

A New Chance: Recovery of Nymphalidae diversity twelve years after mining in a peri-urban Andean Forest of Colombia (Lepidoptera: Papilionoidea)

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Abstract

Various human activities, including mining, have significantly impacted ecosystems in Colombia, leading to a decline in biodiversity. These activities have led to changes in the distribution and diversity of different species, such as Lepidoptera. A study was conducted to analyze the changes in the diversity of Papilionoidea in a peri-urban forest located in Bogotá, twelve years after the cessation of mining activities in the area. Seven study stations were established, and standardized sampling techniques were employed to collect Papilionoidea. The results showed an increase in Nymphalidae diversity compared to studies conducted in the early years after the end of mining in the area. The most common Nymphalidae belonged to the Pronophilina subtribe. This research demonstrates the success of ecological restoration projects implemented in the area after the cessation of mining activities, which allowed for the recolonization of the region by various species, indicating the regeneration of the Andean Mountain Forest. Further studies focused on ecological restoration in the area are recommended, as positive effects on the assemblage of Andean Lepidoptera fauna have been observed.

Keywords: Lepidoptera, Papilionoidea, Nymphalidae, Pronophilina, ecological restoration, synanthropic species, habitat disturbance, Anthropocene, Colombia.

Una nueva oportunidad: Recuperación de la diversidad de Nymphalidae doce años después de la minería en un Bosque Andino periurbano en Colombia (Lepidoptera: Papilionoidea)

Resumen

Diversas actividades humanas, incluida la minería, han impactado significativamente los ecosistemas en Colombia, provocando una disminución de la biodiversidad. Estas actividades han generado cambios en la distribución y diversidad de diferentes especies, como los Lepidoptera. Se realizó un estudio para analizar los cambios en la diversidad de Papilionoidea en un bosque periurbano ubicado en Bogotá, doce años después de haber cesado las actividades mineras en la zona. Se establecieron siete estaciones de estudio, y se emplearon técnicas de muestreo estandarizadas para la recolección de Papilionoidea. Los resultados mostraron un aumento en la diversidad de Nymphalidae en comparación con los estudios realizados en los primeros años después del fin de la minería en la zona. Los Nymphalidae más comunes pertenecían a la subtribu Pronophilina. Esta investigación demuestra el éxito de los proyectos de restauración ecológica implementados en la zona tras el cese de las actividades mineras, que permitieron la recolonización de la región por diversas especies, indicando la regeneración del Bosque Andino de Montaña. Se recomienda realizar más estudios enfocados a la restauración ecológica en la zona, ya que se han observado efectos positivos en el ensamblaje de la fauna

de Lepidoptera andina.

Palabras clave: Lepidoptera, Papilionoidea, Nymphalidae, Pronophilina, restauración ecológica, especies sinantrópicas, perturbación del hábitat, Antropoceno, Colombia.

Introduction

Papilionoidea constitute one of the most diverse insect groups worldwide, with the highest species richness reported in the Neotropical realm, comprising approximately 7,700 species (Lamas, 2000; De-Silva, et al. 2015). Colombia is the second species-rich country after Peru, a total of 3,877 species is reported currently (Garwood et al. 2022). Lepidoptera play a specific and important role in ecosystems (e.g., as pollinators) and serve as valuable conservation bioindicators of habitat health. They frequently contribute to elaborate and carry out of conservation programs (Andrade, 1998). Besides, the Papilionoidea are considering as the umbrella species in biology conservation (New, 1997; Weibull et al. 2000; Díaz-Suárez et al. 2022).

In Colombia, as in other countries around the world, many anthropogenic practices have caused a sharp decline in the total area of ecosystems and many local extinction processes (Mahmoud & Gan, 2017; Murillo-P. et al. 2018; Ouyang et al. 2018; Le Roux et al. 2019; Fowler et al. 2021; Díaz-Suárez et al. 2022; Méndez-Zambrano & Fajardo-Medina, 2024), causing a negative impact on populations of plant and animal native species which may disappear from the face of the planet (Andrade, 1998; Van der Hammen & Andrade, 2003; Le Roux et al. 2019; Fowler et al. 2021). High Andean forests are among the ecosystems most heavily impacted by human population density, agriculture, livestock, and industrial activities that exploit natural resources (Méndez-Zambrano & Fajardo-Medina, 2024). This negative impact is notably reflected on the fauna-flora from the surrounding Andean forests of large cities, such as Bogotá in Colombia (Mahecha-Jiménez et al. 2011; Marín et al. 2014; Ouyang et al. 2018).

Additionally, the urbanization processes have generated the fragmentation of different forest communities, leading to the evolution of secondary forest patches, which in many cases, have lost connectivity between them, reducing the gene flow between populations. As a result, it may reduce the local genetic biodiversity (Van der Hammen & Andrade, 2003; Fahrig, 2003; Mckinney, 2008; While & Whitehead, 2013; Ouyang et al. 2018; Méndez-Zambrano & Fajardo-Medina, 2024). Further, urbanization has been linked to negative effects on biodiversity, which is often greatly reduced by intense urban development but can flourish in suburban and peri-urban areas (Aronson-Myla et al. 2017; Ouyang et al. 2018). The habitat in the peri-urban fragmentation areas allows highlighting many changes that occur between rural and urban ecosystems. It shows that different environmental factors proper to urban areas impact the surrounding ecosystems, by transforming their soil, surface, and groundwater resources (Fahrig, 2003; Mckinney, 2008). Therefore, these peri-urban areas show particularly high ecological fragility due to intensive activities that take place in their proximity and are often described as critical areas for biota (Capel, 1994; Marín et al. 2014).

The Serranía del Zuque is a peri-urban forest that constitutes a source of ecosystem and environmental services for the south-eastern part of Bogotá city. Currently, due to ongoing urban expansion, the natural habitats in this area are under severe anthropogenic pressure, leading to a gradual loss of native vegetation (Aguilar-Garavito, 2010, 2015) and, consequently, a decline in faunal diversity, including Papilionoidea (Mahecha-Jiménez, 2008; Mahecha-Jiménez et al. 2011). The introduction of non-native tree species, including *Acacia decurrens* Willd., *Acacia melanoxylon* Brown, and *Ulex europaeus* L., has disrupted the natural balance of plant and animal communities in the area (Solorza, 2012). This has altered the relationships between different species, changed the functioning of the ecosystem, and displaced native species (Mack et al. 2000; Fahrig, 2003; Mckinney, 2008; Solorza, 2012).

