Orchid bees respond to landscape composition differently depending on the multiscale approach

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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 the nested 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 bee communities combining coupled and decoupled multiscale approaches.

Methods The Euglossini males were sampled in forest patches from 15 landscapes within the Atlantic Forest, southeast Brazil. For simplicity, we defined that the coupled approaches represented the local scales and decoupled 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 a trend of positive effects of landscape heterogeneity on species richness for decoupled regional scales. Forest cover and landscape heterogeneity on coupled local scales positively affected the Euglossini species abundance. The scale of effect for Euglossini species abundance was on coupled local scales.

Conclusions Combining coupled and decoupled multiscale approaches was essential to determine the scale of effect of the landscape composition on bee communities. Therefore, it is crucial to measure the influence of the landscape context on biodiversity. Maintaining landscapes with larger forest cover and spatial heterogeneity is important for bee requirements.
Keywords  Landscape structure · Spatial heterogeneity · Forest cover · Scale of effect · Pollinator

Introduction

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

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

Multiscale approaches have been used to detect the scale of effect of landscape structure on biological attributes or ecological responses related to different taxonomic groups, such as terrestrial mammals (Lyra-Jorge et al. 2010; Nagy-Reis et al. 2017; Amiot et al. 2021), primates (Nagy-Reis et al. 2017; Gestich 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; Franceschini et al. 2017; Montagnana et al. 2021). 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 quantification within various buffer sizes (Allen and Starr 1982; Wu 2004; Gestich et al. 2018; Collevatti et al. 2020). For instance, when a landscape attribute such as forest cover is measured in the coupled scales (i.e. nested), regardless of the increase in the spatial extent, the forest cover measured at a larger scale (e.g. 1000 m) includes the same forest patches of smaller scale (e.g. 500 m). Thus, even if a scale of effect of a landscape variable on an ecological response is the largest spatial extent, there is a correlated effect of landscape attributes from the adjacent smaller scales (Herrmann et al. 2005; Rhodes et al. 2009; Jackson and Fahrig 2015). One way around this issue is to decouple the smaller nested scales through buffer rings. In this approach, landscape metrics are measured in a larger spatial extent, excluding the smaller nested scales (Herrmann et al. 2005; Silva et al. 2005; Rhodes et al. 2009; Shukla...
and Jain 2019). If the forest cover is quantified in the decoupled scales, for example, counts on a smaller scale (e.g. 500 m) are not aggregated into the nearest larger one (e.g. 1000 m). In this case, the smaller scale (i.e. 500 m) is cut out of the system and quantifies only the forest cover between 500 and 1000 m. Although the current trend is to use a nested multiscale approach (i.e. various buffers surrounding the sample point), here we proposed to use a combination of both coupled (i.e. nested scales) and decoupled (i.e. buffer rings) multiscale approaches to evaluate the 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 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; Pokorný 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. 2011; Cândido et al. 2018; Frantine-Silva et al. 2021), but these bees 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 (Brosi 2009), highlighting the importance of assessing these bee communities with multiscale approaches.

