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Diversity and habitat affinities of butterfly families in Central Guyana South America

Gyanpriya Maharaj, Doreen Winstanley and Godfrey R Bourne

Abstract

Our aim was to document butterfly diversity, assemblage structure and biogeographic distribution in the Iwokrama Forest Reserve and North Rupununi District, Guyana. Butterflies were collected by hand netting along line transects in three habitat types-forest, forest-savanna ecotone and savanna. Six butterfly families were recorded, Papilionidae, Pieridae, Nymphalidae, Lycaenidae, Riodinidae, and Hesperidae. Butterfly family counts were influenced by the size of the natural butterfly populations. Specific families showed preferences for various habitat types such that the Riodinidae were mostly found in forests, Pieridae in forest-savanna ecotones, and Hesperidae in savannas. However, the Nymphalidae, Lycaenidae and Papilionidae showed no such patterns, as they exhibited similar richness in all habitats. The presence and absence of all butterfly families seemed to be linked to the distribution of larval food plants and adult food flower in the different habitats, i.e., resource availability.

Keywords: Butterflies, diversity, forest, savanna ecotone, Guyana

Introduction

Communities vary greatly in the number and kinds of taxa they encompass^[1], such that biodiversity at the species, genus or family levels are characteristics unique to the community level of biological organization and are expressions of community structure and organization¹⁻². A community or its subset, called an assemblage is considered to have a high species, or genera, or family diversity if many equally or nearly equally abundant species, genera, or families are present^[1, 2]. Conversely, if a community is comprised of only a few species, or if only a few species are abundant, then species, genera, or family diversities are low^[3, 4]. Higher taxon diversity indicates a highly complex community or assemblage, because a greater number of heterogeneous taxa live in the same geographical area simultaneously^[4].

The actual factors contributing to higher levels of diversity in some communities rather than in others are not known with certainty, and remain a topic of scientific contention^[1, 2]. Diversity appears to be partly a function of the variety within the habitat, heterogeneity. The more heterogeneous habitats tend to be inhabited by a larger number of species than the less heterogeneous ones, as in the case of mixed tropical forests which have higher insect and bird diversity than Neotropical savannas^[1, 2, 4, 5]. A second factor appears to be either the length of time that environments have existed or have been available to organisms as places to live; older habitats tend to contain more species, genera, and families than younger ones^[1, 2, 4, 5]. Other factors that may contribute to diversity include climate and the availability of resources-with warmer, more constant, temperatures and reduced seasonal differences coupled with stable diverse food availability appears to result in high levels of biological diversity^[6, 7]. A clear and repeatable pattern of how these factors interact is the latitudinal diversity gradient in terrestrial and shallow marine environments, where diversity is highest at the equator and gradually decreases toward the poles^[8]. In addition to these natural factors, the effects of human induced climate change and land use alterations on diversity *viz.* poleward shifts of latitudinal ranges, upslope shifts of elevational ranges, and species endangerment and extinctions, have also been clearly documented in many recent studies^[9-12].

The aim of this study was to begin to interpret and describe the structure and organization of Neotropical butterfly family communities in three biome types in Central Guyana, South America. We did not focus on lower taxonomic groupings because of low counts for many genera and species, which prevented meaningful statistical comparisons. Our specific goal was to determine whether mixed rainforest, rainforest-savanna ecotone, and savanna habitats differed in structure and organization using the different habitat types in the Iwokrama Forest,

forest-savanna ecotone and savannas of the North Rupununi Region in Guyana. Family richness, family information-theoretic indices and family preference distributions were studied.