The factors mentioned above increase the likelihood of human-induced land-use disturbances, including erosion, landslides, alterations to hydrological cycles, and changes in the physical and chemical properties of the soil (Solorza, 2012). These disturbances could have impacted the ecological succession dynamics in the Serranía del Zuque (Mahecha-Jiménez et al. 2011; Aguilar-Garavito, 2015). Moreover, the Serranía del Zuque was subject to mining activities from 1960 to 1996, and asphalt production occurred between 1987 and 2006. During this period, frequent avalanches were reported due to the instability of the terrain. Following several slope stabilization efforts, the area was eventually abandoned. In 2009, approximately 35.6 hectares of the Serranía del Zuque were invaded by *U. europaeus* L. (Aguilar-Garavito, 2010, 2015). This invasion resulted in mixed thickets with native vegetation or dense monospecific thickets along the internal road, the

network of roads, edges of ravines, in the old mining area, in forest plantations undergrowth, and within native successional bushes (Aguilar-Garavito, 2015).

The Serranía del Zuque is currently threatened by unregulated urban development, contributing to the progressive loss of native vegetation. Mining activities, wildfires, and water pollution caused by human land-use are contributing to high fragmentation in the peri-urban forest (Aguilar-Garavito, 2010, 2015; Mahecha-Jiménez et al. 2011). This promoted the invasion of *U. europaeus* L., causing a displacement of the native plant populations of the Andean forest and possible local extinctions (Aguilar-Garavito, 2010, 2015; Mahecha-Jiménez et al. 2011; Solorza, 2012). In addition, it has triggered forest fires during the dry season, particularly during El Niño events (Aguilar-Garavito, 2015).

However, the Serranía del Zuque was designated as part of the Forest Reserve East of Bogota in 2006. Subsequently, a management plan was established (CAR, 2006a). This resulted in restrictions on human land use (Aguilar-Garavito, 2010, 2015; Mahecha-Jiménez et al. 2011). In addition, the District Environmental Department from Bogotá initiated the ecological restoration of 10.4 hectares invaded by *Ulex europaeus* in the Serranía del Zuque in 2009-2010 (Aguilar-Garavito, 2010, 2015).

This study aimed to analyze the changes in Papilionoidea diversity at the Serranía del Zuque peri-urban Andean forest twelve years after mining operations ceased. We hypothesized that, after the completion of mining operations in the study area, there would be an increase in diversity due to the native vegetation recovery at the Serranía del Zuque, allowing the establishment of host plants for mountain Papilionoidea such as Poaceae and Melastomataceae (Devries, 1987; Pyrcz et al. 2009; Greeney et al. 2009; Montero & Ortiz, 2013; Mahecha et al. 2019). Our results indicate an increase in the diversity of Papilionoidea at the Serranía del Zuque, suggesting that the peri-urban forest is progressively regenerating after mining, contrasting with the findings of Mahecha-Jiménez (2008) and Mahecha-Jiménez et al. (2011).

Material and methods

STUDY LOCATION AND SAMPLING METHODS

This study took place in the peri-urban Andean forest of Serranía del Zuque, situated in the southeastern part of the eastern hills of Bogotá, on the eastern slopes of the Cordillera Oriental of the Andes in Colombia (4°2'30.38"N and -74° 4'22.40"W; altitude: from 3000 to 3400 m) (Figure 1) (Aguilar-Garavito, 2015). The Serranía del Zuque is an ecotone between high Andean forest and sub-páramo (Mahecha-Jiménez, 2008; Aguilar-Garavito, 2015). The average annual rainfall is 1.500-3.000 mm/year, although this value can vary considerably depending on the ecosystem, with two wet seasons during the year, the first between April and May and the second from October to November (Camelo et al. 2009). The eastern hills have a varied topography in their entirety, where different soil types vary widely in the area since these soils were formed by the interaction between the geological formation, the vegetation cover and the influence of climate. Besides, due to the slow degradation of organic matter and the geological structure results in very acid soils and low fertility (Mahecha, 2000; CAR, 2006b). The climate of the study area is Tropical Mountain, humid with zenithal showers. Its geographical location and the presence of warm and cold currents influence the development of many microclimates. The Eastern Cordillera serves as a barrier against the winds coming from the Llanos and Magdalena Valley that can affect both the rainfall as well as the average temperature of the zones. Temperatures vary between 6 °C and 13 °C. (Mahecha, 2000).

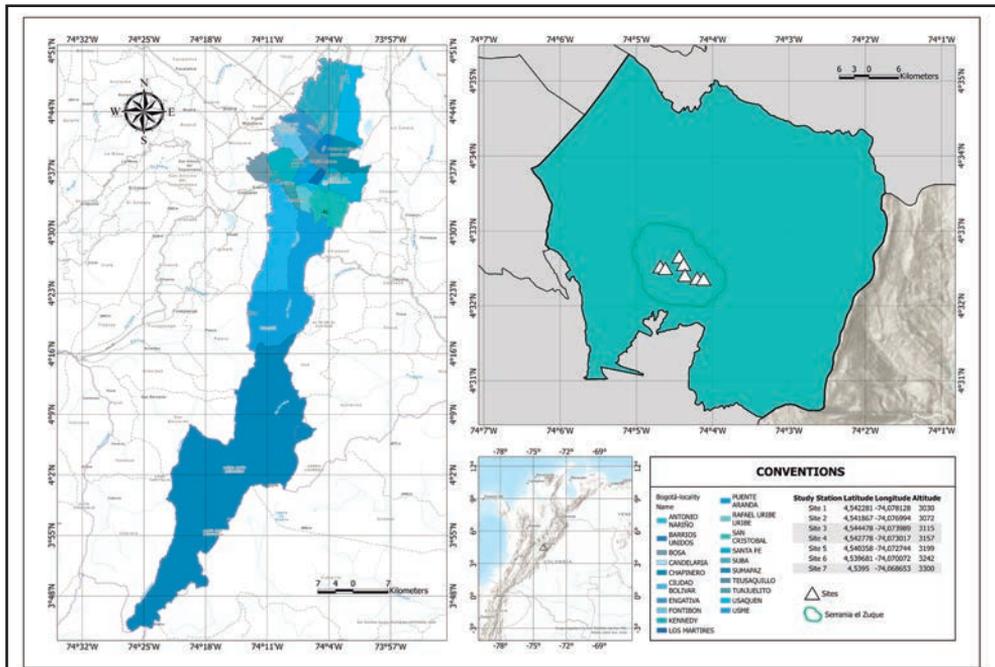
The native vegetation from the Serranía del Zuque consists of cloud forests dominated by *Weinmannia tomentosa* L.F, *Bejaria Mutis*, *Clusia* sp., *Drymis granadensis* L.F, *Eugenia* spp., *Macleania rupestris* Kunth A.C. Smith., *Espeletia* sp., *Puya* sp., and *Calamagrostis effuse* Adans. Epiphytic shrubs and vines, such as *Tillandsia* spp., dominate in the sub-canopy, as well as lichens and mosses, and *Chusquea* spp. (Aguilar-Garavito, 2010, 2015). Additionally, the native vegetation has been recovering, the populations of *Chusquea* spp., *W. tomentosa*, *Espeletia* spp., *Sellaginella* spp., and *Puya* spp. have increased their coverage in comparison to previous years (Aguilar-Garavito, 2010, 2015).

