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Biological corridors as important habitat structures for maintaining bees in a tropical fragmented landscape

Catalina Gutiérrez-Chacón[1,2] · Carlos Valderrama-A[3,4] · Alexandra-Maria Klein[1]

Abstract
Biological corridors are an important conservation strategy to increase connectivity between populations—mainly vertebrates—in fragmented landscapes, which often require habitat restoration to achieve physical connections. Non-target groups such as bees could benefit from corridors while contributing to the restoration process given their role as pollinators, but little is known about the use of corridors by bees. Here we assessed the habitat value for bees of four biological corridors in the Colombian Andes by comparing bee species richness, community composition and functional diversity between corridors (which had two land-cover sections: riparian forest and restored forest), forest patches being connected by corridors and surrounding pastures. We found a higher species richness in riparian than in restored sections of corridors, which was comparable to that in forest and higher than in pasture. Community composition in forest and riparian sections were similar and differed from that in pasture. In contrast, functional diversity was similar among all land-use types, suggesting a higher species redundancy in forest and riparian corridors, given the higher species richness, compared to pastures. Our results show that riparian corridors are holding forest-associated species that could not survive in pastures, and given the higher redundancy, can significantly contribute to the maintenance of pollination services in fragmented landscapes. Our results also indicate that 13 years of restoration process have not been sufficient to reach reference levels (i.e. forest/riparian) in terms of bee species richness, but the recovery of some forest-associated species points to the potential of biological corridors to functionally connect forest patches.

Keywords Restoration · Species traits · Tropical forest · Connectivity · Colombia

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Introduction

Reestablishing connectivity to enable wildlife movement and the flux of ecological processes is a central approach to mitigate deleterious effects of habitat loss and fragmentation (Crooks and Sanjayan 2006). Biological corridors, which are in general linear landscape elements serving as physical connections between otherwise isolated habitat remnants, have been widely promoted as a strategy to increase landscape connectivity (Beier and Noss 1998; Hilty et al. 2012; Rudnick et al. 2012). While corridors are established with the goal of connecting populations of vertebrates (Bennett 1999), other non-target groups such as insects, which are important providers of ecosystems services (Kremen and Chaplin-Kramer 2007; Losey and Vaughan 2006), could benefit from corridors (Cranmer et al. 2012; Herrera-Rangel et al. 2015; Hill 1995). However, evidence is limited across ecosystems and biological groups (Hunter 2002; Öckinger and Smith 2008).

The implementation of biological corridors often requires the restoration of disturbed habitats, that have potential to become near-natural habitats to achieve physical connections (Hilty et al. 2012). As most wild flowering plant species depends to some extent on wild pollinators for their reproduction (Ollerton et al. 2011), recovery of pollinators is crucial to restore functional plant communities. Nevertheless, few studies have assessed the response of key pollinators such as bees to habitat restoration (but see Williams 2011; Winsa et al. 2017), particularly in the context of biological corridors aimed to connect tropical forest patches.

The tropical Andes reaches its higher complexity in Colombia, resulting in an outstanding ecosystem and high biodiversity (Kattan et al. 2004). A substantial portion of this biodiversity, however, survive in fragmented landscapes as cattle ranching and agriculture have largely diminished natural habitats (Etter et al. 2006; Mendoza et al. 2006). Since the late 90s, an increasing number of initiatives aimed at enhancing landscape connectivity through corridors has been developed in Colombia (Cracco and Guerrero 2004). The *Barbas-Bremen* biological corridors, implemented by the Colombian Biodiversity Research Institute Alexander von Humboldt, has been a national reference given its successful implementation through agreements and incentives to landowners (Gutiérrez-Chacón et al. 2013; Lozano-Zambrano 2009). Four corridors were established to connect two large patches of sub-Andean forests, the Barbas canyon (790 ha) and the Bremen Forest Reserve (747 ha) (henceforth 'forest'), which are isolated mostly by a matrix of pasture for cattle ranching (henceforth 'pasture'). To achieve forest corridors, existing riparian forests strips already connected to the forest patches were used; pasture gaps between forest strips were subjected to an active restoration process with native plant species in 2004 (Vargas 2008). Hence, each corridor is composed of two land-use types, riparian forest (henceforth 'riparian section') and a restored forest (henceforth 'restored section'). Target vertebrate species such as the Cauca Guan (*Penelope perspicax* Bangs), the Red-Howler monkey (*Alouatta seniculus* Linnaeus), Ocelot (*Leopardus pardalis*) and Jaguarundi (*Herpailurus yagouaroundi*) have been reported using the corridors, including the restored sections (Gutierrez-Chacón; Valderrama-A, data no published), but long-term monitoring studies are lacking. A recent study focused on hunting ants (Formicidae), however, suggest that restored sections have not yet reached the necessary conditions to harbor a similar community to that in forests patches (Herrera-Rangel et al. 2015).

