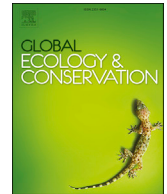


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Original Research Article

Temporal analysis of butterfly diversity in a succession gradient in a fragmented tropical landscape of Mexico

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ABSTRACT

We analyze changes in the diversity of butterflies under a scheme of secondary succession in a fragmented landscape of the Huasteca of Hidalgo, Mexico over two seasons (rainy and dry) and four successional stages (cattle pasture, early secondary succession, intermediate secondary succession and advanced secondary succession). We recorded a total of 3,559 individuals of 124 species of adult butterflies. A higher number of species (104) and higher abundance (2588 individuals) were found during the rainy season than the dry season. *Memphis pithyusa* was the most abundant species in all successional stages. We evaluated the effect of secondary succession and seasonality on the alpha diversity of butterflies through three orders of Hill numbers as measures of diversity (0D = species richness, 1D = measure of abundance in the community, and 2D = common species). We found that in q^0D , cattle pasture and early SS maintained the greatest diversity compared to the last two stages; in q^1D , early SS maintained the lowest diversity, which was significantly different from the rest of the stages; and in q^2D , we found the opposite pattern to q^0D ; the two most advanced stages were the ones that maintained the greatest diversity. Beta diversity analysis was conducted with abundance and species presence/absence data. Species composition was different between the rainy and dry seasons (both as evaluated by abundance and by species presence/absence). Species composition measured by abundance was different between the cattle pasture successional stage in the dry season and all other successional stages. Considering only presence/absence, species composition was different between the cattle pasture successional stage and all other successional stages in both seasons. Although our analysis lacks a primary forest for reference, we highlight here the importance of these secondary forests from Huasteca Region of Hidalgo State of Mexico as reservoirs of butterfly diversity. Considering that these forests generally maintain a close relationship with productive activities for human well-being, this would imply that they should be included in public policies for their maintenance and conservation.

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1. Introduction

The tropical rain forests of the world harbor high species diversity, approximately two thirds of the planet's terrestrial biodiversity (Gardner et al., 2009). These forests maintain a wide range of ecosystem services, provide 33% of the world's net primary terrestrial production, store around 25% of terrestrial carbon, and regulate global climate patterns, especially rainfall and temperature (Godoy et al., 2000; Ferraz et al., 2014). However, despite this, in the tropical forest changes from land use caused by agricultural activities have altered more than 50% of its original coverage worldwide (Gardner et al., 2009; Hooke and Martín-Duque, 2012). In Mexico, particularly for evergreen rainforests, there has been a documented a reduction of 61.54% of the original coverage of 17.82 to 9.47 million hectares for 2005 (of this 67% corresponds to secondary forests; for more details see Challenger and Soberon, 2008). Therefore, we currently observe landscapes with mosaics of forests embedded in matrices of agricultural areas, forest plantations and/or secondary forests at different stages of succession.

Studies on secondary succession have therefore become increasingly important, because they enable us to evaluate the biodiversity response to changing environmental conditions resulting from forest recovery (Guariguata and Ostertag, 2001). Especially in fragmented landscapes, these studies help us to understand the mechanisms and processes that regulate biodiversity in secondary forests (Barlow et al., 2007); it has even been argued that secondary forests can cushion biodiversity loss from deforestation (Brook et al., 2006; Wright and Muller-Landau, 2006; Gardner et al., 2007). However, many of these arguments come from a wide range of plant studies (Breugel et al., 2006; Lohbeck et al., 2015; Sanaphre-Villanueva et al., 2017), and little has been done regarding other taxonomic groups (Brown, 1984; Bowman et al., 1990).

Butterflies have been recognized as a suitable group for the study of the community's response to different environmental conditions (Bowman et al., 1990; Spitzer et al., 1993, 1997), which makes them a good model for studies of this type. However, few works in this vein have been conducted on secondary succession (Barlow et al., 2007). In some studies it has been found that primary forests usually contain a greater diversity of butterflies than secondary forests (Beck and Schulze, 2000; Barlow et al., 2007), while in others it has been found that young secondary forests have greater diversity than older forest (Beck and Schulze, 2000). However, none of these works shows the factors influencing patterns of change in the diversity of butterflies across successional gradients. In other works in secondary forests, no differences were found in species richness, marked differences were found in species composition (Hernández et al., 2014; Nyafwono et al., 2014).

Moreover, it has also been noted that in forest gaps, butterfly diversity can be higher than in closed forest, although this diversity is usually dominated by generalist butterflies, which can use other types of habitats that are generated from the succession (Spitzer et al., 1997). The presence of butterflies in landscapes dominated by secondary vegetation can be seen a favorable and important factor, because their presence implies that desirable pollinators are also present and their presence in turn also implies a reliable food source for many predators (e.g., insectivorous birds, frogs, mammals and spiders) within the site (Bawa et al., 1985; Price, 1997).

The Huasteca region of Mexico has been noted for being an important area for both crop and livestock farming (Rzedowski, 1962). Currently, its landscapes are shaped by a matrix of pasture, cropland and secondary vegetation zones (García-Morales, 2010), where the absence of large patches of original vegetation is notable, particularly in the northern area of the state of Hidalgo. Some studies in this region have documented that the species richness of bats does not vary much in fragments with different forest cover (Ávila-Gomez et al., 2015), but in other taxonomic groups, such as dung beetles, pastures have been found to maintain less diversity than secondary forest (Barragán et al., 2014). This leads us to assume that the environmental dynamics of the landscape (biotic and abiotic conditions) are what modulates the composition and distribution of communities, without this necessarily following a pattern related to the age of abandonment (Cowles, 1901).