Materials and Methods

Study sites

Data were collected from the Iwokrama Forest and the North Rupununi District of Guyana, a country situated along the north eastern coast of South America between 1° 10' N and 8° 35' N and 56° 20' W and 61° 23' W [13]. Three habitat types representing forest, savanna, and forest-savanna ecotone were intensely censused. Transects were located within the boundaries of the Iwokrama Forest Reserve (Forested Site) at Turtle Mountain (4° 43' 54'' N 58° 43' 4'' W), the Canopy Walkway (4° 14' 58'' N 58° 54' 34'' W), and Fair View Village (4° 39' 20'' N 58° 40' 55'' W). The Iwokrama Rainforest is part of the Potaro-Siparuni Administrative Region that is predominantly forested highland with a small portion of a hilly sand and clay belt [14]. Most of the forest comprises a mixture of forest types, with approximately twelve types classified and with no species dominating [15]. In the North Rupununi District, in the Upper Takutu-Upper Essequibo administrative region, the savanna-forest ecotone transects were located on the Surama (4° 6' 3'' N 59° 3' 39'' W) and Burro Burro (4° 9' 54'' N 59° 3' 31'' W) access roads. This area is characterized by forested mountains and hills with interspersed savannas located on fresh water flooded depositary flat lands [16].

Savanna transects were established in the North Rupununi Administrative District at Kwatamang School (3° 56' 32'' N 59° 6' W), Kwatamang Landing (3° 55' 43'' N 59° 6' 12'' W), and Clarence Aranaputa Mountain (3° 58' 28'' N 59° 10' 57'' W). The North Rupununi District in south-west Guyana is a mix of low land-shrub savanna, forest and wetland ecosystems [16]. In general, the North Rupununi savannas form a seasonally flooded plain characterized by fire-climax savanna vegetation usually comprised of *Curatella-Byrsonima* plant associations [16-18].

Butterfly collection and sampling protocol

Butterflies were hand-netted by two teams consisting of either four or five persons. Butterfly-nets were of the type described by DeVries [19], and sampling was carried out along line transects four times/day (twice between 0930–1230 h and twice between 1330–1630 h; GST), when there was maximum sunlight and highest butterfly activity [20]. One and a half days were spent capturing butterflies along each transect, and a total of 6 d were surveyed each month, totaling 72 collection days for the year-long study from 2007–2008. A total of 864 netting hours were executed over the course of the survey (at 36 netting hours/month/team) using methods described by Alonso and Dallmeier²¹ and Neild [22].

Killing, storing and recording specimens

Butterflies were killed using methods described in Alonso and Dallmeier [21] and then individually placed into glassine envelopes. Field information on collection sites, date, time, collector, weather conditions, behavior just prior to capture, and genus and/or species identifications as appropriate, were recorded on the envelopes, and later transcribed onto a database.

Relaxing, setting, storing and identifying specimens

Butterflies were relaxed and set as described by Smart [23]. Specimens were subsequently oven dried, pinned and stored in mounting cases. Butterflies were identified using specialist reference texts [19, 22-32], and also by visual matching of wing patterns to specimens in collections housed at the Centre for the Study of Biological Diversity, University of Guyana, and the Natural History Museum in London, United Kingdom.

Statistical analyses

The butterfly count data collected over the 12-month period were used to estimate several biodiversity indices for butterfly families across eight transects in three habitats in Central Guyana. The relative abundance (percentages) for the butterflies caught in each 100 m⁻¹ transect walked for each habitat type was determined. A 2-way ANOVA model was used to first determine whether relationships exist between butterfly count and family and then compare the effect of habitat on butterfly family diversity. The assumptions for using a parametric approach were tested using the Kolmogorov and Smirnov method, and the data log transformed to permit the aforementioned approach [33]. These data were further analysed by estimating Least Significant Differences (LSDs) to identify pairs of compared data that contributed to the overall significance [33]. All statistical tests were performed using the statistical programme, GenStat Discovery for Windows, Version 12.

The family richness index was employed to determine the extent and patterns of taxon diversity among butterflies of forest, ecotone and savanna habitats. This index relied on the total number of families present in a habitat type, and two information-theoretic indices of Shannon [34], because these are related to the concept of uncertainty [3]. Thus, when there is low diversity, it is possible to accurately predict the identity of a family chosen at random. However, in a highly diverse community, it would be difficult to predict the family identity of a randomly picked individual [3]. Because data were randomly sampled from family abundances from larger communities it is appropriate to use the Shannon [34] information-theoretic index as a measure of family diversity [3].

$$H' = -\sum p_i \ln p_i$$

where, H' is the value of the diversity index, p_i is the proportion of the total number of individuals sampled that belong to family i , and \ln is the natural log.

