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RESEARCH ARTICLE

Responses of bees to habitat loss in fragmented landscapes of Brazilian Atlantic Rainforest

Patrícia A. Ferreira · Danilo Boscolo · Luísa G. Carvalheiro · Jacobus C. Biesmeijer · Pedro L. B. Rocha · Blandina F. Viana

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Abstract

Context Loss of natural habitat can isolate pollinator populations and negatively affect sexual reproduction of animal-pollinated plants.

Objective We evaluated how the loss of natural forest affects pollinator diversity in the understory of the Atlantic Rainforest in Northeastern Brazil.

Methods We focused on bees, the main group of pollinators for angiosperms. We assessed how changes in forest cover at regional (36 km^2) and local (0.36 km^2) scales affect bee richness and abundance.

Results We sampled 492 bees from 59 species, of which 58 % were above ground nesting species and 73 % exhibited some level of sociality. Our results show that the loss of forest had negative effects on understory bee abundance, which was particularly accentuated for species that nest above ground. However, for social bees the effect of changes in forest cover at a local scale depended on regional forest cover, negative effects being only detected when landscapes had at least 35 % of forest. For bee richness, the null model was among the best models bringing considerable uncertainty about landscape effects on bee richness.

Conclusions These findings suggest that management strategies and conservation practices must integrate proper actions that consider both local and regional scales. For existing fragmented landscapes, it is important to increase forest availability at the regional scale, while also maintaining high environmental heterogeneity at the local scale. We believe that with proper landscape planning this multiscalar approach can be not only more effective, but also easier to implement.

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P. A. Ferreira (✉) · D. Boscolo
Biology Department, Faculty of Philosophy, Sciences and Letters, University of São Paulo, Ribeirão Preto,
SP 14040-901, Brazil
e-mail: patybio13@yahoo.com.br

L. G. Carvalheiro
School of Biology, University of Leeds, Leeds LS2 9JT, UK

L. G. Carvalheiro · J. C. Biesmeijer
Naturalis Biodiversity Center, Leiden University,
2300 RA Leiden, The Netherlands

L. G. Carvalheiro
Departament of Ecology, University of Brasília, Brasília,
DF 70910-900, Brazil

J. C. Biesmeijer
Institute for Biodiversity and Ecosystem Dynamics,
University of Amsterdam, Science Park, 904,
1098 XH Amsterdam, The Netherlands

P. L. B. Rocha · B. F. Viana
Biology Institute, Federal University of Bahia, Salvador,
BA 40170-290, Brazil

Keywords Pollinators · Forest understory · Tropical · Landscape changes · Multiscalar approach · Bahia · Brazil

Introduction

Despite the well-established knowledge on the ecological and economic importance of bees (Brosi et al. 2007; Winfree et al. 2009, 2011), little is known about the effects of habitat loss on tropical bee communities especially across different spatial scales (Brosi et al. 2008). While in temperate regions the multiple drivers of changes in wild bee populations and communities are well understood (Potts et al. 2010), most studies are done at relatively restricted spatial scales and only few cover wider or even multiple scales (Schweiger et al. 2005; Dormann et al. 2007; Hendrickx et al. 2007; Schweiger et al. 2007; Billeter et al. 2008). Even in the well-studied temperate regions, little is known about the effects of habitat loss on bee food and nesting resources at the landscape level (but see Murray et al. 2012; Schueepp et al. 2014). Most studies compare habitat patches within restricted regions to assess how landscape structure affects pollinators. Few studies have compared whole landscapes as sampling units to answer similar questions (see Viana et al. 2012; Ferreira et al. 2013). Such narrow-ranging studies may miss landscape effects which are only detectable at wider scales. Since single patches within highly fragmented landscapes will hardly support viable populations on their own (Boscolo and Metzger 2011). Ignoring the influence of the quantity or quality of surrounding habitat can compromise the understanding of regional extinction processes. For example, patch recolonization by bees is only detectable when considering the regional scale (Osborne et al. 1999; Steffan-Dewenter et al. 2002; Tscharntke et al. 2002). Although bees spend most of their lives in a single suitable habitat patch it still remains important for bee populations to move among a set of patches (McIntyre and Wiens 1999). The landscape structure must be adequate for bee populations be able to move among a set of patches. It is necessary to have an approach that explicitly considers the interplay between surrounding landscape structure or resource availability at wider scales with nearby habitat availability in order to unveil how species will be maintained amidst severe habitat loss.

