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Research Article

Butterfly conservation within cities: a landscape scale approach integrating natural habitats and abandoned fields in central Mexico

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Abstract

Growing urbanization and the expansion of the agricultural frontier in tropical ecosystems have generated patchy landscapes composed of remnants of natural habitats and abandoned fields. This scenario offers an opportunity to develop urban reserves in order to preserve local fauna in expanding cities. We propose that if native animals are able to use these two habitat types, reserves composed of a mixture of natural habitats and abandoned fields would contain more diversity than reserves composed only of natural habitats. However, to be useful for conservation, these reserves must harbor specialized organisms that depend on natural habitats. To test this proposal, we focused on diurnal butterflies inhabiting an urban reserve located within the city of Puebla (Mexico), which contains relics of oak forests and abandoned fields. Butterfly assemblages were sampled and compared in the different habitat types of the reserve. The data were then pooled and analyzed for the reserve as a whole. These analyses discriminated between habitat generalist and forest specialist butterflies. Our results indicated that the different habitat types of the reserve harbor different forest specialist butterflies, which in turn enhanced the diversity of forest-dwelling butterflies at the landscape scale. This suggests that the inclusion of abandoned fields together with natural habitats in the design of urban protected areas could help to preserve at least part of the regional biodiversity.

Keywords: habitat diversity, habitat loss, land use change

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Introduction

The world is currently going through the largest wave of urban growth in its history. More than half of the human population now lives in towns and cities, and by 2030 it is predicted that this number will increase to some 5 billion people [1]. Much of this urban growth is taking place in the developing countries of Latin America, Africa and Asia, bringing huge environmental transformations to natural ecosystems [1]. Urbanization has powerful effects on biogeochemical cycles and local climatic conditions [2-6], which in turn results in loss of biodiversity [7]. Together with the expansion of the agricultural frontier, urbanization has generated patchy landscapes in the areas surrounding cities, which are largely composed of the remnants of natural habitats and agricultural fields [8, 9].

In forest ecosystems, these anthropogenic processes have endangered several animal species that depend on natural habitats for developing their life cycles [10-14]. However, the increasing migration of rural people to urban areas is currently resulting in the abandonment of agricultural land, and this may offer an opportunity to develop conservation strategies aimed at preserving part of the local fauna. Indeed, several authors have proposed that the extinction risk of forest-dwelling animals in anthropogenically disturbed ecosystems may decrease if they are able to use abandoned fields as alternative sources for food, refuge and mating sites [15-19]. Furthermore, if forest relicts and abandoned fields are used by different animal species, this increased habitat heterogeneity could even enhance faunal diversity at the landscape spatial scale -i.e., the spatial scale that embraces more than one habitat type [20].

Following this line of reasoning, it can be hypothesized that reserves containing a mixture of native habitats and abandoned fields should harbor higher faunal diversity than reserves composed only of natural habitats. Although this may sound somewhat counterintuitive to the mainstream principles of conservation biology, which emphasize the preservation of natural ecosystems [21], such a hypothesis can be useful for designing urban reserves in the areas surrounding growing cities before all relicts of natural habitats and abandoned fields are claimed for urban development [22, 23]. The main drawback of this hypothesis is establishing whether the organisms that are intended to be protected can survive in these kinds of reserves. For instance, the conservation aim of these reserves might fail if they only harbor generalist species that are anyway able to use the relicts of native habitats or abandoned fields

to survive and reproduce. Conversely, if they can sustain specialized organisms that usually depend on natural habitats to complete their life cycles, but which are also able to use abandoned fields as supplementary habitats, then the conservation aims will be fulfilled. According to the conceptual framework of conservation biology [21], these reserves will be useful if - and only if - they meet this latter condition.

To test this hypothesis, we focused on diurnal butterflies in a forest reserve located within the city of Puebla, Mexico. We chose this group of insects because they are important for a number of ecosystem functions, including pollination and nutrient recycling [10], and because they are highly appreciated by people as an aesthetic component of nature [24]. The study site preserves one of the last stands of oak forest that originally covered this region, also including abandoned fields immersed in the forest matrix [22]. Our hypothesis stated that if natural and man-made habitats provide refuge for different butterfly assemblages, then species diversity at the landscape spatial scale (i.e., the entire reserve) should be higher than that expected within forest relics. However, to be valuable for conservation, these different habitat types must harbor native butterflies that require forests to develop at least part of their life cycles.

Methods

Study area

This study was conducted in the Ecological Park *Flor del Bosque* (19° 02'N, 98° 06'W), located within the metropolitan area of the city of Puebla, State of Puebla, Mexico (Fig. 1). Mean annual temperature in this region is 16.3 °C and annual precipitation oscillates between 750 and 950 mm [25]. Up to 90% of rainfall events occur in summer (June-September), while a markedly dry season occurs during the rest of the year [25]. The original vegetation of this region was composed of oak forests (*Quercus* spp., Fagaceae), but these woodlands were systematically logged during the last three centuries and cleared areas were converted into grazing fields [22]. These fields were abandoned in the second half of the 20th century because of their low productivity and, about 50 years ago, some of them were converted into plantations of the exotic tree *Eucalyptus camaldulensis* (Myrtaceae) to reduce soil erosion [22]. Thus, the current landscape of this natural protected area comprises a mixture of oak forest, abandoned grasslands and *Eucalyptus* plantations. Since 1985 the city of Puebla has experienced rapid population growth, largely due to the migration of people from Mexico City [26], which has resulted in the areas surrounding the reserve coming under ever increasing pressure from urbanization [22].

The reserve covers 675 ha and contains two types of oak forest that differ in their species composition. The north-facing slopes of the reserve harbor relics of mesic oak forest (11% of the reserve, Fig. 1), mainly composed of *Quercus candicans*, *Quercus castanea*, *Quercus crassipes*, *Quercus glaucoides*, *Quercus laeta*, *Quercus laurina*, *Quercus mexicana* and *Quercus rugosa*. The south-facing slopes are covered by relics of xeric oak forest (58% of the reserve, Fig. 1) composed of *Quercus castanea*, *Quercus glabrescens*, *Quercus laeta* and *Quercus obtusata*. Tree density in the mesic oak forest is about 480 tree/ha, while it is 240 tree/ha in the xeric oak forests [27]. The understory of both forest types is open and is composed of scattered short bushes (30-50 cm tall) of *Montanoa tomentosa* (Asteraceae), *Karwinskia humboldtiana* (Rhamnaceae), and *Mimosa aculeaticarpa* (Fabaceae) [27]. The understory of the xeric oak forest also contains monocots (Poaceae and Commelinaceae) and forbs (Verbenaceae, Rubiaceae and Sapindaceae) [27]. At the time of our fieldwork, abandoned fields within the reserve were covered by secondary grasslands (23% of the reserve) and *Eucalyptus* plantations (6% of the reserve) (Fig. 1).

