Open and Disturbed Habitats Support Higher Diversity of Syrphidae (Diptera)? A Case Study During Three Yr of Sampling in a Fragment of Araucaria Forest in Southern Brazil

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ABSTRACT. The diversity of hoverflies in five different habitats of the Parque Estadual de Vila Velha, Ponta Grossa, Paraná, Brazil, from September 1999 to August 2002 was studied. These five areas had been exposed to various types of anthropogenic disturbance at different times, which resulted in different stages of plant succession. In total, 2,841 specimens of 151 species of Syrphidae were collected using malaise traps. The highest species richness and abundance were found at the edge of the forest (Forest Edge), whereas the lowest was found in the most conserved areas. Evenness values increased along the succession gradient. The accumulation curve of new occurrences of syrphid species nearly approached an asymptote starting on the third month of the third year. Estimates of syrphid species richness using different methods indicated that between 155 and 288 species are found in the study area, according the Michaelis–Menten and the Chao2 estimators, respectively. The richness and abundance of representatives of the subfamily Syrphinae were higher in more open areas, where herbaceous plants predominate. Nineteen hoverfly species can be considered as environmental indicators, as they were collected exclusively or mainly in one of the defined habitat types. The degree of opening of the vegetation seems to be the factor determining the distribution of Syrphidae species, a conclusion based on the finding that grassy clearings in Araucaria Forests had more species. Hence, we conclude that, to become established, Syrphidae communities need conserved mosaic landscapes.

Key Words: indicator species, hoverfly, malaise trap, plant succession, species richness estimator

Insects provide easy, sensitive, and inexpensive ways to measure the effects of anthropogenic stress on the biodiversity and the environment (Kim 1993). Among them, the species of Syrphidae have great potential as indicators of the environmental quality of forests (Thompson 1999, Smith et al. 2008). This is mainly because they are easily found in nearly all terrestrial ecosystems, and their larvae have highly diverse feeding habits (Sommaggio 1999).

Entomofaunistic surveys are relevant for understanding how insect communities are structured and may broaden our knowledge on Neotropical Syrphidae. Thus, this study is an extension of the one developed by Jorge et al. (2007) on the syrphid diversity at the Parque Estadual de Vila Velha (PEVV), Paraná State, Southern Brazil. Jorge et al. (2007) studied the species collected during the first year of the project “Levantamento da Fauna Entomológica no Parque Estadual de Vila Velha, Ponta Grossa, Paraná – PROVIVE” (Ganho and Marinoni 2003). Our investigation, carried out over a period of 3 yr, has gathered more striking results. We were able to perform both spatial and temporal assessments of the diversity of Syrphidae and to establish relationships between community structure in each of the five surveyed areas and their conservation status. Because differences in species composition decrease with increasing mobility of the organisms studied, we also evaluated whether syrphid species, known for their outstanding capacity to fly, are distributed evenly across the environment. Furthermore, this study revealed potential indicator species of Araucaria Forest habitats.

Materials and Methods

Characterization of the Biome. The vegetation formation Campos Gerais do Paraná is located in the Eastern region of the second plateau of Paraná (Southern Brazil), immediately following the Devonian ridge, including a broad north–south stretch of natural grassland formations. It is characterized as a phytogeographical zone of “campos limpos” associated with the Mixed Ombrophilous Forest (Araucaria Forest), which may form gallery forests or isolated woods across the landscape, where the presence of the Araucaria angustifolia (Bertol.) Kuntze (Parana-pine) is evident (Maack 1981, Veloso and Góes Filho 1982).

The survey was carried out in an area of Araucaria Forest at the PEVV. Five sites, characterized by varying degrees of plant succession (or environmental conditions due to management) were chosen: 1) forest edge (located between the arboreal vegetation and the open area), 2) Araucaria (planted forest of A. angustifolia); 3) Phase 1 (native forest in an initial to intermediate stage of plant succession); 4) Phase 2 (native forest in an intermediate to advanced stage of plant succession); and 5) Phase 3 (native forest in the most well conserved stage). The information on the history of the anthropogenic disturbance and floristic differences among the areas provided the basis for their recognition as different habitats across the landscape (Ganho and Marinoni 2003).

Collection, Mounting, and Identification. Insects were collected using malaise traps (Towmes 1972). This collecting method has been particularly useful in quantitative studies of Syrphidae (Owen and Owen 1990, Sommaggio 1999), even though it is logistically costly, which makes it necessary to reduce replications (Burgio and Sommaggio 2007). Even if a small number of malaise traps are used, the information provided by long-term monitoring can be very useful because these traps can sample both singletons and the most abundant species (Fraser et al. 2008). A trap was placed in each site, and the material was removed weekly for 3 yr (September 1999 to August 2002), totaling 153 samples per area.

