 individuals for analysis without the two most common genera. We calculated rarefied Hill numbers with the iNEXT package (Hsieh et al. 2016) and plotted diversity profiles using the Entropart package (Marcon and Hérault 2015). For community similarity, we used the axis 1 of a non-metric multidimensional scaling (NMDS) analysis based on Bray-Curtis similarity for bee genera and for bee tribes.

We used 13 explanatory variables in our models (Table S1). To select explanatory variables for analyses, we grouped 22 local factors (measured within 25 m × 25 m quadrants, 15 m × 15 m plots, and 2 m × 2 m sub-plots) and 15 landscape features (factors measured within 200 m, 500 m and 1000 m around farms) and ran Pearson's correlations within each group. We identified 11 non-correlated variables, 6 local factors (flower abundance; % bare soil cover; max. height of non-arboreal vegetation; % canopy cover; tree height; % vegetation 1–3 m) and 5 landscape factors (% unshaded crop cover; % pasture cover; distance to nearest unshaded crops, complex habitat, and to nearest water source), and used them in our models (Table S2). Two variables (e.g., management and elevation) did not fit within any group and were also included. Two other variables (mulch cover and percentage of eroded soils at 1 km landscape buffer) had high numbers of zeros and were excluded (Table S1). Before conducting analyses we ran Mantel tests to test for potential autocorrelations between location, elevation, and local and landscape factors, and found no significant autocorrelations among those variables chosen for analysis.

To test whether local and landscape factors influence bee response variables, we ran generalized linear models (GLM) and multi-model selection (Burnham and Anderson 2004) using the glmulti package (Calcagno and de Mazancourt 2010) in R (R Development Core Team 2014). We used a Gaussian error distribution for all models. We tested the fit of different statistical models including all combinations of explanatory factors, compared conditional Akaike Information Criterion (AICc) values (recommended for small sample sizes), and selected the model with the lowest AICc as the best model. If other models were within 2 AICc points of best models, we used the MuMIn package to run average models of up to the top 10 models (Bartoń 2013). For each GLM we report model factors included in the best or averaged models with their corresponding estimated effect (β), standard error (SE), t-values in non-averaged models and z-values for averaged models, and significance (p-values). For best models, we present the AICc values, degrees of freedom (*df*) and pseudo coefficients of determination (R^2). For averaged models, we report AICc models and weights for all models within 2 AICc points of the best model in the supplementary material (Table S3). To test whether explanatory factors influenced community similarity, we ran a permutational multivariate analysis of variance on bee genera and tribe similarity matrices using the R vegan package, for which we report f values, degrees of freedom, and coefficients of determination (R^2) (Dixon 2003).

To evaluate whether the availability of land use types influenced bee abundance and diversity, we ran Pearson's Chi square tests of independence. We tested whether the frequency of occurrence of each land use type (number of 25 m × 25 m quadrants) across study sites was associated with the number of (1) captured bees, (2) abundance of the

three most common bee tribes, (3) bee genera, and (4) bee tribes. All analyses were conducted in R.

Results

We surveyed 3290 bees from 57 genera, 23 tribes, 8 subfamilies, and all five families reported for Colombia. We captured 1512 bees, and visually sampled 1778 bees. The most abundant genus was *Apis* (38.26% of individuals) followed by *Trigona* (cf. *amalthea* and cf. *fulviventris*) (24.79%); of other genera surveyed, 50 represented fewer than 5% of individuals surveyed (Fig. S1). The most abundant tribes were Meliponini ($n = 1515$), Apini ($n = 1573$) and Augochlorini ($n = 99$). Diversity profiles showed large drops in the effective number of genera as the order of diversity (q) increased indicating high levels of dominance in local bee assemblages (Fig. S2).

