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Bee responses to landscape composition on coupled and decoupled multiscale approaches

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Abstract

Context

Multiscale approaches are essential for understanding ecological processes and detecting the scale of effect. However, nested multiscale approaches retain the effect of the landscape attributes from the smaller spatial scales into the larger ones. Thus, decoupling local vs. regional scales can reveal detailed ecological responses to landscape context, but this multiscale approach is poorly explored.

Objectives

We evaluated the scale of effect of the forest cover (%) and landscape heterogeneity on Euglossini bees combining coupled and decoupled multiscale approaches.

Methods

The Euglossini males were sampled in forest patches from 15 landscapes within the Atlantic Forest biodiversity hotspot, southeast Brazil. For simplicity, we defined that the coupled approaches represented the local scales and decoupled approaches the regional scales. We

decoupled the scales by cutting out the smaller scales inserted into larger ones. We estimated the relationship of the bee community attributes with forest cover (%) and landscape heterogeneity in local and regional scales using Generalized Linear Models.

Results

We found positive effects of landscape heterogeneity on species richness for regional scales. Forest cover (%) and landscape heterogeneity in local scales showed positive effects on the euglossine abundances. The scale of effect for euglossine richness was higher than species abundances.

Conclusions

Combining coupled and decoupled multiscale approaches showed adequate capture of the scale of effect of the landscape composition on bee communities. Therefore, it is of paramount importance to measure the influence of the landscape context on biodiversity. Maintaining landscapes with larger forest cover and spatial heterogeneity is essential to keep euglossine species requirements.

Keywords: landscape structure, spatial heterogeneity, forest cover, scale of effect, pollinator

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69 **1 Introduction**

70 One of the main goals in Ecology is to establish relationships between patterns (e.g. spatial
71 heterogeneity) and processes (e.g. pollination) at different spatio-temporal scales (Turner 1989;
72 Wu 2007; Turner and Gardner 2015). The use of multiscale approaches is essential since
73 ecological systems are hierarchically structured in different levels of space and time (Allen and
74 Starr 1982; Wiens 1989; Levin 1992; Jackson and Fahrig 2015). Nonetheless, the use of incorrect
75 scales for landscape analysis, for example, can result in flaws or observations of spurious
76 relationships between these patterns and processes, even when they exist (Cushman and Landguth
77 2010; Jackson and Fahrig 2015).

78 The ecological responses to spatial heterogeneity patterns have been influenced by changes
79 in the habitat and the landscape structure, often driven by habitat loss and fragmentation processes
80 (Haddad et al. 2015; Püttker et al. 2020). This process modifies the landscape structure by
81 increasing the edge effect, patch number, and spatial isolation, as well as by reducing habitat patch
82 and functional connectivity (Kupfer et al. 2006; Fahrig 2017). Landscape disturbances and spatial
83 heterogeneity interact in different ways, influencing ecological processes in different spatio-
84 temporal scales (O'Neill et al. 1996; Wu 2004; Newman et al. 2019). Therefore, it is expected that
85 the relationship between biodiversity and landscape parameters will be stronger at a specific
86 spatial scale, i.e. the scale of effect (Milne 1991; Holland et al. 2004; Miguet et al. 2016).
87 Individuals and species within populations and communities can perceive and respond to the
88 environment differently, resulting in different scales of effect (Boscolo and Metzger 2009; Miguet
89 et al. 2016; Amiot et al. 2021). The scales of effect of landscape attributes on biological responses
90 are generally unknown (Miguet et al. 2016; Martin 2018). The criteria of which spatial scales will
91 be used are often based on the researcher's perception of the species features, such as dispersal
92 distance and home range (Jackson and Fahrig 2012; Amiot et al. 2021). However, studies have
93 generally sub-optimized the accurate detection of the scale of effect because they use one or a few
94 spatial scales or these scales are larger or smaller than the true scale of effect (Jackson and Fahrig
95 2015; Miguet et al. 2016). Determining the scale of effect is challenging for ecologists and
96 conservationists, and at the same time, it is crucial for understanding how natural processes and
97 human pressures interact in space-time.

