Sociobiology 63(2): 819-825 (June, 2016) DOI: 10.13102/sociobiology.v63i2.1038

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - BEES

Orchid bee fauna responds to habitat complexity on a savanna area (Cerrado) in Brazil

Y Antonini[1], RA Silveira[1], ML Oliveira[2], C Martins[1], R Oliveira[1]

1- Universidade Federal de Ouro Preto, Ouro Preto-MG, Brazil
2- Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus-AM, Brazil

Article History

Edited by
Evandro Nascimento Silva, UEFS, Brazil
Received 06 April 2016
Initial acceptance 17 May 2016
Final acceptance 29 May 2016
Publication date 15 July 2016

Keywords
Orchid bee assemblage, habitat complexity, species composition.

Corresponding author
Yasmine Antonini
Laboratório de Biodiversidade
Universidade Federal de Ouro Preto
Campus Morro do Cruzeiro, s/n
35400-000, Ouro Preto-MG, Brazil
E-Mail: antonini.y@gmail.com

Abstract

Here we investigated responses of orchid bee assemblages to habitat complexity, with the aim of assessing complexity as a useful surrogate for species diversity of this group. For the purposes of our study, we defined habitat complexity as the heterogeneity in the arrangement in physical structure of habitat (vegetation), although there is a large range of operational definitions in the literature. We test the following hypotheses: (i) There is a greater species richness and abundance of orchid bee in sites with high habitat complexity than lower habitat complexity; (ii) High habitat complexity sites have a different species composition of orchid bee than lower habitat complexity sites. In fact, orchid bee species richness was higher in high complexity areas while community composition was not affected by habitat complexity, due to the effect of dominant species. Habitat complexity, measured as a function of differences in multiple strata in forests, may be of great worth as a surrogate for the diversity of a range of arthropod groups including orchid bees.

Introduction

Habitat structure and complexity may broadly affect the diversity and composition of a variety of fauna in terrestrial systems (Lassau & Hochuli, 2004; 2005; Lassau et al., 2005). In general, species diversity of terrestrial arthropod communities has been found to be positively associated with habitat complexity (Lassau & Hochuli, 2005 2007; Lassau et al., 2005).

It has been proposed that community composition is strongly influenced by differences in species pool sizes (the number of species in the species pool) and hence by factors that vary at broad spatial scales and trickle down to local scales (Kraft et al., 2011). Such factors include habitat area, the evolutionary history of lineages and regions (Whittaker et al. 2001; Kraft et al., 2011; Lessard et al., 2012), the cumulative effects of stochastic variation or sampling constraints (Chao et al., 2006; Tuomisto, 2010, a;b).

Orchid bee communities have been widely sampled in different Neotropical ecosystems in recent decades, however, few included the savanna (Cerrados) of central Brazil (Nemésio & Faria, 2004; Alvarenga et al., 2007; Faria & Silveira, 2011; Viotii et al., 2013). These studies have shown structural differences in bee communities from distinct biogeographical regions, particularly in relation to composition, richness and patterns of dominance. Usually the differences have been attributed mainly to historical factors, although regional differences in community structure at less encompassing spatial scales can be analyzed based on current ecological characteristics related to climatic, geomorphological, and/or vegetational parameters (Sydney et al., 2010; Nemésio & Vasconcelos, 2013)

Recently, Nemésio and Vasconcelos (2013) evaluated the beta diversity of Euglossine in the Atlantic forest and noted that climate variations explain twice as much variation in the species data than the spatial variation in species distribution. Nevertheless, part of the observed latitudinal changes in community composition appears to be explained by a concomitant seasonal gradient of precipitation. Similarly, low temperatures and a seasonal rainfall may help explain the

Open access journal: http://periodicos.uefs.br/ojs/index.php/sociobiology
ISSN: 0361-6525

relative specificity of the fauna of some of the most western Atlantic forest.