Influence of local and landscape factors on bee abundance and diversity

Bee abundance varied with local and landscape factors. Total bee abundance increased with flower abundance ($\beta = 2.3 \times 10^{-4}$, SE $= 6.29 \times 10^{-5}$, t $= 3.652$, P $= 0.002$), unshaded crop cover within 1 km ($\beta = 0.759$, SE $= 0.246$, t $= 3.082$, P $= 0.009$), and with elevation ($\beta = 0.001$,

SE $= 5.29 \times 10^{-4}$, t $= 2.670$, P $= 0.019$) (AICc $= 16.24$, df $= 13$, $R^2 = 0.69$, Fig. 3). Bee abundance without the two most abundant genera, *Apis* and *Trigona*, increased with flower abundance and marginally decreased with pasture cover within 1 km (Table 1). Number of Apini (i.e., *Apis*) bees increased with flower abundance ($\beta = 0.039$, SE $= 0.014$, t $= 2.80$, P $= 0.015$), tree cover ($\beta = 2.050$, SE $= 0.559$, t $= 3.66$, P $= 0.003$), elevation ($\beta = 0.523$, SE $= 124$, t $= 4.20$, P $= 0.001$), and intensive agricultural management ($\beta = -41.408$, SE $= 11.038$, t $= -3.75$, P $= 0.002$) (AICc $= 197.16$, df $= 12$, $R^2 = 0.77$). While the total number of Meliponini individuals marginally increased with maximum height of non-arboreal vegetation, *Trigona* abundance increased with elevation and with vegetation between 1 and 3 m. Augochlorini abundance increased with flower abundance, decreased with vegetation between 1 and 3 m, and marginally decreased with pasture cover within 1 km (Table 1).

Bee diversity (richness, evenness, and dominance) varied with local and landscape factors. Bee richness (^{0}D) decreased with elevation ($\beta = -0.025$, SE $= 0.003$, t $= -6.406$, P < 0.001) and vegetation between 1 and 3 m ($\beta = -18.063$, SE $= 7.820$, t $= -2.31$, P < 0.001), but did not vary with unshaded crop cover within 1 km ($\beta = 2.986$, SE $= 2.158$, t $= 1.384$, P $= 0.189$) (AICc $= 84.84$, df $= 13$, $R^2 = 0.76$, Fig. 4). When we excluded the two most abundant genera, *Apis* and *Trigona*, partial bee richness decreased
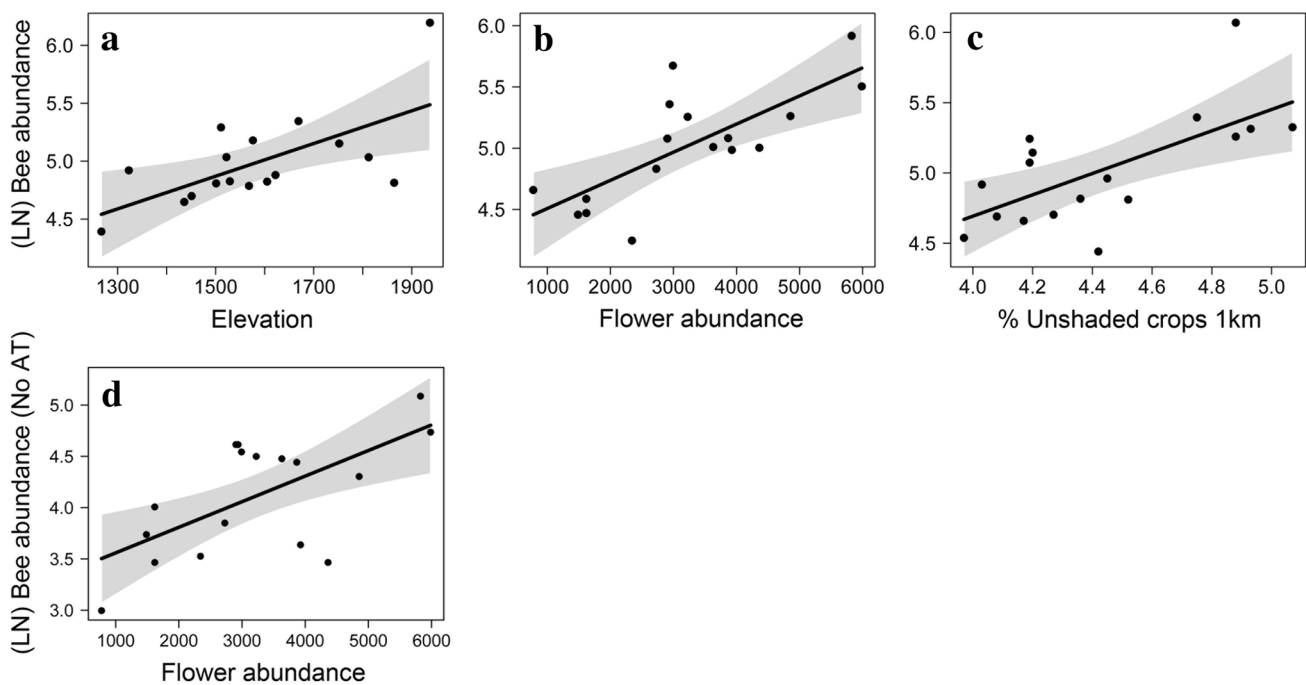

