Vertical diversity patterns and biotic interactions of trap-nesting bees along a fragmentation gradient of small secondary rainforest remnants

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Abstract – Secondary rainforest remnants might contribute to biodiversity conservation and preservation of healthy interspecific interactions with ongoing fragmentation. We studied the vertical distribution of trap-nesting bees along a fragmentation gradient of secondary forest remnants in Costa Rica. Fragment size did not affect bee abundance, diversity, and parasitism and mortality rates. However, height and edge effects influenced bee communities. Bees were more abundant in the canopy and the understory compared to an intermediate height, and bee diversity was higher in the canopy. Tree location (forest edge, intermediate distance, forest center) did not affect abundance but did affect bee diversity since most species preferred the forest interior. The cuckoo bees *Aglaoelissa duckei* and *Coelioxys* sp. 1 only partly followed their hosts' patterns, two *Centris* species. We conclude that an increasing amount of edge habitat will have negative consequences for bee communities and will reduce the conservation value of secondary forest fragments.

fragmentation effects / parasitism rate / mortality rate / secondary forest fragments / vertical stratification

1. INTRODUCTION

Global environmental change threatens biodiversity, species persistence and distributions as well as antagonistic and mutualistic interactions (Barlow et al. 2007). In the tropics, ongoing deforestation results in a mosaic of forest fragments distributed between pastures and plantations (Vitousek et al. 1997; Tilman et al. 2001). Habitat fragmentation is a major threat to biodiversity (Davies et al. 2000; Fahrig 2003) as it leads to declines in species richness and populations (Donovan and Flather 2002) and loss of genetic diversity (Gibbs 2001) and to disruption

of trophic interactions, e.g., predation and parasitism. The remaining forest fragments are influenced by edge effects because of the new matrix. Edge effects in turn are known to change both the microclimate and the biotic communities (Laurance et al. 2011), which is, however, dependent on edge structure and the difference between matrix and habitat (Didham and Lawton 1999; Laurance et al. 2011). On the other hand, secondary forest fragments can be valuable for biodiversity (Turner and Corlett 1996), since their coverage is expanding while that of continuous primary forest habitat is limited, and they enhance landscape connectivity (Barlow et al. 2007).

In tropical rainforests, arthropods have been shown to be equally or more diverse in the canopy than in the understory (Erwin 1982; Stork and Grimbacher 2006), but canopy diversity, especially its community patterns, is understudied (Kays and Allen 2001; Ulyshen et al. 2010). Some

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studies have found vertical stratification of bees with respect to flight height and floral resource use (Frankie and Coville 1979; Roubik et al. 1982; Bawa 1990; Ramalho 2004; Ulyshen et al. 2010), whereas others have not (Roubik 1993). Many trap-nesting bees in tropical rainforests prefer the canopy, at least in primary forest and large fragments (Morato and Campos 2000; Thiele 2003). However, studies along a fragmentation gradient of small secondary forest remnants are lacking.

Most studies investigating whole communities of trap-nesting bees with large sample sizes in tropical countries have been done in agro-ecosystems or along land-use gradients (Klein et al. 2002; Tylianakis et al. 2005; Klein et al. 2006), but few studies have investigated the trap-nesting bee communities in tropical forests (Morato and Campos 2000; Morato 2001; Thiele 2003; Loyola and Martins 2006; Loyola and Martins 2011). None of the studies investigated a fragmentation gradient that included different tree locations in order to measure edge effects of secondary forest remnants, which is important due to their potential for conservation and maintenance of ecosystem services for agricultural areas (Klein et al. 2003; Brosi et al. 2007a; Ngo et al. 2013).

