ABSTRACT. The diversity (Shannon-Weaver) of butterflies throughout the urbanized area of Porto Alegre, Brazil, was analyzed using 109 sampling areas within three characteristic zones of urbanization: buildings (B), houses and buildings (HB), and houses (H). Highest diversity was found in the periphery of the houses zone (H) one to two kilometers beyond the perimeter of the houses and buildings zone (HB). From zone H to zone HB we observed a significant decrease in diversity and a small overlap in community composition (Renkonen’s PS). From zone HB to a central zone of buildings (B), there was a relatively small change in community composition demonstrated by statistically similar diversity indices and a high species similarity. These findings suggest the existence of two macrohabitats for butterflies in the city: 1) B + HB and 2) H. Samples from areas within the same urbanized zone showed the highest degree of similarity. Diversity decreased in the B + HB macrohabitat mainly owing to a reduction in species richness (S). Biotic and abiotic factors that may be involved in this reduction are discussed. For late spring and midsummer samples, nearly 50% of the variation in diversity was explained by vegetation cover and distance from the city center. This value rises to 63% for the total diversity and 70% for the log transformation of species richness. These high proportions emphasize the importance of regional urban environmental conditions for butterfly diversity. In the winter, only vegetation cover presented a partial regression coefficient that was significant, accounting for less than 20% of the variation in diversity. Also, a scattered distribution of areas with high butterfly diversity associated with high vegetation cover was observed during the winter.

Additional key words: urban ecology, urban Lepidoptera, insect diversity, man-made habitats, community structure.

The structure and diversity of biotic communities within urban environments are important for theoretical and practical reasons. Urban biotas can be studied from a genetic and evolutionary perspective, as
exemplified by Bishop and Cook (1981), or from an ecological perspective as demonstrated by Ruszczyk (1987). The ecological consequences of urbanization for particular groups of plants and animals can indicate the degree of disturbance of such environments and may be useful in developing strategies for conservation.

In a previous study, Ruszczyk (1987) presented maps of the distributions of 29 species of butterflies within the urbanized area of Porto Alegre, Brazil. Species exhibited variable rates of decline toward the highly-developed urban center. The border between a predominantly house-occupied zone (H) and a zone of houses and buildings in equal proportions (HB) was found to be the main area of transition for the urban fauna, acting as an ecological barrier for species typically associated with woods or natural fields. Species that are associated with open areas, that are highly vagile, and that have larvae that utilize both native and exotic cultivated plants were dominant in the city. Distance of the sampling areas from the center of the city was found to be a better predictor of butterfly numbers than average elevation or vegetation cover.

In this study we further analyzed butterfly diversity for 109 sampling points. We also investigated factors influencing spatial patterns of diversity and species richness within the city as well as the similarities in the structure of butterfly communities in regions within different levels of urbanization.

**Materials and Methods**

**Study area.** Porto Alegre is a large urban area in Rio Grande do Sul in southern Brazil (30°02'S 51°14'W; 1,000,000 inhabitants). It has a temperate-subtropical climate with high humidity and moderately high temperatures in the summer. Mean annual temperature is 13.8°C, and average annual rainfall is 1322 mm. Three characteristic zones of urbanization were identified (Ruszczyk 1987): a buildings zone (B) with buildings more than four stories high and vegetation cover below 20%; a houses-and-buildings zone (HB) with equal proportions of lower buildings and houses and vegetation cover between 20 and 40%; and a houses zone (H) with mostly houses but including open areas within the city, and vegetation above 40% (Fig. 1a). The urbanized zones illustrated in Fig. 1A were simplified by drawing tangential lines to the borders of the different urbanized zones (Fig. 1b).

**Data collection.** A 1 km grid was superimposed on the map of the urbanized zones resulting in 109 contiguous sample areas within the city. Sampling areas (SAs) were arbitrarily delineated as 600 m diameter circles (Fig. 1b). SAs were surveyed for butterflies during three sampling periods: November–December 1980, March–April 1981, and June–July
FIG. 1. Urbanized zones of Porto Alegre in 1981 (a), and distribution of sampling areas in a simplified map (b). The triangle in Fig. 1b indicates the center of the buildings zone. 1, buildings zone; 2, houses-and-buildings zone; 3, houses zone; 4, marshes; 5, extraurban area.