After sorting and mounting the specimens, we identified them based on keys available in the literature (Thompson 1999, Borges and Pampolina 2003, Marinoni et al. 2007, Borges and Couri 2009) by comparing them with reference material in the Coleção Entomológica Padre Jesus Santiago Mouré of the Zoology Department at the
Universidade Federal do Paraná (DZUP-UFPR) and using the help of Dr. Christian F. Thompson of the National Museum of Natural History, Smithsonian Institution. As a result of our investigations, some changes in the definition of complexes of cryptic species, as well as species with high intraspecific variability, were made, resulting in slight differences between the current data and those presented by Jorge et al. (2007). These differences, however, have not resulted in a noticeable effect in the comparisons of species richness and abundance and, therefore, have not altered the interpretations made in that study.

The material has been deposited in the Coleção Entomológica Padre Jesus Santiago Moura (DZUP-UFPR). All the data are at the database of the Taxonline - Rede Paranaense de Coleções Biológicas (www.taxonline.ufpr.br) and the species list is in Appendix 1.

Data Analysis

Abundance and Species Richness. Abundance and species richness were compared among the areas and the subfamilies of Syrphidae (Eristalinae, Microdonitinae, and Syrphinae) using generalized linear models with a Poisson error distribution. Analyses and graphs were carried out in STATISTICA software 7.1 (StatSoft 2005).

Evenness Index. The Simpson’s index (SD) provides the probability that two randomly selected individuals from an infinitely large community belong to the same species. It is one of the most popular and robust diversity measures, because it captures the variance in the distribution of species abundance. It is heavily weighed by the most abundant species in the sample and less sensitive to species richness (Magurran 2004). The complement of this index (1 – SD = SE) can be considered a way of expressing the Simpson’s evenness index. The dominance index of Berger and Parker (BPD) is defined by the ratio of the number of individuals in the most abundant species by the total number of captured individuals. The reciprocal of this index (1/BPD = BPE) is the Berger and Parker evenness index. This index, in addition to being simple and informative, is considered as one of the most satisfactory measures of diversity (Magurran 2004). Because of the sensitivity of the first index to species abundance distribution, and of the second one to species richness, we used both evenness indexes.

Estimate of Species Richness. To assess syrphid richness estimates of the areas, the following methods were used: Bootstrap, Chao 1, Chao 2, first-order Jackknife, second-order Jackknife, and Michaelis–Menten. According to Palmer (1990), nonparametric estimators obtain better results than their alternatives. These calculations were conducted using the software EstimateS Version 8.0 (Colwell 2006), with 50 randomizations with abundance classes equal to 10. Calculations were conducted using both the classical and the corrected Chao, always recording in the table the highest value obtained by either method, which in our case resulted from the classic Chao. The estimates were first calculated with the data from the first annual cycle (~52 wk) for each area separately and for PEVV as a whole. Then, the same procedure was followed using the combined 2-yr effort, and finally, using the data for the entire survey (three annual cycles, for a total of 153 wk).

Community Structure. The nonmetric multidimensional scaling (NMDS) was used to assess the general dissimilarity pattern in the community structure among the five areas surveyed. This analysis was performed using both total abundance of Syrphidae and abundance of each subfamily separately. Data were log transformed prior to analyses, and the nonparametric estimator was used to generate dissimilarity matrices. NMDS was performed using R 2.13.1 (R Development Core Team 2011) with the package MASS (Venables and Ripley 2002), and graphs were generated in STATISTICA 7.1 (StatSoft 2005).

Indicator Species. Based on floristic differences previously noticed (Ganho and Marinoni 2003), evenness values, number of shared species, and community structure analyses, some groups of areas were defined before conducting the analysis on the indicator species: 1) Edge, an environment with open vegetation, corresponding to a contact zone between forest and gaps; 2) Araucaria + Phase 1, forest areas in their initial and intermediate stages of succession, corresponding to a disturbed habitat with significant canopy opening, intense luminosity and low humidity; 3) Phase 2 + Phase 3, forest areas in their intermediate and advanced succession stages, better-conserved than (2), with less canopy openings, lower luminosity, and higher humidity; 4) Araucaria + Phase 1 + Phase 2 + Phase 3, that encompassed all the woody vegetation, not considering successional level and interior environmental conditions.

