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Authors: Álvarez, Yosiel, and Corso, Andy Joel

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Diversity of Butterfly Assemblages Within Disturbed Habitats of Jardines de Hershey, Mayabeque, Cuba

YOSIEL ÁLVAREZ* AND ANDY JOEL CORSO

Facultad de Biología, Universidad de La Habana, La Habana, Cuba

**Corresponding author: alvarezzyosiel@gmail.com*

ABSTRACT—Butterflies have proven to be excellent indicators of the disturbance and biodiversity of habitats. Cuban butterflies are well known taxonomically, but the state of knowledge of their ecology is still insufficient and no studies have been carried out in some ecosystems. Here we characterize and compare the richness and diversity of butterfly assemblages associated with secondary forest and secondary thicket habitats in Jardines de Hershey, Mayabeque, Cuba. 86 butterfly species belonging to five different families were found. The forest assemblage was found to be the richest and with more evenness, which could be related to the presence of forest-exclusive butterflies in these patches. There is a high similarity in species composition due to the proximity of the sampling sites, and we detected no differences in abundance in the dry season, but there were differences in the humid season related to different abundance peaks of common species in both habitats. Abundance patterns of regularly observed species were similar in both habitats, except for the genus *Calisto*, and differences in these patterns could be related to habitat preferences of these species. The forest assemblage was more stable in time than the thicket assemblage, presumably due to a more stable environment. The locality could represent a shelter for butterfly fauna in a highly modified urban landscape. Further work should focus on the influence of environment in the diversity and replacement of the assemblages, and in the fauna of adjacent, more conserved forest patches.

Species of Lepidoptera play a major role as pollinators of several plant species; hence, they have a great ecological importance (Schoonhoven et al. 2005). Furthermore, butterflies are considered biological indicators, since the composition of species of an assemblage is strongly influenced by the conservational status and the environmental condition changes of the locality in which it is found, chiefly those induced by human activity (Footitt and Adler 2009; Bergerot et al. 2011; Miller et al. 2011). Previous studies have found that butterfly diversity in disturbed habitats is considerably smaller than in semi-natural and conserved ones (Addo-Fordjour et al. 2015; Gallou et al. 2017; León-Cortés et al. 2019). Thus, understanding the dynamics of butterfly assemblages can provide significant information about certain ecosystems, with a high value from a conservational viewpoint (Begon et al. 2006).

Cuba has 201 species of butterflies (Núñez and Barro 2012; Núñez et al. 2012, 2013; Núñez 2015; Núñez et al. 2019). Taxonomic lists of butterflies from all over the country are often published (Núñez 2004; Aborrezco 2006; Fernández 2007; Núñez 2010, 2012; Lauranzón et al. 2013; Luna and Hernández 2013; Bermúdez et al. 2016) but the studies on assemblages are scarcer (Fontenla 1987a, 1987b, 1989; Núñez and Barro 2003). The state of knowledge of their ecology, although improving, is still insufficient and no studies have been carried out in particular ecosystems such as

mangroves, lowland serpentine scrub-woodlands, and some synanthropic habitats such as pasturelands and secondary thickets. The information gathered by a butterfly assemblage study in these habitats would be useful as a measure of their stability and status, with the aim of designing proper management and protection plans.

The Touristic Center “Jardines de Hershey” is located 3 km south of Santa Cruz del Norte, in the municipality of the same name, on the north coast of Mayabeque province, western Cuba (Fig. 1). The landscape of this locality is composed by patches of secondary forest surrounded by anthropic thickets where invasive plants are abundant. Human influence has damaged the original vegetation and these habitats are disturbed. Although the area was selected for management by the National Enterprise for Protection of Flora and Fauna (ENPFF) and systematic bird monitoring surveys are carried out, no studies about the biota of the locality have ever been published. Furthermore, butterfly assemblages inhabiting these habitats in Cuban territory have never been studied. Thus, in order to provide knowledge of the conditions of this locality through a representative and indicative group, we characterize and compare richness and diversity of butterfly assemblages within habitats of secondary forest and secondary thickets of Jardines de Hershey.

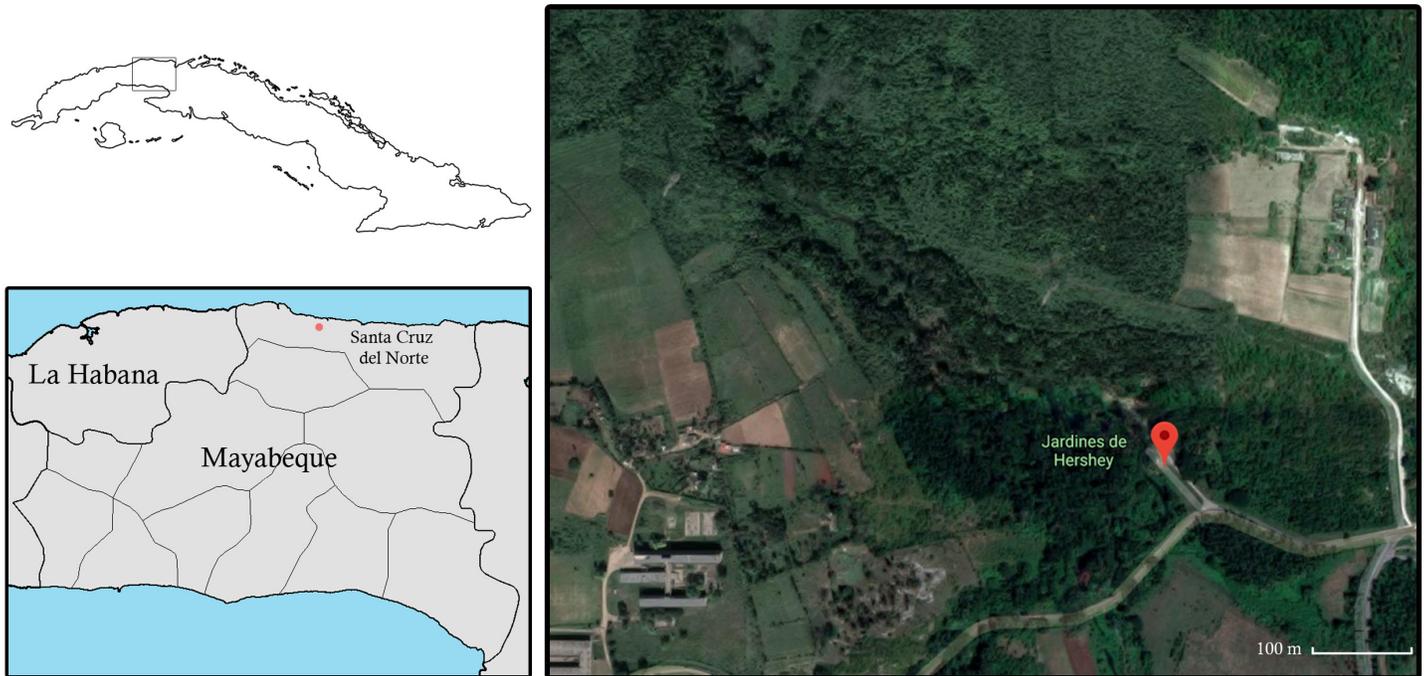


FIG. 1. Geographic location and satellite image of Jardines de Hershey, Mayabeque, Cuba. Satellite image © Google.

MATERIALS AND METHODS

Description of Sampling Sites

According to the criteria of Capote and Berazaín (1984), two habitats are present in this locality: a secondary forest and secondary thickets surrounding forest patches. To conduct the study, trails through these habitats were selected as sampling sites, one trail per habitat. The trails were located along the periphery of each habitat at a distance of 500 m from the other. Taxonomic treatment for plant species included in the description of the habitats followed the criteria of Greuter and Rodríguez (2017).

The secondary forest (Fig. 2) is a modified old growth woodland of approximately 300 m² area of tall tree stratus on a small hill. The phytocenosis is dominated by the expansive species *Trophis racemosa* (L.) Urb. Scattered trees of *Bursera simaruba* (L.) Sarg., *Cecropia peltata* L., *Casearia aculeata* Jacq., *Cordia gerascanthus* L., *Ficus microcarpa* L.F., *Guarea guidonia* (L.) Sleumer, *Roystonea regia* (Kunth) O. F. Cook, *Samanea saman* (Jacq.) Merr., and other species, are also present. The undergrowth comprises a stratum of *Syngonium auritum* (L.) Schott, an invasive species. The forest is crossed by the main road of the touristic center and on its northern limits by a wide clearing. This clearing comprises a lower bush stratus dominated by *Lippia alba* (Mill.) N. E. Br. ex Britton &

P. Wilson, *Bidens pilosa* L. and *Phylla nodiflora* (L.) Greene, being present other scattered plants, such as *Comocladia dentata* Jacq., *Erythroxylum havanense* Jacq., *Koanophyllon villosum* (Sw.) R. M. King & H. Rob. subsp. *villosum*, *Piper auritum* Kunth, *Platygyne hexandra* (Jacq.) Müll. Arg., *Ruellia blechum* L., *Sida ulmifolia* Mill., *Stachytarpetta jamaicensis* (L.) Vahl. and *Wedelia rugosa* Greenm. North-westwards the forest descends to plain terrain and becomes a wider clearing along Santa Cruz river, where a small patch of *Sida ulmifolia* dominates in the undergrowth.