Climatic variables

Because climate strongly influences the presence and abundance of butterflies [29, 30], we measured air temperature, air relative humidity and photosynthetic active radiation (PAR) in the four vegetation types described above (mesic and xeric oak forests, abandoned grasslands and *Eucalyptus* plantations). These variables were recorded during the warm-rainy season (summer 2012, from July 1st to September 30th) and the cold-dry season (winter 2013, from January 1st to March 30th), which correspond to the periods of the year in which butterfly samplings were conducted (see below). These variables were recorded with automatized dataloggers (HOBO Onset Computer Corporation), which were set up to record these data every hour. Three dataloggers were randomly distributed within each vegetation type, always maintaining a minimum distance of 100 m between them. Their sensors were fixed on woody stakes 1.2 m above the ground to avoid interference from understory vegetation.

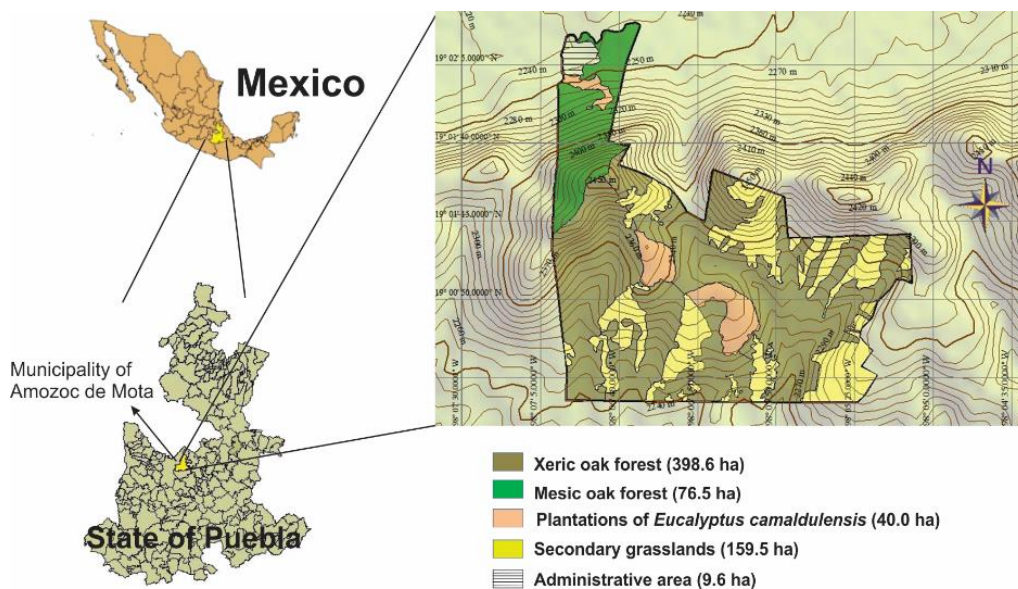


Fig. 1. Location of the ecological park Flor del Bosque at the municipality of Amozoc de Mota, State of Puebla, Mexico. The figure shows the polygon of the park and the area covered by the different vegetation types, including xeric and mesic oak forest, *Eucalyptus* plantations and abandoned secondary grasslands. The projection of the figure is given in geographical coordinates (Datum WGS84; scale 1:50000).

Butterfly sampling

Diurnal butterflies were sampled in the warm-rainy season and the cold-dry season in the four vegetation types described above. This was because the specific composition of butterfly assemblages can change with changes in climatic conditions [28, 29]. Sampling was conducted on nine days in each season, at intervals of 9-12 days. All samples were taken on days of full sun because previous studies indicate that Neotropical butterflies reduce their activity in cloudy conditions [29, 30]. Because the mesic and xeric oak forests are continuous habitats (Fig. 1), their butterfly assemblages were sampled by randomly distributing three 300-m linear transects within each of these vegetation types on each sampling day. Because transects were not placed at the same site, data taken across sampling days can be considered as independent samples. We were careful to set up these transects at least 50 m away from the edge of neighboring vegetation types in order to avoid interference. On the other hand, because abandoned grasslands and *Eucalyptus* plantations constitute discrete habitat patches immersed in the forest matrix (Fig. 1), we selected three patches of these vegetation types on each sampling day and laid out a 300 m linear transect within each of them. If the same vegetation patch was selected on different sampling days, the transects were placed at different sites from those used in previous samplings. Thus, our sampling protocol provided three independent sub-samples (i.e., pseudoreplicates) of butterfly assemblages within each vegetation type on each sampling date.

A well-trained observer (M.N. Barranco-León) walked each transect for an hour to sample butterfly assemblages. She identified and counted all butterfly species in a visual range of 6 m around each

transect. Because most plants in the understory of forests and *Eucalyptus* plantations are composed of scattered, low-growing plants (i.e. below the visual range of the observer), it is unlikely that vegetation interfered with the counting of butterflies in these habitats. These sampling sessions were conducted between 10:00 and 16:00 because preliminary faunal samplings conducted between 2009 and 2011 in the study area indicated a peak of diurnal butterfly activity at this time of day [31]. To confirm the identity of butterflies recorded on transects, we captured 2-3 specimens of each species with aerial nets and identified them to the lowest taxonomic level that was possible. For this we used the guides of Garwood and Lehman [33-34], and the electronic databases of Lotts and Naberhaus [35] and Warren et al. [36]. Collection of specimens was in compliance with the laws of Mexico and they were deposited in the entomological collection of the University of the Americas Puebla. We also conducted extensive searches on the webpages of the iNaturalist Network (www.inaturalist.org), Butterflies and Moths of North America (www.butterfliesandmoths.org) and Butterflies of America (www.butterfliesofamerica.com) to classify species according to their habitat requirements. This allowed us to categorize species into two main groups: (1) habitat generalist butterflies, including species adapted to human-disturbed habitats that do not require forests to develop their life cycles, and (2) forest specialist butterflies, including species that require forested habitats for developing at least part of their life cycles.

Statistical analyses

Data of air temperature and air relative humidity were used to construct daily average curves for each vegetation type at both the warm-rainy and the cold-dry season. For this, we averaged the data of each datalogger for each hour of the day across the respective seasons. In the case of PAR, these curves were constructed using data recorded during daytime only (8:00 - 18:00 h). These values were compared among vegetation types with repeated measures ANOVA, where hours were considered as repeated measures and dataloggers as replicates ($n = 3$ per vegetation type). These analyses were conducted with R 3.0 [37].

Butterfly data were analyzed to determine if the different species were associated with particular vegetation types. These analyses were conducted separately for each season by pooling the data of all samplings conducted on each vegetation type (i.e. the three 300 m transects on which butterflies were recorded on the nine sampling dates) and calculating the absolute observed occurrence frequency of each species. We used Monte Carlo randomization tests to compare the observed occurrence frequency of each species on each vegetation type against the expected occurrence frequency that the species would have if it was randomly distributed across vegetation types. In these tests, the randomly expected distribution of each species was generated by resampling 1000 times its observed occurrence frequency among vegetation types. After that, we computed the probability (P) for coincidence between observed and expected occurrence frequencies [38]. The null hypothesis of these tests states that if the spatial distribution of a given species is regulated by stochastic processes, then it must display neutral association patterns across vegetation types. This is acceptable if $P \geq 0.05$ but, if $P < 0.05$, then it can be assumed that the spatial distribution of the species is regulated by deterministic processes (for example, habitat preferences) [39]. These analyses were conducted with the Monte Carlo module of PopTools 3.2 [40].