Herein, we address the main question: what is the scale of effect of the landscape composition on Euglossini community attributes (i.e. richness, total abundance, and abundance of common, intermediate, and rare species)? For this, we quantified the forest cover (%) and landscape heterogeneity through multiscale approaches exploring a combination of the coupled and decoupled scales as a proxy of local and regional scales, respectively. Because landscape structure and ecological parameters have many interaction levels (Migué et al. 2016; Amiot et al. 2021), we address several questions with the main hypotheses summarized in Fig. 1. Regarding the variable’s explanation, we hypothesized (1) forest cover and landscape heterogeneity would have more explanatory power on coupled local and decoupled regional scales, respectively (Fig. 1a). The forest is a required habitat for many euglossine species, providing essential floral and nesting resources for these bees (Roubik and Hanson 2004; Aguiar et al. 2015). Since forest cover on local scales mainly reflects the focal forest patch of the bee sampling and coupled scales retain the forest cover as the spatial scales increase, the accumulation of nesting sites and floral resources available will be linked to this landscape variable. Thus, forest cover on coupled local scales must influence ecological responses driven by these local factors (Jackson and Fahrig 2014; Migué et al. 2016). On the other hand, landscape heterogeneity may indicate complementary environments for euglossine species (Opedal et al. 2020; Carneiro et al. 2021). This spatial heterogeneity may influences euglossine bees on regional scales (i.e. decoupled) as they disregard the correlated effect of the landscape attributes on coupled local scales (Herrmann et al. 2005; Rhodes et al. 2009). The spatial heterogeneity on decoupled regional scales may represent niche opportunities influencing response variables driven by ecological dynamics (e.g. dispersal, colonization) on larger scales (Migué et al. 2016). In addition, since forest cover and landscape heterogeneity positively influence bees at different spatial scales (Boscolo et al. 2017; Montagnana et al. 2021), we also hypothesized that (2) bee abundance and richness increase with forest cover and heterogeneity in both coupled local and decoupled regional scales (Fig. 1b). We expected positive and negative responses of each euglossine community attribute regarding forest cover and landscape heterogeneity on a respective scale as described in Fig. 1c to 1f. Because of the previously mentioned hypotheses, we expected the scale of effect of forest cover on the euglossine abundance to be at coupled local scales (Steffen-Dewenter 2002; Brosi 2009; Migué et al. 2016). Finally, we also expected...
the scale of effect of landscape heterogeneity on euglossine richness to be at decoupled regional scales (Miguet et al. 2016; Jackson and Fahrig 2014, 2015).

Material and methods

Study area

We carried out this study in 15 fragmented landscapes in Southeast Brazil, an area originally covered by the Atlantic Forest (Fig. 2). This tropical rain forest is threatened by human activities that have 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 can be found in Carneiro et al. (2021).

Euglossini bee sampling

We sampled the euglossine males with five bait traps (eucalyptol, eugenol, methyl cinnamate, methyl salicylate, and vanillin) at a sampling point within a forest patch in each landscape. The distance from the patch edge was 200 m, the minimum and maximum sizes of the chosen forest patches were 5.0 ha and 478.2 ha, respectively (Mean = 104.4 ± 126.2) (Carneiro et al. 2021). The minimum and maximum distance between the sampling points were 2.5 km and 47.7 km, respectively (Mean distance = 25.4 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 3 days in the rainy season (November 2019 to March 2020) and 2 days in the dry season (August to September 2019 and July 2020), totaling 45 h of sampling effort in each landscape (9 h day × 5 sampling days). The specimens are deposited in the pollinating insect’s collection of the Experimental Ecology Sector, Laboratório de...
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 the Occurrence Frequency (OF = number of samples with species i/number of total samples × 100) and species Dominance (D = abundance of species i/total abundance × 100) to rank the species into three groups: common species (OF ≥ 50%, and D ≥ 5% in the community), rare species (OF < 25%, and D < 2.5%), and intermediate species (other combinations between OF and D) (Carneiro et al. 2021).

**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 10.2.1 software as background (Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, Aerogrid, IGN, and the GIS User Community). Satellite images were from 2019. We used 14-class thematic resolution for mapping (Fig. 2) on a scale of 1:2500, 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.

**Fig. 2** Location and land use composition of the 15 landscapes in Southeast Brazil with sampling points of Euglossini bees. The buffer size shown is 1500 m.
Multiscale approaches and landscape metrics