The thickets (Fig. 3) are a wider area surrounding the forest patches both north and southwards. This habitat is more disturbed and stands in the area previously occupied by logged forest. We performed observations in the southern area, which is an extension of small-growing Poaceae with a low bush stratus composed mainly of *Vachellia farnesiana* (L.) Wight & Arn., *Dichrostachys cinerea* (L.) Wight & Arn., and *Viguiera dentata* Spreng (considered highly invasive species by Gonzalez et al. 2016), and also *Lippia alba* and *Bidens pilosa*. Bushes of *Bourreria divaricata* (DC.) G. Don, *Ipomoea nil* (L.) Roth, *Koanophyllon villosum* subsp. *villosum*, *Varronia bullata* subsp. *humilis* (Jacq.) Feuillet, and *Lantana camara* L., amongst other plants, are scattered throughout the zone. Many plants are often blooming in these patches.

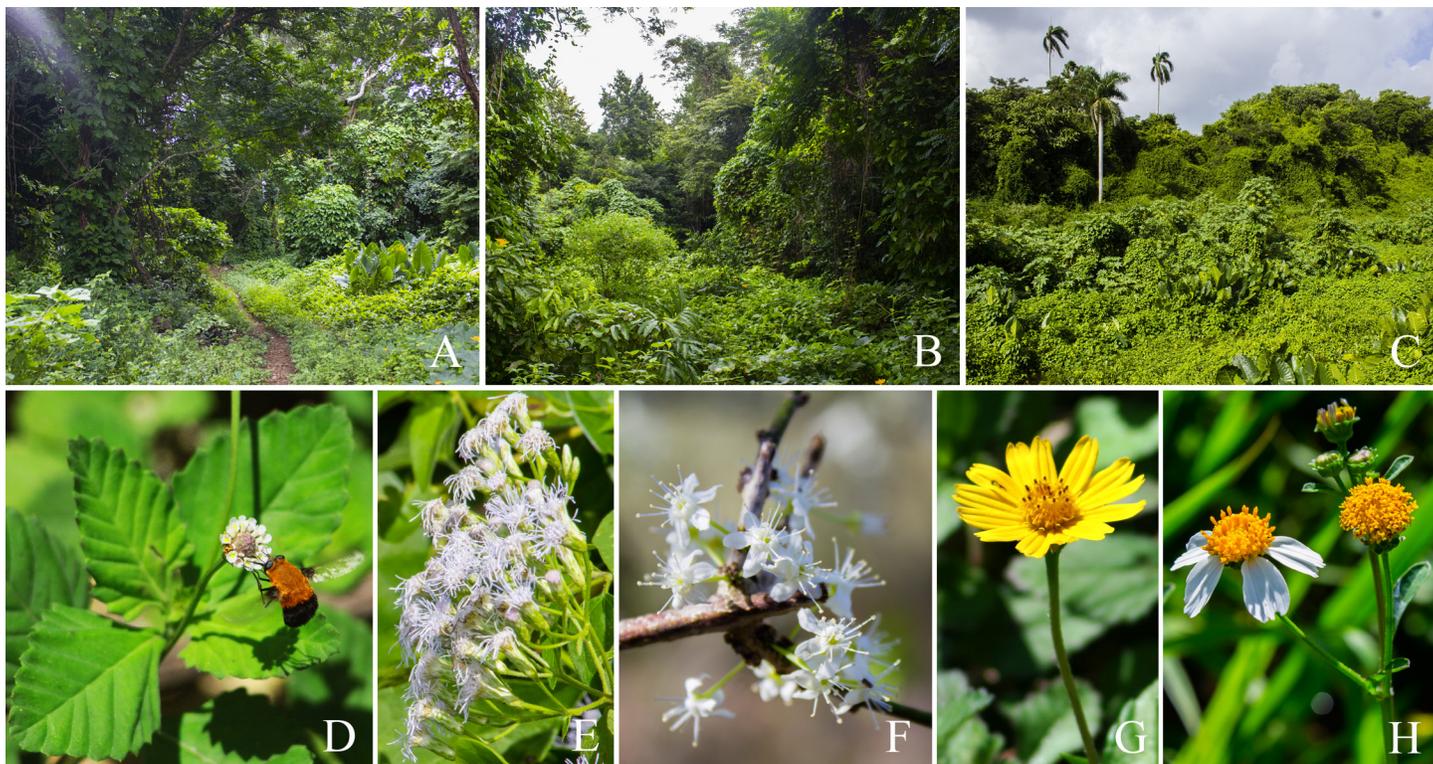


FIG. 2. Habitat and floral resources in the forest patches of Jardines de Hershey, Mayabeque, Cuba. A–C, Secondary forest patches. D. *Phylla nodiflora*. E. *Koanophyllon villosum* subsp. *villosum*. F. *Erythroxylum havanense*. G. *Wedelia rugosa*. H. *Bidens pilosa*.

Sample Design

Fieldwork was carried between November 2018 and September 2019. We employed a one-hour trail method to count butterflies (Andrade-C. et al. 2013). This method does not restrict our sampling trails to a particular length or width. Butterflies were counted during the period between 9:00 and 13:00 hours, but during daylight saving time between 9:30 and 13:30 hours, these being the hours of maximum activity of butterflies (Andrade-C. et al. 2013). In each habitat and for each day of sampling, four consecutive one-hour walks along each trail were carried out, with the authors alternating between habitats every time a trail was completed. Unidentifiable butterflies were collected to secure identification, and were released afterwards. Individuals of rare species were kept as voucher specimens. We divided our sampling to cover both humid and dry seasons of western Cuban climate (Borhidi 1996). After the study concluded, 10 sampling days were conducted in the dry season (November–March, two sampling days per month) and 9 in the humid season (May–September, two sampling days per month, except September when it was conducted only once due to severe weather conditions). The month of April

was excluded from sampling to allow the change of environmental conditions between seasons and obtain a higher contrast in the results, and the month of October was also excluded to ensure that both sampled seasons had the same number of sampling units. In total, 19 sampling days were completed in both habitats and 76 one-hour walks along the trails in each habitat, for a total of 152 one-hour trail walks. Taxonomic treatment of butterfly species followed the criteria of Warren et al. (2020), except for species of the genus *Aphrissa* Butler, which are now considered to belong to *Phoebis* Hübner (Murillo-Ramos et al. 2018).

From the outset of the study, we suspected that there was another *Calisto* species in the locality besides the ubiquitous *C. herophile*, because some individuals were darker and lacked the first white dot in the underside of hindwings. However, the absence of material for comparison resulted in our assuming all individuals as *C. herophile*. To clarify the situation, several individuals of the morphological distinct form were collected. COI barcodes of the material indicated that these exemplars were *C. disjunctus* (R. Núñez, pers. comm.), which is sympatric with *C. herophile* at Hershey. Unfortunately, the initial assumption avoided the determination of the abundance of both species. The collected material pro-

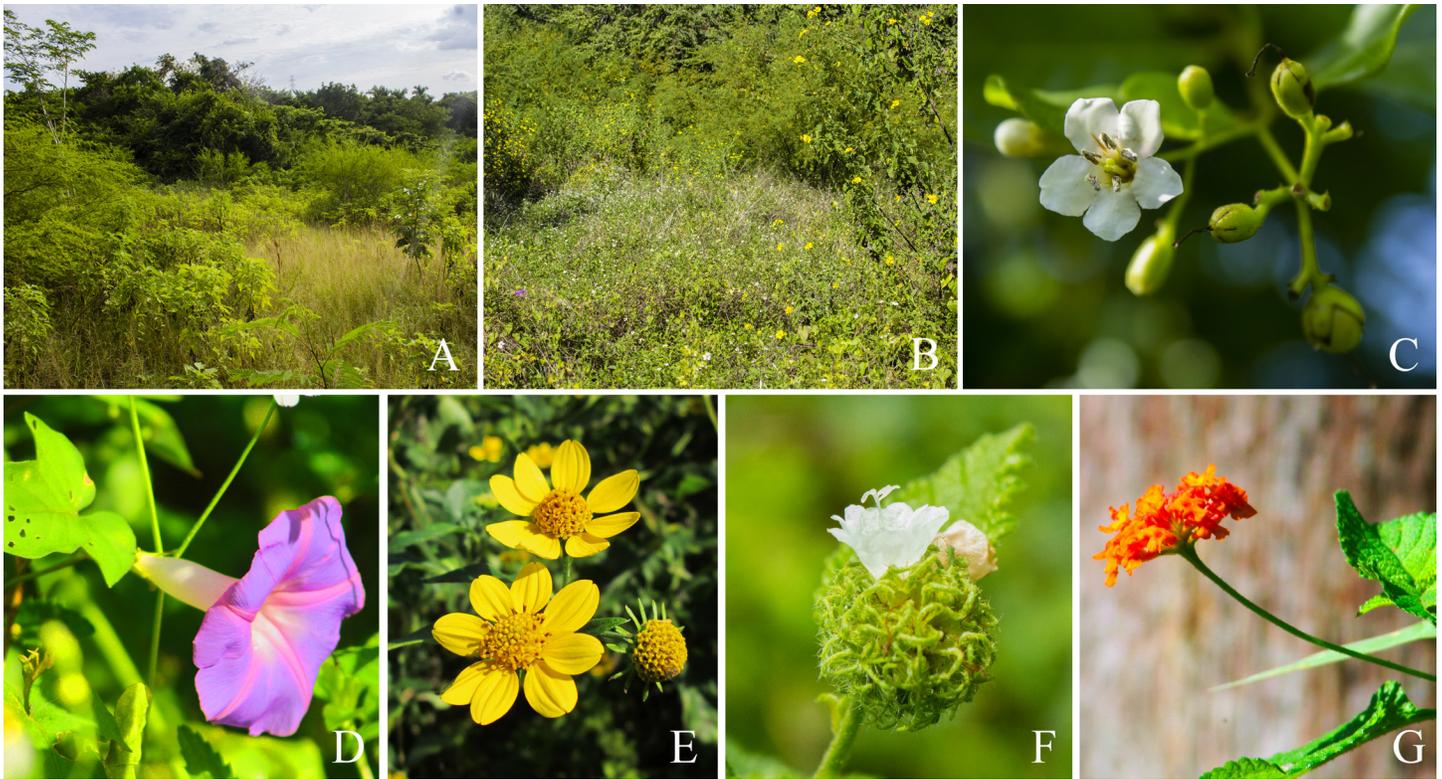


FIG. 3. Habitat and floral resources in the thickets patches of Jardines de Hershey, Mayabeque, Cuba. A-B. Secondary thickets patches. C. *Bourreria divaricata*. D. *Ipomoea nil*. E. *Viguiera dentata*. F. *Varronia bullata* subsp. *humilis*. G. *Lantana camara*.

