Abundance and Diversity of Euglossine Bees in the Fragmented Landscape of the Brazilian Atlantic Forest

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ABSTRACT

Male euglossine bees were sampled with chemical baits every two months from September 1997 to July 1999 at nine sites in the Desengano mountain range, Rio de Janeiro State, Brazil. Four sites were located in Atlantic Forest mature second growth, two sites in disturbed forest, and three sites in forest fragments of 200, 156, and 14 ha, respectively. We collected 3653 male euglossine bees from at least 21 species. Analyses of variance indicated no differences among the three habitat types for total number of bees, and 5 of the 6 dominant species. Bootstrapping indicated significant variation in species richness and diversity for some sites, but there was no clear indication of differences among habitats. Similarity as measured with the Morisita–Horn index was inversely related to distance between sites, but relatively high for most site combinations. These results suggest that the euglossine bee community in the three habitats was essentially the same. Although some species were associated with each habitat type, most appeared to respond to temporal local conditions. Our results do not support the hypothesis that forest fragmentation or habitat alteration reduces abundance and diversity of euglossine bees.

Key words: Atlantic Forest; Brazil; diversity; Euglossini; forest fragmentation; Hymenoptera; semi-deciduous forest.

THE ATLANTIC FOREST (MATA ATLÂNTICA) ONCE EXTENDED for over 4000 km along the Brazilian coast; but after centuries of deforestation, it has been reduced to between 5 and 12 percent of the original 35 million ha (Saatchi et al. 2001). Because of its biological diversity, endemism, number of endangered species, and continuing deforestation, the Atlantic Forest is considered one of the world’s “hot spots” for conservation (Myers et al. 2000). Most remnant Atlantic Forest is composed of relatively small fragments, including protected areas (Jorge & Garcia 1997). Evaluating the impact of fragmentation on plant and animal communities and the characteristics of isolated forest patches are key issues in conservation, particularly for tropical forests. The overall pattern emerging from many studies is that biotic and abiotic characteristics of the original sites may be profoundly altered, with resulting reduction in biodiversity (Turner 1996, Laurance & Bierregaard 1997). Fragmentation of the Atlantic Forest as well as other tropical ecosystems may have additional indirect consequences, such as reduction in the number of visits to plants by pollinating insects (Fisher 1998, Kearns et al. 1998).

Euglossine bees (Hymenoptera: Apidae: Euglossini) are common throughout moist–wet tropical and subtropical forests in Central and South America, and they pollinate many plant species in all layers of the vegetation (Kress & Beach 1994). Euglossine bees are also indispensable pollinators of economically important plants and hundreds of orchid species (Dressler 1982). Male euglossine bees collect fragrances produced by flowers for reasons not yet clearly understood, pollinating them in the process. The object of our study was to compare the abundance and diversity of male euglossine bees at nine sites within a highly fragmented area of the Atlantic Forest and test the hypothesis that fragmentation and forest degradation affect the species composition of euglossine bee communities.

MATERIALS AND METHODS

This study was conducted in the vicinity of the Desengano mountain range, the largest remnant of Atlantic Forest in northern Rio de Janeiro State, Brazil (ca 22,000 ha). Desengano is characterized by an edge of secondary vegetation that gradually shifts into a semi-deciduous primary tropical rain forest toward its interior. The forest is surrounded by a heterogeneous landscape of cattle ranches, abandoned pasture, and second-growth vegetation. Forest fragments of different sizes and stages of preservation cover many of the surrounding hills. Nine sampling sites were selected within an area of ca 230 km² around the village of Sossego...
do Imbé (21°53'S, 41°48'W; Fig. 1). Sites 1 to 4 were located in well developed, second-growth forest contiguous with the main forest. According to local people, these areas have not been disturbed for the last 20–30 years. The remaining sites were located in disturbed forest with high densities of Attalea humilis, a palm species very common on regenerating slopes in this region of the Atlantic Forest (Souza et al. 2000). Sites 5 and 6 were located in an area contiguous with the main forest but comprising a mosaic of second-growth and scrubby vegetation with no clear transition between vegetation types. Sites 7, 8, and 9 were forest fragments surrounded by pasture, and their sizes were 200, 156, and 14 ha, respectively. Hereafter sites 1–4, 5–6, and 7–9 will be referred to as forest, disturbed forest, and forest fragments, respectively.