In each season we also compared the composition and diversity of butterfly assemblages among vegetation types. To perform these analyses, we pooled the butterfly data of the three sub-samples taken within each vegetation type on each sampling date (i.e. in the three transects). Therefore, the statistical analyses focused on these community attributes treated the different sampling dates as independent replicas of the butterfly assemblages recorded on each vegetation type. This was because of the spatial complexity of the reserve (Fig. 1), in which some vegetation types were continuous (i.e. the mesic and xeric oak forest) and other vegetation types constituted discrete patches (such as abandoned grasslands and *Eucalyptus* plantations). This treatment of the data allowed us to avoid

pseudoreplication within vegetation types and, hence, to perform robust statistical analyses comparing the composition and diversity of butterfly assemblages. These analyses were firstly conducted including all butterfly species, irrespective of their habitat preferences, which allowed us to identify whether natural habitats (mesic and xeric oak forests) and man-made habitats (abandoned grasslands and *Eucalyptus* plantations) harbor different species assemblages. However, because these analyses did not allow for the determination of the conservation value of the reserve for forest-dwelling butterflies, they were repeated including forest specialist butterflies only.

The composition of butterfly assemblages among vegetation types was compared with non-metric multidimensional scaling ordinations (NMDS). These analyses were conducted separately for each sampling season with presence/absence matrices where sampling dates were considered as replicates ($n = 9$ for each vegetation type, see details above). Ordinations were performed in PC-ORD 6.12 [41] and the Sørensen coefficient was used to measure species similarity among samples [42]. NMDS firstly included all butterfly species and, later, these analyses were conducted with forest specialists only. All NMDS were started by using six-dimensional configurations, but dimensionality (i.e. the number of ordination axes) was stepped-down until the best solution for each ordination was reached (i.e. the number of axis that best explained the distribution of samples in the ordination space) [43]. We then averaged the values defining the position of samples on each ordination axis to compute the centroids and their 95% confidence intervals for each vegetation type [43]. Species composition was assumed to differ among vegetation types if confidence intervals of centroids did not overlap on at least one ordination axis.

To compare butterfly diversity among vegetation types we focused on species richness because it is the most intuitive and simplest diversity metric [42]. These comparisons were conducted separately for each sampling season, where species richness was firstly estimated by including all butterfly species and, later, it was estimated by including forest specialists only. To avoid biases in these comparisons, we constructed sample-based rarefaction curves with EstimateS 9.1 [44]. These curves estimate the accumulated number of species at each vegetation type as sampling size increases (i.e., number of sampling days). Species richness at each sampling size was estimated by performing 1000 without-replacement random permutations. The resulting values were averaged for each sampling size and their 95% confidence intervals were computed [44]. Species richness was assumed to differ among vegetation types if confidence intervals did not overlap at the asymptote of rarefaction curves. It is important to note that asymptotic rarefaction curves indicate that sampling effort was large enough to fully capture the diversity and composition of species assemblages [45]. However, as additional criterion to assess the completeness of samplings, we also computed the *Chao2* species richness estimator at the maximum number of samples [44]. *Chao2* was computed as the observed number of species plus the ratio between the number of species detected once and twice at each vegetation type [44]. Thus, *Chao2* is a maximum likelihood estimator of species richness and the degree to which this metric exceeds the highest number of species estimated in rarefactions indicates how thoroughly the species assemblage was sampled [45]. *Chao2* was computed 1000 times for each vegetation type using rarefaction procedures. These values were averaged and their 95% confidence intervals were calculated [44]. Complete samplings were assumed if 95% confidence intervals of *Chao2* contained the value of species richness estimated at the maximum number of samples in rarefaction curves.

After comparing the composition and richness of butterfly assemblages among vegetation types, we focused on assessing whether the inclusion of natural and man-made habitats within the reserve enhances butterfly diversity at the landscape spatial scale. For this we pooled data from the four vegetation types in a single dataset for each season. These datasets were used to construct landscape rarefaction curves that were compared against those estimated for each particular vegetation type. However, because valid comparisons of rarefaction curves must be performed at the same sampling size [46], landscape curves were constructed until nine samples were accumulated to equalize their

sizes with those of the different vegetation types. These analyses were conducted separately for the entire butterfly assemblage and for forest specialist butterflies only. It is important to note that there are several possible results for these comparisons, which lead to different conclusions. Firstly, rarefaction curves of all vegetation types can drop below the landscape curve and, consequently, all of them would be required to support butterfly richness in the reserve. Secondly, the curves of all vegetation types may overlap with that of the landscape, indicating that all these habitats contain all species and, consequently, any of them can be used to maintain local diversity. Finally, if a single habitat type overlaps its rarefaction curve with that of the landscape, while curves of all the other vegetation types drop below them, only that vegetation type is required to support the butterfly richness of the reserve. Because the hypothesis of this study proposes that both natural and man-made habitats are important to preserve butterfly diversity within urban reserves, this would only be supported if the first of these conclusions is reached.

Results

Climatic variables

Air temperature differed among vegetation types in both the warm-rainy season ($F_{(3,8)} = 140.904$, $P < 0.001$) and the cold-dry season ($F_{(3,8)} = 150.720$, $P < 0.001$). Daytime temperature in the warm-rainy season was higher in the abandoned grasslands and *Eucalyptus* plantations than in the mesic and xeric oak forests (8:00 - 18:00 h), but no differences among vegetation types were observed during the night (19:00 - 7:00 h) (Fig. 2A). In the cold-dry season, the temperature in the abandoned grasslands and *Eucalyptus* plantations was always higher than in both forest types, irrespective of the hour of the day (Fig. 2B).

Air relative humidity differed among vegetation types in both sampling seasons (warm-rainy season: $F_{(3,8)} = 48249.892$, $P < 0.001$; cold-dry season: $F_{(3,8)} = 20395591.376$, $P < 0.001$). The values of this variable were always higher in the mesic and xeric oak forests than in the abandoned grasslands and *Eucalyptus* plantations, but these differences were smaller in the warm-rainy season (Fig. 2C) than in the cold-dry season (Fig. 2D).

Photosynthetic active radiation (PAR) also differed among vegetation types at both sampling seasons (warm-rainy season: $F_{(3,8)} = 10332064.497$, $P < 0.001$; cold-dry season $F_{(3,8)} = 125449.569$, $P < 0.001$). PAR was always higher in the abandoned grasslands than in the other vegetation types (Fig. 1E, 1F). Nevertheless, the values of this variable in the *Eucalyptus* plantations were higher than in the oak forests, while the mesic and xeric oak forests showed similar PAR values (Fig. 2E, 2F).