ceeded from the forest patches in the end of the humid season, where the “darker form” was more often seen, but it was also seen in the thickets. Thus, to refer to the abundance of these taxa in further analyses, we will address them as *Calisto* spp.

Data Analyses

Butterfly daily abundance was taken as the maximum number of individuals observed per species in a day after the four one-hour surveys. With this value, monthly mean abundance and seasonal mean abundance were calculated. To evaluate the quality of our surveys estimating butterfly richness in the sampled habitats, we constructed sample unit-based rarefaction curves and sample coverage curves, using the incidence data approach (Chao and Jost 2012). We employed 100 bootstraps replicates and retained the extrapolated richness value and sample coverage value until 50 sampling units, with 95% confidence intervals. The analyses were implemented in iNEXT Online (Chao et al. 2016).

We plotted both monthly mean total butterfly abundance for all butterflies and monthly mean butterfly abundance for the 30 species most regularly observed.

To test differences in monthly mean total butterfly abundance between both assemblages, we employed a Monte Carlo test for each month evaluating differences in effect size. A SIMPER multivariate analysis was also carried out to estimate the percentage dissimilitude between the two studied habitats, analyzing both composition and structure. This analysis also indicates which species contributed the most to this dissimilitude. The analysis was run using Past 4.02 (Hammer et al. 2001).

Rank-abundance distributions were analyzed for each habitat during each season, in order to compare dominance, evenness and richness, employing maximum seasonal proportional abundance. Spatial replacement (dissimilitude between the composition of species in both sites) was estimated through the Complementarity Index of Colwell and Coddington (1994). Temporal replacement (substitution of the species in the assemblages between consecutive months) was estimated through the equation $D = 1 - S_1$, where S_1 is Czekanowski Index (described by Wolda 1981).

RESULTS

A total of 4857 observations from 86 butterfly species, belonging to five of the six butterfly families known to inhabit Cuba, were registered (Appendix 1). The family with the greater number of species was HesperIIDae with 28, followed by Nymphalidae with 26, Pieridae with 16, Lycaenidae with nine, and Papilionidae with seven. Eight endemic species were found, representing 18% of Cuba's 43 endemic species. Furthermore, 15 endemic subspecies were found, representing 46% of the 32 total endemic subspecies known for Cuba (Appendix 1). Photographs of adults in their habitats are shown in Figures 4–5. Voucher specimens of some of the observed species (Figs. 6–7) are stored in the Yosiel Álvarez Collection (YAC).

Sample unit-based rarefaction curves (Fig. 8A) revealed that surveys were relatively complete within the 19 sampling days, with 79 species registered for the forest assemblage, and 69 for the thicket assemblage. Sample coverage curves (Fig. 8B) indicated that a high sample coverage (0.98 for both assemblages) was achieved within the 19 sampling days. Extrapolation until completeness (sample coverage = 1) estimated an expected richness of 82 ± 8 species for the forest assemblage and 72 ± 8 species for the thicket assemblage. Thus, we recorded a 97% and 95% of the expected richness for the forest and thicket assemblages, respectively.

When the monthly mean butterfly abundance is plotted (Fig. 9A), it is shown that from November on its value decreases progressively in both assemblages, until February–March when it begins to increase again, first in February for the thicket assemblage and later in March for the forest assemblage. In the early humid season, the values of abundance are considerably higher than the previous season and perform equally for both assemblages until June, when a change occurs: the forest assemblage continues to increase abundance values until it reaches a peak in September, but the thicket assemblage begins to decrease mean abundance proportionally. During the dry season, monthly mean butterfly abundance was statistically different between both habitats only in December, and in the humid season abundance was statistically different in June and August. For September we were unable to test differences as we only had one value, but this value was very dissimilar between both habitats. When we disregard

the abundance of *Calisto* spp. (the most abundant species) from the analysis (Fig. 9B), there were not statistical differences in the dry season, except in March, and in the humid season abundance in all tested months was statistically different except for June. For September, again the only obtained value was very dissimilar.

For regularly observed species in the locality, the general pattern detected in monthly mean butterfly abundance curves (Fig. 10) is a decremented butterfly abundance in the dry season and an increment in the humid season. Although with some differences, the ongoing of abundance of these species was similar for both habitats. Some species were more abundant in the thicket assemblage, such as *Calisto* species and *H. charithonia*, but most species with differences in abundance between both habitats were more abundant in the forest assemblage, such as *M. chiron*, *A. jatrophae*, *L. cassius*, *P. dina* and *S. malitiosa*. These species had abundance peaks in different moments of the year: *L. cassius* in May, *Calisto* species (in the thicket assemblage) and *P. dina* in June, *M. chiron* in July, and *A. jatrophae*, *Calisto* species (in the forest assemblage) and *S. malitiosa* in September. Some species appeared more frequently in the thicket assemblage, such as *D.*

TABLE 1. Contribution of species to the average dissimilarity between butterfly assemblages in secondary forest and secondary thickets during November 2018–September 2019 in Jardines de Hershey, Mayabeque, Cuba, estimated through SIMPER analysis.

Taxon	Contribution %	Cumulative %
<i>Calisto</i> spp.	23.340	23.34
<i>Leptotes cassius</i>	8.192	31.53
<i>Marpesia chiron</i>	5.781	37.32
<i>Pyrisitia dina</i>	4.984	42.30
<i>Anartia jatrophae</i>	4.871	47.17
<i>Pyrisitia nise</i>	3.714	50.89
<i>Synapte malitiosa</i>	3.434	54.32
<i>Cyclargus ammon</i>	2.812	57.13
<i>Pyrgus oileus</i>	2.218	59.35
<i>Heliconius charithonia</i>	2.157	61.51
<i>Dryas iulia</i>	2.000	63.50
<i>Lucinia sida</i>	1.970	65.47
<i>Siproeta stelenes</i>	1.949	67.42
<i>Phyciodes phaon</i>	1.841	69.27
<i>Doxocopa laure</i>	1.744	71.01



FIG. 4. Butterflies of Jardines de Hershey, Mayabeque, Cuba. Family Nymphalidae. A. *Calisto herophile*. B. *Calisto disjunctus*. C. *Asterocampa i. idyja*. D. *Lucinia s. sida*. E. *Marpesia chiron chironides*. F. *Marpesia e. eleuchea*. G. *Heliconius charithonia ramsdeni*. H. *Anartia jatrophae Guantanamo*. I. *Historis o. odius*. J. *Junonia evarete zonalis*. K. *Siproeta stelenes biplagiata*. L. *Libytheana motya*.



FIG. 5. Butterflies of Jardines de Hershey, Mayabeque, Cuba. Families Lycaenidae, Pieridae and Hesperidae. A. *Electrostrymon a. angelia*. B. *Strymon martialis*. C. *Cyclargus ammon*. D. *Leptotes cassius theonus*. E. *Nathalis iole*. F. *Zerene c. cesonia*. G. *Pyrisitia n. nise*. H. *Pyrisitia messalina*. I. *Asbolis capucinus*. J. *Choranthus radians*. K. *Perichares p. philetes*. L. *Cabares p. potrillo*.



FIG. 6. Pinned butterfly specimens collected in Jardines de Hershey, Mayabeque, Cuba. Families Nymphalidae and Papilionidae. A–B. *Archaeoprepona demophoon crassina* (A: dorsal view; B: ventral view). C–D. *Colobura dirce wolcottii* (C: dorsal view; D: ventral view). E–F. *Hypanartia paullus* (E: dorsal view; F: ventral view). G–H. *Adelpha iphicleola iphimedia* (G: dorsal view; H: ventral view). I–J. *Heraclides caiguanabus* (I: dorsal view; J: ventral view).