This diversity index takes into account both family richness (the number of families) and the evenness of the individuals' distribution among the families. Yet, it is usually desirable to estimate both the aforementioned components of diversity so that evenness may be expressed by considering how close a set of observed family abundances are to those from a sample of families with maximum diversity for a given N and f [3]. Thus, the evenness of a distribution of N individuals among the families in a data-set is expressed as the nearness of the diversity index for the observed data to the index of maximum diversity³. Evenness was estimated using the expression:

$$E = e^{D/f}$$

Where e is a constant 2.7, $e^{D/f} = H'$ which is the value of the

information-theoretic indices of Shannon’s equation [34], and *f* is the number of species in a sample (family richness). Patterns in family preferences for habitat types were examined using the butterfly family data-set to assess which best explained the current family distributions in Central Guyana; because the patterns of biogeography that Darwin [35], Wallace [36, 37] and current researchers [38] reported, provide robust evidence that evolutionary forces are responsible for these patterns. Species, genera, or families usually more closely resemble other taxa that live less than 100 km away but in very different habitat types than do taxa that live thousands of kilometers away in similar habitats [36, 37].

Results

A total of 2,274 butterflies were caught in the Iwokrama forest and North Rupununi District. These comprised six families, Papilionidae, Pieridae, Nymphalidae, Lycaenidae, Riodinidae, and Hesperidae. A significant relationship was found between butterfly counts and families, $F_{5, 25} = 27.31$, $p < 0.001$. This overall significance was contributed by the following LDS pairwise comparisons of family means (Table

1)-Nymphalidae and Papilionidae were significantly different from all other families and they exhibited the highest and lowest means, respectively. The means for Hesperidae, Lycaenidae and Riodinidae were similar, while Pieridae were significantly different from Lycaenidae and Riodinidae, but Pieridae was similar to the Hesperidae.

Table 1: Log means for butterflies grouped in their respective families with s.e.d. (Std. error of difference of means) = 0.0781, Rep. = 8, d.f.= 25. The means with the same letters in the superscripts do not differ significantly from one another when compared to the computed LSD value with *t* value in 25 d.f. at 5%.

Family	Mean
Hesperidae	0.404 ^{B, C}
Lycaenidae	0.326 ^B
Nymphalidae	0.934 ^D
Papilionidae	0.092 ^A
Pieridae	0.552 ^C
Riodinidae	0.283 ^B

Overall mean familial densities were similar across all habitats; however, there was unequal evenness within each habitat (Table 2).

Table 2: Descriptors showing butterfly familial compositions in the three habitat types.

Habitat	H	Evenness	Family richness	Mean family density 100m ⁻¹
Forest	1.30	0.61	6	15.86
Ecotone	0.12	0.19	6	18.58
Savannah	0.10	0.18	6	14.36

Comparisons also indicated no significant difference between habitat and butterfly counts ($F_{2, 5} = 0.03$, $p = 0.970$; Fig. 1).

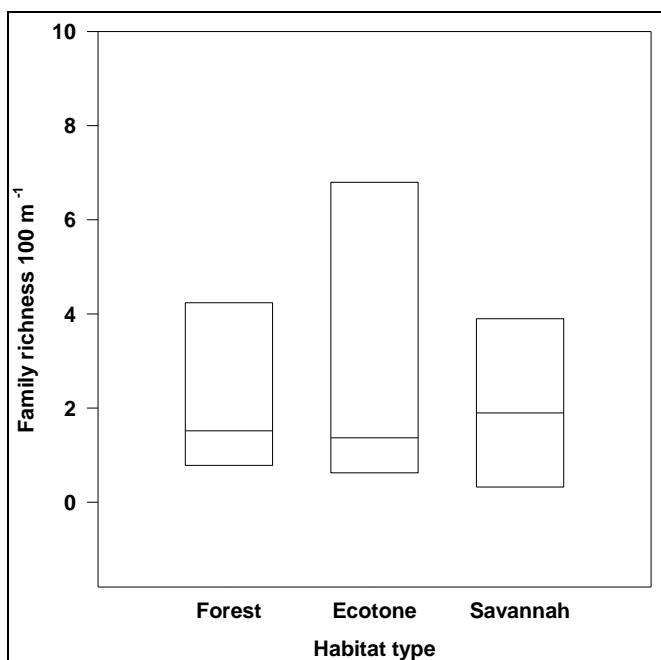


Fig 1: Box plots showing distribution of butterfly families by habitat. The top of the box represents the 75th and the bottom the 25th percentiles. Horizontal lines in each box indicate median values.