We decoupled the scales with 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 MapBiomas raster map (30-m resolution) only for landscape analysis in the decoupled approach, in the spatial extension between 1500 and 3000 m (Fig. 3). Initially, we calculated two landscape composition metrics in all coupled scales (250, 500, 1000, and 1500 m) and decoupled scales (500, 1000, 1500, 2000, and 3000 m). The landscape heterogeneity was quantified using the Shannon diversity index (SHDI) (McGarigal 2015). We measured the forest cover (%) from the Percentage of Landscape (PLAND) index. These two metrics were obtained in the R landscapemetrics package with the lsm function (Hesselbarth et al. 2019). We quantified Pearson’s correlation between the landscape metrics in three steps to avoid multicollinearity between the explanatory variables (Rhodes et al. 2009). First, we correlated the forest cover and landscape heterogeneity between all coupled scales (250, 500, 1000, and 1500 m) (Fig. S1). In the second step, we correlated the forest cover and heterogeneity only between decoupled scales (500, 1000, 1500, 2000, and 3000 m) (Fig. S2). Finally, we correlated the forest cover and landscape heterogeneity between coupled and decoupled 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). Then, we considered as explanatory variables: (a) forest cover (500 m) and landscape heterogeneity (1000 m) on coupled scales (Fig. 3), and (b) forest cover (1000 and 3000 m) and landscape heterogeneity (1500, 2000 and 3000 m) on decoupled scales (Fig. 3). Since euglossine bees have a different relationship with landscape structure at local and regional scales (Brosi 2009; Storck-Tonon and Peres 2017; Carneiro et al. 2021), we used the landscape metrics on coupled and decoupled scales to quantify the scale of effect on expected local and regional ecological responses. Given this analytical approach, besides avoiding multicollinearity in these multiscale approaches (Rhodes et al. 2009), we defined that the coupled approaches represented the local scales and decoupled approaches the regional scales (Fig. 3).

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.
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 (coupled local scales: 500 and 1000 m; decoupled regional scales: 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 by regressing response variables against altitude. If this relationship showed $R^2_{\text{adjusted}} > 0.4$, we prefer to use response variable residuals to exclude the major effect of altitude and keep the model simplicity. Then, we analyzed two possible scenarios for bee richness: (a) richness $\sim$ explanatory variables and (b) residual richness $\sim$ explanatory variables. Since abundance data generally requires log-transformation in base 10, we analyzed four LMs possibilities for each of the abundance variables (i.e. total abundance, abundance of common, intermediate, and rare species): (a) abundance $\sim$ explanatory variables, (b) residual (abundance) $\sim$ explanatory variables, (c) log10 (abundance) $\sim$ explanatory variables, and (d) residual [log10(abundance)] $\sim$ explanatory variables.

After, we chose one response variable type based on the gain or loss of explanatory power ($R^2$) of the landscape variables in each of these LMs scenarios (Tables S1–S3). Thus, the response variable chosen was the one that presented the highest $R^2$ associated with the higher set of explanatory variables in the coupled local and decoupled regional scales. Based on these criteria, we chose the following response variables: richness, residual of log10(total abundance), residual of log10(common species abundance), log10(intermediate species abundance), and log10(rare species abundance) (Tables S1–S3).

After these exploratory steps, we chose the LMs with $R^2 > 0.1$ of each of these selected response variables for analyses through Generalized Linear Models—GLMs. Because species richness is count data, we built GLMs with Poisson distribution with log function for this response variable, and we used the Gaussian distribution with identity function for abundance variables. We aimed to understand the ecological responses to the explanatory variables interacting on coupled local and decoupled regional scales. Then, besides univariate GLMs, we used bivariate GLMs to combine landscape attributes in local and regional scales (Table S4). The null model was also used in the model competition, which represented the absence of an 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 ΔAICc. Models with ΔAICc < 2.0 and model weight ($w_i$) > 0.1 were also considered equally plausible for explaining the patterns. We checked GLMs assumptions, including overdispersion and residual normality distribution through Q–Q plots. Moreover, when two or more GLMs were plausible, we used a model-averaging approach (Burnham et al. 2011) in all top models with ΔAICc < 2.0 and $w_i$ > 0.1. In this method, it is possible to determine the relative importance of each explanatory variable of plausible models through the sum of the Akaike weights (Burnham and Anderson 2002; Burnham et al. 2011). All analyses were performed in the R software, and we used the $ICtab$ function from the bbmle package to model selection (Ben Bolker and R Development Core Team 2020) and the $model.avg$ function from the MuMIn package to model-averaging (Barton 2020).

Results

We found four plausible models to explain the Euglossini bee richness. The best model was the null model (Table 1). The other models showed a trend of positive effects of regional heterogeneity on bee richness but with low explanatory power (Table 2).

