Microclimate Variability Significantly Affects the Composition, Abundance and Phenology of Butterfly Communities in a Highly Threatened Neotropical Dry Forest

Authors: Checa, Maria F., Rodriguez, Jacqueline, Willmott, Keith R., and Liger, Belen

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MICROCLIMATE VARIABILITY SIGNIFICANTLY AFFECTS THE COMPOSITION, ABUNDANCE AND PHENOLOGY OF BUTTERFLY COMMUNITIES IN A HIGHLY THREATENED NEOTROPICAL DRY FOREST

MARIA F. CHECA[1,2], JACQUELINE RODRIGUEZ[2], KEITH R. WILLMOTT[1] AND BELEN LIGER[2]
[1]Museo QCAZ de Invertebrados, Pontificia Universidad Catolica del Ecuador, Av. 12 de Octubre, Quito, Ecuador

[2]McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Powell Hall on Hull Road, Gainesville, FL, USA

Corresponding author; E-mail: mfcheca@ufl.edu

ABSTRACT

In temperate areas, microclimate is a key factor affecting the population dynamics of insects, but very few studies have examined the potential significance of microclimate in diverse tropical insect communities. We quantified the diversity and structure of butterfly communities in 2 different microhabitats, over seasons, and examined which abiotic (microclimate) and biotic (vegetation structure) components affected community composition. The study was performed from Jun 2009 to May 2010 at a dry forest in Ecuador, a globally threatened habitat with high levels of endemism. Two transects were established, one in each microhabitat, where baited traps were located in the understory and canopy to record butterfly species abundance. Humidity and temperature were recorded during the sampling period and vegetation variables were measured. A total of 3,731 individuals representing 93 species were collected. Higher species richness and abundances were found during the wet season. Linear regression models and CCA analyses showed microclimatic variability and vegetation structure (e.g., vegetation density) were significant predictors of the composition and abundance of butterfly communities. Major lineages of butterflies differed in their response to microclimate and microhabitat, explaining some of the spatial variation in community structure. In addition, some of the most abundant species changed their microhabitat preferences in the dry season. The tight relationship between butterfly communities, microclimate and microhabitat suggests that global climate change and habitat alteration are likely to act synergistically on tropical dry forest insect faunas, and these processes should thus be considered together in predicting future impacts on biodiversity.

Key Words: bait-attracted butterflies, climate change, microhabitat, relative humidity, temperature, vegetation structure

RESUMEN

En las zonas templadas, el microclima es un factor clave que afecta la dinámica poblacional de los insectos, pero muy pocos estudios han examinado el potencial significado del microclima de diversas comunidades tropicales de insectos. Hemos cuantificado la diversidad y estructura de las comunidades de mariposas en dos microhábitats diferentes, durante toda la temporada y examinamos cuales son los componentes abióticos (microclima) y bióticos (vegetación, estructura) que afectan la composición de la comunidad. Se realizó el estudio entre junio del 2009 y mayo del 2010 en un bosque seco en Ecuador, un hábitat amenazado a nivel mundial con un alto nivel de endemismo. Se establecieron dos transectos, uno en cada microhábitat, donde se encuentran las trampas con cebo en el sotobosque y el dosel para registrar las especies de mariposas y su abundancia. Se registraron la humedad y la temperatura durante el período de muestreo, y se midieron las variables de la vegetación. Se recogieron un total de 3,731 individuos que representan unas 93 especies. Se encontró una mayor riqueza en la diversidad de especies y su abundancia durante la temporada húmeda. Los modelos de regresión lineal y el Análisis de Correspondencia Canónica mostraron variabilidad microclimática y estructura de la vegetación (por ejemplo, la densidad de la vegetación) fueron estimadores significativos de la composición y abundancia de las comunidades de mariposas. Las principales líneas varían en su respuesta al microclima y microhábitat, la cual explica alguna de las variaciones espacialmente en la estructura de la comunidad. Además, algunas de las especies más abundantes cambiaron sus preferencias de microhábitat en la temporada seca. La estrecha relación entre las comunidades de mariposas, microclima y microhábitat sugiere que el cambio climático global y la alteración del hábitat son propensos a actuar sinérgicamente sobre las faunas de insectos del bosque

seco tropical, y estos procesos por lo tanto se deben considerar en conjunto para predecir el impacto sobre la biodiversidad en el futuro.

Palabras Clave: mariposas atraídas con cebo, cambio climático, microhábitat, humedad relativa, temperatura, estructura de la vegetación

Climate is one of the most influential factors controlling seasonal changes in the abundance of tropical insects (Wolda 1978, 1988 and citations therein). Furthermore, it has long been recognized that individual insect species are sensitive to microclimate (Cloudsley-Thompson 1962), and studies in temperate areas have also shown that microclimate plays a significant role in metapopulation dynamics. For example, a suitable microclimate is essential for the survival and development of butterfly species by directly affecting diapause or larval growth, or indirectly by affecting food availability (Hellmann et al. 2004). At the community level, therefore, microclimatic constraints may be critical in the evolution of life history strategies and niche segregation, allowing diverse communities to persist (see WallisDeVries & Van Swaay 2006).

Segregation in microhabitat niche among tropical insect species has been documented in a number of studies, including both horizontal (e.g. Estrada & Jiggins 2002; Amédégnato 2003; Fleishman et al. 2005; Jarin & Balakrishnan 2011) and vertical (e.g. Mallet & Gilbert 1995; Beccaloni 1997; DeVries et al. 1997, 1999; DeVries & Walla 2001; Fermon et al. 2005; Dial et al. 2006) dimensions. In butterflies, one of the best-studied groups, microhabitat segregation has been shown to significantly affect ecology and community structure. For example, mimicry complexes in Ithomiini and Heliconiinae nymphalid butterflies are segregated by microhabitat, with co-mimics flying in areas of similar disturbance, topography and at a similar height above the ground (Mallet & Gilbert 1995; Beccaloni 1997; Estrada & Jiggins 2002; Elias et al. 2008; Hill 2010). In these butterflies, it is likely that divergence in both mimicry and microhabitat have played a role in generating reproductive isolation (Estrada & Jiggins 2002). Other butterfly guilds, such as tropical fruit-feeding nymphalids, have been consistently reported to show flight height segregation (e.g. DeVries et al. 1997; Fermon et al. 2005 and citations therein). On a broader scale, topography is a little explored but potentially key factor affecting fine-scale species distributions, because hilltops and river valleys are important sites for males of insects engaged in mate-locating behavior (see Shields 1967; Callaghan 1983; Navez & Ishii 2007; Prieto & Dahners 2009).