Bees are the most important group of pollinators (Didham et al. 1996; Ollerton et al. 2011), especially for native plants in tropical forests, where animal-mediated pollination is more frequent than in temperate regions (Bawa 1990; Ollerton et al. 2011). Trap-nesting bees inhabiting native forest are considered sensitive to habitat fragmentation (Morato and Campos 2000) since they depend on nesting sites (Potts et al. 2005), materials for nest construction such as mud and plant materials (wood chips, resin, leaves, oil) (Taki et al. 2008), and food resources (Tscharntke et al. 1998). There is less knowledge of species interactions (Godfray et al. 1999) especially in the canopy. Trap nests are well suited for gaining information on biodiversity, abundance, and community parameters such as mortality and parasitism rates (Tscharntke et al. 1998) and were used in a variety of studies to measure habitat quality (Loyola and Martins 2006, 2011; Tylianakis et al. 2006, 2007). Higher trophic levels are more affected by habitat modification (Valladares et al. 2006; Fenoglio et al. 2012)

because their interactions are more sensitive to phenology, behavior, physiology, and abundances of multiple species (Suttle et al. 2007; Tylianakis et al. 2007).

This study investigated the vertical distribution of bee communities, single species patterns, and community parameters along a fragmentation gradient including locations at different distances from the forest border of small secondary forests in the Sarapiquí region in Costa Rica. We hypothesized that larger fragments would contain a more species-rich and abundant bee community that would sustain a more abundant and diverse community of antagonists and therefore higher parasitism rates. We also expected lower mortality rates in larger fragments because of a higher variety of microhabitats and more natural microclimatic conditions. We expected a higher abundance and species diversity in the canopy and at the forest edge, although individual species may respond differently. We assumed that mortality rates would be lower in the forest center compared to the edge and that the rate would not respond to different heights, because this would be species dependent. Concerning the parasitism rate of *Centris* species and their cuckoo bees, we expected that cleptoparasites would be more affected by fragmentation due to their sensitivity to environmental changes and their higher trophic level (Holt et al. 1999).

2. MATERIAL AND METHODS

2.1. Study region and study sites

This study was conducted in lowland rainforest fragments in the Sarapiquí region in northeastern Costa Rica during a 1-year period, between February 2011 and February 2012. To test for the effects of fragment size, we selected 12 differently sized secondary forest fragments (0.9–16.62 ha) with no recent management activities and with at least a 2-km distance between each. To minimize the influence of landscape and of foraging bees, every fragment had a similar landscape context with a forest cover of approximately 30 % forest cover and 70 % coverage of plantation (banana, pineapple, ornamental plants) or pasture in a 2-km radius.

2.2. Study design

In each of the 12 fragments, three trees, one in the forest fragment center, one at an intermediate distance, and one at the forest edge, were selected along a transect line to measure the influence of edge effects. We selected trees with a low and comparable vine cover. None of the selected trees flowered during the study period, and there was no mass flowering observed in the direct neighborhood. Overstory density increased from the edge to the center of forest fragments, but not with fragment size.

We also did not include % cover of understory in our analysis, because it is significantly negatively related to the fragment size and also to the forest interior. At each tree, three packages of three trap nests were placed at three heights (2, 10, and 20 m), amounting to 27 trap nests per fragment. Trap nests consisted of a PVC tube filled with different diameters of about 120 reed internodes (*Phragmites australis*) cut to 20 cm length (Tscharntke et al. 1998).

During regular inspections (1–2 months) completed nests, recognized by closures of soil or plant materials (Krombein 1967), were collected and replaced by empty internodes of similar diameters. In the lab, nests were opened and identified to morpho-species; living, dead, and parasitized cells were counted in order to calculate number of brood cells and the mortality and parasitism rates. Only cells containing bees that died of unknown causes, most likely due to mold or other pathogenic microbiota (Keller et al. 2013), were included in the mortality rate. The nests were then placed in pieces of transparent plastic tube and closed with cotton at both ends. After emergence, adults were killed for later identification to species or morpho-species level.

2.3. Statistics

The Shannon index and the incidence-based coverage estimator (ICE) were calculated with the software EstimateS (Vs. Win 910, 2014).

