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DISTRIBUTION PATTERNS OF CHARAXINAE (LEPIDOPTERA: NYMPHALIDAE) IN YUCATAN PENINSULA, MEXICO

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ABSTRACT. The objectives of this work were to ascertain which environmental, anthropogenic or geographic factors influence the present distribution of Charaxinae in Yucatan Peninsula and to identify distribution patterns which might be linked to biological conservation in the region. We obtained records from collections, literature and field, and analyzed the data with DCA and CCA. We analyzed both matrices, species data (17 species, 151 sites) and environmental data (11 independent variables, 151 sites). Six environmental, physiographic and anthropic descriptors, namely latitude, distance to Caribbean coast, mean annual temperature, distance to present-day urban settlements, altitude, and humidity were statistically significant. Distribution abundance of Charaxinae was higher towards north and south and lower in mid-latitude of the Yucatan Peninsula. We discerned five distribution patterns of Charaxinae in Yucatan Peninsula; each one formed by different species and with different optima along those six variables, confirming that seven species are indicative of conserved environments. We obtained distributional limits for some species according to latitude and humidity (*Anaea troglodyta aidea*).

Key words: Biodiversity, butterflies, conservation, ecological biogeography, humidity gradient, indicator species, latitude, multivariate analysis.

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RESUMEN. El objetivo de este trabajo fue reconocer qué factores ecológicos, antrópicos o geográficos determinan la distribución actual de los Charaxinae en la península de Yucatán e identificar los patrones de distribución que sean útiles para la conservación biológica del la región. Se obtuvieron registros de colecciones biológicas, literatura y campo y se analizaron los datos por medio de DCA y CCA, a partir matrices de datos de especies (17 especies por 151 sitios) y de datos ambientales (11 variables

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independientes por 151 sitios). Seis descriptores ecológicos, fisiográficos y antrópicos, denominados latitud, distancia a la costa del Caribe, temperatura, distancia a los centros urbanos actuales, altitud y humedad fueron estadísticamente significativos. La abundancia general de Charaxinae presentó una relación con la latitud de la Península, teniendo valores mayores hacía las latitudes extremas y una disminución hacia el centro. Se obtuvieron cinco patrones de distribución de los Charaxinae en la península de Yucatán, cada uno formado por diferentes especies y con diferentes óptimos a lo largo de las seis variables independientes seleccionadas, se confirmó que siete especies son indicadoras de ambientes conservados. Se obtuvieron límites de distribución para algunas de las especies según la latitud y la humedad, en particular para *Anaea troglodyta aidea*.
Palabras clave: Biodiversidad, mariposas, conservación, biogeografía ecológica, gradiente de humedad, especies indicadoras, latitud, análisis multifactorial.

INTRODUCTION

Distribution and abundance patterns of organisms depend on several factors, either ecological-environmental (recent or past), geographical, historical, or related to extinction-recolonization (peninsular effect). However, biogeography studies, either ecological or historical, usually use only one kind of (potentially) explanatory variables; analyses that combine ecological and historical approaches are not very common (Simpson 1964; Lee 1980; Murray *et al*. 1999; Cowley *et al*. 2001a; Cowley *et al*. 2001b; Espadas-Manrique *et al*. 2003; Matter *et al*. 2003; Espadas-Manrique 2004; Wiens & Donoghue 2004). In this work we present a biogeography analysis with an ecological approached, in which we considered conditions of the Yucatan Peninsula (YP) that are related to the development and distribution of the butterflies; the humidity (precipitation and evapotranspiration) gradient, decreasing from south to north, is a major factor explaining the distribution of other kind of organisms (Mandujano *et al.* 2008). The geological youth of the northern and eastern parts of YP (Pleistocene) is another relevant factor (Delgadillo 1984; Schmitter-Soto & Salazar-Vallejo 1993; Pozo *et al.* 2003; White & Hood 2004).

We consider a series of independent variables (environmental, ecological, geographical and anthropic), to explain the distributional patterns of Charaxinae in this region, based on the hypothesis that this distribution is influenced not only by the present-day conditions in YP, but also by the Mayan culture pressure and the geologic age of YP. We analyze presence-absence of species, and patterns of richness and abundance, which are determined by environmental heterogeneity (Brown & Opler 1990; Murray *et al*. 1999; Kocher & Williams 2000; Cowley *et al*. 2001a; Cowley *et al*. 2001b; Matter *et al*. 2003). Also, we will try to discard a possible peninsula effect in the distribution patterns of the Charaxinae of the PY (Simpson 1964; Seib 1980; Brown 1987; Brown & Opler 1990; Martin & Gurrea 1990). This study also examines topography (altitude), a factor that used to be overlooked in YP, because the relief in the YP is low, usually much below 300 m, although Cortés-Castelán & Islebe (2005) proved that topography can be relevant to explain distribution of tree species in YP.