In this study we evaluated diversity and species turnover of butterfly communities, comparing spatial and seasonal patterns in a chronosequence analysis (three successional stages from 1 to 30 years, and one site with active livestock). First we evaluate whether the secondary succession holds an increasing gradient in the diversity of butterflies, and a gradual change of species; second, we determine whether seasonality affects the relationship; and thirdly, we determine which environmental factors influence species composition during secondary succession.

2. Methods

2.1. Study site and field procedures

The fieldwork was carried out in the municipality of San Felipe Orizatlán in the Huasteca of Hidalgo, in the eastern region of Mexico (21° 10' 19" N, 98° 36' 23" W). This region has an average annual temperature of 24 °C and average annual rainfall of 1705 mm, and is characterized by plains and mountains, with an elevation range from 18 to 200 m.a.s.l. The climate is warm and humid semiwarm. The rainy season occurs from June to October with annual precipitation of 1200–3000 mm, and the dry season from November to April (Puig, 1991).

This part of the Huasteca is characterized by being a complex mosaic with areas of tropical forest in different states of ecological succession, as well as extensive livestock and crop farming areas, the latter mainly oranges. Originally the area was covered by extensive fragments of mid-elevation perennial forest, which at present are no longer found (Supplementary Material 1).

2.1.1. Study site selection

Selection of the study sites was based on environmental homogeneity, topographic and management history, and characteristics proposed by the CATIE (2016), such as basal area level, diameter distribution of trees, canopy structure, presence of lianas/epiphytes and presence of large logs and/or very large trees. Four stages were identified (Table 1). Three replicates were sought to represent each of the stages of succession, attempting to distribute sampling sites throughout the landscape. Due to the complexity of the landscape, these replicates were chosen, as much as possible, to be at least 1500 m apart (see Supplementary Material 1), in order that the sampled butterfly communities be as independent as possible.

2.1.2. Sampling design

At each site, a 100 m-long transect was drawn (12 transects for the entire chronosequence). The specimens of diurnal butterflies were recorded and sampled by a two methods: (i) Five traps (similar to Van Someren-Rydon traps), which are used principally for species of the Nymphalidae family (Torres et al., 2009), baited with fermented fruit (orange and banana), were placed every 25 m at a height of 1.5 m above the ground. Each trap was left for three days, and reviewed daily between 9 a.m. and 12 p.m. (Martínez-Sánchez and Vázquez-Mendoza, 2010). This method is complementary to the use of entomological nets and necessary in population and community studies (Andrade-C, 2013). (ii) The second method was the use of entomological nets. The butterflies were collected in a circle with a 5 m radius, with the trap in the center. Sample collection was recorded for 25 min (one session per day). All specimens were identified at the species level. The use of both methods maximizes the capture of individuals regardless of their eating habits.

Sampling was carried out during the dry season (April) and rainy season (August) of 2017, for a total of 18 effective days of sampling (3 sites \times 3 days \times 2 seasons) for each stage of the succession. Most of the material collected was identified in the field with the support of specialized guides; Pyle (1981), Garwood and Lehman (2005), and Sada and Madero-Farías (2011). Taxonomic identity was corroborated with the support of specialists from the Universidad Autónoma del Estado de Morelos (Dr. Luc Legal) and Instituto Tecnológico de Ciudad Victoria (Dr. Jesús García Jiménez), both in Mexico. A website devoted to the study and enjoyment of American butterflies was also consulted; <https://www.butterfliesofamerica.com> (Butterflies of America, 2018).

2.1.3. Environmental characterization

At the local level, the canopy was characterized for each sampling station. Canopy image analysis techniques (Plant Canopy Analysis System CI-110) were used to record solar rays, leaf area index, and transmission coefficient. Physical-environmental parameters were also measured; temperature, humidity, and luminosity, with the use of HOBO-type sensors (HOBO U23 Series Pro v2 Loggers).

The landscape level was categorized in a 500-m buffer zone around each site, using the land use and vegetation map of the 1:250,000 INEGI series (2014), and the CONABIO geoinformation website, the DigitalGlobe orthophoto of Google Earth and the coordinates of the sampling points in UTM projection. Land use was mapped using AutoCAD vector drawing software. Soil type percentage data were obtained for the buffer areas, using CivilCAD.

2.2. Data analysis

2.2.1. Completeness of the sampling

We assessed the completeness of inventories at two levels of analysis: total diversity, and diversity in the dry and the rainy season, for each successional stage. We calculated sample coverage, which is a measure of inventory completeness that gives the proportion of the total number of butterflies in a community that belong to each species represented in the sample. Sample coverage is based on the total number of butterflies recorded, and on the number of rare species, particularly singletons (f_1) and doubletons (f_2), which are the species represented by one and two individuals respectively. Coverage takes on values from 0 to 100; when it is close to 100%, the sample is more complete and diversity values (qD) can be compared directly (Chao and Jost, 2012). For these analyses, we used R version 3.5.2 (R Core Team, 2018), employing the SpadeR package (Chao et al., 2016). This analysis was complemented with rank-abundance curves, which make it possible to describe the relationship between populations of species for each stage of succession, and identify rare, abundant and very abundant species (see Whittaker, 1972).

Table 1

Description of the main characteristics of pasture and successional stages used for this study.