The ANOVA model showed that the distribution of the butterfly means for families were similar across the different habitats ($F_{10, 25} = 1.28$, $p = 0.292$; Fig. 2).

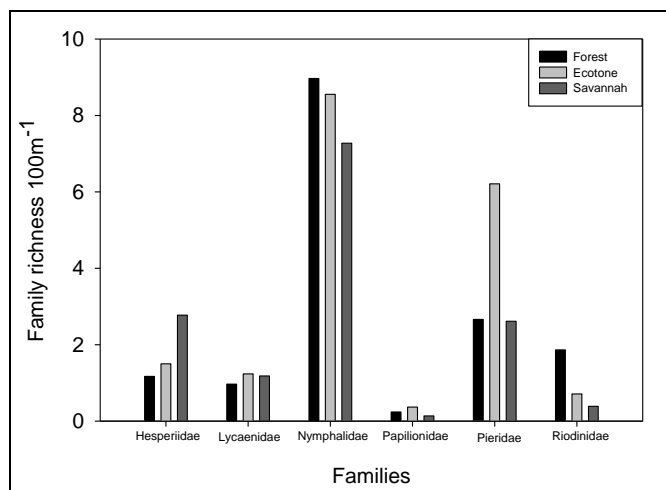


Fig 2: Grouped bar graphs showing butterfly family richness by habitat type.

Discussion

All six butterfly families were caught in each of the three habitat types. This suggested that hand netting was an effective sampling tool for families. However, the level of difficulty in hand netting butterflies varied with family type. Butterflies that proved difficult to catch such as the elusive Riodinids and high flying Papilionids, and certain Nymphalids [24], especially *Prepona* spp. and *Morpho* spp., may have been under-represented in this study. In addition, since only short handled hand nets were used, our sample may

have been biased in favor of forest-floor dwelling and low-flying butterfly species [24]. In spite of the inherent biases in the collection method, many individuals of the same species were caught.

Three of the six families (Papilionidae, Pieridae and Nymphalidae) observed in this study were also recorded by McDonough [39]; while two families, Papilionidae and Nymphalidae, were recorded by Wright [13] in Kurupukari Village and Iwokrama Forest base camp. However, they both conducted their studies in two forested areas consisting of one habitat type. Additionally, these studies were of shorter durations, and focused only on fruit feeders sampled along shorter transects [13, 19]. However, data obtained from surveys by Fratello (pers. comm.) indicated that all six butterfly families were present in different regions of Guyana. In this study we presented evidence that the sizes of butterfly populations were mirrored by the number of species recorded for each family such that Papilionids are the smallest family represented by 550 species [40], and Nymphalids are the largest with about 6000 species [41]. We also found a relationship between butterfly species richness and the families they represented. Thus, we concluded that the more species rich families may have larger populations than less species rich families. Because of the exclusionary competition theory [42], it is expected that the more species rich taxon can exploit, as larvae and adults, a wider range of plant resources than less species rich families. Additionally, the less diverse families may have smaller populations because they are dependent on a more restricted plant resource base and therefore their population sizes may be limited by the availability of these specific resources. Yet another possibility is that larger families may have greater colonizing and reproducing abilities than families with smaller species populations [19]. However, these factors were not examined in this study.