For the variables (1) number of brood cells, (2) parasitism rate, (3) mortality rate, (4) raw species richness, (5) mean ICE, and (6) Shannon index, we calculated linear mixed effect models containing all interactions of size, location, and height with

the statistical program R (R Development Core Team VS R 3.0.3). The number of brood cells was analyzed with a Poisson model, whereas the mortality and parasitism rates were analyzed with a binomial model and the species diversity measures with a Gaussian model (Crawley 2002). To account for the nested design, the random term “fragment” was included. Where necessary, an overdispersion correction term was included in the final models. During model selection, we also tested for the effects of overstory density on abundance, diversity and parasitism, and mortality rate. Since it never was one of the most important factors and was related to tree location, we did not include this factor in our final models.

The effects of fragment size on the variables (1) species richness per fragment, (2) percentage of *Centris* cells of all brood cells, and (3) percentage parasitism per fragment were analyzed with linear models. The same procedure was chosen to analyze the preferences of individual species with sufficient sample size with respect to fragment size, tree location, and height. The best models were chosen according to the lowest AIC (Burnham and Anderson 2002).

3. RESULTS

We found a total of 2340 brood cells of 16 different bee species, comprising 10 non-parasitic and 6 parasitic bee species. Fragment size alone had no impact on the response variables (Table 1). Location (tree 1 at the forest edge, tree 2 at an intermediate distance, tree 3 at the forest center) and height (2, 10, and 20 m) had significant effects on the response variables. $\text{1x}^{\text{(Xin_styles)}}$

3.1. Fragment size effects on species diversity, percentage of *Centris*, and parasitism rate

Fragment size did not affect species diversity calculated per fragment (species richness: $P=0.112$; ICE: $P=0.256$; Shannon: $P=0.09$). The percentage of the most abundant genus and the parasitism rates calculated per fragment did not respond to fragment size (% *Centris*: $P=0.25037$; parasitism rate: $P=0.835090$).

Table I. Effects of fragment size, tree location, and height on bee abundance, parasitism and mortality rates, species richness, ICE, and Shannon diversity index.

Response variable	Explanatory variable	Chisq	<i>P</i> value
Abundance	Size	0.035	0.85155
	Height	29.8031	3.376e-07***
	Tree	/	/
	Height×size	7.0591	0.02932*
Parasitism rate	Size	/	/
	Height	7.1048	0.02866*
	Tree	5.3139	0.07016
	Size	3.9077	0.04806*
Mortality rate	Height	8.6998	0.01291*
	Tree	/	/
	Size	/	/
Species richness	Height	19.3844	6.176e-05***
	Tree	1.9138	0.3841
	Size	1.4499	0.2285514
ICE	Height	265.9556	<2.2e-16***
	Tree	51.0429	8.245e-12***
	Height×size	17.35	0.0001708***
	Height×tree	42.7262	1.179e-08***
	Size×tree	4.7773	0.0917519
	Size	3.5135	0.06087
	Height	638.3852	<2.2e-16***
Shannon index	Tree	51.0422	8.248e-12***
	Height×size	18.5935	9.172e-05***

P* < 0.05; **P* < 0.001

3.2. Vertical distribution of bee abundance and diversity patterns

Bee abundance was significantly lower at 10 m compared to other heights (*P* < 0.001, Figure 1).

Species richness was lower at 10- and 20-m heights (*P* < 0.001, Table I), whereas ICE and Shannon index indicated a higher species diversity at 10 and 20 m (ICE: *P* < 0.001; Shannon: *P* < 0.001, Figure 2). We found a significantly lower species diversity at 10 and 20 m in larger compared to smaller fragments (ICE: 10 m: *P* < 0.05, 20 m: *P* < 0.001; Shannon: 10 m: *P* < 0.05, 20 m: *P* < 0.001). With ICE, diversity was estimated to be lower at heights of 10 and 20 m on both inner trees (see Table I, *P* < 0.01 for 10 m at the intermediate distance, *P* < 0.001 for 20 m at the intermediate tree, and 10- and 20-m heights for the inner tree).