FIELDWORK

Fieldwork was performed every 15 days from June 2017 to June 2018 (29 field trips during all study),

to cover both rainy and dry season (Freitas et al. 2021; Díaz-Suárez et al. 2022); each sampling consisted of five days of collection (145 days at the end of the fieldwork). Papilionoidea were sampled using 20 × 20 m (400 m²) collecting stations, systematically established at 42-meter intervals, yielding a total of seven stations, covering an altitude between 3000 and 3300 m (Figure 1). These stations were located in areas where Mahecha-Jiménez (2008) and Mahecha-Jiménez et al. (2011) identified significant human impact, including deforestation, the introduction of non-native plant species (e.g. *U. europaeus*), and illegal mining activities. The ecological impact of mining activities during 2006-2007 was reflected in a pronounced decrease in Papilionoidea species richness in the study area (Mahecha-Jiménez, 2008; Mahecha-Jiménez et al. 2011). Following this, Aguilar-Garavito (2010) initiated an ecological restoration project in the affected areas to recover ecological functionality.

Figure 1. Location map of the study stations in the Serranía del Zuque peri-urban Andean forest in Bogotá, Colombia. The white triangles indicate the study stations.



Two collect forms were used: passive and active collect. To passive collect, five Van Someren-Rydon traps baited with dog feces, and decaying fish were placed, as this kind of bait has proven to be very attractive for many groups of cloud forest Lepidoptera (Pyrz & Wojtusiak, 2002; Pyrcz & Garlacz, 2012; Díaz-Suárez et al. 2022; Cerdeña et al. 2024). Each trap was spaced by 5 m from each other and were located between 1 and 3 m. from the ground surface and at least 100 m altitudinal distance from each other (Freitas et al. 2014; Clavijo-Giraldo et al. 2020). Traps were checked every three hours between 09:00 and 17:00. Active sampling was conducted manually using entomological nets from 08:30 to 17:00. At each study station, four longitudinal transects, spaced 5 meters apart, were established to cover the entire area. Each transect was walked for approximately 30 minutes (Andrade-C et al. 2013; Freitas et al. 2021).

TAXONOMIC ANALYSIS

The biological material was determined and deposited in the Museum of Natural History at the Universidad Distrital Francisco José de Caldas, Bogotá, Colombia. Taxonomic determination was conducted using an analysis of morphological characters as alar pattern and, the structure of male genitalia. The latter was

extracted following the standard procedure and macerated in a warm 10% KOH solution, and subsequently, they were preserved in glycerol vial. Taxonomic arrangement was based on the works of Adams (1985, 1986), Andrade & Amat (1996), Pycrz (2004a, 2004b), and Pycrz et al. (2009, 2010, 2013). Comparative material deposited in the Instituto de Ciencias Naturales (ICN) of the Universidad Nacional de Colombia, and the collection of the Nature Education Centre of the Jagiellonian University, Krakow, Poland, was examined. The nomenclature was checked against the checklists of Lamas et al. (2004), Pycrz et al. (2010, 2013), and Warren et al. (2013). The collected material was covered under the “Permiso Marco de Recolección de Especímenes de Especies Silvestres de la Diversidad Biológica con Fines de Investigación Científica No Comercial”, granted to the Universidad Distrital Francisco José de Caldas through Resolution 0738 of July 8, 2014, issued by the Autoridad Nacional de Licencias Ambientales – ANLA.

DATA ANALYSIS

Diversity estimates were calculated in terms of effective species or Hill numbers, which enables a better approach to species richness, incorporates the relative abundance of the same, allowing to give importance to the less abundant and rare species, or taking into account the dominance. That is to say, this method sets a greater emphasis on the most abundant species, thus handling the problem of “abundance”, a subject frequently discussed in different studies on diversity when making comparisons between assemblages and communities (Hill, 1973; Jost, 2006; Moreno et al. 2011; Chao et al. 2014). Likewise, it has been shown that for a better analysis of diversity in an assemblage, the numbers of effective species are best compared with the estimates based on the theory of communication such as the index of Shannon entropy (Ellison, 2010; Moreno et al. 2011; Chao et al. 2014). Therefore, Hill numbers are parameterized by a diversity order q , which determines the measures’ sensitivity to species relative abundances (Hsieh et al. 2016). Hill numbers include the three most widely used species diversity measures: species richness ($q = 0$), Shannon diversity ($q = 1$) and Simpson diversity ($q = 2$) (Moreno et al. 2011; Chao et al. 2014; Hsieh et al. 2016). In addition, a Bootstrap was calculated as estimated in the expected range for the order 0 (0D), the estimate of Chao & Shen (2003) for the expected diversity of order 1 (1D) and the expected diversity of order 2 (2D) the MVUE estimator (*Minimum variance unbiased estimator*) (Gotelli & Colwell, 2011; Moreno et al. 2011; Gotelli & Chao, 2013).

The Relative Abundance Distribution (RAD) was estimated to characterize the sampled community (Chao et al., 2015; Cusack et al., 2015). In this approach, the relative abundance of each species is plotted on the y-axis-often log₁₀-transformed to account for several orders of magnitude-while species are ranked from the most to the least abundant along the x-axis (Chao et al. 2015). The Akaike’s Information Criteria (AIC) was carried out to select the best RAD model for the study area (Cusack et al. 2015).

Coverage-based rarefaction/extrapolation (R/E) sampling curves were generated for each sampling station. The R/E method estimates species diversity (Hill numbers) for both rarefied and extrapolated samples, using sample completeness (measured as sample coverage) up to a coverage value equivalent to twice the reference sample size (Hsieh et al., 2016). However, Hill numbers of any order are influenced by sample size and inventory completeness. To address this, Chao et al. (2014) and Hsieh et al. (2016) proposed a unified framework for estimating species diversity through sample-size- and coverage-based R/E, allowing for statistically robust comparisons across communities. Likewise, a R/E curve can compare sites that have different sizes in their samples (Cleary & Genner, 2006; Gotelli & Colwell, 2011; Chao & Jost, 2012; Chao et al. 2014; Hsieh et al. 2016).