Fig. 3 Local and landscape drivers of bee abundance in agroecosystems in Anolaima. Panels represent the drivers of bee abundance including all bees (**a–c**) and excluding the two most abundant genera (*Apis* and *Trigona*) (**d**), as a function of elevation (m.a.s.l) (**a**), flower abundance in 2 m × 2 m plots (local factor) (**b, d**), and the % of unshaded crops in 1 km landscape buffers (landscape factor) (**c**)

Table 1 General linear models (GLM) predicting bee abundance, richness and evenness of local bee assemblages after excluding the two most abundant genera, *Apis* and *Trigona;* and GLMs predicting abundance of tribes Meliponini and Augochlorini, and of the genus *Trigona*

Dependent variable	Predictors included in averaged GLM model	β	SE (adj)	z	P
Abundance (no *Apis—Trigona*)	Flower abundance	*0.017*	*0.006*	*2.965*	*0.003*
	% pasture cover within 1 km	− 0.442	0.252	1.752	0.080
	Tree cover	0.311	0.205	1.516	0.129
	Height of non-arboreal vegetation	0.163	0.105	1.549	0.121
	Elevation	− 0.062	0.048	1.290	0.197
	Distance to complex forest/agroforest	11.841	7.673	1.543	0.123
Richness (no *Apis—Trigona*)	Tree cover	*− 0.023*	*0.010*	*2.373*	*0.018*
	% vegetation 1–3 m	*− 14.123*	*4.594*	*3.074*	*0.002*
	Elevation	*− 0.005*	*0.003*	*2.153*	*0.031*
Evenness (no *Apis—Trigona*)	Flower abundance	*0.000*	*0.000*	*2.801*	*0.005*
	Tree cover	*0.002*	*0.001*	*2.948*	*0.003*
	% bare soil	− 0.002	0.001	1.539	0.124
	% vegetation 1–3m	0.500	0.368	1.357	0.175
Meliponini abundance	Height of non-arboreal vegetation	0.239	0.130	1.847	0.065
	% unshaded crops within 1 km	8.938	6.492	1.377	0.169
	Distance to complex forest/agroforest	33.295	30.456	1.093	0.274
Trigona abundance	% vegetation 1–3 m	*159.800*	*65.220*	*2.618*	*0.012*
	Elevation	*0.111*	*0.036*	*3.106*	*0.002*
	Height of non-arboreal vegetation	0.102	0.076	1.345	0.179
	Flower abundance	0.006	0.005	1.219	0.223
Augochlorini abundance	Flower abundance	*0.003*	*0.001*	*2.605*	*0.009*
	% pasture cover within 1 km	− 0.075	0.043	1.745	0.081
	Elevation	− 0.017	0.013	1.310	0.190
	Tree cover	0.033	0.028	1.188	0.232
	% vegetation 1–3 m	*− 35.980*	*12.680*	*2.837*	*0.005*
	Agricultural management	*− 1.407*	*0.594*	*2.370*	*0.018*

Italic values estimates for predictors with statistical significance (P ≤ 0.05)

β estimated effect or standardized slope, *SE (adj)* adjusted standard error

with elevation, tree cover, and vegetation between 1 and 3 m (Table 1). Evenness ($^1D/^0D$) decreased with elevation (β=− 2.66×10^{-4}, SE = 9.29×10^{-5}, t = − 2.860, P = 0.012) and with increased unshaded crop cover within 1 km (β = − 0.109, SE = 0.048, t = − 2.258, P = 0.040) (AICc = − 39.86, df = 14, R^2 = 0.55, Fig. 5). Dominance ($^2D/^0D$) decreased with the maximum height of non-arboreal vegetation (β = − 0.001, SE = 0.001, t = − 3.379, P = 0.004) and increased with unshaded crop cover within 1 km (β = 0.149, SE = 0.041, t = 3.664, P = 0.002) (AICc = − 45.012, df = 14, R^2 = 0.63).