From the definition of these habitat types, the species that better characterize each of them were determined using an indicator value index (Dufrêne and Legendre 1997), whose significance was obtained after 999 permutations. This analysis was performed using R 2.13.1 (R Development Core Team 2011) with the package labdsv (Roberts 2010). The indicator value index considered: 1) the specificity of a given species to the area and 2) its fidelity to the same area over the 3 sampled years. When analyses were performed with the same sample units, but combined in five, three, or two groups, we found that the specificity and fidelity components are more easily achieved when a smaller number of sample units are considered for each group. Therefore, for the only area that was not grouped with any other (Forest edge), the significance was taken from the preliminary analysis that considered the classification into five areas, without any grouping. This procedure minimized possible biases in the significance of the specific indicator values. Only the taxa identified to species level were considered in this analysis. Only statistically significant values (α = 0.05) were reported, implying that the Syrphidae species that presented such values would have a preference for a particular type of habitat in the Araucaria Forest.

Results

Abundance. At the end of the 3 sampling years, a total of 2,841 syrphids had been collected in all five areas, as follows: 1,345 in the first year, 698 in the second, and 798 in the third. When the data of all years were analyzed together, the Forest edge had the largest number of syrphids, followed by Phase 1, Araucaria, Phase 3, and Phase 2, respectively (Table 1). There was a significant effect of the interaction between area and subfamily on Syrphidae abundance (Wald Stat. = 383.06, df = 8, P < 0.001). In this case, Syrphinae was more

| Year          | Area          | Total  | Eristalinae | Microdonitinae | Syrphinae | Syrphidae |
|---------------|---------------|--------|-------------|----------------|-----------|-----------|
| 2001–2002     | Forest edge   |        |             |                |           |           |
| 1999–2002     | Forest edge   | 26 (1) | 19 (1)      | 1,656 (98)     | 1,699     |           |
| 1999–2002     | Araucaria     | 24 (8) | 95 (30)     | 197 (62)       | 316       |           |
| 1999–2002     | Phase 1       | 6 (2)  | 4 (1)       | 45 (5)         | 56        |           |
| 1999–2002     | Phase 2       | 10 (3) | 52 (14)     | 284 (76)       | 374       |           |
| 1999–2002     | Phase 3       | 18 (6) | 72 (23)     | 106 (49)       | 216       |           |
| Total         |               | 26 (1) | 19 (1)      | 1,656 (98)     | 1,699     |           |
| 2000–2001     | Forest edge   | 4 (1)  | 10 (4)      | 452 (47)       | 473       |           |
| 2000–2001     | Araucaria     | 8 (2)  | 25 (30)     | 39 (72)        |           |           |
| 2000–2001     | Phase 1       | 6 (4)  | 14 (48)     | 68 (68)        |           |           |
| 2000–2001     | Phase 2       | 5 (3)  | 26 (22)     | 53 (53)        |           |           |
| 2000–2001     | Phase 3       | 4 (3)  | 13 (15)     | 32 (32)        |           |           |
| Total         |               | 27 (1) | 88 (53)     | 698 (698)      |           |           |
| 2001–2002     | Forest edge   | 4 (1)  | 4 (1)       | 534 (534)      | 542       |           |
| 2001–2002     | Araucaria     | 5 (1)  | 28 (49)     | 82 (82)        |           |           |
| 2001–2002     | Phase 1       | 6 (2)  | 5 (45)      | 56 (56)        |           |           |
| 2001–2002     | Phase 2       | 7 (4)  | 20 (33)     | 60 (60)        |           |           |
| 2001–2002     | Phase 3       | 4 (3)  | 14 (40)     | 58 (58)        |           |           |
| Total         |               | 20 (8) | 81 (30)     | 388 (388)      | 2,841     |           |
seven most abundant species accounted for 51% of all syrphids collected, namely \textit{Toxomerus polygraphicus} (Hull, 1940), \textit{Syrphus phaestigma} Wiedemann, 1830, \textit{Allograpta neotropica} Curran, 1936, \textit{Toxomerus procrustanus} Metz, 2001, \textit{Toxomerus croesus} (Hull, 1940), and \textit{Ocyptamus funebris} Macquart, 1834 (Appendix 1). \textit{Ocyptamus arabella} Hull 1947 was recorded for the first time in the state of Parana. All of these species belong to the subfamily Syrphinae.