98 Multiscale approaches have been used to detect the scale of effect of landscape structure on
99 biological attributes or ecological responses related to different taxonomic groups, such as
100 terrestrial mammals (Lyra-Jorge et al. 2010; Nagy-Reis et al. 2017; Amiot et al. 2021), primates

(Nagy-Reis et al. 2017; Gestisch et al. 2018), plants (Collevatti et al. 2020), birds (Boscolo and Metzger et al. 2009; Morante-Filho et al. 2016) and insects (Steffan-Dewenter 2002; Rossi & van Halder 2010; Franceschinelli et al. 2017). Most of these studies were developed using a focal patch design (Brennan et al. 2002; Miguet et al. 2016), wherein the quantification of the landscape structure occurs in each of the landscapes nested in different sizes (e.g. 500, 1000, 1500 m). There are changes in spatial heterogeneity attributes with the increase in the spatial scales (i.e. landscape size) because new elements are added to the system (Allen and Hoekstra 1991; Milne 1991; Turner and Gardner 2015). Although the evaluation of larger scales (nesting the smaller ones) might detect the influence of the new elements on the patterns and ecological processes, those effects might also be inherently correlated to those observed in the smaller spatial scales, which is very common on nested landscape quantifications within various buffer sizes (Allen and Starr 1982; Wu 2004; Gestich et al. 2018; Collevatti et al. 2020). Thus, even if a certain scale of effect of an explanatory variable on an ecological response one would be the largest spatial extension evaluated, it is expected that there will also be detected influences from the adjacent smaller scales or buffer sizes (Rhodes et al. 2009). Although the current trend is to use a nested multiscale approach (i.e. various buffers surrounding the sample point varying buffer sizes), here we proposed to use a combination of both coupled (i.e. nested scales) and decoupled (i.e. local vs. regional) multiscale approaches to evaluate the best scale of effect of the forest cover and the landscape heterogeneity on Euglossini bees communities. With this, we call attention to the importance of decoupling local and regional scales of effect on exploring different taxonomic groups or ecological processes within human-dominated landscapes.

The Euglossini bees are essential pollinators in the neotropical forests, associated with more than 40 botanical families and hundreds of orchid species exclusively pollinated by euglossine males (Dressler 1982; Roubik and Hanson 2004). Most of these bee species depend on the forest for nesting sites and floral resources (Roubik and Hanson 2004), which the individuals can access using their astonishing flight capacity to explore large continuous landscape areas (Wikelski et al. 2010; Pokorny et al. 2015). Because of this, euglossine bees are important bioindicators for assessing the effects of forest cover loss and landscape degradation at different spatial scales. These processes can negatively affect the euglossine abundance and gene flow (Freiria et al. 2012; Cândido et al. 2018; Frantine-Silva et al. 2021), but may also respond positively to increased compositional heterogeneity (Opedal et al. 2020; Carneiro et al. 2021). Indeed, these results and others elsewhere (e.g. Aguiar et al. 2015; Cândido et al. 2018; Allen et al. 2019) indicate the importance of the landscape context surrounding forest patches on the

euglossine communities. However, specific responses to different spatial scales and the scale of effect are still allusive, highlighting the importance of assessing these bee communities in multiscale approaches.