Orchid bee seems to be an excellent taxon for examining species composition changes in low and high complexity habitats. First, relatively small forest patches, even in urban areas, can sustain viable populations of at least some species of these insects (Bezerra & Martins, 2001; Storti et al., 2013). Second, as vagile, long-flighted organisms (Wikelski et al., 2010), orchid bees are able to fly many kilometers daily in search for food and other resources (Wikelski et al., 2010), what theoretically presumes a relatively high ability to colonize different kinds of environments and finally, their males are easily attracted to synthetic compounds that mimic floral fragrances, making field studies easy to conduct.

Since a greater distance can be covered by air for an equal energy cost, we expect orchid bee species to be highly ‘spatially mobile’, and the effects of habitat complexity (if any) to be less pronounced (Chust et al., 2004). To our knowledge, there have been no comparative studies describing orchid bee community patterns in relation to habitat complexity on a landscape scale. Our aim was to assess differences in orchid bee assemblages between low and high complexity habitats, within the same vegetation type, considering that habitat complexity may affect orchid bee fauna at various levels of vegetation strata (Aguiar et al., 2014).

In this study, we test the following hypotheses: (i) There is a greater species richness and abundance of orchid bee in sites with high habitat complexity than low habitat complexity; (ii) High habitat complexity sites have a different species composition of orchid bee than low habitat complexity sites. For the purposes of our study, we defined habitat complexity as the heterogeneity in the arrangement in physical structure of habitat (vegetation), although there are a large range of operational definitions in the literature.

Methods

Study area

The vegetation of Espinhaço mountain range is a mosaic of savanna vegetation, patches of semideciduous Atlantic forest and outcrop fields (Menezes & Giulietti, 2000). For the study we selected 15 sampling sites, in this “mosaic” located in the conservation unity “Parque Estadual do Rio Preto” (PERPRETO), in the municipality of São Gonçalo do Rio Preto, Minas Gerais, Brazil (6758200 E-7990420 S) (Figure 1). The climate in PERPRETO is classified as Cwa Köppen (Alvares et al., 2013), with dry winter and hot summer (with an average total annual rainfall of approximately 1350 mm). During the study year, the total precipitation was 1300 mm, with temperatures varying from 18º C to 20º C.

Sampling

Male Euglossine bees were sampled once a month from July, 2011 to July, 2012. At each collecting day, fragrance baits (methyl cinnamate, vanillin, cineole, benzyl acetate, methyl salicylate, beta-ionone and eugenol) were exposed from 08:00 A.M. to 03:00 P.M. , using traps following Bezerra and Martins (2001) totalizing 252 sampling hours (seven traps by each sampling plot) were placed 1.5 m from the