1981. Each SA was sampled sequentially, five SAs per day between 1000–1600 h. SAs were censused by walking continually along the streets and recording the number of each butterfly species observed during a 45 minute period (see Ruszczyk 1987 for further details of the sampling program and study area). The distance between each SA and the SA at the center of the building zone (marked with a triangle in Fig. 1b) was considered the “distance from the city center.” The average elevation of each SA was calculated as the arithmetic mean of its highest and lowest points.

Data analysis. The Shannon-Weaver index (Margalef 1958, Lloyd & Ghellardi 1964, Pielou 1966) was used to calculate diversity ($H'$) for each SA. The SAs were grouped in three sets related to the three urbanized zones. The differences between the calculated indices for these sets were compared using a t-test modification proposed by Poole (1974) for evaluating diversity calculations. In addition, a one-way analysis of variance was applied to the three sampling periods (Nov–Dec/80; Mar–Apr/81; Jun–Jul/81) disregarding the zones, to test the effects of seasonality on mean diversity. The degree of similarity among samples was measured using Renkonen’s Percentage of Similarity (PS). For this analysis, SAs were combined into 11 regions with similar area within a single urbanized zone. This reduced the area matrix from 109
FIG. 2. Diversity index (Shannon-Weaver) of butterfly communities in the urbanized zones of Porto Alegre. Clear areas indicate less than 12 individuals recorded; bold lines separate urbanization zones (see Fig. 1b).

sampling points to 11 contiguous areas and permitted detection of patterns among city regions rather than local faunal similarities. Grouping of regions in the principal matrix followed the simple average method (Sneath & Sokal 1973). The relative influence of 1) percentage of area covered by vegetation, 2) distance from the city center, and 3) mean elevation of each SA on butterfly diversity and on the total number of species was calculated using multiple regression. The explained variation ($R^2$) of the dependent variables was partitioned into components attributed to each independent variable following the standard regression method (Kim & Kohout 1975).

RESULTS

Highest diversity values were found in zone H, typically one to two km beyond the perimeter of zone HB (Fig. 2). In late spring and midsummer (Figs. 2a & 2b), patterns of diversity were strongly correlated with urbanized zones—zone H typically had diversity values greater than $H' = 2.4$ (Fig. 2, diversity class no. 3) and zone HB had lower values. During winter (Fig. 2c) there was greater variability in the diversity indices. However, the peripheral area of the houses zone (H) continued to support greater diversity.

Papilionini and Heliconiini, two tribes that are abundant in the city, showed the same tendencies as described above (Fig. 3). A considerable decrease in the number of species in these two groups was observed at the border between zones H and HB. In zone B the number of species was fairly constant—one or two. The highest number of species was recorded in the periphery of zone H. In the winter, the number of species decreased greatly, especially in zones B and HB (Fig. 3).

Multiple regression of diversity (using pooled seasonal data) with the
number of species and species evenness showed a greater interaction with the number of species in the explained variance of diversity ($R^2 = 0.90$) than with the species evenness ($R^2 = 0.10$). The standardized regression coefficient (variables transformed to have unit variance allowing the comparison of variables measured in different units) of the number of species (0.98) was nearly three times greater than for evenness (0.35), indicating that diversity decreased in zones B and HB mainly due to the reduction in the number of species in these zones. Diversity indices for the entire zone H (summation of SA data) were significantly higher than for zones HB and B. On the other hand, the indices for zone HB and B were not statistically different (Table 1).

**TABLE 1.** Diversity of butterflies in three urbanized zones of Porto Alegre. The lines indicate indices that were statistically similar ($P < 0.05$). Differences between indices were compared using a $t$-test modification proposed by Poole (1974).