Indices based on species richness have commonly been used to describe biodiversity (e.g. Magurran 1988) and how it respond to conservation efforts, including habitat restoration (Wortley et al. 2013). Although species richness is the simplest way to describe community and regional diversity (Gotelli and Colwell 2010, 2001), this measure alone does not provide information on which species compose local communities and how they contribute to ecosystems functioning (Cadotte et al. 2011). The responses of species to environmental conditions and their effects on ecological processes and ecosystem functions are determined by functional traits, which are morphological, physiological, phenological, or behavioral features that have an effect on the organism fitness (Carmona et al. 2016; Kaluza et al. 2018). Thus, quantitative measures of trait variation or multivariate trait differences within a community (referred to as 'functional diversity') have been increasingly used to understand ecosystems functioning (Carmona et al. 2016; Laliberté and Legendre 2010; Petchey and Gaston 2006; Villéger et al. 2008). Combined measures of species richness, community composition and functional diversity can thus provide a comprehensive understanding on how conservation actions influence different aspects of biodiversity (De Arruda Almeida et al. 2018; Díaz and Cabido 2001).

In this study, we assessed the habitat value of the *Barbas-Bremen* biological corridors combining measures of taxonomical, compositional and functional diversity. Specifically, we asked whether bee species richness, community composition, and functional dispersion differ between restored and riparian sections of biological corridors, forest and pasture. Since the abundance of floral resources and the amount of surrounding natural habitat may influence bee diversity at a specific site (Winsa et al. 2017; Gutiérrez-Chacón et al. 2018), we also evaluated these variables to explain the relative importance of habitat succession, resource availability and landscape context for bee diversity and composition.

Materials and methods

Study area and biological corridors

The four biological corridors are located in the Municipality of Filandia, Department of Quindío, in the western versant of the Central cordillera of the Colombian Andes (4° 41 ′N, 75° 40 ′W), 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). Length of corridors connecting the Barbas river canyon and the Bremen-La Popa Forest Reserve vary between 800 and 2500 m, and 50–100 m wide. Distance among corridors range between 500 and 1300 m. Restored sections of corridors connecting riparian forest strips were previously covered with grass (*Pennisetum clandestinum* Hochst. Ex Chiov.) for cattle grazing. In 2010, restored sections had not reached similar conditions in terms of canopy cover as compared to riparian forest strips, showing lowers values

of canopy cover (Herrera-Rangel et al. 2015).We measured canopy cover at three random points in each corridor section with a spherical densiometer (Lemmon Forest Densiometers®), held at 1.5 m. We also found a significantly higher canopy cover in riparian sections ($94 \pm 4\%$, $n = 12$) than in restored sections ($67 \pm 31\%$, $n = 12$) ($t = 2.55$, $df = 8.18$, $p = 0.03$).

Bee sampling

Bees were surveyed in four sites within each land-use type, i.e. forest, pasture, riparian and restored sections of corridors, for a total of 16 sampling sites (Fig. 1). In forest and corridor sections, bees were sampled along edges to avoid differences due to edge effects between riparian strips and continuous forest (Winfree et al. 2007), and because capture rates of bees inside tropical forest are usually low even combining several sampling methods (Brosi et al. 2008). Sites in pasture were distanced at least 100 m from any forest area. In each site, bees were sampled along a 150×4 m plot, which was surveyed during two periods, June–July 2014 and January 2015. In each period, we sampled every site three times combining the following methods: (i) aerial netting for 40 min between 8:00 and 14:30; (ii) four pan-trap sets of three colors each (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 water). Sets of pan traps were placed every 50 m, elevated 3–7 m (except in pasture where bowls were set in the floor) 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 (4 drops) and the other with methyl salicylate (2 drops), located at the transect extremes. These baits are commonly used for studying orchid bees (Brosi 2009a; Nemésio 2012) and similar to Brosi (2009a), we used smaller quantities than have been used in previous studies to avoid deleterious impacts on local orchid bees' populations and to have a smaller radius of attraction. Baited traps were exposed for the same duration as pan traps. Collected bees were pinned for reference collection and voucher specimens of each species will be deposited in the Alexander von Humboldt Institute (Colombia) according to the research permit, and the ICESI University (Colombia). Bees were identified to the lowest possible taxonomic level using available keys and with the help of taxonomic experts. Still, identification to morphospecies (at least genus level) was necessary because many bee species in the tropics are not yet described (Michener 2007).