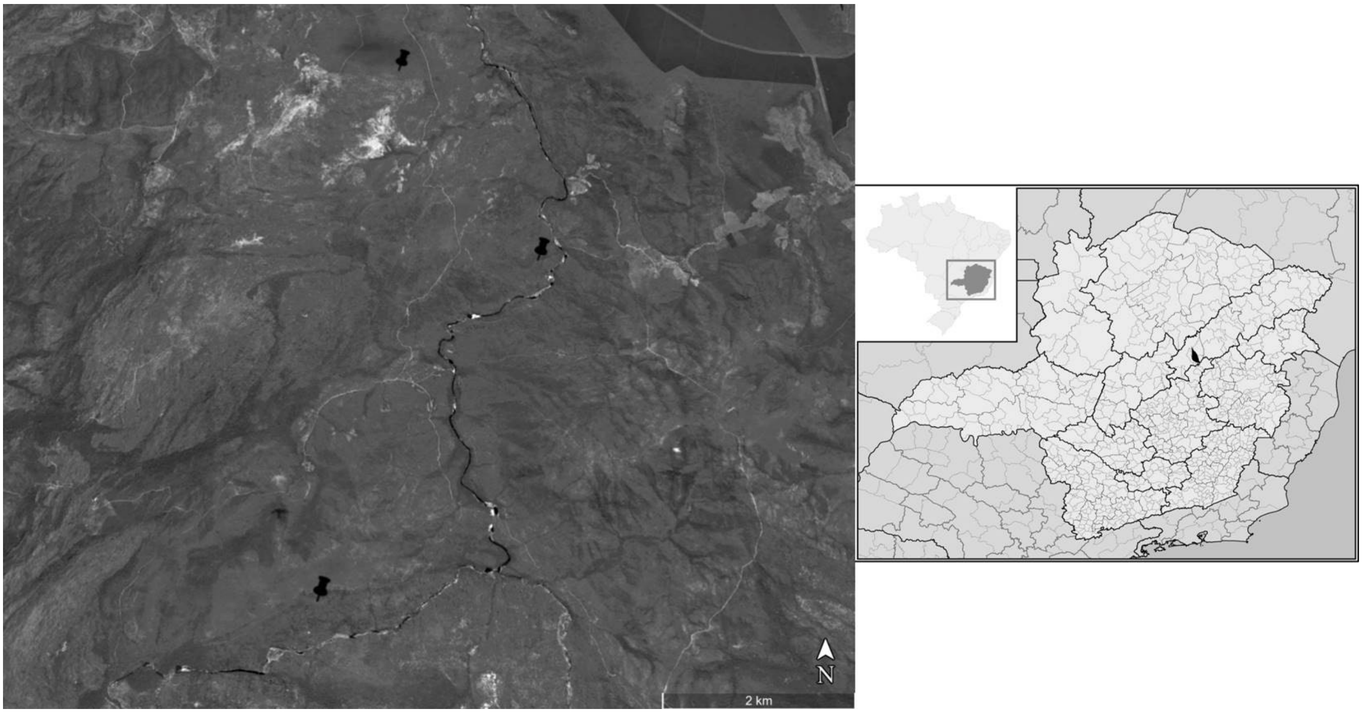

Fig 1. Map showing collecting localities of Euglossine bee at the Parque Estadual do Rio Preto, São Gonçalo do Rio Preto municipality, State of Minas Gerais, southeastern of Brazil. Source of Map: Google Maps Pro.

ground and 2 m apart each other. Sampling was consistently undertaken on sunny days, and never during periods of atypical low temperatures. Orchid bees were identified by Márcio Oliveira. All voucher specimens are deposited in the Entomological Collection of the Laboratory of Biodiversity at the Federal University of Ouro Preto and in the Collection of Invertebrates of Instituto de Pesquisas da Amazonia (INPA).

Each sampling area was selected in habitats of riparian forest, savannah and outcrop fields so that it contained high and low complexity plots. This resulted in 15 sampling plots in 3 areas over the PERPRETO. The minimum distance between each sampling point in each sampling sites was 500 m and the the distance between each sampling site was of approximately 5 km. Each of the 15 plots was characterized for habitat complexity (in the end of the sampling period), using scores between 0 and 3 for three habitat variables (Table 1). This is a modified version of the technique used by Coops and Catling (1997) and Lassau and Hochuli (2005). The scoring of sampling points, in each sampling site, results in 6 plots being categorized as low complexity (LCH), after scoring 2-5 (of a total of 9), and 9 as high complexity (HCH), scoring 6 or greater on the habitat complexity scores. The differences in habitat complexity did not appear to reflect a different successional state, but rather the patchy mosaic of different physiognomies.

Table 1. Visual Method for scoring habitat complexity (modified from Coops and Catling 1997).

Structure	Score			
	0	1	2	3
Tree canopy (% cover)	0	<30	30-70	>70
Shrub canopy	0	<30	30-70	>70
Ground flora (height in m)	Sparse* (<0,5 m)	Sparse (>0.5m)	Dense** (<0.5m)	Dense (>0.5m)

*Sparse ground flora refers to grasses covering < 50% of a study site;
** Dense ground flora refers to grasses covering > 50% of a study site.

Statistical comparisons

We examined differences in the species richness and abundance of orchid bees at high and low habitat complexity sites using single-factor Analysis of Variance (ANOVA). We created individual-based rarefaction curves within each treatment using Estimates (Colwell et al., 2012). Rarefaction was used to ensure that any responses we detected were not a product of sampling bias (Krebs, 1989), caused by trapping methods in habitat with varying structure (Melbourne, 1999). Correlations between orchid bee species richness and individual habitat variable scores were tested using Spearman Rank Correlation (SRC). We also tested correlations between habitat variables using SRCs.

We assessed differences in composition of orchid bee assemblages between areas of low and high habitat complexity using PERMANOVA. We constructed a Bray-Curtis dissimilarity matrix of the data from our orchid species using a fourth root transformation to allow a more equal contribution of rare species (Clarke, 1993). Non-standardized data were used, since throughout the study all collection sites were treated with equal importance. The differences in the abundance of the genus of orchid bee fauna in low and high complexity habitats were accessed using a *t* test.

Results

A total of 1,833 male Euglossine bees were collected, belonging to tree genera and 12 species. *Euglossa melanotricha* and *E. leucotricha* were the dominant species, representing more than 60% of the individuals collected (Table 2). In the HCH habitat 1,276 individuals belonging to 11 species were collected, while 557 individuals belonging to 12 species were collected in the LCH (Table 2).

Table 2. Abundance of orchid bee species in sampling sites with high complexity (HCH) and low complexity (LCH) at PERPRETO, MG, Brazil.

Orchid bee species	HCH	LCH
Euglossa melanotricha	439	162
Euglossa leucotricha	175	106
Euglossa securigera	142	83
Eulaema nigrita	100	72
Euglossa imperialis	120	44
Eulaema cingulata	126	13
Euglossa fimbriata	80	58
Eufriesea nigrohirta	63	2
Euglossa truncata	13	12
Euglossa annectans	13	1
Eufriesea auriceps	0	2
Euglossa violaceifrons	5	2

Effects of habitat complexity on orchid bee assemblage

The species richness and abundance of orchid bee were higher in more complex habitat types (ANOVA $F_{1,14}$= 33.01, $P < 0.001$) however, the species abundance was not significantly different (Figure 2). Average abundance was higher in more complex habitat types only for *Euglossa* species ($t = 7.25$, $P < 0.001$) (Figure 3). Individual based rarefaction curves suggest that the orchid bee species richness may be higher in high complexity habitats (Figure 4). The species composition of orchid bee fauna was not different in habitats of high and low complexity (Permanova R = 0.27, P = <0.2).

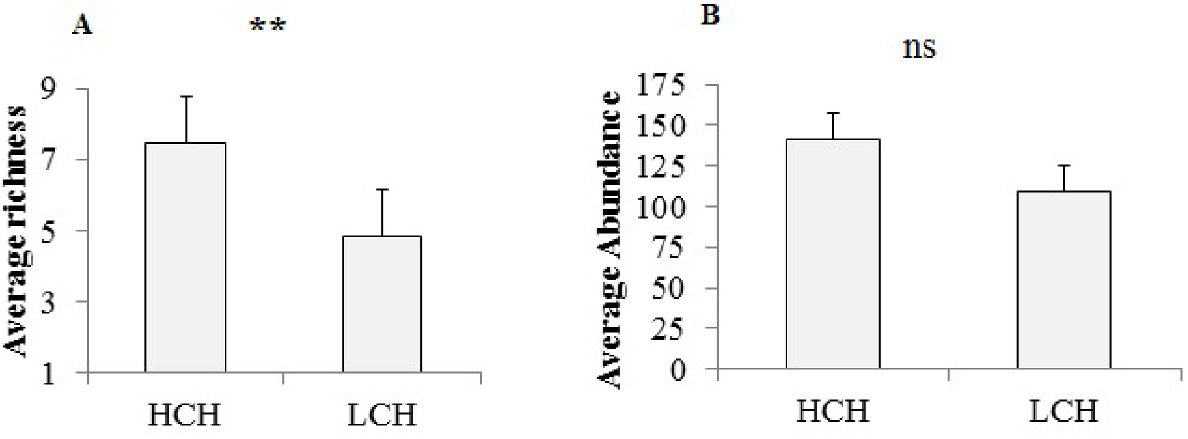

Fig 2. Orchid bee species richness (a) and abundance (b) in high and low complexity habitats. (±SE) ** Anova p<0.05.

The species richness of orchid bees was positively associated to the total score of habitat variables (Spearman Rho = 0.62, n = 15, P = 0.012). The species richness of orchid bees was positively associated with the shrub canopy cover (Spearman Rho = 0.45, n = 15, P = 0.034), and ground flora (Spearman Rho = 0.47, n = 15, P = 0.042). Among habitat variables, tree canopy cover was negatively associated with ground flora (Spearman Rho = -0.43, n = 15, P < 0.001) and shrub canopy cover negatively associated with ground herb cover (Spearman Rho = -0.40, n = 15, P < 0.05).

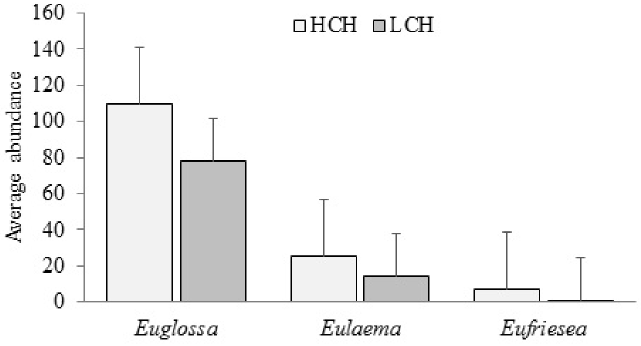

Fig 3. Orchid bee genus abudance in high and low complexity habitats (±SE)

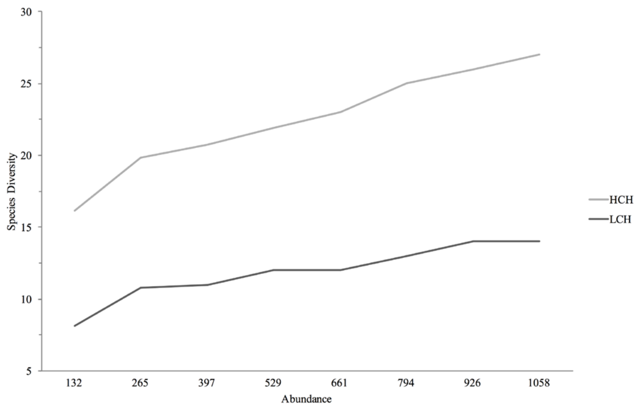

Fig 4. Rarefaction curves of orchid bee fauna sampled in high (HCH) and low (LCH) complexity habitats PERPreto, MG, Brazil.

Discussion

The results of the present study, plus those obtained by Viotti et al. (2013), Justino and Augusto (2012) Faria and Silveira (2011), Alvarenga et al. 2007 and Nemésio and Faria (2004), in other areas of savanna (Cerrado) in Minas Gerais state, revealed a total of 16 orchid bee species for this region. So far there is no list for the orchid bee fauna in the Cerrado of Minas Gerais. Considering the result of the rarefaction curves and richness estimators, the orchid bee fauna in Cerrado areas was underestimated and the real number of species may be higher.

The species richness in Parque do Rio Preto is higher to those found in other inventories carried out in the Cerrado domain (e.g Nemésio & Faria, 2004; Alvarenga et al., 2007; Justino & Augusto, 2010; Faria & Silveira, 2011; Viotti et al., 2013) and in fragments of the semideciduous “low mountain rain forest”, at elevations of 300-900 m, in the Atlantic forest domain (Rebêlo & Garófalo, 1997; Sofia & Suzuki, 2004; Nemésio & Silveira, 2010; Silveira et al., 2011; Ferreira et al., 2013). These forests are characterized by relatively open canopy, 15-25 m tall, and occur under climates with two well defined seasons, rainy and dry. This suggests that the species richness of local faunas in the Cerrado is comparable to those more complex forests, in the so-called “inland forests” or semideciduous forests within the Atlantic forest domain. Such species richness, however, are much smaller than those found in coastal Atlantic forest sites (perennial forests) in southeastern Brazil (e.g. Tonhasca-Jr. et al., 2002; Nemésio & Vasconcelos, 2013).