Overall species diversity was higher in the canopy, but individual species responded differently (Figure 3). *Centris labrosa* preferred the forest understory at 2 m for nesting (*P* < 0.001), and *Centris analis* followed the general abundance pattern, preferring 2 or 20 m (*P* < 0.01). The two parasitic species *Aglaoelissa duckei* and *Coelioxys* sp. 1 followed the patterns of their hosts *C. labrosa* and *C. analis* and preferred to attack nests at 2 m (*A. duckei*: *P* < 0.05, *Coelioxys* sp. 1: *P* < 0.01). In contrast, *Hylaeus* sp. 1 was a canopy nester (*P* < 0.05) and did not construct a single nest at 2 m, which was also the case for *Anthodiocetes gualanense* (*P* = 0.0552).

3.3. Edge effects on bee abundance and diversity patterns

The different tree locations did not affect overall bee abundance (Table I), but species diversity

Figure 1. Vertical distribution of bee abundance (** $P<0.001$, height in meters).

was higher in the forest center compared to the forest edge. All three diversity variables (raw species diversity, ICE, and Shannon index) responded positively to the forest center (observed species richness: $P<0.05$; ICE: $P<0.001$;

Shannon: $P<0.001$; Figure 4). ICE and Shannon estimated species diversity to be higher at the intermediate tree (ICE: $P<0.001$; Shannon: $P<0.05$). However, larger fragment sizes resulted in a lower ICE at the forest center ($P<0.05$, Table I).

Most species preferred forest conditions, but individual species responded differently. We found that *Megachile* sp. 2 ($P<0.05$), *Hylaeus* sp. 1 ($P<0.05$), *C. labrosa* ($P<0.05$), and their cleptoparasites *A. duckei* ($P<0.01$) and *Coelioxys* sp. 1 ($P<0.05$) preferred the forest interior for nesting (Figure 5), whereas *C. analis* ($P<0.05$) and *Tetrapedia maura* ($P<0.01$) preferred edge conditions.

3.4. Effects of fragment size, tree location, and height on the mortality and parasitism rate

Mortality rates did not change significantly with fragment size but tended to increase in larger fragments ($P=0.0703$). However, height significantly affected mortality rates, being highest in the understory and lowering with height, slightly non-significant for 10 m ($P=0.0637$) but significant for 20 m ($P=0.0124$, Figure 6).

Parasitism rates were not significantly related to fragment size and location but tended to be

Figure 2. Vertical distribution of species diversity with **a** the estimator ICE and **b** Shannon diversity index (** $P<0.001$, height in meters).

Figure 3. Vertical distribution of the abundance of individual species (*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$, height in meters).

lower at 10- and 20-m heights (Table I). As shown in Figure 6b, the parasitism rates of the cuckoo bees *A. duckei* and *Coelioxys* sp. 1 on both *Centris* species were higher in the forest center than at the edge ($P < 0.05$).

4. DISCUSSION

4.1. Fragment size effects on species diversity, percentage of *Centris*, and parasitism rate

Contrary to our expectations, fragment size had no effect on bee diversity. Previous studies in tropical systems relating bee diversity to size have revealed variable results, some showing an

increase in diversity with size (Chacoff and Aizen 2005; Brosi 2009; Meneses Calvillo et al. 2010) and others finding no relationships between fragment size and diversity (Brosi et al. 2007b; Gazola and Garófalo 2009). This variability could be due to many factors, since little is known about the nesting behavior of bees in tropical forests. The presence or absence of specific tree species, occurrence of natural nesting sites, and food availability (Tscharntke et al. 1998; Viana et al. 2001; Morato and Martins 2006) among other factors can affect bee species diversity unrelated to fragment size. However, our small-sized fragments appear to offer nesting opportunities and food resources for bees since we found similar species numbers as Morato and Campos (2000) in large

Figure 4. Edge effects on species diversity with **a** the estimator ICE and **b** Shannon diversity index (*** $P < 0.001$; * $P < 0.05$; tree 1 at the forest border, tree 2 at intermediate distance, and tree 3 in the forest center).

Amazonian fragments. Possibly size would have had a significant impact if we had included larger fragments, since the latter contain more tall dead trees with nesting sites for bees (Didham and Lawton 1999; Thiele 2003; Morato and Martins 2006).