Natural habitat loss at a regional scale (e.g. thousands of hectares) leads to reduction in overall habitat availability and, potentially, to increased patch isolation. This may limit gene flow and population sizes (Suni and Brosi 2012). It also can lead to abundance declines or even local extinctions (Pardini et al. 2010), depending on the movement capability of species (Jackson and Fahrig 2012). On the other hand, habitat loss at the local scale (e.g. tens of hectares) causes increases in the average distance to the nearest forest fragments, which reduces the likelihood of multi-patch foraging strategies while withholding local resource availability. As central-place foragers, bees are highly dependent on resources available in the vicinity of their nests (local scale; Garibaldi et al. 2014) and therefore, proximal land cover changes can directly affect individual survival probability, locally reducing species abundance.

In addition to the effects of loss of forest cover at different scales, recent habitat fragmentation research shows that buffering effects among scales also exist (Pardini et al. 2010). Given the high dependency of forest bees on natural habitat for feeding and nesting (Brosi et al. 2007; Kremen et al. 2007; Winfree et al. 2007; Ricketts et al. 2008; Lander et al. 2010; Garibaldi et al. 2011), bee communities are probably more diverse and abundant in landscapes where forest cover is higher at both local and regional scales. In such landscapes the effects of local habitat loss are predicted to be less intense than in landscapes with reduced overall forest cover (Pardini et al. 2010). In landscapes with more remaining forest at a regional scale there are greater availability of resources, since the vegetation tends to be better preserved and structured. In such systems there may also be a better connection among the remaining habitat patches allowing better movement of individuals (McIntyre and Wiens 1999). On the other hand, with less forest at the regional scale, one can expect greater isolation among the remaining patches and less available resources at local scales. Even if there are large populations at the local scale, it would be harder for individuals to find enough resources to maintain their density. These inter-scale relationships, however, have not yet been assessed for bees in tropical environments (Viana et al. 2012; Ferreira et al. 2013). In this study, we conducted a multiscalar evaluation of how forest habitat loss affects bee diversity in the understory of fragmented Brazilian

Atlantic Rainforest in Bahia, Northeastern Brazil. We hypothesize that greater forest cover at wider landscape scales will lead to less accentuated effects of habitat loss for bee richness and abundance at the local scale. Conversely, in landscapes with reduced forest cover, we expected to find stronger effects of local forest loss. In such situations, local diversity is expected to lower on both scales when forest loss increases due to the extinction of more sensitive and area demanding species.

Also, we expected to find functional differences in the responses of bees with dissimilar biology. Local forest destruction affects solitary wild bees more than social bees (Steffan-Dewenter et al. 2002; Sheffield et al. 2008). Social bees are likely to be more generalists than solitary bees (Ricketts et al. 2008; Williams et al. 2010). Therefore, we expected the social bees to be less affected by habitat loss and fragmentation than solitary bees. At the same time, species that nest above the ground, especially in trees, are obviously more dependent on the forest. Species that nest on the ground may cope better in open environments where they can more easily find substrate to build their nests. Nevertheless, this last group would still need the forest to forage. These characteristics may influence the resistance of those species to habitat modifications (Williams et al. 2010). Therefore, we expected ground-nesting bees to be less affected by forest loss than bees that nest above ground.

Materials and methods

Study area

This study was conducted in tropical Atlantic Rainforest in the state of Bahia (Fig. 1), an area that encompasses some of the largest remnants of the Atlantic Rainforest in northeastern Brazil. The climate of this region is tropical humid (*Af*—Koppen–Geiger) with average temperatures varying between 24 and 27 °C and total yearly rainfall higher than 2000 mm (Peel et al. 2007). Among the tropical forests, the Brazilian Atlantic Rainforest is an extremely biodiverse environment containing about 1–8 % of the world's total species and a high endemism rate due to its geographical and altitudinal range. However, this biome is still poorly studied. Moreover, it has been historically subjected to degradation with only about 12 % of its original forest remaining intact, and most forest patches being very isolated and smaller than 50 ha (Ribeiro et al. 2009). In tropical rainforests, such as Atlantic Rainforest, where plant diversity is extremely high, pollination by animals, mostly bees (Bawa 1990; Ramalho 2004), is important for the reproduction of most plant species and, hence, for the maintenance of plant communities (Bawa 1990; Lopes and Buzato 2007; Ebeling et al. 2008; Tabarelli et al. 2008).