A paradox was observed in this study because the family Pieridae exhibited similar population sizes as the Hesperidae. The Pieridae is a small family with about 1,100 species [43], while the Hesperidae is a larger taxon with more than 4,500 species worldwide [44, 46]. Additionally, we showed that Pierids also had larger populations than Lycaenids, another more species rich family with approximately 5,955 species [44-46]. This suggested that certain butterfly families such as the Pierids were more prolific in the habitats that we examined as compared to Lycaenids and Hesperids. Our study sites may have provided more favorable conditions for the Pierids in comparison to other family groups, such as resource availability, suitable climate, shelter, and other related habitat variables for this family to thrive, and therefore sustain larger population sizes. The high numbers of Pierids observed in this study exhibit aggregating migratory behavior during certain months of the year, which could contribute to the high Pierid populations. The low numbers observed for small families may be because many of these butterflies were difficult to net. For example, the Papilionids are high- and mid-elevation fliers and Riodinids are elusive in nature, because they typically settle on the underside of leaves [44-47].

Sharp *et al.* [48] reported that the environmental features needed for survival and reproduction, such as shelter, or food provide the most important cues in habitat selection for butterflies. Therefore, in our study the presence of all butterfly families in each of the habitats suggested that these habitats had supporting familial features. This finding was also supported by researchers such as Kerr [49] and Stefanescu

et al. [50] who indicated that the richness of butterflies responds to a number of basic environmental factors, while Hanspach *et al.* [51] and Lewthwaite *et al.* [12] showed butterfly distribution and turnover of their assemblages were correlated to climatic factors. We also found that there was an inclination (no statistical significance) for butterflies to be associated with particular habitats. However, when each family collected was considered separately, some families showed greater preferences for specific habitat types, while others were well represented in all habitat types. This suggested that some families of butterflies are habitat specialists because they thrive under a narrow range of conditions, and therefore their populations are habitat dependent and are sensitive to small environmental changes [52]. Other butterflies are habitat generalists and do well under a wider range of environmental conditions such that there is minimal variation in their population sizes regardless of habitat type [52, 53].

In this study, butterfly family populations differed when compared to each other within habitats. This suggested that these habitats may have been more suitable for certain families (possibly because of differential resource availability), by sustaining larger populations of some families. This was further illustrated by the Shannon³⁴ informatic on- index which suggested that individuals of the butterfly families in the ecotone and savanna habitats were unequally distributed, further suggesting the dominance of a few numerical abundant families (Table 2). However, in the forest habitat, the distribution of individuals among families was more even because of habitat heterogeneity which provided a greater variety of resources, diverse food and micro-habitats. Thus, the forest habitat could support more individuals of all families compared to familial distributions in other habitat types we investigated [1, 2].

Families such as the Hesperidae are habitat specialists. Fifty-one percent of individuals collected were caught in the grass and sedge rich savannas, where their primary larval host plants are grasses [44, 54]. When compared to the more preferable habitats, the ecotone and forest, the savanna habitat seemed to lack appropriate types and quantities of host plant foods, oviposition vegetation and other environmental resources needed for most butterfly life-histories. Here, the savanna is primarily characterized by *Trachypogon--Curatella--Byrsonima* plant associations [16].

Fifty-four percent of the Pieridae were found in the ecotone habitat where members of the genera *Phoebis*, *Aphrissa* and *Rhabdodryas* were observed to migrate in large numbers during July and August (G. Maharaj & G.R. Bourne pers. obs.), as is their nature [55]. They were also observed "mud puddling" next to small bodies of water; this allows them to obtain micronutrients critical for powering their migrations and reproduction [13, 56]. Additionally, numerous leguminous host plants exploited by the Pieridae in the families, Caesalpiniaceae, Fabaceae, and Mimosaceae were present in this habitat¹³. Sixty-three percent of the Riodinids preferred the forest habitat. This family assemblage was also acknowledged by Hall [47] as usually being present in primary forests.

The Lycaenidae is a large well represented family of butterflies worldwide, and as expected for a large taxon they exploit a wide range of food host plants [23]. Therefore, their ability to inhabit a variety of habitat types is greater in comparison to the more specialized families. Although, Papilionids are not as diverse as the Lycaenids they are also

found in every habitat type throughout the world ^[19]. Thus, these families would be expected to show minimal, if any, proclivity towards specific habitat types. The Nymphalids observed in this study were seen typically in relatively high abundances in comparison to the other butterfly families in all habitats. They are categorized as generalists because they exploit diverse food types, are flexible in their habitat requirements, and are strong long-distance dispersers with great colonizing abilities ^[52, 57]. These same characteristics were observed in the Guyanan populations in this study. Overall the general trend in family habitat preferences seemed to parallel resource availability ^[58]. Thus, the habitat attracts the butterfly families that can be supported.