Therefore, when producing an R/E curve, it is possible to evaluate how representative the sampling was at each station, and in general, the whole study area, allowing us to reduce the effect of “sample size” in research (Chao et al. 2014). To determine the similarity between sampling stations according to the abundance and species composition, a cluster analysis was done, using the Bray-Curtis similarity index and as the cluster method the UPGMA (Unweighted Pair Group Method with Arithmetic Mean). Additionally, to support the results of the cluster analysis was conducted by a test ordination Non-Metric Multidimensional Scaling (NMDS) using the similarity Bray-Curtis index (Brehm et al. 2003b; Addo-Fordjour et al. 2015).

To assess significant differences in species abundance and composition between sampling stations, non-parametric statistical tests were used, as the data did not follow a normal distribution according to the Shapiro-Wilk test (p -value= 0.00002, $p < 0.05$). Consequently, a Kruskal–Wallis test (Zar, 1974; Sá, 2007) and

an ANOSIM test, based on the Bray–Curtis dissimilarity index with 999 permutations (Binz et al., 2014; Addo-Fordjour et al., 2015; Marín et al., 2015), were performed. Combined both methods (ANOSIM and NMDS) complement visualization of group differences along with significance test (Buttigieg & Ramette, 2014). All analyses were conducted at a 95% significance level. Statistical and diversity analyses were performed in R version 4.2.3 (R Development Core Team, 2023) by iNEXT package (Hsieh et al. 2016), and BiodiversityR (Kindt & Coe, 2005).

Results

A total of 685 individual Lepidoptera were reported, belonging to 4 families, 34 genera and 52 species. The majority (80% of the sample) belonged to the Nymphalidae family, followed by Lycaenidae and Pieridae. Papilionidae was represented by a single species, making it the family with the lowest species richness in the dataset. The most representative subfamilies were Satyrinae (29 species) and Theclinae (10 species). The three most diverse genera in the sample, *Pedaliodes* Butler, *Corades* Doubleday, and *Lymanopoda* Westwood, all belong to the subtribe Pronophilina (Satyrinae) (Table I).

Considering the abundance for each species, *Pedaliodes ochrotaenia* (C. Felder & R. Felder) and *Pedaliodes polla* Thieme had a higher abundance than other species registered in the zone and were the co-dominant species for each sampling station. However, species such as *Colias dimera* Doubleday, *Pedaliodes cocytia* (C. Felder & R. Felder), *Lymanopoda samius* Westwood, *Viloriodes manis* (C. Felder & R. Felder), and *Pedaliodes phoenissa* (Hewitson) presented a high abundance in the study area in comparison to other species as *Junea doraete* (Hewitson), *Cyanophrys agricolor* (Butler & H. Druce) and *Papilio polyxenes* Fabricius. Sequentially, three of the less abundant species correspond to Lycaenidae: *Salazaria sala* (Hewitson), *Marachina maraches* (H. Druce), and *Lamprospilus* sp. Geyer. Nevertheless, something to highlight in the results is that several species of Lycaenidae are reported, although they presented a low abundance.

Table II. RAD models with AIC values at the Serrania del Zuque peri-urban forest.

Model	Serrania del Zuque
Null	304.2
Preemption	233.9
Log-normal	226.4
Zipf	263.2
Zipf-Mandelbrot	226.9

Table III. The observed and estimated Hill numbers diversity values (effective species) obtained for each study station.

Study Station	Observed			Estimated		
	0D	1D	2D	0D	1D	2D
Station 1	33	30.45	28.09	35	32.23	29.86
Station 2	42	38.33	35.34	46	39.16	36.23
Station 3	40	36.25	33.15	42	38.02	34.12
Station 4	36	33.3	31.39	39	35.23	32.67
Station 5	32	29.74	27.92	35	31.12	29.3
Station 6	30	27.46	25.33	33	29.56	27.02
Station 7	27	23.8	21.18	30	25.34	23.36

* Kruskal-Wallis test: p -value = 0.169. There isn't significant difference between observed and estimated Hills numbers values.

Five models of RAD were tested (null, preemption, lognormal, Zipf and Zipf-Mandelbrot models) and according to the AIC criterion, the best adjustment for the Alto del Zuque turned out to be the lognormal and Zipf-Mandelbrot distribution models, as a kind mix model (Table II). This result provides evidence of a similar pattern in the abundance distribution between dominant and rare Papilionoidea species in the study area.

Figure 2. Sample Coverage curve based on R/E analysis.

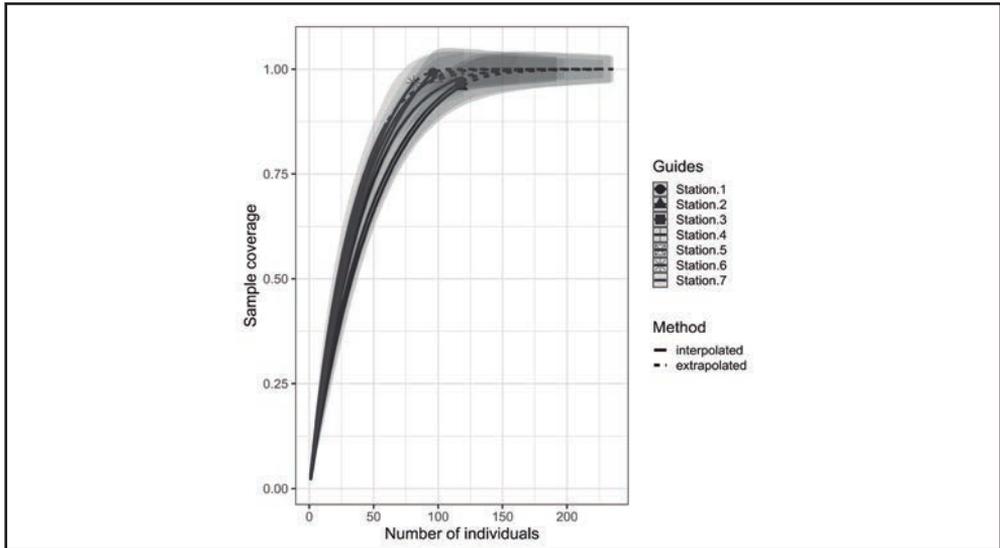
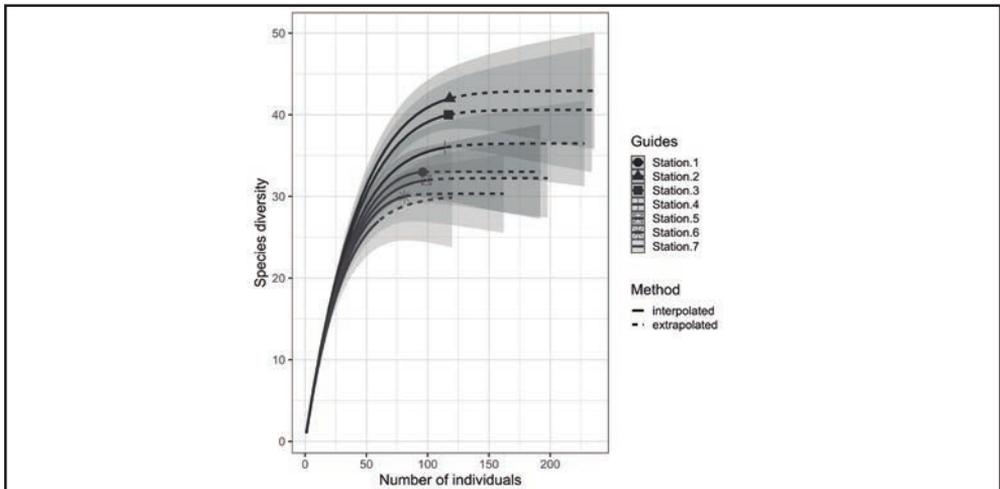


