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From primary forest to pasture: Diversity and distribution of fruit-feeding butterflies of the Western Andes, Colombia

Margarita Rosa López Garcia
Master of Science in Ecology

Acknowledgement

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Abstract

Tropical forests are under immense pressure from agricultural expansion and other human disturbances, and the deforestation leads to forest fragmentation and accelerated biodiversity loss. The tropical Andes of Colombia, a global biodiversity hotspot, is an area that has undergone severe land-use change and where the remaining primary forest is highly fragmented. Previous studies show that this land-use change and fragmentation of primary forest have severely affects a variety of different taxonomic groups. Yet, apart from for dung beetles, no study to date has assessed the impacts of land-use change on insects in the Colombian Andes. Fruit-feeding butterflies are good candidates to study effects of land-use change because they are easy to capture, and they are relatively well known taxonomically and ecologically. Butterflies are also an indicator taxon, used to measure ecosystem health. Here I examine the patterns of fruit-feeding butterfly assemblage structure and composition along an altitudinal gradient (1319-2683 masl) in primary forest, secondary forest and pasture in the western Andes of Colombia. Fruit-feeding butterflies were sampled using baited butterfly traps in 400 x 400m squares distributed across the three habitats. Each square contained 10 traps and a total of 30 squares were sampled. I found that pasture contained the highest species richness and abundance, largely dominated by Satyrinae butterflies. However, primary and secondary forests were more diverse and had a similar species composition. Pasture assemblages were significantly different to those of primary and secondary forest. Altitude significantly affected butterfly abundance, but not richness, across the habitats. In addition, several species had a very narrow altitudinal range at the very lowest elevations, perhaps suggesting that these species belong to the lowlands and are at their altitudinal limits. The results show that butterfly assemblages are severely affected by land-use change. However, the fact that secondary forests contain a similar species composition to that of primary forest suggests that secondary forest retain significant biodiversity and plays a vital role in supporting biodiversity in regions where most of the primary forest has been lost. It also suggests that secondary forests are recovering towards a primary forest state. I therefore conclude that primary forests should be a conservation priority in the region, but investing in secondary forest recovery by reforesting marginally profitable cattle pastures may be a good way to aid the protection of the highly endangered biota across the Andes.

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1. Introduction

In the last century, the world has experienced an accelerated global biodiversity loss and an increase in the world's human population is the major cause of decline. Human interventions in ecosystems, such as agricultural and infrastructural expansion and wood extraction have led to an increasing loss of natural habitats, particularly in the tropics (Food & Nations 2010; Geist & Lambin 2002; Nyafwono et al. 2014). Consequently, natural habitats have also become highly fragmented, affecting the occurrence of ecosystems and species (Barlow et al. 2007a; Tscharntke & Brandl 2004). Yet, biodiversity provides ecological services highly beneficial to humans (Gómez-Baggethun et al. 2010; Singh 2002), suggesting that biodiversity conservation is essential for human survival, economic well-being, ecosystem functions, structure and stability (Norgaard 2010).

In the Neotropics, where most of the world's species diversity is concentrated, forest fragmentation caused by deforestation is a major driver of biodiversity loss (Etter et al. 2006; Gibbs et al. 2010; Sala et al. 2000; Turner 1996). The tropical Andes of Colombia, for example, is one of the most biodiverse regions in the world and has a high degree of endemism due to geographical variability a large altitudinal range, complex topography and the contrasting soil mosaics caused by a geologic heterogeneity ((Etter & van Wyngaarden 2000; Kattan et al. 1996). However, this region is also a hotspot of extinction risk as a result of intensive land-use change, mainly extensive agricultural crops and cattle (Basham et al. 2016; Kattan et al. 1996; Myers et al. 2000). Indeed, previous studies in the western Andes show that land-use change and fragmentation of primary forests severely affect a variety of different taxonomic groups, such as dung beetles, birds and amphibians (Gilroy et al. 2014a; Gilroy et al. 2014b). However, as well as advocating the critical importance of protecting the remaining contiguous primary forest in this region, the authors found that secondary forests on abandoned cattle pastures support a high number of primary forest species. Secondary forests may therefore represent an important asset in the conservation of rare and endangered species, and protecting distinct evolutionary lineages (Basham et al. 2016; Edwards et al. 2017; Gilroy et al. 2014a; Gilroy et al. 2014b).

Yet, apart from for dung beetles, no study to date has assessed the impacts of land-use change on insects in the Colombian Andes. Insects are one of the groups of organisms most affected by forest fragmentation in the Neotropics. Approximately 40.000 insect species are estimated to have gone extinct over the past 600 years, although only 70 have been documented, half of which were Lepidoptera (Bonebrake et al. 2010). Of all insects, butterflies are probably the best known taxonomically and ecologically (Bonebrake et al. 2010; Schulze et al. 2004). The study of butterfly biology has a long history and has contributed greatly to understanding the ecology, evolution, biogeography and conservation of several ecosystems and habitats(Bonebrake et al.

2010; Devries 2001; Devries et al. 2009; Schulze et al. 2004). For example, it is now well known that butterflies are very sensitive to changes in habitat, vegetation structure and composition, as well as climate change. Therefore, they are important candidates for monitoring impacts generated by processes such as habitat degradation and land-use change (Bonebrake et al. 2010; Molleman et al. 2006). Yet, despite the rampant deforestation and degradation of Neotropical forests, relatively few studies have assessed the effects of disturbance on butterfly communities and compared species richness and community composition to intact primary forest (Barlow et al. 2007b). Investigating this group in little-known tropical habitats due to their rapid destruction is therefore urgent.

To redress the shortfalls above, I here explore the patterns of fruit-feeding butterfly assemblage structure and composition along an altitudinal gradient in primary forest, secondary forest and pasture in the western Andes of Colombia. Butterflies were collected using standard baited fruit traps from two locations: Montezuma and La Mesenia. I compare butterfly richness, abundance and composition patterns between habitats and discuss my results in light of previous research in the region and elsewhere. This will help us understand the state of the remaining forests.

2. Materials and methods

2.1 Study area

The current work was carried out in the National Natural Park of Tatamá (Montezuma), in the department of Risaralda (Fig. 1) and at La Mesenia-Paramillo Natural Reserve in the department of Antioquia (Fig. 2), western Andes, Colombia. Butterfly sampling was carried out during January and February 2015 at La Mesenia and February to March 2015 at Montezuma. This coincides with the dry season in the region.

Montezuma (5°03′46″N 76°10′30″E) is characterized by topography with very steeply slopes, generally between 50-70% deep valleys and sharp edges. This topography, combined with weather conditions, has created a great variety of environments, with an average annual rainfall of over 3000 mm and temperatures that fluctuate between 4 and 22° C (Ballesteros et al. 2005). The park begins at 2000 meters above sea level (masl) and covers 51.900ha. However, natural forests start being common from 500masl. Tatamá is the highest point of the Western Andes in Colombia and reaches 4250m (Ballesteros et al. 2005). This protected area is of great scientific interest since it contains a a large tract of intact Andean cloud forest with much endemic vegetation and fauna. In fact, over 90% of the National Natural Park of Tatamá area is covered by Andean natural forest (Ballesteros et al. 2005) (Etter et al. 2006).

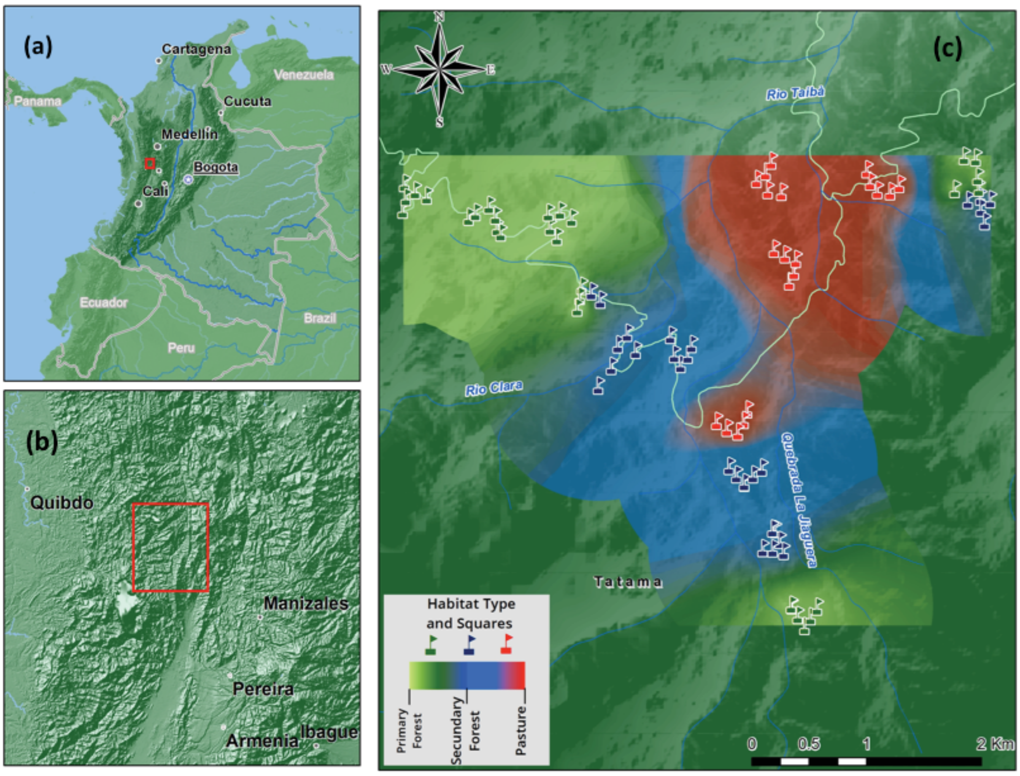

Figure 1. The location of Montezuma in the western Andes of Colombia (a, b) and of the individual sampling points (flags) overlaid different land-uses in the region (c).

At La Mesenia (5°30′11″N, 75°51′7″ E), there is an undisturbed and slightly disturbed cloud forest surrounded by cattle pastures (Cuartas-Hernández & Gómez-Murillo 2015). The Hummingbird Conservancy administrates the reserve and is in charge of its conservation. La Mesenia covers an area of 1723 ha and comprises an elevation gradient from 2150 to 3100 masl. This area is typified by a topography of steep slopes, while mean annual temperature ranges from 13 and 23°C. The mean monthly rainfall as reported by Cuartas-Hernández and Gómez-Murillo (2015) is 161 mm, varying between 61 and 225 mm.

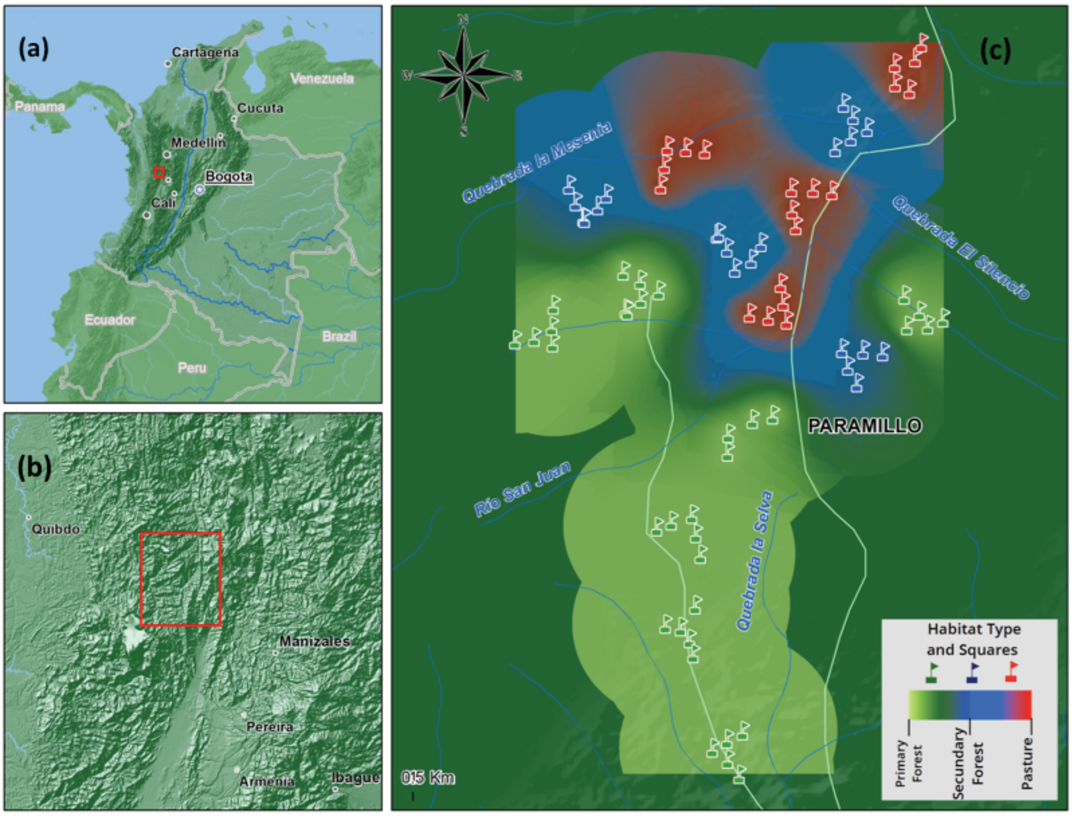

Figure 2. The location of La Mesenia in the western Andes of Colombia (a, b), and of the individual sampling points (flags) overlaid different land-uses in the region (c).