Sites were sampled for euglossine bees during 12 field trips conducted every two months from September 1997 to July 1999. Sampling occurred twice during the first field trip and once thereafter. Usually three sites were sampled on the same day, and weather permitting, all sites were sampled during three consecutive days. Site 4 was not sampled during September 1998 and site 7 was added to the study beginning in May 1998. Sampling sites were set up 30–100 m inside the forest. At each site, ca 10 m of string was tied ca 1.5 m above the ground between two trees, with the string perpendicular to ground declivity; the direction of prevailing winds. Six pieces of blotter paper (7 × 7 cm) were fixed at equal distances along the string, and each was impregnated with 2 ml of one of the following chemicals: cineole, eugenol, methyl salicylate, methyl cinnamate, skatole, or vanillin. The last three chemicals are crystals and were dissolved in ethanol until reaching saturation point. These synthetic products mimic natural components found mainly in orchid flowers and are collected by male euglossine bees (Dressler 1982). Fragrances were replenished every 1.5 hours except for cineole, which was replenished every 30 minutes. These intervals were based on our previous observations of the chemicals’ volatility. Male euglossine bees landing on the pieces of paper were captured with insect nets. Sampling started between 0900 and 1000 h and continued until 1500 h, weather permitting. Voucher specimens were deposited at the entomological museum of the Universidade Estadual do Norte Fluminense.

To compare habitats (forest, degraded forest, and fragments) we conducted analyses of variance (ANOVAs) for the total number of bees collected and for each of the six most abundant species, which comprised 88.7 percent of all samples (see Results). For the analysis, we averaged the number
of bees collected per field trip and transformed the data to \( \log(x + 1) \) to homogenize variances. Statistical power was expected to be low in these analyses because of the small number of replicates; therefore, we did not correct the experiment-wise error resulting from multiple tests (so that power would not be further reduced) and considered a critical level of \( \alpha = 0.10 \). These measures decrease the probability of accepting false null hypotheses (Toft & Shea 1983, Zar 1984).

To compare bee diversity in the three habitats, we plotted the log number of individuals against their rank to obtain estimates of species richness and evenness (Whittaker 1965). To compare the number of species among sites, we added the samples from the 12 field trips and used bootstrapping (Simon 1999) to generate 1000 samples from each site and obtain 95 percent confidence intervals for the number of species (richness). Diversity was expressed as the Simpson–Yule diversity index, \( D \), calculated as \( D = (1)/(\Sigma(N_j/N_r)^2) \), where \( N_r \) is the number of individuals in the \( r \)th species and \( N_r \) is the total number of bees at each site (Magurran 1988). Therefore, \( D \) can be used as a measure of dominance and distribution of individuals among species in a community. Although diversity indices have no intrinsic biological meaning (Ludwig & Reynolds 1988), they are useful for comparing the combination of the number of species (richness) and their relative abundance (evenness) among communities (Peet 1974).

The community similarity between sites was estimated with the Morisita–Horn index, \( MH \), calculated as \( MH = (2 \sum(an_i \times bn_j)/((da + db) \times N_a \times N_b) \), where \( an_i \) and \( bn_j \) are respectively the number of individuals in communities \( a \) and \( b \). \( N_a \) and \( N_b \) are the total number of individuals in each community, and \( da = (\sum an_i^2)/((N_a)^2) \), \( db = (\sum bn_j^2)/((N_b)^2) \) (Southwood & Henderson 2000). \( MH \) approaches 1.0 when species in both communities have similar ranking and densities, and it is zero when there is no species overlap between communities.

**RESULTS**

We collected 3653 euglossine bees representing at least 21 species (Table 1). Bees classified as *Euglossa cordata* may actually belong to more than one species (R. Dressler, pers. comm.). Sampling duration throughout the study ranged between 4.9 and 5.6 hours because of the time required to reach different sites; however, few bees were collected before 1000 h, when usually all sampling stations were set up. Therefore, differences in sampling duration are not likely to have biased the results.

The ANOVAs indicated no significant differences in the total number of bees or in the number of the dominant species except for *Eulaema nigrita* (\( F = 4.37, P = 0.06, df = 2, 6 \)). *Eulaema nigrita* was the most common species, but it was concentrated (42.5% of the total) in the two disturbed forest sites (Table 1). Richness estimates generated by bootstrapping demonstrated that random samples of euglossine bees were likely to contain more species at site 2, whereas all the other sites had equivalent richness (Fig. 3a). The diversity index accentuated the differences among sites, with lower values for sites 1, 5, and 6 (Fig. 3b). The strong dominance by *E. nigrita* was responsible for the considerably lower diversity index values at sites 5 and 6 (Fig. 3b). A similar pattern occurred at site 1, where the second most abundant species, *E. cordata*, comprised a relatively larger proportion of the total number of individuals compared to the dominant species of the remaining sites. Similarity decreased with increasing distances between sites, but values of the Morisita–Horn index were relatively high for most site combinations (Fig. 4). The species list in Table 1 clearly shows the similarity among sites in relation to euglossine bees. Excluding the rare species, species composition and their relative abundance were alike at all sites.