In Microdontinae, the following species were noteworthy: \textit{Mixogaster polistes} Hull, 1954, \textit{Microdon aureolapis} Marini, 2004 and \textit{Microdon aurifex} Wiedemann, 1830, which occurred in all areas (Appendix 1). In the case of Eristalinae, the most abundant species included \textit{Copestylum macquarti} (Curran, 1926), \textit{Chalcosyrphus armatipes} (Curran, 1941), and \textit{Copestylum selectum} (Curran, 1939) (Appendix 1).

The survey resulted in a large number of species represented by a few specimens and a few species represented by many individuals. From the 151 species collected, 110 were represented by fewer than 10 specimens, which correspond to 73% of all species.

**Evenness Index.** With respect to both indexes applied, the Forest edge was the least uniform area, particularly due to the presence of dominant species such as \textit{T. polygraphicus} (495 individuals) and \textit{S. phaestigma} (397 individuals). Evenness, according to the Simpson's index, was higher for the forested areas. In contrast, evenness as calculated by the Berger and Parker's index increased with the level of plant succession (Table 3).

**Species Accumulation Curve.** The cumulative number of species throughout the survey in all five areas indicates that more than half of the species (52%) had already been collected in the first 5 mo of sampling, and at the end of the first year, 67% of the species had been sampled. In each of the following years, the number of species sampled increased by 16% (Fig. 3). The curve did not reach an asymptote before the third year of sampling, i.e., there were new records of species for nearly every month during the first 2 yr. This indicates that the 3-yr sampling effort was important to provide more robust results to the survey of syrphid fauna of PEVV. In the last months of the third year, the curve tended toward stability (Fig. 3).
The species accumulation curves for the forested areas indicate that >55% of the species had been captured in the first 5 mo. The patterns for the rate at which new species are found in the most conserved areas (Phases 2 and 3) were similar to one another during the 3 yr. More than 70% of the species in those areas had been collected during the first year of the survey, contrasting with the Forest edge, where only 57% of the species had been collected during the same period. In the Forest edge, the number of species found continued to increase throughout the 3 yr and tended to stabilize during the last 5 mo (Fig. 3).

**Species Richness Estimators.** To determine which index shows best results as an indicator of the likely species richness at a given environment (Table 4), we tested several indexes in this study. The number of species collected was always lower than the number of species predicted by all indexes. This is true for each area considered individually, as well as for all areas combined, and for each year or for all years combined. The closest estimate for PEVV resulted from the Michaelis–Menten index, which was only 3% higher than the number of species collected at the end of the third year. Estimates by the Chao 1 and Chao 2 indexes were the highest, 83 and 91% higher than the number of species collected. With increased sampling effort, the values estimated with the Michaelis–Menten index differed less and less from the number of species collected: 14% difference in the first year, 6% in the second, and 3% in the third. In contrast, the difference between the estimated and observed number of species became increasingly larger each year when the remaining indexes were used. For instance, the Chao 2 estimate was 73% higher than the number of collected species in the first year, 72% in the second, and 91% in the third.

**Table 3. Number of species (S), abundance of individuals (N), the Simpson’s evenness index (SE), and the Berger and Parker’s evenness index (BPE) of Syrphidae resulting from a survey using malaise traps in five areas of the PEVV, Ponta Grossa, Paraná (September 1999 to August 2002)**

|                | S     | N    | SE   | BPE  |
|----------------|-------|------|------|------|
| Forest edge    | 98    | 1,686| 0.88 | 3.43 |
| Araucaria      | 50    | 315  | 0.93 | 4.57 |
| Phase 1        | 63    | 373  | 0.94 | 5.74 |
| Phase 2        | 40    | 216  | 0.93 | 6.17 |
| Phase 3        | 40    | 236  | 0.94 | 7.38 |
| PEVV           | 101   | 168  | 0.88 | 3.43 |
| Araucaria      | 19    | 76   | 0.88 | 3.43 |
| Phase 1        | 45    | 203  | 0.94 | 5.74 |
| Phase 2        | 34    | 135  | 0.94 | 6.17 |
| Phase 3        | 34    | 118  | 0.94 | 7.38 |
| PEVV           | 35    | 217  | 0.94 | 5.74 |

**Fig. 3. Cumulative numbers of species of Syrphidae captured using malaise traps in all five areas surveyed in the PEVV, Ponta Grossa, Paraná (September 1999 to August 2002).**