Figure 3. Species diversity curve according to R/E analysis.



The observed and estimated Hill numbers of diversity (0D, 1D, and 2D) were similar, showing no significant differences between them (Table III), so that we can infer to the community is homogeneous among all the stations in the study area. Moreover, the analysis of the sample Coverage-R/E curve (Figure 2) indicates that the sampling effort was appropriate for all the established stations, although it is noteworthy that no curve reached an asymptote, this suggests that a more extensive sampling could potentially increase the

number of species in the study area. However, when comparing the 0D, 1D, and 2D diversity values (Table III) with the species diversity curve based on the R/E analysis (Figure 3), it can be inferred that the sampling effort was adequate. The number of species observed closely matched the number of species expected at each sampling station, supporting the validity of the R/E curve results.

Figure 4. Cluster analysis with the Bray- Curtis index and UPGMA.

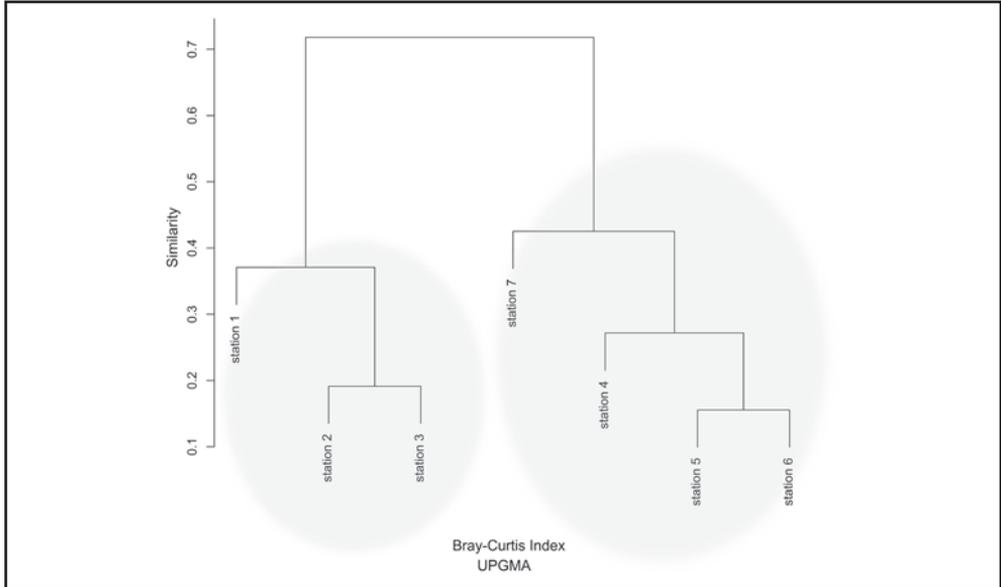
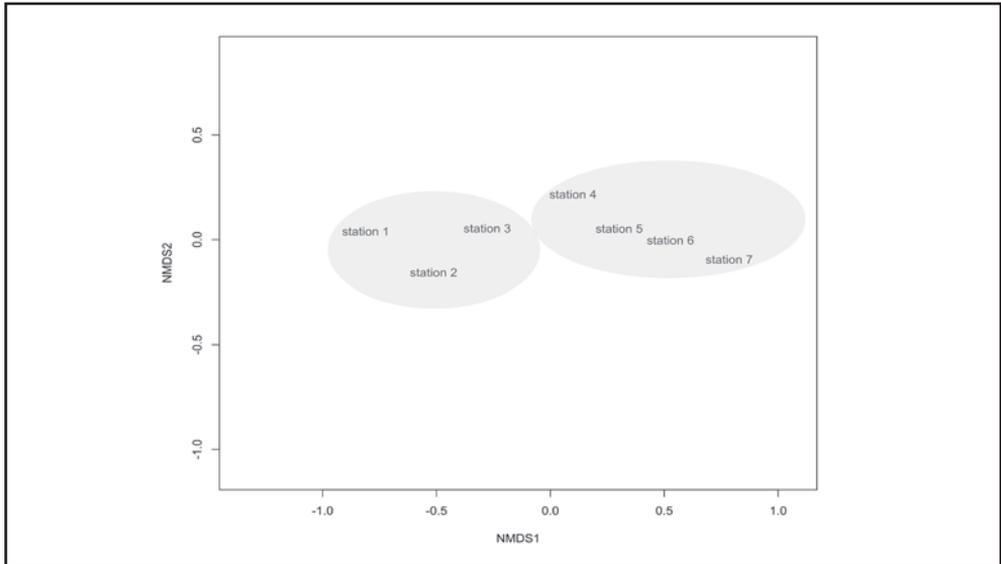


Figure 5. NMDS analysis using the similarity Bray-Curtis index.



On the other hand, based on the similarity analysis, a clear difference in species turnover is uncovered and grouping into two groups, the first group had stations 1, 2, and 3 (72.3% similarity), and the second group

contained stations from 4 to 7 (68.8% similarity). Also, there is a high degree of similarity between station 2 and 3 (84.4% similarity), and between station 5 and 6 (85.8% similarity) (Figure 4). The NDMS ordination analysis results (*Kruskal stress* = 0, *R* = 1) corroborated these results (Figure 5). Therefore, there was a significant difference in the composition of species among sampling units (*ANOSIM test*: *R* = 0.346, *p-value* = 0.001).