Cattle pasture	Early secondary succession (early SS)	Intermediate secondary succession (intermediate SS)	Advanced secondary succession (advanced SS)
- Are active paddocks mainly for cattle	- Sites with 2–10 years abandonment of farming activities	- Sites with 10–20 years abandonment of farming activities	- Sites with more than 30 years of abandonment of farming activities
- Presence of native trees inside	- Generally with a regular canopy	- Regular canopy	- Canopy at different heights
- Live fences	- Few open areas	- Some clearings within the forests	- Well-defined forest clearings
	- Absence of trees with large trunks	- With few tall trees, as well as some liana presence	- Presence of spiny lianas

2.2.2. Species diversity

For analysis of alpha diversity, we compare the magnitude of change between communities in each stage of the secondary succession and season. We combined all the information obtained from 3 day at each of five experimental stations, and adopt the analytic method of [Chao and Jost \(2015\)](#) to obtain diversity profiles in which diversity is evaluated in terms of “effective numbers of species” (qD), an approach that is equivalent to Hill’s numbers ([Hill, 1973](#)). The exponent q determines the influence of species abundance on diversity values and ranges from 0 to infinity ([Jost, 2006](#)). In this study, we use three orders: 0D measures species richness; 1D (exponential of Shannon’s index) assumes that the weight of a particular species is proportional to its abundance in the community; and 2D (the inverse of the Simpson index) is based mainly on the most common species ([Jost, 2006](#); [Moreno et al., 2011](#)). Also following the proposal of [Chao and Jost \(2015\)](#), we apply a novel analytic method to obtain accurate, continuous, low-bias diversity and entropy profiles with a focus on low orders of q ($0 \leq q \leq 3$). For $q = 0$, their estimator reduces to the Chao1 estimator; for $q = 1$, their estimator reduces to the Shannon diversity estimator proposed in [Chao et al. \(2013\)](#); and for $q = 2$, their estimator reduces to the inverse of the minimum variance unbiased estimator of the Simpson index; see [Gotelli and Chao \(2013\)](#). We obtained 95% confidence intervals calculated using a bootstrap method based on 1000 replications. For these analyses, we used R version 3.5.2 ([R Core Team, 2018](#)), employing the SpadeR package ([Chao et al., 2016](#)).

2.2.3. Beta diversity

Beta diversity analysis was carried out from a spatial approach (comparing the different stages of ecological succession) and a temporal approach (comparing the two seasons of the year: rainy and dry). For this analysis we followed Baselga’s proposal ([2010 and 2013](#)), which suggests using two types of analysis: 1) with species abundance (beta.bray) and 2) with species presence–absence data (beta.jac).

For beta.bray, Baselga divides total β diversity into two independent components: i) beta.bray.bal (balanced variation in abundance), in which individuals of some species at one site are substituted for the same number of individuals of different species in another site; and ii) beta.bray.gra (abundance gradients), in which some individuals are lost from one site to the other. For beta.jac, total β diversity is divided into two components: i) beta.jne (nestedness), which occurs when the biotas of sites with smaller numbers of species are subsets of the biotas at richer sites; and ii) beta.jtu (spatial turnover), in which some species are replaced by others as a consequence of environmental sorting or spatial and historical constraints. For more details, see [Baselga \(2010, 2013\)](#) and the references cited there.

To partition beta diversity into its components, the “betapart” R package was used ([Baselga and Orme, 2012](#); [R Core Team, 2018](#)). Both the “beta.pair” function (used to calculate measures between pairs of sites) and “beta.multi” (used to calculate matching measures between multiple sites) were used for analysis of abundance and presence of species. These analyses were graphically represented using NMDS (non-metric multidimensional scaling), and the significance of these similarities was evaluated by a permutational multivariate analysis of variance (PERMANOVA), using PAST 2.07 ([Hammer et al., 2001](#)).

2.2.4. Environmental factors

To explore the relationship of environmental factors (at the landscape and local level) with the values of diversity (0D , 1D and 2D) between the sites of each stage of the secondary succession, we calculate Spearman rank order correlations. For this analysis, we used the diversity data obtained at each sampling site separating them by seasons of the year ($n = 24$); these were correlated with the environmental variables obtained at the local and landscape level. For this analysis we used the “MASS” and “ggplot2” R packages.

3. Results

We registered a total of 3,559 individuals of 124 species of adult butterflies. The species were distributed in the families *Hesperiidae* (subfamily *Eudaminae*, *Hesperiinae* and *Pyrginae*), *Lycaenidae* (subfamily *Polyommatae* and *Theclinae*), *Nymphalidae* (subfamily *Apaturinae*, *Biblidinae*, *Charaxinae*, *Cyrestinae*, *Danainae*, *Heliconiinae*, *Ithomiini*, *Libytheinae*, *Limenitidinae*, *Nymphalinae* and *Satyrinae*), *Papilionidae* (subfamily *Papilioninae*), *Pieridae* (subfamily *Coliadinae* and *Pierinae*), and *Riodinidae* (subfamily *Riodininae*) (Supplementary Material 2).

The sample coverage estimator indicated that our inventories were 95–98% complete. In [Table 2](#), we give the observed and proposed diversity estimates (by [Chao and Jost, 2015](#)) and confidence intervals for $q = 0, 1$ and 2 for each successional stage and season. We can see that the confidence intervals overlap between the two measures for all cases, which means that there are no significant differences between the two methods.