**Table 4. Observed and estimated species richness of Syrphidae based on the estimators Chao 1, Chao 2, Jackknife 1, Jackknife 2, Bootstrap, and Michaelis–Menten, separately for each area and for the entire dataset in PEVV, based on weekly data obtained using malaise traps in the PEVV, Ponta Grossa, Paraná (September 1999 to August 2002)**

|                | Sobs. | Chao 1 | Chao 2 | Jackknife 1 | Jackknife 2 | Bootstrap | Michaelis–Menten |
|----------------|-------|--------|--------|-------------|-------------|-----------|------------------|
| 1999–2000      |       |        |        |             |             |           |                  |
| Forest edge    | 55    | 97 ± 24| 108 ± 31| 81 ± 6       | 99 ± 3       | 66 ± 1    | 65               |
| Araucaria      | 36    | 69 ± 26| 64 ± 21| 51 ± 4       | 61 ± 1       | 42 ± 1    | 53               |
| Phase 1        | 50    | 98 ± 29| 95 ± 25| 75 ± 5       | 92 ± 3       | 60 ± 1    | 69               |
| Phase 2        | 30    | 42 ± 9 | 47 ± 13| 43 ± 3       | 51 ± 1       | 36 ± 1    | 43               |
| Phase 3        | 31    | 43 ± 9 | 43 ± 9 | 43 ± 4       | 49 ± 2       | 36 ± 1    | 42               |
| PEVV           | 101   | 168 ±30| 175 ±33| 141 ±7       | 169 ±3       | 118 ±1    | 115              |
| 1999–2001      |       |        |        |             |             |           |                  |
| Forest edge    | 80    | 124 ±20| 124 ±20| 115 ±6       | 135 ±3       | 95 ±1     | 89               |
| Araucaria      | 47    | 77 ±19 | 76 ±18 | 67 ±4       | 80 ±2       | 56 ±0     | 62               |
| Phase 1        | 56    | 128 ±47| 97 ±24 | 80 ±5       | 97 ±2       | 66 ±1     | 72               |
| Phase 2        | 34    | 43 ±7  | 46 ±9  | 47 ±3       | 53 ±1       | 40 ±0     | 44               |
| Phase 3        | 34    | 44 ±8  | 44 ±8  | 46 ±4       | 51 ±2       | 40 ±1     | 44               |
| PEVV           | 126   | 208 ±32| 217 ±35| 179 ±8       | 215 ±2       | 148 ±1    | 134              |
| 1999–2002      |       |        |        |             |             |           |                  |
| Forest edge    | 98    | 203 ±45| 203 ±45| 146 ±7       | 182 ±2       | 118 ±1    | 105              |
| Araucaria      | 50    | 91 ±29 | 91 ±29 | 68 ±4       | 82 ±1       | 58 ±1     | 61               |
| Phase 1        | 63    | 119 ±31| 102 ±20| 91 ±6       | 109 ±2      | 75 ±1     | 78               |
| Phase 2        | 40    | 56 ±11 | 64 ±16 | 57 ±4       | 68 ±1       | 47 ±0     | 49               |
| Phase 3        | 40    | 48 ±6  | 48 ±6  | 53 ±4       | 55 ±1       | 46 ±0     | 50               |
| PEVV           | 151   | 276 ±45| 288 ±49| 218 ±9      | 267 ±2      | 179 ±1    | 156              |

Sobs. = observed number of species.
Exclusive and Shared Species. From all identified species, 12% were common to all areas studied, whereas 62% were exclusive to only one of the five areas. Among the exclusive species, only six were represented by >10 specimens. The Forest edge had the largest number of exclusive species, which represented more than half of the local richness. In contrast, the most conserved forest areas (Phases 2 and 3) had the smallest number (<20%).

The number of species shared between areas ranged between 23 and 37 but did not exceed half of the number of species found in each of the areas (Table 5). The highest percentage share of species was between Phases 2 and 3 (48%)—the most conserved and geographically distant from each other—and the lowest was between these areas and the Forest edge (20%). Considering that light availability and vegetation characteristics of Phase 1 and Araucaria areas are more similar to those in the Forest edge, Phase 1 and Araucaria were the areas that shared more species with the Forest edge (Table 5).

Community Structure. The ordination analysis based on Syrphidae species occurrence and their relative abundance in the different sample areas (Fig. 4) indicated that the Forest edge is strongly different from the forested areas, reflecting their unique floristic and environmental characteristics. The strongest structural similarity occurred between the forested areas where the canopy opening had more gaps (Araucaria and Phase 1), and the most conserved areas, with high humidity, formed a third group, not very cohesive. When the Syrphidae subfamilies were ordered separately, a different arrangement of the areas was observed for the species of Eristalinae and Microdontinae. In the case of Eristalinae, the forested areas nearly overlapped on the diagram, revealing high similarity. Conversely, when Microdontinae were considered not only the Forest edge but also the best-conserved area (Phase 3) showed a quite distinct community structure when compared with the other areas.