The main objective of this investigation was to evaluate the scale of effect of the landscape composition on Euglossini community attributes (richness, total abundance, and abundance of common, intermediate, and rare species). We quantified the forest cover (%) and landscape heterogeneity through multiscale approaches exploring a combination of two multiscale approaches: coupled and decoupled scales. Before we present our expectations on our focal taxonomic group, it is important to emphasize that we advocate that researchers worldwide would adapt our proposal to any ecosystem, taxa, or ecological processes, just adapting what can be considered local, regional (or even macroregional) levels. In the scope of this study, we defined that the coupled multiscale approach represents the local landscape composition, and the decoupled multiscale approach the regional landscape composition. Because landscape structure and ecological parameters have many interaction levels (Miguet et al. 2016; Amiot et al. 2021), we address several questions with the main hypotheses summarized in Fig. 1. Regarding the explanation of the variables, we hypothesized that forest cover and landscape heterogeneity would have more explanatory power in local and regional scales, respectively (Fig. 1a). Likewise, we hypothesized that bee abundance and richness would increase with forest cover and heterogeneity in both local and regional scales (Fig. 1b). We hypothesized positive and negative responses of each euglossine community attribute on a respective scale as described in Fig. 1c-1f. We expected the scale of effect of forest cover on the euglossine abundance to be at local scales (Steffan-Dewenter 2002; Brosi 2009; Miguet et al. 2016). Finally, we also expected the scale of effect of landscape heterogeneity on euglossine richness to be at regional scales (Miguet et al. 2016; Jackson and Fahrig, 2014; 2015).

2 Material and Methods

2.1 Study area

We carried out this study in 15 fragmented landscapes from Southeast Brazil, an area originally covered by the Atlantic Forest (Fig. 2). This tropical rain forest is threatened by human actions that resulted in a high fragmentation and forest cover loss (Ribeiro et al. 2009; Fundação SOS Mata Atlântica and INPE 2021). Besides forest cover, coffee crops and pastures are the main landscape covers in the region (Fig. 2). More information about the study area in Carneiro et al. (2021).

2.2 Euglossini bee community

We sampled the euglossine males through five bait traps (eucalyptol, eugenol, methyl cinnamate, methyl salicylate, and vanillin) at a sampling point within a forest patch in each landscape. The minimum size of the chosen forest patches was 5 ha, and the minimum distance between the sampling points was 2,5 km (Carneiro et al. 2021). The bait traps were placed in the early morning and removed in the afternoon. We carried out the sampling expeditions for three days in the rainy season (November 2019 to March 2020) and two days in the dry season (August to September 2019 and July 2020), totaling 45 hours of sampling effort in each landscape (9 hours day x 5 sampling days). The specimens are deposited in the pollinating insects collection of the Experimental Ecology Sector, Laboratório de Ciências Ambientais, Universidade Estadual do Norte Fluminense - UENF.

We evaluated five variables from the Euglossini bee communities: richness, total abundance, common species abundance, intermediate species abundance, and rare species abundance. The alpha diversity of euglossine communities are measures that show robust responses to forest loss and landscape degradation processes (Cândido et al. 2018; Allen et al. 2019). We combined frequency of occurrence (FO) and species dominance (D) to rank the species into three groups: common species ($FO \geq 50\%$, and $D \geq 5\%$ in the community), rare species ($FO < 25\%$, and $D < 2.5\%$), and intermediate species (other combinations between occurrence frequency and dominance) (Carneiro et al. 2021).

2.3 Delimitation and classification of the landscape structure

We delimited buffers of 1500 m for the landscape classification from the bee sampling points. The landscapes were mapped by delimiting polygons and visual classification. We used high-resolution satellite images accessed within the ArcGis software as background (Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community). We used 14-class thematic resolution for mapping (Fig. 2) on a scale of 1:2,500, the same as defined in Carneiro et al. (2021). We converted the vectorized maps into raster files (5-m resolution) to analyze the landscape structure. Because we aimed to assess the influence of the landscape composition on larger spatial scales on euglossine bees, we used the rasterized maps (30-m resolution) of the Brazilian Annual Land Use and Land Cover Mapping Project [collection 4.1, 2020] (available at <www.mapbiomas.org>). From this map, we delimited buffers up to 3000 m from the bee sampling points.