We found that the distribution of butterfly population means by family was similar across the three habitat types. This may have ensued because the overall differences between the total abundances were not pronounced enough to be detected by the statistical procedure used. Additionally, no significant interaction was demonstrated because in the statistical analysis the variation among habitats was compared with the variation among transects, and there was considerable between-transect variation in the abundance distributions across families. Habitat preferences seemed to be related to the presence or absence of larval food plants. However, it may also be related to host plant abundance and richness, especially for polyphagous species as found by Quinn *et al.* ^[51], Kunte ^[59] and Shree Kumar & Balakrishnan ^[57] also showed that the specificity of habitat occupancy by butterflies is directly linked to the availability of food plants on peninsular India and at Kerala, respectively. Most butterfly species use specific plant resources as larval and adult foods, and in many locations, there is congruence between host plant diversity and butterfly diversity ^[60]. Additionally, Gutiérrez ^[61] showed that certain vegetation types are occupied by characteristic butterfly assemblages, while Singer ^[62] reported that populations of adult *Euphydryas editha* (Lepidoptera; Nymphalidae) fluctuate annually by tracking fluctuations in their host plant species. Furthermore, Rabasa *et al.* ^[63] pointed out that larvae are usually relatively immobile, their growth and survival depending on the choices of food plants made by their active mothers. Most butterfly species deposit eggs directly onto their larval host plant, with ovipositing females actively searching for plants on which larval growth and development is optimal ^[64-66]. Therefore, many butterfly species avoid habitats in which larval growth and development are poor. Other studies suggest that some butterfly species choose habitats with nectar rich patches even though alternative host plants may be sub-optimal in nutritional quality ^[67, 68].

Conversely, Sharp *et al.* ^[48] found evidence that with the exception of two small, sedentary species, there is no correlation between the micro-distribution of butterflies and that of their exploited plant resources for adult sub-alpine butterflies in the mountain meadow flora in Gunnison County, Colorado. Here, the food plants favored by adult butterflies were abundantly scattered across the habitat and butterflies therefore wandered indiscriminately to exploit the nectar and pollen of these plants; this random distribution pattern is also exhibited by the larval food plants ^[48]. This was supported by Hanspach *et al.* ^[51] that concluded that host plants presence/absence represent more of a limiting factor for butterfly distribution in stressful environments with harsh conditions and Friberg *et al.* ^[69] that found *Leptidea* butterflies will choose suitable habitats first and subsequently

search for host plants. It is recognized that a combination of biotic and abiotic environmental factors, were probably involved; these are reported to be influential in studies in Pune City, India ^[70], at the Comoro Islands of western Indian Ocean ^[71], in the Bumbuna Forest Reserve in Sierra Leone ^[72], in Bedfordshire, United Kingdom ^[73], and in Sweden ^[11].

We surmised that butterfly family population sizes were influenced by their species diversity, yet we recognized that there were environmental factors such as availability of larval and adult food plants that attracted butterflies to specific habitat types. Thus, these butterflies showed preferences for various habitat types while others exhibited generalists' behaviors and were capable of thriving in all habitat types. At the same time, collection method biases may have resulted in specific groups being poorly represented in our samples. Few ecological studies focused on butterflies have been conducted in Guyana, which means that there is great scope for future work. The data generated from this study can be used as a baseline to monitor outcomes of anthropological, biotic and abiotic factors affecting country-wide butterfly diversity patterns. Furthermore, the methods used in this project to ascertain butterfly family diversity in relation to habitat heterogeneity can be applied to other areas of Guyana to investigate patterns in butterfly species diversity. We especially endorse long-term studies with intensive sampling because they reveal better the nature of tropical communities and emphasize the challenges of measuring species diversity¹ ^[2, 74, 75].

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