The two best models to explain the total abundance residuals indicated a high explanatory power of landscape composition on local scales (Table 1). Forest cover (500 m) had a strong and positive effect on total abundance residuals (Table 2; Fig. 4a).

The landscape composition on local scales best explained the common species abundance residuals, and intermediate and rare species abundance (Table 1). Moreover, models including forest cover and landscape heterogeneity on regional scales also explained the euglossine species abundance (Table 1). The local forest cover (500 m) had greater explanatory power with a positive effect on common species abundance residuals and intermediate species abundance (Table 2; Fig. 4b, c). On the other hand,
Table 1  The most parsimonious Generalized Linear Models-GLMs ($\Delta AICc < 2.0$ and $wi > 0.1$) to explain the five attributes of the Euglossini bee community [richness, total abundance residuals (log10), common species abundance residuals (log10), intermediate species abundance (log10), and rare species abundance (log10)]

| Response variable                  | Model                                                                 | $\Delta AICc$ | df | $wi$ | Slope |
|-----------------------------------|-----------------------------------------------------------------------|---------------|----|------|-------|
| 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 | +     |
| Total abundance residuals (log10) | Local forest cover (500 m)                                           | 0.0           | 3  | 0.49 | +     |
|                                  | Local forest cover (500 m) + Local heterogeneity (1000 m)            | 1.81          | 4  | 0.20 | +/-   |
| Common species abundance residuals (log10) | Local forest cover (500 m)                                           | 0.0           | 3  | 0.38 | +     |
|                                  | Regional forest cover (1000 m)                                       | 1.79          | 3  | 0.15 | +     |
| Intermediate species abundance (log10) | Local forest cover (500 m)                                           | 0.0           | 3  | 0.32 | +     |
|                                  | 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 |       |
| Rare species abundance (log10)    | Local heterogeneity (1000 m)                                         | 0.0           | 3  | 0.21 | +     |
|                                  | Local heterogeneity (1000 m) + Regional forest cover (3000 m)       | 0.55          | 4  | 0.16 | +/-   |
|                                  | Local heterogeneity (1000 m) + Regional heterogeneity (2000 m)      | 0.75          | 4  | 0.14 | +/-   |
|                                  | Regional forest cover (3000 m)                                       | 1.42          | 4  | 0.10 | −     |

The forest cover (%) and landscape heterogeneity were the explanatory variables on local and regional scales. Local scales represent coupled scales, and regional scales represent decoupled scales. The symbols on the “Slope” indicate the effect of each explanatory variable on response variables: + positive effect, − negative effect; “df” indicates Degrees of Freedom; and “$wi$” the Akaike weight.

local landscape heterogeneity (1000 m) positively influenced rare species abundance (Table 2; Fig. 4e).

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, and 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 on regional and local scales, respectively. We rejected the hypothesis that the combination of forest cover and landscape heterogeneity on local and regional scales positively influences bee abundance and richness. Our results highlight that the scale of effect of landscape composition on euglossine species abundance was on local scales. The scale of effect for species richness tended to be regional scale, but this result is inconclusive because of the higher explanatory power of the null model.

Landscape context on coupled local scales explains the euglossini species abundance.

The importance of forest cover and landscape heterogeneity for bees have been reported (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 land covers of the compositional heterogeneity (Aguiar et al. 2015; Carneiro et al. 2021). The landscape...
structure that we analyzed has been altered by different land uses. It resulted in mosaics of forest patches scattered in agricultural areas such as coffee crops and other matrices with different management (e.g. agroforestry, managed and unmanaged pastures) (Carneiro et al. 2021). Our results corroborated the positive influence of forest cover and landscape heterogeneity for the euglossine species abundance (Brosi 2009; Cândido et al. 2018; Carneiro et al. 2021).