Both Montezuma and La Mesenia are located at an interface between farmland and large contiguous tracts of forest that is dominated by primary forests and some patches of secondary forest (age range 6–30 years, determined from interviews with reserve managers and local residents;(Gilroy et al. 2014a; Gilroy et al. 2014b). The sites were selected to cover the frontier between agricultural developments and remaining contiguous forests (Gilroy et al. 2014a). The main agricultural practice at these two sites is cattle farming, accounting for more than 90% of farmed lands. Other land-uses included small areas of maize, orchards of Tamarillo or Tomate de Arbol (*Solanum betaceum*) and ecotourism (mainly bird-watching). For this study I sampled primary forest, secondary forests and pasture at each site (Fig. 3). All sampled secondary forests had some degree of connectivity to primary forest and pasture (Gilroy et al. 2014a).

Figure 3. (a) Primary forest, (b) secondary forest and (c) pastures sampled in this study. Photos: M. Lopez.

2.2. Butterfly sampling

The current study focuses on fruit-feeding nymphalid butterflies. This guild is generally represented by species in the subfamilies Biblidinae, Charaxinae, Nymphalinae and Satyrinae. Butterfly trapping was conducted at points arrayed within 400 x 400m squares in primary forest, secondary forest and pasture, following Gilroy et al. (2014a). At Montezuma, there were 6 squares located in primary forest, 5 squares in secondary forest and 4 squares in pasture, while at La Mesenia there were 7 squares in primary forest, 4 squares in secondary forest and 4 in pasture. In total, 30 squares were sampled across the two study areas; 13 in primary forest, 9 in secondary (aged 4-8 years old) and 8 pasture. Every square included five sampling points, separated by 100m to allow community independence. Each sampling point consisted of 2 traps erected 10m apart. Thus, each square consisted of 10 traps and the total effort across the two study areas was 150 sampling points (= 300 traps). Traps were hung from existing vegetation in the understory (approx. 1m above ground) in primary and secondary forest. Due to a lack of trees in pasture, traps were hung from bamboo poles around 1m above ground.

Fruit-feeding butterflies were captured using Van Someren baited traps. These are cylindrical traps measuring 1,10m in height and 35 cm in diameter and are commonly used to survey butterflies in the tropics (DeVRIES et al. 1997; Devries & Walla 2001; Devries et al. 2009; DeVries et al. 2012); Fig 4). A plastic plate were placed around 3cm below the cylindrical net and used for bait. Traps were baited with mashed and fermented banana. I sampled 3 squares (30 traps) simultaneously, normally one in primary forest, secondary forest and pasture. Traps were run for 4 days, checked every day, and new bait was added to any remaining bait (from day 1) in the trap on day 3. If sampling was interrupted by persistent rain, I rebaited the trap and added extra day(s) to the trapping in the given squares depending on the number of days lost to rainfall.

Figure 4. (a) Figure 4. (a) Van Someren traps used to trap butterflies, (b) the fermented banana bait and (c) the triangular glassine envelopes used to conserve butterflies in the field. Photos: M. Lopez.

All individuals captured in the traps were collected and stored in triangular glassine envelopes. These were kept in a hermetically sealed plastic box with silica gel to avoid humidity and decomposition of the specimens, until they could be transported to the biological collections of the Alexander von Humboldt Institute at Vila de Leyva to be identified. Specimens from the first sampling location (La Mesenia) were frozen in sterilize conditions until the second sampling site (Montezuma) was finished and all specimens were ready for identification (Fig. 4). The Humboldt reference collection and on-site expert entomologists aided identification, and all butterflies were identified to species, except six specimens from the *Pedaliodes* genus, which were not in the best condition to be morphologically identified. At least one specimen of each species was mounted and included in the collections (Fig. 5). Identifications herein follow the classification and nomenclature of Lamas et al. (1999) and Lamas (2004).

Figure 5. Fruit-feeding butterflies pinned and mounted after being identify at the Von Humboldt institute station in Villa de Leyva, Colombia. Photo taken by the author.

2.3. Data Analysis

I followed Devries and Walla (2001) and define rare species as those species with four or fewer individuals captured. Shannon (H') and Simpson (1-D) indices were used as biodiversity measures and are some of the most commonly used measures of species diversity and species richness (Lande 1996). Shannon (H') is good as a diversity measure, because this method is independent of sample size (Jost 2006). These indices were calculated using the statistical software EstimateS version 9 (Colwell 2013).

To evaluate sampling efficiency, I created a sample-based species accumulation curve for the study as a whole (all habitats across both study areas combined) using the vegan package (Jari 2016) in RStudio version 3.3.1 (R development Core Team 2016). Individual-based accumulation curves for each habitat type (primary forest, secondary forest and pasture) were created using the statistical software PAST version 3.14 (Hammer et al. 2001). To assess if there were significant differences in species richness between habitats and site, an analysis of variance (ANOVA) was done using Mixlm package (Liland 2016) and a Tukey's post-hoc test using the Agricolae package (Mendiburu 2016) RStudio version 3.3.1. The number of species recorded in each habitat or site was considered species richness, while the number of individuals recorded was considered abundance.

An initial test of normality indicated that species abundance data needed transformation. Box-Cox transformations were used to find the best fit and fourth root $y=\sqrt[4]{x}$ was subsequently used on the data. This transformation allowed to accomplish with homogeneity of variance assumptions and normality as the abundance varied across sites (Li 2005). In order to test for the variation in abundance across sites, species and habitat, I used an ANOVA using general linear model (GLM) analysis with nested effect using SAS software version 9.4 (SAS Institute Inc. 2012) establishing species abundance as a dependent variable. The statistical model of the structure of the data for abundance is presented in the formula:

$Y = \alpha_i S_i + \mu_j H_j + \sigma_k SP_k + \varepsilon_{\iota}$ (1) Where:
Y_{ijk} = Abundance (number of individuals) collected by species in each of the five points per square in the i sites, j habitats and k species
$\alpha_i S_i$ = Is the linear function of the independent coefficients of site, $_{i = 1 \text{ to } 2}$
$\mu_j H_j$ = Is the linear function of the independent coefficients of habitat, $_{j = 1 \text{ to } 3}$
$\sigma_k SP_k$ = Is the linear function of the independent coefficients of species, $_{k=1 \text{ to } 66}$
ε_{ι} = error

Butterfly assemblage structure and composition across study areas and habitats were visualized using a non-metric multi-dimensional scaling (NMDS) with a Bray-Curtis similarity index. Composition data were processed using the vegan package (Jari 2016) in RStudio version 3.3.1. For this analysis, it was necessary to code each species name (Appendix. 3). To test for significant differences in assemblage composition across habitats, I used an analysis of similarities (ANOSIM) with Bray-Curtis similarity index. A similarity percentages (SIMPER) procedure was used to determine which species contributed the most to differences between different habitats. These analyses were done using PAST version 3.14 (Hammer et al. 2001).

A linear regression was applied to test for the effect of altitude on species richness and abundance. The altitude used in the analysis was the average altitude of each sampling square. To run the regression the data was Log n+1 transformed. This produces more homogeneous data, especially when there are many low values close to zero (Keene 1995). Moreover, to test for significant differences in the overall species richness and abundance along the altitudinal gradient, and its interaction with all habitat and sites, a General Linear Model (GLM) was implemented using the *MASS* package (Ripley 2002) in RStudio version 3.3.1. For richness, I used the *"glm"* function and the *"poisson"* model. For abundance, the *"poisson"* model was used in the "*glm.nb*" function. Both for species richness and abundance, I selected the model with the lowest Akaike's information criterion (AIC) value (Crawley 2012). Finally, I calculated the altitudinal range for all species at Montezuma and La Mesenia, using the minimum and maximum altitude registered for each species at each sampled square. All the specimens were captured within a range of altitude between 1319 and 2683(masl), Montezuma (1319-1703 masl) and La Mesenia (2055-2583 masl; Appendix 1).

3. Results

3.1 The La Mesenia and Montezuma fruit-feeding nymphalid community

In total, 1065 individuals and a minimum of 65 species in the subfamilies Satyrinae (33), Charaxinae (11), Morphinae (7), Nymphalinae (6), Biblidinae (4), Limenitidinae (3), and Riodininae (1) were captured during this study (Appendix 1). Of these, 968 individuals (90.9%) were captured at Montezuma and 97 individuals (9.1%) at La Mesenia (Appendix 1). At Montezuma, 7 subfamilies were registered, while 5 were registered at La Mesenia. The most abundant subfamily at Montezuma (902 individuals) and La Mesenia (88 individuals) was Satyrinae.

3.2 Species richness and abundance

I registered a similar number of species in primary forest (36 species), secondary forest (36 species) and pasture (32 species; Table 1). However, the sample-based species rarefaction curve showed that the curve is still not reaching an asymptote after 30 squares sampled at Montezuma and La Mesenia (Fig 6). The individual-based rarefaction curves show that sampling in primary forest and secondary forest are far from complete, whereas the sampling in pasture captured more of the expected species richness (Fig 7). Further, the Shannon H' and Simpson 1-D estimations indicate a higher level of diversity and expected total species richness in primary and secondary forest than in pasture (Table 1). Yet, the highest butterfly abundance was recorded in pasture (805 individuals), followed by primary (133 individuals) and secondary (127 individuals) forest (Appendix 1, Table 1).

Most species caught were rare (Appendix 1). Overall, species with 4 or fewer captures accounted for 61.5% of the total species (n = 40), but only 7.5% of the captured individuals (n = 80; Table 1). In primary forest at Montezuma, rare species accounted for 34.6% of species (n = 9) and 25.3% of the individuals (n = 20), in secondary forest 32.1% of species (n = 9) and 13% of the individuals (n = 14), and in pasture 40% of species (n = 12) and 2.05% of the individuals (n = 16). At La Mesenia, rare species in primary forest represented 28.6% of species (n= 4) and 42.6% of individuals (n=23), secondary forest 45.5% of species (n=5) and 31,6% of individuals (n=6), and for pasture 45.5% of species (n=10) and 4.2% of individuals (n=1; Table 1).

The highest number of species unique to a single habitat was found in pasture at Montezuma, followed by primary forest at both sites. Species turnover between the three habitat types was high; 17 species were only found in primary forest, 10 in secondary forest and 12 in pasture (Table 1, Appendix 2). In total, the highest number of unique species was registered at Montezuma (Table 1).

Table 1. Species richness, diversity and abundance in primary forest, secondary forest and pasture at Montezuma and La Mesenia, western Andean cordillera, Colombia. PF = primary forest, SF = secondary forest, P = pasture, Total = all habitats of each site combined. Unique species are those present only in one habitat (PF, SF, P) at a particular site or unique to a particular site (Sub-total). Rare species are those represented by ≤ 4 individuals. Values in brackets are the percentages of the total number of species.

	Montezuma				**La Mesenia**				
	PF	**SF**	**P**	**Sub-total**	**PF**	**SF**	**P**	**Sub-total**	**Total**
No. of species	26	28	30	51	14	11	4	22	65
No. of unique species	9 (34.6)	6 (21.4)	11 (36.7)	26 (51)	9 (64.3)	5 (45.5)	2 (50)	16 (72.7)	42 (64.6)
No. of rare species	9 (34.6)	9 (32.1)	12 (40)	30 (58.8)	4 (28.6)	5 (45.5)	1 (25)	10 (45.5)	40 (61.5)
Individuals	79	108	781	968	54	19	24	97	1065
Shannon H'	2.9	2.9	0.9	1.7	2.1	2.3	0.9	2.6	2.0
Simpson 1-D	0.9	0.9	0.3	0.5	0.8	0.9	0.3	0.9	0.6

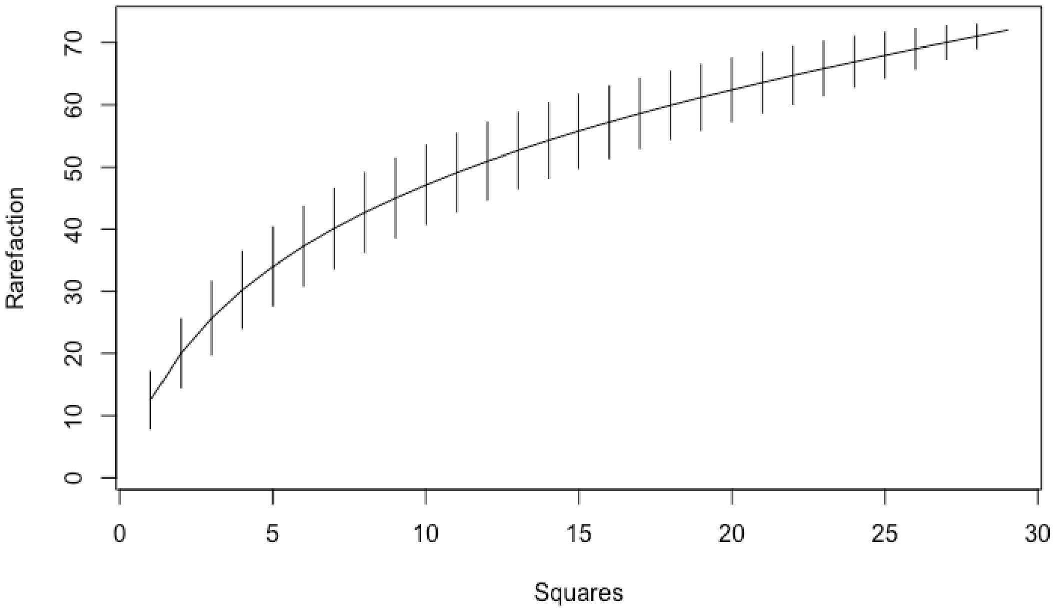

Figure 6. Sample-base species rarefaction curve of the fruit feeding butterflies community for primary forest, secondary forest and pasture at La Mesenia and Montezuma combined. The bars indicate the 95% confidence interval (CI) based on standard deviation.

