Forest-edge associated bees benefit from the proportion of tropical forest regardless of its edge length

Catalina Gutiérrez-Chacón[a,b,*], Carsten F. Dormann[c], Alexandra-Maria Klein[a]

[a] Faculty of Environment and Natural Resources, Chair of Nature Conservation and Landscape Ecology, University of Freiburg, Tennenbacher Straße 4, 79106 Freiburg, Germany
[b] Wildlife Conservation Society – Colombia Program, Av 5N # 22N-11, Cali, Colombia
[c] Faculty of Environment and Natural Resources, Chair of Biometry and Environmental System Analysis, University of Freiburg, Tennenbacher Straße 4, 79106 Freiburg, Germany

ABSTRACT

Natural areas are important for wild bees in human-dominated landscapes as they provide permanent feeding and nesting resources. Understanding how bee communities vary with the amount of natural areas is thus key to guide conservation measures. This information, however, is largely lacking in montane tropical ecosystems. Here we explore to what extent the amount of forest area or forest edge (as landscape variables) influence the species richness and abundance of forest-edge associated bees in the Colombian Andes. In addition, we assess the effects of flower species richness and abundance (as local variables) to better understand the individual and interactive effects of forest conservation. Bees were surveyed along 20 forest edges differing in forest proportion and forest edge length within four spatial scales (250, 500, 1000 and 1500 m radii). We conducted trait-specific analyses as bees with different traits associated to body size, sociality and nesting behavior might differ in their response to local and landscape variables. We found that overall bee species richness and abundance increased with an increasing proportion of forest within 1000 m radius, but also with flower abundance. Similarly, the species richness and abundance of social, large and above-ground nesting bees increased with an increasing proportion of forest area, mainly within 500 and 1000 m radii. However, only the abundance (not the species richness) of solitary and small bees were positively related to the proportion of forest within 1000 m. Below-ground nesters did not respond to the individual effect of forest area at any spatial scale. Interactive effects between local and landscape variables were mainly found between flower richness and the proportion of forest. Forest edge length influenced only the abundance of solitary bees. These findings highlight the importance of conserving and/or restoring forest areas – at meaningful spatial scales – to promote diverse bee communities in montane tropical regions.

1. Introduction

The conservation and restoration of natural areas are key strategies contributing to the maintenance of biodiversity (Gibson et al., 2011; Phalan et al., 2011; Sodhi et al., 2010) and ecosystem services in human-dominated landscapes (De Marco and Coelho, 2004; Tscharntke et al., 2012). Natural areas usually refer to different land-cover types of native vegetation (e.g. native forests) and semi-natural areas (e.g. hedgerows and some grasslands), which differ from managed lands in their lower or non-existent human perturbation (Garibaldi et al., 2011; Scolozzi and Geneletti, 2012). However, the amount of natural areas in a given landscape that should be preserved to maintain diverse communities and viable populations remains unknown for most animal groups (Sodhi et al., 2010; Swift and Hannon, 2010). Moreover, universal diversity responses to the loss of natural areas are difficult to detect due to variation among species (Lindenmayer et al., 2008) and even within a biological group in different biomes (Brosi et al., 2008; Winfree et al., 2007). Nonetheless, empirical studies on the relationship between different biological groups and the availability of natural areas (e.g. Radford et al., 2005; Rodrigues et al., 2016) can collectively assist land managers to set meaningful conservation/restoration goals (Swift and Hannon, 2010) as long as the information is derived from the region of interest (Viana et al., 2012).

Bees, the main pollinators of wild and cultivated plants (Klein et al., 2007; Ollerton et al., 2011; Winfree et al., 2011), often rely on natural areas to obtain permanent feeding and nesting resources in human-

---

dominated landscapes (Garibaldi et al., 2011). Therefore, the effects of available natural areas on bee species richness and abundance have been increasingly studied from a landscape perspective over the last two decades (Basu et al., 2016; Pisanty and Mandelik, 2015; Viana et al., 2012). However, knowledge development has been rapid in temperate regions, while bee diversity responses to the amount of natural areas in the tropics still require more research (Brosi et al., 2008; Freitas et al., 2009; Viana et al., 2012). Understanding landscape features that enhance bee diversity is crucial in the tropics, as pollinator shortages can threaten not only the remarkable plant biodiversity via pollen limitation (Vamosi et al., 2006), but also the production of globally and locally important crops that benefit from bee pollination (Klein et al., 2007).

In Neotropical montane landscapes, forest cover has been extensively transformed into pastures for cattle ranching and croplands (Ayram et al., 2017; Etter et al., 2006). Yet, montane forest remnants hold a great portion of the world's biodiversity and provide multiple ecosystem services (Armenteras et al., 2007; Churchill et al., 1995), including crop pollination. For example, coffee yields, which represent incomes for many farmers in mountain regions of Latin America, increased in close proximity to forest fragments as an effect of the spill-over of pollinating bees from forests into crop fields (Bravo-Monroy et al., 2015; Olschewski et al., 2006; Ricketts, 2004). Nonetheless, the response of bee communities to different amounts of montane forests across landscapes is largely unexplored in the Neotropics. One difficulty in addressing this knowledge gap is the structural complexity of tropical forests, which make commonly used bee-sampling methods such as pan traps, sweep netting, and visual observations rather ineffective and biased towards certain taxa (Prado et al., 2017). In addition, the steep slopes can limit bee sampling in montane forest interiors, as many forests remnants are found in inaccessible areas. Hence, the few studies assessing the effects of montane forest loss and fragmentation have been focused on bees associated with forest edges, as these bees can be sampled more easily than bees inside the forest (Brosi et al., 2008; Brosi, 2009a).

Species richness and abundance are expected to increase as the amount of habitat providing their main foraging and nesting resources increases in the landscape (Fahrig, 2013; Tscharntke et al., 2012). Bees collected in natural and semi-natural areas, both in temperate and tropical areas, have been found to benefit from a larger proportion of such areas in the landscape (Ferreira et al., 2015; Holzschuh et al., 2008; Steffan-Dewenter, 2003). However, bees collected in forest edges have not been related to the proportion of forest (Brosi et al., 2008), except when focusing on particular bee groups (Brosi, 2009a), or have even responded negatively to the proportion of forest habitat in the landscape (Winfree et al., 2007). The amount of habitat edges and not their total areas, conversely, may better explain bee diversity of forest-edge specialists (Fahrig, 2013). Still, as bees foraging in forest edges may also come from the forest interior (Brosi et al., 2008; Nemésio and Silveira, 2006), understanding whether their diversity is influenced by the amount of edge or by the total forest area is important for management purposes. Since both variables are usually negatively correlated (Fahrig, 2003), they are rarely assessed simultaneously.

Responses of bee communities to changes in landscape features are largely shaped by species traits such nest location, sociality, and foraging capability (Benjamin et al., 2014; Williams et al., 2010). Above-ground nesting bees, for instance, are more sensitive to the loss of natural areas than below-ground nesting bees, as nest substrates such as trees, dead wood, and shrub stems are more likely found in such habitats (Williams et al., 2010). Likewise, small species, which tend to have limited dispersal capacity, are more adversely affected by habitat loss than large species (Bommarco et al., 2010; Jauker et al., 2013). Consequently, communities with a prevalence of species with particular traits can drive the response to habitat loss of the entire bee community (Garibaldi et al., 2011). Moreover, the response of a species or groups of species sharing a particular trait varies across spatial scales (Pisanty and

Mandelik, 2015; Winfree, 2013), hence a better understanding of the effects of habitat loss on bee communities can only be achieved when considering species traits under a multi-scale approach (Ferreira et al., 2015; Pisanty and Mandelik, 2015).

In this study, we explore to what extent the amount of forest area or the amount of forest edge (landscape variables) influence the species richness and abundance of forest-edge bee communities at several landscape scales in a montane region of the Colombian Andes. For this, we first test whether bees prefer to use forest edges compared to the surrounding pastures. We hypothesize that i) bee community diversity is driven by the amount of habitat (whether forest proportion or forest edge length) in the landscape, and ii) the response to habitat amount varies across groups of species sharing specific traits, in conjunction with the landscape scale. We thus expect overall bee species richness and abundance to increase with an increasing amount of habitat, and this response should be stronger for small than for large bees (or vice versa as small species may require fewer resources than large bees), for social than for solitary bees, and for above- than for below-ground nesting bees, particularly at smaller spatial scales. Finally, as floral resource availability is an important driver of bee diversity (Roulston and Goodell, 2011), we also test the effect of flower species richness and abundance (local variables) on bee species richness and abundance, allowing us to understand the individual and interactive effects of local and landscape variables on forest-edge associated bee communities.