2.4 Local and regional multiscale approaches

We used a multiscale approach in two combined approaches: coupled local and decoupled regional scales. The first approach refers to the usual coupled multiscale approach (Jackson and Fahrig 2015; Miguet et al. 2016), where the landscape structure is measured in nested scales with different spatial extensions from the focal patch where we sampled the biological variables (Brennan et al. 2002; Jackson and Fahrig 2014). In the second approach, landscape structure metrics such as forest cover and heterogeneity are measured using a decoupled part of the larger spatial extent, without using the smaller nested extents (Rhodes et al. 2009; Silveira 2014) (Fig. 3). Then, there are differences in the landscape context between these two multiscale approaches. If the forest cover, for example, is measured in the coupled scales (i.e. nested), the forest cover of a smaller spatial scale (e.g. 500 m) influences the forest cover observed on a larger spatial scale (e.g. 1000 m). Although there is an increase in spatial extent, the forest cover measured at a larger scale includes the same forest patches of a smaller scale. However, if we measure the forest cover in the decoupled scales, the forest cover on a smaller scale is not aggregated to the forest cover considered on a larger scale. This is because a smaller scale (i.e. 500 m) is cut out of the system and quantifies only the forest patches between 500 and 1000 m (Fig. 3). For these reasons, we considered that the coupled approach represents the local scales, and the decoupled approach - disregarding the local landscape attributes, the regional scales (Fig. 3).

The scale decoupling was performed using the “extract by mask” tool in ArcGIS software. We decoupled the following scales: 500-250 m (i.e. cut the 250 m scale in the 500 m scale), 1000-500 m (cut the 500 m scale in the 1000 m scale), 1500-500 m, 2000-1500 m, and 3000-1500 m. We used our raster map (5-m resolution) in the coupled and decoupled multiscale approaches in the spatial extension up to 1500 m. We used the MapBiomass raster map (30-m resolution) only for landscape analysis in the decoupled approach, in the spatial extension between 1500 and 3000 m (Fig. 3).

2.5 Landscape metrics

We calculated two landscape composition metrics. The landscape heterogeneity was measured through the Shannon diversity index (SHDI) (McGarigal 2015). We measured the forest cover (%) from the Percentage of Landscape (PLAND) index. These metrics were obtained in the R landscapemetrics package with the *lsm* function (Hesselbarth et al. 2019). We previously quantified these two landscape metrics in all coupled local scales (250, 500, 1000, and 1500 m) and decoupled regional scales (500, 1000, 1500, 2000, and 3000 m). We quantified Pearson's correlation between the landscape metrics in three steps to avoid the correlation between the explanatory variables. First, we correlated the forest cover and landscape heterogeneity between

local scales (Fig. S1). In the second step, we correlated the forest cover and heterogeneity only between regional scales (Fig. S2). Finally, we correlated the forest cover and landscape heterogeneity between local and regional scales (Fig. S3). In each of these steps, the metrics with high Pearson's correlation ($r > 0.65$) on the same spatial scale or between scales were removed for the subsequent correlation analyses (Rhodes et al. 2009). In the last correlation step, we selected the landscape metrics with Pearson's correlation $r < 0.65$ (Fig. S4). Thus, we considered as explanatory variables: (a) forest cover (500 m) and landscape heterogeneity (1000 m) on local scales (Fig. 3), and (b) forest cover (1000 and 3000 m) and landscape heterogeneity (1500, 2000 and 3000 m) on regional scales (Fig. 3).