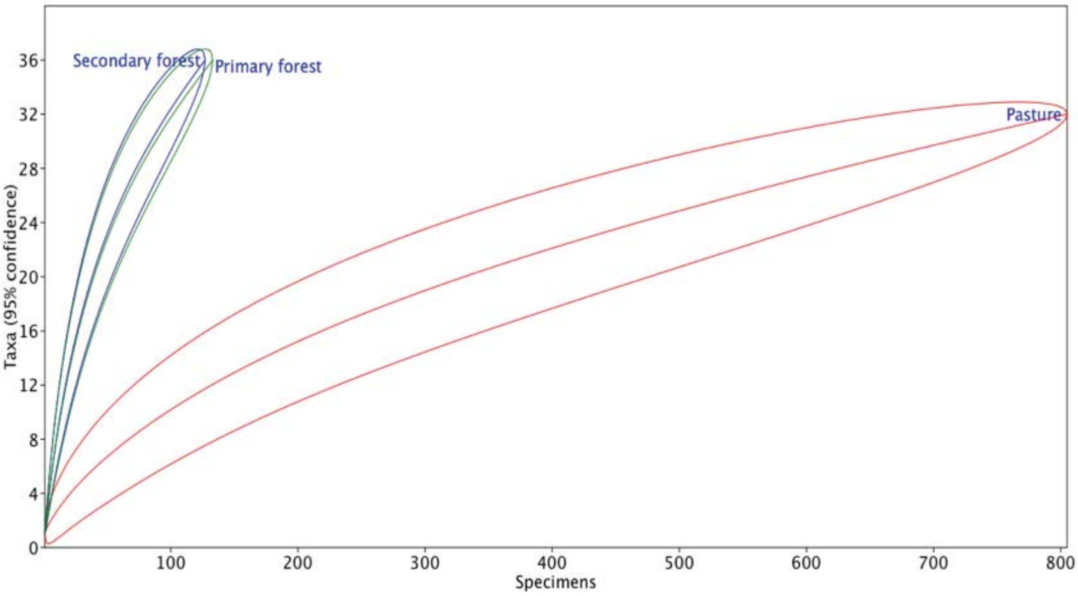

Figure 7. Individual-based species rarefaction curves for each habitat combined across both study sites (La Mesenia and Montezuma).

Species richness was higher at Montezuma than at La Mesenia for all habitat types. In Montezuma, pasture had the highest species richness whereas primary forest had the lowest. At La Mesenia, the richest habitat was primary forest followed by secondary forest and pasture (Fig. 8). When the study sites were combined, primary and secondary forest portrayed an equal species richness (Fig. 8).

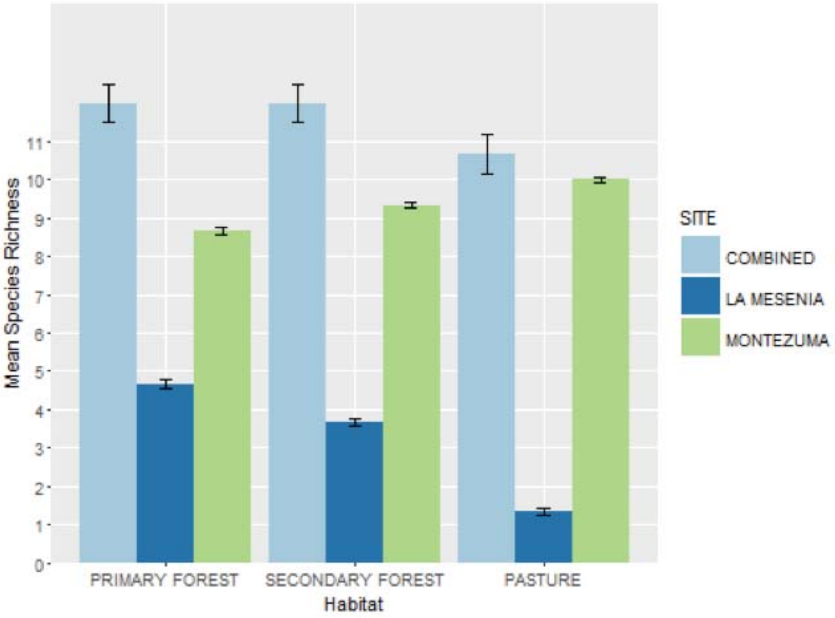

Figure 8. Mean butterfly (±SE) species richness for all habitats (primary forest, secondary forest and pasture) at La Mesenia and Montezuma. Combined = mean species richness at Montezuma and La Mesenia combined.

The analysis of variance (ANOVA) showed that there was a significant difference in species richness between the two study sites ($F = 33.2$ p=0.001). Species richness did not vary significantly between primary forest, secondary forest and pasture (Table 2). A Tukey post-hoc test identified several significant differences in species richness between different sample combinations. The most prominent difference was found between pasture samples at La Mesenia and all the habitat samples (primary forest, secondary forest and pasture) from Montezuma (Table 3).

Table 2. Analysis of variance (ANOVA) examining differences in species richness between study sites and habitats.

Variable	DF	Sum Sq	Mean Sq	F Value	Pr(>F)
Site	1	504.2	504.2	33.2	0.001 **
Habitat	2	10.3	5.2	0.0	0.973

Table 3. Results of Tukey's post-hoc test showing all the combinations between habitats from each study site that were significantly different.

Habitat by Site	Variables (interactions)	Estimate β	Std. Error	z	*p*-value
Montezuma Primary forest	Secondary forest La Mesenia	-0.860	0.360	-2.39	0.01 *
La Mesenia Primary forest	Primary forest Montezuma	0.619	0.332	1.87	0.005 .
	Secondary forest Montezuma	0.693	0.327	2.12	0.01 *
La Mesenia Secondary	Secondary forest Montezuma	0.934	0.356	2.63	0.001 **
Montezuma Pasture	Primary forest La Mesenia	-0.762	0.324	-2.36	0.01 *
	Secondary forest La Mesenia	-1.003	0.352	-2.85	0.001 **
La Mesenia Pasture	Pasture Montezuma	2.015	0.532	3.79	0.0001 ***
	Primary forest La Mesenia	1.253	0.567	2.21	0.01 *
	Primary forest Montezuma	1.872	0.537	3.49	0.0001***
	Secondary forest La Mesenia	1.012	0.584	1.73	0.05 .
	Secondary forest Montezuma	1.946	0.535	3.64	0.0001 ***

Variation in abundance across site, habitat and species was analyzed using a GLM. The overall model, considering all the independent variables (site, habitat and species), was highly significant (Table 4). Abundance also differed significantly when considering all the independent variables separately (Table 5). The abundance was significant different when I compared against all independent variables

Table 4. Parameter estimates from an ANOVA using a general linear model (GLM) with the overall abundance at sampled square level as the dependent variable.

Source	**DF**	**Sum of Squares**	**Mean Square**	**F Value**	***p*-value**
Model	133	489.9	3.68	194.61	<.0001
Error	10442	197.6	0.01		
Corrected Total	10575	687.5			

Table 5. Parameter estimates from an ANOVA using general linear model (GLM) with the overall abundance at sampled square level as the dependent variable. Site= Montezuma and La Mesenia, habitat (primary forest, secondary forest and pasture), species= total number of species.

Variables	**DF**	**Mean Square**	**F Value**	***p*-value**
Site	1	0.110	5.81	0.0159
Habitat	2	3.907	206.42	<.0001
Species	64	0.433	22.85	<.0001
Species-Site	5	0.469	24.78	<.0001
Species-Habitat	34	2.187	115.56	<.0001

The 10 most abundant species accounted for 87.2% of all individuals (n= 968) at Montezuma and 83.5% of all individuals (n= 97) at La Mesenia. *Hermeuptychia hermes* was the most abundant species and accounted for 62.1% of all captures (n = 661), followed by *Yphthimoides renata* (6.5%, n = 69), *Parataygetis lineata* (2.3%, n = 25), *Magneuptychia alcione* (2.3%, n = 24) and *Pareuptychia ocirrhoe* (2.3%, n = 24; Table 3). The most abundant species at Montezuma were *H. hermes* (66.6%, n=645), *Y. renata* (7.1%, n= 69), *M. alcione* (2.5%, n= 24). At La Mesenia *Mygona irmina* (17.5%, n= 17), *H. hermes* (16.5%, n= 16), *Parataygetis lineata* (12.4%, n=12; Table 6) were most abundant.

Table 6. Ten most important species, listed in descending order of number of individuals (No. ind.) captured at each site. % = percent of total number of captures.

Rank	**Montezuma**	**No. ind.**	**%**	**La Mesenia**	**No. ind.**	**%**	**Combined**	**No.ind**	**%**
1	*Hermeuptychia hermes*	645	66.6	*Mygona irmina*	17	17.5	*Hermeuptychia hermes*	661	62.1
2	*Yphthimoides renata*	69	7.1	*Hermeuptychia hermes*	16	16.5	*Yphthimoides renata*	69	6.5
3	*Magneuptychia alcione*	24	2.5	*Parataygetis lineata*	12	12.4	*Parataygetis lineata*	25	2.3
4	*Pareuptychia ocirrhoe*	24	2.5	*Pedaliodes manis*	10	10.3	*Magneuptychia alcione*	24	2.3
5	*Taygetis chrysogone*	16	1.7	*Forsterinaria inornata*	6	6.2	*Pareuptychia ocirrhoe*	24	2.3
6	*Magneuptychia tiessa*	15	1.5	*Lasiophila zapatoza*	6	6.2	*Mygona irmina*	17	1.6
7	*Manataria maculata*	14	1.4	*Pedaliodes pacifica*	5	5.2	*Taygetis chrysogone*	16	1.5
8	*Parataygetis lineata*	13	1.3	*Catonephele chromis*	3	3.1	*Magneuptychia tiessa*	15	1.4
9	*Oxeoschistus puerta*	12	1.2	*Corades chelonis*	3	3.1	*Manataria maculata*	15	1.4
10	*Taygetomorpha celia*	12	1.2	*Euptychoides griphe*	3	3.1	*Oxeoschistus puerta*	14	1.3
Σ 1-10		**844**	**87.2**		**81**	**83.5**		**880**	**82.6**

At Montezuma, the 10 most abundant species in primary forest represented 72% (n= 57), secondary forest 25% (n= 81) and pasture 97.1% (n=758) of the total number of captures in each habitat. *P. lineata* (16.5%, n= 13) was the most abundant species in primary forest, *P. ocirrhoe* (20.4%, n= 22) most abundant in secondary forest and *H. hermes* (81.8%, n=639) most abundant in pasture (Table 7).

The 10 most abundant species in primary forest at La Mesenia comprised 92.6% of the total number of individuals captured in this habitat. For secondary forest this percentage was even higher (94.7%, n=18) and only four species were captured in pasture (Table 7). *Mygona irmina* was the most abundant species in primary forest (29%, n=16), *Pedaliodes manis* (21.1%, n=4) in secondary forest and *H. hermes* (66.7%, n=16) in pasture (Table 7).

Table 7. Ten most important species, listed in descending order of number of individuals (No. ind.) captured in each habitat at each site. % = percent of total number of captures. Combined = Montezuma and La Mesenia combined.

Montezuma

Rank	Primary forest	No. ind.	%	Secondary forest	No. ind.	%	Pasture	No. ind.	%
1	*Parataygetis lineata*	13	16.5	*Pareuptychia ocirrhoe*	22	20.4	*Hermeuptychia hermes*	639	81.8
2	*Taygetis chrysogone*	8	10.1	*Oxeoschistus puerta*	10	9.3	*Yphthimoides renata*	59	7.6
3	*Taygetomorpha celia*	7	8.9	*Pareuptychia metaleuca*	10	9.3	*Magneuptychia alcione*	19	2.4
4	*Pseudohaetera mimica*	6	7.6	*Yphthimoides renata*	8	7.4	*Magneuptychia tiessa*	8	1.0
5	*Catonephele chromis*	5	6.3	*Taygetis chrysogone*	7	6.5	*Forsterinaria neonympha*	8	1.0
6	*Pirella helvina*	5	6.3	*Taygetis asterie*	6	5.6	*Memphis perenna*	8	1.0
7	*Manataria maculata*	4	5.1	*Hermeuptychia hermes*	5	4.6	*Manataria maculata*	6	0.8
8	*Magneuptychia tiessa*	3	3.8	*Magneuptychia alcione*	5	4.6	*Pronophila unifasciata*	5	0.6
9	*Corades pannonia*	3	3.8	*Taygetomorpha celia*	4	3.7	*Panacea prola*	3	0.4
10	*Memphis lyceus*	3	3.8	*Manataria maculata*	4	3.7	*Historis odious*	3	0.4
	Σ 1-10	**57**	**72.2**	**Σ 1-10**	**81**	**75**	**Σ 1-10**	**758**	**97.1**