We compared the species diversity data (effective number of species) for Papilionoidea reported by Mahecha-Jiménez (2008) (Table IV) and for Pronophilina by Mahecha-Jiménez et al. (2011) (Table V) at the Serranía del Zúque. Our current observations revealed a significant increase in both abundance and species richness. The number of Papilionoidea species increased from 26 to 52, while Pronophilina species rose from 13 to 30, reflecting a substantial enrichment of the butterfly community in the study area. Finally, it is noteworthy that a newly identified species in the genus *Eretris* Thieme, 1905 has been reported. It will be described in an upcoming monograph (Pyrzcz et al. in prep.) (see Table I).

Table IV. Comparison of Hill numbers values (numbers of effective species) observed in Mahecha-Jiménez (2008) and the results from the current study for Papilionoidea at the Serranía del Zúque.

Study	Hill Numbers values		
	0D	1D	2D
Mahecha-Jiménez (2008)	26	24.7	21.2
Mahecha-J. et al. current one	52	50.4	47.3

Table V. Comparison of Hill numbers values (numbers of effective species) observed in Mahecha-Jiménez et al. (2011) and the results from the current study for Pronophilina at the Serranía del Zúque.

Study	Hill Numbers values		
	0D	1D	2D
Mahecha-Jiménez et al. (2011)	13	10.07	9.40
Mahecha-J. et al. current one	30	27.46	25.33

Discussion

A total of 52 species of Papilionoidea were identified, representing a significant increase compared to the 26 species previously reported by Mahecha-Jiménez (2008). Likewise, 30 species of Pronophilina were recorded, exceeding the 13 species reported by Mahecha-Jiménez et al. (2011) for the Serranía del Zúque. An ecological restoration process was implemented in the study area between 2009 and 2010 to facilitate the regeneration of natural habitats (Aguilar-Garavito, 2010, 2015), this restoration process appears to have played a key role in enhancing Papilionoidea diversity in the area. Additionally, the area is undergoing ecological succession from a mix of pasture and forest to a closed forest (Aguilar-Garavito, 2015). This transition is leading to changes in the habitats and the composition of Lepidoptera communities in the area (Waltz & Wallace, 2004; De Souza et al. 2013), because we reported a high increase in the diversity values compared to previous diversity study data reported in the same zone by Mahecha-Jiménez (2008) and Mahecha-Jiménez et al. (2011). Some species related to cloud forests in good conditions previously not recorded in the Serranía del Zúque (Mahecha-Jiménez, 2008; Mahecha-Jiménez et al. 2011) have colonized the area, such as Pronophilina Satyrinae: *Daedalma dinias* Hewitson, 1858, *Manerebia levana* (Godman, 1905), *Lymanopoda lebbaea* C. Felder & R. Felder, [1867] and Lycaenidae: *Salazaria sala* (Hewitson, 1867).

There was an increase in Lycaenidae species in the study area, and we found abundant species in forest edge areas and clearings with varying levels of human disturbance such as *Rhamma comstocki* Johnson, 1992, *Hemiargus hanno bogotana* Draudt, 1921 and *Penaincisalia loxurina* (C. Felder & R. Felder, 1865) (Pulido & Parrales, 2011; Henao-P & Stiles, 2018; Henao-Bañol et al. 2018). However, we reported rare and endemic

species of Papilionoidea at the Serranía del Zuque, for example, Nymphalidae: *Daedalma dinias* Hewitson, 1858, *Lymanopoda samius* Westwood, *Lymanopoda lebbaea* C. Felder & R. Felder, 1867, *Idioneurula erebioides* Felder, 1867, *Manerebia levana* (Godman, 1905), and *Manerebia apiculata* (C. Felder & R. Felder, 1867); Lycaenidae: *Salazaria sala* (Hewitson, 1867) and *R. comstocki* Johnson, 1992; Pieridae: *Catasticta semiramis* (Lucas, 1852) and *Catasticta chrysolopha* (Kollar, 1850); Papilionidae: *Papilio polyxenes* Fabricius, 1775 (Henao-Bañol et al. 2018b). Moreover, *Junea doraete* Hewitson, 1858, is considered a bioindicator of natural forests in a state of good conservation (Duran-Prieto & Molina-Fonseca, 2020).

On the other hand, species such as *Pedaliodes polla* Thieme, *Viloriodes manis* (C. Felder & R. Felder), *Pedaliodes ochrotaenia* (C. Felder & R. Felder), *Pedaliodes phoenissa* (Hewitson, 1862), *Corades chelonis* Hewitson, 1863, *Lasiophila circe* C. Felder & R. Felder, 1859, *Pedaliodes empusa* C. Felder & R. Felder, 1867, and *L. samius* Westwood are often associated with Andean secondary forests. These species may be considered potential generalists capable of colonizing early stages of ecological succession in montane habitats (Díaz-Suárez et al., 2022). Henao-Bañol et al. (2018) also found that several Pronophilina species are associated with forest edges and clearings with varying degrees of human disturbance, and tend to be more abundant in moderately disturbed areas.

Furthermore, the genus *Chusquea* serves primarily as a host plant for several Pronophilina species in the Neotropical region (Pyrz, 2004a, 2004b; Pyrcz & Viloría, 2005; Greeney et al., 2009; Pyrcz et al., 2009; Montero & Ortiz, 2013; Mahecha et al., 2019; Díaz-Suárez et al., 2022). Most *Chusquea* species readily colonize disturbed sites (Judziewicz et al., 1999; Fisher et al., 2014), exerting long-term influence on the structure and diversity of dynamic plant communities and contributing to habitat resilience (Beckage et al., 2000; Holz & Veblen, 2006; Raffaele et al., 2007; Giordano et al., 2009; Muñoz & González, 2009; Muñoz et al., 2012). As pioneer species in forest succession, *Chusquea* plays an ecologically important role in facilitating tree cover regeneration (González et al., 2002; Pacheco, 2013). This ecological context may help explain the observed increase in Pronophilina species in the study area.

Three lines of evidence support the recovery of Papilionoidea diversity in the Serranía del Zuque: (1) an increase in the total number of species; (2) the recolonization by forest specialist species typically found in undisturbed habitats; and (3) a shift in the proportion of synanthropic species within the sample. For instance, species such as *Viloriodes manis* (C. Felder & R. Felder), *Pedaliodes polla* Thieme, *Panyapedaliodes drymaea* Forster, and *Colias dimera* Doubleday & Hewitson, 1847, exhibited lower abundances compared to previous studies.