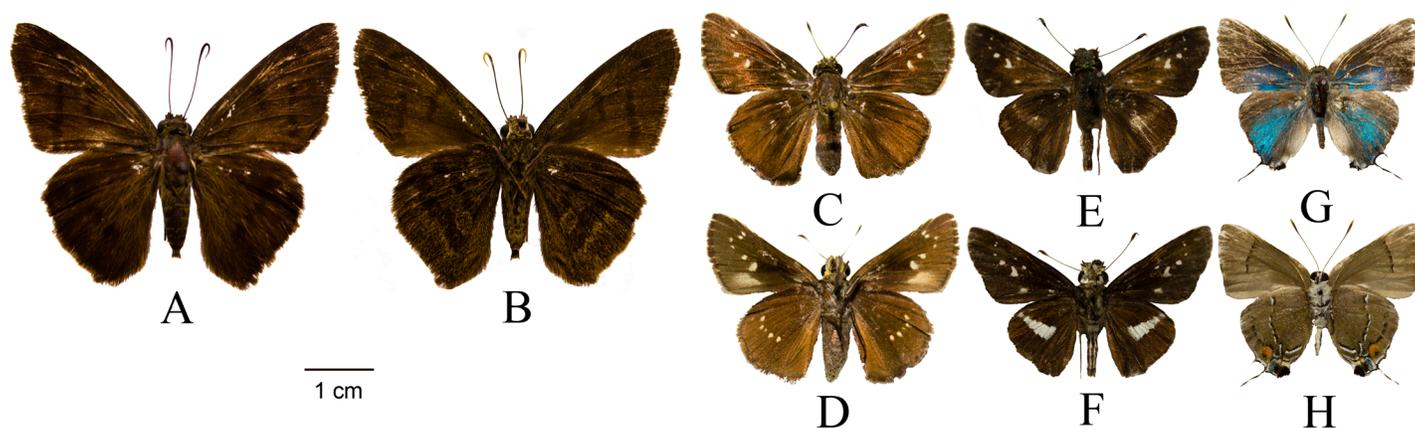


FIG. 7. Pinned butterfly specimens collected in Jardines de Hershey, Mayabeque, Cuba. Families Hesperiidae and Lycaenidae. A–B. *Astrartes anaphus anausis* (A: dorsal view; B: ventral view). C–D. *Euphyes c. cornelius* (C: dorsal view; D: ventral view). E–F. *Panoquina corrupta* (E: dorsal view; F: ventral view). G–H. *Allosmaitia coelebs* (G: dorsal view; H: ventral view).

gilippus, and others in the forest assemblage, such as *A. idyja* and *N. iole*.

The SIMPER multivariate analysis detected a dissimilarity between habitats of 69.92%. Table 1 shows which species contributed up to a 70% of this dissimilarity, being the most significant contribution that of *Calisto* species complex, near 24%, due to the marked difference in abundance of these taxa between the studied habitats. *Calisto* species were more abundant in the thicket assemblage, and were in overall the most abundant taxa in the study, reaching a maximum mean abundance of 84 individuals in the thickets on June 2019.

Rank-abundance distributions (Fig. 11) show similar patterns for both assemblages and for both sampled seasons. No curve has a marked slope, indicating the presence of evenness in all seasons and habitats; at the end of the curve there is a group of species of minimal abundance; and species in the first part of the curve have similar and decreasing abundances. In the dry season, both abundance and richness were lower than in the humid season for both habitats. There was a constant dominant species in each habitat and season, but other dominant species switched their position from the dry season to the humid season. Particularly, *M. chiron* and *P. dina* became noticeably abundant in the humid season in comparison to the dry season. In the forest rank-abundance distribution, a greater evenness was noted for both seasons, and the dominating species was *L. cassius*. In the thicket rank-abundance distribution, a lesser evenness is perceived and the *Calisto* species complex was dominant in both seasons.

Spatial replacement estimated through the

Complementarity Index of Colwell and Coddington was 0.24. Of the 86 reported species, 64 were shared by both assemblages, and 22 were exclusive from one or another; specifically, 16 were exclusive of the forest and six of the thickets. Temporal replacement values estimated through the Czekanowski Index (Table 2) suggest that the forest assemblage has a low replacement rate and is more stable in time. Forest values were low and very similar for each pair of consecutive months in both seasons. On the other hand, the thicket assemblage had different patterns in the replacement rate, indicating that this assemblage is more unstable. In the middle of the dry season replacement was elevated and the assemblage was not stable. Thickets replacement values were similar to those of the forest at the beginning and end of the season. Through the humid season, replace-

TABLE 2. Temporal replacement (estimated through 1 - Czekanowski Index) of butterfly assemblages in secondary forest and secondary thickets for consecutive month pairs during November 2018–September 2019 in Jardines de Hershey, Mayabeque, Cuba.

Pair of Months	Forest	Thickets
November-December	0.30	0.32
December-January	0.38	0.50
January-February	0.35	0.52
February-March	0.34	0.30
May-June	0.31	0.17
June-July	0.32	0.14
July-August	0.34	0.14
August-September	0.34	0.40

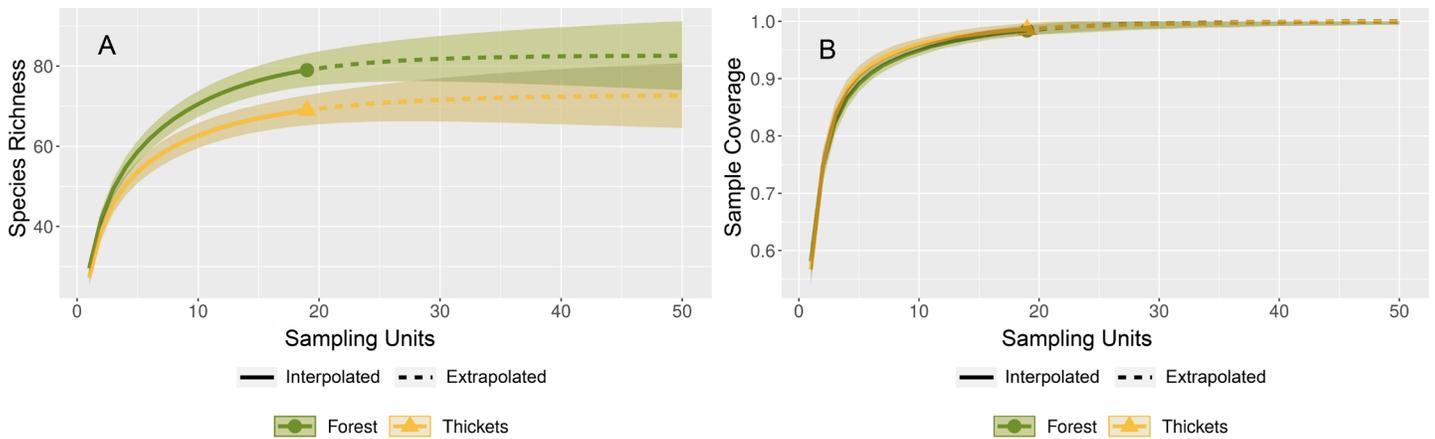


FIG. 8. Sample completeness analyses implemented in iNEXT Online for the butterfly assemblages in secondary forest and secondary thickets in Jardines de Hershey, Mayabeque, Cuba. A. Sample unit-based rarefaction curves. B. Sample coverage curves.

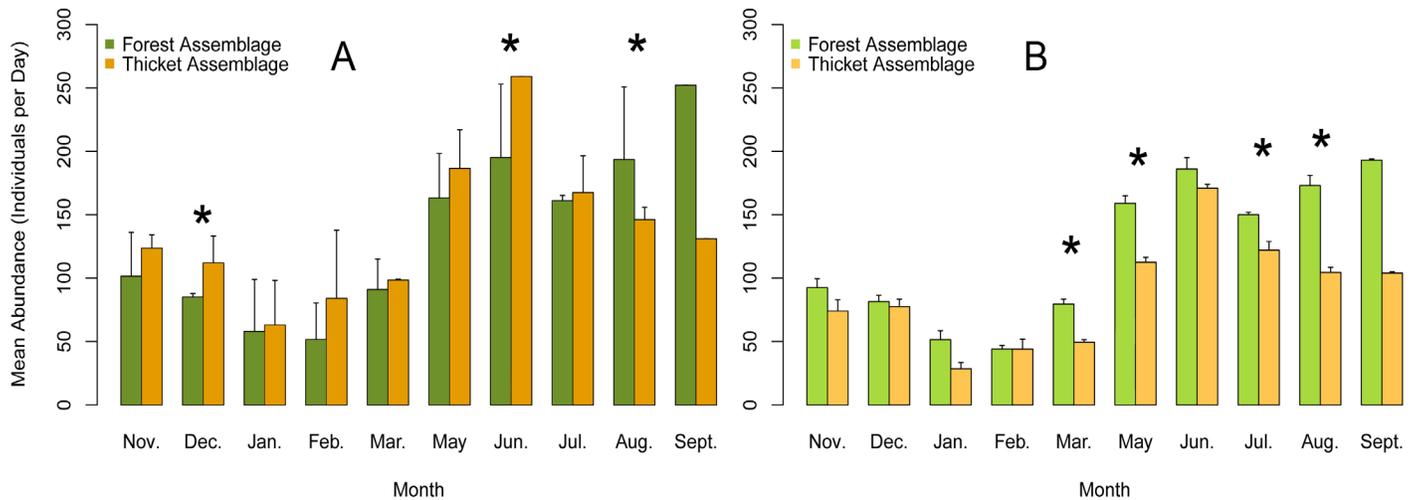


FIG. 9. Monthly mean butterfly abundance between November 2018 - September 2019 for the butterfly assemblages in secondary forest and secondary thickets in Jardines de Hershey, Mayabeque, Cuba, including *Calisto* spp. abundance (A) and excluding *Calisto* spp. abundance (B). Lines above bars represent standard deviation and asterisks denote significant statistical differences according to Monte Carlo test for effect size (the test was not applied to September as only one abundance value was available).