La Mesenia

Rank	Primary forest	No. ind.	%	Secondary forest	No. ind.	%	Pasture	No. ind.	%
1	*Mygona irmina*	16	29.6	*Pedaliodes manis*	4	21.1	*Hermeuptychia hermes*	16	66.7
2	*Parataygetis lineata*	12	22.2	*Euptychoides griphe*	3	15.8	*Pedaliodes manis*	6	25.0
3	*Forsterinaria inornata*	6	11.1	*Lasiophila zapatoza*	2	10.5	*Catonephele chromis*	1	4.2
4	*Pedaliodes pacifica*	5	9.3	*Adelpha saundersii*	2	10.5	*Perisama humboldtii*	1	4.2
5	*Lasiophila zapatoza*	4	7.4	*Oxeoschistus puerta*	2	10.5			
6	*Corades chelonis*	3	5.6	*Mygona irmina*	1	5.3			
7	*Catonephele chromis*	1	1.9	*Catonephele chromis*	1	5.3			
8	*Opsiphanes camena*	1	1.9	*Opsiphanes camena*	1	5.3			
9	*Pedaliodes sp 1*	1	1.9	*Pedaliodes sp 1*	1	5.3			
10	*Daedalma dianias*	1	1.9	*Fountainea nessus*	1	5.3			
	Σ 1-10	**50**	**92.6**	**Σ 1-10**	**18**	**94.7**	**Σ 1-10**	**24**	**100**

Combined

Rank	Primary forest	No. ind.	%	Secondary forest	No. ind.	%	Pasture	No. ind.	%
1	*Parataygetis lineata*	25	18.8	*Pareuptychia ocirrhoe*	22	17.3	*Hermeuptychia hermes*	655	81.4
2	*Mygona irmina*	16	12.0	*Oxeoschistus puerta*	12	9.4	*Yphthimoides renata*	59	7.3
3	*Taygetis chrysogone*	8	6.0	*Pareuptychia metaleuca*	10	7.9	*Magneuptychia alcione*	19	2.4
4	*Taygetomorpha celia*	7	5.3	*Yphthimoides renata*	8	6.3	*Magneuptychia tiessa*	8	1.0
5	*Catonephele chromis*	6	4.5	*Taygetis chrysogone*	7	5.5	*Forsterinaria neonympha*	8	1.0
6	*Forsterinaria inornata*	6	4.5	*Taygetis asterie*	6	4.7	*Memphis perenna*	8	1.0
7	*Pseudohaetera mimica*	6	4.5	*Hermeuptychia hermes*	5	3.9	*Manataria maculata*	6	0.7
8	*Manataria maculata*	5	3.8	*Magneuptychia alcione*	5	3.9	*Pedaliodes manis*	6	0.7
9	*Pedaliodes pacifica*	5	3.8	*Taygetomorpha celia*	4	3.1	*Pronophila unifasciata*	5	0.6
10	*Pirella helvina*	5	3.8	*Manataria maculata*	4	3.1	*Panacea prola*	3	0.4
	Σ 1-10	**89**	**66.9**	**Σ 1-10**	**83**	**65.4**	**Σ 1-10**	**777**	**96.5**

3.3 Butterfly assemblage structure and composition

A non-metric multi-dimensional scaling (NMDS) plot based on Bray-Curtis similarities of species composition and abundance showed a loose clustering by habitat. Most of the primary forest samples are grouped in the left part of the diagram, while most samples belonging to pastures are clustered to the right, indicating that the butterfly communities in these two habitats are dissimilar. The secondary forest samples are placed in the center of the diagram, indicating that secondary forests contain a mix of primary forest and pasture species (Fig. 9).

Species such as *Eretris apuleja* (ErAp), *Opsiphanes camena* (OpCa), *Narope anartes* (NaAn), *Memphis pseudiphis* (MePs), *Memphis lyceus* (MeLy), *Colobura annulata* (CoAn), *Teratophthalma monochrome* (TeMo), *Pseudodebis celia* (PsCe), *Pedaliodes pacifica* (PePa) *Lasiophila zapatoza* (LaZa), *Pedaliodes pacifica* (PePa), and *Mygona irmina* (MyIr) were characteristic of primary forest. *Taygetis chrysogone* (TaCh), *Oxeoschistus puerta* (OxPu), *Taygetis thamyra* (TaTha), *Tirgridia acesta* (TiAc), *Manataria maculata* (MaMa), *Fosterinaria neonympha* (FoNe), *Fountainea nessus* (FoNe1), *Pedaliodes manis* (PeMa) and *Parataygetis lineata* (PrLi) were species characteristic of secondary forest (Fig. 9).

Pastures were represented by species such as *Historis odious* (HiOd), *Opsiphanes quiteria* (OpQu), *Adelpha salmoneus* (AdSA), *Pareuptychia ocirrhoe* (PaOc), *Taygetis asterie* (TaAs), *Prepona laertes* (PrLa), *Pronophila unifasciata* (PrUn), and *Memphis philumena* (MePh). There were also species located in a transition between secondary forest and pasture. These species were *Panacea prola* (PaPr1), *Hermeuptychia hermes* (HeHe), *Memphis perenna* (MePe), *Magneuptychia alcione* (MaAL), *Panacea procilla procilla* (PaPr), *Yphthimoides renata* (YpRe), *Pareuptychia ocirrhoe* (PaOc) and *Pareuptychia metaleuca* (PaMe; Fig. 9).

The analysis of similarity (ANOSIM) showed that there is a significant difference in the butterfly assemblages between habitats (ANOSIM, R = 0.395, p=0.001). Pairwise comparisons show that the most significant difference was found between primary forest and pasture (p=<0.001). There were also significant differences between secondary forest and pasture (p= 0.002), whereas primary and secondary forest did not differ significantly (p=0.114).

According to the Similarity percentages (SIMPER) analysis, the species contributing most to the difference between primary forest and secondary forest were *P. lineata* (10.6%), *M. irmina* (8.2%), *O. puerta* (6.1%) and *P. ocirrhoe* (5.6%). The difference between pasture and the two forest habitats is largely due to the extremely high abundance of *H. hermes* in pasture (Table 8).

Table 8. Ten most important species as indicated by SIMPER analysis contributing to differences in butterfly assemblages between primary forest *vs* secondary forest, primary forest *vs* pasture and secondary forest *vs* pasture. Species are listed in descending order percentage contribution (Contrib. %)

Primary forest vs Secondary forest		**Primary forest vs Pasture**		**Secondary Forest vs Pasture**	
Species	**Contrib. %**	**Species**	**Contrib. %**	**Species**	**Contrib. %**
Parataygetis lineata	10.6	*Hermeuptychia hermes*	51.7	*Hermeuptychia hermes*	53.8
Mygona irmina	8.2	*Pedaliodes manis*	7.2	*Pedaliodes manis*	8.1
Oxeoschistus puerta	6.1	*Yphthimoides renata*	5.4	*Yphthimoides renata*	5.7
Pareuptychia ocirrhoe	5.6	*Parataygetis lineata*	5.4	*Oxeoschistus puerta*	3.4
Taygetis chrysogone	4.7	*Mygona irmina*	3.9	*Pareuptychia ocirrhoe*	3.2
Lasiophila zapatoza	3.8	*Catonephele chromis*	1.9	*Pareuptychia metaleuca*	2.0
Taygetomorpha celia	3.6	*Taygetis chrysogone*	1.8	*Magneuptychia alcione*	1.8
Pareuptychia metaleuca	3.4	*Manataria maculata*	1.6	*Catonephele chromis*	1.8
Catonephele chromis	3.3	*Taygetomorpha celia*	1.4	*Lasiophila zapatoza*	1.5
Manataria maculata	3.1	*Magneuptychia alcione*	1.3	*Fosterinaria neonympha*	1.4

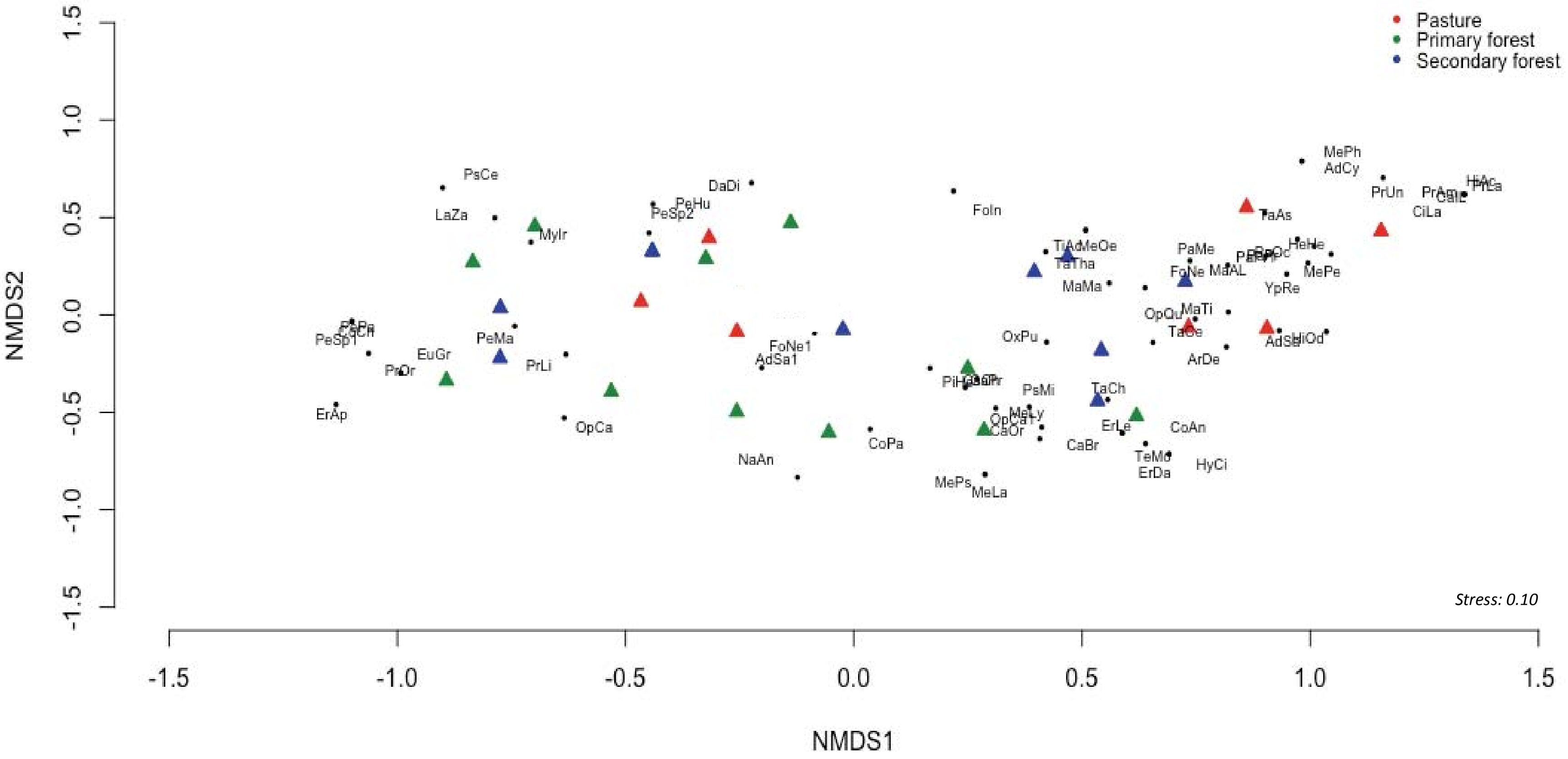

Figure 9. Non-metric multi-dimensional scaling (NMDS) plot based on Bray-Curtis similarities, across primary forest (green triangles), secondary forest (blue triangles) and pasture (red triangles) western Andes, Colombia. Black dots indicate the location of individual species.

3.4 Altitudinal range profiles

Species richness and abundance declined with increasing altitude, but primary and secondary forest expressed a less abrupt decline compared to pasture (Fig 10 and 11). Indeed, the GLM analysis indicates that altitude has a significant negative effect on both species richness and abundance (Table 9 and 10).

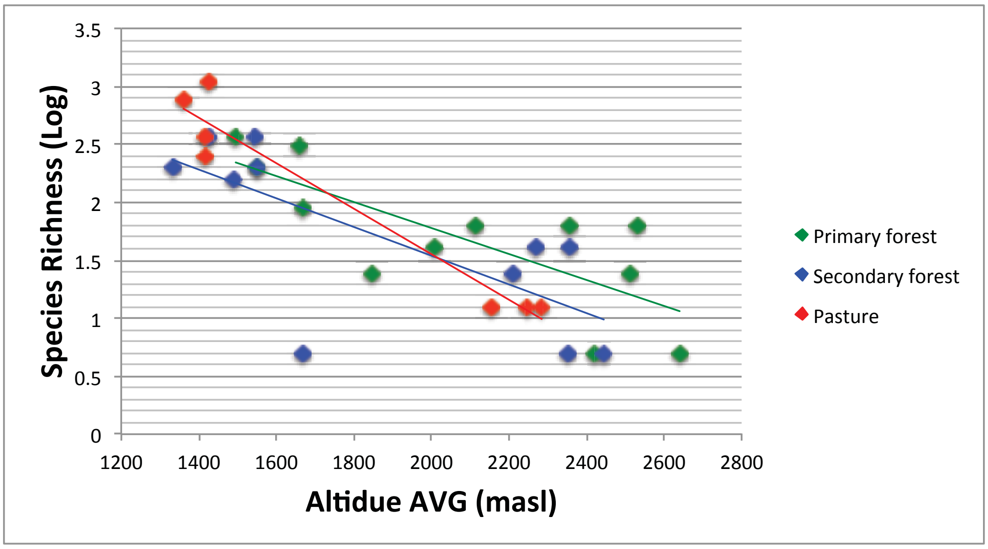

Figure 10. Linear regression showing the richness trend in each square sampled along the altitude (AVG= average) gradient, at each habitat (Primary forest: y = -0.0012x + 4.7173 R^2 = 0.4472, Secondary forest: y = -0.0016x + 5.0924 R^2 = 0.46411 and Pasture: y = -0.0038x + 10.46 R^2 = 0.90468). Each diamond represents a sampled square.