Understanding the factors responsible for microhabitat segregation is thus fundamental in the study of community and evolutionary ecology in tropical insects. Most authors assume that because microclimate is linked to vegetation structure, it must be the key factor in controlling microhabitat distribution (e.g. Dial et al. 2006). However, although a few studies have quantified differences in vegetation structure among microhabitats (e.g., Dial et al. 2006; Barlow et al. 2007; Dolia et al. 2008; Elias et al. 2008; Jain & Balakrishnan 2011), very few studies have determined which microclimate variables are significant in explaining community composition (but see Dial et al. 2006, for a study of vertical stratification). Our study is thus the first to examine which microclimatic variables are most strongly correlated with variation in composition of a tropical insect community, across spatial (horizontal) and temporal (seasons) dimensions. Our research focused on butterflies, one of the best-studied tropical insect groups, and one that has previously been studied in relation to microhabitat segregation.

Understanding how microclimate and microhabitat interact to control insect communities is important not only to understanding their evolutionary ecology, but also to better predict the responses of these communities to climate and habitat change. The majority of studies of temporal and spatial patterns in tropical insects have focused on wet, relatively aseasonal forests. By contrast, the more pronounced seasonality of dry forests suggests that important new insights might be gained from studies over multiple seasons in this type of habitat. Furthermore, dry forests are typically of high significance from a conservation perspective. We therefore based our study in west Ecuadorian dry forest, part of the Tumbesian area of endemism (Davis et al. 1997), where many species are known from only one or few localities (e.g. Gentry 1992; Hall & Willmott 1996; Willmott & Hall 2010). High endemism and extensive habitat loss combine to make west Ecuadorian dry forests a global conservation priority; by 1998 the Tumbesian region of Ecuador had less than 5% of its original dry forests remaining and was facing exceptional threats of extinction (Dodson & Gentry 1991; Stattersfield et al. 1998). In recent years, deforestation has increased in western Ecuador (Checa 2008), and the percentage of original vegetation cover has decreased still further, underlining the urgency of increasing our knowledge about the biodiversity of this unique region.

The goals of this study were, therefore, to identify which microclimatic and microhabitat components are most significant in structuring a

tropical dry forest butterfly community, and how seasonality affects this relationship.

Materials and Methods

Site Description

Western Ecuador supports a sharp gradient of life zones due to uneven distribution of annual rainfall. The presence of 2 opposite ocean currents is responsible for this pattern. The cold Humboldt Current coming from the south turns westward away from land near 2° S latitude, while the warm Equatorial Current El Niño comes from the north (Lynch & Duellman 1997). As a result, pluvial and wet forests dominate in the north, but change increasingly to moist and dry forest southward to around 2° S latitude, where several months of drought occur (see Cañadas & Estrada 1978). From Jan through Mar El Niño shifts further south before moving westward, producing increased precipitation in the north and the arrival of the rainy season in dry and moist forests (Lynch & Duellman 1997). Lalo Loor Dry Forest Reserve (LLDFR) is located at the transition between moist and dry forest, a vegetation type that is nearly extinct in the region due to deforestation (Clark et al. 2006). The reserve has 200 ha of primary forest ranging from 10 to 300 m above sea level. The dry season starts in Jun and may last 5 months, and the trees of the lower hillsides and coastal plain are thus deciduous (Clark et al. 2006). In addition, trees on some ridgetops that are exposed to direct sunlight, and thus to greater variability in temperature and humidity, are also deciduous. Moist evergreen forests are present on hillsides and in valleys between ridges, and this micro-environmental complexity makes the reserve especially suitable for studies of butterfly communities on a local scale.

Experimental Design

A transect approximately 280 m long was established in each of 2 microhabitats (ridgetop and valley) that differed by 150 m in elevation (Fig. 1). The ridgetop transect was through deciduous forest and the valley transect through evergreen forest. Each transect consisted of 8 sample points spaced about 40 m apart (Fig. 1). Previous field research showed that 40 m is the minimum distance between sample points to be considered independent replicates, since traps located less than 40 m apart are likely to have overlapping zones of attraction. The assumption of independence is supported by the results of a mark-recapture study of 12 species performed over a period of 11 months, using the same trapping protocol and transects described here. During that study, 1,329 butterflies were marked and released, and 9% were recaptured (118 individuals). Approximately 8% (9 individuals) of the recaptured butterflies were trapped at the closest neighboring sample points (separated by 40-60 m), with the great majority recaptured at the same sample point.

At each sample point one baited trap was placed in each of 2 different strata, understory (1.5 m above ground) and canopy, to control for and enable studying vertical stratification in the butterfly community (DeVries & Walla 2001; Fermon et al. 2003). The canopy height varied between the microhabitats, ranging from 18-22 m in the valley and 14-17 m in the ridgetop.

A thermo-hygrometer was placed in each transect to record the maximum and minimum temperature and relative humidity during the 7 days of monthly sampling. Forest structure was quantified by establishing 5 m radius circles in each of the sample points centered on the understory butterfly trap. Several variables were measured in each circle to capture variation in forest structure, following the methodology of Elias et al. (2008): (1) canopy cover; (2) ground cover; (3) number of trees > 1 cm diam at breast height (dbh); (4) average number of markings visible on a 2 m pole marked at 20 cm intervals held at 4 evenly spaced points around the perimeter of the circles; and (5) average tree diam for all trees greater than 1 cm dbh. Canopy cover and ground cover were measured qualitatively: 2 observers estimated the percentage of cover in the 5 m circle and an average of both estimates were used. These variables were measured twice, once during the middle of the dry season (Nov) and once during the middle of the wet season (Feb).

Census Techniques

Butterflies were sampled using traps with 2 different baits, carrion (rotting shrimp fermented for 13-18 days) and fruit (banana fermented for 2 days). Fruit and carrion baits attract different butterfly guilds (Hall & Willmott 2000; Hamer et al. 2006), thus use of different baits increases the diversity of species sampled. We alternated baits between sample points so that neighboring sample points had different types of bait, while canopy and understory traps at the same sample point were baited with the same type of bait. Traps were checked daily during the first 7 days of each month from Jun 2008 to May 2009. The traps were opened and baited on the first trapping day, and over the next 6 days traps were checked and all trapped butterflies were collected and placed in glassine envelopes. The bait was renewed every day. All collected material was examined and identified in the laboratory. The taxonomic classification follows the checklist by Lamas (2004). All collected specimens were deposited in the Section of Invertebrates, Museo QCAZ of the Pontificia Universidad Católica del Ecuador, and the McGuire Center for Lepidoptera, Florida Museum of Natural History, University of Florida.

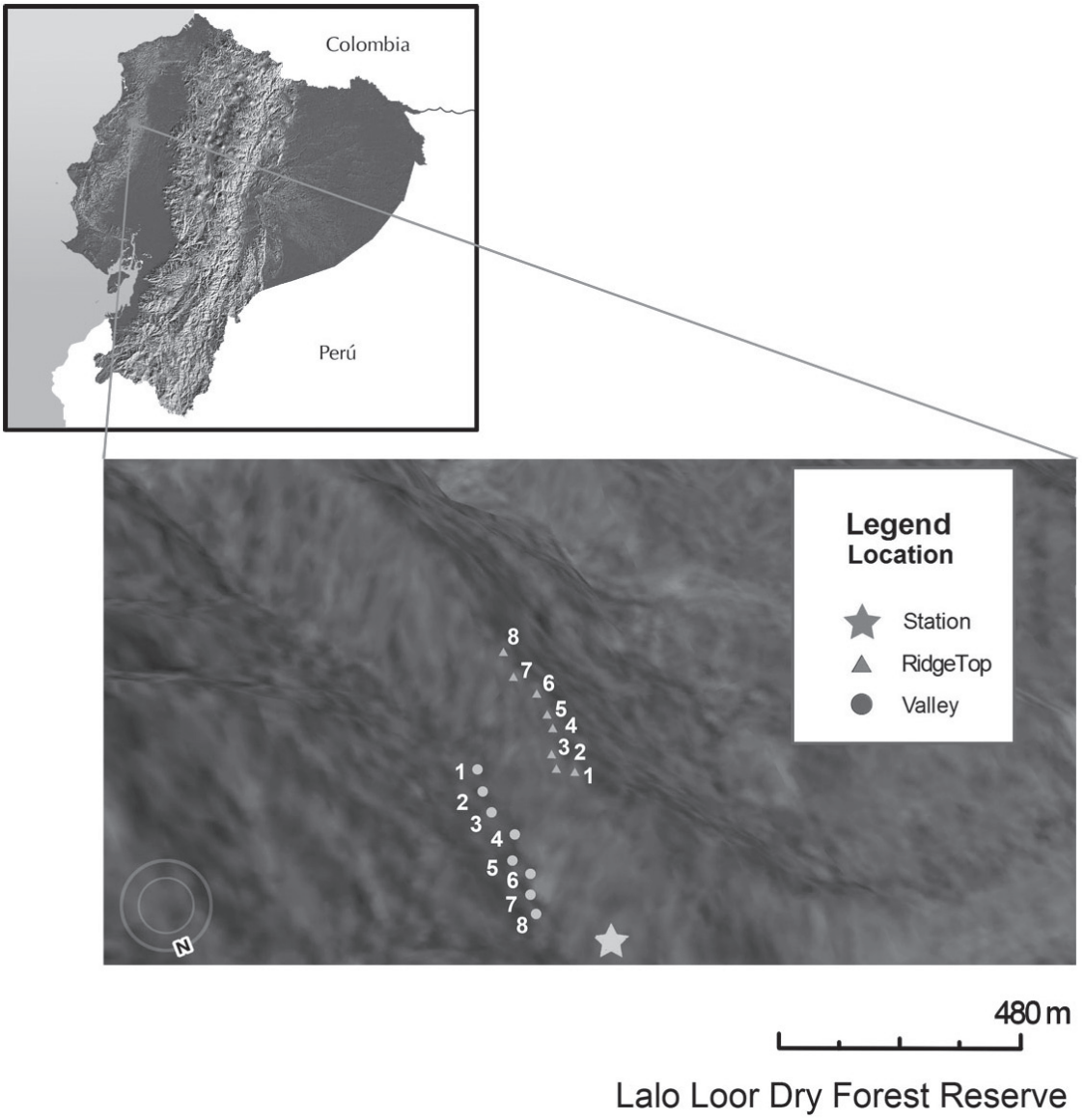

Fig. 1. Lalo Loor Dry Forest Reserve located in northwest Ecuador and transects with 8 sample points established in ridgetop and valley microhabitats.

Statistical Analyses

Four different attributes of butterfly communities were analyzed: abundance (i.e., number of individuals), species richness (i.e., number of species), composition (i.e., species present in the community) and structure (i.e., distribution of abundance among species). Different statistical analyses are appropriate depending on which attribute will be analyzed and our objectives. To analyze the structure and composition of butterfly communities, a Canonical Correspondence Analysis (CCA) and a Cluster Analyses were performed. Linear regression models were constructed to analyze butterfly abundance and species richness. As described below, CCA and linear regression models are also used to determine how variation in environmental variables was related to the corresponding variation in butterfly communities.

A Canonical Correspondence Analysis (CCA) was used to examine the relationship between the composition and structure of butterfly communities and environmental variables in different microhabitats and across seasons. In other words, the analysis tested whether environmental variables (i.e., microclimate and vegetation structure)

were good predictors of butterfly community attributes. These analyses are useful to predict how climatic and habitat variation might affect butterfly communities and their conservation.

Monte Carlo simulation methods were used to test the statistical significance of the results obtained in the CCA (Legendre & Legendre 1998; Leps & Smilauer 2003). CCA is a robust analysis that performs quite well with noise in species abundance data and highly intercorrelated environmental variables (see Palmer 1993). The matrix corresponding to butterfly data consisted of species and their abundance registered for each sample point (8 for each microhabitat) in the valley and ridgetop during dry and wet season, and thus data from different strata and months (corresponding to either wet or dry season) were pooled. In a similar way, values of environmental variables corresponded to measurements obtained during the dry and wet season in each microhabitat. Another CCA was done including the subfamilies of Nymphalidae (Biblidinae, Heliconiinae, Danainae, Limenitidinae, Nymphalinae, Morphinae and Satyrinae) and Hesperiidae as dependant variables instead of including species and their abundance. The families Lycaenidae, Riodinidae and Pieridae were not included as each was only represented by a single species.

Initial analysis of this dataset showed that different baits attract different butterfly species, thus affecting the overall dispersion of sites (sample points in each transect) in the diagram. Therefore, in the CCA analysis bait type was included as a covariable, so the variation produced by this variable was accounted for (see ter Braak &Verdonschot 1995) and would not influence the results observed in the diagram.

The environmental variables included the SD of maximum and minimum temperature and relative humidity as well as all measurements of forest structure. Climatic conditions on the ridgetop were more variable than those in the valley, and because the SD of maximum and minimum values reflects the range of seasonal variability SD was preferred over mean or maximum/minimum values. Also, CCA analysis including SD of temperature and humidity better separated butterfly communities over time compared to CCA with mean values. Finally, ground cover was excluded from the analysis because it was highly correlated with canopy cover and climatic variables (see Results). The CCA diagram was interpreted following guidelines provided by ter Braak (1986, 1996).

The CCA qualitatively (through diagrams) shows differences in the composition and structure of butterfly communities on the ridgetop and in the valley over seasons. However, in order to detect the statistical significance of this variation, it is necessary to perform additional analyses. Hence, we performed a Cluster analysis (complete linkage) with a Simprof permutation test for significant differences, using Primer 6 (Clarke & Warwick 2001). The Bray-Curtis similarity index was used to cluster sample sites because it performs well for comparing species abundance among sites (Gotelli & Ellison 2004). The abundance data were squared-root transformed so that common and rare species would contribute more equally to variation, and transformed data were used in all of the following analyses.

Finally, linear regression models (generalized linear models) were used to test for a relationship between changes in butterfly species richness and abundance, and environmental variables (climate and vegetation structure). Generalized linear models have applications in circumstances where the assumptions of the standard linear model do not hold, as in the case where the distribution of the data is not normal (Littell et al. 1996). Typically, count data do not follow a normal distribution, but rather a Poisson or a negative binomial. Indeed, our dataset was better fit by a negative binomial distribution. The Kenward-Roger (1997) adjustment to the denominator degrees of freedom in F-tests was used to account for bias in the estimation of the variance-covariance matrix of the errors. Two different models were constructed to analyze each dependent variable, butterfly species richness and abundance; the independent variables in both models were the microclimatic (SD of temperature and relative humidity) and vegetation variables (canopy cover, number of markings, average tree diam and number of trees) recorded in each butterfly sampling point. Data from Jan to Jun were pooled to represent the wet season while data from Jul to Dec where pooled and treated as dry season. This separation by season was done using the values of temperature and relative humidity of months. Data from each of the 2 sampled strata were pooled for each sample point. Each point in the analyses thus consisted of the number of butterflies collected (number of species or individuals) and the microclimatic and vegetation variables registered at each sample point of the 2 locations (ridgetop and valley) in each of the 2 seasons (wet or dry). The best model for species richness and abundance, according to Akaike's Information Criterion (AIC) and Scaled Pearson Chi-square values, was obtained by including canopy cover, vegetation density (number of markings), average tree diam, and the SD of temperature and relative humidity. The SD represents the variability of temperature and relative humidity (using maximum and minimum values) recorded during each microhabitat in the dry or wet season. The negative binomial distribution fit the data better than Poisson. Therefore, the outputs of these models were used for further interpretation. Linear regression models were carried out with SAS 9.2.

Results

A total of 3,731 individuals were collected, representing 93 species (Nymphalidae, Hesperiidae, Riodinidae, Lycaenidae and Pieridae). The most abundant family was Nymphalidae, with 2,864 individuals. In general, the samples were dominated by only a few species, and 7 species accounted for approximately 71% of individuals. The most abundant species were *Fountainea ryphea* (Charaxinae, 1138 individuals), *Smyrna blomfildia* (Nymphalinae, 480), *Myscelia cyaniris* (Biblidinae, 294), *Hamadryas amphichloe* (Biblidinae, 259) and *Taygetis nympha* (Satyrinae, 197). More species were collected in the valley (79 species compared to 66 in the ridgetop), but abundance was higher in the ridgetop (1,381 individuals) (Table 1). In both microhabitats, higher species richness and abundance were registered during the wet season (Table 1).

Mean temperature over the year was significantly higher in the ridgetop (27.1 °C) compared to the valley (25.2 °C), according to the Mann-Whitney test analyzing the mean temperature between microhabitats ($U = 31.5$, $P = 0.017$) (Fig. 2). In addition, mean relative humidity was lower in the ridgetop (average across all months 76.45%) compared to the valley (79.73%). However, the results of the Mann-Whitney Test comparing the mean relative humidity between ridgetop and valley showed this difference was not significant ($U = 62$; $P = 0.59$).

In the CCA analysis where individual species were used as dependent variables, 61% of the variance was explained by the environmental variables along the first 2 axes and the explanatory effect of all of the environmental variables on species representation was significant (Monte Carlo test, $P = 0.005$). This means that all vegetation structure and climatic variables included in the analysis are significantly related to the variation found in butterfly communities in terms of composition and structure. The eigenvalues of the axes 1 and 2 were 28.9 and 12.6, respectively.

The most important environmental variables were the SD of temperature and relative humidity, as indicated by the length of the arrows in Fig. 3. Axis 1 was highly correlated with vegetation density (-0.74). Axis 2 was mainly a climatic gradient, as the SD of temperature and relative humidity were positive and highly correlated with this axis, while canopy cover and dbh of trees were negatively correlated with this axis. This means that sites with higher variability of humidity and temperature (sites located in the upper part of the diagram) thus had less canopy cover and lower tree dbh. This was particularly true for sites in the ridgetop during the dry season, a result that was expected, as this microhabitat seems to be physically more exposed (see Fig. 3). It was also apparent that the valley forest had lower climatic variability and higher values of canopy cover during the wet season.

Additionally, the CCA revealed that butterfly communities from ridgetop and valley differed more markedly in structure and composition in the dry season, with variation in the wet season being more or less continuous with some overlap among sample points (Fig. 3). During the wet season, butterfly communities from the ridgetop and valley were mainly separated along axis 2, hence the variation found among these communities was explained mainly by the SD of relative humidity and temperature, which were highly correlated with this axis. More specifically, in the case of the ridgetop, the variability of relative humidity and temperature explained the variation found among butterfly communities between the dry and wet seasons. However, butterfly communities in the valley were separated by season mainly along axis 1; vegetation density thus better explained the differences in structure and composition of communities between the dry and wet season in this microhabitat.

The results of the Cluster analysis and the Simprof test confirmed the separation qualitatively observed in the CCA; butterfly communities from the ridgetop and valley were significantly different in terms of structure and composition during the dry season ($P < 0.05$), but not during the wet season (Fig. 4).

The CCA diagram with the subfamilies of Nymphalidae and the family Hesperiidae as dependent variables also showed that environmental variables (variability of temperature and humidity, along with vegetation density, average tree diam and canopy cover) were significantly related to the structure and composition of butterfly communities ($F = 2.62$, $P = 0.005$), and 85.9% of the variance was explained by environmental variables along the first 2 axes. The first axis was also defined, as in the previous CCA analysis, by

Table 1. Species richness and abundance of butterflies attracted to baits recorded on the ridgetop and in the valley from the Lalo Loor dry forest reserve.

	Valley		Ridgetop		
	Wet season	Dry season	Wet season	Dry season	TOTAL
Abundance	1171	210	1973	377	3731
Species richness	64	43	56	42	93

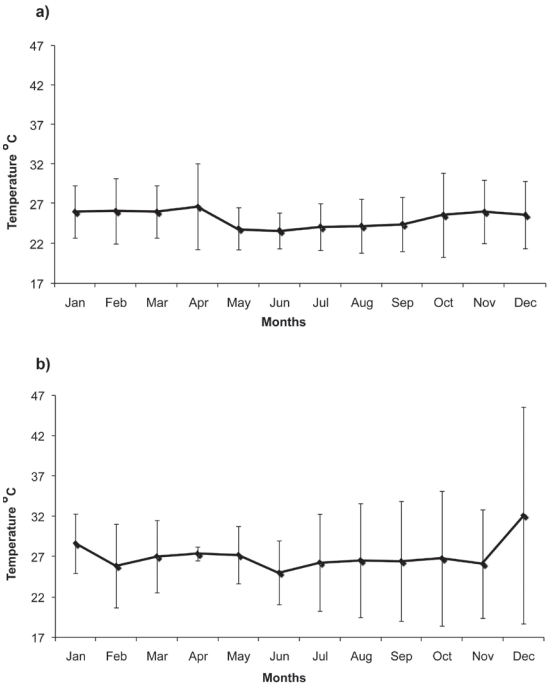

Fig. 2. Temperature (ºC) recorded in the valley (a) and ridgetop (b) from Jun 2009 to May 2010. Error bars represent the mean ± SD of temperature, which were calculated using the maximum and minimum values of temperature of each month. Mean temperature significantly varied between ridgetop and valley over seasons (Mann-Whitney test $U = 31.5$, $P = 0.017$).

vegetation density, whereas the second axis was correlated with variability in relative humidity, temperature and, to a lesser extent, canopy cover and average tree diam. This means that Biblidinae and, to a lesser extent, Charaxinae and Morphinae, occurred mainly at sites with higher variability in both humidity and temperature, and lower canopy cover (Fig. 5). On the other hand, Danainae were found mainly at sites with low vegetation density and intermediate microclimatic variability, and Heliconiinae, Nymphalinae and Limenitidinae were found mainly at sites with low microclimatic variability and high vegetation density.

The linear regression models demonstrated that the SD of relative humidity was negatively correlated with variation in butterfly abundance (b= -0.38; F = 15.94; df = 1,26) and species richness (b= -0.18; F = 10.85; df = 1,26) in the ridgetop and valley communities over seasons, and these relationships were highly significant ($P < 0.001$ and $P = 0.003$, respectively) (Table 2). These results showed that in conditions where humidity is highly variable, a lower number of butterfly species and individuals were present in the butterfly community. On the other hand, the SD of temperature was positively correlated with butterfly abundance (b= 1.57; F = 13.84; df = 1,26) and species richness (b= 0.72; F = 9.42; df = 1,26), and these relationships were highly significant (P = 0.001 and P = 0.005, respectively) (Table 2). In the case of vegetation variables, only canopy cover had a significant effect on butterfly abundance (b= 0.016; F = 12.02; df = 1,26; P = 0.002), with the other variables not significant in the linear models where species richness or abundance was the dependent variable. When the average of both temperature and relative humidity were included in the models (instead of SD), similar results were obtained except that temperature was not a significant variable related to variation in butterfly abundance (F = 0.62; df = 1,26; P =0.43) or species richness (F = 0.21; df = 1,26; P =0.64).

Discussion

Our study showed that microclimatic variables (relative humidity and temperature) as well as vegetation (canopy cover, vegetation density and average tree diam) were significant predictors of the structure and composition of butterfly communities between seasons and microhabitats (Fig. 4). Moreover, canopy cover and microclimate (variability of both humidity and temperature) were also significantly related to the variation of species richness and abundance on the ridgetop and in the valley with season (Table 2). When average temperature and humidity were analyzed instead of SD (representing variability of climatic variables), microclimate was not a significant factor. Thus, microclimate variability and vegetation structure variables are significant factors influencing species richness and abundance over seasons in each microhabitat and, as far as we know, this represents the first study to identify the importance of microclimate seasonal variability in affecting the composition of a tropical insect community.

In temperate areas, microclimate strongly affects the distribution and abundance of larvae and adult butterflies, with temperature and moisture availability being critical determinants of plant senescence and larval growth rates (Hellmann et al. 2004). An appropriate microclimate is also essential for butterfly species hibernating as eggs or larvae in the cool margins of their geographical distributions (WallisDeVries & Van Swaay 2006), emphasizing that microclimate can differentially affect butterfly species with different life history strategies.

Butterfly communities from both microhabitats, ridgetop and valley, showed highest species richness and abundance in the wet season (Table 1). The results of this study agree with those of other studies carried out in Neotropical dry forests (Shahabuddin et al. 1999; Pozo et al. 2008; Torres et al. 2009), where peaks of species richness and abundance oc-

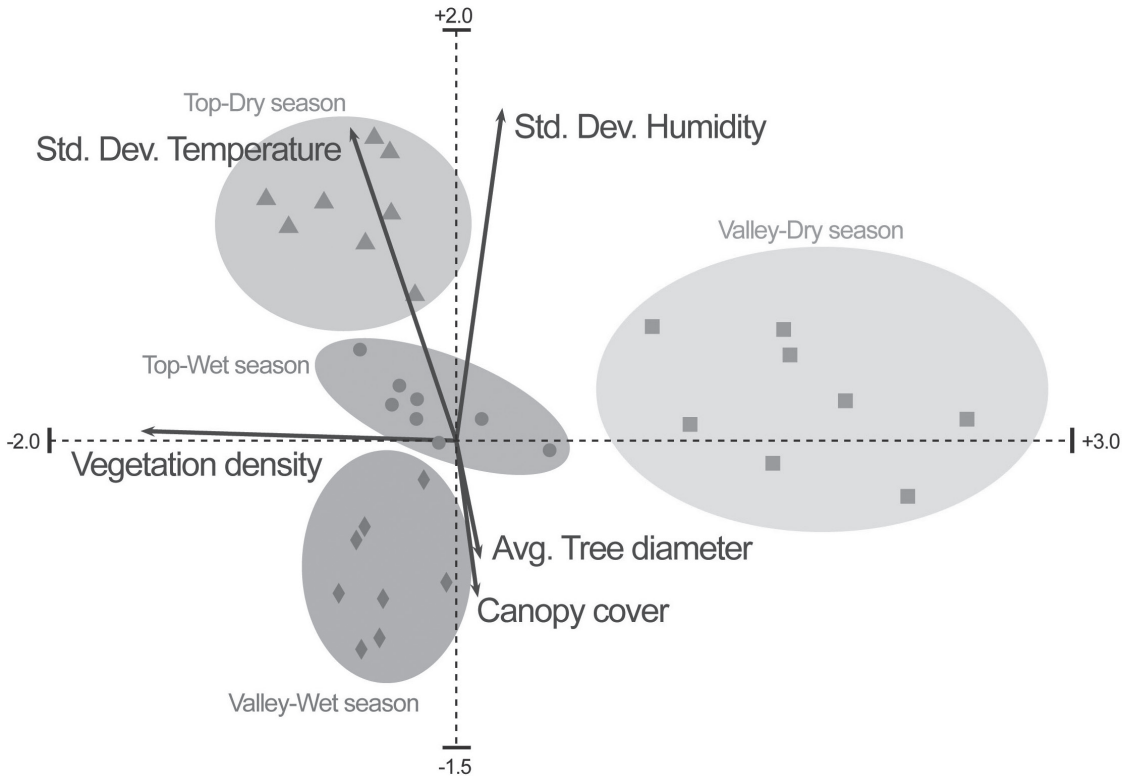

Fig. 3. Results of the Canonical Correspondence Analyses (CCA) showing the relationship between environmental variables and butterfly communities sampled in the valley during the dry (squares) and wet season (diamond), and the ridgetop over the dry (triangles) and wet season (circles). Each point represents one of the 8 sample points established in transects located in the valley and ridgetop. The environmental variables (represented as arrows) included were SD of relative humidity (Std. Dev. Humidity), SD of temperature (Std. Dev. Temperature) and variables representing vegetation structure (Canopy cover, Average tree diam and vegetation density). The explanatory effect of all of the environmental variables on the composition variation of butterfly communities was significant (permutation test, $P < 0.001$).

curred during the months with highest precipitation and relative humidity. This pattern of peak occurrence in the rainy season has also been reported for other insect groups in the tropics (Wolda 1978; Novotny & Basset 1998 and citations therein). In contrast, the results of this study differ from studies that focused on butterfly communities of relatively aseasonal forests in the Ecuadorian Amazonia, where higher species richness and abundance were recorded after the time of the year with the highest precipitation (see DeVries & Walla 2001; Checa et al. 2009; Grøtan et al. 2012). This contrasting pattern could be explained by the presence of different limiting climatic factors in seasonal dry forests compared to aseasonal rain forests, and the associated phenology of the flora and fauna. In other words, water availability is critical in drier habitats where dehydration of both host plants and butterflies is likely, whereas maintaining a sufficiently high thoracic temperature for adequate flight performance is a greater problem for butterflies in cloudier, wetter habitats.

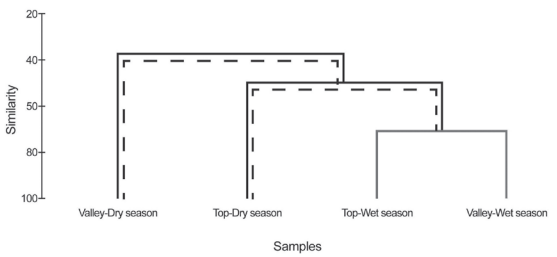

Fig. 4. Results of the cluster analysis using Bray-Curtis index and complete linkage revealing similarities among butterfly communities from valley and ridgetop microhabitats over seasons. Dashed line indicates significant differences ($P < 0.05$) exist between clusters according to the Simprof test.

Our data suggest that ecological differences among major butterfly lineages might explain some of the observed spatial and temporal variation in community structure and composition.

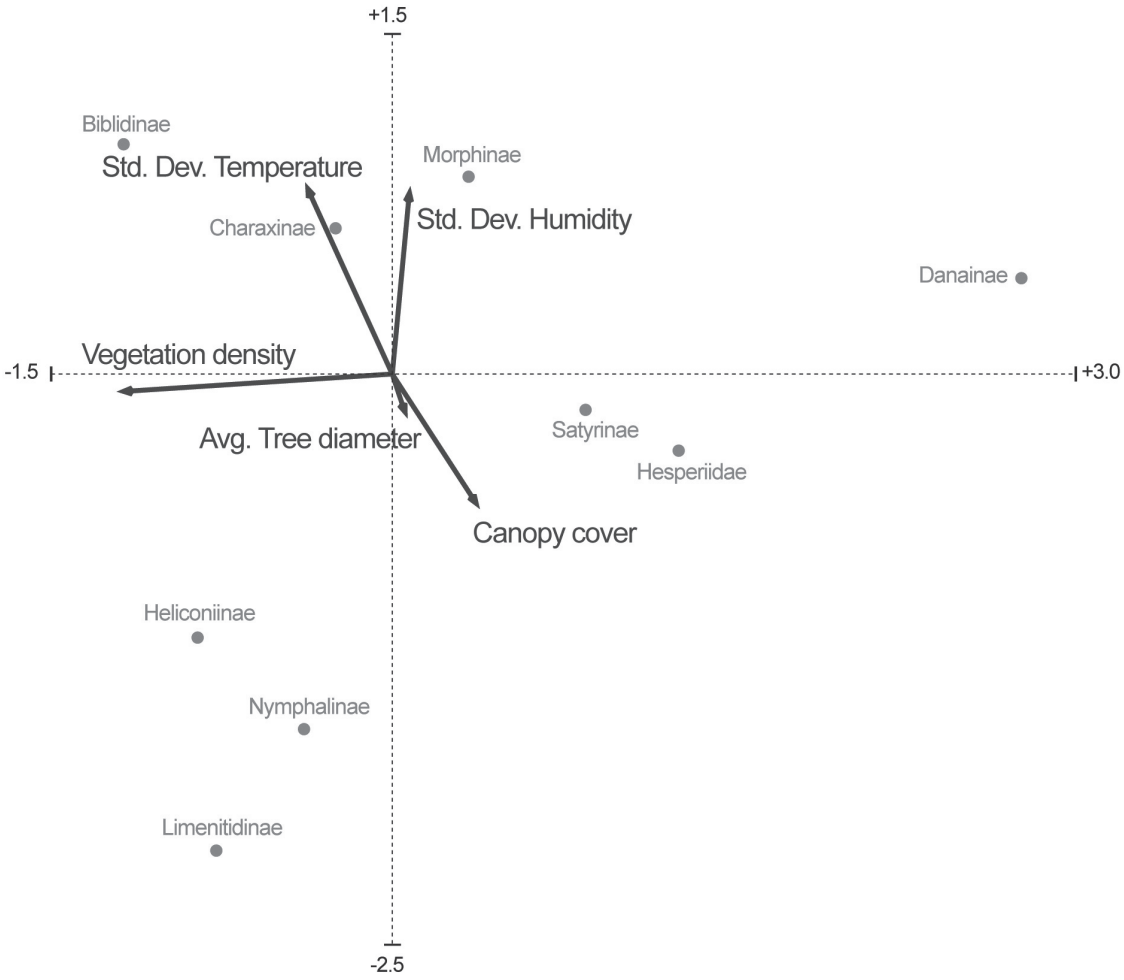

Fig. 5. Results of the Canonical Correspondence Analyses (CCA) including subfamilies of Nymphalidae and Hesperiidae as dependent variables are shown. The explanatory effect of the environmental variables included on the composition variation of butterfly communities was significant (permutation test, $P < 0.001$).

Biblidinae, and to a lesser extent Charaxinae and Morphinae, were associated with higher microclimate variability and low canopy cover (Fig. 5), and were more abundant on the ridgetop than in the valley. On the other hand, Danainae were found mainly in the valley during the dry season, areas with low vegetation density and intermediate microclimatic variability (a preference shown in the CCA analysis, Fig. 5). Limenitidinae were also mainly collected in the valley and more than 98% of the individuals were recorded only during Mar and Apr. A similar pattern was found in Heliconiinae, with 99% of individuals recorded during the wet season. These results support earlier observations that different subfamilies of Nymphalidae have different seasonality patterns (see Checa et al. 2009; Ribeiro & Freitas 2011), and suggest that differences in microhabitat and associated microclimate may be part of the explanation.