Trait assignment

For each species, we assigned information on four traits that have been extensively used in previous studies, as they are known to respond to disturbance, extinction sensitivity and ecological interactions: body size, nest location, method of nest construction 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). ITD was measured from pinned specimens and averaged by species from 10 individuals, or the maximum number available. Second, each bee species was classified as below or aboveground nester, the latter group including species that nest in pre-existing cavities in trees and those that burrow tunnels into wood. Third, in terms of method of nest construction, we use the term 'rent' for species that nest in existing holes or cavities either above or below ground; 'construct' for species that build the nest exterior using collected materials, and 'excavate' for species that drill the tunnel/cavity in which the brood cells are constructed (following Williams et al. 2010). Finally, species were classified as social or solitary bees. Only the honeybee *Apis mellifera* (in our sites they are feral) and all stingless bees (tribe Meliponini) were assigned to 'social' to group species with a behavior that improves foraging efficiency (Nieh 2004); all other species were categorized as solitary. Information on sociality, nest location and construction method were mostly obtained from the primary literature and complemented with direct observations in the field, particularly on nesting behavior. 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* spp.), therefore these morphospecies were excluded from our functional diversity analysis.

Functional diversity

We calculated functional diversity at each sampling plot using the functional dispersion metric (FDis), as it accounts for different trait types, including qualitative and quantitative traits. FDis estimates the mean distance of each species from its community centroid in a multivariate space defined by all included traits (Laliberté and Legendre 2010). This metric can account for species abundances by shifting the position of the centroid toward the more abundant species, and weighting distances of individual species by their relative abundances (Laliberté and Legendre 2010). To calculate FDis, we used the function dbFD in package FD, with the Cailliez correction for non-Euclidean distances generated by
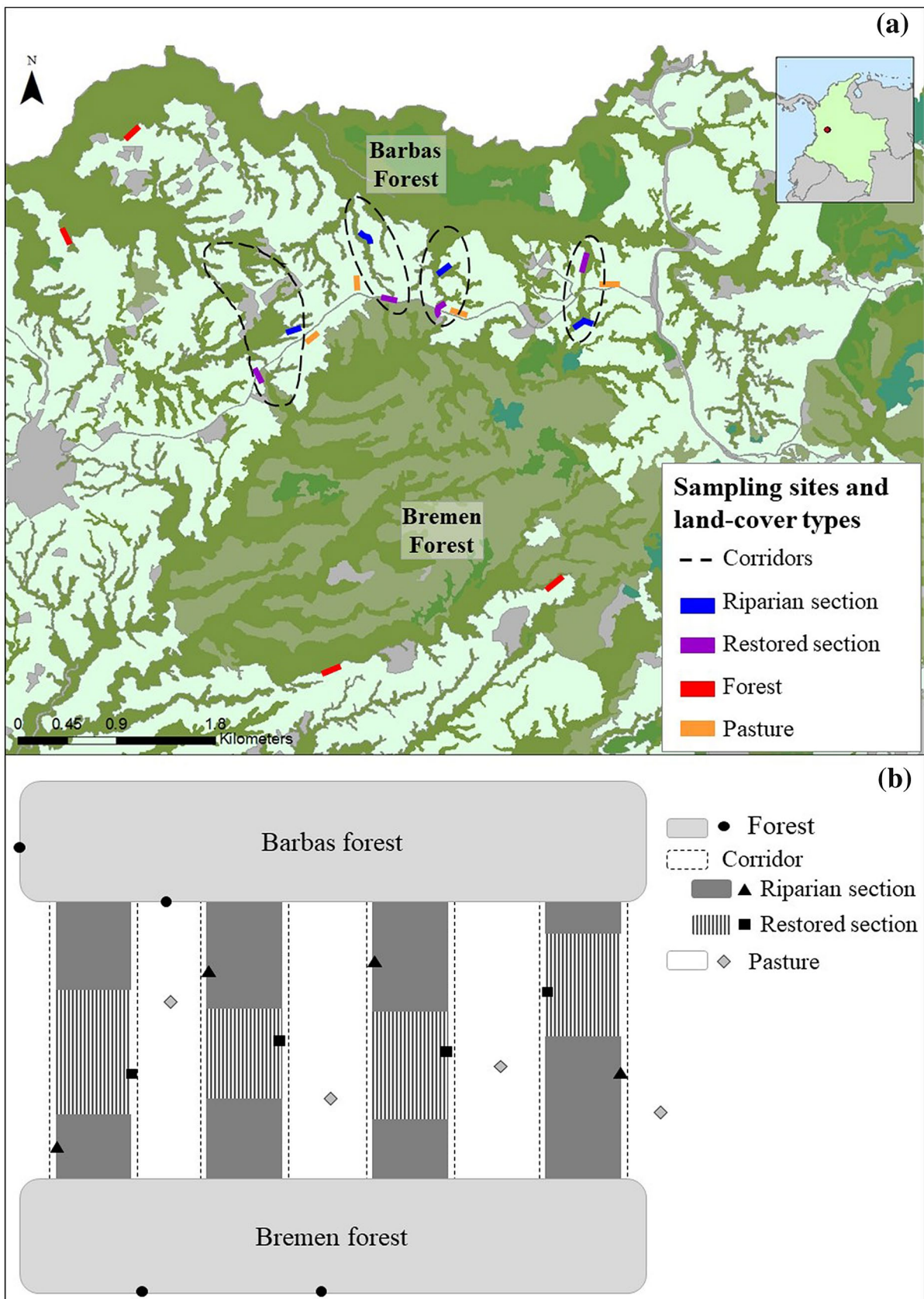
Fig. 1 Map (**a**) and schematic presentation (**b**) of the study area and location of the sampling sites in the studied land-cover types: forest (circles), riparian sections of corridors (triangles), restored sections of corridors (squares) and pasture (rhombus)