Changes in the composition of bee communities

Generic similarity was explained by elevation (F = 3.34, R^2 = 0.17, P = 0.02) and flower abundance (F = 2.49, R^2 = 0.12, P = 0.05). Tribe similarity was also explained by elevation (F = 5.67, R^2 = 0.21, P = 0.007) and, marginally, by flower abundance (F = 2.82, R^2 = 0.10, P = 0.07).

Influence of land uses on bee abundance and richness

The number of available units of each land use across farms was not independent from the number of bees (χ^2 = 122.53, df = 7, P < 0.001), number of genera (χ^2 = 59.66, df = 7, P < 0.001), or number of tribes (χ^2 = 35.277, df = 7, P < 0.001) captured on different land uses. Generic and tribe richness were higher in fallow lands, constructions and borders of roads; and lower in forest-agroforests and in unshaded crops under conventional management (Table 2). Bee abundance of the three most common tribes changed across land use types (χ^2 = 5874, df = 7, P < 0.001). Representation of Meliponini was the highest across land uses, followed by Apini (17% of individuals ± 32%) and Augochlorini (2% ± 3%) (Fig. 6). Apini was the most abundant in conventionally managed crops (73%) and in crops with simplified shade (37%). Augochlorini abundance, as well as the abundance of other bee tribes, was highest in areas
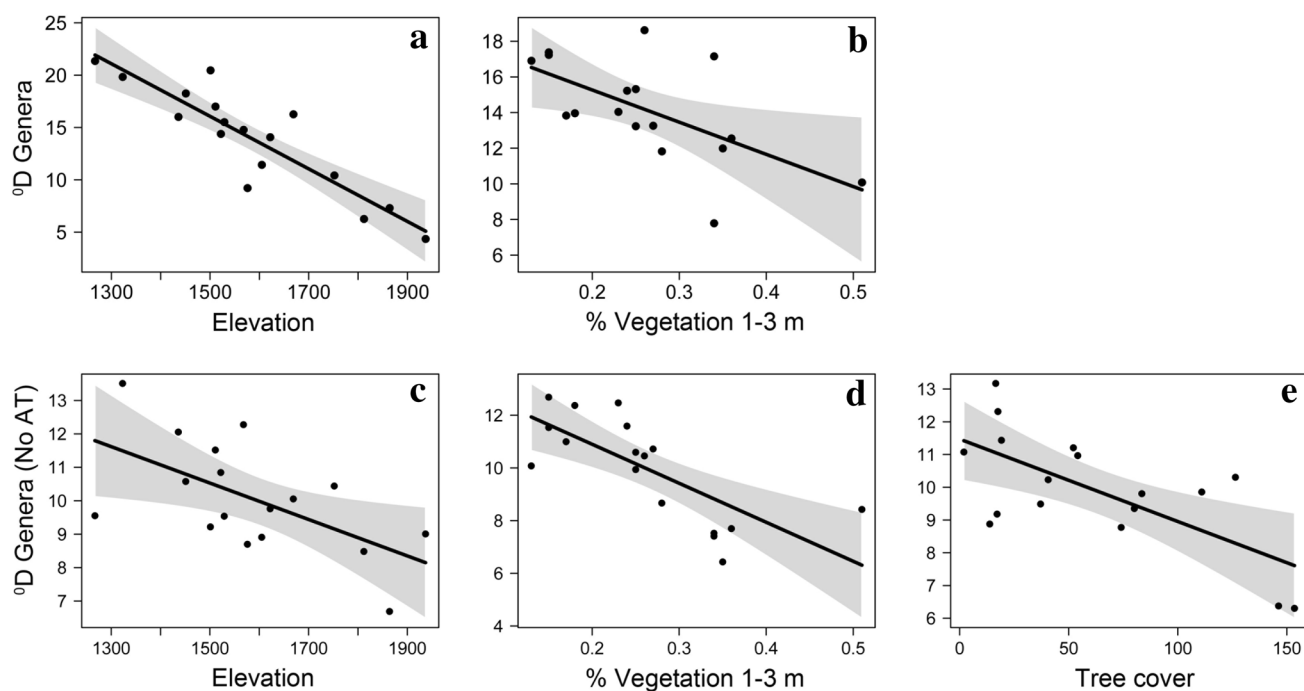
Fig. 4 Local and landscape drivers of bee richness in agroecosystems in Anolaima. Panels represent the drivers of bee generic richness including all bees (**a, b**) and excluding the two most abundant genera (*Apis* and *Trigona*) (**c–e**), as a function of elevation (m.a.s.l) (**a**), the % of vegetation between 1 and 3 m (middle-low strata) (local factor) (**b, d**), and canopy cover in 25 × 25 quadrants (local factor) (**e**)