Tropical lowland rainforests in medium to advanced regeneration stages were the predominant vegetation type in our study areas (Veloso et al. 1991). Seven square landscapes of 36 km^2 covering a range of 15–55 % of natural forest cover were selected. The size of the landscapes (i.e. 36 km^2) was determined arbitrarily, but we consider this spatial scale large enough to encompass relevant community-level ecological processes linked to our hypothesis, such as bee dispersal between patches and possible local extinctions of bees derived from patch area and edge effects. The altitude of the sampled habitats varied between 23 and 416 m (Table 1). Due to this variation we tested altitude as a covariate in the data analyses to avoid potentially confounding effects on our results.

In order to standardize sampled landscapes and minimize the effects of varying environmental conditions, we established three criteria of landscape context. First, each 36 km^2 landscape was located in the center of a 324 km^2 larger square, each of which had a similar percentage of forest cover with an acceptable variation of ±2 %. Second, both 36 and 324 km^2 landscapes had a similar largest patch index (LPI, McGarigal and Marks 1995) (Fig. 1a). We intended to maintain the proportions of remaining forest between 36 and 324 km^2 landscapes. The LPI determines the percentage of all forest within the landscape occupied by the largest forest patch. Third, at least 80 % of the inter-forest patch area of both 36 and 324 km^2 landscapes consisted of deforested areas mostly composed of low vegetation height such as pasture and/or herbaceous/shrub plantations and non-urban areas. Based on the map from the Atlas of Forest Remnants of the Atlantic Rainforest (see www.sosma.org.br, www.inpe.br) we randomly selected seven 36 km^2 landscapes of 15, 25, 30, 35, 40, 45 and 55 % of forest cover (Fig. 1b). Each of the seven landscapes was divided in 100 squares of 0.36 km^2 (Fig. 1b). We