2.6 Statistical analysis

First, we used linear models (LMs) to fit models between the response variables and the landscape attributes (forest cover and heterogeneity) in each spatial scale (local: 500 and 1000 m; regional: 1000, 1500, 2000, and 3000 m). Since altitude influences these euglossine communities (Carneiro et al. 2021), we also previously analyzed how altitude influences our understanding and the explanatory power of the system. For this, we used the response variable residuals in the LMs analysis. Since abundance data generally requires log-transformation in base 10, we analyzed four LM for each of the abundance variables (i.e. total abundance, abundance of common, intermediate, and rare species): (a) abundance ~ explanatory variables, (b) residual (abundance) ~ explanatory variables, (c) $\log_{10}$ (abundance) ~ explanatory variables, and (d) residual ($\log_{10}$ (abundance)) ~ explanatory variables. We chose the response variable based on the gain or loss of explanatory power (R^2) of the variables in each of these LMs scenarios. We also considered the association strength (R^2) between response variables and altitude (Table S1, S2 and S3). Based on these criteria, we used the response variables: richness, residual of $\log_{10}$ (total abundance), residual of $\log_{10}$ (common species abundance), $\log_{10}$ (intermediate species abundance), and $\log_{10}$ (rare species abundance) (Table S1, S2 and S3).

After these exploratory steps, we chose the LMs with $R^2 > 0.1$ for analyses through Generalized Linear Models - GLMs. Because species richness is count data, we built GLMs with Poisson distribution for this response variable, and we used the Gaussian distribution for abundance variables. We aimed to understand the ecological responses to the explanatory variables interacting in both local and regional scales. Then, besides univariate GLMs, we used bivariate GLMs combining as explanatory variables the landscape attributes in local and regional scales (Table S5). The null model was also used in the competition between models, which represented the absence of effect. We used Akaike's Information Criterion corrected for small samples (AICc)

to rank the models (Burnham and Anderson 2002). We considered the most parsimonious model to have the lowest $\Delta AICc$. Moreover, models with $\Delta AICc < 2.0$ and model weight (w_i) > 0.1 were considered equally plausible for explaining the patterns. All analyses were performed on the R software, and to model selection, we used the *ICtab* function from the *bbmle* package (Bolker and R Development Core Team 2020).

3 Results

We found four models to explain the Euglossini bee richness. The best model was the null (Table 1). However, other model sets were statistically plausible to explain the euglossine richness ($\Delta AICc < 2.0$ and $w_i > 0.1$). The regional landscape heterogeneity (1500, 2000 m) and local forest cover (500 m) had a positive effect on species richness (Table 1, Fig. 4a, 4b). The landscape composition on local scales had a high explanatory power on residual total abundance. The model with a positive effect of local forest cover (500 m) and the model that combined a positive effect of local heterogeneity (1000 m) and a negative effect of the local forest cover (500m) best explained the residual total abundance (Table 1, Fig. 4c, 4d).

The landscape composition on local scales had a higher explanatory power on the euglossine abundance. The models of regional scales also explained the species abundance. The forest cover on local (500 m) and regional (1000 m) scales positively explained the residual common species abundance (Table 1, Fig. 5a, 5b). The model of forest cover on local scale (500 m) best explained the intermediate species abundance through a positive relationship (Table 1, Fig. 5c). Another three models were also statistically plausible to explain these species' abundance. These models included a combination of the positive effect of the regional forest cover (3000 m) with a negative effect of the local forest cover (500 m) (Table 1, Fig. 5d), the model with the positive effect of regional forest cover (3000 m), and the null model (Table 1). The model presenting a positive effect of local landscape heterogeneity (1000 m) best explained the rare species abundance (Table 1, Fig. 5e). The second plausible model combined the positive effect of regional forest cover (3000 m) and the negative effect of local heterogeneity (1000 m) (Fig. 5f). The other plausible model to explain the rare species abundance combined a positive effect on regional heterogeneity (2000 m) and a negative effect on local heterogeneity (1000 m). Finally, this euglossine species abundance responded negatively to the regional forest cover (3000 m).

4 Discussion

We showed the different ecological responses of Euglossini bees to the landscape composition combining coupled and decoupled multiscale approaches. Overall, the results corroborated most of our hypotheses and expectations. The forest cover had a high explanatory power on a local scale. This landscape attribute positively influenced the total abundance, abundance of common and intermediate species. Furthermore, the landscape heterogeneity had a high explanatory power on both local and regional scales. There was a higher euglossine richness and rare species abundance when the landscape heterogeneity was high in regional and local scales, respectively. Our results highlight that the scale of effect of landscape composition on euglossine species abundance was in local scales. The scale of effect for species richness tends to be regional scale, but this result is inconclusive because of the higher explanatory power of the null model.