inclusion of categorical traits. Traits were given equal weight and species were weighted by their relative abundance.

Local and landscape variables

Both flower abundance (as a local habitat variable) and proportion of forest (as a landscape variable) have been found to influence bee diversity and composition in our study area (Gutiérrez-Chacón et al. 2018). Therefore, we tested whether these two variables differ among the four land-use types (forest, riparian and restored section of corridors, and pasture) to determine whether differences in bee communities among land-use types could be explained by differences in the availability of floral resources or by the amount of natural habitats surrounding the sampling sites. We estimated flower abundance in each site counting individual flowers along 150×2 m transects. This was carried out once per survey and always by the same person. 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 panicle (e.g. *Verbesina nudipens*). Availability of natural habitat was estimated as the proportion of forest within a buffer of a 500 m radius. Land-use information was obtained from http://www.sigquindio.com by webmap service and digitalized with the software ArcGIS® 10.2.1.

Statistical analyses

All bees captured by the three methods across the two surveys were pooled to provide a count of species richness, community composition and FDis per site. We assessed the bee sample completeness in each habitat 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). As sample coverage in each land-use type was over 96%, we used observed rather than extrapolated bee species richness. To assess the recovery of bees in restored sections of corridors and how they differ with the other land-use types, we compared mean species richness and FDis between habitats with a one-way ANOVA. The change in bee community composition between habitats was analyzed using Kruskal Non-metric Multidimensional Scaling (NMDS), calculated as Bray–Curtis distances and with three-axis solution (k = 3), followed by a one-way analysis

of similarities (ANOSIM, Clarke and Gorley 2006) to test for significance of differences and a sequential Bonferroni adjustment of p values as a post hoc. The percentage contribution of each taxon to the average dissimilarity between habitats was assessed with a similarity percentage analysis (SIMPER). Differences in mean flower abundance and forest proportion (within 500 m radius) between forests, riparian and restored section of corridors, and pastures were tested in two separate one-way analysis of variance (ANOVA) and post hoc Tukey tests. All analyses were performed in R 3.3.2 (http://www.r-project.org) except pairwise test (sequential Bonferroni adjustment of p values) which was performed in the program PAST (Ryan et al. 1994).