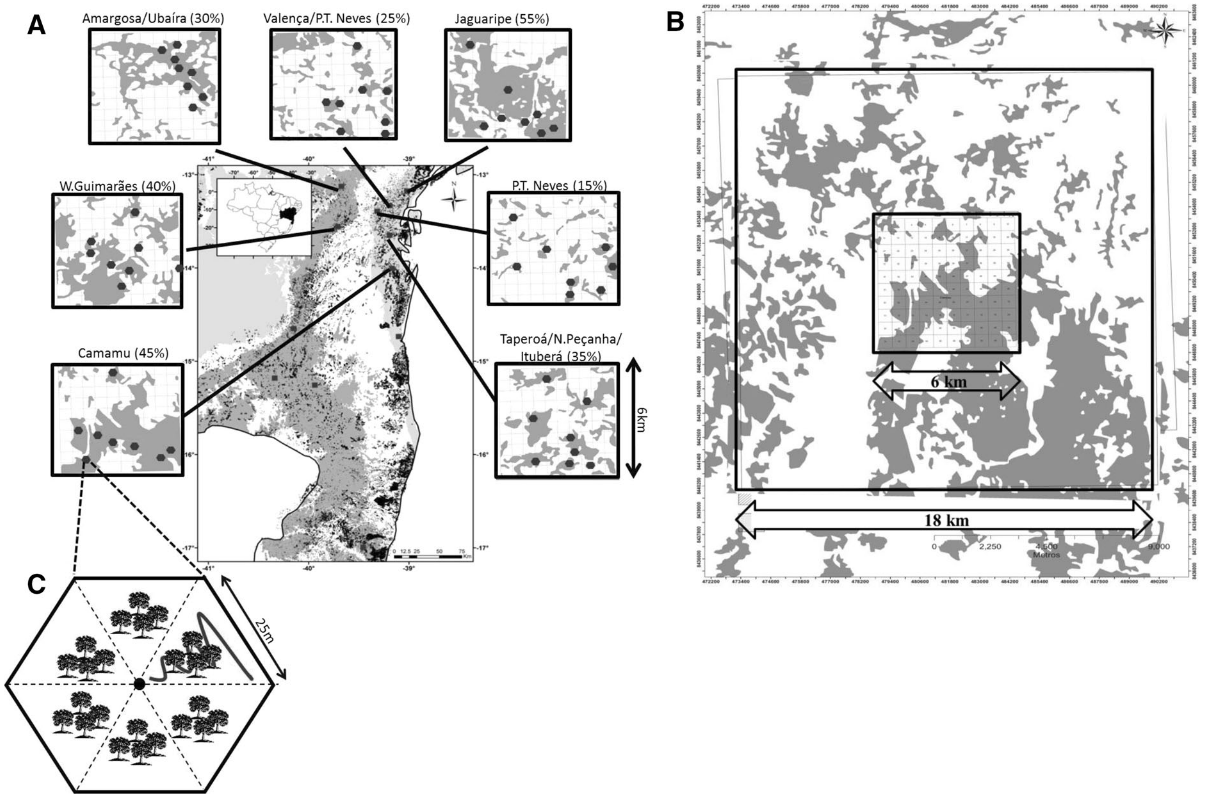

Fig. 1 **a** Atlantic Rainforest of Bahia in northeastern Brazil, showing in detail the seven square sampled 36 km^2 (6 × 6 km) landscapes with forest cover along a gradient from 15 to 55 %. *Dark gray dots* represent sampled hexagonal plots. **b** Example of a 36 km^2 landscape surrounded by an area of 324 km^2 (18 × 18 km) with similar LPI and overall forest cover. This same criteria was used to select all sampled landscapes (see text for details on selection criteria); *gray* forest, *white* non-forest matrix. **c** Hexagonal plots with 25 m sides. In detail, the inner line represents the standardized path to sample flower visiting bees from the center to the edges of the hexagons

selected eight of these squares located at least 600 m apart from each other to avoid spatial autocorrelation and ensure data independency (Taki and Kevan 2007). In each of the selected 0.36 km^2 squares we established a regular hexagonal plot with 25 m sides, which were completely within forest patches and at least 50 m distant from each edge of the patches (Fig. 1c). This led to a total of 55 plots (one plot could not be sampled because it did not fulfill the criteria described above).

Data collection

In each of the hexagonal plots, data on plant-pollinator interactions was collected in 2011 during two seasons (January to April and August to November). We avoided the rainy season because the frequency of bee flower visits is typically much lower in this period (PAF; personal observation), and access to the selected landscapes was difficult. We surveyed each hexagonal plot for flower visiting bees during warm dry days (20–31 °C), between 6:00 and 17:00 h. We sampled two landscapes per month, each for a period of 8 days, with one hexagon sampled each day. For logistic reasons we did not repeat the sampling at each plot, but considered each plot within a landscape as a replicate. In each hexagonal plot, the sampling was done by walking through a path from the center to the edges, and repeating this for each of the six subsections of the hexagonal plot (Fig. 1c), pausing for 15 min in all flowering plant detected. All flowers present in the strata up to 2 m above the ground were considered during sampling, and all insects visiting flowers were collected.

Table 1 Location of the seven square landscapes of 36 km^2 (6 × 6 km) sampled along a gradient of forest cover from 15 to 55 % of the Atlantic Rainforest in Bahia, Brazil

Location (cities covered)	Forest cover at regional scale (%)	Forest cover at local scale mean (SD)	Altitude (m)	Successional stage	Height (m)	Geographic coordinates
Pres. Tancredo Neves	15	31.0 (29.4)	181	Medium	8–11	13°23′28″S 39°19′06″W
Valença/Pres. T. Neves	25	41.8 (17.3)	144	Medium	10–13	13°20′32″S 39°11′43″W
Amargosa/Ubaíra	30	64.1 (20.7)	416	Advanced	12–15	13°07′19″S 39°39′34″W
Taperoá/Nilo Peçanha/Ituberá	35	60.9 (27.5)	31	Advanced	11–14	13°38′58″S 39°12′37″W
Wenceslau Guimarães	40	43.6 (23.6)	249	Medium/advanced	11–14	13°33′14″S 39°42′07″W
Camamu	45	80.9 (14.8)	23	Medium/advanced	11–14	14°00′51″S 39°10′56″W
Jaguaripe	55	72.8 (26.7)	47	Medium	10–13	13°11′44″S 39°01′26″W

Although our sample procedures included all flower-visiting insects, we focused the analyses on bees, the main group of pollinators for angiosperms (Bawa 1990; Roubik 1995), and the most abundant group in our study sites. Bees were killed in ethyl acetate and later desiccated in a small (30 cm base × 40 cm height × 30 cm depth) wooden greenhouse with an incandescent 40 volts lamp. After drying, bees were kept frozen until arrival at the laboratory and deposited in the Zoological Museum—Federal University of Bahia (UFBA). All bees were identified by regional experts (F.F. Oliveira and T. Mahlmann) at the most specific taxonomic level possible, following the classification proposed by Michener (2007).

Landscape data

Forest cover was measured at two different spatial scales: regional (a region being considered an area of 36 km^2) and local (square of 0.36 km^2 where sampling took place). In this way we could assess the effects of variations in forest cover on bee diversity at different spatial scales. The size of our sampling units (0.36 km^2) was based on the mean foraging range for solitary bees described by Gathmann and Tscharntke (2002). Despite the ability to fly long distances, both solitary and social bees tend not to make use of their maximum foraging ability, foraging on average in an area of 100–300 m radius away from their nest (Zurbuchen et al. 2010). Therefore, by having our sampling units at least 600 m apart we ensured spatial independence. We used Quantum GIS 1.8.0 software to calculate forest cover (%) at both scales.