<table>
<thead>
<tr>
<th>Sample</th>
<th>Buildings</th>
<th>Houses-and-buildings</th>
<th>Houses</th>
</tr>
</thead>
<tbody>
<tr>
<td>Late spring, 1980</td>
<td>2.5414</td>
<td>3.0304</td>
<td>3.4785</td>
</tr>
<tr>
<td>Midsummer, 1981</td>
<td>2.6344</td>
<td>3.0145</td>
<td>3.3108</td>
</tr>
<tr>
<td>Total</td>
<td>2.9277</td>
<td>3.2251</td>
<td>3.4873</td>
</tr>
</tbody>
</table>
Figure 4 illustrates the results of PS calculations. Two distinct clusters of regions are evident: 1) regions I to VIII, all but the last of which are located in zone H, with a high internal PS; and 2) regions IX and X in zone HB and region XI in zone B, with a comparatively low internal PS.

Standardized regression coefficients of distance from the city center and vegetation cover with diversity and the log number of species, were similar; but distance had a slightly greater value (Table 2). In midsummer, distance was almost twice that of vegetation cover. In the winter, vegetation cover showed a significant partial regression coefficient with diversity, though accounting for less than 20% of the explained variation in diversity. In late spring and midsummer, about 50% of the variation in diversity was explained by vegetation cover and distance from the city center. This value increased to 63% for the total diversity and 70% for the log number of species. These high proportions demonstrate that such variables are important determinants of butterfly community structure in Porto Alegre. However, the contribution of each variable alone was, in general, less than 11%. More than 30% of the variation was due to the interaction of vegetation cover and distance, whose effects on butterfly diversity and species number was neither indepen-
TABLE 2. Decomposition of the explained variation in butterfly diversity (Shannon-Weaver index) in three sampling periods, and total number of species (ln S) into components attributed to the independent variables percentage of area covered by vegetation of the sampled area ($X_1$) and distance from the city center ($X_2$). Standardized regression coefficients in parentheses. Angular transformation was used for $X_1$ and logarithmic for $X_2$.

<table>
<thead>
<tr>
<th>Dependent variable (Y)</th>
<th>Proportion of variation explained by $X_1$ and $X_2$ ($R^2$)</th>
<th>Increment due to vegetation cover ($X_1$)</th>
<th>Increment due to distance from the city center ($X_2$)</th>
<th>Not attributed to either $X_1$ or $X_2$ alone</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diversity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late Spring 1980</td>
<td>0.456</td>
<td>0.058</td>
<td>0.075</td>
<td>0.323</td>
</tr>
<tr>
<td>Midsummer 1981</td>
<td>0.489</td>
<td>0.043</td>
<td>0.108</td>
<td>0.338</td>
</tr>
<tr>
<td>Winter 1981</td>
<td>0.171</td>
<td>0.171</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total 1980–1981</td>
<td>0.630</td>
<td>0.078</td>
<td>0.107</td>
<td>0.445</td>
</tr>
<tr>
<td>Log no species</td>
<td>0.703</td>
<td>0.096</td>
<td>0.109</td>
<td>0.498</td>
</tr>
</tbody>
</table>

(—), partial regression coefficient not significant after the inclusion of the variable in the multiple regression equation.

Diversity nor additive (Table 2). The biological mechanism underlying the strong association between these two variables affecting butterfly diversity and species number cannot be inferred from these data alone. Average elevation was excluded from this analysis because in the presence of the other variables its partial regression coefficient was not significant.

A marked seasonality in diversity was observed in Porto Alegre (Fig. 5), with mean diversity of each sampling period significantly different even when the zone data were pooled (Table 3).

**DISCUSSION**

The buildings zone (B) did not form a subset isolated from the houses-and-buildings zone (HB) (Fig. 4), and the diversity indices for these zones were statistically similar (Table 1) revealing their similar butterfly diversity.
TABLE 3. Results of the one-way ANOVA for mean diversity in three sampling periods, independently of urbanized zone. \( H_1 \) = Late Spring 1980; \( H_2 \) = Midsummer 1981, \( H_3 \) = Winter 1981.