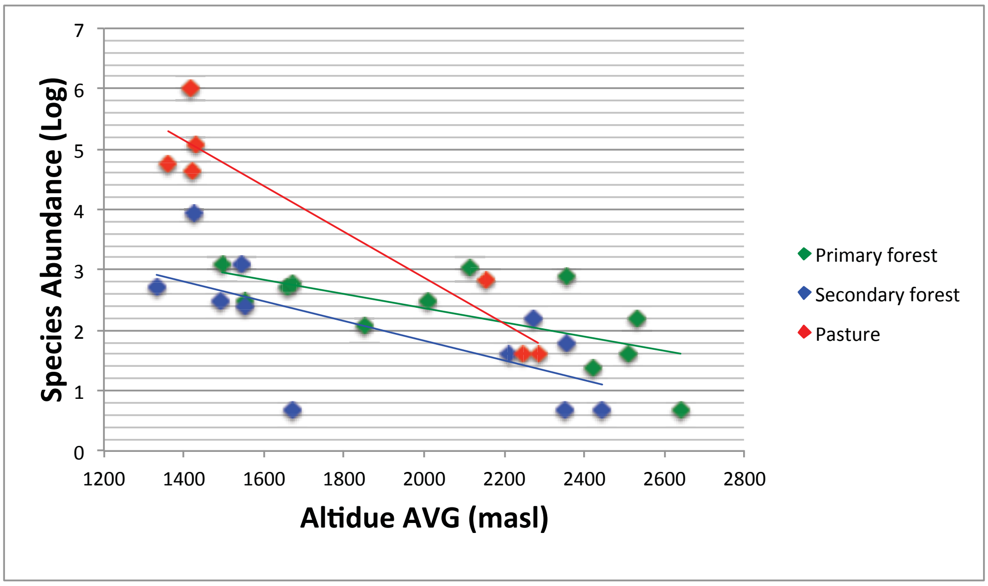

Figure 11. Linear regression showing the abundance trend in each square sampled along the altitude (AVG= average) gradient, at each habitat (Primary forest: y=-0.0011x + 4.0191, Secondary forest: y = -0.0012x + 4.016 R^2 = 0.53334 and Pasture: y = -0.002x + 5.4786 R^2 = 0.9409). Each diamond represents a sampled square.

Examining the two sites and the different forest types therein separately, GLM analysis showed that altitude significantly influences species richness and abundance at La Mesenia, but only species richness at Montezuma. Pasture showed a significant decline in species richness with altitude, whereas primary and secondary forest did not (Table 11). Abundance portrayed the opposite trend with abundance decreasing significant with altitude in primary and secondary forest, but not in pasture (Table 12).

Table 9. Parameter estimates of the GLM model for overall species richness across the altitude gradient (average of total sampled squares altitude). Intercept is presented as the dummy variable "Species richness".

Variables	Estimate	Std. Error	z	*p*-value
Intercept	4.808	0.35	13.73	< 2e-16 ***
Altitude	-0.002	0.00	-7.99	1.31e-15 ***

Table 10. Parameter estimates general linear model (GLM) of altitude (average of altitude at each sampled square) with overall species abundance as a "depended variable. Intercept is presented as the dummy variable "Species abundance".

Variables	Estimate	Std. Error	z	*p*-value
Intercept	8.497	0.85	9.99	< 2e-16 ***
Altitude	-0.003	0.00	-6.67	2.5e-11 ***

Table 11. Results of GLM analysis showing the effect of altitude on butterfly species richness at the two study sites (Montezuma and La Mesenia) and the three habitats (primary forest, secondary forest and pasture).

Variables (Interactions)	Estimate	Std. Error	z	*p*-value
Altitude*Montezuma	-2.8E-03	7.2E-04	-3.84	0.0001 ***
Altitude*La Mesenia	-2.4E-03	5.0E-04	-4.74	2.11e-06 ***
Altitude*Primary forest	1.3E-04	1.3E-04	1.02	0.307
Altitude*Secondary forest	-9.7E-05	1.1E-04	-0.85	0.397
Altitude*Pasture	6.5E+00	1.0E+00	6.32	2.70e-10 ***

Table 12. Results of GLM analysis showing the effect of altitude on butterfly abundance at the two study sites (Montezuma and La Mesenia) and the three habitats (primary forest, secondary forest and pasture).

Variables (Interactions)	Estimate	Std. Error	z	*p*-value
Altitude*Montezuma	0.000	0.001	-0.251	0.802
Altitude*La Mesenia	7.624	2.269	3.361	0.001 ***
Altitude*Primary forest	-0.003	0.001	-2.803	0.005 **
Altitude*Secondary forest	-0.003	0.001	-2.627	0.009 **
Altitude*Pasture	-0.002	0.001	-1.857	0.05 .

Most species sampled at Montezuma and La Mesenia had a very narrow altitudinal range, and no species were present across the entire altitudinal range at any of the two sites (Fig. 12). The broadest altitudinal range was portrayed by *Pedaliodes manis*, *Corades chelonis* and *Pedaliodes pacifica* at La Mesenia and *Parataygetis lineata* at Montezuma (Fig. 12)

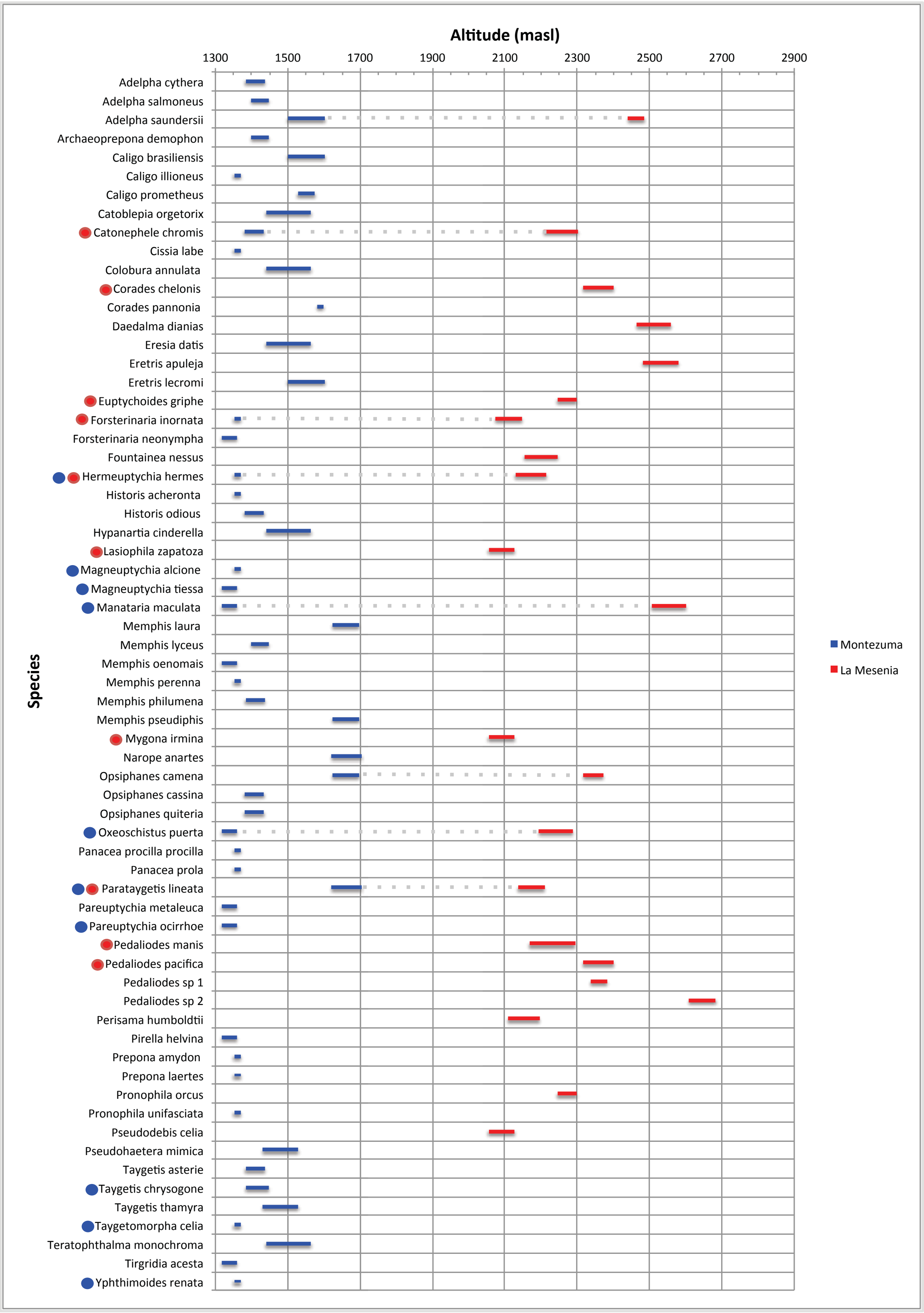

Figure 12. Altitudinal range profile of fruit-feeding butterflies captured at Montezuma and La Mesenia, western Andean Cordillera, Colombia. No sampling sites were located between 1750-2000m. Dotted lines connect the ranges for species observed at both sites. Blue and red dots indicated the ten most abundant species at Montezuma and La Mesenia, respectively.

4. Discussion

4.1 The fruit-feeding Nymphalid community

This is the first study to investigate fruit-feeding butterfly assemblage structure and composition at Montezuma and La Mesenia. It is also the first study to examine the effects of land-use change on butterflies in Colombia. The subfamilies captured in the current study are typical members of the fruit-feeding nymphalid butterfly community, with a diet consisting of fermented fruits or nectar from flowers in the Neotropics (Jenkins 1983; Jenkins 1984). The sub-family and species composition registered in this study is similar to other studies from the Colombian Andes (García-Perez et al. 2007; Garcia-Robledo 2002; Mahecha-Jiménez et al. 2011) and other Andean sites (Pyrcz & Wojtusiak 2002)

Most of the individuals in this study were captured in Montezuma. This is likely due to more periods of continuous rain at La Mesenia, even though the sampling was conducted during the dry season at both study sites. Indeed, rainfall is known to negatively affect butterfly presence, richness and diversity (Benedick et al. 2006; Pollard 1988; Roy et al. 2001). Yet, high rainfall in the western Andes is a normal, as the mountains intercept humid coastal winds that come in from the Pacific Ocean, making the Chocó region one of the wettest places in the world (Durán-Quesada et al. 2012).

4.2 Species richness and diversity

The fruit-feeding nymphalid species richness registered in this study is similar to or higher than other studies conducted in the Colombian Andes. Marín et al. (2014) reported a similar number of species (75) from an Andean cloud forest in the Aburra valley, whereas Mahecha-Jiménez et al. (2011) registered 13 species in a Andean forest outside Bogotá(central Andean cordillera), and García-Perez et al. (2007) registered 34 species at Tolima in the central Andean cordillera. However, it is much lower than that obtained in Amazonian forests, where well over a hundred species are captured at a single location (DeVRIES et al. 1997; Devries & Walla 2001; Lilleengen 2016).

The sample-based rarefaction curve suggests that the sample effort was reasonable. However, the species accumulation curves for primary and secondary forest did not reach an asymptote, indicating that the sample has not captured the full diversity of fruit-feeding nymphalids in these habitats. More species are therefore expected to be discovered in these two habitats and more sampling is clearly needed to obtain a more representative fruit-feeding butterfly community. In addition, butterfly communities commonly vary both within and between years (DeVries et al. 2012; Grøtan et al. 2014) (Checa et al. 2009) and so further sampling across seasons and years may thus be necessary to achieve a more precise estimation of total fruit-feeding nympalid species richness in the region. Including a vertical component to future studies would also improve estimates, as many tropical forest butterflies are canopy-dwellers (Dumbrell & Hill 2005; Hamer & Hill 2000). The sample effort for pasture was sufficient to represent the majority of the fruit feeding butterflies species in this habitat.

Primary and secondary forests had the highest number of unique species at both study sites. Unique species contribute to the functional diversity of natural systems and are usually present in high numbers in habitats with high species richness (O'Gorman et al. 2010). However, surprisingly, pasture at Montezuma had the highest percentage of unique species. A high number of unique species is usually expected to be found in primary forest (Koh & Sodhi 2004; Weibull et al. 2003). Yet, agro-ecosystems, cattle pasture or farming ecosystems could also have a high number of unique species due to landscape heterogeneity, for example created by a patchwork of forest fragments and farming land(Gilroy et al. 2014a). Indeed, pasture at Montezuma was very different from pasture at La Mesenia in terms of landscape heterogeneity and land-used change. The fact that Montezuma lies within a national park, some activities like logging are more regulated than at La Mesenia. There were also different varieties of crops and patches of secondary forest within the sample squares in pastures at Montezuma. This variety of different habitats imbedded within pasture at Montezuma may therefore explain the observed results.

Most butterfly species found in the current study were rare. Most rare species were found in pasture at Montezuma and secondary forest at La Mesenia. This is possibly a result of a strong dominance of only a few species or very low butterfly abundance. It could alternatively be a sign of an unstable and constantly changing butterfly fauna. However, rare species make up a large number of the sample in most studies (e.g. DeVRIES et al. (1997)). In more intact ecosystems, the loss of rare species can affect local ecosystem processes (Bracken & Low 2012; Mouillot et al. 2013) and rare species can contribute significantly to long-term and large-scale ecosystem functioning (Lyons et al. 2005). They are thus often targets for conservation action (Devries & Walla 2001).