Results

We collected 658 bees of four families, 27 genera and 41 (morpho) species. Aerial netting and pan traps collected 24 and 23 species, respectively; 14 species were collected by the two methods while nine species were exclusively collected by each method. Eight additional bee species from genus *Euglossa* were found in chemical baited traps. A total of 32 species were recorded in forest, 24 in corridors (22 in riparian sections and 14 in restored sections), and eight species in pasture (Table 1).

Mean species richness was significantly different between forest, pasture, riparian, and restored sections of corridors (F = 23.32, df = 3, p < 0.01). According to the post hoc Tukey tests, riparian sections of corridors showed a significantly higher species richness than restored sections and pastures, but species richness did not differ between restored sections and pastures (p > 0.05). Bee species richness was higher in forests compared to the other habitat types (p > 0.05) (Fig. 2a). Similarly, bee community composition was significantly different among habitats (R = 0.41, p < 0.01, Fig. 2b), but differences were observed between forest and restored sections of corridors, forest and pasture, and pasture and riparian sections (p < 0.05). Bee species composition was not significantly different between the restored and the riparian sections (p > 0.05). The stingless bee species *Trigona amalthea* Olivier and *Scaptotrigona barrocoloradensis* Schwarz where highly abundant in forest, driving to a great extent the difference with restored areas in corridors and pastures. While the stingless bee *Partamona peckolti* Friese was highly abundant in restored sections of corridors, *Lasioglossum* sp4 was dominant in pastures (Online Resource 1, SIMPER results).

Mean values of FDis were not significantly different among land-use types (F = 1.156, df = 3, p = 0.34), even performing the analysis excluding the *Euglossa* species given the uncertainty in their sociality traits (F = 1.555, df = 3, p = 0.25). Although FDis in restored and pasture were lower

Table 1 List of bee species recorded in the study area, with information on functional traits and presence in the four habitat types evaluated: forest patches being connected by corridors (forest), riparian sections of corridors (riparian), restored sections of corridors (restored) and surrounding pastures (pasture). Functional traits included inter-tegular distance (ITD); nest location, either above-ground (above) or below-ground (below) nesting bees; method of nest construction, which could be 'rent' for species that nest in existing holes or cavities, 'construct' for species that build the nest exterior using collected materials, and 'excavate' for species that drill the tunnel/cavity; and sociality, with eusocial species (Apis mellifera and stingless bees (tribe Meliponini)) categorized as 'social' and all other species as solitary

Bee species	ITD	Sociality	Nest location	Nest construction	Forest	Riparian	Restored	Pasture
Apidae								
Apis mellifera	2.68	Social	Above	Rent	x	x	x	x
Centris similis	5.81	Solitary	Above	Excavate			x	
Euglossa cf. variabilis	3.45	NI[a]	Above	Rent		x		
Euglossa crassipunctata	3.52	NI[a]	Above	Rent	x	x		
Euglossa dissimula	3.30	NI[a]	Above	Rent	x			
Euglossa maculilabris	3.53	NI[a]	Above	Rent	x			
Euglossa modestior	3.53	NI[a]	Above	Rent		x		
Euglossa trinotata	3.32	NI[a]	Above	Rent	x		x	
Eulaema cf. meriana	4.96	Solitary	Above	Rent	x			
Eulaema nigrita	5.40	Solitary	Above	Rent		x		
Exomalopsis sp1	1.81	Solitary	Below	Excavate		x		x
Melipona nigrescens	3.04	Social	Above	Rent	x	x	x	
Nannotrigona cf. perilampoides	1.27	Social	Above	Rent	x			
Parapartamona caliensis	1.38	Social	Above	Excavate	x	x	x	x
Paratetrapedia sp1	1.99	Solitary	Below	Excavate		x	x	
Paratetrapedia sp2	1.71	Solitary	Below	Excavate	x			
Paratrigona rinconi	1.26	Social	Above	Construct	x	x		
Partamona peckolti	1.56	Social	Above	Construct	x	x	x	x
Plebeia sp1	1.24	Social	Above	Rent	x	x	x	
Scaptotrigona barrocoloradensis	1.68	Social	Above	Rent	x	x	x	x
Thygater aethiops	3.19	Solitary	Below	Excavate	x			
Trigona amalthea	2.01	Social	Above	Construct	x	x	x	x
Trigona fulviventris	1.39	Social	Above	Rent	x			
Xylocopa lachnea	6.51	Solitary	Above	Excavate	x			
Colletidae								
Hylaeus sp1	1.17	Solitary	Above	Rent	x			
Halictidae								
Augochlora sp1	1.39	Solitary	NI	NI	x	x	x	
Augochloropsis sp1	1.86	Solitary	Below	Excavate	x			
Caenaugochlora sp1	1.24	Solitary	Below	Excavate	x			
Caenohalictus sp1	1.11	Solitary	Below	Excavate	x			
Chlerogella sp1	1.49	Solitary	NI	NI		x		
Habralictus sp1	1.12	Solitary	Below	Excavate	x			
Habralictus sp2	0.97	Solitary	Below	Excavate		x		
Lasioglossum sp1	1.65	Solitary	Below	Excavate	x	x		
Lasioglossum sp2	1.37	Solitary	Below	Excavate	x			
Lasioglossum sp4	0.99	Solitary	Below	Excavate	x	x	x	x
Neocorynura sp1	1.34	Solitary	Below	Excavate	x	x	x	
Neocorynura sp5	1.80	Solitary	Below	Excavate	x			
Neocorynura sp6	0.95	Solitary	Below	Excavate	x	x		
Neocorynura sp8	1.57	Solitary	Below	Excavate	x	x	x	
Pseudaugochlora graminea	2.28	Solitary	Below	Excavate				x
Megachilidae								
Megachile sp1	3.28	Solitary	Above	Rent	x			