surrounding human constructions (7%) and in traditionally managed crops (6%).

Discussion

We present evidence for the effects of different local and landscape factors on bee abundance and diversity in agricultural lands in the Colombian Andes. Bee abundance and diversity were influenced by habitat factors including flower availability, elevation, and unshaded crop cover within 1 km. Contrary to our hypotheses, bee abundance decreased, although diversity increased, in farms with higher habitat complexity. Local factors greatly influenced individual bee groups, yet landscape factors were important at explaining the presence of two bee genera with disproportionate influence in the community: *Apis* and *Trigona*.

We first examined which local and landscape factors influenced bee abundance and diversity. In general, bee abundance was predicted by flower abundance and elevation. Our results coincide with other studies documenting a positive response of bee density to floral resources (Torné-Noguera et al. 2014), although we found that overall bee abundance in areas with high flower abundance was greatly influenced by abundance of *Apis* and *Trigona*. Other studies have documented the positive responses of *Apis* to the spatial aggregation of floral resources (Plascencia and Philpott

2017) and mass-flowering crops (Rader et al. 2009; Holzschuh et al. 2011, but see; Boreux et al. 2013). This trend may also be influenced by intraspecific interactions in the bee community. *Apis* and Meliponini are both social, generalist bees. Although there is resource partitioning among Meliponini species, *Apis* and Meliponini may share (and compete) for resources (Wilms et al. 1996). In fact, *Apis* prevents flower access for other species via interference or exploitative competition (Montero-Castaño et al. 2016; Wilms et al. 1996), as do *Trigona cf. amalthea* and *T. spinipes* (Breed et al. 2002; Nieh et al. 2005).Therefore, differential influence of flower abundance on different bee groups may be mediated by their competitive interactions with *Apis* and *Trigona* bees.