The uniformity in the distribution of species abundance of diurnal butterflies is indicated by the slope of the rank-abundance curve. Only cattle pasture and early SS in the rainy season showed a steeper slope. The rest of the stages, including all those of the dry season, presented a gradual slope in their abundances, but with a predominance of rare species (that is, species represented by one or by two individuals; [Fig. 1](#)). In the rainy season cattle pasture had 55% of the species ($n = 20$), early SS 59% ($n = 25$), intermediate SS 47% ($n = 13$) and advanced SS 58% ($n = 16$). In the dry season cattle pasture had 47% of the species ($n = 12$), early SS 62% ($n = 12$), intermediate SS 46% ($n = 9$) and advanced SS 60% ($n = 14$) ([Fig. 1](#)).

In the rainy season, *Memphis pithyusa* was the most abundant species in all stages of secondary succession, with 369 individuals in cattle pasture (54%), 678 individuals in early SS (61%), 144 individuals in intermediate SS (32%) and 93 individuals in advanced SS (26%). In the dry season the most abundant species in cattle pasture was *Hermeuptychia hermes*

Table 2

Abundance, diversity (⁰D, ¹D and ²D) observed (cumulative data for the three replicates) and estimated by Chao and Jost method (2015). The completeness of inventories (sample coverage) of diurnal butterflies of the Huasteca of Mexico is also shown for different successional stages and seasons of the year.

Suc. Stages	Abun	⁰ D		¹ D		² D		Sample Coverage
		Observed	ChaoJost	Observed	ChaoJost	Observed	ChaoJost	
Cattle pasture								
All	834	68 (61.2–74.8)	90 (63–1117)	14 (12.3–15.7)	14.8 (13.0–16.7)	4.7 (4–5.3)	4.7 (4.1–5.3)	0.97
Rainy season	684	56 (50.1–61.9)	74.1 (50.4–97.9)	9 (7.8–10.2)	9.6 (8.3–10.9)	3.3 (2.9–3.7)	3.3 (2.9–3.7)	0.97
Dry season	150	32 (26.6–37.4)	55.8 (12.8–98.8)	19.6 (16.3–22.8)	23.6 (18.6–28.5)	13.6 (10.5–16.7)	14.8 (11.1–18.5)	0.92
early SS								
All	1337	69 (60.1–77.2)	115.5 (67–164)	7.7 (6.9–8.4)	8 (7.2–8.9)	3.2 (2.9–3.4)	3.2 (2.9–3.4)	0.98
Rainy season	1106	59 (53.1–64.9)	90.2 (35.3–145)	5.9 (5.4–6.5)	6.2 (5.6–6.8)	2.5 (2.4–2.7)	2.5 (2.4–2.7)	0.98
Dry season	231	26 (21.0–30.9)	43.9 (4.5–83.3)	9.4 (8.1–10.8)	10.4 (8.8–12.0)	6.2 (5.3–7.1)	6.3 (5.4–7.3)	0.95
intermediate SS								
All	724	49 (42–56)	85.1 (35–135)	12.4 (11–13.7)	13.1 (11.6–14.6)	6.9 (6.2–7.5)	6.9 (6.3–7.6)	0.98
Rainy season	445	34 (28.0–40.0)	62.1 (9.1–115)	9.8 (8.5–11.1)	10.5 (8.9–12.0)	5.9 (5.1–6.7)	6.0 (5.2–6.8)	0.97
Dry season	279	28 (23.7–32.3)	38.1 (14.3–61.9)	9.3 (8.0–10.5)	10.0 (8.5–11.4)	4.7 (3.7–5.7)	4.7 (3.7–5.7)	0.97
advanced SS								
All	664	49 (43.3–54.6)	61.8 (39.4–84.2)	11.3 (10–12.6)	11.9 (10.5–13.3)	6.2 (5.6–6.9)	6.3 (5.6–6.9)	0.98
Rainy season	353	34 (28.0–40.0)	59.5 (9.3–109)	9.7 (8.3–11.1)	8.9 (12.2–9.7)	6.1 (5.4–6.9)	5.5 (7.0–6.1)	0.96
Dry season	311	35 (29.4–40.6)	48.9 (12.4–85.5)	10.2 (8.5–12.0)	9.2 (13.1–10.2)	5.5 (4.5–6.5)	4.5 (6.6–5.5)	0.96