Species distribution patterns

Within the reserve we recorded 91 butterfly species. Of these species, 54 were detected in both sampling seasons, 21 were only detected in the warm-rainy season, and 16 were only detected in the cold-dry season (Appendix 1). All butterfly species were native to Mexico and belonged to six families: Hesperidae (25 species), Lycaenidae (13 species), Nymphalidae (29 species), Papilionidae (2 species), Pieridae (19 species) and Riodinidae (3 species). The classification of species according to their habitat preferences indicated that 41 of them are forest specialist butterflies (23 were detected in both sampling seasons, nine were detected only in the warm-rainy season, and another nine species were only detected in the cold-rainy season; Appendix 1), while 48 species were habitat generalist butterflies (31 were detected in both sampling seasons, 10 were detected only in the warm-rainy season, and seven only in the cold-rainy season; Appendix 1). Only two species could not be classified according these criteria (*Celaenorrhinus* sp. and *Choranthus* sp.; Appendix 1) because we did not find information about their habitat preferences.

In both sampling seasons, most forest specialist butterflies were positively associated with the mesic and xeric oak forests. However, the number of positive associations with these forests increased from the warm-rainy season (12 species with the mesic oak forest and 21 species with the xeric forest; Appendix 1) to the cold-dry season (15 species with the mesic oak forest and 24 species with the xeric forest; Appendix 1). Furthermore, several forest specialist butterflies were positively associated with the abandoned grasslands in both sampling seasons (12 species in the warm-rainy season and four species in the cold-dry season; Appendix 1). More than half of the habitat generalist butterflies from the warm-rainy season were positively associated with the abandoned grasslands (27 species), but several of them were also associated with the oak forests (nine species with the mesic oak forest and 11 species with the xeric oak forest; Appendix 1). The number of habitat generalist butterflies positively associated with the abandoned grasslands decreased towards the cold-dry season (16 species), while the number of positive associations with the oak forests increased in this season (17 species with the mesic oak forest and 13 species with the xeric oak forest; Appendix 1). Although several butterfly species were recorded in the *Eucalyptus* plantations in both sampling seasons, there were no positive associations with this vegetation type (Appendix 1).

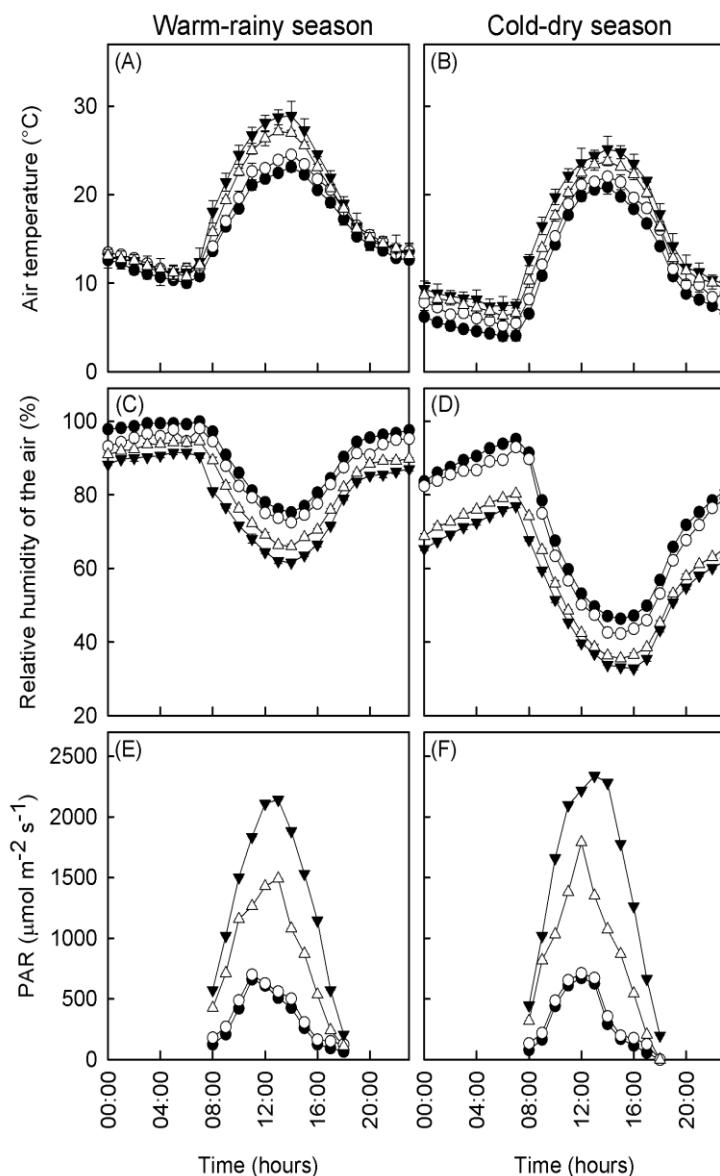


Fig. 2. Daily curves of environmental variables measured in the warm-rainy season (left panels) and the cold-dry season (right panels). Values are averages (\pm 95% confidence intervals) of air temperature (A, B), relative humidity of the air (C, D) and PAR (E, F) in the mesic oak forest (solid circles), the xeric oak forest (empty circles), abandoned grasslands (solid triangles) and the *Eucalyptus* plantations (empty triangles).

Species composition

Two-dimensional configurations were indicated as the best solution for all NMDS ordinations addressed to compare the composition of butterfly assemblages among vegetation types. When all butterfly species were included (i.e. irrespective of their habitat preferences), NMDS explained 78% of variance among samples in the warm-rainy season (final stress for the two-dimensional solution = 13.431; Fig. 3A) and 69% of variance among samples in the cold-dry season (final stress for the two-dimensional solution = 15.349; Fig. 3B). Species composition differed among all vegetation types in the warm-rainy season (Fig. 3A). Conversely, the mesic and xeric oak forests showed similar butterfly composition in the cold-dry season, but species assemblages in these vegetation types differed from those recorded in the abandoned grasslands and the *Eucalyptus* plantations (Fig. 3B).