This is the first biogeographical study concerning YP butterflies, aside from a few ones of inventory and monitory (de la Maza & Gutierrez-Carbonell 1992; Pozo *et al*. 2003; Maya-Martínez *et al.* 2005), and previous isolated records (*e.g*., Godman & Salvin 1879-1901; Godman *et al*. 1887-1901; Hoffman 1941; Comstock 1961).

MATERIAL AND METHODS

Study area. The study area was defined as the portion of YP in a precipitation range of 500 to 1500 mm, which corresponds, approximately, to the Mexican portion of YP. The area has humidity and vegetation gradients (Fig. 1; Miranda 1958; Miranda & Hernández-X 1963; Martínez & Galindo-Leal 2002; Pozo *et al*. 2003). Soils are shallow, recently formed, with rendzines and litosoles in the north, gleysoles towards the coasts, luvisoles in mature karstic plains and vertisoles in the south and northeast (Bautista-Zúñiga *et al*. 2003). The most important vegetation types are medium semi-evergreen tropical forest (especially where precipitation is 1100-1400 mm); high statured semi-deciduous tropical forest (1200-1400 mm); low deciduous tropical forest (to the north and northeast, 500-600 mm), and floodable low tropical forest (in poorly drained soils throughout YP). There are mangroves and other aquatic vegetational associations too (Carnevali *et al*. 2003). Historically, YP has experienced several climates. During the last glacial, climate was dry, with savannas and juniper scrub; during the early Holocene, vegetation changed to tropical forest; towards the years 1000 and 500 BP forest cover was reduced and savanna area increased (Orellana *et al*. 2003). Geologically, YP consists of two main subregions: to the north, areas of Miocene-Pliocene age; to the south, Miocene tectonic uplifts, as well as Eocene hills and residual plains. The Caribbean coast is Pleistocene in age (Bautista-Zúñiga *et al*. 2003).

Studied taxon. The Charaxinae (Lepidoptera: Nymphalidae) include 19 genera and 400 species approximately, most of them live in tropical areas around the globe; in the Neotropics the majority of the species dwell in southeastern Mexico, Central America and the Amazonas (Comstock 1961; Ackery 1984; DeVries 1987; Joly 2003; Mielke *et al*. 2004). The subfamily is well known taxonomically, although its phylogeny remains poorly known (Wahlberg *et al*. 2003). Many Charaxinae adults prefer the canopy rather than the forest undergrowth, but all can be attracted to carrion and fermented fruit (Queiroz 2002; Mielke *et al*. 2004).

The ecological and environmental interaction between vegetation and butterflies has been recognized, since the larvae eat plants and the adults are pollinators; in addition, they are an important part of the food chain to the being food of insectivores or parasitoids (Scoble 1995). Moreover, frugivorous butterflies, such as Charaxinae, have been considered excellent bioindicators of environmental quality, candidates to be included in management plans of the sites where they occur (Uehara-Prado *et al*.

2007). DeVries & Walla (2001) and Barlow *et al.* (2007) mentioned that this group displays clear diversity patterns, with variations in temporal and space scale.

Data analysis. Distributional records were taken from the literature (Godman & Salvin 1879-1901; Godman *et al*. 1887-1901; Comstock 1961; de la Maza 1987; d'Abrera 1988a; d'Abrera 1988b; Vargas-Fernández *et al*. 1991; de la Maza & Gutiérrez-Carbonell 1992; Vargas-Fernández *et al.* 1996; Warren *et al.* 1998; Pozo *et al*. 2003; Maya-Martínez *et al*. 2005; among others), collections (Colección Lepidopterológica del Museo de Zoología "Alfonso L. Herrera" and Colección Nacional de Insectos, consulted through REMIB; Colección Lepidopterológica del Museo de Zoología de ECOSUR and McGuire Center of Lepidoptera, visited) and new data from fieldwork (Fig. 1). Sampling effort focused on northern YP, between 500 and 1000 mm precipitation, because literature and collection records were sparse in this area. We used standard collecting techniques (entomological net and traps: Rydon 1964; Brown 1972; Howe 1975; Llorente *et al*. 1990), during 54 days in 2006-07.