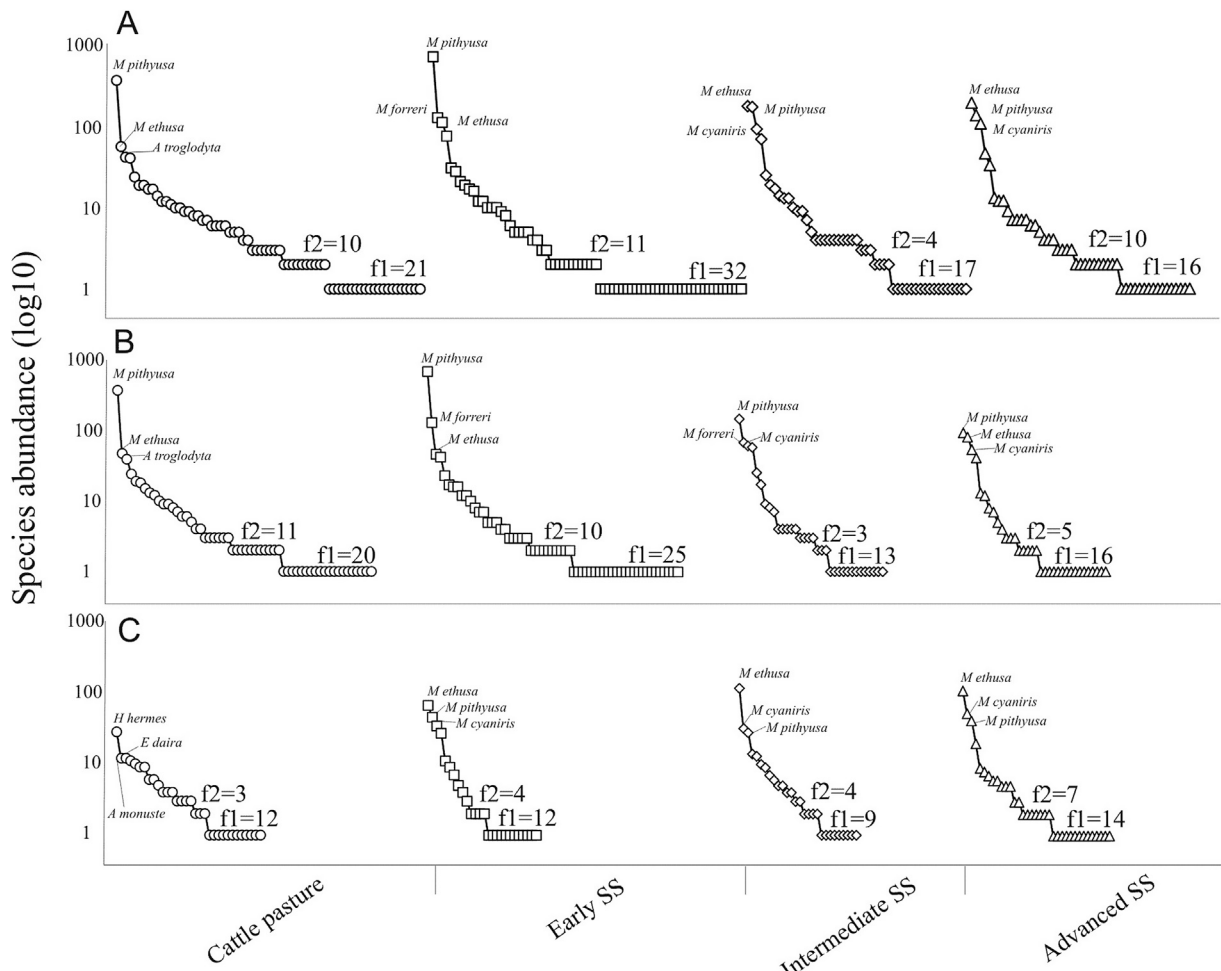


Fig. 1. Rank-abundance curves of diurnal butterfly communities for the four stages of secondary succession in a tropical forest of the Huasteca of Hidalgo. For all stages of secondary succession (A), and separated by rainy season (B) and dry season (C).

($n = 28$ individuals; 9%), and the most abundant species for all the other stages was *Myscelia ethusa*, with 66 individuals (44%) in early SS, 119 individuals (52%) in intermediate SS, and 111 individuals (40%) in advanced SS (Fig. 1).

3.1. Alpha diversity

The rainy season had a higher number of species (104) and a greater abundance (2588 individuals), while in the dry season there were 69 species and 971 individuals. We found that the early SS stage had the greatest richness and abundance (69 species and 1337 individuals; Table 2). In q^0D we found that the first two stages (cattle pasture and early SS) had the greatest diversity and these were significantly different (with 95% confidence intervals) with respect to the last two stages (intermediate SS and advanced SS). For q^1D we found that early SS had the lowest diversity, which was significantly different from the rest of the stages. We found the opposite pattern for 2D diversity as with q^0D ; the two most advanced stages were the ones that had the greatest diversity (Fig. 2, Table 2).

With respect to seasonality (rainy and dry season) we only found significant differences between the two seasons in cattle pasture and early SS, in the entire diversity profile (0D , 1D and 2D ; Fig. 2). Within seasons, in the rainy season, the confidence intervals for cattle pasture and early SS showed significant differences in q^0D diversity compared to the rest of the rainy season. For this same diversity metric, in the dry season there were no significant differences between any of the stages (Fig. 2, Table 2).

For the analysis based on the values of the effective number of species (1D index; Shannon exponential), we found significant differences in the dry season for cattle pasture compared to all other stages of the same season, while in the rainy season, only early SS was significantly less than all the other stages (Fig. 2, Table 2).

In the analysis of 2D diversity values (inverse of the Simpson index), significant differences were found in the first two stages (cattle pasture and early SS) compared to the final two stages of the succession (intermediate SS and advanced SS), but in the rainy season these first two stages were smaller than the final two stages, while in the dry season the initial stages had the highest values (Fig. 2, Table 2).