Butterfly diversity was highest in primary and secondary forest at both sites. This could be an artifact of the smaller number of squares sampled in pasture compared to the number of squares sampled in primary and secondary forest at both study sites. However, previous studies in the region show that several other taxa, such as birds, dung beetles and ants, have a much reduced diversity in pasture compared to secondary and primary forest(Gilroy et al. 2014a; Gilroy et al. 2014b; Gilroy et al. 2015). It is therefore more likely that these results are directly linked to the conversion of forest to pasture.

4.3 Species distribution and composition among habitat

Of all habitats, pasture at Montezuma and primary forest at La Mesenia portrayed the highest butterflies abundance. *Hermeuptychia hermes* hugely dominated the pasture samples at both sites. This is consistent with previous studies showing that this species is occurring in high densities in disturbed ecosystems (e.g. Ramos (2000)). *H. hermes* is attracted to the vegetation of disturbed forest or disturbed ecosystems, such as pastures. It is a sun-loving and opportunistic species that is common in open biomes like the Cerrado in Brazil (Pinheiro & Ortiz 1992; Ramos 2000).

Mygona irmina and *Parataygetis lineata* were species typical of primary forest in this study*. M. irmina* is the only representative of the genus in the entire northern Andes of Venezuela and Colombia. It has a particular, lazy, slow flapping flight. It usually stays in the sub-canopy, but occasionally comes to the ground to feed on decomposing organic matter (Viloria et al. 2010).*P. lineata* is mainly restricted to lowlands, although it occurs in montane habitats on the eastern slope of the Andes in lower Andean and/or southeast Brazilian montane habitats (Matos-Maravi et al. 2013). Both species are specialists and prefer habitats with vegetation structures more complex usually at higher altitudes (Tobar 2000). Also, these species belong to the Satyrinae (Pronophilini tribe), which most common hostplants are members of the plant families Selaginallaceae and Bryophytes (DeVRIES et al. 1997), predominant between 2000 and 2400 masl across the Andean forest (Pyrcz et al. 2009).

Butterfly abundance was lower in primary and secondary forest at Montezuma than in pasture, and secondary forest had fewer butterflies than pasture at La Mesenia. However, the butterfly assemblages in these habitats were not dominated only by a few super abundant species, as was the case in pasture. Primary and secondary forest had a much more homogeneous abundance distribution among the species captured. This promotes assemblage variation and most likely higher phylogenetic diversity, which is an important measure of evolutionary history (Graham & Fine 2008). Indeed, Edwards et al. (2017) found that converting Andean forest to cattle farming dramatically reduces avifaunal phylogenetic diversity and increases phylogenetic clustering. Investing in the conservation of primary and secondary forests in the Andes therefore offers substantial benefits for the conservation of evolutionary distinct biodiversity, and emphasizes that preventing primary tropical forest loss to agriculture remains extremely important.

Butterfly assemblages in primary forest, secondary forest and pasture were significantly different. These results are similar to those found for butterflies in the Brazilian Amazon(Barlow et al. 2007b) and for amphibians (Basham et al. 2016), birds and dung beetles (Gilroy et al. 2014b) the western Colombian Andes. However, primary and secondary forest shared a similar butterfly fauna, while pasture tended to have a different set of species than the other two habitats. Secondary forest was less diverse than primary forest and the intermediate positioning of secondary forest assemblages in the ordination suggests that these assemblages contain both pasture and primary forest species. Yet, the non-significant difference between primary and secondary forest butterfly assemblages suggests that these secondary forests appears to be on a gradual road of recovery, moving towards a primary forest butterfly community. Indeed, fruit-feeding nymphalid butterfly diversity is well-known to be related to light conditions in tropical forests and to be very sensitive to changes in light levels (Veddeler et al. 2005). In a very fragmented landscape heavily influenced by pastures, secondary forest could provide refuge for more forest dependent species in addition to providing dispersal potential for species restricted to primary forests. Indeed, del Pliego et al. (2016) show that secondary forests support critical thermally buffered microhabitats, recovering towards primary forest levels. Secondary forests may therefore be extremely important to retain primary forest species and will directly boost population sizes of many evolutionary distinct species(Basham et al. 2016; Edwards et al. 2017) especially in regions where the majority of primary forest cover has already been lost. Consequently, secondary forest holds high conservation value and underlines the importance of reforestation in areas where cattle farming is performed with marginal profit (Basham et al. 2016; Gilroy et al. 2014a; Gilroy et al. 2014b)

In addition, although the primary and secondary forest butterfly community was different from pasture, species such as *Pedaliodes manis* and *Catonephele chromis* were found in pasture even though they were more characteristic of primary and secondary forest in this study. This is probably why some of the squares sampled in pasture mingle with primary and secondary forest sites in the NMDS ordination diagram. These squares were all from La Mesenia. The likely reason for these species to be present in pasture at this site is that those squares were all surrounded by contiguous primary and secondary forest. Perhaps they were attracted by the bait in the traps and moved into pasture to feed. However, this should not lead to the conclusion that these species are moving across these habitats looking for food sources, as the abundance of such species was very low in pasture compared to primary or secondary forest. The similarity analysis showed that some species were more likely to be found in one habitat more than the other, suggesting that species were associated to different habitats. This is supported by the fact that the pasture species were typically light-loving species (*H. hermes* and *Y. renata*) and those associated to primary and secondary forests are found to be more shade loving species (*P. lineata* and M. irmina; (Pardonnet 2010)).

4.4 Species across altitudinal range

Species richness and abundance declined with increasing altitude, but primary and secondary forest expressed a less abrupt decline compared to pasture and the effect of altitude was not significant on richness and abundance in these two habitats. Both a monotonic decrease and a hump-shape relationship with elevation (where the highest richness occurs in the mid-elevation zone), have been documented in a variety of habitats and taxa across the globe (Sanders 2002). Colwell and Lees (2000) suggests that perhaps mid-elevational peak are more common. However, since only a small fraction of the altitudinal gradient in the Andes was sampled in this study, it is uncertain if the overall richness and abundance decreases across the altitudinal gradient or conforms to some other trend. Indeed, a variety of trends have been described for butterflies in the Neotropics. For example, Pyrcz and Wojtusiak (2002) who investigated the effect of altitude on the diversity of Pronophilini (Satyrinae) butterflies in a cloud forest at the Cordillera de Merida, Venezuela, found that richness remained high up to an elevation of about 2700 masl and then gradually decreased towards the upper timberline. However, abundance did not increase as richness increased – the higher the elevation, the lower the abundance. Investigating the diversity and distribution of Satyrinae between 433 a 3600 masl in the Coello river basin, Colombia, García-Perez et al. (2007) found trends contrasting significantly from those found in the current study; they found that richness and abundance increased along the altitudinal gradient. Based on results presented in this thesis, Satyrinae was the most abundant group of butterflies occurring in the lower altitudes considered in this study (1300-1700 masl). This group of butterflies usually uses hostplants from families such as Poaceae, which is characteristic of pastures (DeVRIES et al. 1997). In addition, generalist Satyrinae butterfly species tend to predominate in pasture habitats, strongly influenced by human activities, compared to more specialist forest species (Tobar 2000).

The higher abundance of this butterfly group at lower altitudes in the current study therefore makes sense, since most pasture sites were located at the lower altitudinal range covered in both study sites in the current study sites (Montezuma 1300-1500 masl and La Mesenia 2055-2300 masl). In addition, the higher richness and abundance at lower altitudes may be due to the proximity of nearby core areas for these ‘’low elevation’’ species, but these species cannot persist at higher elevations. Indeed, several species with a very narrow altitudinal range at the very lowest elevations of Montezuma are species that belong to the lowlands and are just about at their altitudinal limit at this elevation (Stevens 1992).

The reason why primary and secondary forest expressed a less abrupt decline than pasture and richness was not significantly affected by altitude could be that more of the squares sampled in primary and secondary forest occurred at higher altitudes than pasture at both study sites. Much of the remaining primary forest in the Andes occurs at higher altitudes in remote and inaccessible places. This is also indicated by the butterfly species composition at the highest elevations at each study site. For example, at Montezuma the highest altitudes (from 1623 to 1700 masl.) included species such as *Memphis laura*, *Memphis pseudiphis*, *Narope anartes*, *Opsiphanes camena* and *Parataygetis lineata*. These species are considered more specialist shade-lovers, typically occurring in primary forest understory (Devries 2001; DeVRIES et al. 1997). At La Mesenia, which included sites at even higher altitudes, butterflies such as *Mygona irmina, Parataygetis lineata, Forsterinaria inornata, Lasiophila zapatoza* , *Corades chelonis* and *Pedaliodes pacifica* are among the most abundant species. This is consistent with previous work along Andean transects in Venezuela, Colombia and Peru, where butterfly genera such as *Corades, Pedaliodes, Forsterinaria, Hermeuptychia, Lasiophila* and *Mygona* are more abundant at higher than lower elevations (Pyrcz & Wojtusiak 2002; Pyrcz 2004; Pyrcz & Viloria 2005).

4.5. Conclusions

In summary, this study demonstrates that fruit-feeding butterfly diversity in the western Andes is affected by habitat disturbance due to land-use change. Even though In summary, this study demonstrates that fruit-feeding butterfly assemblages in the western Andes are affected by land-use change. Even though species richness was high in pasture, the sample-based rarefaction curves suggest that many more species are yet to be catalogued in primary and secondary forest. More survey effort is therefore likely to reveal large differences in species richness between forests and pasture. In addition, butterfly assemblage composition varied substantially form pasture to primary and secondary forest. The fact that secondary forests contain a similar species composition to that of primary forest suggests that secondary forest retain significant biodiversity. Secondary forests therefore appear to be extremely important for conservation, particularly in regions where the majority of primary forest cover has already been lost. The results also underline the importance of reforestation in areas where cattle farming is marginally profitable in the western Andes of Colombia. Species richness and abundance declined with increasing altitude. However, as there was only a small fraction of the altitudinal gradient in the Andes sampled in this study. It is thus uncertain if the overall richness and abundance indeed decreases across the altitudinal gradient in the Andes. Surprisingly, species richness was not significant affected by altitude. Yet, much of the remaining primary forest occurs at higher altitudes, so it is possible that a higher the higher diversity of microhabitats provided by this habitat is the reason for this trend. In conclusion, primary forests should be a conservation priority in the region and reforesting marginal cattle pastures might be a good way to further protect the highly endangered biota across the Andes.

5. References

Ballesteros, H., Ríos, C., Hernández, J., Restrepo, R., Gallego, L., López, F., Rendon, L., Ruiz, J., Rodríguez, Y. & Ramírez, J. (2005). Plan básico de manejo 2005–2009, Parque Nacional Natural Tatamá. *Parques Nacionales Naturales de Colombia, Dirección Territorial Noroccidente, Santuario, Risaralda*.

Barlow, J., Gardner, T. A., Araujo, I. S., Avila-Pires, T. C., Bonaldo, A. B., Costa, J. E., Esposito, M. C., Ferreira, L. V., Hawes, J., Hernandez, M. I., et al. (2007a). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proc Natl Acad Sci U S A*, 104 (47): 18555-60.

Barlow, J., Overal, W. L., Araujo, I. S., Gardner, T. A. & Peres, C. A. (2007b). The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon. *Journal of Applied Ecology*, 44 (5): 1001-1012.

Basham, E., González del Pliego, P., Acosta-Galvis, A., Woodcock, P., Medina Uribe, C., Haugaasen, T., Gilroy, J. & Edwards, D. (2016). Quantifying carbon and amphibian co-benefits from secondary forest regeneration in the Tropical Andes. *Animal Conservation*, 19 (6): 548-560.

Benedick, S., Hill, J., Mustaffa, N., Chey, V., Maryati, M., Searle, J., Schilthuizen, M. & Hamer, K. (2006). Impacts of rain forest fragmentation on butterflies in northern Borneo: species richness, turnover and the value of small fragments. *Journal of Applied Ecology*, 43 (5): 967-977.

Bonebrake, T. C., Ponisio, L. C., Boggs, C. L. & Ehrlich, P. R. (2010). More than just indicators: a review of tropical butterfly ecology and conservation. *Biological Conservation*, 143 (8): 1831-1841.

Bracken, M. E. & Low, N. H. (2012). Realistic losses of rare species disproportionately impact higher trophic levels. *Ecology Letters*, 15 (5): 461-467.

Checa, M. F., Barragán, A., Rodríguez, J. & Christman, M. (2009). Temporal abundance patterns of butterfly communities (Lepidoptera: Nymphalidae) in the Ecuadorian Amazonia and their relationship with climate. . *Annalesde la Société entomologique de France: Taylor &Francis*: 470-486.

Colwell, R. K. & Lees, D. C. (2000). The mid-domain effect: geometric constraints on the geography of species richness. *Trends in ecology & evolution*, 15 (2): 70-76.

Colwell, R. K. (2013). *EstimateS: Statistical estimation of especies richness and shared species from samples.* . 9. ed. University of Connectitcut, USA

Crawley, M. J. (2012). *The R book*. The Atrium, Southern Gate, Chicherter, West Sussex, England: John Wiley & Sons, Ltd. 941 pp.

