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

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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 spillover 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.