NI no available information

[a]Likely solitary. Thus, we first run the analyses with the *Euglossa* species as solitary, and then excluding these species
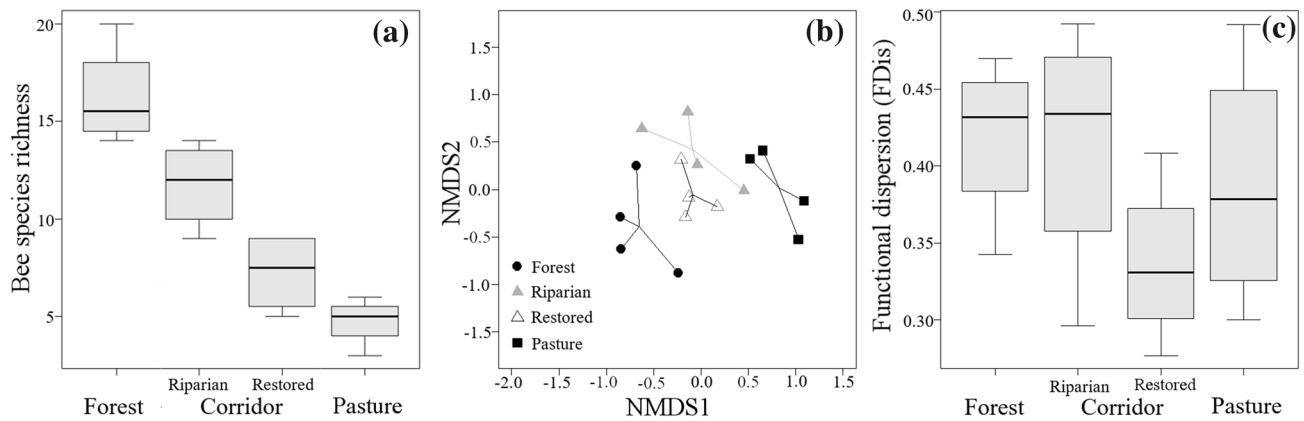
Fig. 2 Comparison of bee species richness (**a**), community composition (**b**) and functional dispersion (FDis) (**c**) between forest, corridors (riparian and restored sections) and pasture. Box indicates quartiles with median marked as a horizontal line. NMDS with a three axis solution (k = 3) and resulting stress of 0.09

than forest and riparian sections of corridors, there was a high variability in FDis values in each habitat type (Fig. 2c).

Looking at the vegetation, mean flower abundance did not differ between forest, riparian and restored sections of corridors and pasture (F = 0.948, p = 0.45). However, differences were found to be significant in flower composition between the habitat types (ANOSIM R = 0.40, p ≤ 0.01), specifically between pasture and the other habitat types (Online Resource 2). Similarly, the proportion of forest within a 500 m radius around the study sites were also different between habitat types (F = 4.94, p = 0.02), being significantly higher around forest patches (Mean ± SD = 0.44 ± 0.12) than around pastures (Mean ± SD = 0.24 ± 0.09) (p < 0.05). The proportion of surrounding forest was not different between restored and riparian sections of corridors.