4.1 Landscape context on a local scale explains the Euglossini species abundance

The importance of forest cover and landscape heterogeneity for bees have been reported (Boscolo et al. 2017; Cândido et al. 2018; Opedal et al. 2020) mainly on small spatial scales (Steffan-Dewenter 2002; Basu et al. 2016). Forest environments provide nesting sites and floral resources (e.g. nectar and pollen) for Euglossini species (Roubik and Hanson 2004; Rocha-Filho et al. 2012). These bees can also benefit from other covers (e.g. pasture and crops) of the compositional heterogeneity (Aguiar et al. 2015; Carneiro et al. 2021). Our results corroborated those findings because they presented a positive influence of forest cover and landscape heterogeneity for the euglossine species abundance.

The total abundance, abundance of common and intermediate species were positively correlated to local forest cover (i.e. 500 m). On the other hand, the rare species abundance was positively related to local landscape heterogeneity on a larger spatial scale (i.e. 1000 m). Despite the forest cover had a significant contribution to the abundance of several species in the community, such as common and dominant species (e.g. *Eulaema nigrata* L., *Euglossa cordata* (L.)), the spatial context is an important predictor for rare species abundance (Basu et al. 2016; Arroyo-Rodríguez et al. 2016). The rare species group represented the highest species richness in the euglossine communities evaluated (Carneiro et al. 2021). However, since we measured these landscape attributes on coupled scales, it is important to consider that the patterns and ecological processes predicted on the larger local scale may be related to those found on the smaller scale (Allen and Starr 1982; Allen and Hoekstra 1991; Gestich et al. 2018). Thus, if the forest cover on a local scale (e.g. 500 m) is not accompanied by a high adjacent spatial heterogeneity (e.g. 1000 m), the bees dispersion in the landscape can be affected because individuals are in forest patches

surrounded by low quality environments (Boscolo et al. 2017; Machado et al. 2020). The importance of heterogeneity in the spatial context is supported by the second model explaining total abundance. The landscapes with high heterogeneity on a 1000 m scale positively influence the total abundance, even when the forest cover on a smaller scale (i.e. 500 m) was low.

4.2 Landscape context on a regional scale explains Euglossini species richness

Despite the low statistical support through the high explanatory power of the null model, we observed a significant positive influence of regional heterogeneity on species richness. The landscape structure that we analyzed has been altered by different land uses. It resulted in mosaics of forest patches scattered in agricultural areas with different management systems (e.g. agroforestry, coffee crops, managed and unmanaged pastures) (Carneiro et al. 2021). Landscape compositional heterogeneity can positively influence the responses of biodiversity in fragmented ecosystems, particularly euglossine bees. Landscapes with higher land cover diversity can provide complementary resources or habitats essential to organism life cycles (Dunning et al. 1992; Fahrig et al. 2011; Boscolo et al. 2017). The positive response of euglossine species richness on regional scales supports predicting that more complex and heterogeneous landscapes have more species (Fahrig et al. 2011; Tscharntke et al. 2012). In addition, the spatial heterogeneity in regional scales represents the cover and environment diversity used for euglossine species in a spatial extension outside the forest patch context where the bees were sampled.