Indicator Species. From the 151 Syrphidae species identified, 19 were considered environmental indicators and were collected exclusively or mainly in a particular habitat type. Twelve of them were associated with the open vegetation, and seven with the forest vegetation (Table 6). The other species sampled were not good indicators of any particular habitat.

Discussion

The outcome of our 3-yr survey of the insects of the PEVV corroborates the interpretations based on the data of the first year provided by Jorge et al. (2007). Our extended study, however, has not only provided more consistent data but has also advanced the knowledge on the family Syrphidae. The highest species richness and abundance were found in the subfamily Syrphinae, followed by Microdontinae and Eristalinae. The richness in hoverfly species and abundance of individuals were associated with the floristic characteristics and the level of conservation of the different areas. The more open, initial, or disturbed areas had more species and more individuals. In addition, the species distribution within the different habitat types in Araucaria Forest was heterogeneous, and the community structure in the Forest edge was clearly distinct when compared with the other areas sampled.

| Table 5. Total number and percentage of Syrphidae species shared between pairs of areas, resulting from malaise trap sampling, in five areas of the PEVV, Ponta Grossa, Paraná, between September 1999 and August 2002 |
|-----------------|-----------------|-----------------|-----------------|-----------------|
| Forest edge | Araucaria | Phase 1 | Phase 2 | Phase 3 |
| Forest edge | 98 | — | — | — |
| Araucaria | 33 (29%) | 50 | — | — |
| Phase 1 | 37 (30%) | 34 (43%) | 63 | — |
| Phase 2 | 23 (20%) | 27 (43%) | 30 (41%) | 40 |
| Phase 3 | 23 (20%) | 26 (41%) | 28 (37%) | 26 (48%) | 40 |

Fig. 4. NMDS ordination of abundance data of hoverflies collected with malaise traps in five areas sampled in the PEVV, Ponta Grossa, Paraná, between September 1999 and August 2002. The first graph is based on all species of Syrphidae (NMDS stress < 0.001), the second refers only to species of Eristalinae subfamily (NMDS stress = 0.008), the third to Microdontinae (NMDS stress = 0.003), and the last to Syrphinae (NMDS stress < 0.001).
Syrphidae larvae are more strongly affected by particular environmental conditions than are the adults (Ricarte et al. 2011). Given the lack of efficient protocols for sampling the entire hoverfly larval community (Ricarte et al. 2011) and the importance of the highly diverse larval habitats in the evaluation of the environmental conditions of a site (Sommaggio 1999), it is necessary to consider the ecological requirements of both adults and larvae when assessing hoverfly communities collected as adults (Meyer et al. 2009).

The highest species richness and abundance of Syrphidae in the Forest edge and in the areas at the initial to intermediate stages of plant succession can be a result of the higher productivity in these areas, which can be associated with a higher incidence of light and a greater availability of flowers—the preferred food source for Syrphinae and Eristalinae adults (Vockeroth and Thompson 1987). This was expected based on the literature, given that open and sunny areas are generally considered suitable habitats for syrphids (Owen 1991, Gittings et al. 2006). Moreover, grassy clearings may promote the entry of insects from the surrounding areas (Taki et al. 2010), providing conditions for migrant, pioneer, and eurytopic species to establish temporary populations. Hence, the high species richness in such areas might also be the result of a large number of vagrant species.

On the other hand, areas in the most advanced stage of conservation had the lowest abundance and species richness. A general decrease in these community descriptors with increasing forest structural retention had been previously reported (Deans et al. 2007). Similarly, a study on the effects of plant succession and the type of forest management on Syrphidae communities in Belgium documented a decrease in the total diversity in advanced forest succession stages (Dekoninck et al. 2005). Moreover, the area in initial to intermediate stages of forest succession (Phase 1) had elevated species richness and abundance of Syrphidae, though lower than in the Forest edge, a pattern consistent with data obtained for hoverflies in general. Our results confirm an evaluation of different habitats in China, where the highest diversity of flower-visiting hoverflies occurred in the secondary forest habitats that were only slightly disturbed (Du et al. 2009). The richness of Syrphidae decreased with an increase in the level of plant succession, which results in flowers and short plants becoming scarce in the understory. Despite the scarcity of studies on the subject, one can assume that, in forested areas, syrphids are most abundant in the canopy, which is where flowers are more widely available.