Data Analyses

We analyzed data using a multi-model selection approach. To assess the impact of forest loss on bee diversity (richness and abundance), we used generalized linear mixed models (GLMM) assuming a Poisson error distribution with a log link function using the R package lme4. To account for differences in the effects of habitat loss at different spatial scales we included forest cover at local and regional scales as explanatory variables as well as their interaction. As expected, the amount of forest at regional and local spatial scales was significantly correlated but since the Pearson correlation coefficient was low ($r < 0.45$) both variables were included in the models (Supplementary material 1). Altitude and day of sampling were also used as explanatory variables. To avoid statistical problems due to pseudoreplication and to handle overdispersion of data, we considered plots nested within sites as a random effect for all models (Crawley 2007; Zuur et al. 2009). For each response variable (bee richness and abundance), we tested the spatial autocorrelation in the best model residuals using a Mantel test with 9999 permutations. We tested the correlation between the explanatory variables and only considered models which did not include highly correlated variables. Since the successional stages of sampled forests were very similar, we decided to not include it in the models.

For each selected response variable we ordered models based in Akaike information criterion with a second-order correction for small sample sizes (AICc), and we also calculated the Akaike weight (w) for each model. The most parsimonious model was selected as that with the lowest AICc. Models with ΔAICc smaller than 2 were considered equally plausible. The null model (without considering the effect of any of the explanatory factors) was included in the model selection to verify if the models containing explanatory variables performed better than the null model, which considers only the intercept (Burnham and Anderson 2002; Zuur et al. 2009). All analyses were performed using the software R 2.15.1 (R Development Core Team 2009).

To evaluate if species' traits influenced how the loss of forest cover affected bees, we grouped bees by both their nesting substrate (above ground, which includes bees that nest on trees and dead wood; and ground) and social structure (social species, for bees species that exhibit any level of sociability; and solitary species). Information on traits was compiled from the primary literature (Michener 2007; Moure et al. 2012). If published data were unavailable, we relied on a consensus of experts opinions (approximately 20 % of this information was obtained in this fashion). Whenever information about the social status and/or the nest type for a given species was not available we used available knowledge on closely related species within the same genus of bees (Kennedy et al. 2013). To assess the importance of traits in the response of bees to changes in forest cover, we conducted analyses similar to that used for richness and abundance of species. We considered sociality (social vs. solitary) and nesting type (above ground vs. ground) as well as the interaction between each of the trait variables and forest cover at both scales.

Results

We collected 492 bees representing 59 species (see Supplementary material 2). Among all species, 34 (58 %) were above ground nesters, while the remaining nest in the ground. The majority of the sampled species (73 %) exhibited some level of sociality, and 16 species (27 %) were considered solitary, with six species of the latter group (10 % of total) nesting above ground and ten species (17 % of total) nesting below the ground. For social bees only 15 species (25 % of total) were ground nesters, with the remaining 28 species (47 %) establishing their colonies on trees. There was no spatial autocorrelation in the residuals of the best model of bee abundance (Mantel test, $r = -0.0728$, p value $= 0.9579$) nor for bee richness (Mantel test, $r = 0.0166$, p value $= 0.3464$). No effect of altitude was detected for bee richness or abundance (Table 2).

Overall, loss of forest at both studied scales has affected bee communities (Table 2). For bee richness, the null model had very similar plausibility ($\Delta\text{AICc} < 2$) to the first and second best models, bringing considerable uncertainty to the landscape effects on the number of species. Nevertheless, our results showed that there was an interactive effect between forest cover at regional and local scales (Table 2; Supplementary material 3). Similar, but clearer, effects were found for bee abundance (Table 2), which increased with the amount of forest at the regional scale, but only when there was very low forest cover at the local scale (Fig. 2). We detected a positive increase in overall abundance relative to forest cover at the local scale only when forest cover at the regional scale was very high. The effect was negative when forest cover at the regional scale was low (Supplementary material 4). Contrary to what was expected, our models predicted very low bee abundance with large amounts of forest at both spatial scales, a similar pattern found for places where forest was mostly depleted (low amount of forest at both scales). The high abundance on such sites was mainly due to the presence of a highly generalist bee species, *Trigona* sp. (Apidae).