4.3 Local and regional scales interacting to explain the Euglossini community

The local scale of effect for the Euglossini species abundance may be due to different biotic factors on small spatial and temporal scales (e.g. natality, floral resources availability, or parasitism) interacting with abiotic factors distributed in the space (e.g. nesting substrates) (Miguet et al. 2016; Galán-Acedo et al. 2018; Stuber and Fontaine 2019). Moreover, the species abundance is a consequence of the population dynamics such as immigration and emigration on larger spatio-temporal scales (Miguet et al. 2016). This issue was elucidated when we observed that forest cover on a regional scale (i.e. 3000 m) also positively influenced the abundance of common, intermediate, and rare species. The euglossine bees have high flight capacity and can keep the same routes to obtain resources in the landscape, a.k.a. trapline behavior (Ackerman et al. 1989; Whikelski et al. 2010). Thus, we consider that the conservation of forest cover (%) on regional scales might be essential for maintaining foraging habitats and population dynamics (e.g. source/sink) in these fragmented landscapes. In contrast, the association of euglossine richness with landscape heterogeneity on regional scales may be related to population events on larger spatial-temporal scales, such as colonization (Miguet et al. 2016). From the general context of our

results, it seems plausible to say that Euglossini bee responses depend on the interaction between forest cover and landscape heterogeneity in different spatial scales. These pollinators can benefit when landscape areas of high forest cover are interspersed with areas of high spatial heterogeneity associated with cover types that can be friendly to bees (e.g. unmanaged pastures, agroforestry) (Boscolo et al. 2017; Opedal et al. 2020; Machado et al. 2020; Carneiro et al. 2021).

5 Final remarks

Euglossini communities responded well to both forest cover and spatial heterogeneity in different spatial scales. We confirmed the importance of assessing multiscale interactions to understand the patterns and processes in the landscape. To our knowledge, this was the first time that a study combined these multiscale approaches (coupled and decoupled scales) to understand ecological responses to the landscape context. We encourage new studies comparing how the landscape composition and configuration metrics behave when measuring the landscape structure using local and regional scales independently or even combined. These multiscale approaches can help researchers find more solid answers about the influence of landscape structure and human disturbances on biodiversity in different ecosystems.

In addition, we showed the importance of the spatial context surrounding the forest patches for biodiversity parameters through the scale decoupling. Our results indicate that the conservationist concern about local patches without considering the surrounding areas may not be enough to maintain organism populations that depend on forest patches, although species present high mobility potential in the landscape. Because we observed the importance of incorporating regional level landscapes when assessing biodiversity and ecological processes, we can extrapolate the discussion toward the importance of buffer zones associated with conservation units. These areas are essential to minimize the adverse effects of human pressures on biodiversity on the neighborhoods of conservation units. In Brazil, for example, the conservation of buffer zones is still endorsed by environmental laws (e.g. Law N° 9.985/2000).

Finally, we highlight the importance of maintaining forest cover in different landscape spatial extensions for Euglossini bees within agroecosystem-dominated regions at the Atlantic Forest biodiversity hotspot. We also emphasize that the spatial context around these forest patches must be kept heterogeneous through low intensity in land use practices (e.g. agroforestry, unmanaged pasture), providing more friendly landscapes for these pollinators.

Declarations

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Conflicts of interest

Not applicable.

Ethics approval

The authorization for collect biological material was provided by Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis-IBAMA (Nº 71013-3).

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

Additional data is available in supplementary material.

Code availability

Not applicable.

Authors' contributions

MCG, LSC, and WMA idealized the study design. MCR delimited the multiscale approaches. LSC and MCR idealized the main hypotheses and quantified the landscape metrics. LSC, MCR, and WFS analyzed the data. CFP and LSC did the spatial analysis. All authors contributed to the manuscript revision.