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between ( (H_1 \cdot H_2) ) vs. ( H_3 )</td>
<td>3.7050</td>
<td>2</td>
<td>1.8525</td>
<td>15.47</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>( H_1 ) vs. ( H_2 )</td>
<td>2.1274</td>
<td>1</td>
<td>2.1274</td>
<td>17.77</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Within</td>
<td>31.9676</td>
<td>267</td>
<td>0.1197</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>35.673</td>
<td>269</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

community structure. Zone B can be seen as a portion of the zone B + HB macrohabitat where environmental conditions are more harsh for butterflies, but without divergence of the typical community of butterflies of zone HB. In this community (B), several species of butterflies that are relatively abundant in zone H, are scarce or absent. These include woodland species, such as *Heliconius erato phyllis* (Fabricius), *Eunica margarita* (Godart), *Adelpha* spp. (Nymphalidae), *Battus* spp., *Parides* spp. (Papilionidae); Nymphalidae that feed on fruit and sap (*Hamadryas* spp., *Anaea* spp.); species characteristic of fields, such as *Colias lesbia pyrrhothea* (Huebner), *Eurema* spp. (Pieridae), *Euryades corethrus* (Boisduval) (Papilionidae), *Junonia evarete* (Cramer), *Vanessa* spp. (Nymphalidae); and some eurytopic species, such as *Dryas iulia* (Fabricius), *Anartia amathea* (Eschscholtz) (Nymphalidae), *Papilio hectorides* Esper, and *Papilio astyalus* (Papilionidae). All species found in zones B and HB also were observed in zone H. These species [e.g., *Papilio scamander* Boisduval, *Papilioanchisiades capys* Huebner (Papilionidae), *Ascia monuste orseis* (Latreille), *Tatochila autodice* (Huebner), *Phoebis philea* (Johansson) (Pieridae), and *Dryas iulia*) are the most widespread in the city, attaining high densities in all urbanized zones (Ruszczyk 1987). The impoverishment of the butterfly community in the B + HB urbanized zone is likely the result of the considerable environmental disturbance in this area as compared to zone H. Abiotic and biotic factors are harsher in zone B + HB than in zone H. Abiotic factors include the following: a) dry and strongly illuminated habitat (e.g., all watercourses are channelized, there are few shaded areas, and there is high sunlight penetration to the ground); b) greater air pollution owing to traffic; c) habitat disturbance from intense human movement and traffic; and d) streets and sidewalks completely paved and a large percentage of the area occupied by buildings, diminishing the resources at the soil surface. Biotic factors include the following: a) lower percentage of area covered by vegetation which acts to decrease diversity within these zones by lowering primary productivity (Connell & Oris 1964), and the accentuated fragmentation of the vegetation probably reduces colonization
and dispersion of butterflies; b) relative homogeneity of vegetation (in zones B and HB relicts of native vegetation were not observed, and many plants that are common in outlying areas were very scarce, giving a qualitative decrease in nectar sources and potential food plants for larvae); and c) smaller contribution of elements of the extraurban fauna (zones B and HB probably have small participation of the transitory species from peripheral areas than zone H, which is in direct contact with remnants of natural habitats).

The formation of butterfly diversity gradients in the city is in contrast to the results obtained in studies of soil arthropods, which seem to respond more to local (soil) variables than to urban environmental gradients (Kühnelt 1955, Topp 1972, Lussenhop 1973, Maurer 1974). More recently, Klausnitzer and Richter (1983) demonstrated the presence of an urban gradient for carabids in the city of Leipzig, Germany. As for butterflies, the distance from the center of the city showed a greater influence on diversity than vegetation cover or mean elevation, emphasizing the importance of macrohabitat conditions for these insects.

Distance correlated well with butterfly abundance (Ruszczyk 1987) and diversity (present paper) in Porto Alegre, Brazil, probably because many parameters that are important for butterflies are radially dispersed in the city due to the radial pattern of the urbanized zones.

The non-significance of the partial regression coefficient of distance from the city center during winter, and the island character of the class distribution of diversity (Fig. 2c), suggest that winter butterfly diversity depends on qualitative variables such as presence of habitat refugia. When compared to other zones, zone H showed greater possibilities for the presence of such refugium. In the winter, a higher diversity was scattered among 26 SAs, all but one of which was situated in zone H; 19 of these SAs possess vegetation cover greater than 45%. This provides evidence of the biotic value of urban vegetation, and suggests that fragments of habitat within the urbanized areas, especially urban forest fragments (Rodrigues et al. 1992), may perform a vital role in maintaining local biodiversity.

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LITERATURE CITED


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