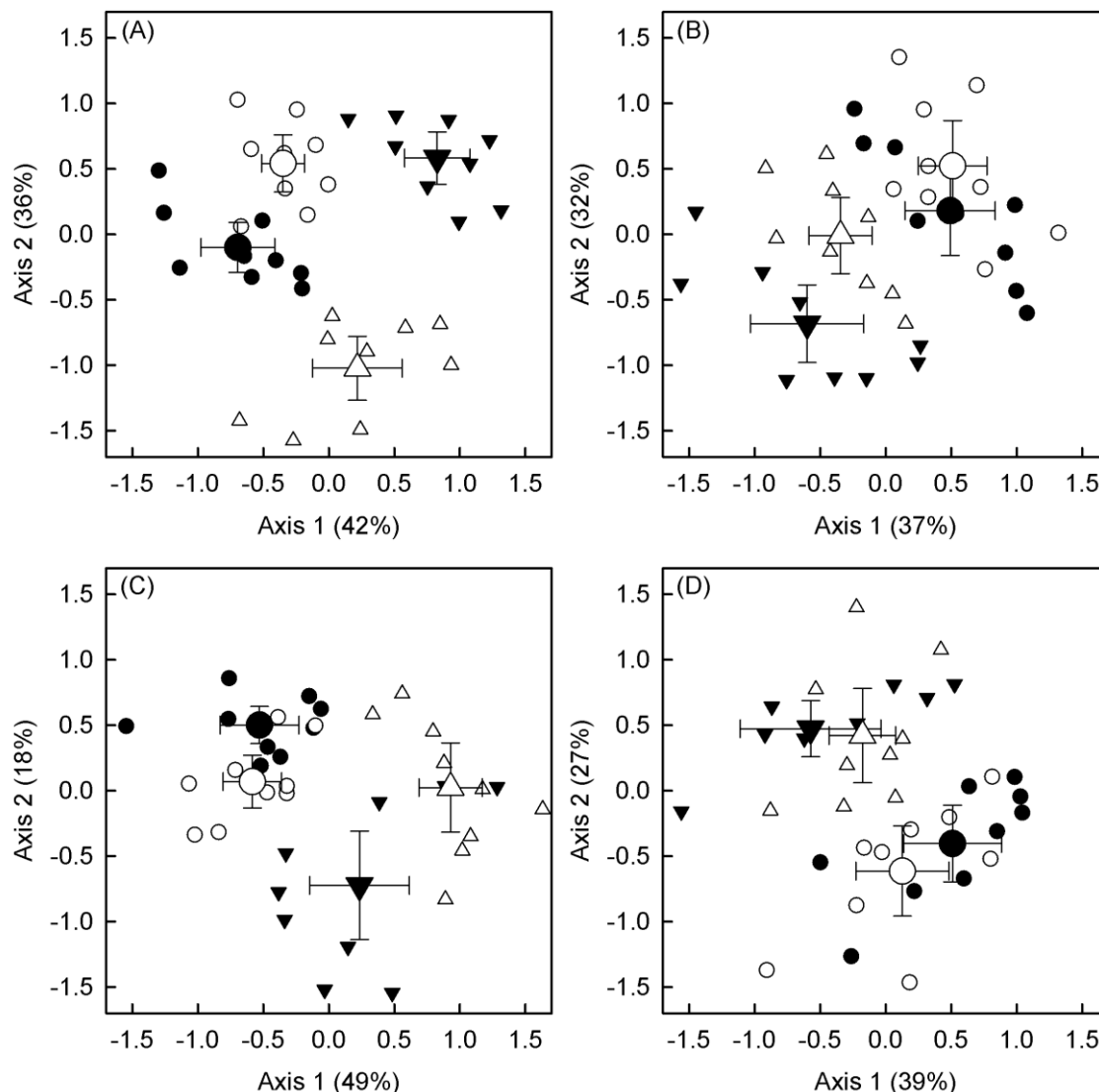


Fig. 3. NMDS ordinations comparing the composition of butterfly assemblages among vegetation types (solid circles = mesic oak forest; empty circles = xeric oak forest; solid triangles = abandoned grasslands; empty triangles = *Eucalyptus* plantations). These analyses were conducted separately for the warm-rainy season (left panels) and the cold-dry season (right panels) by including all butterfly species, irrespective of their habitat preferences (A, B), and by including forest specialist butterflies only (C, D). Larger symbols are the ordination centroids (\pm 95% confidence intervals) of each vegetation type. Significant differences in species composition are assumed if 95% confidence intervals of centroids do not overlap.

Similar results were obtained when only forest specialist butterflies were included in the NMDS ordinations. In this case, NMDS explained 67% of variance among samples in the warm-rainy season (final stress for the two-dimensional solution = 14.915; Fig. 3C) and 66% of variance among samples in the cold-dry season (final stress for the two-dimensional solution = 15.450; Fig. 3D). NMDS conducted with data collected in the warm-rainy season indicated differences in the composition of forest specialist butterflies among all vegetation types (Fig. 3C). In the cold-dry season, however, the mesic and xeric oak forests contained similar species assemblages, which differed from those recorded in the abandoned grasslands and the *Eucalyptus* plantations (Fig. 3D).

Species richness

Rarefaction curves of all vegetation types reached the asymptote after including six days of sampling (Fig. 4). Further, in all cases, the 95% confidence intervals of the *Chao2* estimator contained the values of species richness estimated at the maximum number of samples (Fig. 4). This indicates that sampling effort in both sampling seasons was large enough to fully capture the composition and diversity of butterfly assemblages in the different vegetation types.

Comparisons of species richness at the asymptote of rarefaction curves when all butterfly species were included indicated significant differences among vegetation types. In the warm-rainy season, the xeric oak forest and the abandoned grasslands had higher butterfly richness than the other vegetation types (Fig. 4A). In the cold-dry season, the highest species richness was recorded within the xeric oak forest, followed by the mesic oak forest and the abandoned grasslands (Fig. 4B). The *Eucalyptus* plantations had the lowest species richness in both sampling seasons (Fig. 4A, 4B). The landscape rarefaction curve constructed by including all butterfly species leveled off above those obtained for each particular vegetation type in both sampling seasons (Fig. 4A, 4B). This indicates that, when habitat preferences of butterflies are not taken into account, all vegetation types in the reserve contribute equally to support the diversity of this insect community.

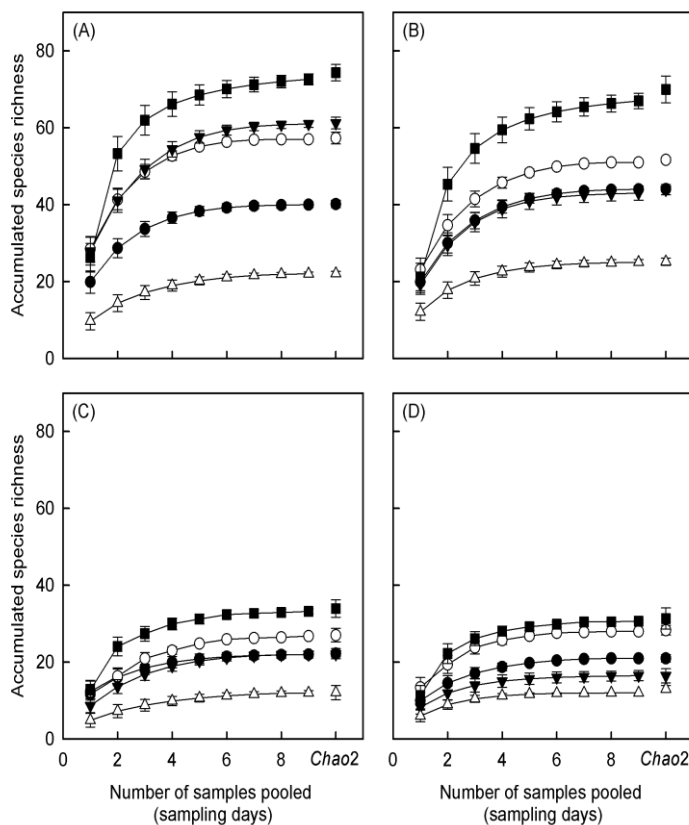


Fig. 4. Species richness rarefaction curves and *Chao2* estimators (\pm 95% confidence intervals) computed for the mesic oak forest (solid circles), the xeric oak forest (empty circles), the abandoned grasslands (solid triangles), the *Eucalyptus* plantations (empty triangles), and the landscape including all these vegetation types (solid squares). These analyses were conducted separately for the warm-rainy season (left panels) and the cold-dry season (right panels) by including all butterfly species, irrespective of their habitat preferences (A, B), and by including forest specialist butterflies only (C, D). Significant differences in species richness are assumed if 95% confidence intervals do not overlap at the asymptote of curves.