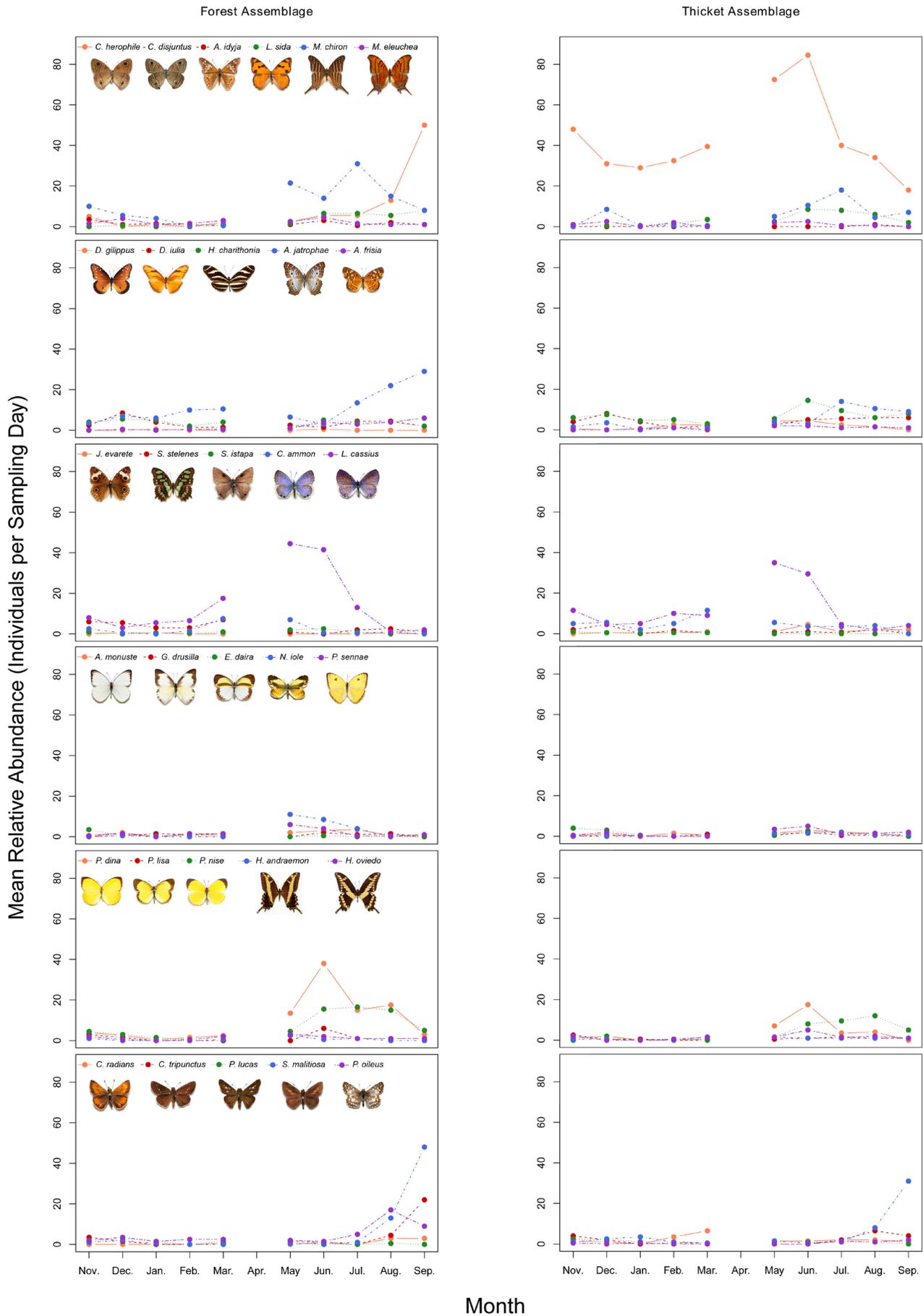
ment was very low in comparison to the previous season and to the forest assemblage, indicating that the assemblage turned more stable, except in the final month when replacement rate increased.

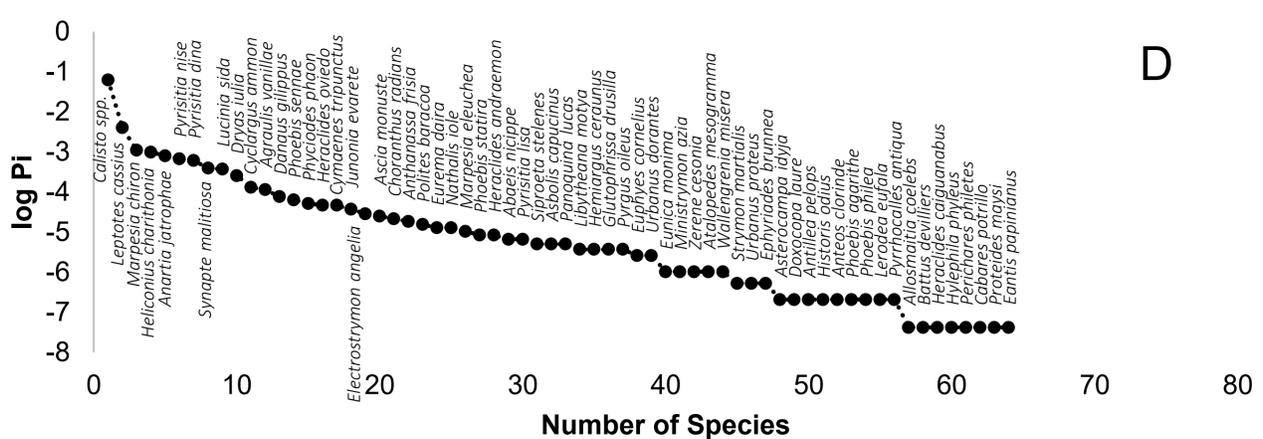
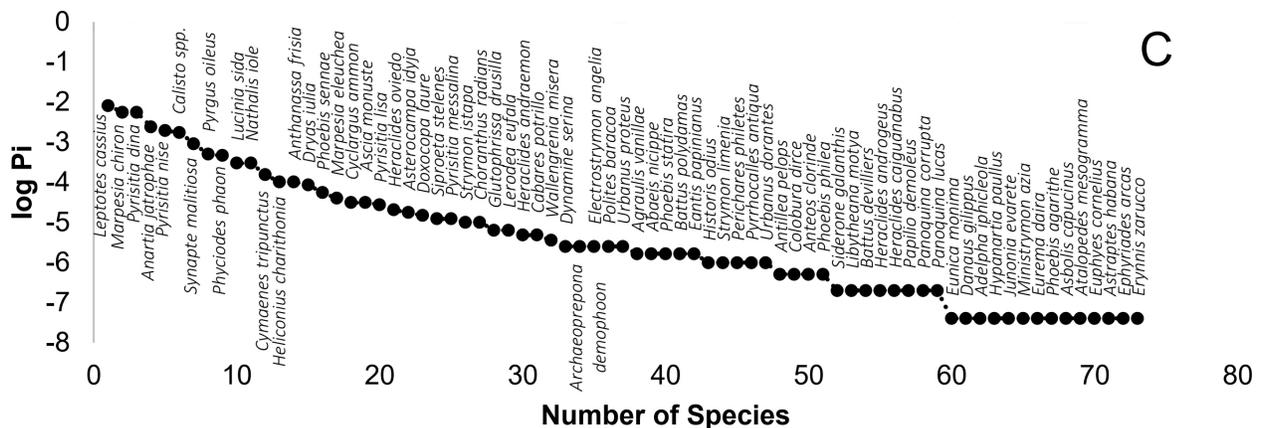
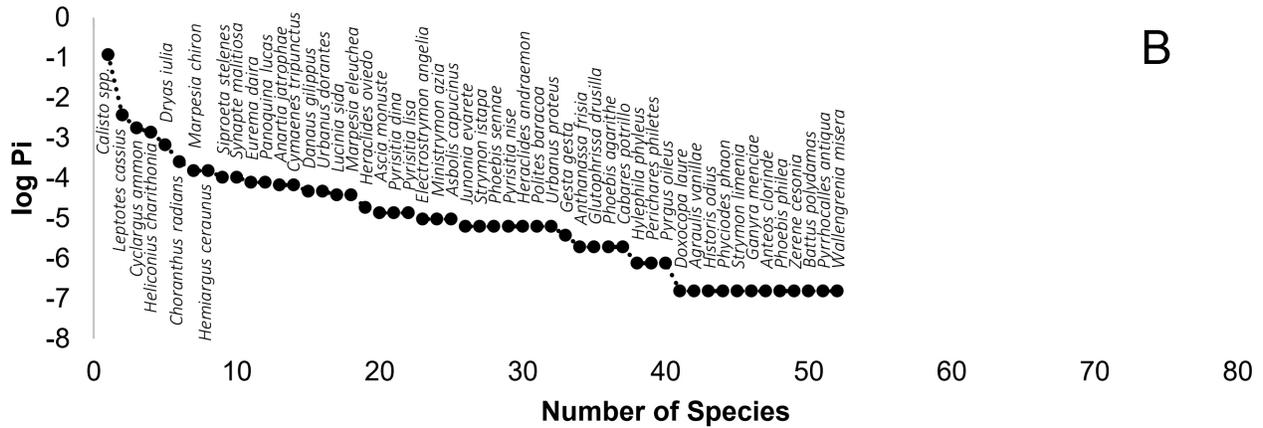
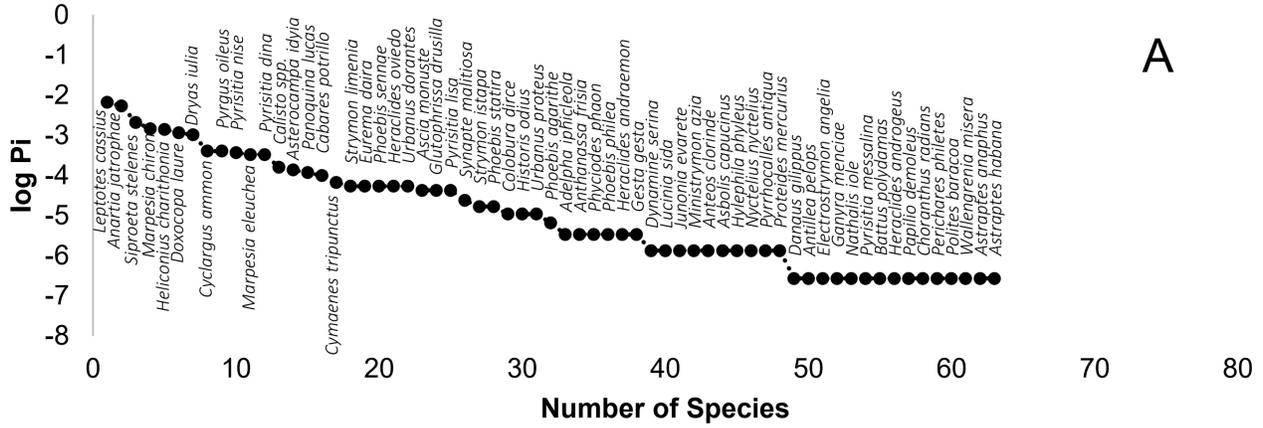
DISCUSSION