We found contrasting results for groups of bees with different functional traits. Above ground nesting bees had a higher abundance when there was plenty of forest at the regional scale, but were negatively affected by increased forest cover at the local scale (Fig. 3). On the other hand, in landscapes with reduced forest cover at the regional scale, increasing forest cover at the local scale resulted in higher bee abundance of the above-ground nesting bees. This

Table 2 Results of bee richness, abundance and functional groups models: three best models for each response variable, from generalized linear mixed models, with Poisson error distribution ordered by AICc (small sample Akaike information criterion)

Model (explanatory variables)	AICc	ΔAICc	W
Overall bee abundance			
LargeScale:SmallScale	307.4	0.00	0.28
Day:LargeScale:SmallScale	307.9	0.48	0.22
LargeScale + SmallScale	308.2	0.77	0.19
Bee richness			
LargeScale:SmallScale	232.4	0.00	0.29
LargeScale + SmallScale	232.8	0.39	0.24
Null model	233.1	0.78	0.19
Bee abundance within functional groups			
LargeScale:SmallScale:factor (social):factor (nest)	855.0	0.00	1.00
Altitude:SmallScale:factor (social):factor (nest)	869.4	14.40	0.00
LargeScale + SmallScale:factor (social) + factor (nest)	881.6	26.70	0.00

Explanatory variables, ΔAICc Akaike weight of evidence (w) are presented

Number of observations was 55 in seven sampled landscapes. Number of observations was 219 for four functional groups in seven sampled landscapes (plots within site as random variables). When interactions effects are shown we also always included the main effects in the model

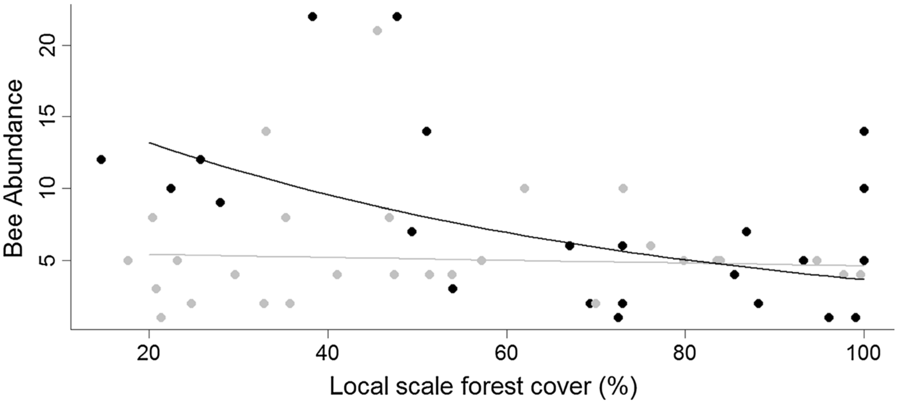

Fig. 2 Effects of forest cover on bee abundance at regional and local scale. The effect of forest cover at a local scale depended on regional forest cover. To visualize such interactive effect *gray circles* represent plots in landscapes with less than 35 % forest cover, while *black circles* represent plots in landscapes with more than 35 % forest cover. *Lines* represent the values predicted by the best model. For statistical details see Table 2

trend was more evident for social than for solitary bees. Conversely, landscapes with less forest cover at the regional scale have a higher abundance of ground-nesting bees. Indeed, the abundance of social ground nesting bees was higher when there was less forest cover at both scales (Fig. 3). When regional forest cover was low, social ground nesting bees declined with increasing forest cover at the local scale, while for landscapes with high regional forest cover no significant effect of forest cover at local scale was detected. No clear patterns were detected for solitary ground nesting bees.

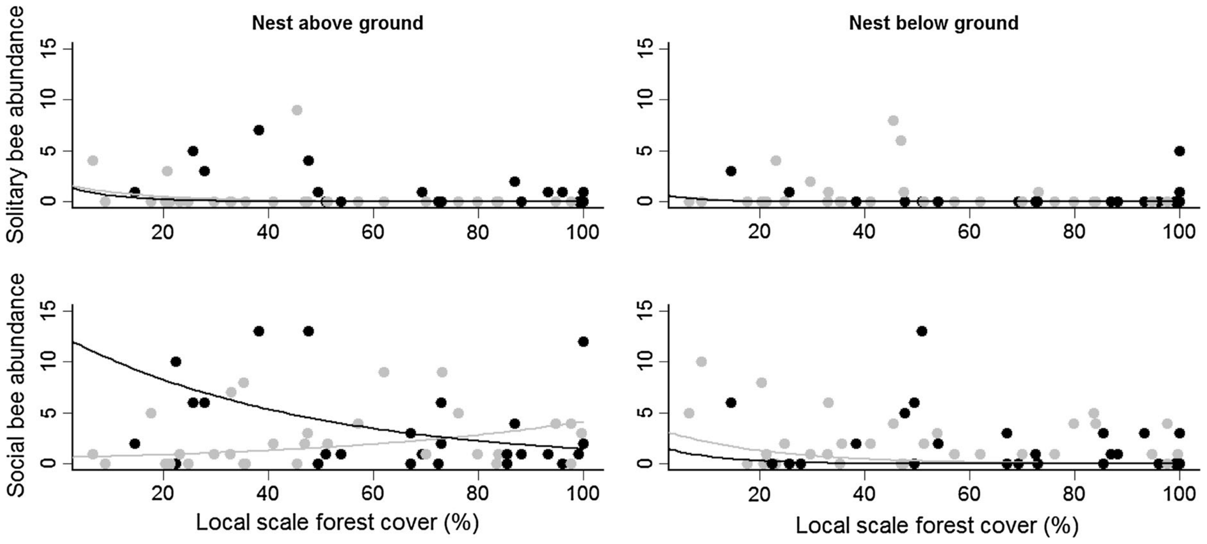

Fig. 3 Effects of forest cover at regional and local scale on the abundance of four groups of bees: solitary and social bees that nest above ground; solitary and social bees that nest on the ground. For social bees, the effect of changes in forest cover at a local scale depended on regional forest cover. To visualize the interactive effect, *gray circles* represent plots in landscapes with less than 35 % forest cover and *black circles* represent plots in landscapes with more than 35 % forest cover. *Lines* indicate the predicted values based on the best model. For statistical details see Table 2

Discussion

The tropical Atlantic Rainforest is one of the World's conservation hotspots most affected by habitat loss and fragmentation. And yet, little is known about how such landscape changes are impacting bee communities (e.g. Brosi et al. 2008). We analyzed the effects of varying forest cover at regional and local scales on bee communities and showed that the loss of forest at regional scale had negative effects on their abundance, particularly for those that nest above ground in live or dead trees. Given that the availability of feeding and nesting resources is the main determinant of bee establishment and survival (Kremen et al. 2007; Lander et al. 2010; Garibaldi et al. 2011; Hudewenz and Klein 2013), such findings were not completely surprising. However, we found landscape scale interactions and differences among functional groups, which indicated that the overall response of the bee community arises from different processes. Those processes must be considered when planning for the conservation of a large number of species and ecological processes provided by them.

Bees depend on flower resources throughout their life cycle (Potts et al. 2006; Grundel et al. 2010). Since we sampled bees that were foraging on flowers, the information we collected specifically indicates bee presence as a surrogate for foraging habitat use. As a result, we found that areas with locally low amounts of remaining habitat sustained mostly generalist bee species, such as *Trigona* sp. (Apidae), which are able to forage on almost any flower existing inside the forest. However, more specialized species, which have very specific feeding and/or nesting requirements, may not be able to survive under such scenario of habitat changes. For populations of more specialized species to be maintained, resource complementation in nearby environments is needed, making them more susceptible to forest loss. Indeed, the high importance of forest to social bees that nest above ground is likely due to enhanced nesting opportunities within the available forest patches (Brosi et al. 2008). For social bees living in groups with many individuals, the presence of a forested habitat was important to supply their needs not only for flowers, but also for upright trees which allow them to nest within forests. In contrast, when there was less local forest, ground-nesting bees were more abundant because these bees typically need to find open areas with exposed ground (see Cane et al. 2006). This effect of deforestation was only detected when forest cover at the regional scale was reduced. This suggests that species' composition of bee communities within regions of low forest cover differ from regions with high forest cover, the first community likely being mostly composed by species that are more adapted to disturbed regions. Indeed, in our sampled landscapes we observed bees, which usually forage within forest fragments, near places with enough open land close to flowering forests, even if those forests were small in area (PAF personal observation).

The fact that the effect of forest loss was stronger for social than for solitary ground nesting bees, can be due to the larger number of individuals per nest that social species have, which makes this group more resource demanding than the solitary ones. Furthermore, the more effective foraging strategies of social bees facilitate the discovery and acquisition of feeding resources amidst scattered forests for social species.

There is little evidence in the literature about the effects of the amount of forest in different spatial scales on the maintenance of bee communities in tropical environments (for temperate environments see, Steffan-Dewenter et al. 2002). Landscapes with higher proportions of natural habitat usually have greater connectivity, increasing the probability of recolonization among patches, and decreasing the risk of local extinctions (Andrén 1994). This may make bees less susceptible to forest loss (McIntyre and Wiens 1999; Osborne et al. 1999; Steffan-Dewenter et al. 2002). However, contrary to our expectations, the highest abundance of social ground nesting bees was found at low forest cover at both local and regional scales. A possible explanation is that in such regions the number of species that can persist is lower, providing an opportunity for hyper-abundant opportunistic species (Fig. 3).