The specific factors influencing abundance of different bee groups may relate to species traits. For example, elevation strongly influenced *Apis* and *Trigona* abundance, but not abundance of other groups. Elevation, and associated changes in temperature, may influence species distributions based on their tolerance to cold environments (McCoy 1990; Rahbek 2004) and to climatic and other biophysical fluctuations (Hodkinson 2005). *Apis* and native *Trigona cf. amalthea* and *T. cf. fulviventris* have broad altitudinal and geographic ranges (Gonzalez and Engel 2004; González et al. 2005; Nates-Parra 2016), as well as high reproductive capacities (Roubik 2006), unlike other bees (Nates-Parra 2001). This combination of factors may partially explain
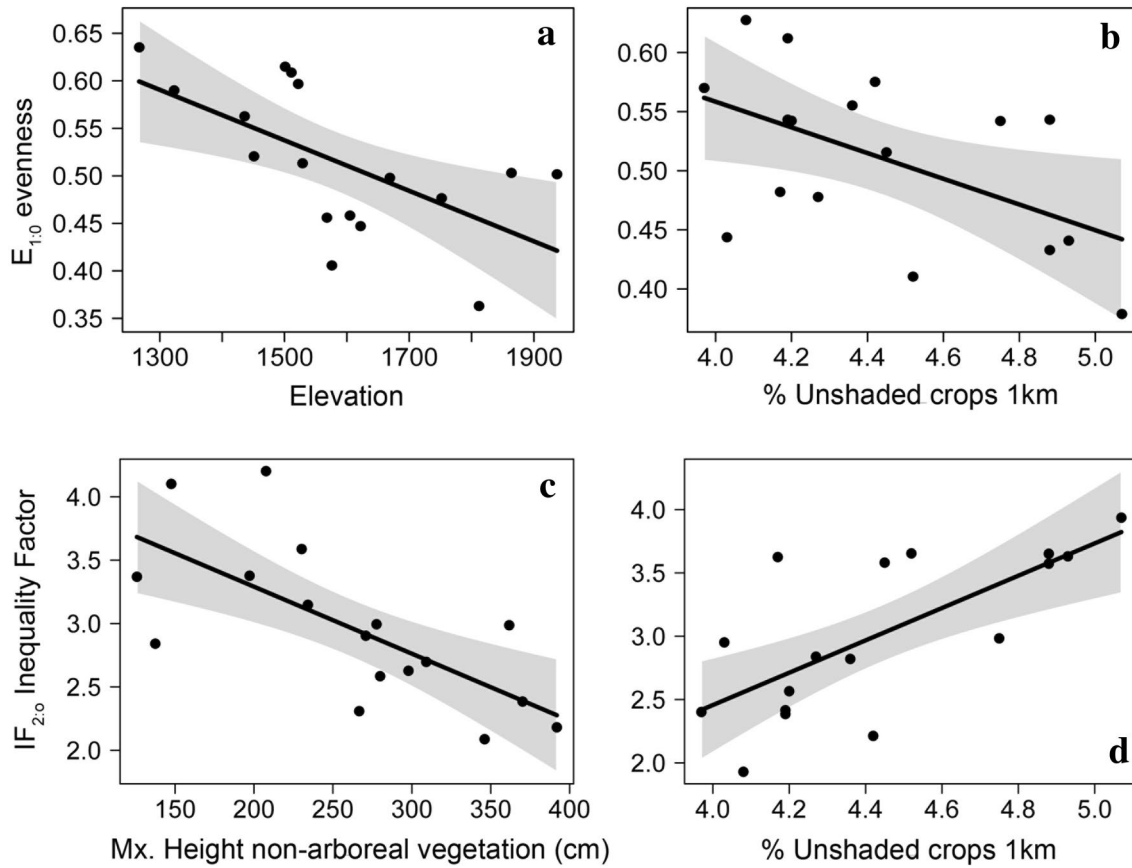
Fig. 5 Local and landscape drivers of bee evenness and dominance. Evenness corresponds to the ratio $^1D/^0D$ (relative abundance of species/richness) (**a, b**), and the inequity factor, an estimate of dominance within communities, corresponds the ratio $^2D/^0D$ (Simpsons' concentration index/richness) (**c, d**). The panels represent drivers of evenness or dominance as influenced by elevation (m.a.s.l) (**a**), the % of unshaded crops in 1 km landscape buffers (landscape factor) (**b, d**), and the maximum height of non-arboreal vegetation in 2 m×2 m subplots (local factor) (**c**)

Table 2 Bee generic and tribal richness across land use types

Land use type	Number of land units	Generic richness	Tribal richness	Genera/land units	Tribes/land units
Unshaded crops—conventional	129	17	8	0.13	0.06
Border of roads	69	30	15	0.43	0.22
Pastures	261	38	19	0.15	0.07
Constructions	79	34	15	0.43	0.19
Fallow lands	53	13	6	0.25	0.11
Unshaded crops—traditional	235	44	16	0.19	0.07
Simplified shade	88	20	9	0.23	0.10
Forest/agroforest	211	30	15	0.14	0.07

Values correspond to the number of different genera or tribes (richness) captured on the different land uses found across study sites. Number of land units corresponds to the total number of quadrants (25 m×25 m) on each land use type sampled across study sites

high abundance of *Apis* and *Trigona*. Similarly, abundance of Augochlorini decreased with pasture cover within 1 km, a factor inversely correlated with forest or agroforest cover, and increased with percent vegetation between 1 and 3 m.

Augochlorini are typically forest associated (Brosi et al. 2007a, b; Wcislo et al. 2003; Zillikens et al. 2001), are soil or wood nesters, and use flowering herbs and vines as feeding resources (Wilms et al. 1996). Hence, decreased
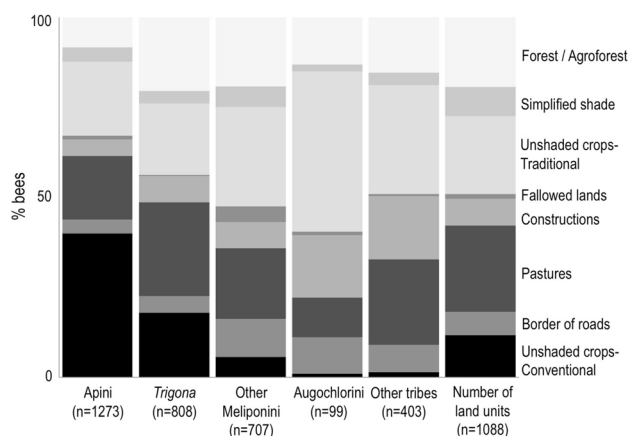
Fig. 6 Relative abundance of bee tribes in different land use types, and of land use types sampled across study sites within 25 m × 25 m quadrants