Most species present in the locality correspond to Cuba’s most common butterflies (Alayo and Hernández 1987; Hernández 2004; Barro and Núñez 2011). This is to be expected, due to the disturbed characteristics of

the habitats included in this study. Butterflies depend on their hostplants to breed; therefore, their distribution is highly dependent on their hostplant’s presence (Schoonhoven et al. 2005). Species with the highest abundance in the study are generalists: species of wide-spread distribution, found in several habitats and with a wide range of food and hostplants, including plants that benefit from disturbance (Alayo and Hernández 1987) and can easily adapt to a wide range of environmental conditions. These results are in conformance

FIG. 10 [next page →]. Monthly mean butterfly abundance for regularly observed species between November 2018–September 2019 in the butterfly assemblages in secondary forest and secondary thickets in Jardines de Hershey, Mayabeque, Cuba. Images of butterflies were obtained from Butterflies of America (<http://butterfliesofamerica.com/>) and Núñez et al. (2019) for *Calisto disjunctus*. Specimens are not at scale.





with previous studies in which generalist butterflies are found to be widespread and abundant (Kitahara et al. 2000; Kitahara and Sei 2001). The only Cuban butterfly family absent in the locality, Riodinidae, includes just one species in Cuba, *Dianesia carteri*, of a local and restricted distribution (Riley 1975).

The number of endemic species and subspecies detected in the locality, 23, is superior to the expected number of endemics by Azor and Barro (2014) for this region of the country. Although the results of these authors were obtained through modeling and are preliminary, this number of endemic taxa could suggest that this region of Cuba might have high values of endemism. Previous work in Mayabeque province corroborates this hypothesis (Núñez and Barro 2003).

The occurrence of *Calisto disjunctus* in this locality is noteworthy. This is a newly described species of the genus, and at the timing of this description, the known range of the species was restricted to marsh grasslands of Estero de las Piedras, in the southeastern portion of Isla de la Juventud (A. Barro, pers. comm.), and semideciduous forest in El Taburete, at the eastern tip of the Guaniguanico mountains (Núñez et al. 2019). This is the third known locality for this endemic insect. The presence of this species in disturbed habitats of Mayabeque suggests that it might be more widespread in Western Cuba, living in semideciduous forest of the Guaniguanico Cordillera and the Habana-Matanzas Hills, but overlooked due to its external resemblance with *C. herophile*. This species might have been inhabiting these hills for a long time and still subsists because its hostplant still persists in the remaining forest patches.

Heraclides caiguanabus is a rare insect, found often in coastal woodlands, scarce in the mountains and commoner in the eastern provinces (Alayo and Hernández 1987). It was found by Núñez and Barro (2003) in Boca de Canasí, 15 km east of Hershey. As the studied sites are relatively near the coast, the observed individuals could have moved from a coastal forest where the species is found, something possible due to the great dispersal capacity of swallowtails (Tyler et al. 1994). Other scarce species found during the study are *Archaeoprepona*

demophon, *Hypanartia paullus*, *Astraptes anaphus*, *Proteides maysi*, and *Ephyriades arcas*.

The skippers *Cabares potrillo*, *Synapte malitiosa*, and *Choranthus radians* were found to be abundant in both sites, contrasting with the descriptions of Alayo and Hernández (1987), Fontenla and de la Cruz (1992) and Smith et al. (1994) about the restricted distribution and apparent scarcity of these insects in western Cuba. A possible explanation might reside in the occurrence of an expansion event during the last few decades from east to west. Evidence is provided by Núñez and Barro (2003), who commonly found these species in Boca de Canasí. Hernández (2004) also noticed an increment of abundance in the western region for *S. malitiosa*, and this could have occurred similarly for other species.

These records, alongside the elevated number of species detected in the locality, confirm the idea of Fontenla (1992) about the wide but discontinuous distribution of butterflies throughout Cuba. This elevated richness may be explained by the intermediate disturbance hypothesis of Connell (1978). This author stated that medium-disturbed habitats are prone to have a higher richness and diversity of species than those entirely disturbed or entirely conserved. The substitution of only a part of the native plants impacts moderately butterfly assemblages, while simultaneously introduces new vegetation, which is used by generalist species to subsist in the modified habitat. Thus, new resources are accessible to species that in other ways could not inhabit the locality. The result is a higher richness and diversity in medium-disturbed areas than those fully disturbed or fully conserved (Wilson 1994). This could explain why almost half of Cuban butterfly species can be found in such a disturbed locality. Long-term butterfly assemblages' studies in Cuban conserved and slightly disturbed semideciduous and evergreen forest of Sierra del Rosario (Rodríguez 2012) and the "mogote" vegetation complex of Viñales Valley (Fontenla 1987b), have found a lesser richness than our results. These localities lack several generalists detected in Jardines de Hershey, such as *S. limenia*, *P. agarithe*, *P. demoleus*, *N. nyctelius*, and *M. azia*, the latter known as an inhabitant of disturbed ecosystems dominated by *D. cinerea*

FIG. 11 [previous page ←]. Rank-abundance distributions plotted with the logarithm of proportional abundance (P_i) for the butterfly assemblages in secondary forest and secondary thickets during November 2018 – September 2019 in Jardines de Hershey, Mayabeque, Cuba. A. Forest assemblage, dry season. B. Thicket assemblage, dry season. C. Forest assemblage, humid season. D. Thickets assemblage, humid season.

and *V. farnesiana* (Hernández 2004), like the thickets we sampled. Some specialists (butterflies with limited geographic distribution, marked habitat preference and a restricted range of food plants and hostplants) detected in Hershey were also absent in these localities, such as *H. paullus*, *A. coelebs*, *H. caiguanabus*, and *A. anaphus*. A lesser richness is also perceived for studies in highly disturbed habitats, such as coastal anthropic thickets and highly anthropized secondary forests (Fontenla 1987a), where specialist species detected in our study, such as *A. demophoon*, *A. iphicleola*, *H. paullus*, *G. menciae*, *H. androgeus*, *E. arcas*, and *P. maysi*, were not found. The distribution of hostplants in different habitats and in same habitats of different phytogeographic regions may be the cause of these distribution patterns, particularly for specialists detected in Hershey that could be inhabitants of the more conserved localities cited before. Núñez and Barro (2003), studying a disturbed semideciduous forest, detected a species richness similar to the results of this study, and most of these species were also present in Jardines de Hershey.

Previous observations indicate that *Colobura dirce* and *Perichares philetus* are common species in the locality. Nonetheless, *C. dirce* is abundant in the darkest and closed patches of the forest, which were not included along the walking due to their inaccessibility. On the other hand, *P. philetus* has crepuscular habits and is more visible during the early hours of the morning (Alayo and Hernández 1987), when sampling was not proceeding yet due to the inactivity of most species at these hours. These factors may have negatively influenced these insects being detected. Moreover, the lycenid *A. coelebs* is more active in the late afternoon (Alayo and Hernández 1987), so this could explain why it was barely represented in our sampling (which finished around 13:00 hours, and around 13:30 in daylight saving time), although it was only observed during the sampling period and not before.