In conclusion, our findings highlight the importance of considering multiple scales when evaluating responses of bee species to fragmentation. Single patches in highly fragmented landscapes hardly support diverse bee communities and different bee functional groups on their own. Therefore, approaches that consider both local forests as well as the whole regional set of patches as the sampling units (i.e. the landscapes) tend to provide better insights on the effects of landscape change on biological populations and communities (Boscolo and Metzger 2011). Recent habitat fragmentation research showed the possibility of buffering effects among scales, regulating the biotic responses to landscape structure in a top–bottom system (see, Pardini et al. 2010). We found evidence that such intricate nonlinear scale interactions, driven by forest cover at the regional scale, regulates the biological response of bees at the local scale. The local scale also depends on the immediate amount of habitat surrounding sampled plots.

Implications for conservation and ecosystem services

Knowledge consolidation concerning ecological processes such as pollination at the landscape level is of extreme importance for the management of natural areas because of the relevance of conserving ecosystem functioning and services (Tscharntke and Brandl 2004; Nazareno and Carvalho 2009; Olschewski et al. 2010; Viana et al. 2012). As the reproduction of most plants depends on natural bee communities (Winfree et al. 2009; Ollerton et al. 2011), the loss of bee abundance may have important ecological (Ollerton et al. 2011) and economic impacts (Garibaldi et al. 2013). We showed that in the Atlantic Rainforest, natural habitat loss at the regional scale negatively affected bees. Such changes in pollinator communities within tropical forest landscapes are likely to be important for the reproduction of understory plants, affecting the quality and quantity of plant gene flow (Ghazoul and McLeish 2001) and also for pollination services in surrounding agricultural fields (Ricketts 2004; Klein et al. 2007; Morreale and Sullivan 2010). Our data corroborates the proposition of Pardini et al. (2010) who indicate that at intermediate levels of overall forest cover, where landscape diversity is still reasonably high, opportunities for enhancing biodiversity through local scale management are greatest. Similarly, we saw that in already fragmented landscapes, the maintenance of greater landscape heterogeneity may favor the conservation of several functional groups of bees at the same time (also see Moreira et al. 2015).

The key aspect to consider when developing bee conservation initiatives in tropical fragmented environments, is how to maintain habitat availability and landscape connectivity. At the regional scale variations in forest cover influences the direct availability of resources for foraging individuals (McIntyre and Wiens 1999). Conservation of forest cover at this scale can be more important for bees than the conservation of selected isolated forest patches. When the remaining habitats of fragmented landscapes are enlarged and better connected, the overall conditions for population maintenance are also increased (Brosi et al. 2008). Thus, keeping enough habitat at the regional scale has great importance in the reduction of extinction probabilities and in the increase of the probability of bee recolonization among patches. However, taking care of only the regional scale is probably not enough for effective conservation of bees and their services to the ecosystems. Bee species with different traits may have different functions in the ecosystem, for they might pollinate different plant species (Fontaine et al. 2006; Hoehn et al. 2008). To ensure and conserve the reproductive success of a vast number of plant species, it is also important to conserve trait diversity of bee communities (Hoehn et al. 2008). To effectively do this, management strategies must also consider the local scale in an effort to provide nesting areas available for bee populations through the restoration of connectivity between different kinds of environments used by bees. Because of the great variety of resource demands by different species, at the local scale higher landscape heterogeneity is crucial to maintain bee diversity in already fragmented landscapes (Moreira et al. 2015). While the regional scale affects population sizes, the local scale is directly related to foraging individuals. For them, the environments surrounding their nests must provide enough variety of resources for all their needs. Bee diversity can thus be maintained only if local forests are interspersed by some open land patches which can provide nesting sites also for ground nesters.

Conservation practices must integrate proper actions that consider both local and regional scales. In Atlantic rainforest fragmented landscapes, it is important to increase forest availability at the regional scale, while also maintaining high environmental heterogeneity at the local scale. Even though this might seem difficult to achieve, we believe that with proper landscape planning this multiscalar approach can be not only more effective, but also easier to be implemented along with land development. For example, land owners can be motivated to establish their land use activities interspersed by small but interconnected native vegetation patches, which would create functionally connected sets of forested environments, allowing economic activity concomitant with the conservation of bees and their pollination services.

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