Cuartas-Hernández, S. & Gómez-Murillo, L. (2015). Effect of Biotic and Abiotic Factors on Diversity Patterns of Anthophyllous Insect Communities in a Tropical Mountain Forest. *Neotropical entomology*, 44 (3): 214-223.

del Pliego, P. G., Scheffers, B. R., Basham, E. W., Woodcock, P., Wheeler, C., Gilroy, J. J., Uribe, C. A. M., Haugaasen, T., Freckleton, R. P. & Edwards, D. P. (2016). Thermally buffered microhabitats recovery in tropical secondary forests following land abandonment. *Biological Conservation*, 201: 385-395.

Devries, P. (2001). Species diversity and community structure in neotropical fruit-feeding butterflies. *Biological Journal of the Linnean Society*, 74 (1): 1-15.

DeVRIES, P. J., Murray, D. & Lande, R. (1997). Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological journal of the Linnean Society*, 62 (3): 343-364.

Devries, P. J. & Walla, T. R. (2001). Species diversity and community structure in neotropical fruit-feeding butterflies. *Biological journal of the Linnean Society*, 74 (1): 1-15.

Devries, P. J., Austin, G. T. & Martin, N. H. (2009). Estimating species diversity in a guild of Neotropical skippers (Lepidoptera: Hesperiidae) with artificial lures is a sampling problem. *Insect Conservation and Diversity*, 2 (2): 125-134.

DeVries, P. J., Alexander, L. G., Chacon, I. A. & Fordyce, J. A. (2012). Similarity and difference among rainforest fruit-feeding butterfly communities in Central and South America. *Journal of Animal Ecology*, 81 (2): 472-482.

Dumbrell, A. J. & Hill, J. K. (2005). Impacts of selective logging on canopy and ground assemblages of tropical forest butterflies: implications for sampling. *Biological Conservation*, 125 (1): 123-131.

Durán-Quesada, A., Reboita, M. & Gimeno, L. (2012). Precipitation in tropical America and the associated sources of moisture: a short review. *Hydrological Sciences Journal*, 57 (4): 612-624.

Edwards, D. P., Massam, M. R., Haugaasen, T. & Gilroy, J. J. (2017). Tropical secondary forest regeneration conserves high levels of avian phylogenetic diversity. *Biological Conservation*, 209: 432-439.

Etter, A. & van Wyngaarden, W. (2000). Patterns of Landscape Transformation in Colombia, with Emphasis in the Andean Region. *AMBIO: A Journal of the Human Environment*, 29 (7): 432-439.

Etter, A., McAlpine, C., Wilson, K., Phinn, S. & Possingham, H. (2006). Regional patterns of agricultural land use and deforestation in Colombia. *Agriculture, Ecosystems & Environment*, 114 (2): 369-386.

Food & Nations, A. O. o. t. U. (2010). *Global forest resources assessment 2010: Main report*: Food and Agriculture Organization of the United Nations.

García-Perez, J. F., Ospina-López, L. A., Villa-Navarro, F. A. & Reinoso-Flórez, G. (2007). Diversidad y distribución de mariposas Satyrinae (Lepidoptera: Nymphalidae) en la cuenca del río Coello, Colombia. *Revista de Biología Tropical*, 55 (2): 645-653.

Garcia-Robledo, L. M. C., M. Dolores & G. Kattan. (2002). Mariposas comunes de la cordillera Central de Colombia. *Feriva, Colombia*: 130.

Geist, H. J. & Lambin, E. F. (2002). Proximate Causes and Underlying Driving Forces of Tropical Deforestation Tropical forests are disappearing as the result of many pressures, both local and regional, acting in various combinations in different geographical locations. *BioScience*, 52 (2): 143-150.

Gibbs, H. K., Ruesch, A. S., Achard, F., Clayton, M. K., Holmgren, P., Ramankutty, N. & Foley, J. A. (2010). Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences*, 107 (38): 16732-16737.

Gilroy, J. J., Edwards, F. A., Medina Uribe, C. A., Haugaasen, T. & Edwards, D. P. (2014a). Surrounding habitats mediate the trade-off between land-sharing and land-sparing agriculture in the tropics. *Journal of applied ecology*, 51 (5): 1337-1346.

Gilroy, J. J., Woodcock, P., Edwards, F. A., Wheeler, C., Medina Uribe, C. A., Haugaasen, T. & Edwards, D. P. (2014b). Optimizing carbon storage and biodiversity protection in tropical agricultural landscapes. *Global change biology*, 20 (7): 2162-2172.

Gilroy, J. J., Medina Uribe, C. A., Haugaasen, T. & Edwards, D. P. (2015). Effect of scale on trait predictors of species responses to agriculture. *Conservation Biology*, 29 (2): 463-472.

Gómez-Baggethun, E., De Groot, R., Lomas, P. L. & Montes, C. (2010). The history of ecosystem services in economic theory and practice: from early notions to markets and payment schemes. *Ecological Economics*, 69 (6): 1209-1218.

Graham, C. H. & Fine, P. V. (2008). Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecology letters*, 11 (12): 1265-1277.

Grøtan, V., Lande, R., Chacon, I. & DeVries, P. (2014). Seasonal cycles of diversity and similarity in a Central American rainforest butterfly community. *Ecography*, 37 (5): 509-516.

Hamer, K. & Hill, J. (2000). Scale-Dependent Effects of Habitat Disturbance on Species Richness in Tropical Forests. *Conservation Biology*, 14 (5): 1435-1440.

Hammer, Ø., Harper, D. A. T. & Ryan, P. D. (2001). *PAST: Paleontological statistics software package for education and data analysis*. 3.09 ed. Natural History Museum, U. o. O. (ed.).

Jari, O. (2016). *Vegan: Community Ecology Package*. R package version 2.4-0 ed.

Jenkins, D. W. (1983). *Neotropical Nymphalidae I. Revision of Hamadryas*: Florida State Museum. 146 pp.

Jenkins, D. W. (1984). *Neotropical nymphalidae, II. Revision of Myscelia*: Florida State University, University of Florida. 64 pp.

Jost, L. (2006). Entropy and diversity. *Oikos*, 113 (2): 363-375.

Kattan, G. H., Alvarez-Lopez, H., Schelhas, J. & Greenberg, R. (1996). Preservation and management of biodiversity in fragmented landscapes in the Colombian Andes. *Forest patches in tropical landscapes*: 3-18.

Keene, O. N. (1995). The log transformation is special. *Statistics in medicine*, 14 (8): 811-819.

Koh, L. P. & Sodhi, N. S. (2004). Importance of reserves, fragments, and parks for butterfly conservation in a tropical urban landscape. *Ecological Applications*, 14 (6): 1695-1708.

Lamas, G., Bauer, E. & Frankenbach, T. (1999). *Butterflies of the World: Nymphalidae Ii, Ithomiinae*: Goecke & Evers. 17 pp.

Lamas, G. (2004). Checklist: Part 4A. Hesperioidea-Papilionoidea. *Atlas of neotropical Lepidoptera*, 5: 439.

Lande, R. (1996). Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos*: 5-13.

Li, P. (2005). Box-Cox transformations: an overview. *presentation,* http://www*. stat. uconn. edu/~ studentjournal/index_files/pengfi_s05. pdf*.

Liland, K. H. (2016). *mixlm: Mixed Model ANOVA and Statistics for Education*.

Lilleengen, P. (2016). *Assemblage structure of fruitfeeding nymphalids (Lepidoptera, Nymphalidae) in floodplain and upland forest at Cocha Cashu, Peru.*: Norwegian University of Life Science.

Lyons, K. G., Brigham, C., Traut, B. & Schwartz, M. W. (2005). Rare species and ecosystem functioning. *Conservation Biology*, 19 (4): 1019-1024.

Mahecha-Jiménez, O., Dumar-Rodríguez, J. & Pyrcz, T. (2011). Efecto de la fragmentación del hábitat sobre las comunidades de Lepidoptera de la tribu Pronophilini a lo largo de un gradiente altitudinal en un bosque andino en Bogotá (Colombia)(Lepidoptera: Nymphalidae, Satyrinae). *SHILAP-Revista de Lepidopterología*, 39: 117-126.

Marín, M. A., Álvarez, C. F., Giraldo, C. E., Pyrcz, T. W., Uribe, S. I. & Vila, R. (2014). Butterflies of an Andean periurban cloud forest in the Aburra valley, Colombia. *Revista Mexicana de Biodiversidad*, 85: 200-208.

Matos-Maravi, P. F., Pena, C., Willmott, K. R., Freitas, A. V. & Wahlberg, N. (2013). Systematics and evolutionary history of butterflies in the "Taygetis clade"(Nymphalidae: Satyrinae: Euptychiina): towards a better understanding of Neotropical biogeography. *Molecular Phylogenetics and Evolution*, 66 (1): 54-68.

Mendiburu, F. d. (2016). *agricolae: Statistical Procedures for Agricultural Research*.

Molleman, F., Kop, A., Brakefield, P. M. & Zwaan, B. J. (2006). Vertical and temporal patterns of biodiversity of fruit-feeding butterflies in a tropical forest in Uganda. *Biodiversity & Conservation*, 15 (1): 107-121.

Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S. & Mouquet, N. (2013). Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biol*, 11 (5): e1001569.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403 (6772): 853-858.

Norgaard, R. B. (2010). Ecosystem services: From eye-opening metaphor to complexity blinder. *Ecological economics*, 69 (6): 1219-1227.

Nyafwono, M., Valtonen, A., Nyeko, P. & Roininen, H. (2014). Butterfly Community Composition Across a Successional Gradient in a Human-disturbed Afro-tropical Rain Forest. *Biotropica*, 46 (2): 210-218.

O'Gorman, E. J., Yearsley, J. M., Crowe, T. P., Emmerson, M. C., Jacob, U. & Petchey, O. L. (2010). Loss of functionally unique species may gradually undermine ecosystems. *Proceedings of the Royal Society of London B: Biological Sciences*: rspb20102036.

Pardonnet, S. (2010). *Effect of tree-fall gaps on fruit-feeding Nymphalidae assemblages in a Peruvian rainforest.*

Pinheiro, C. E. & Ortiz, J. V. (1992). Communities of fruit-feeding butterflies along a vegetation gradient in central Brazil. *Journal of Biogeography*: 505-511.

Pollard, E. (1988). Temperature, rainfall and butterfly numbers. *Journal of Applied Ecology*: 819-828.

Pyrcz, T. W. & Wojtusiak, J. (2002). The vertical distribution of pronophiline butterflies (Nymphalidae, Satyrinae) along an elevational transect in Monte Zerpa (Cordillera de Mérida, Venezuela) with remarks on their diversity and parapatric distribution. *Global Ecology and Biogeography*, 11 (3): 211-221.

Pyrcz, T. W. (2004). Pronophiline butterflies of the highlands of Chachapoyas in northern Peru: faunal survey, diversity and distribution patterns (Lepidoptera, Nymphalidae, Satyrinae). *Genus*, 15 (4): 455-622.

Pyrcz, T. W. & Viloria, A. L. (2005). Adiciones a la fauna de mariposas de la reserva forestal de tambito (colombia): descripción de cuatro subespecies nuevas de la subtribu Pronophilina (Nymphalidae, Satyrinae). *Boletín Científico-Centro de Museos-Museo de Historia Natural*, 9: 258-277.

Pyrcz, T. W., Wojtusiak, J. & Garlacz, R. (2009). Diversity and distribution patterns of Pronophilina butterflies (Lepidoptera: Nymphalidae: Satyrinae) along an altitudinal transect in north-western Ecuador. *Neotropical Entomology*, 38 (6): 716-726.

R development Core Team. (2016). *R: A Language and Environment for Statistical Computing*. Computing, R. F. f. S. (ed.).

Ramos, F. A. (2000). Nymphalid butterfly communities in an amazonian forest fragment. *Journal of Research on the Lepidoptera*, 35 (1): 29-41.

Ripley, W. N. V. a. B. D. (2002). *Modern Applied Statistics with S*, Fourth. New York: Springer.

Roy, D. B., Rothery, P., Moss, D., Pollard, E. & Thomas, J. (2001). Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology*, 70 (2): 201-217.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B. & Kinzig, A. (2000). Global biodiversity scenarios for the year 2100. *science*, 287 (5459): 1770-1774.

Sanders, N. J. (2002). Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. *Ecography*, 25 (1): 25-32.

SAS Institude Inc. (2012). *The SAS system for Windows*. 9.4 ed. Cary, NC, USA.: SAS Intititude Inc.

Schulze, C. H., Waltert, M., Kessler, P. J., Pitopang, R., Veddeler, D., Mühlenberg, M., Gradstein, S. R., Leuschner, C., Steffan-Dewenter, I. & Tscharntke, T. (2004). Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecological Applications*, 14 (5): 1321-1333.

Singh, J. (2002). The biodiversity crisis: a multifaceted review. *Current Science*, 82 (6): 638-647.

Stevens, G. C. (1992). The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *The American Naturalist*, 140 (6): 893-911.

Tobar, L. (2000). *Diversidad de mariposas (Lepidoptera: Rhopalocera) en la parte alta del rio Roble (Quindío, Colombia).* Bogotá: Pontificia Universidad Javeriana, Basic Biology. 182 pp.

Tscharntke, T. & Brandl, R. (2004). Plant-insect interactions in fragmented landscapes. *Annual Reviews in Entomology*, 49 (1): 405-430.

Turner, I. (1996). Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of applied Ecology*: 200-209.

Veddeler, D., Schulze, C. H., Steffan-Dewenter, I., Buchori, D. & Tscharntke, T. (2005). The contribution of tropical secondary forest fragments to the conservation of fruit-feeding butterflies: effects of isolation and age. *Biodiversity and Conservation*, 14 (14): 3577-3592.