The high similitude in composition suggested by the low value of Colwell and Coddington's Complementarity Index and the similarities of the rank-abundance distributions might be attributed to the scarce separation of the sampled sites and the forest patches being a poorly differenced habitat. As was mentioned, a portion of the forest was wide open and received as much sunlight as the thickets do. Similar results were found by Fontenla (1987a). This could

explain the 64 species shared, and that most species exclusive from forest patches are strictly woodland insects such as *C. dirce*, *A. demophoon*, *S. galanthis*, and species of genus *Astrartes*. The presence of these forest exclusive specialist species is the cause of the greater richness in this habitat. The shared species include the generalists previously mentioned (Alayo and Hernández 1987).

Due to this, the high dissimilitude suggested by the SIMPER analysis might be related to the differences in abundance rather than composition, as the Colwell and Coddington's Complementarity Index indicates a great overlap in the present species. While in the dry season abundance was not different between habitats, at the beginning of the humid season abundance was higher in the thicket assemblage and in the following months was higher in the forest assemblage (Fig. 9A). This can be explained by the abundance pattern of *Calisto* species (Fig. 10). The peak of abundance of these species was in June, a month in which abundance between habitats differed statistically and was higher in the thicket assemblage. In the following months, with the decrement in abundance of *Calisto*, abundance was higher in the forest, and statistically different between both habitats, as other abundant species (*A. jatrophae*, *M. chiron*, *L. cassius*, and *P. dina*) were more abundant in the forest. When we disregard *Calisto* abundance (Fig. 9B), from May on butterfly abundance was higher (and statistically different) in the forest, except in June, when *P. dina* reached an abundance peak, more pronounced in the forest assemblage, but also perceived in the thicket assemblage. *Calisto* species were the taxa that contributed the most to the dissimilitude of habitats according to the SIMPER analysis (Table 1). The great abundance of *Calisto* species in the thickets can be related to the dominance of their hostplants (grasses) (Núñez et al. 2012) in this habitat.

Phenology of Cuban butterflies has been poorly studied. Most authors provide information regarding flight period and voltinism of several species (Riley 1975; Smith et al. 1994) but do not deepen in abundance shifts throughout the year. Only Fontenla (1987b) and Núñez and Barro (2003) have provided patterns of abundance for a few common butterflies. The results of these authors are congruent to our species abundance patterns, particularly for *A. jatrophae*, *C. herophile*, *C. tripunctus*, and *S. malitiosa*. This suggests that these species have a stable phenological pattern. Fontenla

(1987a) attributed the asynchrony of their abundance peaks to temporal niche segregation between dominant species to avoid competition for nectar resources, which could explain why we obtained similar results. Our findings provide insights into other species' phenology. Abundance patterns of these species are similar in both sampled habitats, except for *Calisto* spp. This could be explained by different abundance patterns for *C. herophile* and *C. disjunctus*. As we stated, we were unable to isolate each species' abundance, but we noted *C. disjunctus* more common in the last months of the humid season in the forest patches. Thus, the peak of *C.* spp. in this habitat at the end of the humid season could be the abundance peak of this species. In the thickets, *C. herophile* was dominant and the abundance pattern detected could be the one of this species. This suggests that *C. disjunctus* prefers more conserved and shaded habitats, thriving in forests and gathering in great numbers in clearings to feed, as it was seen in the forest assemblage at the end of the humid season, while *C. herophile* favors more disturbed, open lands.

Differences in abundance between habitats may suggest habitat preference by butterfly species, as this factor is known to determine butterfly distribution and abundance (Thomas et al. 2001; Olivier et al. 2016). For example, species of the genus *Danaus* are known to prefer open, sunny habitats (Alayo and Hernández 1987), such as the thickets we sampled, where *D. gilippus* was frequently seen. *A. idyja*, *M. chiron*, and *P. dina* are examples of forest species, the latter two species often abundant in forest patches. *A. idyja* is a rarer species, found only in scattered forest patches in which *Celtis iguanaea* is found (Hernández 2004). Given the importance of phenological studies to the comprehension of distribution and abundance patterns, a deeper study in the phenology of Cuban butterflies would be very promising.

Species that were present in all the sampling months and constituted the permanent, basic core of the assemblages (e.g. *A. jatrophae*, *C. herophile*, *L. cassius*, *D. iulia*, *H. charithonia*, etc.) are examples of widespread and common generalists (Alayo and Hernández 1987). Other species were complementary and appeared frequently but not constantly (e.g. *Strymon* species, *Lucinia sida*, *Electrostrymon angelia*, etc.) and other species were rare and infrequent (e.g. *H. paullus*, *A. coelebs*, *Astraptus anaphus*, etc.). Although we cannot consider these as residents in the community, most but-

terflies are territorial and sedentary insects (Footitt and Adler 2009), therefore these species must be resident in the vicinity of the study sites. At the beginning of the humid season, *Libytheana motya* and *Eunica monima* were found frequently and stayed in the locality for a few weeks, disappearing afterwards. These species are seldom constant in their range, and are strong migrants that appear and disappear sporadically throughout the country (Alayo and Hernández 1987; Smith et al. 1994).

Replacement rate indicates that the forest assemblage is more stable in time than the thicket assemblage. Brown and Freitas (2002) found that stable ecosystems harbor more diverse and stable butterfly communities. Hence, the influence of environment stability could have led to the results obtained herein, although more evidence is necessary to verify this.

Núñez and Barro (2003) suggested that the great diversity of butterflies in the semideciduous coastal forest and sea grape forest of Boca de Canasí (Santa Cruz del Norte) could be an indicative of these habitats representing a shelter for insect fauna within an anthropic landscape, as a great part of Cuba's western coast forest have been whipped out. Considering that the locality of this study is placed in the same biogeographic area, in an even more urbanized and disturbed environment, Jardines de Hershey and surrounding forest patches, though disturbed habitats, could also represent a potential shelter for butterfly fauna, and thus are home to a great number of species, including rare and infrequent ones.

Although beyond the focus of this work, a relationship between butterfly abundance and flowering periods was detected. A succession in floral species through the year was observed, although annual species such as *Bidens pilosa* and *Wedelia rugosa* were always available as nectar sources. Different species flowered at different times of the year, during which butterfly abundance was higher (e.g. *Koanophyllon villosum* subsp. *villosum* at early December, *Viguiera dentata* in January–February, and *Bourreria divaricata* in May–June and late August). During these periods, butterflies, if not more abundant, were at least more visible as they gathered around blooming plants to feed. Previous studies have detected the existence of this relationship between the presence of flowering plants and butterfly abundance (Kubo et al. 2009), so it could be a pattern to study in Cuban assemblages.

CONCLUSIONS

The pattern that we detected in two butterfly assemblages in disturbed habitats is a high number of species in comparison to other Cuban localities with long-term butterfly fauna studies, as evidence of the wide distribution of Cuban butterflies and the possible effects of moderate disturbance in the biodiversity of habitats. The forest assemblage was richer in species, and there were not significant differences in abundance during the dry season, while in the humid season abundance rose first in the thicket assemblage (due to an abundance peak of *Calisto* species in this habitat) and later in the forest after an abundance increment of species in this habitat and the decrement of abundance of *Calisto* species in the thickets. The two assemblages shared several species due to their close proximity, but the presence of exclusive forest butterflies in this habitat contributed to its higher richness. Similar abundance patterns were observed for the most frequent species in both habitats, but differences in abundance and frequency may suggest the influence of habitat preference. Stability and replacement patterns seem to be related to environmental changes, but additional information is necessary to establish a clear relationship. The core species in both assemblages are common, widespread, generalist butterflies with a wide range of hostplants. Uncommon and rare species were found in less number, but their presence indicates that they are surely resident near the study locality. Thus, further studies around this area could lead to the discovery of butterfly hotspots in more conserved forested hills.

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APPENDIX 1. List of butterflies detected during November 2018–September 2019 in forest and thicket habitats in Jardines de Hershey, Mayabeque, Cuba, with annual and seasonal mean abundance in each site. *Endemic species. **Endemic subspecies. ****Calisto herophile* Hübner, 1823 + *C. disjunctus* Núñez and Barro, 2019 (both endemic species).

Species	Annual Abundance		Dry Season		Wet Season	
	Forest	Thickets	Forest	Thickets	Forest	Thickets
Nymphalidae						
<i>Calisto</i> spp. ***	6.52	44.66	1.60	36.00	11.44	53.33
<i>Asterocampa i. idyja</i> (Geyer, 1828)	1.53	0.11	1.50	-	1.56	0.22

APPENDIX 1. Continued.