Despite Faria and Silveira (2011) explain the low richness and abundance of orchid bees in Cerrado areas, as a result from relative food scarcity, which, in turn, would be a consequence of a combination of low soil fertility and relatively low seasonal precipitation, our results are going in an opposite way. The Cerrado is a very rich floristic region with many different habitat types (Joly et al., 1999) and that habitat heterogeneity may provide the necessary resources for orchid bee species. It should be considered that the orchid bees present in the Cerrado domain are able to explore both high and low complexity habitats (the savannic and the forest environments). It is important to notice that the species composition of orchid bee, in our study, was not different in habitats of high and low complexity. It is possible, then, that orchid bees vague through both environments, exploiting whatever resources they can find in each of them. For example, riparian forests would be important for orchid bees, offering them nesting sites, food resources and protection against intense solar radiation and winds (Neves & Viana 1999, Wikelski et al., 2010).

Habitat complexity

The higher average species richness in more complex habitat was expected and is in agreement with our findings since the individual rarefaction curves shown that the expected richness of HCH was always higher than that in LCH. Nevertheless, for abundance, the result was the opposite since the "more common" orchid bee species (*E. melanotricha* and *E. leucotricha*) present higher abundance both in high and less complex habitat types.

Shrub canopy cover and ground flora cover all had significant positive associations with species richness of orchid bees. The interpretation of this result is somewhat complicated by the negatively correlations between tree canopy cover and ground flora and shrub canopy cover negatively associated with ground herb cover.

For the three genera of orchid bee, habitat complexity may not be important in determining bee richness but abundance. For the most rich genera – *Euglossa* – there was no difference in richness but the abundance. It should be notice that the abundance of the three more abundant *Euglossa* species (*E. melanotricha*, *E. leucotricha* and *E. securigera*) was also higher in sites with LCH when compared with the other species. For *E. melanotricha* and *E. leucotricha*, previous studies had demonstrated that these species are much abundant in mosaic of Cerrado and outcrop fields as well as in a mosaic of Cerrado and *Eucalyptus* plantation (see Faria and Silveira, 2011; Viotti et al., 2013). It should also be considered that mosaic of physiognomies may be favoring the occurrence of orchid bees, as demonstrated by Aguiar et al. (2014).

Recently, Nemésio and Vasconcelos (2013) evaluated the beta diversity of orchid bees in the Atlantic forest and noted that climate variations explain twice as much variation in the species data than the spatial (latitudinal) variation in species distribution. Nevertheless, part of the observed latitudinal changes in community composition appears to be explained by a concomitant seasonal gradient of precipitation. Overall, our results agree with a growing body of evidence (e.g. Myster, 2009; Sydney et al., 2010; Vasconcelos et al., 2010) showing that environmental gradients affect the turnover of animal and plant species in tropical forests more strongly than geographic gradients.

Our study reinforces the importance of habitat complexity to preserve high local and regional species richness, as the composition of orchid bees communities, as well as their patterns of abundance and species dominance have been found to differ among habitat with high and low complexity. The mechanisms driving associations between habitat complexity and patterns in orchid bee communities may also provide a basis for maintenance of ecological services and the genetic diversity of their host plant populations, and attention should be given to studies focusing on these points.

Acknowledgements

We thank CAPES and FAPEMIG fellowships to the first and last author. CNPq for the PQ scholarships to YA CAPES for PD scholarships to RO. IEF, Antonio Tonhão de Almeida and Parque do Rio Preto staff, for logistic support. Erik Wild for English Revision.

References

Aguiar, W.M., Melo, G.A.R. & Gaglianone, M.C., (2014). Does forest physiognomy affect the structure of orchid bee (Hymenoptera, Apidae, Euglossini) communities? A study in the Atlantic Forest of Rio de Janeiro state, Brazil. Sociobiology, 61: 68–77.

Alvarenga, P.E.F., Freitas, R.F. & Augusto, S.C. (2007). Diversidade de Euglossini (Hymenoptera: Apidae) em áreas de cerrado do Triângulo Mineiro, MG. Bioscience, 23: 30–37.

Alvares, C.A., Stape, J.L., Sentelhas, P.C., Gonçalves, J.L.M. & Sparovek, G. (2013). Köepen's climate classification map for Brazil. Meteorologische Zeitschrift, 22: 711–728.

Bezerra, C.P. & Martins, C.F. (2001). Diversidade de Euglossinae (Hymenoptera, Apidae) em dois fragmentos de Mata Atlântica localizados na região urbana de João Pessoa, Paraíba, Brasil. Revista Brasileira de Zoologia, 18: 823–825.

Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.J. (2006). Abundance-based similarity indices and their estimation when there are unseen species in samples. Biometrics, 62: 361–371.

Chust, G., Pretus, J.L., Ducrot, D., Ventura, D. (2004). Scale dependency of insect assemblages in response to landscape pattern. Landscape Ecology, 19: 41–57.

Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology, 18: 117–143.

Coops, N.C. & Catling, P.C. (1997). Predicting the complexity of habitat in forests from airborne videography for wildlife management. International Journal of Remote Sensoring, 18: 2677–82.

Colwell, R.K., Dunn, R.R. & Harris, N. C. (2012). Coextinction and persistence of dependent species in a changing world.

Annual Review of Ecology, Evolution and Systematics, 43: 183-203.

Faria, L.R.R. & Silveira, F.A. (2011). The orchid bee fauna (Hymenoptera, Apidae) of a core area of the Cerrado, Brazil: The role of riparian forests as corridors for forest-associated bees. Biota Neotropica, 11: 87–94.

Ferreira, R.P., Martins, C., Dutra, M.C., Mentone, C.B & Antonini, Y. (2013). Old Fragments of Forest Inside an Urban Area Are Able to Keep Orchid Bee (Hymenoptera: Apidae: Euglossini) Assemblages? The Case of a Brazilian Historical City. Neotropical Entomology 42: 466–473.

Justino, D.G & Augusto, S.C. (2012). Avaliação da eficiência de coleta utilizando armadilhas aromáticas e riqueza de Euglossini (Hymenoptera, Apidae) em áreas de Cerrado do Triângulo Mineiro. Revista Brasileira de Zoociências, 12: 227–239.

Joly, C.A., Aidar, M.P.M., Klink, C.A., McGrath, D.G., Moreira, A.G., Moutinho, P., Nepstad, D.C., Oliveira, A.A., Pott, A., Rodal, M.J.N. & Sampaio, E.V.S.B. (1999). Evolution of the Brazilian phytogeography classification systems: implications for biodiversity conservation. Ciência e Cultura, 51: 331–348.

Kraft, N.J.B, Comita, L.S., Chase, J.M, Sanders, N.J, Swenson, N.G, Crist, T.O, Stegen, J.C., Vellend, M., Boyle, B., Anderson, M.J., Cornell, H.V., Davies, K.F., Freestone, A.L., Inouye, B. Harrison, S.P & Myers J.A. (2011). Disentangling the drivers of beta diversity along latitudinal and elevational gradients. Science, 333: 1755–1758.

Krebs, C. J. (1989). Ecological Methodology. Harper & Row, New York.

Lassau, S.A. & Hochuli, D.F. (2004). Effects of habitat complexity on ant assemblages. Ecography, 27: 157–64.

Lassau S. A., Hochuli D. F., Cassis G., Reid C. (2005) Effects of habitat complexity on forest beetle. Diversity and Distributions, 11: 73–82.

Lassau, S.A. & Hochuli, D.F., (2005). Wasp community responses to habitat complexity in Sydney sandstone forests. Austral Ecology, 30: 179–187.

Lassau, S.A. & Hochuli, D.F., (2007). Associations between wasp communities and forest structure : Do strong local patterns hold across landscapes ? Austral Ecology, 32: 656–662.

Lessard, J.P., Borregaard, M.K., Fordyce, J.A., Rahbek, C., Weiser, M.D., Dunn, R.R. & Sanders, N.J. (2012). Strong influence of regional species pools on continent-wide structuring of local communities. Proceeding of the Royal Society of Botany, 266: 1–9.

Melbourne, B.A. (1999). Bias in the effect of habitat structure on pitfall traps: an experimental evaluation. Australian Journal of Ecology, 24: 228–39.

Menezes, N.Z. & Giulietti, A.M. (2000). Campos rupestres. Pp. 65-73. In: M.P. Mendonça & L.V. Lins (eds.). Lista vermelha das espécies ameaçadas de extinção da flora de Minas Gerais. Minas Gerais, Belo Horizonte, Fundação Biodiversitas & Fundação Zoo-Botânica de Belo Horizonte.