These results demonstrated that, as a whole, the euglossine bee community in the three habitats was essentially the same. There was greater variability among sites at the species level, and in two cases (*E. nigrita* and *Euglossa analis*) differences among sites are likely to be associated with habitat types. Despite the nonsignificant statistical result, none of the 178 *E. analis* were collected from degraded forest or the two smallest fragments, suggesting that it is mostly restricted to large, relatively undisturbed forests. In samples collected from the same area during subsequent years, we rarely found *E. analis* in degraded sites (A. Tonhasca and C. L. Albuquerque, pers. obs.). For most other species, densities were comparatively high at specific sites regardless of the habitat type, such as *Euglossa pleisticta*.

The accumulation of individuals at particular sites was not the result of preference throughout the season, but rather originated from momentary local increases in the number of bees. This pattern of local and temporal concentration was clear for four of the six dominant species (Fig. 5). Considerable seasonal variation in euglossine bee abun-
<table>
<thead>
<tr>
<th>Species</th>
<th>Site:</th>
<th>1</th>
<th>2</th>
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<th>5</th>
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<td></td>
<td>100</td>
<td>95</td>
<td>140</td>
<td>112</td>
<td>52</td>
<td>143</td>
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<td>32</td>
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<td>6</td>
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<td>17</td>
<td>9</td>
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<td>7</td>
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<td>10</td>
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<td><em>Euglossa surinamensis</em></td>
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<td><strong>Total</strong></td>
<td></td>
<td>366</td>
<td>591</td>
<td>435</td>
<td>300</td>
<td>308</td>
<td>677</td>
<td>404</td>
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dance was expected (Roubik 2001), and in this study it probably was caused in part by weather patterns. Although the number of bees per site or field trip was not correlated with temperature or relative humidity (AT, JLB, and GSA, pers. obs.), the field trips with the fewest dominant species (and lowest total number of bees) were the coldest; average temperatures during sampling were below 22°C. Results in Figure 5 also support Roubik's (2001) view that short-term census of euglossine bee populations can be misleading; although E. cordata and Euglossa securigera were among the dominant species, their numbers during the first year of sampling corresponded to only 3.3 and 8.7 percent, respectively, of the total.

DISCUSSION

Although it is reasonable to assume that similar habitats have similar bee communities, to consider sites as habitat replicates is not appropriate because of differences, for example, among site size, vegetation type and density, degree of disturbance, and topography. The influence of the naturally high variability among sites could be diluted by a significant increase in the number of replicates, but this is clearly not practical or feasible. Reduced or improper replication, and consequently low power, are among the most serious limitations of experiments with forest fragmentation (Crome 1997).

Despite these caveats, our results revealed some aspects of euglossine bee responses to habitat quality. Forest fragmentation has been associated with population decline of euglossine bees (Powell & Powell 1987) and native bees in general (review in Cane 2001), but we found no clear association between abundance and richness of the euglossine bee community and habitat type. The total number of bees was lowest in the smallest fragment, but this result was determined mostly by the relative low abundance of two species. Although the results sug-
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suggest that numbers of some euglossine bees may decline in fragments or disturbed forests, most species appear to respond to specific and ephemeral local conditions. Euglossine bee populations have relatively high stability, but substantial seasonal fluctuations occur possibly because of nesting and adult emergence patterns (Roubik & Ackerman 1987, Roubik 2001). Microhabitat characteristics may also play a major role in bees’ local abundance; for example, sometimes we observed *E. nigrita* and *Eulaema cingulata* concentrating in high numbers around trees exuding sap and on banks with exposed earth. Brown (1991) proposed that many insects could be used as indicators of habitat quality, and Peruquetti et al. (1999) attributed this role to *E. nigrita* because of its high abundance in disturbed areas (Rebêlo & Cabral 1997, Peruquetti et al. 1999). Our data suggest that *E. nigrita* and *E. analis* are the most likely candidates for indicator species of disturbed and primary (or less disturbed) areas, respectively.

Euglossine bees are able to locate isolated food and fragrances and use resources far away from their reproductive sites due to their exceptional flight capacity and plant fidelity (Dressler 1968, Janzen 1971, Janzen et al. 1982). These characteristics ensure the cross-pollination of many plant species inside forest (Kress & Beach 1994). Murren (2002) noted the reproductive success of an euglossine bee-pollinated orchid on islands in the Panama Canal due to visits of mainland euglossine bees. In our area, some species are capable of flying almost 2 km over open areas to trace fragrances located on the opposite side of steep hills (Tonhasca et al. in press), suggesting that the mountainous landscape of the Atlantic Forest does not obstruct bees’ movements. Bee numbers and species composition in different sites are probably similar because their capacity to disperse and locate fragrances compensate for possible negative effects of forest isolation or forest degradation. Moreover, much of the research area, and a great portion of the remaining Atlantic Forest, form a matrix of regenerating vegetation, a landscape that increases connectivity of sites and may greatly reduce deleterious effects of fragmentation (Gascon et al. 1999). Bees from many species are present in highly disturbed or fragmented sites, attesting to their resilience to habitat disturbance (Cane 2001).

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LITERATURE CITED