In small fragments, there is often a dominance of few abundant species (Laurance et al. 2002; Zhu et al. 2004), but the amount of *Centris* was not influenced by size since all our fragments were relatively small.

We expected that antagonists suffer more from habitat fragmentation (Valladares et al. 2006; Fenoglio et al. 2012), but parasitism rates did not respond to fragment size. Fragments in our size range seem to provide sufficient hosts, but further research is needed to see whether a size effect would occur when larger fragments or primary forest are included.

4.2. Vertical distribution of bee abundance and diversity patterns

The higher bee abundances in the understory can be explained through the abundant *C. labrosa* and their cleptoparasites *A. duckei* and *Coelioxys* sp. 1. There were less abundant species like *Hylaesus* sp. 1 and *A. gualanense* that preferred the canopy, and *C. analis* was abundant in the understory and the canopy. However, none of the

species preferred the intermediate height of 10 m. The reasons for strata preference could be microclimate and natural nesting availabilities (Morato 2001; Thiele 2003). Natural cavities are possibly more abundant in the canopy due to sunlight exposure whereas higher humidity in the understory leads to the higher activity of fungi (Morato and Martins 2006).

Species richness declined with height, which was opposite to the trends of the ICE and the Shannon index. The latter two variables are more sensitive for changes in community structure since they include species numbers and abundance data and because of their better suitability for greater numbers of rare species (Pianka 1966). In this study, the dominant *Centris* species and their related cleptoparasites mainly occurred at the 2-m height, whereas all other species were less abundant and mainly occurred at other heights. We conclude that species diversity of trap-nesting bees was higher at the canopy level. The abundant species in the understory can be considered rainforest specialists, e.g., *C. labrosa* (Thiele 2003), whereas the majority of bees preferred the sunny dry conditions in the canopy. Moreover, bee pollination is especially predominant in the canopy of tropical lowland forest (Bawa et al. 1985), so nesting closer to their food resources might be more attractive. Our results suggest that the canopy preference could also be due to the

Figure 5. Edge effects on the abundance of individual species (*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; tree 1 at the forest border, tree 2 at intermediate distance, and tree 3 in the forest center).

lower mortality rate and the lower risk of being parasitized. Previous studies investigating the vertical distribution of trap nesting bee communities in tropical rainforest found a canopy preference by bees in primary forest and large fragments (Morato 2001; Thiele 2003) like we did in small

secondary forest remnants. Therefore, it is important to monitor bees and other insects at the canopy level.

Species diversity at 10 and 20 m was lower in larger compared to smaller fragments and at the forest fragment center at 10 and 20 m, which can

Figure 6. **a** Mortality rate in relation to different heights (2, 10, 20 m). **b** Parasitism rate of *Centris* and their cuckoo bees in relation to different locations in the forest (tree 1 at the forest border, tree 2 at intermediate distance, and tree 3 in the forest center; * $P < 0.05$).

be explained through our study design. Ten and 20 m have different microclimatic conditions depending on forest structure since canopy height is lower in smaller fragments and at the edge (Didham and Lawton 1999). The trap nests at 20 m at the edge and in smaller fragments were more sun exposed than those in larger fragments or in the forest center, where there are taller trees, resulting in more humid conditions, which affects nesting success. Bees also find more natural nesting sites in larger fragments and the forest center, which could result in a lower colonization probability of trap nests (Viana et al. 2001).

4.3. Edge effects on bee abundance and diversity patterns

Total bee abundance did not vary from edge to center due to opposing preferences of individual species. *C. labrosa*, *Megachile* sp. 2, *Coelioxys* sp. 1, *A. duckei*, and *Hylaeus* sp. 1 preferred the forest interior, whereas *T. maura* and *C. analis* preferred the forest edge. This suggests that single species responses can be more informative than aggregated abundance and richness data in tropical forest remnants (Nemésio and Silveira 2006), and species-based analyses can help to understand

contradictory responses to habitat fragmentation in the tropics.