Myster, R.W. (2009). Plant communities of western Amazonia. Botanical Review, 75: 271–291

Nemésio, A. & Silveira, F.A. (2010). Forest fragments with larger core areas better sustain diverse orchid bee faunas (Hymenoptera: Apidae: Euglossina). Neotropical Entomology, 39: 555-561

Nemésio, A. & Vasconcelos, H.L. (2013). Beta diversity of orchid bees in a tropical biodiversity hotspot. Biodiversity and Conservation, 22: 647–1661.

Nemésio, A. & Faria, L.R.R. (2004). First assessment of orchid bee fauna (Hymenoptera: Apidae: Apini: Euglossina) of Parque Estadual do Rio Preto, a cerrado area in southeastern Brazil. Lundiana, 5: 113–117.

Neves, E.L. & Viana, B.F. (1999). Comunidade de machos de Euglossinae (Hymenoptera: Apidae) das matas ciliares da margem esquerda do Médio Rio São Francisco, Bahia. Anais da Sociedade Entomológica do Brasil, 28: 201–210.

Rebêlo, J.M.M. & Garófalo, C.A. (1997). Comunidades de machos de Euglossini (Hymenoptera, Apidae) em matas semidecíduas do nordeste do estado de São Paulo. Anais da Sociedade Entomologica do Brasil, 26: 787–799.

Silveira, G.C., Nascimento, A.M., Sofia, S.H. & Augusto, S.C. (2011). Diversity of the euglossine bee community (Hy-(Hy- menoptera, Apidae) of an Atlantic Forest remnant in southeast- ern Brazil. Revista Brasileira de Entomologia, 55: 109–115.

Sofia, S.H. & Suzuki, K.A. (2004). Comunidade de machos de abelhas Euglossina (Hymenoptera: Apidae) em fragmentos florestais no sul do Brasil. Neotropical Entomology, 33: 693-702.

Storti, E.F., Oliveira, M.L., Storti Filho, A. (2013). O papel dos fragmentos florestais da cidade de Manaus na manutenção da fauna de abelhas das orquídeas (Apidae: Euglossini). In: Bermúdez, E.G.C., Teles, B.R., Keppler, R.L.M. (orgs.). Entomologia na Amazônia Brasileira, 2: 227–234.

Sydney, N.V., Gonçalves, R.B. & Faria, L.R.R. (2010). Padrões espaciais na distribuição de abelhas Euglossina¸ (Hymenoptera, Apidae) da região Neotropical. Papeis Avulsos de Zoologia, 50: 667–679

Tonhasca Jr., A., Blackmer, J.L. & Albuquerque, G.S. (2002). Abundance and diversity of euglossine bees in the fragmented landscape of the Brazilian Atlantic Forest. Biotropica, 34: 416-422.

Tuomisto, H. (2010a). A diversity of beta diversities: straightening up a concept gone away. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography, 33: 2-22

Tuomisto, H. (2010b). A diversity of b diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. Ecography, 33: 23–45.

Vasconcelos, H.L.; Vilhena, J.M.S., Facure, K.G. & Albernaz A.L.K.M. (2010). Patterns of ant species diversity and turnover across 2000 km of Amazonian floodplain forest Journal of Biogeography, 37: 432–440.

Viotti, M.A., Moura, F.R. & Lourenço, A.P. (2013). Species diversity and temporal variation of the orchid-bee fauna (Hymenoptera, Apidae) in a conservation gradient of a rocky field area in the Espinhaço Range, state of Minas Gerais, southeastern Brazil. Neotropical Entomology, 42: 565–575.

Whittaker, R.J., Willis, K.J & Field, R. (2001). Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography, 28: 453–470.

Wikelski, M., Moxley, J., Eaton-Mordas, A., Lopez-Uribe, M.M, Holland, R., Moskowitz, D., Roubik, D.W. & Kays, R. (2010). Large-Range Movements of Neotropical Orchid Bees Observed via Radio Telemetry. Plos One. doi: 10.1371/journal.pone.0010738