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Table 1 The most parsimonious Generalized Linear Models ($\Delta AICc < 2.0$ and $w_i > 0.1$) to explain the five attributes of the Euglossini bee community (richness, residual total abundance, residual common species abundance, intermediate species abundance, and rare species abundance). The forest cover (%) and landscape heterogeneity were the explanatory variables on local and regional scales

Response variable	Models	$\Delta AICc$	df	weight (w_i)
Richness	Null	0.0	1	0.26
	Regional heterogeneity (2000 m)	0.97	2	0.15
	Regional heterogeneity (1500 m)	1.12	2	0.14
	Local forest cover (500 m)	1.65	2	0.11
Residual Total	Local forest cover (500 m)	0.0	3	0.49
Abundance (log10)	Local forest cover (500 m) + Local heterogeneity (1000 m)	1.81	4	0.20
Residual Common	Local forest cover (500 m)	0.0	3	0.38
Species Abundance (log10)	Regional forest cover (1000 m)	1.79	3	0.15
Intermediate	Local forest cover (500 m)	0.0	3	0.32
Species Abundance (log 10)	Local forest cover (500 m) + Regional forest cover (3000 m)	0.09	4	0.31
	Regional forest cover (3000 m)	1.03	3	0.19
	Null	1.44	2	0.15
	Local heterogeneity (1000 m)	0.0	3	0.21
Rare Species	Local heterogeneity (1000 m) + Regional forest cover (3000 m)	0.55	4	0.16
Abundance (log10)	Local heterogeneity (1000 m) + Regional heterogeneity (2000 m)	0.75	4	0.14
	Regional forest cover (3000 m)	1.42	4	0.10

Figure captions

Fig. 1 Expectations contributions and patterns for the relationship of Euglossini community and landscape attributes: (a) expected contribution of each independent variable (forest cover - FOR; and landscape heterogeneity - HET) on the explanatory power of the models at local (lower L) and regional (lower R) scales; (b) expected relationship between ecological responses and landscape attributes at local and regional scales, warmer colors refers to more positive ecological responses; (c-f) predictions of the Euglossini community responses to landscape composition on local scales and regional scales

Fig. 2 Location and land use composition of the 15 landscapes in Southeast Brazil with sampling points of Euglossini bees

Fig. 3 Multiscale landscape in coupled and decoupled approaches used to quantify the landscape composition. The black dashed line refers to the 500 m scale in coupled local scales and decoupled regional scales, while the red dashed line refers to the 1500 m scale decoupled at the regional scales

Fig. 4 Relationship between richness (a-b) and residual total abundance (c-d) of Euglossini species with forest cover (%) and landscape heterogeneity at local (L.) and regional (R.) scales. The black line is the GLM fit, and the gray shadow the 95% confidence interval

Fig. 5 Relationship between residual common species abundance (a-b), abundance of intermediate (c-d) and rare species (e-f) with forest cover (%), and landscape heterogeneity quantified on local (L.) and regional (R.) scales. The black line represents the GLM fit, while the gray shadow is the 95% confidence interval

Figures

Figure 1

Expectations contributions and patterns for the relationship of Euglossini community and landscape attributes: (a) expected contribution of each independent variable (forest cover - FOR; and landscape heterogeneity - HET) on the explanatory power of the models at local (lower L) and regional (lower R) scales; (b) expected relationship between ecological responses and landscape attributes at local and regional scales, warmer colors refers to more positive ecological responses; (c-f) predictions of the Euglossini community responses to landscape composition on local scales and regional scales

Figure 2

Location and land use composition of the 15 landscapes in Southeast Brazil with sampling points of *Euglossini* bees

Figure 3

Multiscale landscape in coupled and decoupled approaches used to quantify the landscape composition. The black dashed line refers to the 500 m scale in coupled local scales and decoupled regional scales, while the red dashed line refers to the 1500 m scale decoupled at the regional scales

Figure 4

Relationship between richness (a-b) and residual total abundance (c-d) of Euglossini species with forest cover (%) and landscape heterogeneity at local (L.) and regional (R.) scales. The black line is the GLM fit, and the gray shadow the 95% confidence interval

Figure 5

Relationship between residual common species abundance (a-b), abundance of intermediate (c-d) and rare species (e-f) with forest cover (%), and landscape heterogeneity quantified on local (L.) and regional (R.) scales. The black line represents the GLM fit, while the gray shadow is the 95% confidence interval

Supplementary Files

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