Species diversity was higher in the forest center, and most bees preferred forest conditions, probably due to the more stable microclimatic conditions (Didham and Lawton 1999). Bee diversity was shown to be higher in continuous forest and natural gaps in the Amazon, and bees are highly sensitive to fragmentation (Morato and Campos 2000). With ongoing deforestation and fragmentation and the resulting increase of edge conditions, aboveground nesting solitary bees could become more threatened in the future.

The lower ICE estimates at the inner trees in larger fragments could be the result of more available natural nesting cavities inside larger fragments with taller trees and a higher amount of dead trees. The availability of natural nesting sites is known to affect nesting frequency in trap nests (Viana et al. 2001).

Most study species preferred the forest center, but a few species preferred edge conditions, e.g., *C. analis*, which have a broad geographical range from Brazil to Mexico (Moure 1960) and are known to be remarkably generalized (Vieira de Jesus and Garófalo 2000; Roubik and Villanueva-Gutiérrez 2009). These two species seem to be better adapted to tolerate steeper temperature and

humidity fluctuations and will probably profit from ongoing fragmentation and increased edge conditions. Morato and Campos (2000) also found that despite an overall preference for continuous forest and natural gaps, some species preferred disturbed habitats and deforested areas. With respect to the effects on pollination, we conclude that small forest fragments can help to sustain bee communities and to stabilize pollination services, which has been shown for stingless bees (Brosi et al. 2007b). However, further fragmentation leading to an even greater increase in edge conditions will negatively affect trap-nesting bees.

4.4. Effects of fragment size, location, and height on the mortality and parasitism rate

Mortality rates tended to increase in larger fragments which is probably due to higher humidity that results in a higher fungal infestation rate of nests (personal observation). However, larger fragments contain more tall trees (Didham and Lawton 1999), providing natural nesting opportunities for the majority of bees (Morato and Martins 2006), so that larger fragments may be more suitable for some of the scarcer species. Tree location did not affect mortality rates, because of the preferences of individual species. Species probably prefer certain locations due to their advantage in survival, which is dependent on individual species traits (Nemésio and Silveira 2006).

The most interesting pattern was the significantly lower mortality in the canopy. Most studied bee species preferred the canopy (Morato 2001; Thiele 2003), probably because it provides better conditions for survival as shown in our data. It is possible that the drier sunnier conditions in the canopy help to reduce infestations by fungi. It is also probably easier for bees to find nectar and pollen resources in the canopy (Bawa 1990), although this explanation has been questioned by some authors (e.g., Roubik 1993).

The overall parasitism rate was not related to fragment size or tree location but did show a tendency of being higher in the understory, which is probably due to the dominance of *Centris* and their related cleptoparasites. The higher parasitism

rate of the two cuckoo bees *A. duckei* and *Coelioxys* sp. 1 on *C. labrosa* and *C. analis* in the forest center was interesting because it did not follow the patterns of host abundance. *C. labrosa* preferred the intermediate distance between edge and forest center and *C. analis* the forest edge. So the two parasite species seem to prefer the forest center for other reasons, for example, the higher humidity and more stable temperature conditions (Didham and Lawton 1999) as long as they find enough hosts. This concurs with the hypothesis that species at higher trophic levels are more susceptible to habitat fragmentation (Nouhuys 2005; Valladares et al. 2006). We conclude that ongoing fragmentation and deforestation will affect diversity and trophic interactions of bee communities, with currently unknown long-term consequences for the survival of forest specialists and plant-pollinator interactions.

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Schémas de diversité verticale et interactions biotiques chez les abeilles nichant dans des nids artificiels, le long d'un gradient de fragmentation de petites parcelles résiduelles de forêt pluviale secondaire

effets de la fragmentation / taux de parasitisme / taux de mortalité / strate verticale

Vertikale Biodiversitätsmuster und biotische Interaktionen von nisthilfenbewohnenden Bienen entlang eines Fragmentierungsgradienten von kleinen Sekundärwaldfragmenten

Fragmentierungseffekte / Parasitierungsrate / Mortalitätsrate / Sekundärwaldfragmente / vertikale Stratifizierung

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