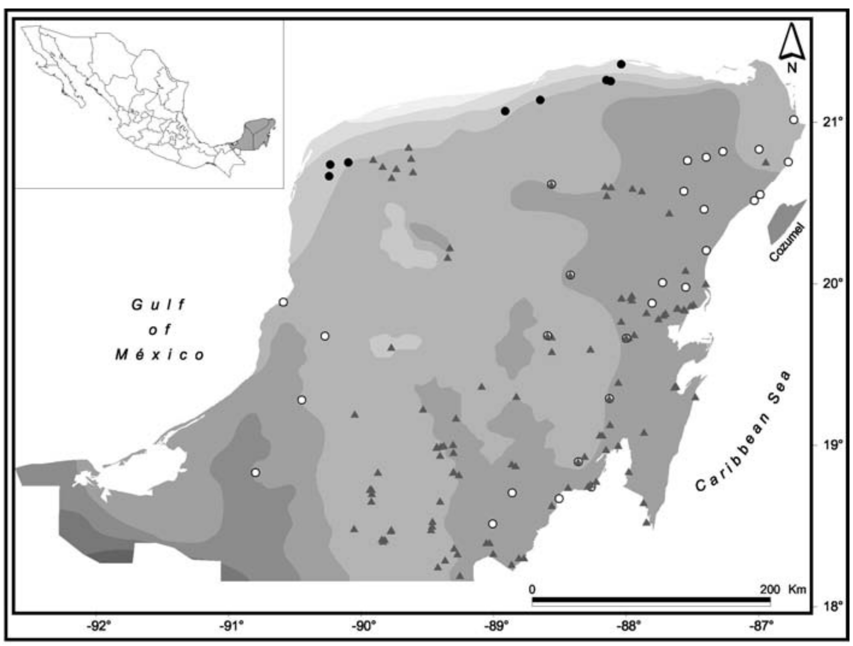

Figure 1. Study area, with humidity gradient (grey scale, lightest is 500-800 mm, darkest 1200-1500 mm precipitation) and projected records, according to source (white circles, literature; black circles, field; triangles, collections).

Every distributional record was characterized with environmental, ecological, physiographical, geological and anthropic descriptors; eleven variables were considered initially (Table 1). Finally, the database included 14,210 records, representing 23 species from 152 sites throughout YP (Table 2). To reduce the bias by the sampling effort, localities with low effort were eliminated, and also species with less than 10% occurrence. The matrix was thus reduced to 17 species (columns; Table 3) from 151 sites (rows).

Table 1. Independent variables for the canonical correlation analysis of the Charaxinae of YP.

Conditions	Variable	Type	Comments
Environmental	Temperature Precipitation	Semiquantitative Semiquantitative	Records were projected on thematic maps,* which were the source of the information.
Ecological	Host plants	Presence/absence	Presence/absence refers to quadrants of 0.5º x 0.5º latitude
Geographical	Geological age Distance to Caribbean coast	Semiquantitative Quantitative	Projection on thematic map Distance of record to the coast, including the eastern coast of large islands (e.g. Cozumel, see Fig. 1), along the usual trajectory of hurricanes, which is east-west.
Geographical	Altitude Latitude	Quantitative Semiquantitative	Data from original sources or estimated
Land use	Plant association (vegetation) Soil	Semiquantitative Semiquantitative	Projection on thematic maps
Anthropic	Distance to present day urban settlements Distance to classic Maya urban settlements	Semiquantitative Semiquantitative	Projection of three buffers around urban centers: 0-3 km, 3-6 km, or more than 6 km**

*Maps from INEGI and CONABIO, projected with ArcView. **Only human settlements above 1000 pop. considered. Classic Maya settlements obtained from Conservation International *et al.* (1995). See figure 4 (Pattern V).

Table 2. Records source of species distribution.

Source	Type	Species	Records
Field	Abundance	14	3764
Collection	Abundance	23	10001
Literature	Presence/absence	19	445
Total		23	14210

Table 3. Checklist of Charaxinae of the Yucatan peninsula. Nomenclature: Tribe and genus level names generally follow Lamas *et al*. (2004); systematics: Kristensen (1976). Species level names follow alphabetical order

Tribe/Species	Abbreviation	Pattern*
Anaeini		
Consul electra electra	cee	I
Siderone syntyche syntyche	sss	III
Siderone sp.	sg	V
Z. callidryas	zc	II
Z. ellops	ze	II
Anaea troglodyta aidea	ata	IV
Fountainea eurypyle confusa	fec	V
F. glycerium yucatanum	fgy	III
Memphis forreri	mf	V
M. hedemanni	mh	I
M. moruus boiduvali	mmb	I
M. oenomais	mo	II
M. pithyusa pithyusa	mpipi	IV
Preponini		
Archaeoprepona demophoon gulina	adg	I
A. demophon centralis	adc	I
Prepona laertes octavia	plo	I
P. pylene philetas	ppp	I

*According to the CCA diagram.

We generated two matrices: species-sites and independent variables-sites. Species data were transformed (square-root), and environmental data were standardized of minimum-maximum values from 0 to 1 (Legendre & Legendre 1998; Herrando-Pérez 2002). Latitude was a proxy for the possible peninsula effect, since the distal part of YP is oriented directly north.

Multivariate analyses were performed with the package Canoco ver. 4.5. A detrended correspondence analysis (DCA) was applied to the species matrix, to visualize the length of the gradient and therefore determine the type canonical analysis that would follow, that is, either a linear (length < 4) or a unimodal model (length >4) (Leps & Smilaurer 2003). Since the matrix was unimodal, a direct analysis of gradient, canonical correspondence analysis (CCA) was performed on both matrices, based on distance between species (giving extra weight to rare species) and performing a Montecarlo test with data randomization.