2. Materials and methods

2.1. Study region

The study region (approximately 81 km^2) is located in the Central Andes of Colombia (4°N, 75°W) in the municipalities of Filandia and Circasia (Quindío Department), between 1800 and 2100 m.a.s.l. The vegetation is sub-Andean forest (sensu Cuatrecasas, 1958); mean annual rainfall is 2817 mm and mean monthly temperature ranges between 16 and 24 °C (Fagua et al., 2013). Dominant land uses in the study region are pasture for cattle ranching (50%) and forest (35%). As in some Neotropical montane landscapes, remaining forest areas are irregularly shaped and interconnected as riparian vegetation along streams and rivers in deep canyons, likely due to access limitation. Isolated forest fragments are thus not commonly found in our study region (Fig. 1).

2.2. Study sites, landscape scales and variables

We selected 20 sites that differed in the proportion of forest and forest edge length within four GIS buffer radii, representing our landscape scales: 250 m (11–57%; 0.9–3 km), 500 m (11–57%; 6–12 km), 1000 m (14–73%; 13–36 km) and 1500 m (19–73%; 34–79 km). In contrast to most situations in which the amount of habitat area and edge are correlated, we did not find a correlation between forest proportion and forest edge length (see Section 2.6). Sites were located a minimum of 1000 m apart. The maximum radius (1500 m) was chosen according to the typical homing distance (THD), estimated a posteriori from our samples using the R package BeeIT (Cariveau et al., 2016), as 93% of the species showed THD within that distance (THD of the remaining 7% of the species ranged between 4.6 and 10 km) (Supplementary Table A1). Despite the fact that land cover area tends to be positively correlated across scales (Steffan-Dewenter, 2002), we individually tested all these spatial scales to identify in which of them the landscape variables had a significant effect on different groups of bees with particular traits. Land-use information was obtained at www.sigquindio.com by webmap service and digitalized with the software ArcGIS® 10.2.1.
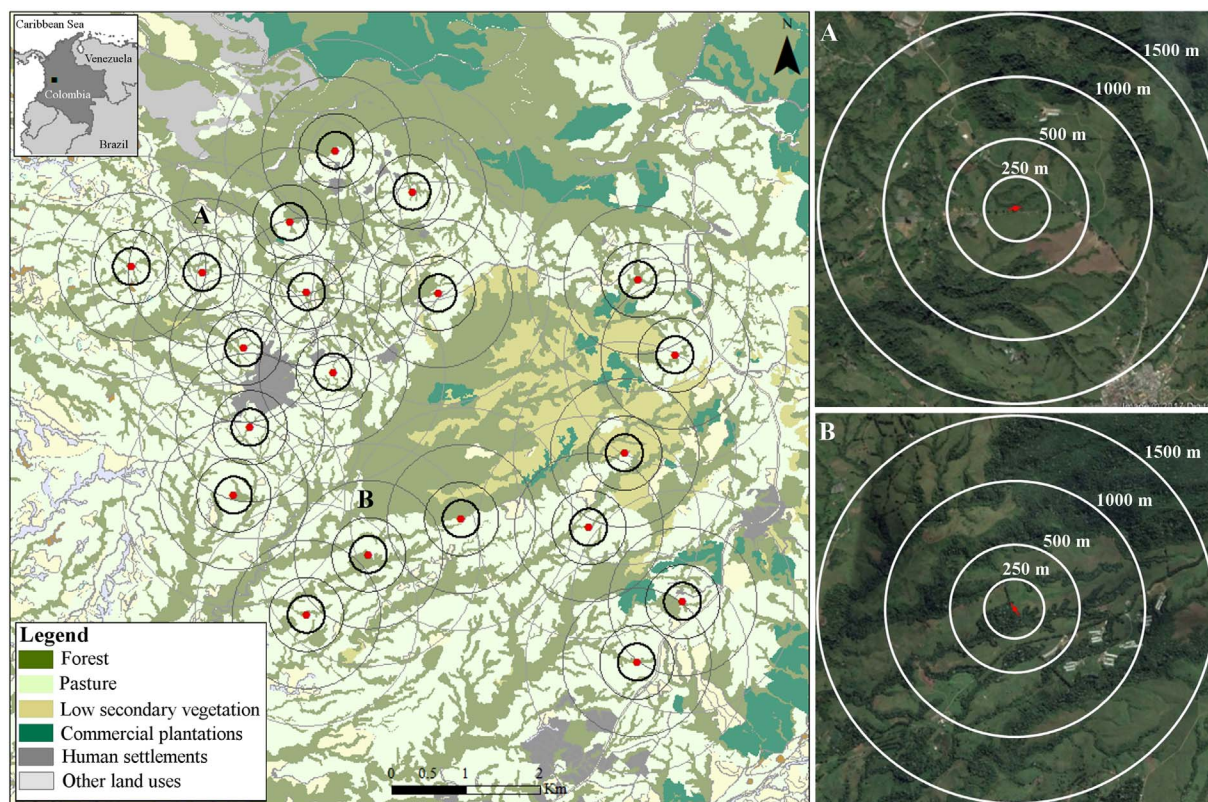
Fig. 1. Map of the study region with sites (red dots) and multiple landscape scales (250–1500 m radii) at which forest proportion and total forest edge length were calculated. Right: satellite images of two sites showing differences in proportion of forest (A = 16%, B = 31%) within 500 m radius and similar edge-forest length (9 and 9.6 km, respectively) (images available at www.sigquindio.com). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.3. Bee sampling

Bees were sampled in each site along a 150 × 4 m transect located in forest edges. We avoided sampling directly in pastures and focused on edge vegetation, such as trees and shrubs. Additionally, bees were sampled in adjacent pastures along 11 transects (150 × 4 m) located 100 m away from any forest area. This allowed us to compare bee composition between forest edges and pastures and confirm whether forest was the land cover predominantly used by forest-edge associated bees. Bees in forest edges were sampled during four surveys between March 2014 and January 2015, therefore including variability throughout the year. In each survey, we sampled every transect three times combining the following methods: (i) aerial netting for 40 min between 8:00 and 14:30; (ii) four sets of pan traps of three colors each (UV-fluorescent yellow, fluorescent blue and white), modified from Nuttman et al. (2011) by placing a small receptacle in each bowl containing 15 ml of industrial honey (inverted sugar and Carboxymethyl cellulose) as bait. Bowls were then filled with a soapy water solution (1 tsp TopTerra® soap per 3 l of water). Sets of pan traps were placed every 50 m, elevated 3–7 m and exposed on average 7 h daily between 8:00 and 17:00; (iii) chemical baited traps for orchid bees (tribe Euglossini) (Vélez and Pulido-Barrios, 2005); two traps were set in each transect, one with cineole (four drops) and the other with methyl salicylate (two drops), located at the transect extremes. These baits are commonly used for studying orchid bees (Brosi, 2009b; Nemésio, 2012) and similar to Brosi (2009b), we used smaller quantities than have been used in previous studies to avoid deleterious impacts on local orchid bee populations, and to have a smaller radius of attraction, although there is no information on the attraction distances of baits (Brosi, 2009b). Baited traps were exposed for the same duration as pan traps. Bees in pastures were sampled using the same methods and sampling effort during the last three surveys (between June 2014 and January

2015). Each survey lasted between 20 and 23 days.

Collected bees were pinned for reference collection and voucher specimens of each species will be deposited in the Humboldt Institute (Colombia) according to the research permit. Bees were identified to the lowest possible taxonomic level (species or morphospecies) using available keys and with the help of taxonomic experts. Still, identification to morphospecies (at least genus level) was often necessary because many bee species in the tropics are not yet described (Michener, 2007).

2.4. Bee life-history traits

To each species, we assigned information on three traits that have been extensively used in previous studies, as they are related to response to disturbance and extinction sensitivity: body size, nesting location and sociality (Bommarco et al., 2010; Jauker et al., 2013; Williams et al., 2010). First, body size was measured as the distance between the two insertion points of the wings (i.e. inter-tegular distance (ITD)). ITD is an indicator of the flight musculature (Cane, 1987) and it is a strong predictor of foraging ranges (Greenleaf et al., 2007). Bee species were categorized as large (ITD ≥ 2.25 mm) or small (ITD < 2.25 mm), following Benjamin et al. (2014). ITD was measured from pinned specimens and averaged by species with measurements from 10 individuals or the maximum number available. Second, each bee species was classified as below or above-ground nester, the latter group including species that nest in pre-existing cavities in trees and those that burrow tunnels into wood. Finally, species were classified as social or solitary bees. Only the honeybee *Apis mellifera* (in our sites they are feral) and stingless bees (tribe Meliponini) were considered 'social' in order to group species with a behavior that improves foraging efficiency (Nieh, 2004); all other species were categorized as solitary. Information on nesting location and sociality was obtained from the primary

literature, but for some morphospecies, information at the genus level was not consistent across all species (e.g. nest location for *Augochlora* spp. or sociality for *Chlerogella* sp.), therefore these morphospecies were excluded from our trait analyses. We estimated the correlation between traits as a rough measure of the extent to which these species traits can be interpreted independently. Species richness of social and above-ground nesting bees were correlated (Supplementary Table A2), as all social bees collected at our sites were above-ground nesters (11 species). However, since not all above-ground nesting bees collected at our sites were social (19 out of 30 species were solitary bees), responses of groups are interpreted individually. Large bees tended to be above-ground nesters, and solitary bees tended to be small bees as well as below-ground nesters.

2.5. Diversity of flowers

We estimated flower species richness and abundance by counting individual flowers along 150 × 2 m transects, both in forest edges and pastures. This was carried out once per survey and always by the same person to avoid differences in biases between researchers. For flowers occurring in inflorescences in the family Melastomataceae (e.g. *Miconia* spp. and *Graffenrieda* sp.), we counted individual functional (open) flowers because we noticed differences in the number of functional flowers among inflorescences between sites and surveys, likely due to the time of the flowering period (beginning/ending vs. peak). For this, and given the large amount of inflorescences in some surveys, we averaged the number of flowers from six inflorescences and multiplied it by the number of total observed inflorescences (to obtain total functional flowers). Similarly, we counted individual capitula in Asteraceae, even for those species in which they occur in a panicle (e.g. *Verbesina nudipens*).

2.6. Statistical analyses

2.6.1. Bee community differences between forest edges and pastures

All analyses were performed in R 3.2.4 (http://www.r-project.org). We analyzed the changes in bee community composition between forest edge and pasture using Non-metric Multidimensional Scaling (NMDS) with the Morisita-Horn index, as it is recommended for different sample sizes (pasture n = 11, forest edges n = 20). We used a three-axis solution (k = 3) to lower final stress below 0.2. A one-way Analysis of Similarity (ANOSIM) was used to test for significant differences (Clarke and Gorley, 2006), and the percentage contribution of each taxon to the average dissimilarity between habitat types was assessed with a similarity percentage analysis (SIMPER) (Bennett and Isaacs, 2014; Clarke, 1993). All multivariate statistics were performed using the R-package vegan (Oksanen et al., 2013).

2.6.2. Landscape and local effects on bee abundance and richness

All bees captured by the three methods in a single survey were pooled to provide a survey-level count of species richness and abundance per site (79 samples in total: four samples in each of the 20 sites, except in one site with three samples). Sample completeness was calculated for each site to make a fair comparison through the concept of sample coverage (Chao and Jost, 2012), estimated in the R-package iNEXT (Hsieh et al., 2016). Sample coverage was above 0.92 for all sites, thus we used observed rather than extrapolated bee species richness and abundance. We then fit generalized linear mixed models (GLMM) with Poisson distribution with species richness and abundance of overall, social, solitary, small, large, above-ground and below-ground nesting bees as the response variable (in individual models). As fixed factors, we included landscape (forest proportion, forest edge length) and local variables (flower species richness and flower abundance) both individually and in two-way interactions (only between landscape and local variables). Survey and site were included as random effects, as we were not interested in their parameter values but rather the explained variance. We fit models with and without the most common species in pasture, *Lasioglossum* sp4 (which explained most of the difference between communities, see Results section). Explanatory variables were not highly correlated ($|r_s| < 0.5$) at any of the spatial scales, according to the Spearman rank test (Supplementary Tables A3), and therefore all variables were included in the models. Given its wide range (186–57,649), flower abundance was the only variable transformed by natural logarithm in order to avoid leverage effect on our analyses. Explanatory variables were centered and scaled allowing effect sizes to be more easily compared (Zuur et al., 2009). We found models to be either under- or over-dispersed, hence we fit GLMM with a penalized quasi-likelihood method of parameter estimation (Harrison, 2014) with log link and Poisson errors, using the glmmPQL function in the R package "MASS" (Breslow and Clayton, 1993; Nelson and Leroux, 2006). There was no spatial autocorrelation according to Moran's I correlograms using model residuals, except for the species richness of small bees within 1500 m radius, but spatial autocorrelation was not detected at smaller scales 250–1000 m thus was not accounted for in further analyses (Supplementary Fig. A1).

3. Results

3.1. Bee and plant communities in forest edges and pastures

In forest edges, we collected 2248 bees belonging to four families, 31 genera and 57 species, which included 29 morphospecies. From the total abundance, social bees were more abundant (60%) than solitary bees (40%), but their species richness (ten species of stingless bees plus the honeybee) represented only 19% of all specimens. Small bees were both more abundant (77%) and diverse (60%) than large bees. The majority of the sampled species and individuals nest above ground (53% and 71%, respectively), while for five species we found no nesting information. In pastures, we collected 880 bees belonging to 24 genera and 30 species (14 morphospecies). Solitary bees were more abundant (62%) and diverse (70%) than social bees, and small bees were both more abundant (70%) and diverse (77%) than large bees. Most individuals nest below ground (58%), although species richness of below-ground nesters was slightly lower (40%) than above-ground nesters (50%); three species had no available nesting information (see species list in Supplementary Table A1). Bee composition in forest edges was significantly different from that in pasture (R = 0.69, p < 0.01) (Supplementary Fig. A2), driven by *Lasioglossum* sp4, which was dominant in pasture (18% of all records, and 48% of the total abundance), and *Partamona* cf. *peckolti* (8%), dominant in forest edges (Supplementary Table A4).

We counted 152 flowering species in forest edges in 87 genera and 46 families. The most species rich families were Melastomataceae (17), Asteraceae (16), Orchidaceae (12), and Solanaceae (12). Highest flower abundances were found in the families Melastomataceae and Asteraceae. In pasture, we found 42 morphospecies in 15 plant families, from which 79% were not found in forest edges. Asteraceae was the most species rich family (9 species). Flower abundance was significantly higher in forest edges than in pastures (t = 4.87, df = 19.12, p-value < 0.01).

3.2. Landscape and local effects on overall bee abundance and richness

Overall bee abundance increased with an increasing forest proportion in a 500 m radius, while overall species richness increased only at 1000 m (Fig. 2a, b; Table 1). This effect on the richness of the overall bee-community was detected even when including the typical pasture species *Lasioglossum* sp4, since its abundance represented only 4% of the forest-edge bee community. Species richness and abundance of the overall bee community was not significantly related to forest edge length (Table 1). The overall bee abundance was related to the increasing flower abundance at all spatial scales, and to the overall bee
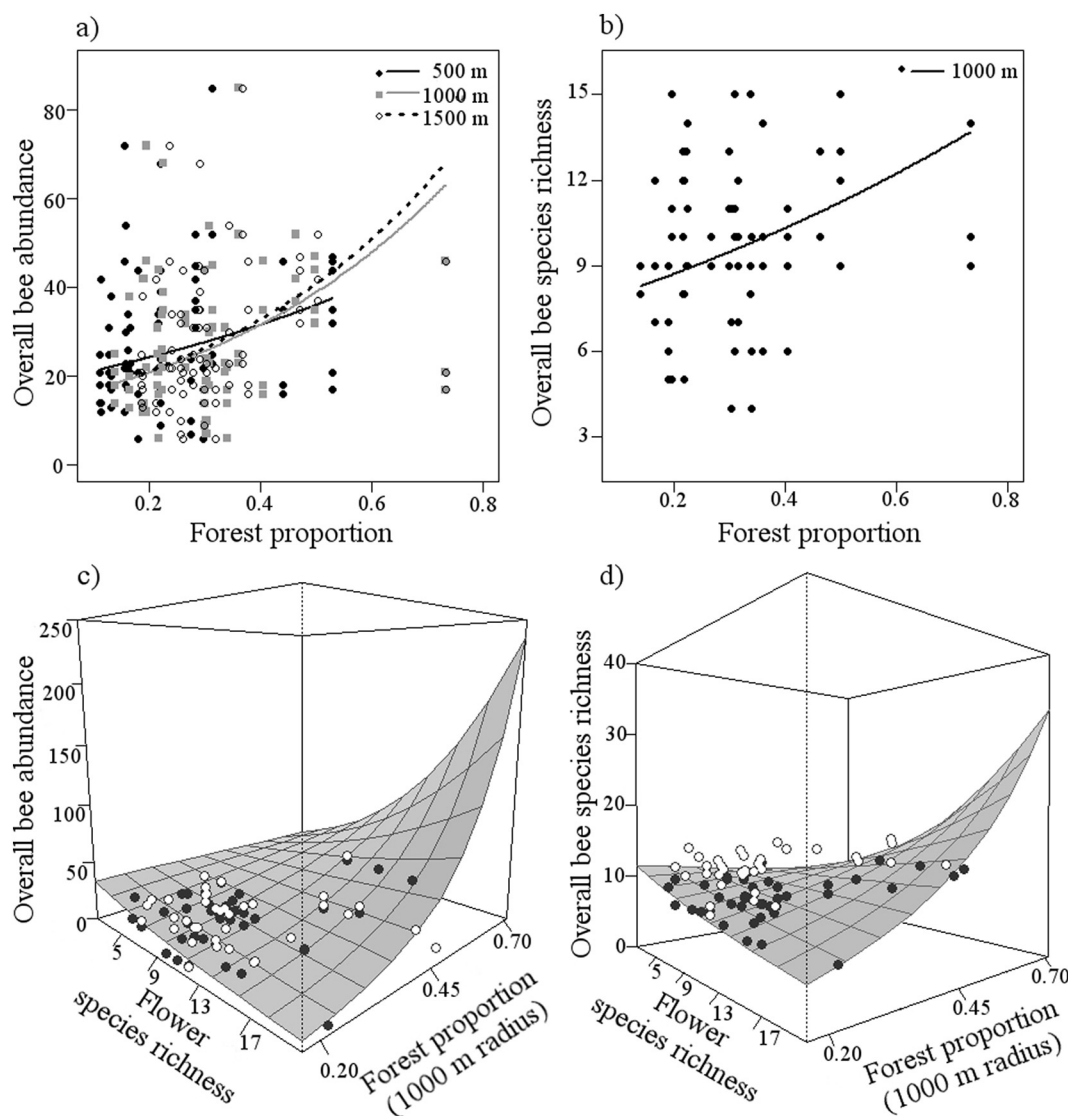
Fig. 2. Relationships between local and landscape variables on the overall bee community: individual effect of forest proportion on (a) the overall bee abundance and (b) species richness across landscape scales (500, 1000 and 1500 m radii), and interactive effect of forest proportion and flower species richness on (c) the overall bee abundance and (d) species richness (only showing effect within 1000 m radius as slope was larger compared to 500 m); values below (black dots) and above (white dots) the model prediction are shown. All relationships are significant at P < 0.05 (see Table 1).