Discussion

Actively restored sections of corridors supported communities of wild bees with lower species richness than those found in the riparian sections of corridors, and similar to those in pastures. Thus, it appears, on the one hand, that restoration time of 13 years is not long enough to harbor several forest-associated species. On the other hand, a lack of protection of some restored areas from cattle intrusion may also be delaying the colonization of these areas by plants and bees. However, the similarity in species composition between restored and riparian sections suggest progress towards the recovery of some species found in the reference systems (i.e. riparian). Likewise, although species richness was higher in forest than in both sections of corridors, the comparable community composition between forest and riparian sections, and the significant differences between forest and pastures, indicate that several forest-associated

species are using well preserved sections of corridors, while pastures seems to be hostile habitats for such species. Functional dispersion, however, did not indicate significant differences between habitat types. This suggest that communities with different species composition may have similar functional diversity, and higher species richness is not necessarily coupled with higher functional dispersion (Cadotte et al. 2011).

Differences in species richness between restored and riparian sections of corridors were not driven primarily by differences in flowering-plant communities, as floral resources availability (flower abundance and flower composition) did not differ between these habitat types. Likewise, proportion of surrounding forest was similar between riparian and restored sections. Thus, differences in bee community richness likely arose from physical differences between restored and riparian sites. Canopy cover was lower in restored sections than in riparian sections, where mature trees were more often observed. This point to other resources such as nesting sites as limiting factors in restored areas. Many bee species depend on a wide variety of nesting resources such as trees, dead wood and twigs, which are more likely found in more advanced successional stages of vegetation. Therefore, the recovery of bee communities in the restored areas also depends on the recovery of such resources. In our study, recovery time of the restored sections may not be sufficient to successfully recuperate several bee species and the resources they require. Contrasting with our results, Williams et al. (2011) found that after 6 years of restoration of riparian vegetation in California, bee species richness was similar between restored and reference sites, although community composition was different. Although recovery time of bee communities might be context-dependent, more research is needed to better understand bee responses to habitat restoration. Information from

other insect taxa show that recovery of reference communities in restored areas can be a slow process. For instance, Audino et al. (2014) found that after 18 years of restoration of tropical low-land rainforest (from pastures), dung beetle (Coleoptera: Scarabaeinae) communities were still depauperated showing no progress from the starting point. Likewise, the only published study conducted in the biological corridors here evaluated also revealed that restoration time has not been enough to recover hunting ant communities in restored sections of corridors, as higher species richness were found in riparian forest (our riparian sections of corridors) after 5–7 years of restoration process (Herrera-Rangel et al. 2015).

Forest patches showed the highest bee species richness compared to corridors and pastures. This pattern is likely the result of higher amounts of forest cover in the surrounding landscape of forest sampling sites, from the patch itself but also from other forest areas. Previous research has demonstrated that bee species richness is enhanced in landscapes with a higher proportion of natural habitats (Brosi 2009b; Park et al. 2015; Gutiérrez-Chacón et al. 2018; Steffan-Dewenter 2002; Viana et al. 2012). Natural areas are important for the survival of bees in human-dominated landscape as they offer permanent food and nesting resources (Garibaldi et al. 2011). Particularly in the Neotropics, the diversity of an important group of pollinators of wild and cultivated plants, the stingless bees (Tribe Meliponini, Roubik 1992, 1995), has been strongly and positively related to the availability of forest areas (Brosi 2009b; Gutiérrez-Chacón et al. 2018). Most of the stingless bee species required trees for building their nests, which are located either in limbs, cavities or between the roots (Roubik 1992). In addition to higher availability of nesting resources in forest, these can offer diverse and abundant floral resources meeting high food demands of large colonies, as all stingless bees are eusocial (Michener 2007).