With the first CCA we selected six variables with the forward selection of environmental variables option, which avoids high correlation between explanatory variables; the six variables were latitude, distance to Caribbean coast, temperature, distance to present-day urban settlements, altitude, and precipitation, that explained more than 10% of the variance (*P=0.0010,* F-ratio=8.542; Table 4a, b and c). Finally distribution patterns of the Charaxinae of YP were located projecting on the ordination diagram, a procedure to determine the optima of each species along the environmental variables (ter Braak 1986; Jongman *et al*. 1995; Roberts & Wuest 1999; Leps & Smilaurer 2003).

RESULTS

The six variables with higher explanatory power and statistical significance refer to present conditions, and are mainly environmental and geographical, including the influence of human settlements (Table 4b, c). These variables were not highly correlated among themselves, except for altitude and latitude, because the highest elevations in YP are found towards the south. There is also a negative relationship between distance to the Caribbean coast and humidity (Table 5a).

The ordination graph generated by the CCA showed that the richness and abundance of the Charaxinae of the YP have a gradient of distribution defined by the latitude, topography (altitude) and humidity, observed that the greater diversity was associated to sites of the south of the YP (lowest latitudes), with pronounced topography and high humidity, with the exception of a group of sites of the north of the YP where it was observed low richness but high abundances (Table 5b; Fig. 2a, b). The distributional patterns were defined by different species with an optimal reaction for each one of the six independent variables.

The pattern I included species in the genera *Archaeoprepona*, *Prepona*, and *Consul*, as well as two *Memphis*, and depended on altitude and humidity (Table 3; Fig. 2c); thus, these species presented optima at high humidity (1000-1500 mm precipitation), pronounced topography (204-261 m), and highest abundances towards the south (17°-18°N), in sites with lower temperatures (22º-24°C), and with little influence of present urban settlements; also, most of the species that are distributed under this pattern prefer sites near the coast of the Caribbean (0-237 km; Figs. 3, 4).

Five species followed the distribution patterns II and III, whose distribution was determined mainly by high humidity and latitude (20°-21°N, towards the north of YP); both patterns cover sites closer to the Caribbean coast, and intermediate distances to present urban settlements (Table 3; Fig. 2c); however, the species that followed the distribution pattern II preferred lower temperatures (22º-26°C, vs. 24-28°C for group III; Figs. 3, 4).

Table 4. Summary CCA: (a) Percentage variation (original eleven variables); (b) Monte Carlo test and report on permutation test; (c) Percentage variation (six variables, $P < 0.05$).

(a)	**AX1**	**AX2**	**AX3**	**AX4**	**Total inertia**
Eigenvalues	0.207	0.101	0.031	0.027	1.331
Species-environment correlations	0.833	0.671	0.564	0.492	
Cumulative percentage variance:					
Of species data					
Of species-environment relation	15.5	23.1	25.5	27.5	
	51.6	76.8	84.5	91.3	
Sum of all eigenvalues					1.331
Sum of all canonical eigenvalues					0.401
Summary of Monte Carlo test*	Test of significance of all canonical axes:				
	Trace = 0.388, F-ratio = 5.196, P-value =				0.0010

(b)	**δ^2m****	**δ^2c*****	**F**	***P***	
Latitude	0.152	0.152	19.253	0.0010	
Distance to Caribbean coast	0.115	0.267	16.023	0.0010	
Temperature	0.030	0.298	4.309	0.0010	
Distance to present-day urban settlements	0.024	0.322	3.456	0.0010	
Altitude	0.016	0.337	0.337	0.0090	
Precipitation	0.012	0.349	1.742	0.0560	

(c)	**AX1**	**AX2**	**AX3**	**AX4**	**Total inertia**
Eigenvalues	0.200	0.095	0.029	0.018	1.331
Species-environment correlations	0.819	0.658	0.544	0.392	
Cumulative percentage variance:					
Of species data	15.1	22.2	24.4	25.7	
Of species-environment relation	57.4	84.6	92.9	98.0	
Sum of all eigenvalues					1.331
Sum of all canonical eigenvalues					0.349
Summary of Monte Carlo test*	Test of significance of all canonical axes:				
	Trace = 0.349, F-ratio = 8.542, P-value =				0.0010

*999 permutations under full model; **δ^2m: variance of species data; ***δ^2c: cumulative variance of species data.

Table 5. Weighted correlation matrix (weight = sample total): (a) among selected variables; (b) among independent variables and species axes from CCA. DCC: Distance to Caribbean coast; DUS: Distance to urban settlements; bold represents higher values.

(a)	**Humidity**	**Temperature**	**DCC**	**Altitude**	**Latitude**	**DUS**
Humidity	1.0000					
Temperature	-0.1085	1.0000				
DCC	**-0.5190**	0.2223	1.0000			
Altitude	-0.1374	-0.3178	0.4051	1.0000		
Latitude	-0.2410	0.2821	-0.0933	**-0.7754**	1.0000	
DUS	-0.1923	-0.1623	0.1629	0.3546	-0.2412	1.0000
(b)	**EnviAx1**		**EnviAx2**			
Humidity	-0.5327		0.5064			
Temperature	0.5248		-0.0905			
DCC	0.4605		**-0.8126**			
Altitude	**-0.5388**		**-0.7561**			
Latitude	**0.7991**		0.4889			
DUS	-0.2285		**-0.5292**			

Anaea troglodyta aidea and *Memphis pithyusa pithyusa* tracked pattern distribution IV. The most influential variable in this case was temperature (26-28°C; Fig. 2c); other conditions favorable for these species were the higher latitude, greater distance to the Caribbean coast, far to the human settlements and lower humidity (Figs. 3, 4); in general, this group distributes better in sites with tenuous or null topography, even though there is a *M. p. pithyusa* population that displayed high abundances in sites with marked topography, having 39% of the individuals (1452) of this species for the rank of the 261 m (Fig. 3).

Under the distribution pattern V we found *Memphis forreri*, *Fountainea eurypyle confusa and* an undescribed species of *Siderone*. The main factor was distance to urban settlements (Fig. 2c); in addition, the greatest abundances of these species occurred in sites away from the coast, altitude 204-261 m, precipitation 800-1200 mm and lower temperatures 22-24°C (Figs. 3, 4); the group of species track a distribution towards the north of the YP, the species of *Siderone* and *F. e. confusa* fulfill this pattern, but *M. forreri* showed high abundances towards the both ends of the YP, with a decrease in the mid-latitudes (Fig. 3).

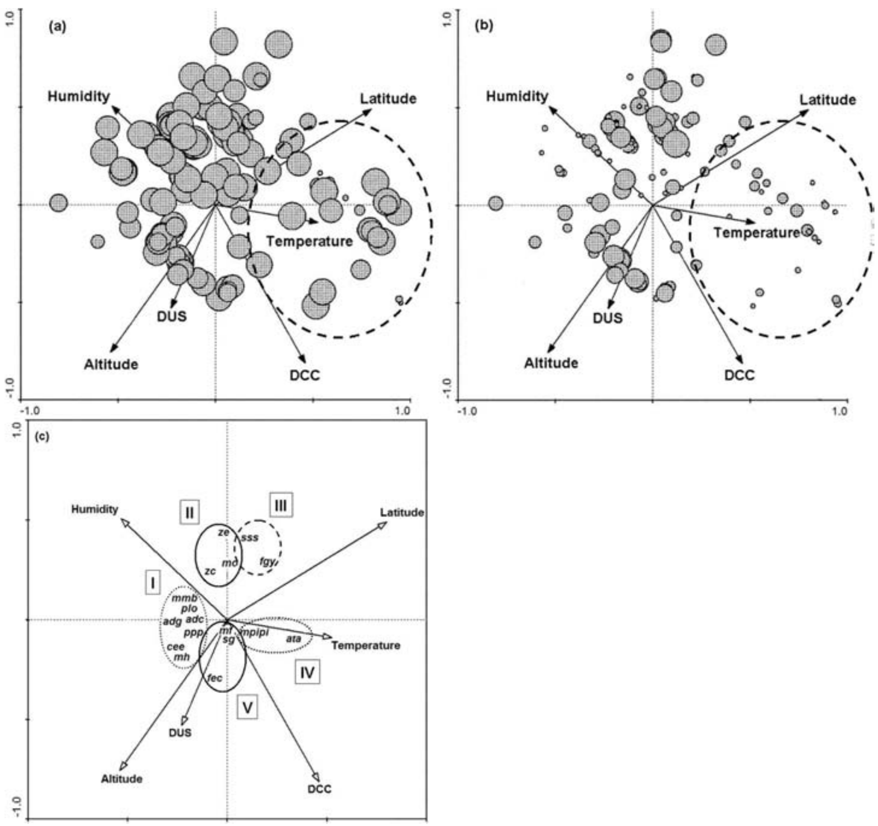

Figure 2. Ordination graph from CCA. (a) Distribution of local species abundance; (b) Distribution of alpha richness; larger circles mean higher abundance and richness. (c) Distributional patterns. DUS: Distance to urban settlements; DCC: Distance to Caribbean coast. For the abbreviations of the species see Table 2.

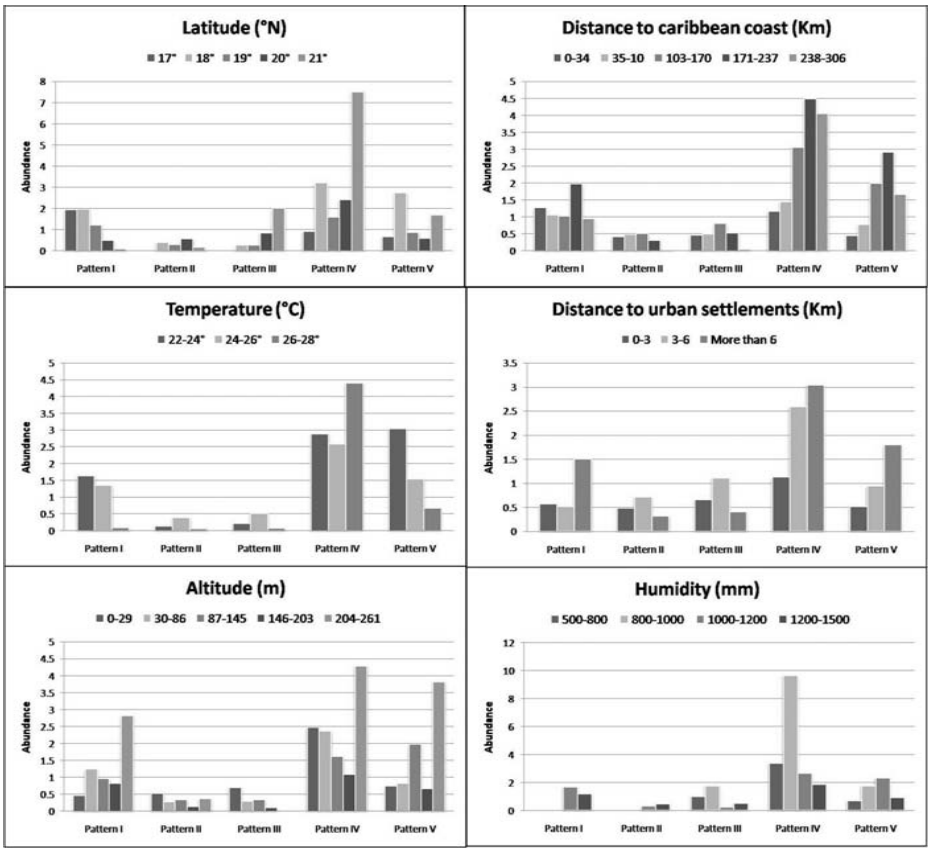

Figure 3. Distribution patterns of Charaxinae according to independent variables obtained from CCA. We show mean abundances transformed by square-root.

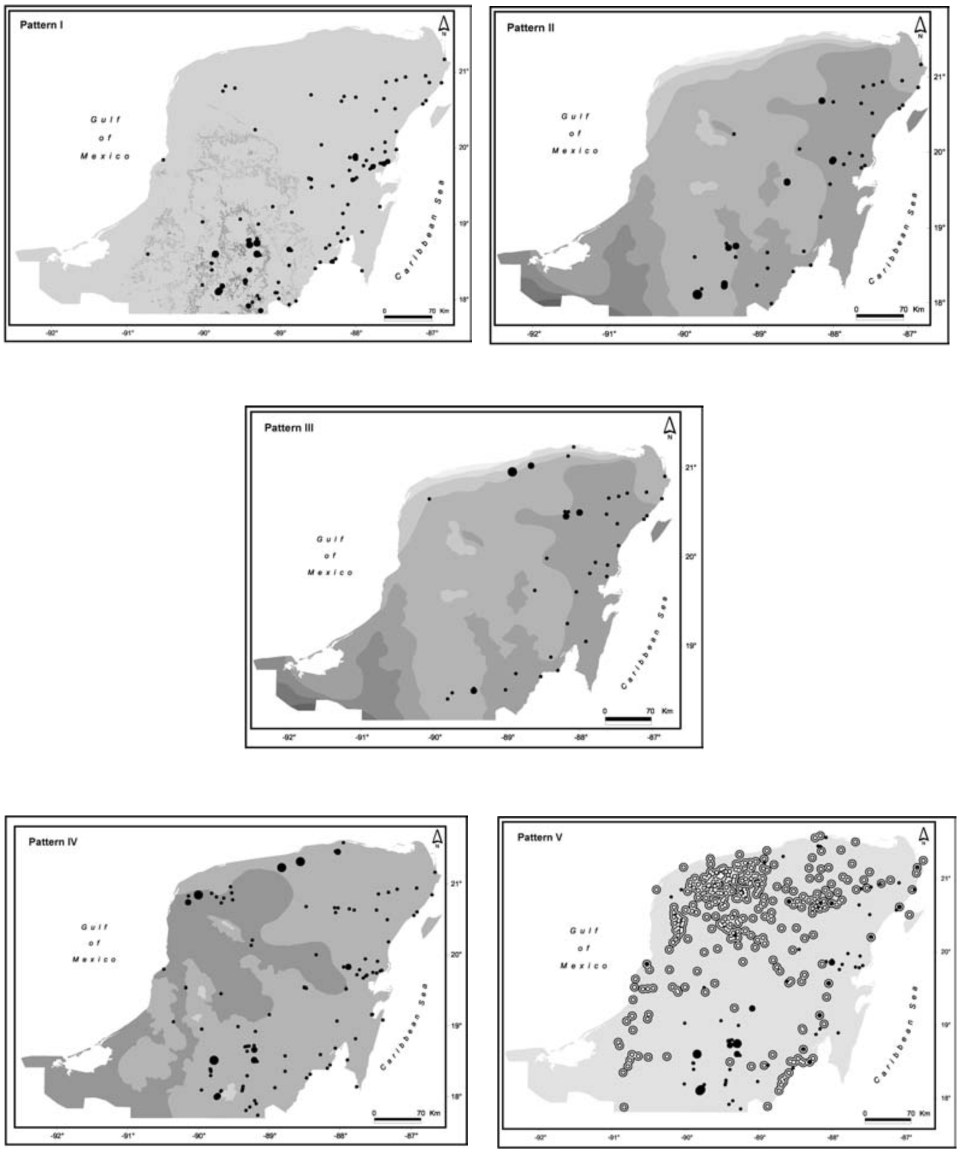

Figure 4. Distribution maps of five patterns of Charaxinae in YP. Every map depicts the most important variable explaining every distribution. Pattern I: altitude (darker: higher); Patterns II and III: humidity (darker: higher); Pattern IV: temperature (darker: warmer); Pattern V: influence of urban settlements (flags). Larger circles mean higher species abundance.

DISCUSSION

According to recent research in YP, the present-day vegetation in the region resulted mainly from events that occurred during the Tertiary, when climate became markedly tropical (Orellana *et al*. 2003). Moreover, for several taxa (Lee 1980; Espadas-Manrique *et al*. 2003; Pozo 2006, among others), distribution is determined by environmental heterogeneity; this is the case for the Charaxinae, since the main factors that explain their distribution are recent and related to the environment. Humidity and temperature are relevant, as are latitude, altitude, distance to the Caribbean coast (a surrogate for risk of impact by hurricanes) and distance to present urban settlements (a surrogate for direct human impact). This heterogeneous arrangement was mentioned by Barlow *et al.* (2007) who discerned that, opposite to other subfamilies, the Charaxinae species are influenced by the surrounding secondary forest and plantations, but mainly by the presence of primary forest.

On the other hand, distribution patterns of biodiversity may vary according to a geographic or environmental gradient (Murray *et al*. 1999; Kocher & Williams 2000). In the present case, latitude (that is, distance to the base of YP or Nuclear Central America, the putative biogeographic origin of most taxa in the region; Bussing [1976]) was not so relevant for richness, which is relatively homogeneous latitudinally, refuting a “peninsular effect” as such. This finding coincides with the results of Simpson (1964), Brown (1987), Brown & Opler (1990), and Martin & Gurrea (1990); peninsulas of Baja California, Florida and Iberian, respectively), who pointed out that distributional patterns of the neotropical lepidopterofauna are largely due to ecological and environmental conditions. The opposite happens with the nearctic lepidopterofauna in all three mentioned peninsulas, where a richness gradient along the axis of the peninsulas was demonstrated.

As for the distribution of abundance, this tended to be higher towards north and south latitudes and lower at mid-latitude. This could be due to the fact that in this intermediate latitude one finds the transition between the wet and the dry subregions of YP, as mentioned by Lee (1980), who found a similar pattern for lizards and snakes. Seib (1980) observed this phenomenon in the rodents of Baja California, and suggested two patterns of peninsular distribution: a geometric pattern (peninsular effect) and a gradient, because towards the border between the southern and northern halves of that peninsula there is a mixture of habitat types, which favors a higher diversity.

Thus, distribution of Charaxinae is marked more by environmental factors, with a gradient, with higher abundance in the extreme south and north; moreover, it is important to note that personal observations of distributional maps of the plants that harbor the larvae of these butterflies follow the same pattern (Maya, in process).

The Charaxinae of YP demonstrate a distributional gradient given by the latitude, the topography and the humidity, thus an environmental gradient explains the distribution (Wet-Dry: South-North), established by others authors for the YP. This gradient has an important influence on the distributional patterns of the organism; for the Charaxinae the result was a richer fauna in the South of the peninsula. Even if the effect of the topography has been considered less of then in the distributional patterns of the organisms in the peninsula, because it is not very much pronounced (0-300 m), it influence must be important in the distributional gradient of the organism, as it is demonstrated with the Charaxinae in this study in accordance with Cortés-Castelán *et al*. (2005). This distributional pattern was observed by Hill (1999), who recorded that populations of Satyridae butterflies were influenced directly by humidity and not properly by vegetation structure.

On the other hand, we observed a group of localities in northern YP (24) that was low in richness (nine species out of 17, on average only three per site), with high dominance of a few species (*M. p. pithyusa* and *A. t. aidea*; 94% of the total abundance in these sites), which are the only ones that display higher abundances in drier environments. This pattern of low equitability has been reported already for tropical environments, especially when productivity is rather low (Bazzaz & Pickett 1980; Murray *et al*. 1999; Magurran 2004), as happens in northern PY.