species richness at 500 and 1000 m, but only when including the most abundant species found in pastures (*Lasioglossum* sp4) (Table 1). Interactive effects of local and landscape variables were also found; in sites with high richness of flowering species, overall bee abundance increased with an increasing proportion of forest within 500 m (Fig. 2c), and bee species richness increased with the increasing proportion of forest within 500–1000 m (Fig. 2d, Table 1).

3.3. Landscape and local effects on functional bee groups

Groups of bees with different life-history traits responded differently to landscape and local variables at different spatial scales. In terms of landscape variables, species richness and abundance of social, large, and above-ground nesting bees had individual and positive responses to the proportion of forest within a 500 and 1000 m radius (Fig. 3a–c; Table 1). Additionally, within the 1000 m radius, the abundance of small and solitary bees increased with the proportion of forest (Fig. 3d). Species richness of above-ground nesting bees (Fig. 3e) and the abundance of large bees (Fig. 3f) increased with an increasing proportion of forest within 1500 m radius and the abundance of solitary bees increased with the individual effect of forest edge length. Considering

local habitat variables, species richness and abundance of social, large, and above-ground nesting bees increased with increasing flower abundance across all spatial scales (Table 1). The abundance of small bees increased with the abundance of flowers across all spatial scales, while the abundance of below-ground nesting bees was only related to the abundance of flowers within 250 m.

Functional bee groups were also significantly affected by the interaction between local and landscape variables. In sites with a higher richness of flowering plant species, species richness of small and below-ground nesting bees increased with an increasing proportion of forest within a 500 m radius (Fig. 4a). The species richness of small bees also increased with an increasing forest proportion within a 1000 m radius (Fig. 4b), as well as the abundance of social (Fig. 4c) and below-ground nesting bees (Fig. 4d) when richness of flowering plants was high (Table 1). The abundance of social bees increased with an increasing forest edge length within 1000 m, but only at higher levels of flower richness (Fig. 4e). Finally, the abundance of large bees increased with an increasing proportion of forest, and flower abundance had a negative interaction effect in a 500 m radius, indicating a positive relationship between large bee abundance and flower abundance, but only at low levels of forest proportion (Fig. 4f; Table 1).

Table 1

Significant results from mixed-effects modelling of the effects of forest proportion (Forest), forest edge length (Edge), flower species richness (FlowerS) and flower abundance (FlowerN) on bee species richness and abundance (overall and by functional groups). Interaction between explanatory variables is indicated by "×" (see results for all variables in Supplementary Table A5).

Response variable	Landscape scale											
	250 m			500 m			1000 m			1500 m		
	Explanatory variable	Estimate ± SE	P	Explanatory variable	Estimate ± SE	P	Explanatory variable	Estimate ± SE	P	Explanatory variable	Estimate ± SE	P
Bee species richness												
Overall	–	–	–	FlowerN[a]	0.08 ± 0.04	0.04	FlowerN[a]	0.07 ± 0.03	0.04	–	–	–
				FlowerS × Forest	0.08 ± 0.04	0.02	Forest	0.12 ± 0.05	0.02			
							FlowerS × Forest	0.11 ± 0.05	0.02			
Social	FlowerN	0.14 ± 0.05	0.01	FlowerN	0.15 ± 0.05	< 0.01	FlowerN	0.14 ± 0.05	< 0.01	FlowerN	0.13 ± 0.05	0.01
				Forest	0.18 ± 0.05	< 0.01	Forest	0.19 ± 0.07	0.02			
Solitary	–	–	–	–	–	–	–	–	–	–	–	–
Above-ground	FlowerN	0.13 ± 0.05	0.01	FlowerN	0.14 ± 0.04	< 0.01	FlowerN	0.13 ± 0.04	< 0.01	FlowerN	0.12 ± 0.04	0.01
				Forest	0.17 ± 0.04	< 0.01	Forest	0.23 ± 0.07	< 0.01	Forest	0.19 ± 0.08	0.03
Below-ground	–	–	–	FlowerS × Forest	0.15 ± 0.06	0.01	–	–	–	–	–	–
Small	–	–	–	FlowerS × Forest	0.08 ± 0.04	0.04	FlowerS × Forest	0.15 ± 0.05	< 0.01	–	–	–
Large	FlowerN	0.22 ± 0.07	< 0.01	FlowerN	0.20 ± 0.07	< 0.01	FlowerN	0.18 ± 0.06	0.01	FlowerN	0.17 ± 0.07	0.01
				Forest	0.16 ± 0.07	0.04	Forest	0.20 ± 0.10	0.04			
Bee abundance												
Overall	FlowerN	0.21 ± 0.06	< 0.01	FlowerN	0.21 ± 0.05	< 0.01	FlowerN	0.23 ± 0.05	< 0.01	FlowerN	0.21 ± 0.05	< 0.01
				Forest	0.17 ± 0.07	0.04	Forest	0.28 ± 0.10	0.01	Forest	0.28 ± 0.12	0.03
							FlowerS × Forest	0.18 ± 0.09	0.04			
Social	FlowerN	0.36 ± 0.09	< 0.01	FlowerN	0.42 ± 0.08	< 0.01	FlowerN	0.46 ± 0.07	< 0.01	FlowerN	0.42 ± 0.08	< 0.01
				Forest	0.28 ± 0.10	0.01	Forest	0.37 ± 0.16	0.03			
							FlowerS × Edge	0.31 ± 0.14	0.03			
							FlowerS × Forest	0.26 ± 0.12	0.04			
Solitary	–	–	–	–	–	–	Edge	0.23 ± 0.08	0.01	–	–	–
							Forest[a]	0.20 ± 0.09	0.04			
Above-ground	FlowerN	0.34 ± 0.08	< 0.01	FlowerN	0.34 ± 0.07	< 0.01	FlowerN	0.38 ± 0.07	< 0.01	FlowerN	0.34 ± 0.07	< 0.01
				Forest	0.26 ± 0.09	0.01	Forest	0.37 ± 0.14	0.02			
Below-ground	FlowerN	−0.17 ± 0.08	0.03	–	–	–	FlowerS × Forest	0.33 ± 0.12	0.01	–	–	–
Small	–	–	–	FlowerN	0.12 ± 0.05	0.03	FlowerN	0.13 ± 0.05	0.02	FlowerN	0.12 ± 0.05	0.02
							Forest	0.28 ± 0.12	0.03			
Large	FlowerN	0.48 ± 0.10	< 0.01	FlowerN	0.51 ± 0.09	< 0.10	FlowerN	0.49 ± 0.08	< 0.01	FlowerN	0.45 ± 0.08	< 0.01
				Forest	0.28 ± 0.10	0.02	Forest	0.39 ± 0.12	0.01	Forest	0.46 ± 0.16	0.01
				FlowerN × Forest	−0.35 ± 0.10	< 0.01	FlowerN × Forest	−0.30 ± 0.13	0.03	FlowerN × Forest	−0.30 ± 0.14	0.04