Differences in community composition between pastures and forests may reflect differences in flower composition but also support the idea that the scarcity of above-ground nesting sites in intensive-production areas act as a strong environmental filter on bee communities (Forrest et al. 2015; Williams et al. 2010). *Lasioglossum* sp4 was dominant in pastures while almost absent from forest samples, which can be explain by the need of species in this genus for bare soil to nest, making them common inhabitants of productive lands (Basu et al. 2016; Ngo et al. 2013). On the contrary, the stingless bee species *T. amalthea* and *S. barrocoloradensis*, which require trees for nesting, dominated forest samples. As those species also dominated riparian sections of corridors, no differences in species composition were observed with forest, indicating that well conserved riparian forest-strips are suitable habitats for forest-associated bees. However, significant differences between forest

and restored sections of corridors suggest that more time is needed for the restored sites to develop suitable nesting sites for stingless bees, specifically large trees, which can more likely offer proper nesting conditions for the diverse requirements of such bees. Yet, the similar bee community composition between riparian and restored sections of corridors reveals some progress towards forest-like conditions of restored sites. This is important particularly for stingless bees, since new nests are usually established only after multiple trips from the old nest to provide it with stored food (Roubik 1992), so genetic flux between isolated and distant habitat patches would be restricted by the low flying capacity of most stingless bees given their small body size (Araújo et al. 2004). Therefore, the establishment of stingless bees´ colonies along biological corridors is a positive signal on the potential role of corridors as landscape linkages for otherwise isolated populations.

Despite differences in species richness between forest, corridors (riparian and restored sections) and pasture, these differences did not translate into differences in functional dispersion. Our results parallel previous findings in which species of pollinators were higher in less intensively managed habitat types, but no differences in functional dispersion were observed (Forrest et al. 2015; Rader et al. 2014). Although positive linear relationships between species richness and FD have been observed, that trend lacks of universal support (Cadotte et al. 2011). That functional diversity remain unchanged despite the loss of species richness may indicate the coexistence of functionally redundant species in the community (Cadotte et al. 2011; Petchey and Gaston 2006). As high functional redundancy buffers ecosystem functioning against environmental changes (Laliberté and Legendre 2010; Tscharntke et al. 2012), forest (with highest species richness) are less likely to decline in the pollination function if some species are lost. Likewise, as corridor sections showed intermediate levels of taxonomical diversity between forest and pastures, their functional redundancy would be higher than in pastures, which highlight their potential contribution to the maintenance of pollination services in fragmented landscapes.

The ability to detect functional differences between species increases with the number of functional traits included in the calculation of functional diversity (Cadotte et al. 2011). As we only included four traits, the likelihood of classifying species as functionally redundant could be high. Yet, there is no a 'correct' number of traits and rather all traits functionally important should be account for (Petchey and Gaston 2006). Although life-history and behavioral traits here included may be relevant to bee conservation and their role as pollinators (Williams et al. 2010), their number was limited by the ease to measure them (e.g. body size) and the available information in literature, which are a general limitations for trait-based approaches (Lichtenberg et al. 2017).

Moreover, some individuals not identified to species but genus level were discarded from the analyses, as information on nest location or sociality was not consistent across all species in the genus (e.g. *Augochlora* and *Chlerogella*). Thus, a better understanding on how functional diversity varies with environmental conditions will require improving of our taxonomic knowledge, particularly of tropical bees (Gonzalez et al. 2013), and the characterization of traits that most importantly influence fitness and the ecosystem functions (Carmona et al. 2016), in this case pollination.

In conclusion, restored sections of corridors appear to be slowly progressing towards the reference riparian sections, although differences in species richness are still significant. Compared to large forest patches, biological corridors immersed in pasturelands appear to have limited carrying capacity, likely due to less available habitat area. However, our results suggest their potential value as habitat for several forest-associated species that otherwise could not find enough resources in open pastures. This is the case of some stingless bee species, whose prevalence in forests and riparian sections of corridors drove the difference in terms of community composition with open pastures. As the restoration process advance, restored sites can improve their offer of nesting sites, in particular, consolidating the role of corridors as linkages in the landscape for bee populations. Our results also show that functional diversity was decoupled from species richness and it was rather similar among habitat types, although the inclusion of more functional-traits and a better taxonomical information in the calculation of functional diversity could influence this result. Still, our findings point to the higher functional redundancy of forest and corridors, and underscore the importance of using complementary biodiversity metrics as one dimension of biodiversity was not a good surrogate for another (Audino et al. 2014; Cisneros et al. 2015).

Compliance with ethical standards

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

Informed consent Informed consent was obtained from all individual participants included in the study.

Research involving human participants and/or animal This article does not contain any studies with human participants or animals performed by any of the authors.

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