The Araucaria area harbored a great number of species. When a forest is planted, as in the case of the Araucaria area, the forest structure has different strata and grows more rapidly than in natural circumstances (Dekoninck et al. 2005). In addition, despite the height of the canopy, the interior of the Araucaria Forest receives more sunlight than the most conserved areas in our study, which had lower syrphid species richness. Although the complexity of the vertical structure increases with successional age and potentially provides physical habitat for species, the lower abundance of herbs and shrubs provides fewer food sources for adults (Humphrey et al. 1999).

Despite not significant, the number of Eristalinae species was higher in more open and less humid areas (Phase 1 and Forest edge). On the other hand, the highest relative frequency of adults in the area at the intermediate to advanced stages of forest succession (Phase 2) could reflect the reproductive characteristics of hoverflies. The lower incidence of light in the interior and the moister, leaf-litter-rich soils of that area provide a suitable microenvironment for the development of larvae with saprophagous feeding habits. In these conditions, the adults would be caught as soon as they emerge from pupa. It has already been shown that, although hoverfly species richness is affected by resource heterogeneity, hoverfly density depends on resource accessibility, such as the availability of larval microhabitats (Meyer et al. 2009).

The relative frequency of Microdontinae was higher in each of the forested areas than in the Forest edge. However, species richness was significantly higher in the three most open areas. It is still not possible to understand the reasons for these results because the biology of Microdontinae is not well documented. All we know is that larvae of a few species are associated with ants (Duffield 1981, Elmes et al. 1999, Hironaga and Maruyama 2004).

The estimates generated by Bootstrap and Jackknife 1 richness estimators were closer to what was posited by Owen and Owen (1990), i.e., if in 3 yr one can uncover ~75% of the syrphid fauna present at a given location, one could expect that the surveyed forest, whose richness was 151 species, might in fact harbor 200 species, which is an intermediate value between the Bootstrap (179) and Jackknife 1 (218) estimates. Granted that the number of new occurrences of species decreases with the increase in sampling effort, one can assume that the index of Michaelis–Menten is also an adequate estimator, as revealed by the

| Species | Subfamily | Condition | IndVal | P  |
|---------|-----------|-----------|--------|----|
| Allograpta neotropica (Curran, 1936) | Syrphinae | Cl | 0.90 | 0.020 |
| Allograpta similis (Curran, 1925) | Syrphinae | Cl | 1.00 | 0.010 |
| Copestylum macquarti (Curran, 1926) | Eristalinae | Fo | 0.83 | 0.040 |
| Microdon aureopilis (Marioni, 2004) | Microdontinae | Fo | 0.83 | 0.041 |
| Microdon mariei (Thompson, 2004) | Microdontinae | Ad | 0.62 | 0.035 |
| Mixogaster polistes (Hull, 1954) | Microdontinae | In | 0.63 | 0.027 |
| Ocyptamus antiphates (Walker, 1849) | Syrphinae | Cl | 1.00 | 0.020 |
| Ocyptamus clarex (Wiedemann, 1830) | Syrphinae | Cl | 1.00 | 0.010 |
| Ocyptamus funebris (Macquart, 1834) | Syrphinae | Cl | 0.68 | 0.020 |
| Ocyptamus gastrostactus (Wiedemann, 1830) | Syrphinae | Cl | 0.96 | 0.010 |
| Paramicrodon flukei (Curran, 1936) | Microdontinae | In | 0.63 | 0.036 |
| Pseudodaros clavatus (Fabricius, 1794) | Syrphinae | Cl | 0.97 | 0.010 |
| Syrphus phaeostigma (Wiedemann, 1830) | Syrphinae | Cl | 0.63 | 0.040 |
| Taxomerus basilis (Walker, 1836) | Syrphinae | Cl | 0.69 | 0.040 |
| Taxomerus croesus (Hull, 1940) | Syrphinae | Ad | 0.58 | 0.027 |
| T. croesus (Hull, 1940) | Syrphinae | Fo | 0.93 | 0.001 |
| Taxomerus pictus (Macquart, 1842) | Syrphinae | Cl | 1.00 | 0.010 |
| Taxomerus polygraphicus (Hull, 1940) | Syrphinae | Cl | 0.99 | 0.010 |
| Taxomerus pulitius (Say, 1823) | Syrphinae | In | 0.67 | 0.040 |
| Taxomerus watsoni (Curran, 1930) | Syrphinae | Cl | 0.99 | 0.010 |

Cl, open vegetation; In, initial and intermediate forest succession areas; Ad, intermediate and advanced forest succession areas; Fo, forested environments.
The highest proportion of common Syrphidae species is probably due to their remarkable ability to fly (Gilbert 1983) and to their diverse eating habits during their life cycle, which leads to greater mobility among the areas surveyed.