3.2. Beta diversity

Species composition was different between the rainy season and the dry season, both as measured by abundance (stress = 0.12; PERMANOVA: $F = 5.16$, $p = 0.0001$) and by presence/absence of species (stress = 0.22; PERMANOVA: $F = 3.33$, $p = 0.0001$) (Fig. 3a and 3c). Species composition measured by abundance was different between cattle pasture in the dry season and all other successional stages (PERMANOVA: $F = 2.16$, $p = 0.0002$), with dissimilarity values of 86% and 87%. In

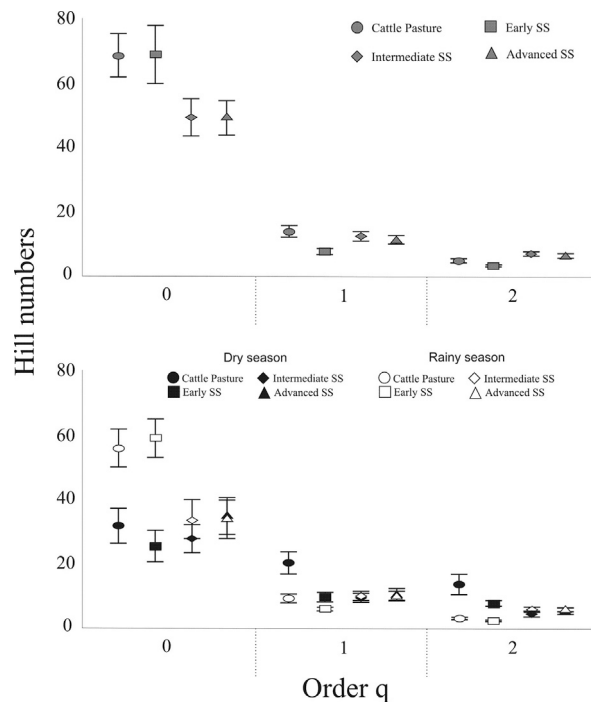


Fig. 2. Diversity profiles alpha of order (0D , 1D and 2D) of butterflies of the tropical forest of the Huasteca of Hidalgo Mexico, along the gradient of secondary succession and by season (dry and rainy). The lines represent 95% confidence intervals.

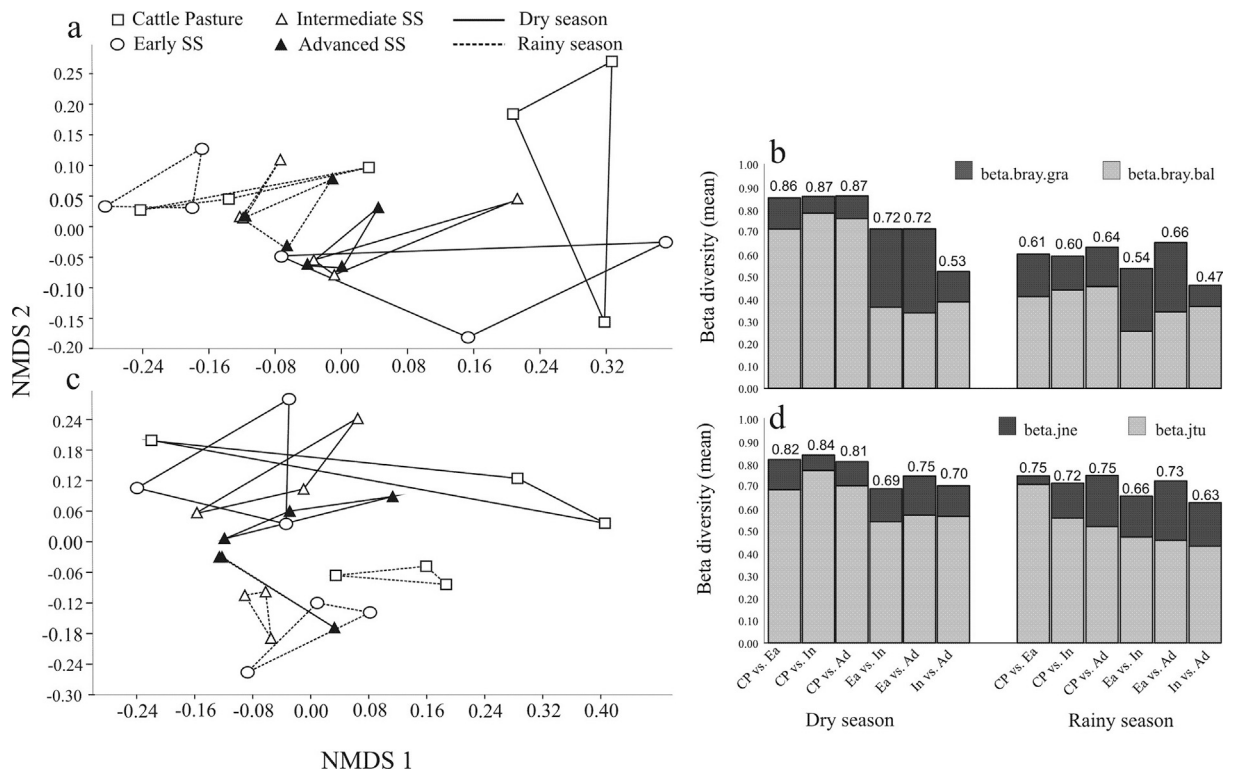


Fig. 3. Analysis of spatial beta diversity between the stages of secondary succession in a tropical forest of the Huasteca of Hidalgo. Using abundance data, we show (a) NMDS and PERMANOVA through the Bray-Curtis index, and (b) one analysis which shows the dissimilarity derived from unidirectional abundance gradients (beta.bray.gra) and from balanced variation in abundance (beta.bray.bal). (c) Also shown are the NMDS and PERMANOVA analyses with presence/absence data, through the Jaccard index, and (d) analysis which shows the dissimilarity derived from turnover (beta.jtu) or by nestedness (beta.jnc).

almost all comparisons of beta diversity, the dissimilarity between stages was given by the beta.bray.bal component (balanced variation in abundance) (Fig. 3b). Species composition as measured only by presence/absence was different between the cattle pasture stage in both seasons and all other successional stages (PERMANOVA: $F = 1.73$, $p = 0.0002$), reaching values of dissimilarity above 80% in the dry season and 75% in the rainy season, and this dissimilarity was highly influenced by spatial turnover (Fig. 3b and 3d).