Different patterns of species richness emerged when only forest specialist butterflies were included in the rarefaction analyses. In both sampling seasons, richness of forest specialists was higher in the xeric oak forest than in all the other vegetation types, while the *Eucalyptus* plantations always had the lowest butterfly richness (Fig. 4C, 4D). However, while the landscape rarefaction curve estimated for the warm-rainy season leveled off above all the curves estimated for each particular vegetation type (Fig. 4C), the landscape rarefaction curve of the cold-dry season fully overlapped with that of the xeric oak forest (Fig. 4D). This indicates that all vegetation types contribute to support the diversity of forest specialist butterflies during the warm-rainy season, but the xeric oak forest is the most important vegetation type for these butterflies in the cold-dry season.

Discussion

Our results support the proposal that urban protected areas including a mixture of natural and man-made habitats can preserve higher butterfly diversity than reserves composed only by relics of natural habitats. Despite the strong urban pressure in the land surrounding the study area, it contained the six taxonomic families of diurnal Lepidopterans (Hesperiidae, Lycaenidae, Nymphalidae, Papilionidae, Pieridae and Riodinidae) that compose the butterfly fauna of Mexican forests [47]. Indeed, butterfly richness within the reserve (91 species) was higher than that reported for larger forest ecosystems in Mexico, such as the oak forests on the slopes of the Tequila Volcano (47 butterfly species) [48] and the pine-oak forests of the UNESCO Biosphere Reserve *La Michilía* (46 butterfly species) [49]. This elevated diversity of butterflies can be linked to the presence of forest relics and abandoned agricultural fields in the study area.

The large number of forest specialist butterflies that were positively associated with the mesic and xeric oak forests in both sampling seasons suggests that these vegetation types are critical to preserve this group of insects. However, several habitat generalists also displayed occurrence frequencies higher than expected by chance within the oak forests (Appendix 1), which indicates that these habitats are important even for those species that can fully develop their life cycles in human-disturbed habitats. Because most species detected in this study reproduce in summer [32-36], the positive associations with oak forests in the warm-rainy season could be explained by their climatic reproductive requirements. In this season, oak forests offer mild temperatures and elevated relative humidity, as compared to the abandoned grasslands and the *Eucalyptus* plantations (Fig. 2), and these environmental conditions are considered favorable for butterfly reproduction because they prevent desiccation of eggs after oviposition and promote the development of larvae [50]. Further, because most plants in the forest understory are in full bloom during this season [27], these positive association patterns may also be due to the elevated diversity of food resources that these habitats offer to adult lepidopterans.

In the cold-dry season, several butterfly species were also positively associated with the oak forest (Appendix 1). However, it is difficult to attribute these distribution patterns to differences in temperature among vegetation types in this season. This is because the values of this variable were lower within forests than in man-made habitats (Fig. 2), and such decreases in temperature reduce rather than promote butterfly activity [29, 30]. Nevertheless, because this season coincides with the driest period of the year, and because the relative humidity of the air is a critical factor influencing water loss in insects [50], the higher relative humidity within oak forests (Fig. 2) may have influenced these distribution patterns. The availability of food resources, on the other hand, is not likely to cause these positive associations because most plants in the forest understory lose their leaves and do not produce flowers during this season [27]. Thus, although the potential influence of microclimate on butterfly distribution patterns deserves more attention in future studies, our results clearly suggest that oak forests are key habitats to preserve butterflies in this urban protected area.

The species distribution patterns detected in this study also suggested that abandoned grasslands are an important vegetation type for preserving native butterflies. Most habitat generalists were associated with the abandoned grasslands of the reserve (Appendix 1) and this could be due to the higher levels of PAR recorded in this vegetation type (Fig. 2), which usually promote the activity of nonspecialized heliophilous species [29, 52, 53]. However, as mentioned before, urban reserves containing abandoned fields are not critical for preserving these generalist species. Yet, abandoned grasslands are relevant to conservation because of the elevated number of forest specialist butterflies that are associated with this vegetation type, especially in the warm-rainy season (Appendix 1). This suggests that some forest-dwelling species require different vegetation types for developing their life cycles. Because forbs and grasses constitute the main sources of nectar for adult diurnal butterflies [54], and because these flowering plants are very common in the abandoned grasslands during the warm-rainy season [27], the positive associations of forest specialist butterflies with this vegetation type may be explained by the presence of abundant food resources. Furthermore, because most species reproduce in this season, it is also feasible that forest-dwelling butterflies are using the abandoned grasslands as courtship and mating sites, as reported in other studies conducted in anthropogenically disturbed forest areas in Mexico [54]. Thus, although further research is required to determine the activities of forest-dwelling butterflies in abandoned grasslands, our results suggest that including this man-made habitat, together with native forests, in the design of urban reserves could be an important strategy for preserving these insects.

The *Eucalyptus* plantations showed intermediate values for all environmental variables measured in this study, as compared to the other vegetation types (Fig. 1). However, no butterfly species was positively associated with the *Eucalyptus* plantations. This lack of positive associations, rather than being related to physical environmental conditions, may be due to the biotic factors that predominate within this vegetation type. For example, the understories of plantations are dominated by bare soil, with a few sparse grasses and leguminous shrubs [22]. Thus, it is possible that butterflies are not able to use this vegetation type as source of food or as suitable habitat for reproduction. Further, *Eucalyptus* trees produce several secondary metabolites that are toxic for insects [55, 56], which could prevent the presence of butterflies within this vegetation type. Irrespective of the factors causing these distribution patterns, our results allow proposing that *Eucalyptus* plantations are not essential for preserving native butterflies within the urban reserve. Those butterflies that were recorded in the *Eucalyptus* plantations may be using them as corridors between the other vegetation types of the reserve, rather than finding plantations as suitable habitat for developing their life cycles.