Our results support the idea that syrphids are appropriate ecological bioindicators (Sommaggio 1999). The values of specific indicators revealed that the 12 indicator species of the Forest edge can be considered primarily species of grassy clearings or disturbed areas. All of them belong to the subfamily Syrphinae. Related species whose biology is known (Rojo et al. 2003) are generally aphid predators, and we think that it is safe to assume that our species have similar habits. The seven indicator species of forested habitats can be considered primarily forest species, three of which occurred exclusively, or mainly, in the initial and disturbed areas, and two occurred in the advanced and most conserved areas. Four of those species belong to the subfamily Microdontinae, three to Syrphinae, and one to Eristalinae. As they are allocated to different groups and have different larval morphologies, their larval feeding habits are varied, ranging from predation to saprophagy (Vockeroth and Thompson 1987). However, their ecological requirements appear to be present especially in forests. A similar analysis performed in Belgium also indicated that the major component determining the distribution of Syrphidae species is the degree of vegetation cover (Dekoninck et al. 2005). Natural or anthropogenic small disturbances, which create a gradient of canopy openness in Araucaria Forest and increase their environmental heterogeneity, may increase the entomological diversity (Marinoni and Ganho 2006, Linzmeier and Ribeiro-Costa 2009).

Although several studies have demonstrated that hoverflies are negatively affected by a reduction in landscape diversity, few studies have used this taxonomic group to evaluate environmental health (Sommaggio 1999). This may be due to the lack of data on the habitats and habitats of Brachycera fly species, especially in the Neotropic region, where the lack of this kind of information hinders ecological research on the group (Beaulieu and Wheeler 2005). Although it is risky to establish habitat associations based only on five areas, the general patterns found in this study have allowed us to make a hypothesis for the distribution of the syrphid fauna of Araucaria Forest. Only more knowledge on the biology of the species may confirm such patterns.

Considering that the habits of foraging, mating, oviposition, and diapause in Syrphidae may require habitats quite different from one another, environmental heterogeneity is fundamental (Meyer et al. 2009). Additionally, there are hoverfly species that are more closely associated with specific vegetation types. Many of them are associated with forest environments (Branquart and Hemptinne 2000) with a high diversity and abundance of microhabitats, as well as refuges in adverse conditions (Ricarte et al. 2011). Other species colonize open and anthropogenic habitats (Branquart and Hemptinne 2000), of which grassy clearings provide additional resources, increasing Syrphidae diversity (Ricarte et al. 2011), as in the disturbed areas of this study. Taking into consideration the availability of exclusive species in both forested and open areas, the results of this study confirm those of Meyer et al. (2009) and Ricarte et al. (2011), highlighting the need to conserve mosaic landscapes for the development of different stages of the life cycle of hoverfly species and thus support highly diverse communities.

**Final Considerations**

This study is the outcome of the longest survey of the syrphid fauna in Brazil using malaise traps. In the case of taxa with highly diverse life histories as Syrphidae species, only intensive and extensive studies can adequately survey its richness and allow the understanding of the role of them in nature. The species accumulation curve, with an asymptote only on the third month of the third year, demonstrates the importance of long periods of collecting for robust surveys of syrphid faunas.

Our data on the richness and abundance of Syrphidae corroborated the hypothesis that more well-preserved forests tend to maintain a smaller number of species with more equitable abundances, when compared with areas that are impacted or are in the early stages of plant succession.

In most syrphid species with known biology, adults are flower visitors and play an important role as pollinators. The larvae have feeding habits that usually characterize them as predators, saprophagous or phytophagous. As a consequence of the different behaviors displayed by adults and larvae, a given species might, throughout its life cycle, occupy environments that are completely at odds with one another—for instance, open areas with high incidence of sunlight and flower availability versus shaded areas with low incidence of sunlight and rich in decomposing matter. Therefore, the interpretation of the results based on the capture of adults using malaise traps is complex, leading to different hypotheses that need to be tested by further biological and ecological studies on the Neotropical Syrphidae fauna. It would be necessary also to identify environmental indicator species in different vegetation types.

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