The RAD analysis for the study area fits a log-normal and Zipf-Mandelbrot distribution model, which indicates that a natural community is extensive, varied and mature (Magurran, 1988), and complies with most of the ecological requirements of a community (May, 1975). It is important to highlight that this result reveals a similar pattern in the abundance distribution between dominant and rare Papilionoidea species in the study area. This pattern may suggest a community structure characterized by hierarchical niche subdivision, in which a small fraction of species exploits a large portion of the available resources. In turn, under as proposed by Hill & Hamer (1998) and Marín et al. (2014) communities that compose log-normal series of distribution models present some level of disturbance (Mouillot & Lepretre, 2000; Matthews & Whittaker, 2015; Nallis, 2021; Cerdeña et al. 2024). According to Wilson (1991), species presence is influenced by initial physical conditions and the presence of other species, which represent ecological ‘costs.’ In this framework, pioneer species require minimal preconditions and thus incur low costs, whereas late-successional species face higher costs—such as greater energy expenditure, longer establishment times, and dependence on ecosystem organization—before they can successfully colonize an area. These temporal and ecological differences among species can result in a Zipf-Mandelbrot distribution pattern. Whereas a log-normal model may result from many factors acting simultaneously, a Zipf-Mandelbrot model is indicative of many factors acting sequentially (Wilson, 1991; Marimon et al. 2015; Nallis, 2021; Cerdeña et al. 2024).

The RAD described by Mahecha-Jiménez (2008) in the same region followed a log-normal distribution, suggesting that the butterfly community at that time was subject to substantial environmental disturbance, causing a rise up in the heterogeneous environment that benefits several times the most dominant species, which causes an increase in the dominance of some species about others, observing a low diversity in the community (Matthews & Whittaker, 2015). We have to point out, however, that these models have been widely debated (Mouillot & Lepretre, 2000; Williamson & Gaston, 2005; Ferreira & Petre, 2008; Matthews & Whittake, 2015; Nallis, 2021; Cerdeña et al. 2024).

As the study area undergoes ecological succession, the formation of diverse ecotones may facilitate

increased species richness and expanded distribution patterns (Uehara-Prado et al. 2005; Weyland & Zaccagnini, 2008; Uehara-Prado & Freitas, 2009; Urbano et al. 2014). Similar diversity estimates across the stations in the Serranía del Zaque may, at least partially, be attributed to the Intermediate Disturbance Hypothesis, which posits that species richness is highest at intermediate levels of disturbance (Townsend et al. 1997; Kershaw & Mallik, 2013), or by the mass ratio hypothesis, which proposes that the biological traits of the dominant species are the critical drivers of ecosystem function and that these species increase in biomass rapidly after disturbance then stabilize. Consequently, species diversity first peaks then declines after a disturbance as a few species dominate the site. Both hypotheses provide a conceptual link among disturbance, species diversity, and productivity (Kershaw & Mallik, 2013). The highest level of species richness often occurs at moderate altitudes due to species turnover between lowland and highland areas. This intermediate zone tends to have greater diversity, a phenomenon known as the mid-domain effect. This may explain why stations 2 and 3 exhibited higher diversity values compared to the other stations and were more similar to each other (Colwell & Lees, 2000; Sanders, 2002; Colwell et al. 2004; Guerrero & Sarmiento, 2010; Giraldo-Cañas, 2021).

Some studies of Papilionoidea in other Colombian Andean forests have reported higher overall species richness, particularly within the subtribe Pronophilina, which was the most representative taxon in our sample. For example, Pycrz & Wojtusik (1999) reported 44 species for Pronophilina in the Tambito Reserve in the Western Cordillera of Colombia, whereas Prieto (2003) reported richness of 40 species in the nearby Cerro Munchique. Pycrz & Rodríguez (2007) found 85 species in the Páramo de Tatamá, Farallones de Citará Cerro Frontino massifs in the Western Cordillera. Pycrz & Vioria (2007) found 54 species of Pronophilina in the Serranía del Tamá, on the Colombian-Venezuelan border. Montero & Ortiz (2013) reported 60 species of Papilionoidea (Papilionoidea + Hesperioidea), including 32 species of Pronophilina, for El Tablazo Andean forest in the Subachoque-Cundinamarca in East Cordillera. Marín et al. (2014) found 75 species of Papilionoidea (Papilionoidea + Hesperioidea), including 38 species of Pronophilina, at the Romeral peri-urban forest of the Central Cordillera in Medellín, southwest of the Aburrá Valley. Olarte-Quiñonez et al. (2016) reported 69 Papilionoidea in the East Cordillera on the Norte de Santander and Santander border. Pycrz et al. (2016) identified 48 species of Pronophilina on the Páramo de Belmira on the Central Cordillera. Clavijo-Giraldo et al. (2020) found 69 species of Papilionoidea (Papilionoidea + Hesperioidea) but they did not find any representative of Papilionidae. Clavijo-Giraldo et al. (2024) reported 108 Papilionoidea species in high-montane ecosystems of the Central Cordillera in Antioquia.

However, some studies have reported a lower richness compared to our research in other Colombian Andean forests, for example, Pérez et al. (2017) reported 31 Papilionoidea species (12 Pronophilina species) for Andean forest at the Santa Rosa de Viterbo in Boyacá-Colombia. Henao-B & Stilles (2018) reported 55 species of Papilionoidea (Papilionoidea + Hesperioidea) in Tabio in East Cordillera on Cundinamarca, where 13 species were Pronophilina. Murillo-P. et al. (2018) identified only eight species of Papilionoidea in Neuta, San Isidro, and Tierra Blanca wetlands in Soacha municipality in East Cordillera. Duran-Prieto & Molina-Fonseca (2020) reported 45 Papilionoidea species, including 18 Pronophilina species, in the Bogotá region of the East Cordillera in Cundinamarca. Olarte-Quiñonez et al. (2021) found 25 Pronophilina species in Cerro de Tierra Negra in the East Cordillera on the Norte de Santander and Santander border. Díaz-Suárez et al. (2022) reported 23 species of Pronophilina in the Frailejón Andean forest in the East Cordillera in Cundinamarca. Nonetheless, the results obtained in these studies cannot be immediately compared due to different sampling methodologies applied, sampling time effort, and the area size.

The relatively low species diversity in the study area is likely a consequence of the long-term habitat degradation resulting from past mining operations (Aguilar-Garavito, 2010). This disturbance led to the formation of forest patches that hindered gene flow between subpopulations, resulting in a reduction in the diversity of various animal and plant taxa (Murillo-P. et al. 2018). Although nearly eight years have passed since the beginning of the ecological restoration process and twelve years since the cessation of mining activities (see Aguilar-Garavito, 2010; 2015), complete recovery of the habitat in the study area has not been observed. However, vegetal coverage has been gradually regenerating. For instance, the cover by the species of Poaceae and Melastomataceae has been increasing (Aguilar-Garavito, 2015). This has allowed for the growth of different plants that serve as hosts for many Papilionoidea species, leading to a gradual recovery of the diversity of Papilionoidea, particularly Pronophilina, in the Serranía del Zaque after the mining activity. Finally, these findings reinforce the need for ongoing ecological restoration initiatives aimed at preserving native montane ecosystems in peri-urban regions of Colombia.