availability of nesting and food resources in pastures may explain abundance patterns for this tribe.

Bee richness and evenness decreased, and dominance increased, with unshaded crop cover at the landscape scale, a factor negatively correlated with complex habitat. Changes in dominance within communities are associated with availability of complex habitat at the landscape scale (Boreux et al. 2013; Brosi et al. 2007a, b; Jha and Vandermeer 2009), and can be explained by the negative responses of rare solitary species to landscape simplification (Brosi et al. 2007a, b; Carman and Jenkins 2016; Le Féon et al. 2013; Zurbuchen et al. 2010), and by the ability of some groups to equally use complex or simplified habitats. For example, *Apis* and *Trigona spinipes*, closely related to *T. cf. amalthea*, are hyper-generalist species that are often unaffected by environmental disturbance and persist in simplified lands unfavorable for other bees (Giannini et al. 2015; Magrach et al. 2017; Veddeler et al. 2006).

Bee richness and evenness were also predicted by elevation. We found fewer bee species at higher elevations, corroborating reports from other studies explained by the narrow thermal tolerance limits of many bee species (e.g., Potts et al. 2010; Rahbek 2004). We suspect, however, that the elevation response in this study may have interacted with disturbance and the simplification of land uses. Across our study sites the number of land units in pasture and conventional unshaded crops significantly increased at higher elevations, along with the percent of eroded soils within 1 km that marginally increased with elevation (Table S4). In this region eroded soils are associated with steep topography as well as cattle ranching—both that are concentrated in the highlands (EOT 2016). Further, farmers report that there is greater disturbance in the highlands because farms receive water from an irrigation

district (EOT 2016) enabling annual row crop production, not possible in the lowlands where water access is limited. Although we cannot differentiate effects of elevation, disturbance and landscape simplification, the combination of these factors may act as filters excluding species associated with forests and complex habitats (Gámez-Virués et al. 2015; Hopfenmuller et al. 2014) and favoring species with high tolerance to disturbance, which may explain the reduction of rare species and the dominance of *Apis* and *Trigona* bees in high elevations.

Bee richness was strongly influenced by vertical vegetation structure and flower abundance. At least one other study reported bee richness and abundance increased in low vegetational strata and decreased in areas with dense canopy cover (Smith-Pardo and Gonzalez 2007). Canopy density influences sunlight reaching the understory, and in turn, flowering of herbs (Holt 1995) and most likely bee activity along the vertical strata (Smith 1972). Although we did not quantify the effects of plant diversity on bee richness, areas with higher plant richness yield high bee richness (Fontaine et al. 2006; Gutiérrez-Chacón et al. 2018; Nicholls and Altieri 2012), which may also happen in Anolaima.

Our second research question addressed changes in bee community composition, which were influenced by elevation and flower abundance. This is consistent with the elevation-richness gradient we found, and may be explained by the distribution and degree of specialization of different bees in our study region. As elevation decreases, species have narrower ecological niches and distributions (Hodkinson 2005; Janzen 1967), and plant-pollinator interactions are more specialized (Rasmann et al. 2014). These trends along elevation gradients may also interact with negative effects of disturbance, thus the changes in community composition we found may indicate either genera turnover or differential loss of species along the altitudinal range, and great vulnerability of species with narrower and more specialized niches to be sort out of local communities in light of further environmental change.

Our final research question evaluated whether the availability of different land uses influenced diversity and abundance of bee genera and tribes. Current land uses in the region can be linked directly to local and landscape habitat factors and their influence on bees. In general, abundance and richness were higher in low-impact land uses, and in areas associated with human constructions. Unshaded traditional crops and fallow lands can have high floral abundance and diversity (Motzke et al. 2016), begetting bee richness in these land uses. We found nests of at least eight bee genera in human constructions and foraging on flower and medicinal gardens and on forbs surrounding houses. Constructions offer areas with favorable features for nest thermoregulation and unmanaged flowering plants may represent continuous floral resources. Thus, human resources may have inadvertent yet important positive impacts on bee populations and

could be used to target conservation measures in agricultural lands.

We did not find high bee abundance or richness in habitats with high structural complexity i.e., forest or coffee agroforests in the vertical strata we sampled (0–3 m above ground). In this region, coffee shrubs typically bloom synchronously only during 2 or 3 days a year and farmers manually exclude forbs, yielding an understory without continuous availability of floral resources for bees. However, flowering trees may offer feeding and nesting resources at the canopy level (Ulyshen et al. 2010). In shaded coffee agroforests in Mexico, flowering tree diversity benefits bee diversity and abundance of solitary bees (Fisher et al. 2017; Jha and Vandermeer 2010). Also, Nates-Parra et al. (2001) found living trees were the most frequent nesting substrate for stingless bees in eastern Colombia, and we frequently found Meliponini nests in *Inga* trees or in abandoned bird nests in coffee agroforests; other studies found Augochlorini nest in wood and epiphytes (Wcislo et al. 2003; Zillikens et al. 2001). Therefore, despite the understory of agroforests is not greatly used by bees, the canopy may offer important resources for bees in Anolaima. However, a dense canopy or the presence of high flowering resources distributed across the landscape may influence negatively the local provision of pollination services to coffee shrubs (Boreux et al. 2013). Thus, level of shade could be managed to provide resources for the bees, yet not abundantly during main harvest seasons to still allow for some local concentration of bees to pollinate crops in agroforests.

We also found that conventional crops (even at small scale) negatively affect bee richness. This region supports conventional monocrops and polycrops managed with high agrochemical use (e.g., carbofurans, organophosphates, chlorpyrifos and neonicotinoids, depending on the crop composition). Chlorpyrifos and neonicotinoids are systematically used twice a week on tomato and peas, and application mixtures include antibiotics to treat cattle from *Dermatobia* flies. Bees have different degrees of tolerance to chemical disturbance (Arena and Sgolastra 2014), yet most bee species are negatively impacted by biocides (Tomé et al. 2017). *Apis* and *Trigona* were among the few bees using floral resources in conventional crops, suggesting they subsidize the pollination of plants in areas with high-impact management that represent a sink for rare bee species. However, heavily sprayed areas pose a potential threat for bees with relative high resistance to pesticides in Anolaima such as *Apis mellifera*, which is already in decline in Colombia (Requier et al. 2018). These bee reductions may have important impacts for agricultural productivity and the maintenance of local and regional pollination networks (Giannini et al. 2015).

Our results suggest interacting effects between elevation, habitat configuration and agrochemical disturbance on tropical bee communities, which could have important implications in light of climate change. Further studies could assess degrees of habitat specialization and distribution of different species to determine their potential vulnerability to environmental change, and target range shifts of bee communities in Anolaima to understand their potential responses to interactive effects of agrarian, environmental and climate change in tropical montane regions.

Conclusions

Different local and landscape factors influence bee abundance and diversity in Anolaima. Some factors were associated with the increase in abundance of two hyper-generalist groups, *Apis* and *Trigona*, and with reductions in the representation of rare species, reflected in changes in evenness and dominance within local bee assemblages. This suggests a process of biotic homogenization with the loss of some species and the spread of others, especially in high-elevation areas. In addition, we found that factors that affect bee physiology, such as elevation, may be interacting with resource availability and space to influence the composition of bee communities. Certain land use types (e.g., unshaded conventional crops) negatively impacted bee abundance and diversity, despite the high heterogeneity of agroecosystems in the study region, while other land uses (e.g., pastures) had different impacts depending on bee groups. This suggests bee communities are highly responsive to agricultural management in small-scale farming systems. Our study highlights the impact of agricultural management and habitat simplification for the homogenization of bee communities, but also the importance of traditional management systems and of smallholder agriculture for bee diversity in transitioning tropical agroecosystems. It also calls for attention to assess the effect of environmental change on bee communities in mountainous regions where climate change may influence elevational range shifts, such as in the Colombian Andes.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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