Butterfly abundance patterns are partly regulated by larval and adult food resource availability (Yamamoto et al. 2007), which is in turn regulated by climate. This relationship with plant phenology results because herbivores tend to use specific plant resources during short periods of time, when the quality of these sources is optimal (Hellmann 2002). Therefore, the observed decrease in butterfly numbers in the dry season could be explained by the limited food sources for adult butterflies (fruits, carrion) and larvae (leaves) in the valley and ridgetop. This could be especially true for the ridgetop communities, where the average of both relative humidity and temperature were more variable than those of the valley, and where the forest is deciduous. In addition, low humidity

Table 2. Results of the type III test of fixed effects of the linear regression models with butterfly abundance or species richness as dependent variables. Effect column corresponds to predictor variables. sD of relative humidity and temperature along with canopy cover were significantly related to changes in butterfly abundance. Similar results were found when species richness was the dependent variable in the model, except that canopy cover was not significant.

	Abundance		Species Richness	
Effect	F^{1}	P	F^{1}	P
SD Relative Humidity	15.94	< 0.001	10.85	0.003
SD Temperature	13.84	0.001	9.42	0.005
Canopy cover	12.02	0.002	0.93	0.340
Average tree diam	1.50	0.23	3.41	0.076
Vegetation density	0.88	0.36	0.92	0.350

[1]df = 1,26.

along with high temperatures may have made the canopy stratum in the ridgetop a less favorable microhabitat for butterflies in the dry season, so that this 'resource' is also seasonally limited.

It has been reported that the attractiveness of baits differs with species (Hamer et al. 2006) and that the level of attraction may vary over seasons (Torres et al. 2009). Although these factors could certainly explain some variation, the bias produced is likely to be negligible because this study included a large number of species from phylogenetically distinct groups, and the differences in abundance among seasons and microhabitats were relatively large.

In terms of structure and composition, butterfly communities from the ridgetop and valley differed significantly during the dry season, although this separation was non-significant and more or less continuous during the wet season (Figs. 3 and 4). Similar results have been found in *Heliconius* butterfly communities, which showed greater overlap of communities among microhabitats during the wet season (Estrada & Jiggins 2002). These results highlight the higher contribution of environmental seasonality (temporal scale) over microhabitat (spatial scale) in shaping the composition and structure of butterfly communities in LLDFR. At our study site the greater difference between ridge and valley communities in the dry season may have been driven partly by variation in microhabitat preference across seasons in the most abundant species. For example, the characteristic dry forest species *Hamadryas amphichloe, Fountainea ryphea* and *Myscelia cyaniris* showed much higher relative abundance on the ridge in comparison with the valley during drier months. By contrast, the understory species *Taygetis nympha* showed the opposite pattern, being more abundant on the ridge in the wet season and more abundant in the valley in the dry season. Vegetation density in the valley during the dry season was conspicuously lower than in other microhabitats and seasons (Fig. 3), although it is unclear whether or why this might have affected the distribution of these species. Clearly, detailed ecological studies of individual species are needed to understand which factors control these different responses to seasonal climate and microhabitat changes. However, the distribution of adult food sources and host plants is one likely candidate playing a key role in the determination of butterfly population structure (Gilbert & Singer 1973; e.g., Srygley et al. 2009); thus, the differential composition of plant communities in the ridgetop and valley is likely to be an important factor influencing butterfly communities in both microhabitats. The distribution of predators can also influence microhabitat use by butterfly species, as suggested by theoretical studies of mimicry complexes (Gompert et al. 2011). Butterfly species may also prefer different microhabitats because of differing thermoregulatory requirements (Bryant et al. 2002).

The close relationship of butterfly communities with microclimatic conditions and vegetation structure (which is directly related to climate) found in this study suggests that habitat alteration and consequent effects on local climates, in addition to global climate change, are likely to have particularly strong effects on the butterfly fauna of the already fragmented dry forests of western Ecuador. This situation could be exacerbated by at least 5 months of drought in these forests, and by the positive feedback among forest fragmentation, drought and climate change that has been reported for the Neotropics (Laurance et al. 2001).

Vegetation structure (mainly canopy openness) and climate (temperature) are known to be significant predictors of butterfly communities at the habitat level (Barlow et al. 2007; Dolia et al. 2008). Our results also suggest that climatic or anthropogenic effects on canopy cover and vegetation density in tropical dry forests will influence microclimate, and thus the studied butterfly communities in a synergistic way. The understory Satyrinae, for example, were clearly associated with microhabitats having higher levels of canopy

cover. An increase in temperature due to global warming could also alter the phenology of butterfly populations, changing times of appearance or peaks in abundance (Roy & Sparks 2000; Stefanescu et al. 2003), which in turn may disrupt the relationship between butterflies and their host plants or adult resources (Hanski et al. 2004). These processes might eventually lead to species extinctions. An increase in climatic seasonality as a result of climate change is also likely to have adverse effects on tropical dry forest butterflies, particularly on groups such as Heliconiinae, Nymphalinae and Limenitidinae, which were found mainly in sites with lower microclimatic variability. Additionally, our results showed that individual species might react in different ways to climate and habitat change; making it difficult to predict the possible effects of changes in climatic variability on butterfly communities.

Further studies are needed to understand clearly the effects of microhabitat factors on butterfly communities; in particular, long-term studies focused on the seasonality of butterflies and their life histories would be highly valuable. Finally, the overall results of this study emphasize the importance of including temporal and spatial dimensions at the microhabitat level in ecological analyses of butterfly communities in the tropics.

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