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Conflict of Interest

The authors declare that there is no known financial interest or personal relationship that could have influence the work presented in this article.

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Table I. List of species of Papilionoidea butterflies found at the Serrania del Zuque with their respective abundances for each study station and the abundance total at the study area.

Family/ Subfamily	Species/Subspecies	Station	Abundance Total						
		1	2	3	4	5	6	7	
Nymphalidae/ Satyrinae	<i>Corades chelonis</i> Hewitson, 1863*□	2	4	3	4	3	2	2	20
	<i>Corades chirone</i> Hewitson, 1863	0	0	0	2	2	3	1	8
	<i>Corades cybele</i> Butler, 1866	0	2	2	3	2	2	1	18
	<i>Corades dymantis</i> Thieme, 1907*□	4	3	3	2	2	1	0	15
	<i>Corades medeba columbina</i> Hewitson, 1850	1	2	2	3	2	1	1	12
	<i>Daedalma dinias</i> Hewitson, 1858	0	0	0	3	3	2	2	10
	<i>Daedalma drusilla</i> Hewitson, 1858	0	0	0	0	0	3	4	7
	<i>Eretris apuleja bogotana</i> E. Krüger, 1924*□	4	3	1	0	0	0	0	8
	<i>Eretris</i> n. sp.	0	0	3	4	3	2	2	14
	<i>Forsterinaria difficilis</i> (Forster, 1964)	2	3	2	3	1	0	0	11
	<i>Idioneurula erebioides</i> Felder, 1867*□	2	2	3	4	3	4	3	21
	<i>Junea doraete</i> (Hewitson 1858)	0	0	0	0	3	2	2	7
	<i>Lasiophila circe</i> C. Felder & R. Felder, 1859*□	0	3	3	4	3	2	1	16
	<i>Lymanopoda ionius</i> Westwood, 1851*□	0	3	3	2	3	2	2	15
	<i>Lymanopoda lebbaea</i> C. Felder & R. Felder, 1867	0	1	2	2	3	1	1	10
	<i>Lymanopoda obsoleta</i> Westwood, 1851	2	3	3	4	3	2	1	18
	<i>Lymanopoda samius</i> Westwood, 1851*□	4	3	4	5	4	3	2	25
	<i>Manerebia apiculata</i> (C. Felder & R. Felder, 1867)	0	2	3	2	3	2	1	13
	<i>Manerebia levana</i> (Godman, 1905)	0	0	0	2	3	3	4	12
	<i>Panyapedaliodes drymaea</i> Forster, 1964*□	0	3	4	4	4	3	2	20
	<i>Pedaliodes polla</i> Thieme, 1905* □	6	7	6	5	5	4	3	36
	<i>Pedaliodes empusa</i> C. Felder & R. Felder, 1867	2	3	5	4	2	2	0	18
	<i>Pedaliodes cocytia</i> (C. Felder & R. Felder, 1867) *□	0	1	2	4	6	6	6	25
	<i>Pedaliodes ochrotaenia</i> (C. Felder & R. Felder, 1867) *□	6	5	7	6	5	5	3	37
	<i>Pedaliodes phoenissa</i> (Hewitson, 1862)	3	5	5	4	4	3	2	26
	<i>Pedaliodes polusca</i> (Hewitson, 1862)	0	3	3	3	2	2	0	13

	<i>Pronophila unifasciata bogotensis</i> Lathy, 1906	2	3	0	0	0	0	5
	<i>Steremnia pronophilia</i> (C. Felder & R. Felder, 1867) *□	0	0	3	3	5	4	18
	<i>Steroma bega andensis</i> Westwood, [1851]	0	0	4	4	3	3	16
	<i>Viloriodes manis</i> (C. Felder & R. Felder, 1867) *□	0	4	5	4	5	4	25
Nymphalidae/ Nymphalinae	<i>Hypanartia kefersteini</i> (E. Doubleday, [1847])	2	3	2	2	1	0	10
	<i>Vanessa virginienensis</i> (Drury, 1773) *	2	4	2	3	2	2	17
Nymphalidae/ Heliconinae	<i>Altinote tinacria</i> (C. Felder & R. Felder, 1862) *	5	4	4	3	2	0	18
	<i>Dione glycera</i> (C. Felder & R. Felder, 1861) *	3	4	3	4	3	2	20
Pieridae/ Pierinae	<i>Catasticta chrysolopha</i> (Kollar, 1850) *	3	2	2	0	0	0	7
	<i>Catasticta semiramis</i> (Lucas, 1852) *	3	4	2	2	0	0	11
	<i>Phulia xanthodice</i> (Lucas, 1852) *	3	3	2	1	0	0	9
	<i>Leodonta zenobia</i> (C. Felder & R. Felder, 1865)	2	2	3	1	0	0	8
	<i>Leptophobia eleone</i> (E. Doubleday, 1847) *	4	2	2	2	0	0	10
Pieridae/ Coliadinae	<i>Colias dimera</i> Doubleday, 1847 *	5	4	4	5	4	4	29
Lycanidae/ Theclinae	<i>Atlides havila</i> (Hewitson, 1865)	2	2	2	0	0	0	6
	<i>Cyanophrys pseudolongula</i> (Clench, 1944)	2	1	1	0	0	0	4
	<i>Cyanophrys agricolor</i> (Butler & H. Druce, 1872)	2	1	0	0	0	0	3
	<i>Lamprospilus</i> sp. Geyer, 1832	2	0	0	0	0	0	2
	<i>Micandra aegides</i> (C. Felder & R. Felder, 1865)	3	2	1	0	0	0	6
	<i>Marachina maraches</i> (H. Druce, 1912)	3	1	0	0	0	0	4
	<i>Penaincisalia loxurina</i> (C. Felder & R. Felder, 1865) *	4	3	3	0	0	0	10
	<i>Rhamma commodus</i> (C. Felder & R. Felder, 1865)	3	2	1	1	0	0	7
	<i>Rhamma comstocki</i> Johnson, 1992 *	2	3	1	0	0	0	6
	<i>Salazaria sala</i> (Hewitson, 1867)	2	2	0	0	0	0	4
Lycanidae/ Polyommatae	<i>Hemiargus hanno bogotana</i> Draudt, 1921*	3	2	0	0	0	0	5
Papilionidae/ Papilioninae	<i>Papilio polyxenes</i> Fabricius, 1775 *	0	2	2	0	0	0	4

* Mahecha-Jiménez (2008) also reported these species of Papilionoidea butterflies.

□ Mahecha-Jiménez et al. (2011) also documented these species of Pronophilina butterflies.