3.3. Environmental variables

Variables recorded at the landscape level, correlated against diversity values, showed that for the rainy season only abundance presented a significant negative relationship ($r = -0.74$, $p < 0.05$) with the percentage of secondary vegetation in the landscape. In the rainy season the 1D and 2D values of diversity were negatively correlated ($r = -0.12$, $r = -0.22$ respectively) with the percentage of grassland in the landscape (Table 3).

On the other hand, when correlations were made with the local variables, we found that only in the dry season were there significant differences ($p < 0.05$); luminosity presented significant correlations with 0D ($r = -0.79$), 1D ($r = -0.71$) and 2D ($r = -0.64$); temperature with abundance and 2D ($r = 0.59$ and $r = -0.58$, respectively); and solar radiation with abundance ($r = -0.57$; Table 3).

4. Discussion

In Mexico, approximately 1825 species of diurnal butterflies have been reported (Llorente-Bousquets et al., 2014). In our study we found 124 species, which represents 6.8% of the total. It is difficult to compare our results with previous work due to methodological differences; however, the number of species registered in other tropical forests of Mexico such as Los Tuxtlas and Calakmul in the south of the country (146 and 123 species respectively; Raguso and Llorente-Bousquets, 1990; Maya et al., 2005) show the importance of the Huasteca region as a zone of high Lepidoptera diversity. Although we did not achieve high completeness of sampling in all communities, since insects are highly seasonal and in the case of butterflies, very diverse, the results of the analysis of sample coverage (based on the total number of butterflies registered and the number of rare species), as well as the results of comparisons between the observed and estimated diversity of Chao and Jost (2015), mean that it is

Table 3

Spearman rank order correlations between environmental variables (local and landscape) against the diversity values of diurnal butterflies in the Huasteca region of Mexico, separated by the rainy and dry seasons. The asterisk (*) indicates significant correlations at a significance level of $p < 0.05$.

Scale	Environmental variable	Dry				Rain			
		Abun	⁰ D	¹ D	² D	Abun	⁰ D	¹ D	² D
Landscape	Pastureland (%)	0.47	0.18	-0.12	-0.22	0.28	-0.03	-0.63*	-0.72*
	Crops (%)	0.33	0.15	0.03	0.08	-0.21	-0.25	0.15	0.43
	Other land use (%)	0.18	-0.19	-0.33	-0.38	-0.06	-0.13	0.15	0.36
	Secondary vegetation (%)	-0.74*	-0.15	0.19	0.26	-0.11	0.17	0.31	0.12
Local	Temperature	0.59*	-0.26	-0.57	-0.58*	0.39	-0.09	-0.41	-0.26
	Humidity	0.45	0.33	-0.02	-0.10	-0.25	-0.15	0.10	0.03
	Luminosity	-0.26	-0.79*	-0.71*	-0.64*	0.36	0.56	0.11	-0.19
	Leaf area index	0.39	0.25	0.10	0.01	-0.50	-0.21	0.13	0.17
	Transmission coefficient	0.27	-0.21	-0.32	-0.26	0.07	0.14	0.00	0.22
	Solar rays	-0.57*	0.03	0.29	0.33	-0.22	0.26	0.48	0.24

possible to make adequate comparisons between butterfly communities along a gradient of secondary succession and between seasons.

Only 15% of the sampled species were present in all stages of succession. *Memphis pithyusa* (1402 individuals) and *Myscelia ethusa* (537 individuals) were the most abundant species. These species have morphological characteristics that enable positive mimicry, which can provide a defense against predators. In addition, the larvae feed on Euphorbiaceae (BMNA, 2018), which have toxins that confer additional protection to these species. These factors may be helping the populations of both species increase with respect to other species, although it could also be a sampling effect since they are a large and very colorful species, so they could be detected more frequently in the sampling. It can also be seen that the intermediate and advanced SS stages do not change their butterfly population structure very much between the dry and rainy seasons, even conserving the same group of dominant species and a similar number of rare species. In contrast, in the cattle pasture and early SS stages, there is more change in the structure, which is more evident in early SS stages, even a total change of the dominant species between seasons. This leads us to suppose that the more advanced stages of succession are serving as a refuge for butterflies in the face of resource scarcity scenarios, which is the case in the dry season, while in the rainy season the high number of butterflies that were observed in the cattle pasture and early SS stages may be due to the presence of visiting species, due possibly to abundant resources in these habitats, since there are more flowering plants in this season.

The diversity profile showed an interesting change from ⁰D to ²D diversity. In the former, where only species richness is considered, it is seen that cattle pastures and early SS present the greatest diversity, while with ²D diversity (dominant species), this pattern is reversed and here the advanced and intermediate stages of succession were the most diverse; this pattern is also seen in the rainy season. As in other works (see Nyafwono et al., 2014), our diversity analysis showed no directional gradient of increased diversity of diurnal butterflies during secondary succession. We found only marginal evidence of an increase in ⁰D diversity in the dry season, and in ¹D and ²D diversity in the rainy season. These results contrast with the original studies on succession, which indicate that during secondary succession, the number of species increases and often also the diversity (Margalef, 1997). Our findings can be explained by the particularities of this part of the Huasteca region of Mexico, where the absence of any fragments of original vegetation is evident. This means that to a certain degree, older secondary forests fulfill the function of original forest. But these secondary forests do not have the capacity to provide the full range of services that a forest with original vegetation could offer, which leads the butterfly species to use other fragments of landscape, such as low impact productive lands (livestock pastures and cropland). Newer forests in secondary successional stages thus play an important role in the landscape, this being the phase that connects the transition of mature secondary vegetation with the productive activities that take place in this area. This successional stage may have increased butterfly diversity at moderate levels of disturbance, as has been noted by several authors (Connell, 1978; Janzen, 1987; Willott et al., 2000).