[a] Significant explanatory variables when including *Lasioglossum* sp4 (the most abundant species in pasture).
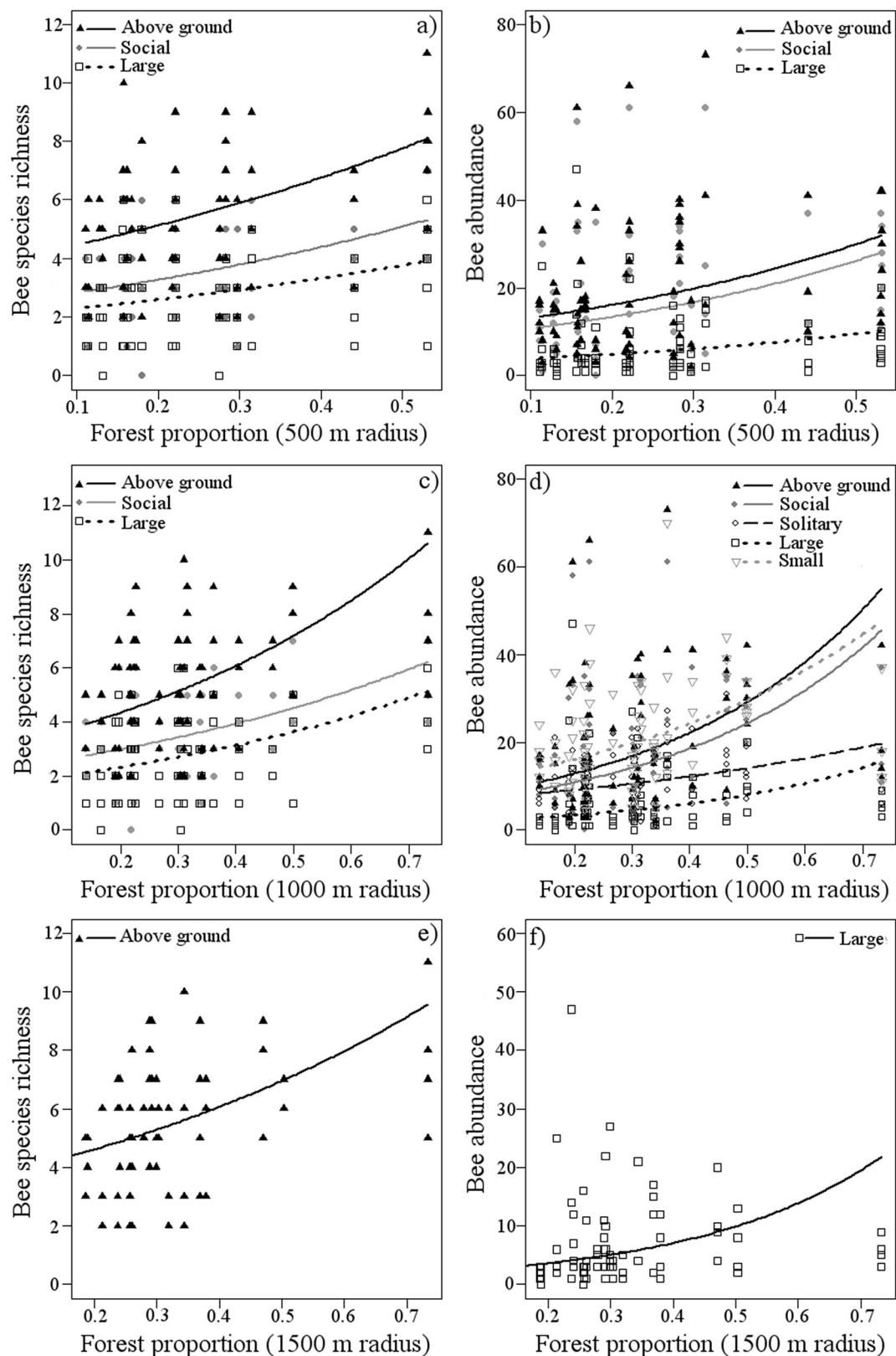
Fig. 3. Relationships between species richness and abundance of functional bee groups and forest proportion within 500 m radius (a, b), 1000 m radius (c, d) and 1500 m radius (e, f). Lines are model-predicted values. All relationships are significant at P < 0.05 (see Table 1).

4. Discussion

Our study shows that bee communities at montane-forest edges were significantly influenced by the amount of forest in the landscape as well as by local floral resources. The total forest amount and not just forest edge length seem to represent the habitat for bees collected in forest edges, given their significant response to forest proportion (mainly within 500–1000 m radii) and the lack of relationships with
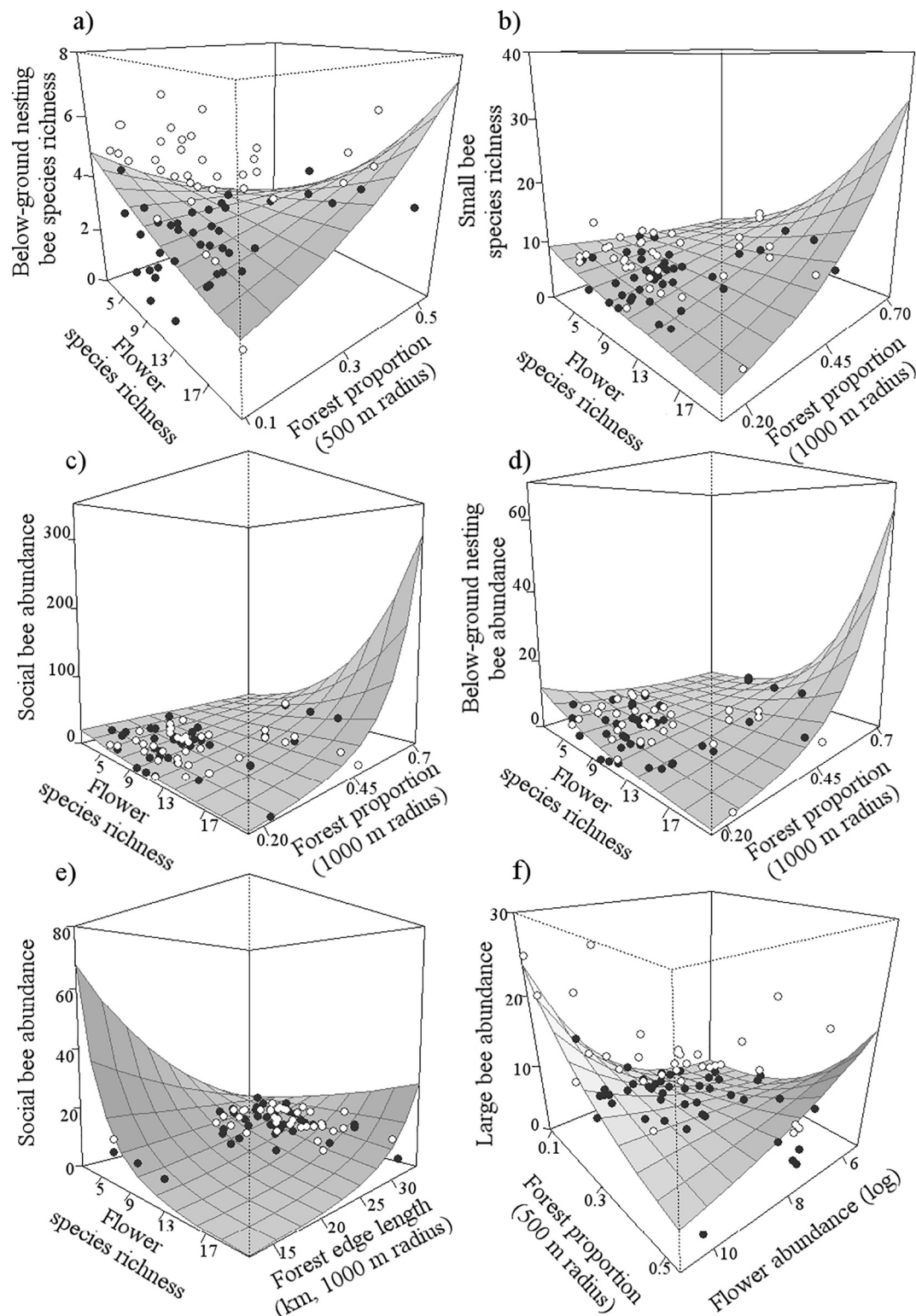
Fig. 4. Interactive effects of landscape and local variables on functional bee groups: forest proportion and flower species richness on the species richness of (a) below-ground nesting bees and (b) small bees (only showing effect within 1000 m radius as slope was larger compared to 500 m), as well on the abundance of (c) social and (d) below-ground nesting bees; (e) Forest edge length and flower species richness on the abundance of social bees, and (f) forest proportion and flower abundance on large bee abundance (only showing effect within 500 m radius as slope was larger compared to 1000 and 1500 m). Values below (black dots) and above (white dots) the model prediction are shown. All relationships are significant at P < 0.05 (see Table 1).

total forest edge length. The strength of the landscape effects and whether they occur individually or in interaction with local variables varied according to the target group of the analysis (i.e. entire bee community versus functional groups), the spatial scale at which habitat was measured, and the bee-community metric (bee species richness versus abundance). Our findings illustrate how forest conservation and/ or restoration could benefit bee communities in montane tropical regions.

Bee-community composition significantly changed from forest edges to pastures (distance 100 m), mainly due to the loss of social bees as well as above-ground nesters. Although we did not measure the availability of nesting substrates, we observed few standing trees within pastures, characteristic of conventionally managed pasturelands in Colombia (Murgueitio et al., 2011). This may partially explain the lower abundance of most social bees, for example stingless bees, which often rely on trees for nest building (Brosi, 2009a) and have a typical homing distance shorter than 100 m for most species in the study region (Supplementary Table A1). In addition, pastures had a lower abundance of floral resources compared to forests, suggesting they were less attractive even for above-ground nesting bees with greater flying capabilities than stingless bees. In contrast, the wide availability of bare soils in pastures enhanced the below-ground nesting bees (all of them solitary), particularly in the genus *Lasioglossum*, which have previously been associated with intensive-production sites in other tropical landscapes (Basu et al., 2016; Ngo et al., 2013).

4.1. Landscape variables: individual effect of habitat (forest) amount

As expected, we found overall bee species richness and abundance to increase with an increasing amount of forest cover in the landscape. However, both community metrics were only simultaneously associated with forest when it was measured within a 1000 m radius. Interestingly, this radius distance is close to the average typical homing distance (THD) of our group of species (895 m), in which the response of species richness (and likely abundance) to the amount of habitat is expected to be stronger (Fahrig, 2013). This further suggests that conserving forest within small landscape scales might not be sufficient to effectively conserve diverse bee communities in tropical landscapes. In contrast to our results, the few studies assessing the effect of forest area on overall bee communities have found no relationship (Brosi et al., 2008; Kleijn and Van Langevelde, 2006; Schüepp et al., 2011; Williams and Winfree, 2013) or even a negative response (e.g. Winfree et al., 2007). On the one hand, forests may not represent habitat for most of the sampled species, either because they were collected in a different land cover type thus including non-forest related species (e.g. Brosi et al., 2008), or because other open habitats, such as agricultural fields, can offer more resources than forests (Williams and Winfree, 2013; Winfree et al., 2007). On the other hand, remaining forest at regional scales can drive the response of bee communities at smaller scales (Ferreira et al., 2015; Winfree et al., 2009). In a highly deforested region in Mexico (< 14% of forest), Jha and Vandermeer (2010) found no relationship between forest proportion and bee diversity, which was dominated by sweat bees (Halictidae, 72%) with many species adapted to open habitats. In contrast, the bee community in our region (with 35% of forest) was dominated by Apidae (56%), which includes tribes with many forest-associated species such as Euglossini and Meliponini. Thus, in highly deforested regions, forest-associated bees may already be lost, and current communities are mostly composed of species well adapted to disturbed areas (Ferreira et al., 2015), meaning that an increase in forest area may not affect bees at any spatial scale.

We also found a positive and stronger response of social and above-ground nesting bees to the proportion of forest compared to solitary and below-ground nesting bees, consistent with previous findings (Brosi, 2009a; Brown and Albrecht, 2001; Ferreira et al., 2015; Winfree et al., 2009). The responses of these two functional groups are usually interrelated in the tropics, as social bees, mainly feral honeybees and stingless bees, often require trees as nesting sites, while in temperate regions, social bees frequently include *Bombus* and sweat bees with many species nesting in the ground (Ricketts et al., 2008; Winfree et al., 2009). In addition to nesting resource limitations, the higher demands of food resources in relation to the large number of individuals per nest make social bees highly sensitive to forest loss (Brosi, 2009b; Ferreira et al., 2015; Ricketts et al., 2008; Winfree et al., 2009). We observed the strongest effect of forest proportion within a 1000 m radius, in which

richness and abundance of social and above-ground nesting bees increased at least twofold with increasing forest proportion (14–73%). This larger scale, as compared to previous reports for stingless bees (250 and 400 m, Brosi, 2009b; Lichtenberg et al., 2017), could be driven to some extent by *A. mellifera*, as the foraging distance of honeybees vary greatly but is usually over 1000 m (Abou-Shaara, 2014). The identity of dominant species might also contribute to these contrasting results, as the most abundant species in our samples, *T. amalthea*, was estimated to cover three times the foraging distance of *T. fulviventris*, the dominant species reported by Brosi (2009a). These findings illustrate the variability of landscape effects on bee communities even in similar systems, and highlight the importance of accounting for species traits to understand such variation.

As central-place foragers, bees with a small foraging range require a greater density of resources per unit area than animals with similar needs, but greater range (Cresswell et al., 2000). Therefore, we expected that small bees would have responded more strongly than large bees to the increasing proportion of forest (as a source of resources), particularly within smaller radii. However, small bee abundance increased with an increasing proportion of forest only at 1000 m. In turn, large bee abundance increased with an increasing proportion of forest within 500–1500 m radii. This confirms that large bees, despite being able to cover long foraging distances, can be sensitive to land use changes even at small spatial scales (Benjamin et al., 2014). These results may be partially explained by the large number of species and individuals belonging to orchid bees, which are more abundant and diverse in larger forest fragments (Nemésio and Silveira, 2007, 2010). Nevertheless, as some studies did not find a relationship between species richness of orchid bees and forest fragment size (Botsch et al., 2017; Brosi, 2009b), further research is needed to test whether the amount of habitat within circular landscapes of appropriate radius is a better predictor than patch size, as posited by the habitat amount theory (Fahrig, 2013).

4.2. Local variables: individual effect of floral richness and abundance

The abundance of most functional groups and the overall bee community increased with increasing flower abundance, regardless of the forest proportion, which is in line with previous investigations in natural and agricultural systems both in temperate and tropical areas (Classen et al., 2015; Pywell et al., 2005, but see Brosi, 2009a; Grundel et al., 2010). In addition, we found a positive relationship between the overall bee species richness as well as the species richness of some functional groups (social, large, and above-ground nesting species) with flower abundance. Although the relationship between bee species richness and floral abundance has not been extensively assessed, similar results were reported by Pardee and Philpott (2014) in urban gardens. Our findings support the idea that habitats with abundant flowers have greater possibilities for partitioning available resources (Potts et al., 2003), hence promoting not only abundance of individuals but also greater species richness (Heithaus, 1979).

4.3. Interactive effects of landscape and local variables

The relationship between species richness of all, small, and below-ground nesting bees, as well as of a higher abundance of social and below-ground nesting bees with flower species richness was stronger at higher levels of forest proportion. Although this interactive effect may suggest a sampling artifact, as the effect of forest amount may only become significant at higher levels of flower richness (which attract many forest-interior bees), the individual positive relationships between overall species richness and abundance and forest proportion suggests that this is not the case. On the contrary, dominant species in pastures, such as below-ground nesting bees, were positively related to higher levels of both forest cover and flowers. However, the relationship with forest cover is not straightforward to explain, as below-

ground nesters benefit from open habitats with more bare and sunny soil available (Williams et al., 2010). One plausible explanation is that given the lack of information on the ecology of many tropical species, coupled with the identification up to the genus level, some morphospecies classified as below-ground nesters may actually be using substrates provided by forests such as hollow stems or dead wood, for example in the genera *Neocorynura* and *Augochlora* (Michener, 2007). Therefore, to better understand the effect of land-use change on native tropical bee fauna, further studies on taxonomy and ecology are needed (Gonzalez et al., 2013).

The positive relationship between bees and flower diversity has been widely described (Fründ et al., 2010; Potts et al., 2003; Ebeling et al., 2008; Rubene et al., 2015) and attributed to the availability of a wide range of foraging niches for different functional groups of bees (Murray et al., 2009). However, whether the effect of flower diversity depends on the amounts of natural habitats has not been frequently studied and results are mixed (Kleijn and Van Langevelde, 2006; Rubene et al., 2015). Despite the fact that pollinators (mostly bees) seem to track floral resources regardless of how they vary with land-use change (Winfree et al., 2011), our results suggest this is not always the case, as the loss of tropical montane forest may limit the positive effect of a high floral offer, which is likely related to the reduction of nesting sites. This suggests that increased forest habitat is associated with higher habitat quality, but this relationship requires further research.

The increase of large bee abundance with increasing flower abundance, which was found only at low levels of forest proportion, was somewhat surprising given the general positive effect of forest proportion on bees with different traits. A similar response was displayed by bumblebees in the Netherlands, which tended to be concentrated in small resource-rich patches (Kleijn and Van Langevelde, 2006). We attribute this pattern to the dominance of *A. mellifera* (comprising 47% of the total number of large bee individuals), which has been reported to decrease with increasing forest area (Brosi et al., 2008), likely due to its preference for foraging in open habitats (Ramalho et al., 1990). Nevertheless, it is important to note that the minimum forest proportion in our study area was 11%, which is higher than what is considered extreme habitat loss (< 5%, Winfree et al., 2009). Feral *A. mellifera*, an important pollinator of many tropical crops (Klein et al., 2007), benefit from forest cover especially in agricultural fields that exhibit poor nesting conditions (Chacoff and Aizen, 2006). We echo the call for more research on the effects of forest loss and isolation on this species (Garibaldi et al., 2011; Winfree et al., 2009), which would require a wider range of habitat amounts than studied here.

5. Conclusion

Our study demonstrates that higher proportions of forest area enhance the species richness and abundance of forest-edge associated bees, especially within 500–1000 m radii distances. Although species that rely on wood-related nesting substrates such as the stingless bees (important pollinators of wild and cultivated tropical plants) benefit particularly from more forest area in the landscape, other species with diverse traits are also positively influenced. Hence, conserving diverse functional bee communities in montane tropical regions will require the conservation and/or restoration of forest areas before extreme forest loss occurs. This can be realistically achieved, for instance, by incorporating information on the relationship between bee diversity and forest areas into programs and policies that promote forest conservation in Neotropical countries (e.g. Hall, 2012), expanding their scope to include pollination services. Future studies could attempt to relate our findings to the responses of bees in more diverse regions in terms of land-use and management practices, as the positive effect of increased habitat amount can be modified by the quality of adjacent habitats (Tscharntke et al., 2012).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.02.009.

References

Abou-Shaara, H.F., 2014. The foraging behaviour of honey bees, *Apis mellifera*: a review. Vet. Med. (Praha) 59, 1–10.

Armenteras, D., Cadena, C.E., Moreno, R.P., 2007. Evaluación del estado de los bosques de niebla y la meta 2010 en Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogota D.C., Colombia.

Ayram, C.A.C., Mendoza, M.E., Etter, A., Salicrup, D.R.P., 2017. Potential distribution of mountain cloud forest in Michoacán, Mexico: prioritization for conservation in the context of landscape connectivity. Environ. Manag. 60, 86–103.

Basu, P., Parui, A.K., Chatterjee, S., Dutta, A., Chakraborty, P., Roberts, S., Smith, B., 2016. Scale dependent drivers of wild bee diversity in tropical heterogeneous agricultural landscapes. Ecol. Evol. 6, 6983–6992.

Benjamin, F.E., Reilly, J.R., Winfree, R., 2014. Pollinator body size mediates the scale at which land use drives crop pollination services. J. Appl. Ecol. 51, 440–449.

Bennett, A.B., Isaacs, R., 2014. Landscape composition influences pollinators and pollination services in perennial biofuel plantings. Agric. Ecosyst. Environ. 193, 1–8.

Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P., Steffan-Dewenter, I., Öckinger, E., 2010. Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. Proc. R. Soc. B Biol. Sci. 277, 2075–2082.

Botsch, J.C., Walter, S.T., Karubian, J., González, N., Dobbs, E.K., Brosi, B.J., 2017. Impacts of forest fragmentation on orchid bee (Hymenoptera: Apidae: Euglossini) communities in the Chocó biodiversity hotspot of northwest Ecuador. J. Insect Conserv. 21, 633–643.

Bravo-Monroy, L., Tzanopoulos, J., Potts, S.G., 2015. Ecological and social drivers of coffee pollination in Santander, Colombia. Agric. Ecosyst. Environ. 211, 145–154.

Breslow, N.E., Clayton, D.G., 1993. Approximate inference in generalized linear mixed models. J. Am. Stat. Assoc. 88, 9–25.

Brosi, B.J., 2009a. The complex responses of social stingless bees (Apidae: Meliponini) to tropical deforestation. For. Ecol. Manag. 258, 1830–1837.

Brosi, B.J., 2009b. The effects of forest fragmentation on euglossine bee communities (Hymenoptera: Apidae: Euglossini). Biol. Conserv. 142, 414–423.

Brosi, B.J., Daily, G.C., Shih, T.M., Oviedo, F., Durán, G., 2008. The effects of forest fragmentation on bee communities in tropical countryside. J. Appl. Ecol. 45, 773–783.

Brown, J.C., Albrecht, C., 2001. The effect of tropical deforestation on stingless bees of the genus *Melipona* (Insecta: Hymenoptera: Apidae: Meliponini) in central Rondonia, Brazil. J. Biogeogr. 28, 623–634.

Cane, J.H., 1987. Estimation of bee size using intertegular span (Apoidea). J. Kansas Entomol. Soc. 60, 145–147.

Cariveau, D.P., Nayak, G.K., Bartomeus, I., Zientek, J., Ascher, J.S., Gibbs, J., Winfree, R., 2016. The allometry of bee proboscis length and its uses in ecology. PLoS One 11, e0151482.

Chacoff, N.P., Aizen, M.A., 2006. Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. J. Appl. Ecol. 43, 18–27.

Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93, 2533–2547.

Churchill, S.P., Balslev, H., Forero, E., Luteyn, J.L., 1995. Biodiversity and conservation of neotropical montane forests. In: Proceedings of the Neotropical Montane Forest Biodiversity and Conservation Symposium. New York Botanical Garden, Bronx, NY, pp. xi–xiv.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Austral Ecol. 18, 117–143.

Clarke, K.R., Gorley, R.N., 2006. User Manual/Tutorial. Primer-E Ltd, Plymouth, pp. 93.

Classen, A., Peters, M.K., Kindeketa, W.J., Appelhans, T., Eardley, C.D., Gikungu, M.W., Hemp, A., Nauss, T., Steffan-Dewenter, I., 2015. Temperature versus resource constraints: which factors determine bee diversity on Mount Kilimanjaro, Tanzania? Glob. Ecol. Biogeogr. 24, 642–652.

Cresswell, J.E., Osborne, J.L., Goulson, D., 2000. An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. Ecol. Entomol. 25, 249–255.

Cuatrecasas, J., 1958. Aspectos de la vegetación natural en Colombia. Rev. Academia Colomb. Cienc. Exactas Fis. Nat. 10, 221–268.

De Marco, P., Coelho, F.M., 2004. Services performed by the ecosystem: forest remnants influence agricultural cultures' pollination and production. Biodivers. Conserv. 13, 1245–1255.

Ebeling, A., Klein, A.-M., Schumacher, J., Weisser, W.W., Tscharntke, T., 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? Oikos 117, 1808–1815.

Etter, A., McAlpine, C., Wilson, K., Phinn, S., Possingham, H., 2006. Regional patterns of agricultural land use and deforestation in Colombia. Agric. Ecosyst. Environ. 114, 369–386.

Fagua, J.C., Cabrera, E., Gonzalez, V.H., 2013. The effect of highly variable topography on the spatial distribution of *Aniba perutilis* (Lauraceae) in the Colombian Andes. Rev. Biol. Trop. 61, 301–309.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 487–515.

Fahrig, L., 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. J. Biogeogr. 40, 1649–1663.

Ferreira, P.A., Boscolo, D., Carvalheiro, L.G., Biesmeijer, J.C., Rocha, P.L., Viana, B.F., 2015. Responses of bees to habitat loss in fragmented landscapes of Brazilian Atlantic Rainforest. Landsc. Ecol. 30, 2067–2078.

Freitas, B.M., Imperatriz-Fonseca, V.L., Medina, L.M., Kleinert, A. de M.P., Galetto, L., Nates-Parra, G., Quezada-Euán, J.J.G., 2009. Diversity, threats and conservation of native bees in the Neotropics. Apidologie 40, 332–346.

Fründ, J., Linsenmair, K.E., Blüthgen, N., 2010. Pollinator diversity and specialization in relation to flower diversity. Oikos 119, 1581–1590.

Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S., et al., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecol. Lett. 14, 1062–1072.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J., Laurance, W.F., Lovejoy, T.E., et al., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378–381.

Gonzalez, V.H., Griswold, T., Engel, M.S., 2013. Obtaining a better taxonomic understanding of native bees: where do we start? Syst. Entomol. 38, 645–653.

Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. Oecologia 153, 589–596.

Grundel, R., Jean, R.P., Frohnapple, K.J., Glowacki, G.A., Scott, P.E., Pavlovic, N.B., 2010. Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. Ecol. Appl. 20, 1678–1692.

Hall, A., 2012. Forests and Climate Change: The Social Dimensions of REDD in Latin America. Edward Elgar Publishing.

Harrison, X.A., 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. PeerJ 2, e616.

Heithaus, E.R., 1979. Community structure of neotropical flower visiting bees and wasps: diversity and phenology. Ecology 60, 190–202.

Holzschuh, A., Steffan-Dewenter, I., Tscharntke, T., 2008. Agricultural landscapes with organic crops support higher pollinator diversity. Oikos 117, 354–361.

Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 2.0.12. URL: http://chao.stat.nthu.edu.tw/blog/software-download/.

Jauker, B., Krauss, J., Jauker, F., Steffan-Dewenter, I., 2013. Linking life history traits to pollinator loss in fragmented calcareous grasslands. Landsc. Ecol. 28, 107–120.

Jha, S., Vandermeer, J.H., 2010. Impacts of coffee agroforestry management on tropical bee communities. Biol. Conserv. 143, 1423–1431.

Kleijn, D., Van Langevelde, F., 2006. Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. Basic Appl. Ecol. 7, 201–214.

Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. Proc. R. Soc. B Biol. Sci. 274, 303–313.

Lichtenberg, E.M., Mendenhall, C.D., Brosi, B., 2017. Foraging traits modulate stingless bee community disassembly under forest loss. J. Anim. Ecol. 86, 1404–1416.

Lindenmayer, D., Hobbs, R.J., Montague-Drake, R., Alexandra, J., Bennett, A., Burgman, M., Cale, P., Calhoun, A., Cramer, V., Cullen, P., et al., 2008. A checklist for ecological management of landscapes for conservation. Ecol. Lett. 11, 78–91.

Michener, C.D., 2007. The Bees of the World. Johns Hopkins University Press, Baltimore (953pp.).

Murgueitio, E., Calle, Z., Uribe, F., Calle, A., Solorio, B., 2011. Native trees and shrubs for the productive rehabilitation of tropical cattle ranching lands. For. Ecol. Manag. 261, 1654–1663.

Murray, T.E., Kuhlmann, M., Potts, S.G., 2009. Conservation ecology of bees: populations, species and communities. Apidologie 40, 211–236.

Nelson, K.P., Leroux, B.G., 2006. Statistical models for autocorrelated count data. Stat. Med. 25, 1413–1430.

Nemésio, A., 2012. Methodological concerns and challenges in ecological studies with orchid bees (Hymenoptera: Apidae: Euglossina). Biosci. J. 28.

Nemésio, A., Silveira, F.A., 2006. Edge effects on the orchid-bee fauna (Hymenoptera: Apidae) at a large remnant of Atlantic Rain Forest in southeastern Brazil. Neotrop.

Entomol. 35, 313–323.

Nemésio, A., Silveira, F.A., 2007. Orchid bee fauna (Hymenoptera: Apidae: Euglossina) of Atlantic Forest fragments inside an urban area in southeastern Brazil. Neotrop. Entomol. 36, 186–191.

Nemésio, A., Silveira, F.A., 2010. Forest fragments with larger core areas better sustain diverse orchid bee faunas (Hymenoptera: Apidae: Euglossina). Neotrop. Entomol. 39, 555–561.

Ngo, H.T., Gibbs, J., Griswold, T., Packer, L., 2013. Evaluating bee (Hymenoptera: Apoidea) diversity using Malaise traps in coffee landscapes of Costa Rica. Can. Entomol. 145, 435–453.

Nieh, J., 2004. Recruitment communication in stingless bees (Hymenoptera, Apidae, Meliponini). Apidologie 35, 159–182.

Nuttman, C.V., Otieno, M., Kwapong, P.K., Combey, R., Willmer, P., Potts, S.G., 2011. The utility of aerial pan-trapping for assessing insect pollinators across vertical strata. J. Kansas Entomol. Soc. 84, 260–270.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., et al., 2013. Vegan: community ecology package. http://CRAN.R-project.org/package=vegan (URL HttpCRAN R-Proj. Orgpackage Vegan).

Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? Oikos 120, 321–326.

Olschewski, R., Tscharntke, T., Benítez, P., Schwarze, S., Klein, A.-M., 2006. Economic evaluation of pollination services comparing coffee landscapes in Ecuador and Indonesia. Ecol. Soc. 11, 1–7.

Pardee, G.L., Philpott, S.M., 2014. Native plants are the bee's knees: local and landscape predictors of bee richness and abundance in backyard gardens. Urban Ecosyst. 17, 641–659.

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

Pisanty, G., Mandelik, Y., 2015. Profiling crop pollinators: life history traits predict habitat use and crop visitation by Mediterranean wild bees. Ecol. Appl. 25, 742–752.

Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G., Willmer, P., 2003. Linking bees and flowers: how do floral communities structure pollinator communities? Ecology 84, 2628–2642.

Prado, S.G., Ngo, H.T., Florez, J.A., Collazo, J.A., 2017. Sampling bees in tropical forests and agroecosystems: a review. J. Insect Conserv. http://dx.doi.org/10.1007/s10841-017-0018-8.

Pywell, R.F., Warman, E.A., Carvell, C., Sparks, T.H., Dicks, L.V., Bennett, D., Wright, A., Critchley, C.N.R., Sherwood, A., 2005. Providing foraging resources for bumblebees in intensively farmed landscapes. Biol. Conserv. 121, 479–494.

Radford, J.Q., Bennett, A.F., Cheers, G.J., 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. Biol. Conserv. 124, 317–337.

Ramalho, M., Kleinert-Giovannini, A., Imperatriz-Fonseca, V.L., 1990. Important bee plants for stingless bees (*Melipona* and *Trigonini*) and Africanized honeybees (*Apis mellifera*) in neotropical habitats: a review. Apidologie 21, 469–488.

Ricketts, T.H., 2004. Tropical forest fragments enhance pollinator activity in nearby coffee crops. Conserv. Biol. 18, 1262–1271.

Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., et al., 2008. Landscape effects on crop pollination services: are there general patterns? Ecol. Lett. 11, 499–515.

Rodrigues, M.E., de Oliveira Roque, F., Quintero, J.M.O., de Castro Pena, J.C., de Sousa, D.C., Junior, P.D.M., 2016. Nonlinear responses in damselfly community along a gradient of habitat loss in a savanna landscape. Biol. Conserv. 194, 113–120.

Roulston, T.H., Goodell, K., 2011. The role of resources and risks in regulating wild bee populations. Annu. Rev. Entomol. 56, 293–312.

Rubene, D., Schroeder, M., Ranius, T., 2015. Diversity patterns of wild bees and wasps in managed boreal forests: effects of spatial structure, local habitat and surrounding landscape. Biol. Conserv. 184, 201–208.

Schüepp, C., Herrmann, J.D., Herzog, F., Schmidt-Entling, M.H., 2011. Differential effects of habitat isolation and landscape composition on wasps, bees, and their enemies. Oecologia 165, 713–721.

Scolozzi, R., Geneletti, D., 2012. A multi-scale qualitative approach to assess the impact of urbanization on natural habitats and their connectivity. Environ. Impact Assess. Rev. 36, 9–22.

Sodhi, N.S., Koh, L.P., Clements, R., Wanger, T.C., Hill, J.K., Hamer, K.C., Clough, Y., Tscharntke, T., Posa, M.R.C., Lee, T.M., 2010. Conserving Southeast Asian forest biodiversity in human-modified landscapes. Biol. Conserv. 143, 2375–2384.

Steffan-Dewenter, I., 2002. Landscape context affects trap-nesting bees, wasps, and their natural enemies. Ecol. Entomol. 27, 631–637.

Steffan-Dewenter, I., 2003. Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. Conserv. Biol. 17, 1036–1044.

Swift, T.L., Hannon, S.J., 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. Biol. Rev. 85, 35–53.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batary, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., et al., 2012. Landscape moderation of biodiversity patterns and processes-eight hypotheses. Biol. Rev. 87, 661–685.

Vamosi, J.C., Knight, T.M., Steets, J.A., Mazer, S.J., Burd, M., Ashman, T.-L., 2006. Pollination decays in biodiversity hotspots. Proc. Natl. Acad. Sci. U. S. A. 103, 956–961.

Vélez, D., Pulido-Barrios, H., 2005. Observations on the vertical stratification of orchid bees (Apidae: Euglossini) in a riparian forest of the Colombian Orinoquia. Caldasia 2, 267–270.

Viana, B.F., Boscolo, D., Neto, E.M., Lopes, L.E., Lopes, A.V., Ferreira, P.A., Pigozzo, C., Primo, L., 2012. How well do we understand landscape effects on pollinators and pollination services? J. Pollinat. Ecol. 7, 31–41.

Williams, N.M., Winfree, R., 2013. Local habitat characteristics but not landscape urbanization drive pollinator visitation and native plant pollination in forest remnants. Biol. Conserv. 160, 10–18.

Williams, N.M., Crone, E.E., Minckley, R.L., Packer, L., Potts, S.G., et al., 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. Biol. Conserv. 143, 2280–2291.

Winfree, R., 2013. Global change, biodiversity, and ecosystem services: what can we learn from studies of pollination? Basic Appl. Ecol. 14, 453–460.

Winfree, R., Griswold, T., Kremen, C., 2007. Effect of human disturbance on bee communities in a forested ecosystem. Conserv. Biol. 21, 213–223.

Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G., Aizen, M.A., 2009. A meta-analysis of bees' responses to anthropogenic disturbance. Ecology 90, 2068–2076.

Winfree, R., Bartomeus, I., Cariveau, D.P., 2011. Native pollinators in anthropogenic habitats. Annu. Rev. Ecol. Evol. Syst. 42, 1–22.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. In: Gail, M., Krickeberg, K., Samet, J.M., Tsiatis, A., Wong, W. (Eds.), Mixed effects models and extensions in ecology with R. NY Springer Sci. Bus. Media, N. Y.