The total abundance, and abundance of common and intermediate species were positively correlated with 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 significant contribution of the forest cover to common and dominant species (e.g. *Eulaema nigrita* Lepeletier. and *Euglossa cordata* (Linnaeus)), it is important to point out that these euglossine species show high environmental plasticity and are abundant in both disturbed and conserved habitats (Ramalho et al. 2009; Aguiar et al. 2015; Cândido et al. 2018). *Eulaema nigrita* and *Euglossa cordata* are food generalists (Ferreira-Caliman et al. 2018; Miranda et al. 2021), display parasocial behaviors with nest re-use over generations (Zucchi et al. 1969; Garófalo 1985), and may disperse through open matrices (Aguiar et al. 2015; Rosa et al. 2015). These ecological attributes indicate an influence of local factors and dispersal processes from nearby patches to the local abundance of these dominant bee species. Nevertheless, the rare species abundance highlights the importance of the spatial context surrounding forest patches for many species in human-modified landscapes (Basu et al. 2016; Arroyo-Rodríguez et al. 2016; Montagnana 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). Therefore, the spatial heterogeneity that has influenced rare bees on a larger local scale (i.e. 1000 m) also includes the forest cover that affected common and intermediate euglossine species on a smaller spatial scale (i.e. 500 m). Given that landscape

**Table 2** Importance of each explanatory variable to explain Euglossini community attributes in the set of all top-ranked models (i.e. ΔAICc < 2.0 and wi > 0.1) using the model-averaging method

| Response variable | Predictor variable                          | Estimate | SE    | Relative importance |
|-------------------|--------------------------------------------|----------|-------|---------------------|
| Richness          | Intercept                                  | 1.473    | 0.700 | –                   |
|                   | Regional heterogeneity (2000 m)            | 0.184    | 0.484 | 0.20                |
|                   | Regional heterogeneity (1500 m)            | 0.136    | 0.378 | 0.19                |
|                   | Local forest cover (500 m)                 | 0.000    | 0.002 | 0.14                |
| Total abundance   | Intercept                                  | −0.097   | 0.421 | –                   |
| residuals (log10) | Local forest cover (500 m)                 | 0.006    | 0.002 | 1.00                |
|                   | Local heterogeneity (1000 m)               | −0.125   | 0.266 | 0.29                |
| Common species    | Intercept                                  | −0.273   | 0.129 | –                   |
| abundance         | Local forest cover (500 m)                 | 0.004    | 0.003 | 0.71                |
| residuals (log10) | Local heterogeneity (1000 m)               | 0.002    | 0.004 | 0.29                |
| Intermediate      | Intercept                                  | 0.706    | 0.242 | –                   |
| species abundance | Local forest cover (500 m)                 | 0.004    | 0.003 | 0.64                |
| residuals (log10) | Regional forest cover (3000 m)             | −0.003   | 0.004 | 0.51                |
| Rare species      | Intercept                                  | −0.573   | 0.594 | –                   |
| abundance (log10) | Local heterogeneity (1000 m)               | 0.510    | 0.336 | 0.83                |
|                   | Regional forest cover (3000 m)             | −0.001   | 0.002 | 0.43                |
|                   | Regional heterogeneity (2000 m)            | 0.104    | 0.230 | 0.23                |

The “Relative Importance” indicates the sum of the Akaike weights and range between 0 and 1, and “SE” the Standard Error. Local scales represent coupled scales, and regional scales the decoupled scales.
heterogeneity increases with patch diversity (Fahrig et al. 2011), the positive effects of this landscape attribute on coupled local scales show the importance of different patches for rare bee species (Boscolo et al. 2017; Montagnana et al. 2021). The land cover diversity is essential for bees because they present different ecological requirements during their life cycle (Montagnana et al. 2021). In fact, some rare species sampled (e.g. Euglossa pleosticta Dressler, Eulaema atleticana Nemésio) can disperse to nearby patches (Ramalho et al. 2013; Aguiar et al. 2015), but the matrices must present high environmental heterogeneity since these rare species tend to avoid homogeneous matrices (Rosa et al. 2015; Aguiar et al. 2015). For this reason, the forest cover on a local scale (e.g. 500 m) must be accompanied by a high spatial heterogeneity associated with diverse and heterogeneous patches in the adjacent spatial scale (e.g. 1000 m). The bee’s dispersion in the landscape can be affected if individuals are in forest patches surrounded by low-quality environments (Boscolo et al. 2017; Machado et al. 2020).

Scale of effect on coupled local and decoupled regional multiscale approaches

We found a low influence of landscape composition on Euglossini richness. One of the reasons for this is that the scale of effect of landscape composition may not have been included in the scale range evaluated (Jackson and Fahrig 2015; Miguet et al. 2016). The accurate detection of the scale of effect is challenging and depends on the choice of the spatial scale that species present the highest interaction with a landscape attribute (Martin 2018; Amiot et al. 2021). Nevertheless, we noted a trend of positive effects of regional heterogeneity on bee richness. Species richness is shaped mainly by ecological events on larger spatio-temporal scales, such as extinction and colonization processes (Miguet et al. 2016). Thus, spatial heterogeneity on decoupled scales may be important
to explain response variables influenced by ecological processes operating on larger spatio-temporal scales (i.e. regional scales). In these human-modified landscapes, the spatial context beyond forest patches is essential to ecological dynamics such as those of metapopulations (Storck-Tonon and Peres 2017).

The association of euglossine abundance with landscape composition on coupled local scales reinforces the robustness of the species abundance index to assess the effects of landscape changes on orchid bees (Cândido et al. 2018; Allen et al. 2019). The local scale of effect for the euglossine 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. 2019; 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).

Indeed, despite the lower explanatory power, we also observed the influence of forest cover and spatial heterogeneity at decoupled regional scales on 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 1989; Wikelski 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 in these fragmented landscapes. 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 may be beneficial to bee species (e.g. unmanaged pastures, agroforestry) (Boscolo et al. 2017; Opedal et al. 2020; Machado et al. 2020; Carneiro et al. 2021).

Our study highlights the importance of combining coupled and decoupled scales in multiscale investigations. For example, these two approaches indicated that euglossine abundance mainly depends on local forest cover, but both forest cover and landscape heterogeneity on regional scales also influence bee species abundance. While landscape attributes on coupled scales primarily characterize the local habitat, these landscape metrics on decoupled regional scales can proxy how human activities and landscape structure act on local ecological processes (Rhodes et al. 2009). We believe it is too early to define if ecological responses are better understood at coupled or decoupled approaches. The use of one or both approaches will depend on the questions and hypotheses to be accessed. Coupled approaches (i.e. nested) seem to be more suitable when the hypothesis for ecological responses is supported by the accumulation of landscape attributes, such as forest cover through spatial extent. On the other hand, decoupled approaches (i.e. buffer rings) may be interesting when the objective is to determine whether an ecological response is correlated through spatial scales (Herrmann et al. 2005; Silva et al. 2005). In this case, an alternative is to break the scale nesting of coupled approaches through scale decoupling. From that, it is possible to detect the spatial scales where landscape attributes have higher explanatory power on variables such as species richness and individual density (Herrmann et al. 2005). Therefore, this multiscale approach can contribute to more effective landscape management strategies by determining which scale these practices should be addressed.

**Final remarks**

In accordance with our hypothesis, forest cover on coupled local scales had a high explanatory power on Euglossini community attributes. On the other hand, contrary to our expectations, the landscape heterogeneity on decoupled regional scales presented low explanatory power. We confirmed the importance of assessing multiscale interactions to understand the patterns and processes in the landscape. We advocate that researchers worldwide would adjust our proposal to any ecosystem, taxa, or ecological processes, just adapting what can be considered local, regional (or even macroregional) levels. We encourage new studies comparing how the landscape composition and configuration metrics behave when measuring the landscape structure using coupled and decoupled scales independently or even combined. These multiscale approaches can help researchers find more strong 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).

We also 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 call the attention 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. Finally, because our study shows the responses of euglossine communities in agricultural landscapes dominated mainly by coffee crops, we emphasize the importance of new studies in other spatial contexts to assess the influence of land-use and landscape changes on bee communities.

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Author contributions MCG, LSC, and WMA idealized the study design. MCR delimited the multiscale approaches. LSC, MCG, and MCR idealized the main hypotheses. LSC and MCR 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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Data availability Additional data is available in supplementary material.

Code availability Not applicable.

Declarations

Conflict of interest Not applicable.

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