The environmental optima observed for species in pattern distribution I (south of YP, near to the Caribbean coast, low temperatures, far to the urban settlements, pronounced topography and high humidity) coincide in general with findings elsewhere for those species (Godman & Salvin 1879-1901; Godman *et al*. 1887-1901; Comstock 1961; DeVries 1987; DeVries & Walla 2001); however below the 1000 mm precipitation, we didn't found any record of this species. We establish here a humidity limit for those species.

Under pattern distribution II and III were including species that do not occur in the south (latitude 17ºN). These species were more prevalent between parallels 20º and 21ºN, but the species that followed the pattern II preferred wetter sites and those of distribution pattern III drier environments; this coincides with the division between the two biotic provinces proposed for PY, Yucatec and Peten, based on diagnostic species of reptiles, birds, fishes, plants, and others (Smith 1941; Lee 1980; Escalante *et al*. 1993; Schmitter-Soto & Salazar-Vallejo 1993; Lee 1996; Espinosa-Organista *et al*. 2002). *Memphis oenomais*, *Zaretis ellops* and *Z. callidryas* (distribution pattern II) were better distributed in the south (Peten) and *S. syntyche syntyche*, and *Fountainea glycerium yucatanum* (pattern III) in the north (Yucatec). Of those species, *F. g. yucatanum* had already been considered (Vargas-Fernández *et al*. 2006) one of the four endemic butterflies (*Anthirrea philoctetes casta*, *F. g. yucatanum* and *Fountainea halice maya*) diagnostic of PY as a biogeographical province. However, this distribution pattern should be confirmed by means of a different sort of analysis (*e.g*., panbiogeographic) to determine whether these groups belong in historically coherent faunas (that is, generalized tracks; Morrone & Crisci 1995).

Although species in distribution patterns IV and V presented particular environmental preferences, they are distributed throughout the peninsula; for example, *A. t. aidea* (included in pattern IV), reported to have a wide distribution, from Costa Rica to the southern United States, but we observed it to prefer drier and hotter regions. Most authors (from Godman & Salvin 1879-1901, to Pozo *et al*. 2003, among others) mention sites where the species of these groups were collected, but omit habitat preferences. An exception is DeVries (1987), who mentioned that *A. t. aidea* is associated with deciduous forest (dry low tropical forest in YP: Martínez & Galindo-Leal 2002). In North America, Scott (1986) usually found *Anaea* at the border of forests, roads and water bodies, although it also occurs in subtropical pine-palmetto scrub and wooded desert areas. Thus, we can conclude that the species in these patterns (*M. p. pithyusa, A. t. aidea, M. forreri*, *Siderone* sp and *F. e. confusa*), particularly *M. p. pithyusa* and *A. t. aidea*, are favored by drier environments, which limit other Charaxinae; although they are widely distributed, they take advantage of these conditions to increment their populations opportunistically.

This work could also detect and confirm (Pozo 2006; Uehara-Pardo *et al*. 2007) that these butterflies are good bioindicators of the conservation state of the vegetation. Therefore, they should be included in management plans: species that followed the distribution pattern I, IV and V prefer conserved sites, far from urban settlements. Hill (1999) mentions that Satyridae populations were impaired by the humidity and habitat fragmentation, being considered as well as a group indicator of conservation status.

Formerly, Pozo (2006) detected seven of these species (*A. t. aidea, F. e. confusa, Memphis forreri, M. moorus boisduvali, M. p. pithyusa, Archaeoprepona demophoon gulina* and *Prepona laertes octavia*) as useful indicators of conserved environments in low and medium tropical forests. However, *Consul electra electra*, *M. hedemanni* and *Siderone* sp., considered indicative of disturbed vegetation by Pozo (2006), were observed here to belong in groups whose optima correspond to conserved sites.

CONCLUSIONS

The distribution, abundance and richness of Charaxinae in YP mainly followed the latitudinal, altitudinal and humidity gradient; a group of sites in dry northern Yucatan showed an inverse correlation between abundance and richness, with dominance of two species opportunistic for drier environments (*A. t. aidea* y *M. p. pithyusa*). Five distribution patterns were identified, each with different species that tracked particular environmental preferences. Species that followed the distribution pattern I was limited by the minimum mean annual precipitation of 1000 mm. Patterns II and III were restricted to northern YP; species of the pattern II preferred wetter sites (*ca*. 1350 mm) and pattern III the drier areas in the region (vary from 700 to 900 mm). Species of patterns IV and V displayed similar distribution, favored by conserved sites, that is, far from urban settlements. *A. t. aidea* is a widespread species, but it shows preference for low humidity and high temperatures, a fact previously overlooked. Seven species are confirmed bioindicators of conserved vegetation (*A. t. aidea, F. e. confusa, M. forreri, M. m. boisduvali, Memphis p. pithyusa, A. d. gulina,* and *P. l. octavia*).

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