<i>Doxocopa laure druryi</i> (Hübner, 1823) **	2.62	0.16	3.80	0.10	1.44	0.22
<i>Dynamine serina calais</i> Bates, 1934 **	0.43	-	0.20	-	0.67	-
<i>Eunica monima</i> (Cramer, 1782)	0.05	0.22	-	-	0.11	0.44
<i>Lucinia s. sida</i> Hübner, 1823 **	2.76	3.44	0.20	1.10	5.33	5.78
<i>Marpesia chiron chironides</i> (Staudinger, 1886) **	11.60	5.61	4.20	2.00	19.00	9.22
<i>Marpesia e. eleuchea</i> (Hübner, 1818) **	2.21	1.16	2.20	1.10	2.22	1.22
<i>Archaeoprepona demophoon crassina</i> (Fruhstorfer, 1904) **	0.38	-	0.10	-	0.67	-
<i>Siderone galanthis nemesis</i> (Illiger, 1802)	0.11	-	-	-	0.22	-
<i>Danaus gilippus berenice</i> (Cramer, 1779)	0.10	2.04	0.10	1.20	0.11	2.89
<i>Agraulis vanillae insularis</i> Maynard, 1869	0.28	1.77	-	0.10	0.56	3.44
<i>Dryas iulia nudeola</i> (Bates, 1934) **	3.35	4.34	3.60	3.80	3.11	4.89
<i>Heliconius charithonia ramsdeni</i> Comstock & Brown, 1950	3.71	6.99	4.10	5.20	3.33	8.78
<i>Adelpha iphicleola iphimedia</i> Fruhstorfer, 1915 **	0.20	-	0.30	-	0.11	-
<i>Anartia jatrophae guantanamo</i> Munroe, 1942	10.31	4.70	7.40	1.40	13.22	8.00
<i>Anthanassa f. frisia</i> (Poey, 1832)	1.81	0.93	0.30	0.30	3.33	1.56
<i>Antillea pelops anacaona</i> (Herrich-Schäffer, 1864) **	0.21	0.11	0.10	-	0.33	0.22
<i>Colobura dirce wolcotti</i> (Comstock, 1942)	0.41	-	0.50	-	0.33	-
<i>Historis o. odius</i> (Fabricius, 1775)	0.47	0.16	0.50	0.10	0.44	0.22
<i>Hypanartia paullus</i> (Fabricius, 1793)	0.05	-	-	-	0.11	-
<i>Junonia evarete zonalis</i> Felder & Felder, 1867	0.15	1.30	0.20	0.50	0.11	2.11
<i>Phyciodes p. phaon</i> (Edwards, 1864)	3.37	1.27	0.30	0.10	6.44	2.44
<i>Siproeta stelenes biplagiata</i> (Fruhstorfer, 1907)	3.11	1.29	4.90	1.70	1.33	0.89
<i>Libytheana motya</i> (Hübner, 1826) *	0.11	0.39	-	-	0.22	0.78
Lycaenidae						
<i>Allosmaitia coelebs</i> (Herrich-Schäffer, 1862) *	-	0.05	-	-	-	0.11
<i>Electrostrymon a. angelia</i> (Hewitson, 1874)	0.38	1.24	0.10	0.60	0.67	1.89
<i>Ministrymon azia</i> (Hewitson, 1873)	0.15	0.52	0.20	0.60	0.11	0.44
<i>Strymon istapa cybira</i> (Hewitson, 1874)	0.91	0.25	0.60	0.50	1.22	-
<i>Strymon limenia</i> (Hewitson, 1868)	0.72	0.05	1.00	0.10	0.44	-
<i>Strymon martialis</i> (Herrich-Schäffer, 1864)	-	0.16	-	-	-	0.33
<i>Cyclargus ammon</i> (Lucas, 1857)	2.20	4.73	2.40	5.80	2.00	3.67
<i>Hemiargus ceraunus filenus</i> (Poey, 1832)	-	1.39	-	2.00	-	0.78
<i>Leptotes cassius theonus</i> (Lucas, 1857)	15.27	12.11	8.10	8.00	22.44	16.22
Pieridae						
<i>Ascia monuste eubotea</i> (Godart, 1819)	1.45	1.24	0.90	0.70	2.00	1.78
<i>Ganyra menciae</i> (Ramsden, 1915)	0.05	0.05	0.10	0.10	-	-
<i>Glutophrissa drusilla poeyi</i> (Butler, 1872)	0.95	0.54	0.90	0.30	1.00	0.78
<i>Abaeis nicippe</i> (Cramer, 1779)	0.28	0.50	-	-	0.56	1.00
<i>Anteos clorinde</i> (Godart, [1824])	0.26	0.16	0.20	0.10	0.33	0.22
<i>Eurema दौरa palmira</i> (Poey, 1852)	0.55	1.41	1.00	1.50	0.11	1.33
<i>Nathalis iole</i> Boisduval, 1836	2.71	0.66	0.10	-	5.33	1.33
<i>Phoebis agarithe antillia</i> Brown, 1929	0.25	0.26	0.40	0.30	0.11	0.22
<i>Phoebis p. philea</i> (Johansson, 1793)	0.31	0.16	0.30	0.10	0.33	0.22
<i>Phoebis s. sennae</i> (Linnaeus, 1758)	1.78	1.58	1.00	0.50	2.56	2.67

APPENDIX 1. Concluded.

<i>Phoebis statira cubana</i> d'Almeida, 1939	0.58	0.55	0.60	-	0.56	1.11
<i>Pyrisitia d. dina</i> (Poey, 1832) **	10.6	3.90	2.20	0.70	19.00	7.11
<i>Pyrisitia lisa euterpe</i> (Ménétriés, 1832)	1.39	0.85	0.90	0.70	1.89	1.00
<i>Pyrisitia messalina</i> (Fabricius, 1787)	0.71	-	0.10	-	1.33	-
<i>Pyrisitia n. nise</i> (Cramer, 1775)	7.15	3.97	2.30	0.50	12.00	7.44
<i>Zerene c. cesonia</i> (Stoll, 1790)	-	0.27	-	0.10	-	0.44
Papilionidae						
<i>Battus devilliers</i> (Godart, 1823)	0.11	0.05	-	-	0.22	0.11
<i>Battus polydamas cubensis</i> (Dufrane, 1946) **	0.33	0.05	0.10	0.10	0.56	-
<i>Heraclides a. andraemon</i> Hübner, [1823]	0.59	0.80	0.30	0.50	0.89	1.11
<i>Heraclides androgeus epidaurus</i> (Godman & Salvin, 1890)	0.16	-	0.10	-	0.22	-
<i>Heraclides caiguanabus</i> (Poey, [1852]) *	0.11	0.05	-	-	0.22	0.11
<i>Heraclides oviedo</i> (Gundlach, 1866) *	1.33	1.56	1.00	0.80	1.67	2.33
<i>Papilio demoleus malayanus</i> (Wallace, 1865)	0.16	-	0.10	-	0.22	-
Hesperiidae						
<i>Asbolis capucinus</i> (Lucas, 1857)	0.15	0.74	0.20	0.60	0.11	0.89
<i>Atalopedes m. mesogramma</i> (Latreille, [1824])	0.05	0.22	-	-	0.11	0.44
<i>Choranthus radians</i> (Lucas, 1857)	0.66	2.08	0.10	2.50	1.22	1.67
<i>Cymaenes t. tripunctus</i> (Herrich-Schäffer, 1865)	2.55	1.86	1.10	1.40	4.00	2.33
<i>Euphyes c. cornelius</i> (Latreille, [1824]) **	0.05	0.33	-	-	0.11	0.67
<i>Hylephila p. phyleus</i> (Drury, 1773)	0.10	0.15	0.20	0.20	-	0.11
<i>Lerodea e. eufala</i> (Edwards, 1869)	0.50	0.11	-	-	1.00	0.22
<i>Nyctelius n. nyctelius</i> (Latreille, [1824])	0.10	-	0.20	-	-	-
<i>Panoquina corrupta</i> (Herrich-Schäffer, 1865) *	0.11	-	-	-	0.22	-
<i>Panoquina lucas</i> (Fabricius, 1793)	0.81	1.19	1.40	1.50	0.22	0.89
<i>Perichares philetus</i> (Gmelin, 1790)	0.27	0.15	0.10	0.20	0.44	0.11
<i>Polites b. baracoa</i> (Lucas, 1857)	0.38	0.97	0.10	0.50	0.67	1.44
<i>Pyrrhocalles antiqua orientis</i> Skinner, 1920 **	0.32	0.16	0.20	0.10	0.44	0.22
<i>Synapte m. malitiosa</i> (Herrich-Schäffer, 1865)	4.68	3.79	0.70	1.70	8.67	5.89
<i>Wallengrenia misera</i> (Lucas, 1857)	0.44	0.27	0.10	0.10	0.78	0.44
<i>Astraptes anaphus anaensis</i> (Godman & Salvin, 1896)	0.05	-	0.10	-	-	-
<i>Astraptes h. habana</i> (Lucas, 1857) **	0.10	-	0.10	-	0.11	-
<i>Cabares p. potrillo</i> (Lucas, 1857)	1.09	0.20	1.30	0.30	0.89	0.11
<i>Proteides maysi</i> (Lucas, 1857) *	-	0.05	-	-	-	0.11
<i>Proteides mercurius sanantonio</i> (Lucas, 1857) **	0.10	-	0.20	-	-	-
<i>Urbanus dorantes santiago</i> (Lucas, 1857)	0.72	0.93	1.00	1.20	0.44	0.67
<i>Urbanus proteus domingo</i> (Scudder, 1872)	0.58	0.41	0.50	0.50	0.67	0.33
<i>Eantis papinianus</i> (Poey, 1832)	0.28	0.05	-	-	0.56	0.11
<i>Ephyriades arcas philemon</i> (Fabricius, 1775)	0.05	-	-	-	0.11	-
<i>Ephyriades b. brunnea</i> (Herrich-Schäffer, 1865)	-	0.16	-	-	-	0.33
<i>Erynnis zarucco</i> (Lucas, 1857)	0.05	-	-	-	0.11	-
<i>Gesta gesta</i> (Herrich-Schäffer, 1863)	0.15	0.20	0.30	0.40	-	-
<i>Pyrgus oileus</i> (Linnaeus, 1767)	4.53	0.49	2.40	0.20	6.67	0.78