We find that seasonality is also an important regulator in the temporal changes in butterfly diversity in the landscape. But these changes were not consistent through the analysis of the diversity profile; for example, in the rainy season, sites with farming activity, along with sites in the initial stages of succession, showed the highest ⁰D diversity, while in the dry season changes of diversity in the succession were not evident. But with the ¹D and ²D diversity analysis, this pattern was different, and in the dry season we can find that the greatest diversity occurs in the early stages of succession and even in the rainy season as ²D diversity (in the early stages) decreases significantly. The pattern that did appear is that the cattle pasture and early SS stages presented more changes by this diversity measure. This can be explained by the marked environmental differences caused by seasonality (rainy and dry season), since, for example, in rainy season the environmental conditions are more favorable and there is more opportunity for a wide variety of niches to be generated than in the dry season (Lorente-Bousquets and Luis-Martínez, 1993; Barlow et al., 2007; Pozo et al., 2008; Luna-Reyes et al., 2010). In addition, butterflies have a seasonal distribution with abundance peaks determined by precipitation (Raguso and Lorente-Bousquets, 1990; Maya et al., 2005).

For the beta diversity analysis, the clearest differences in species composition were between seasons, the rainy season contributing 44%, the dry season 16%, and the two seasons sharing only 40% of species. In the dry season, there was greater

overlap in the composition of butterfly communities between the stages of succession, while in the rainy season, the overlap was lower, particularly between the cattle pasture and early SS stages compared to the other two stages (this pattern was observed with both presence/absence data and abundance). This latter observation may be particularly affected by two factors. The first can be identified by seeing that the beta value is given to a greater extent by species turnover; that is, each stage shows a significant number of species unique to the stage and few shared species, especially between cattle pasture and the early SS stage compared to the other stages. The second factor can be identified by seeing that the beta value was given a greater proportion in the balanced variation of abundance ($\beta_{\text{bray}}_{\text{bal}}$), which means that variation in species abundances is perfectly balanced; that is, abundance increases in some species are matched by decreases in other species (Baselga, 2017).

We can observe a high number of exclusive species in single stages of succession (67 species, corresponding to 54% of total species). The cattle pasture and early SS stage had the highest percentage of exclusive species (48%, 32 species and 30%, 20 species, respectively). Most of these species are considered rare, because there were only one or two species records (21 species in cattle pasture and 18 species in early SS). On the other hand, if we compare the species present in cattle pastures against the secondary forest (made up of all other stages of succession), we observe that the secondary forest has a greater number of exclusive species (56 species), which would represent 45% of the diversity present. This leads us to think that at the landscape level, grazing, cutting, low-intensity burning regimes, and bush intrusion prevention, among other factors, may be necessary, but the presence of secondary forests is essential for the presence of butterflies, since these forests can be considered as the source of the species diversity pool, since maintaining particular host plants or shade regimes can provide the right balance of resources for larvae and adults (New et al., 1995).

It has also been shown there are environmental variables that are closely related to the presence and abundance of butterflies, such as daily radiation, relative humidity and temperature (Schwartz-Tzachor et al., 2008), which together shape suitable microhabitats for these organisms. Our analysis shows that at least temperature and luminosity have an effect on diversity (in the dry season), which is probably because butterflies are forced to seek refuge in covered areas, so as not to be exposed to higher levels of temperature and light, since it is likely to affect their ability to move and therefore decreases the presence of individuals. Finally, although we do not measure it, there is another factor, which is the strong relationship between lepidopterans and their host plants, especially at the larval level (Hernández et al., 2014; Nyafwono et al., 2014). This can also be decisive, such that a butterfly community may or recover or not during secondary succession. Therefore further research following from our investigation would be to consider the larval stage of the group and the relationship with host plants. This would expand our knowledge about the assembly of butterflies during the secondary succession.

5. Conclusions

Our results show that diurnal butterfly diversity from the Huasteca region of Mexico (study region) does not have a linear relationship with the progress of secondary succession, since maximum diversity appears in the younger stages of the succession, reaching an intermediate level in mature stages of succession. These results enable us to understand the internal mechanisms of movement of species within secondary forests and we cannot identify one age as more important than another. What we can say is that the older stages provide greater stability to the system, since their richness and diversity are not affected by seasonality, so they are potential sites for the butterflies to use as a refuge when environmental conditions are adverse.

Although our analysis lacks a primary forest of reference, we can highlight the importance of these secondary forests in the Huasteca Region of Hidalgo as reservoirs of butterfly diversity. It should be noted that this implies that proper management at the landscape level can generate suitable conditions to house these and other organisms.

Today we are facing vast and rapid changes in the original land cover, which are continuously modifying the landscape structure. In Mexico, there are very few regions that host large areas of primary tropical forest in good condition; however, secondary forests are gaining more and more ground, so they could be an important alternative to cushion the loss of biodiversity. These forests generally maintain a close relationship with productive activities for human well-being, which makes their inclusion vital in public policies for their maintenance and conservation.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00847>.

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