The relevance of oak forests and abandoned grasslands to preserve native butterflies was also supported by the comparisons of species composition and richness. When all butterfly species were included in NMDS ordinations, the differences in species composition among vegetation types can be assumed to occur because most habitat generalists were associated with the abandoned grasslands, while most habitat specialist butterflies were associated with the oak forests (Fig. 3). These differences in species composition were responsible of the increased butterfly richness that we found at the landscape spatial scale in both sampling seasons. Indeed, the rarefaction analyses that included all butterfly species indicated that all vegetation types contribute to support the diversity of this insect community within the reserve (Fig. 4). However, it is important to highlight that the conceptual framework of this study states that urban reserves including a mixture of natural and man-made habitats are valuable for the conservation of butterflies if - and only if - the diversity patterns described above are also observed for species that depend on forests to develop at least part their life cycles. The analyses that only included forest specialist butterflies supported this proposal as well. This was particularly evident in the warm-rainy season, when oak forests and abandoned grasslands showed quite different butterfly assemblages (Fig. 3). This resulted in increased richness of forest-dwelling butterflies at the landscape spatial scale (Fig. 4), indicating that the urban reserve meets its conservation aim effectively. Indeed, because the reserve seems to be particularly valuable for forest-

dwelling butterflies during the warm-rainy season, when most species are reproducing [36], such an increase in habitat diversity may reduce their local extinction risk by enhancing their chance of maintaining viable populations.

Implications for conservation

The results of this study indicate that including a mixture of natural habitats and abandoned agricultural fields as part of urban protected areas could help to preserve local fauna within expanding human settlements. As mentioned earlier in this article, such a proposal may be controversial for conservation biologists because it calls for the protection of man-made habitats together with the relics of natural habitats. On this later issue, however, a note of caution must be introduced about the interpretation of this proposal: conservation actions in urban environments will never replace the conservation of extensive natural ecosystems, which provide critical ecosystem services such as water provision and atmospheric depuration. In turn, our proposal to include a mixture of natural and man-made habitats in urban reserves constitutes a realistic strategy of adaptive management. Such a strategy would enable the conservation of particular species within urban environments before they become locally extinct due to the continued expansion of urban areas. Taking this into account, it is important to implement these conservation actions before all relics of natural habitats and abandoned fields in the areas surrounding cities are lost to urban development.

There are also several caveats that decision makers must consider before applying this proposal. Firstly, particular attention should be paid to the proportion of natural and man-made habitats that are required within these protected areas. In our case, oak forests cover up to 69% of the reserve, while abandoned grasslands cover just 23%, and this seem enough to promote butterfly diversity within the study area. However, it is possible that any change in these proportions could alter the diversity patterns of forest-dwelling species. Secondly, our results indicate that not all anthropogenically modified abandoned habitats are suitable for native species. This was the case with the *Eucalyptus* plantations, which did not have any butterfly species positively associated with them. Finally, it is important to point out that prior to applying this design for urban reserves, decision makers should carefully consider which animal species will be the focus of conservation efforts and ensure that the habitats included within the reserves are adequate for allowing the survival and reproduction of the target organisms. Otherwise, the reserve may not be able to support viable populations of the target species.

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APPENDIX 1

Butterfly species detected in the warm-rainy season and the cold-dry season in the different vegetation types of the ecological park *Flor del Bosque* (mesic oak forest = MOF; xeric oak forest = XOF; abandoned grasslands = AG; *Eucalyptus* plantations = EG). Species authorities are indicated according to Warren et al. [33]. The table indicates the taxonomic family, habitat preferences (forest specialist butterflies = FS; habitat generalist butterflies = HG) and the number of times that each species was detected at each vegetation type. Empty cells indicate that the species was not detected. Positive associations of species with a particular habitat type are indicated with an asterisk on the side of their occurrence frequencies (Monte Carlo tests critical $\alpha = 0.05$).

Family	Species	Habitat preferences	Warm-rainy season				Cold-dry season			
			MOF	XOF	AG	EP	MOF	XOF	AG	EP
Hesperiidae	<i>Apyrrothrix araxes araxes</i> (Hewitson, 1867)	FS		19*						
	<i>Atalopedes campestris huron</i> (W. H. Edwards, 1863)	FS	2	12*	11*		13	19*	10	
	<i>Autochton cellus</i> (Boisduval et Le Conte, 1837)	FS						4*		
	<i>Autochton cincta</i> (Plötz, 1882)	FS	43*	20	16	2	7*		6*	
	<i>Celaenorrhinus</i> sp.	Undetermined			7*	4				
	<i>Chiomara georgina georgina</i> (Reakirt, 1868)	FS						5*		
	<i>Choranthus</i> sp.	Undetermined		8*	3					
	<i>Cogia</i> sp.	HG			8*					
	<i>Copaeodes aurantiaca</i> (Hewitson, 1868)	HG	2	2	17*			2	17*	
	<i>Erynnis tristis</i> (Boisduval, 1852)	FS	7*		6*		13*	2	10*	
	<i>Hylephila phyleus</i> (Drury, 1773)	HG		4*						
	<i>Lerema</i> sp.	FS						5*		
	<i>Nastra lherminier</i> (Latreille, 1824)	FS						4*		

APPENDIX 1 (continue)

Family	Species	Habitat preferences	Warm-rainy season				Cold-dry season			
			MOF	XOF	AG	EP	MOF	XOF	AG	EP
	<i>Oarisma garita calega</i> (Godman, 1900)	HG						4*		
	<i>Pellicia arina</i> Evans, 1953	HG	4	4	11				3*	
	<i>Piruna polingii</i> (W. Barnes, 1900)	FS	126*	15	7	5				
	<i>Poanes melane vitellina</i> (Herrich-Schäffer, 1869)	FS	19*	18*		1	9*	11*		
	<i>Poanes zabulon</i> (Boisduval and Le Conte, 1837)	FS		4*						
	<i>Pyrgus communis communis</i> (Grote, 1872)	HG		10	60*	2	2	11*	13*	
	<i>Quasimellana mexicana</i> (E. Bell, 1942)	FS						3*		
	<i>Remella</i> sp.	HG	5*	3	3				4*	
	<i>Urbanus dorantes dorantes</i> (Stoll, 1790)	FS						3*		
	<i>Urbanus proteus</i> (Linnaeus, 1758)	FS		3*						
	<i>Urbanus viterboana</i> (Ehrmann, 1907)	FS		7*	9*		1	5*	6*	
	<i>Zestusa staudingeri</i> (Mabille, 1888)	FS		6*						
Lycaenidae	<i>Arawacus</i> sp.	HG							4*	
	<i>Celastrina echo</i> (W. H. Edwards, 1864)	HG		3*			4*	5*		
	<i>Celastrina gozora</i> (Boisduval, 1870)	FS	65*	16	8	10	15*	4	2	3
	<i>Cyanophrys longula</i> (Hewitson, 1868)	FS					3*	5*		

APPENDIX 1 (continue)

Family	Species	Habitat preferences	Warm-rainy season				Cold-dry season			
			MOF	XOF	AG	EP	MOF	XOF	AG	EP
Nymphalidae	<i>Echinargus isola</i> (Reakirt, 1867)	HG	22*	13*	4	5	12	43*	39*	8
	<i>Electrostrymon denarius</i> (Butler et H. Druce, 1872)	FS						5*		
	<i>Erora quaderna</i> (Hewitson, 1868)	FS		12*	9*					
	<i>Leptotes marina</i> (Reakirt, 1868)	HG	16*	15*	4	3	9*		3	1
	<i>Ministrymon azia</i> (Hewitson, 1873)	HG			4*					
	<i>Rekoa zebina</i> (Hewitson, 1869)	HG	4*					6*		
	<i>Strymon melinus melinus</i> (Hübner, 1818)	HG							4*	
	<i>Strymon</i> sp.	HG					18*		15*	2
	<i>Zizula cyna</i> (W. H. Edwards, 1881)	HG	10*	9*	3					
	<i>Adelpha eulalia</i> (E. Doubleday, 1848)	FS	9*	2	7*	2	3	19*	4	2
	<i>Agraulis vanillae incarnata</i> (N. Riley, 1926)	HG		5	37*		11*	2	4	
	<i>Anaea aidea</i> (Guérin-Ménéville, 1844)	HG	6*		3		9	10	10	8
	<i>Anthanassa frisia</i> (Poey, 1832)	HG							3*	
	<i>Anthanassa texana texana</i> (W. H. Edwards, 1863)	FS	21*	6	1	2	29*	21*	3	5
	<i>Chlosyne ehrenbergii</i> (Geyer, 1833)	HG			5*					
	<i>Chlosyne endeis</i> (Godman et Salvin, 1894)	FS	27	39*	18					

APPENDIX 1 (continue)

Family	Species	Habitat preferences	Warm-rainy season				Cold-dry season			
			MOF	XOF	AG	EP	MOF	XOF	AG	EP
	<i>Chlosyne lacinia</i> (Geyer, 1837)	HG		3	8*					
	<i>Chlosyne marina</i> (Geyer, 1837)	FS	3	45*	7					
	<i>Chlosyne theona</i> (Ménétriés, 1855)	HG	3	4	51*	12				
	<i>Cyllopsis gemma</i> (Hübner, 1809)	HG					8*	4		
	<i>Cyllopsis windi</i> L. Miller, 1974	FS	25*	29*	2	5	38*	40*		3
	<i>Danaus gilippus thersippus</i> (H. Bates, 1863)	HG		4	32*				5*	
	<i>Danaus plexippus plexippus</i> (Linnaeus, 1758)	HG		7	18*				4*	
	<i>Dione moneta poeyii</i> Butler, 1873	FS	16	15	48*	9	77*	26	7	21
	<i>Euptoieta claudia</i> (Cramer, 1775)	HG		5	29*				3*	
	<i>Gyrocheilus patrobas patrobas</i> (Hewitson, 1862)	FS	13	34*	2					
	<i>Junonia coenia coenia</i> Hübner, 1822	FS		3	12*		3	16*	5	5
	<i>Libytheana carinenta mexicana</i> Michener, 1943	HG			3*		3*			
	<i>Mestra dorcas</i> (Fabricius, 1775)	FS	4*	4*				4*		
	<i>Microtia elva elva</i> H. Bates, 1864	HG			5*					
	<i>Manataria hercyna maculata</i> (Hopffer, 1874)	FS	2	1	10*		4*	1		
	<i>Phyciodes batesii</i> (Reakirt, 1866)	HG						9*	9*	
	<i>Phyciodes pallescens</i> (R. Felder, 1869)	HG	17*	4	21*	3		7*	6*	

APPENDIX 1 (continue)

Family	Species	Habitat preferences	Warm-rainy season				Cold-dry season			
			MOF	XOF	AG	EP	MOF	XOF	AG	EP
	<i>Pindis squamistriga</i> R. Felder, 1869	FS					2	6*	3	2
	<i>Siproeta stelenes biplagiata</i> (Fruhstorfer, 1907)	HG		6*	2					
	<i>Smyrna blomfieldia datis</i> Fruhstorfer, 1908	HG			3*		4*	5*		
	<i>Vanessa atalanta rubria</i> (Fruhstorfer, 1909)	HG	3	5	19*			4*		1
	<i>Vanessa virginiensis</i> (Drury, 1773)	HG	13	34*	36*	11	7*		8*	3
Papilionidae	<i>Papilio polyxenes</i> (Fabricius, 1775)	HG			5*		8*	2		
	<i>Pterourus multicaudata multicaudata</i> (W. F. Kirby, 1884)	FS	19*	4	16*		5*			
Pieridae	<i>Abaeis nicippe</i> (Cramer, 1779)	HG	3*		3*		3	13*	3	2
	<i>Anteos clorinde</i> (Godart, 1824)	HG	3	2	18*		12	3	3	1
	<i>Anteos maerula</i> (Fabricius, 1775)	FS	4*				6*	3		
	<i>Catasticta nimbice nimbice</i> (Boisduval, 1836)	HG	13	15	49	5	42*	45*		2
	<i>Catasticta teutila teutila</i> (Doubleday, 1847)	HG			7*		33*			
	<i>Colias eurytheme</i> Boisduval, 1852	HG			3*		11*	4	2	3
	<i>Eurema daira sidonia</i> (R. Felder, 1869)	FS	3	8*		2	2	9*		4
	<i>Eurema mexicana mexicana</i> (Boisduval, 1836)	FS	44	136*	68	63	148*	168*	16	25
	<i>Eurema salome jamapa</i> (Reakirt, 1866)	FS	4	12*	10*		30*	27*	6	5
	<i>Hesperocharis costaricensis pasion</i> (Reakirt, 1867)	HG	5	6	7		15	10	11	12

APPENDIX 1 (continue)

Family	Species	Habitat preferences	Warm-rainy season				Cold-dry season			
			MOF	XOF	AG	EP	MOF	XOF	AG	EP
	<i>Leptophobia aripa</i> (Boisduval, 1836)	FS	8	41*	7	12	5*		2	
	<i>Nathalis iole iole</i> Boisduval, 1836	HG	4	5	7	4	8*	6*	1	
	<i>Phoebis agarithe</i> (Boisduval, 1836)	HG			9*	3				
	<i>Phoebis philea philea</i> (Linnaeus, 1763)	HG		7*	3		11*	14*	2	4
	<i>Phoebis sennae marcellina</i> (Cramer, 1777)	HG			7*		7*	2	2	
	<i>Pontia protodice</i> (Boisduval et Le Conte, 1830)	HG		6	22*				10*	
	<i>Pyrisitia lisa</i> (Boisduval et Le Conte, 1830)	HG		7*			4	7*		
	<i>Pyrisitia proterpia</i> (Fabricius, 1775)	HG	7*	6*			8*	5		
	<i>Zerene cesonia cesonia</i> (Stoll, 1790)	FS	3	8*	12*		4	20*	4	5
Riodinidae	<i>Calephelis nemesis</i> (W. H. Edwards, 1871)	FS		9*	8*			6*	5*	
	<i>Calephelis rawsoni</i> McAlpine, 1939	FS		24*	20*		10	37*	16	18
	<i>Emesis zela zela</i> Butler, 1870	FS	53*	40*			15*	13*	1	4