Viloria, A. L., Pyrcz, T. W. & Orellana, A. (2010). A survey of the Neotropical montane butterflies of the subtribe Pronophilina (Lepidoptera, Nymphalidae) in the Venezuelan Cordillera de la Costa. *Zootaxa*, 2622 (1): 1-41.

Weibull, A.-C., Östman, Ö. & Granqvist, Å. (2003). Species richness in agroecosystems: the effect of landscape, habitat and farm management. *Biodiversity and conservation*, 12 (7): 1335-1355.

APPENDIX 1

Appendix 1. Species and their abundance collected across different habitat types at La Mesenia and Montezuma, western Andes of Colombia. Number on the brackets correspond the percentage of the total capture.

Family	Sub-family	Species	Montezuma					La Mesenia					Total
			Altitude range (masl)	Primary forest	Secondary forest	Pasture	Sub-total	Altitude range (masl)	Primary forest	Secondary forest	Pasture	Sub-total	
Nymphalidae	**Biblidinae**	*Catonephele chromis*	1380-1435	5	2	1	8	2154-2247	1	1	1	3	11
		Panacea procilla	1351-1371		1	2	3						3
		Panacea prola	1351-1371		1	3	4						4
		Perisama humboldtii						2109- 2196			1	1	1
	Sub-total						**15**					**4**	**19**
	Charaxinae	*Archaeoprepona demophon*	1400-1448		1	2	3						3
		Fountainea nessus						2154 2247		1		1	1
		Memphis laura	1623-1696	1			1						1
		Memphis lyceus	1400-1448	3		1	4						4
		Memphis oenomais	1319-1360		1		1						1
		Memphis perenna	1351-1371			8	8						8
		Memphis philumena	1383-1437			1	1						1
		Memphis pseudiphis	1623-1696	1			1						1
		Narope anartes	1621-1703	1			1						1
		Prepona amydon	1351-1371			1	1						1
		Prepona laertes	1351-1371			2	2						2
	Sub-total						**23**					**1**	**24**
	Limenitidinae	*Adelpha cythera*	1383-1437			1	1						1
		Adelpha salmoneus	1400-1448			1	1						1
		Adelpha saundersii	1499-1602		1		1	2338- 2383		2		2	3
	Sub-total						**3**					**2**	**5**
	Morphinae	*Caligo brasiliensis*	1499-1602		1		1						1
		Caligo illioneus	1351-1371			1	1						1
		Caligo prometheus	1527-1575	1			1						1
		Catoblepia orgetorix	1439-1564	3			3						3
		Opsiphanes camena	1623-1696	2			2	2245-2299	1	1		2	4
		Opsiphanes cassina	1380-1435	2	1	1	4						4
		Opsiphanes quiteria	1380-1435		2	1	3						3
	Sub-total						**15**					**2**	**17**

Appendix 1. Continuation

Nymphalidae	**Nymphalinae**	*Colobura annulata*	1439-1564	1	1		2						2
		Eresia datis	1439-1564	1			1						1
		Historis acheronta	1351-1371			1	1						1
		Historis odious	1380-1435			3	3						3
		Hypanartia cinderella	1439-1564	1			1						1
		Tirgridia acesta	1319-1360		1		1						1
	Sub-total						**9**					**0**	**9**
	Satyrinae	*Cissia labe*	1351-1371			1	1						1
		Corades chelonis						2316-2401	3			3	3
		Corades pannonia	1581-1598	3	1		4						4
		Daedalma dianias						2465-2559	1			1	1
		Eretris apuleja						2481-2580	1			1	1
		Eretris lecromi	1499-1602		2		2						2
		Euptychoides griphe						2245-2299		3		3	3
		Forsterinaria inornata	1351-1371			1	1	2055-2128	6			6	7
		Forsterinaria neonympha	1319-1360	1	2	8	11						11
		Hermeuptychia hermes	1351-1371	1	5	639	645	2109-2196			16	16	661
		Lasiophila zapatoza						2055-2128	4	2		6	6
		Magneuptychia alcione	1351-1371		5	19	24						24
		Magneuptychia tiessa	1319-1360	3	4	8	15						15
		Manataria maculata	1319-1360	4	4	6	14	2465-2559	1			1	15
		Mygona irmina						2055-2128	16	1		17	17
		Oxeoschistus puerta	1319-1360	2	10		12	2154-2247		2		2	14
		Parataygetis lineata	1621-1703	13			13	2055-2128	12			12	25
		Pareuptychia metaleuca	1319-1360		10	1	11						11
		Pareuptychia ocirrhoe	1319-1360	1	22	1	24						24
		Pedaliodes manis						2168-2294		4	6	10	10
		Pedaliodes pacifica						2316-2401	5			5	5
		Pedaliodes sp 1						2338- 2383	1	1		2	2
		Pedaliodes sp 2						2609-2683	1			1	1
		Pirella helvina	1319-1360	5	1		6						6
		Pronophila orcus						2245-2299		1		1	1
		Pronophila unifasciata	1351-1371			5	5						5
		Pseudodebis celia						2055-2128	1			1	1
		Pseudohaetera mimica	1431-1529	6	3		9						9
		Taygetis asterie	1383-1437		6	1	7						7
		Taygetis chrysogone	1385-1448	8	7	1	16						16
		Taygetis thamyra	1431-1529		1		1						1
		Taygetomorpha celia	1351-1371	7	4	1	12						12
		Yphthimoides renata	1351-1371	2	8	59	69						69
	Sub-total						**902**					**88**	**990**
Riodinidae	**Riodininae**	Teratophthalma monochroma	1439-1564	1			1						1
	Sub-total						**1**					**0**	**1**
	Total			79	108	781	**968 (90.9)**		54	19	24	**97 (9.1)**	**1065**

APPENDIX 2

Appendix 2. Abundance of unique and rare species for each habitat at Montezuma and La Mesenia. Unique species are those present only in one habitat (Primary forest, secondary forest, Pasture) at a particular site or unique to a particular site (Sub-total). Rare species are those represented by ≤ 4 individuals.

Montezuma	**Primary forest**	**No.**	**%**	**Secondary forest**	**No.**	**%**	**Pasture**	**No.**	**%**	**Total**	**%**
Unique species	*Caligo prometheus*	1	1.3	*Adelpha saundersii*	1	0.9	*Adelpha cythera*	1	0.1	3	0.3
	Catoblepia orgetorix	3	3.8	*Caligo brasiliensis*	1	0.9	*Adelpha salmoneus*	1	0.1	5	0.5
	Eresia datis	1	1.3	*Eretris lecromi*	2	1.9	*Caligo illioneus*	1	0.1	4	0.4
	Hypanartia cinderella	1	1.3	*Memphis oenomais*	1	0.9	*Cissia labe*	1	0.1	3	0.3
	Memphis laura	1	1.3	*Taygetis thamyra*	1	0.9	*Forsterinaria inornata*	1	0.1	3	0.3
	Memphis pseudiphis	1	1.3	*Tirgridia acesta*	1	0.9	*Historis acheronta*	1	0.1	3	0.3
	Narope anartes	1	1.3				*Historis odious*	3	0.4	4	0.4
	Parataygetis lineata	13	16.5				*Memphis philumena*	1	0.1	14	1.4
	Teratophthalma monochroma	1	1.3				*Prepona amydon*	1	0.1	2	0.2
							Prepona laertes	2	0.3	2	0.2
							Pronophila unifasciata	5	0.6	5	0.5
Sub-total		23	29.1		7	6.5		18	2.3	48	5.0
Rare species	*Corades pannonia*	3	3.8	*Catonephele chromis*	2	1.85	*Archaeoprepona demophon*	2	0.3	7	0.7
	Forsterinaria neonympha	1	1.3	*Corades pannonia*	1	0.9	*Catonephele chromis*	1	0.1	3	0.3
	Hermeuptychia hermes	1	1.3	*Fosterinaria neonympha*	2	1.9	*Memphis lyceus*	1	0.1	4	0.4
	Magneuptychia tiessa	3	3.8	*Opsiphanes cassina*	1	0.9	*Opsiphanes cassina*	1	0.1	5	0.5
	Memphis lyceus	3	3.8	*Opsiphanes quiteria*	2	1.9	*Opsiphanes quiteria*	1	0.1	6	0.6
	Opsiphanes camena	2	2.5	*Panacea procilla procilla*	1	0.9	*Panacea procilla procilla*	2	0.3	5	0.5
	Opsiphanes cassina	2	2.5	*Panacea prola*	1	0.9	*Panacea prola*	3	0.4	6	0.6
	Oxeoschistus puerta	2	2.5	*Pirella helvina*	1	0.9	*Pareuptychia metaleuca*	1	0.1	4	0.4
	Pareuptychia ocirrhoe	1	1.3	*Pseudohaetera mimica*	3	2.8	*Pareuptychia ocirrhoe*	1	0.1	5	0.5
	Yphthimoides renata	2	2.5				*Taygetis asterie*	1	0.1	3	0.3
							Taygetis chrysogone	1	0.1	1	0.1
							Taygetomorpha celia	1	0.1	1	0.1
Sub-total		20	25.3		14	13.0		16	2.0	50	4.7

La Mesenia	**Primary forest**	**No.**	**%**	**Secondary forest**	**No.**	**%**	**Pasture**	**No.**	**%**	**Total**	**%**
Unique species	*Corades chelonis*	3	5.6	*Adelpha saundersii*	2	10.5	*Hermeuptychia hermes*	16	66.7	21	21.6
	Daedalma dianias	1	1.9	*Euptychoides griphe*	3	15.8	*Perisama humboldtii*	1	4.2	5	5.2
	Eretris apuleja	1	1.9	*Fountainea nessus*	1	5.26				2	2.1
	Forsterinaria inornata	6	11.1	*Oxeoschistus puerta*	2	10.5				8	8.2
	Manataria maculata	1	1.9	*Pronophila orcus*	1	5.26				2	2.1
	Parataygetis lineata	12	22.2							12	12.4
	Pedaliodes pacifica	5	9.3							5	5.2
	Pedaliodes sp 2	1	1.9							1	1.0
	Pseudodebis celia	1	1.9							1	1.0
Sub-total		31	57.4		9	47.4		17	70.83	57	58.8
Rare species	*Catonephele chromis*	1	1.9	*Catonephele chromis*	1	5.3	*Catonephele chromis*	1	4.2	3	3.1
	Lasiophila zapatoza	4	7.4	*Lasiophila zapatoza*	2	10.5				6	6.2
	Mygona irmina	16	29.6	*Mygona irmina*	1	5.3				17	17.5
	Opsiphanes camena	1	1.9	*Opsiphanes camena*	1	5.3				2	2.1
	Pedaliodes sp 1	1	1.9	*Pedaliodes sp 1*	1	5.3				2	2.1
Sub-total		23	42.6		6	31.6		1	4.2	30	2.8

APPENDIX 3

Appendix 3. Fruit feeding butterfly species and their code for the NMDS ordination analysis (Fig 9).

Species	Species Code	Species	Species Code
Adelpha cythera	AdCy	*Memphis pseudiphis*	MePs
Adelpha salmoneus	AdSa	*Mygona irmina*	MyIr
Adelpha saundersii	AdSa1	*Narope anartes*	NaAn
Archaeoprepona demophon	ArDe	*Opsiphanes camena*	OpCa
Caligo brasiliensis	CaBr	*Opsiphanes cassina*	OpCa1
Caligo illioneus	CaIL	*Opsiphanes quiteria*	OpQu
Caligo prometheus	CaPr	*Oxeoschistus puerta*	OxPu
Catoblepia orgetorix	CaOr	*Panacea procilla procilla*	PaPr
Catonephele chromis	CaCh	*Panacea prola*	PaPr1
Cissia labe	CiLa	*Parataygetis lineata*	PrLi
Colobura annulata	CoAn	*Pareuptychia metaleuca*	PaMe
Corades chelonis	CoCh	*Pareuptychia ocirrhoe*	PaOc
Corades pannonia	CoPa	*Pedaliodes manis*	PeMa
Daedalma dianias	DaDi	*Pedaliodes pacifica*	PePa
Eresia datis	ErDa	*Pedaliodes sp 1*	PeSp1
Eretris apuleja	ErAp	*Pedaliodes sp 2*	PeSp2
Eretris lecromi	ErLe	*Perisama humboldtii*	PeHu
Euptychoides griphe	EuGr	*Pirella helvina*	PiHe
Forsterinaria inornata	FoIn	*Prepona amydon*	PrAm
Fosterinaria neonympha	FoNe	*Prepona laertes*	PrLa
Fountainea nessus	FoNe1	*Pronophila orcus*	PrOr
Hermeuptychia hermes	HeHe	*Pronophila unifasciata*	PrUn
Historis acheronta	HiAc	*Pseudodebis celia*	PsCe
Historis odious	HiOd	*Pseudohaetera mimica*	PsMi
Hypanartia cinderella	HyCi	*Taygetis asterie*	TaAs
Lasiophila zapatoza	LaZa	*Taygetis chrysogone*	TaCh
Magneuptychia alcione	MaAL	*Taygetis thamyra*	TaTha
Magneuptychia tiessa	MaTi	*Taygetomorpha celia*	TaCe
Manataria maculata	MaMa	*Teratophthalma monochroma*	TeMo
Memphis laura	MeLa	*Tirgridia acesta*	TiAc
Memphis lyceus	MeLy	*Yphthimoides renata*	YpRe
Memphis oenomais	MeOe		
Memphis perenna	MePe		
Memphis philumena	MePh		

Norges miljø- og biovitenskapelig universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway