

# Effect of Biotic and Abiotic Factors on Diversity Patterns of Anthophyllous Insect Communities in a Tropical Mountain Forest

SE CUARTAS-HERNÁNDEZ, L GÓMEZ-MURILLO

Instituto de Biología, Universidad de Antioquia, Medellín, Colombia

## Keywords

Arthropods, cloud forest, Colombia, ecological interactions, elevation gradient, species turnover

## Correspondence

SE Cuartas-Hernández, Instituto de Biología, Universidad de Antioquia, Calle 67 N° 53-108, Bloque 7 Oficina 108, Medellín, Colombia; sandra.cuartas@udea.edu.co

Edited by Kleber Del Claro – UFU

Received 11 December 2013 and accepted 10 December 2014

Published online: 17 March 2015

© Sociedade Entomológica do Brasil 2015

## Abstract

The determinants of diversity are a central issue in ecology, particularly in Andean forests that are known to be a major diversity hotspot for several taxa. We examined the effect of abiotic (elevation and precipitation) and biotic (flowering plant diversity) factors considered to be decisive causal factors of diversity patterns on anthophyllous insect communities on mountain forest. Sampling was carried out in 100-m transects at eight elevational levels and during a period of 8 months. All flowering plants in the understory and their flowering visitors were recorded. Species richness and diversity were estimated for each elevation and month. Diversity of flowering plants, elevation, and precipitation were used as independent variables in multiple regressions against insect diversity. The evaluated abiotic and biotic factors had contrasting effects on insect diversity: a significant decrease on insect diversity occurred at high elevation and dry months (i.e., threshold effect), while it showed a positive relationship with flowering plant diversity through time (i.e., linear effect), but not along elevation. Rapid turnover of species of both interacting guilds was observed every 100-m altitude and month. Local insect communities were also divided functionally depending on the plant family they visit. These results indicate that each insect community is distinctive among elevations and months and that diversity of flowering plants, precipitation, and elevation influence their structure and composition. Thus, conservation strategies should involve protection of forest cover at the whole elevation gradient, in order to preserve common and exclusive components of diversity and consequently, the mosaic of plant–pollinator interactions.

## Introduction

Identifying the biotic and abiotic factors determining community diversity is a central issue in ecology and has gained particular importance with the escalating loss of species and habitats at global level in recent years (Kelly & Southwood 1999, Brehm *et al* 2005). As a consequence, resulting shifts in functional sets of species or alterations on patterns of interactions might threaten major ecosystem processes (Tilman *et al* 1997, Díaz & Cabido 2001). Thus, interactions as a component of biodiversity might affect short-term ecosystem dynamics and long-term ecosystem stability (Zak *et al* 1994). In spite of this, the role of biotic and abiotic factors as underlying determinants of diversity of interacting guilds is

barely studied (Power *et al* 1988, Arnott & Vanni 1993, Suárez *et al* 2004, Hoffman 2005, Rico-Gray *et al* 2012, Vilela *et al* 2014). The understanding of how diversity patterns of interacting assemblages of species change or depend from each other is a crucial step toward developing general predictions of responses to environmental change (Power *et al* 1988).

Insects are the dominant pollinators on earth and at least 70% of all angiosperms are insect pollinated (Faegri & Van Der Pijl 1979, Kearns & Inouye 1997). Nevertheless, the patterns of insect diversity in tropical mountain forest have been studied only in few groups, mainly on Hymenoptera, Lepidoptera, and Coleoptera (Fisher 1998, Basset 2001, Pycrc & Wojtusiak 2002, Brehm *et al* 2003, 2005, Escobar

*et al* 2005). Spatial and temporal changes in diversity and structure in communities of insects depend greatly on fluctuations in the micro- and macroclimatic conditions (Wolda 1987, Escobar *et al* 2005). Additionally, for anthophyllous insects, diversity depends also on the variation in the availability and geographic distribution of floral resources (Kelly & Southwood 1999, Bachman *et al* 2004, Dyer *et al* 2007, Condon *et al* 2008). High insect diversity has been related to high plant diversity in temperate and tropical areas (Hoffman 2005, Novotny *et al* 2006) and high level of specialization in the use of plant resources (Dyer *et al* 2007). Diversity and availability of flower resources depend on temporal flowering patterns in plants (i.e., phenology), which depends on climatic conditions at local and regional scale and elevation (Krömer *et al* 2006). In addition, differences in composition of plant species give rise to different phenological patterns in different localities (Carranza-Quiceno & Estévez-Varón 2008). As a consequence, the patterns of host plant use varies also, forming a mosaic of interacting species that varies across time (Pinheiro *et al* 2002, Petanidou *et al* 2008), large geographic areas (Malo & Baonza 2002, Condon *et al* 2008), or even within a locality conditioned to sequential flowering (Vilela *et al* 2014). Simultaneously, the abundance of flowering plants influences insect population dynamics and movements (Rico-Gray *et al* 2012, Alves-Silva *et al* 2013), the responses of species to gradual or seasonal changes in environmental conditions (Pinheiro *et al* 2002, Bachman *et al* 2004, Devoto *et al* 2005, Hodkinson 2005), and the number of associations insects establish with plants (Rico-Gray *et al* 2012).

In mountain habitats, several abiotic and biotic components change rapidly through the elevation gradient (Hodkinson 2005, Korner 2007) and diversity decreases monotonically with altitude (Rahbeck 1995, Vásquez & Givnish 1998). However, for a broad range of organisms, diversity shows a different trend with unimodal peaks at medium elevations (Rahbeck 1995, Pyrcz & Wojtusiak 2002, Brehm *et al* 2003). To date, evidence of relationship between patterns of diversity of flowering plants and pollinators at community level is scarce with a few exceptions (Arroyo *et al* 1982, Hoffman 2005, Kessler & Kromer 2000, Krömer *et al* 2006). Thus, the knowledge of diversity, abundance, and distribution of species of interacting communities (flower-visiting species and flowering plants) through space and time is relevant for the understanding of ecological processes (i.e., the functioning of plant–pollinator systems) and key evolutionary mechanisms of community structure. Few detailed ecological studies of flower visitors at community level that include a systematic sampling through elevation and time exist at present (Lomolino 2001, Pinheiro *et al* 2002, Brehm *et al* 2003). In this work, we aimed to investigate spatial and temporal diversity patterns of flower-visiting communities and their floral resources in a mountain Andean

cloud forest. We focused on the key abiotic (elevation and precipitation) and biotic (flowering plant diversity) factors considered decisive causal factors of diversity on anthophyllous insect communities on mountain forest. The main purpose was to know how species richness of insects visiting flowers and flowering plants are influenced by elevation and precipitation and in which way these interacting communities are related to each other.

In a first survey, we wanted to evaluate any strong effect of altitude and/or precipitation on (1) anthophyllous insects and flowering plant diversity, (2) composition and structure of flower visitor assemblage, and (3) the relationship between diversity of insects and flowering plants. Additionally, we analyzed whether assemblages of insects differ among the plant families they visit along the elevation gradient.

By analyzing data from communities at eight altitudinal transects and eight consecutive months in a mountain forest in Antioquia, Colombia, we describe the altitudinal change in species richness and abundance of flower-visiting insect assemblages and its relationship with flowering plant diversity.

## Material and Methods

### Study site

The study area locates in northern Colombia, within the West Cordillera of the Andes at the Department of Antioquia in the Natural Reserve La Mesenia-Paramillo (5°30'11"N, 75°51'7" E). The area is covered with undisturbed to slightly disturbed pluvial cloud forest and pastures (Ledesma-Castañeda 2011, Cuesta *et al* 2009). The reserve is administrated by The Hummingbird Conservancy. It covers an area of 1723 ha and comprises an elevation gradient from 2150 to 3100 m above sea level (asl). Topography is typified by steep slopes. Mean annual temperature ranges from 13 to 23°C. Precipitation exhibits a bimodal pattern with two rainy seasons (March–May and October–December) and two dry seasons (January–February and June–September). The mean monthly precipitation is 161 mm ranging from 61 to 225 mm (Ledesma-Castañeda 2011).

### Sampling and collection of anthophyllous insects

Within the described area, we traced eight 100×4 m transects transversal to the slope of the mountain every 100-m elevation from 2200 to 2900 m asl (T0–T7, respectively). We sampled along a single transect at each 100-m interval because continuous undisturbed forest was not available in the region to replicate transects through the same elevational range studied. Every month from October 2009 to May 2010, we visited at each transect to record data of insects

visiting flowering plants. This period included two rainy seasons and one dry season. In total, we record data for 64 samples (8 transects  $\times$  8 months). Since herb plants are the most abundant structural components of mountain forests in Antioquia (Callejas & Idarraga 2011), we restricted our study to the understory. All flowering plants below  $\sim$ 2-m height within each transect were recorded and all insects visiting their flowers were collected. Since most insects were minute, identification at glance was not possible. Regular walks along each transect were performed from 9:00 a.m. to 5 p.m. (8 observation hours/day) to record visits. The whole system was observed during a total of 512 h. Flowering plants were collected at the end of the observation period and identified at the Herbario Universidad de Antioquia (HUA). Insects were first sorted to morphospecies, and in general, their identification was possible to family level and eventually to genera, in several cases with the assistance of specialists. The diversity of insects for mountain forest is barely known in Colombia and particularly in the studied forest (Ledesma-Castañeda 2011), so we did not have any previous reference to insect diversity. Vouchers were deposited at the Entomological Collection of the Universidad de Antioquia (CEUA).

### Analysis

The sampling effort was comparable in all sampled units to avoid potential bias in the estimation of diversity (Fisher 1998). Additionally, in order to avoid biases in the estimations in not numerous samples, original data was pooled to make one data set for each transect and each month (Magurran 1988). Pooled samples of monthly records of flowering plant and insect visitor species for each elevation were used as samples of local diversity through the elevation gradient. Similarly, for each month, pooled data from all elevations were used as samples of monthly diversity. For insects, matrices were built based on abundance and presence/absence of data, while for plants, only presence/absence of data was obtained due to the small number of flowering species and individuals present in the overall system.

To quantify insect species richness and diversity at each elevation and month (i.e., alpha diversity), three indices were calculated: (1) species richness  $S$ , the total number of species in the whole sample. (2) Chao 2, a non-parametric incidence-based coverage estimator (ICE) of species richness, which requires presence/absence of data in two or more sampled quadrats of equal size and has been shown to be largely independent of sample size (Colwell & Coddington 1994). From the given set of samples, the estimators are computed from 1000 random resamplings of the samples with replacement (bootstrapping), and their means and standard deviations are obtained. This index was calculated using the

software EstimateS version 8.2.0 (Colwell 2009). (3) Shannon index  $H' = -\sum_{i=1}^S p_i \log p_i$  where  $S$  is the total number of species in a whole sample,  $p_i$  is the proportion of the  $i$ th species in the sample ( $p_i = N_i/N$ ),  $N_i$  is the number of individuals of the  $i$ th species, and  $N$  is the total number of individuals of all species in a sample. This index was estimated using Paleontological Statistics software (PAST software v. 2.12) (Hammer 2011). Since abundance of flowering plant communities was too low, we did not calculate Shannon diversity index for this component but only estimates of richness ( $S$  and Chao 2) based on presence/absence of species data.

Similarity Percentage (SIMPER, Clarke 1993) analysis was used to assess the similarity on species composition between each pair of communities between elevations or months. This analysis obtains the Bray–Curtis dissimilarity measure ( $\times 100$ ) and identifies the taxa primarily responsible for the observed differences. Additionally, this analysis allows the detection of common species and the species occurring exclusively in some altitudes or months. The Bray–Curtis dissimilarity is bound between 0 and 100, where 0 means the two sites have the same composition (i.e., they share all the species), and 100 means the two sites do not share any species. To find out whether differences in species composition associate to differences in elevation or to differences in the month when samplings were performed, we calculated Mantel's correlation coefficient. This coefficient is used to calculate correlations between the two square matrices containing information about the distance between pairs of objects (Manly 1991). These analyses were done using PAST software (v. 2.12) (Hammer 2011).

Data on mean monthly precipitation was obtained from WorldClim software v 1.4 (Hijmans *et al* 2005). This software provides a set of global climate grids with a spatial resolution of about 1 km<sup>2</sup>. Linear and polynomial relationship between estimators of species richness and diversity with altitude and precipitation were evaluated. We used a multiple linear regression to analyze the functional relationship between (1) insect diversity per elevation as dependent variable with altitude and flowering plant diversity per elevation as independent variables and similarly, (2) insect diversity per month with mean monthly precipitation and flowering plant diversity per month. Additionally, for tropical Andean forest, a conspicuous change in climatic and biotic characteristics has been described to occur at 2700 m asl and thermal band changes from mountain to alti-mountain (Cuesta *et al* 2009). To investigate whether the abundance and diversity of the studied communities change at 2700-m asl threshold elevation, we performed  $t$  tests for the parameters from communities below (2200–2700 m, low elevation, T0–T5) vs. above this elevation level (2800–2900 m, high elevation, T6–T7).

To define groups of plant species (families) with similar assemblages of flower-visiting insects along the elevation gradient, non-metric multidimensional scaling (NMDS) was

applied to the four families with higher number of visitors. NMDS was chosen because any kind of similarity matrix may be used, and neither normality nor linearity of data is required (Guisande-González *et al* 2011).

## Results

A total of 2603 insect individuals were collected from 8 transects during 8 months. In some of the 64 possible samples, no flowering plant was observed, which reduced the number of samples per transect or per month in few cases. Calculations were performed by pooling the available data. The entire data set consisted of 53 samples, with 73 insect and 43 plant species, including herbs and shrubs. Insect species belonging to ten orders and 55 families were found in the study area: Blattodea, Coleoptera, Collembola, Dermaptera, Diptera, Hemiptera, Hymenoptera, Socoptera, Scolopendromorpha, Thysanoptera (Online Supplementary Material S1).

## Diversity patterns of anthophyllous insects

Fluctuations in abundance and species number of flower visitors were detected through the gradient of elevation and through time. Mean abundance per transect or month was on average ( $\pm$ SD)  $330\pm 49$  ranging spatially from 156 (T7) to 556 (T5) and through time from 52 (March) to 726 (October). The mean number of species per elevation or month was  $26.33\pm 2.06$ . Higher number of species was found at T3 (32 species), T4 (28), and T5 (28) and during October (28), November (47), and April (29). The abundance and species richness (*S* or Chao 2) of insect assemblages had not relationship with elevation. In contrast, Shannon index was negatively related to elevation (Table 1) and the mean per transect was  $1.88\pm 0.24$ . Insect communities from low elevation (2200–2700 m asl) were more abundant and diverse than communities from high elevation (2800–2900 m asl) (Table 1; Fig 1a, left panel). No linear relationship between precipitation with abundance, *S*, Chao 2, or Shannon index was detected (Table 1). However, differences emerge when comparing rainy

Table 1 Relationship between the abundance and diversity descriptors for flower visitor and flowering plant communities with elevation and precipitation (left), and mean comparison between estimates from low vs. high elevation communities and rainy vs. dry month communities (right).

Community	Descriptor	Elevation					
		Linear relationship				Low vs. high	
		$R^2$	$t$	$b$	$P$	$t$	$P$
Flower visitors	Abundance	0.001	0.008	0.56	0.9323	−6.59	0.0003
	<i>S</i>	0.36	1.84	−0.03	0.1152	−9.54	0.0001
	Chao 2	0.001	0.008	0.01	0.9320	3.70	0.0023
	Shannon	0.54	−2.67	−0.002	0.0366	−2.17	0.0475
		Precipitation					
		Linear relationship				Rainy vs. dry	
	Abundance	0.37	1.88	2.42	0.1084	−3.29	0.0001
	<i>S</i>	0.24	1.39	0.08	0.2122	−5.15	0.0001
	Chao 2	0.07	0.69	0.08	0.5122	−5.28	0.0001
	Shannon	0.001	0.10	0.002	0.9184	−2.50	0.0259
		Elevation					
		Linear relationship				Low vs. high	
		$R^2$	$t$	$b$	$P$	$t$	$P$
Flowering plants	<i>S</i>	0.06	−0.62	−0.003	0.5573	−6.80	0.0001
	Chao 2	0.07	−0.69	0.02	0.5143	−4.26	0.0002
		Precipitation					
		Linear relationship				Rainy vs. dry	
	<i>S</i>	0.06	−0.62	−0.003	0.5573	−3.96	0.0001
Chao 2	0.19	1.09	0.17	0.3252	−3.57	0.0001	

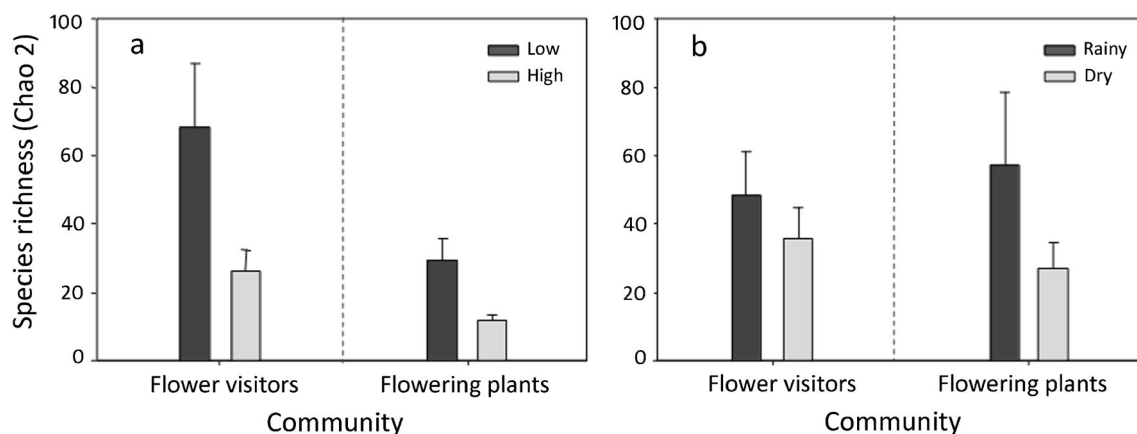


Fig 1 Estimated species richness (Chao 2) for flower visitor and flowering plant communities **a** in low (2200–2700 m asl) vs. high elevation (2800–2900 m asl) and **b** in rainy (>280 mm) vs. dry (<200 mm) months.

months (>280 mm) (October, November, April, May) with dry months (<200 mm) (December, January, February, March). In general, abundance, species richness, and diversity were higher during rainy months (Table 1; Fig 1b, left panel).

#### Species richness of flowering plants

A total of 43 flowering plant species distributed in 12 families and 23 genera was found (Online Supplementary Material S1). The mean number of species per elevation or month was  $16.5 \pm 4.5$ . A higher species number was found at 2400 m asl (T3) (16 species), while the lowest number of species occurred in T0, T3, T7 (7 species in each). Variation in flowering plant species number was more accentuated among months. In February, only 3 species were recorded, while in October and November, 23 and 21 species were recorded, respectively. Species richness of flowering plants as estimated by *S* and Chao 2 did not show a linear relationship with altitude (Table 1). However, communities at low elevation (T0–T5) showed a significant higher species richness compared to communities at high elevation (T6–T7) (Table 1; Fig 1a, right panel). Interestingly, two diversity peaks were observed at T2 (2300 m asl) and T5 (2600 m asl). *S* and Chao 2 did not show a linear relationship with precipitation. However, *S* and Chao 2 were smaller in dry months compared to rainy months (Table 1; Fig 1b, right panel). In general, diversity of insect visitor assemblages was higher than that of flowering plants (mean Chao 2 insects  $57.71 \pm 15.25$ , mean Chao 2 plants  $24.90 \pm 5.24$ ; *t* test  $t=4.46$ ,  $P=0.0001$ ).

#### Composition of communities along the elevation gradient and time

Composition of communities of insects was very different among elevation levels and months. Dissimilarity between pairs of insect communities at different elevations or months was on average 75%. Plant communities were even more

different than insect communities between altitudes (mean 82%) and months (mean 95%). No linear relationship between dissimilarity index with altitude or precipitation was detected. However, dissimilarity index showed a high correlation with distance in elevation (Mantel test: insects  $R=0.76$ ,  $P=0.0001$ ; plants  $R=0.82$ ,  $P=0.0002$ ) and time (distance in number of months) for both insects visiting flowers (Mantel test  $R=0.78$ ,  $P=0.0002$ ) and flowering plant communities (Mantel test  $R=0.89$ ,  $P=0.0018$ ). Figure 2a, b shows the average dissimilarity of each insect or plant community with each other community along the elevation gradient or time (i.e., how different is a particular community from the other communities), respectively. Dissimilarity at small spatial scale, comparing only adjacent communities, showed also high values for both flowering plant and insect communities (data not shown).

A high fraction of unique (i.e., altitudinal restricted) species per elevation was found in both flower visitors and flowering plant communities (on average, 21% for insects and 31% for plants). Moreover, the fraction of species not reaching the superior altitudinal level was 52% and the inferior level was 49% for insect communities (Fig 3a). This trend is more accentuated for flowering plant species; 61% do not cross to the superior level and 57% do not cross to the previous elevational level (Fig 3b).

#### Relationship between diversity of flower visitors with diversity of flowering plants

No correlation among estimated species richness (Chao 2) of flower visitors and flowering plants was detected along the gradient of elevation ( $r=0.59$ ,  $P=0.1223$ ) (Fig 4a), but a significant correlation was detected through time ( $r=0.91$ ,  $P=0.0036$ ) (Fig 4b) also, with a significant linear relationship ( $R^2=0.84$ ,  $t=5.12$ ,  $b=0.66$ ,  $P=0.0036$ ). Multiple linear regressions showed that insect diversity is tightly related to the flowering plant diversity when the relationship is evaluated among temporal communities (i.e., monthly communities).



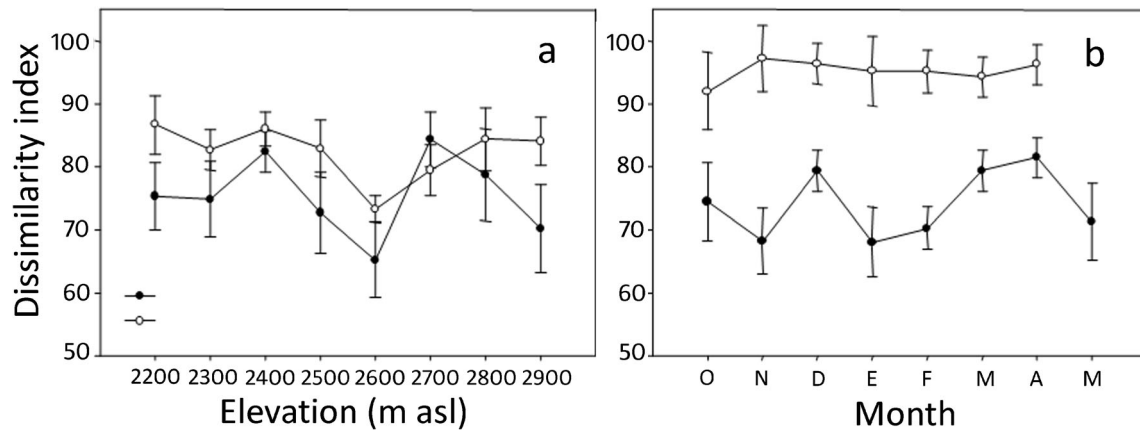


Fig 2 Average Bray–Curtis dissimilarity index **a** between the species composition of the community from each elevation compared to the communities of the other seven elevations and **b** between the species composition of the community of each month compared to the other months.

However, it does not occur when the relationship is evaluated among spatial communities (i.e., altitudinal communities) (Table 2).

#### Are flower visitor assemblages different among plant families?

Forty-two species of plants from 14 families used as floral resources by insects were listed. From these families, the most representative ones were Araceae (17 species), Melastomataceae (7 species), and Piperaceae (4 species). Despite flowering plant species of Araceae were more abundant, Cyclanthaceae with only one species (*Sphaeradenia* sp.) was the family that received the highest number of visits by insects belonging to 22 species.

Dissimilarity index showed that assemblages of flower visitors are very different among plant families (overall average dissimilarity=89.5). The families Araceae, Cyclanthaceae, Melastomataceae, and Rubiaceae had the higher number

of collected insects (data not shown). These plant families are visited by different insect assemblages as suggested by the NMDS (Fig 5).

#### Discussion

The evaluated abiotic and biotic factors had different effects on insect diversity in this Neotropical mountain forest. Species richness of assemblages of flower visitors significantly depended (i.e., linear effect) on the species richness of flowering plants through time (i.e., flowering phenology). Abundance and species richness of both insects and flowering plants fluctuated markedly with altitude and time, but both elevation gradient and precipitation accounted for a high proportion of this variation, not with a linear effect, but in a threshold-like fashion: a significant decline in species richness occurred specifically in the upper part of the gradient and during dry months.

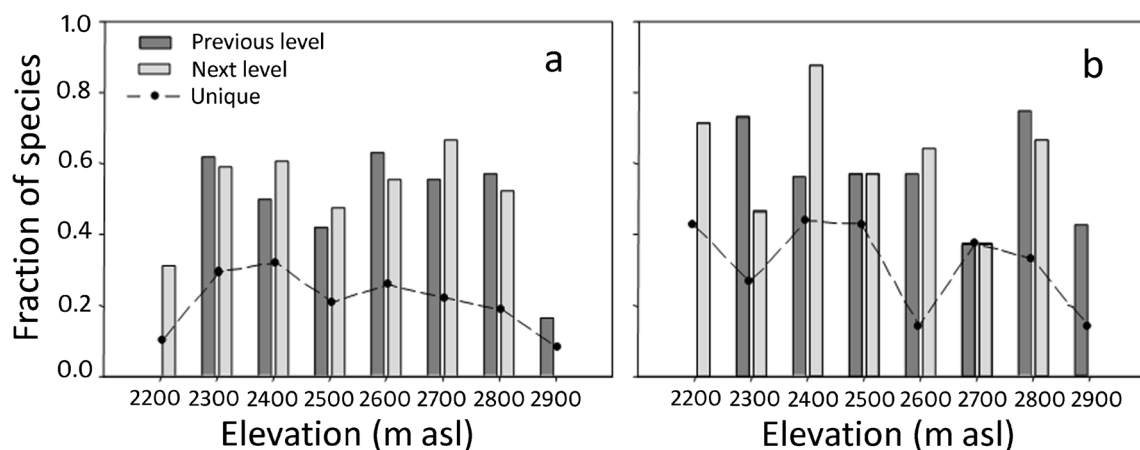


Fig 3 Fraction of species not crossing to the next upper level (*right-hand bar*), fraction of species not crossing to the next lower level (*left-hand bar*), and fraction of species exclusive (*unique*) to the elevation band, **a** for flower visitor communities and **b** for flowering plant communities.

**Table 2** Multiple linear regression between (a) insect species richness (Chao 2) per elevation with altitude and flowering plant species richness (Chao 2) per elevation, and (b) insect species richness (Chao 2) per month with mean monthly precipitation and flowering plant species richness (Chao 2) per month.

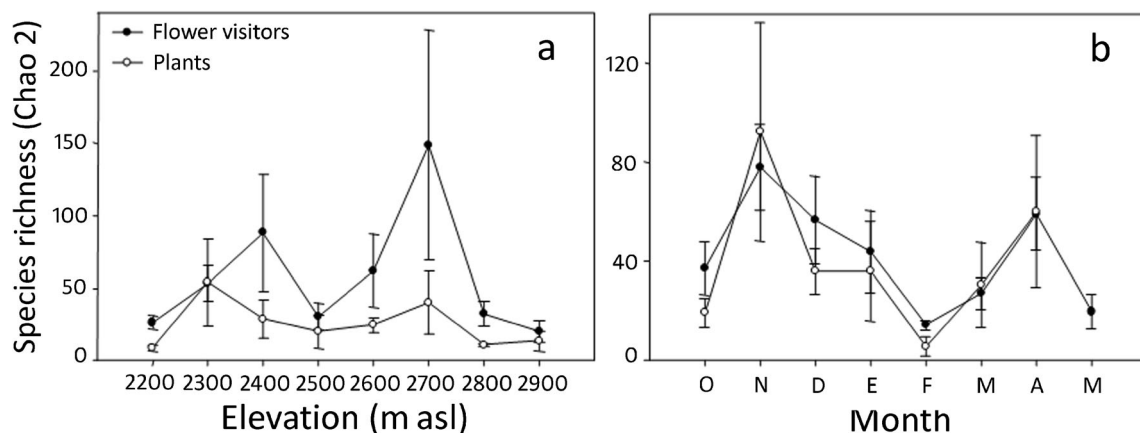
Variable	Slope	Error	Intercept	Error	$R^2$	$P$
(a) Elevation						
Flowering plant species richness (Chao 2)	0.21	0.12	12.49	8.42	0.59	0.1223
Elevation	0.20	2.32	2535.7	163.62	0.04	0.9320
(b) Precipitation						
Flowering plant species richness (Chao 2)	1.22	0.23	-15	11.78	0.92	0.0036
Precipitation	1.63	1.26	153.09	62.73	0.49	0.2532

### Patterns of diversity along the elevation gradient and time

For the studied area, the observed pattern of diversity is remarkable because the decline of insect and flowering plant diversity took place only toward higher altitudes (2800 and 2900 m asl), although a gradual decrease along the entire gradient was expected. The effect of elevation is expressed in a threshold-like fashion, according to Brehm *et al* (2003), who suggested that the decrease of species diversity with altitude may only start at very high altitudes, particularly in the Andes, in the zone of transition between mountain cloud rainforest and the paramo vegetation.

Although few detailed studies about patterns of diversity for insects and floral resources in the tropical mountain forest have been developed, the trends described previously are variable and even specific taxa showed contrasting patterns (Arroyo *et al* 1982, Brehm *et al* 2003). General patterns involve gradual decline in diversity (Wolda 1987, Vásquez & Givnish 1998, Lobo & Halffter 2000) or a peak in richness at middle elevations for several insect groups (Kessler 2000, Escobar *et al* 2005), both patterns contrasting with our findings. In general, insect species richness for the studied area is low compared to other areas in Andean forest (Brehm *et al* 2003, Escobar *et al* 2005), although these studies evaluated diversity at lower elevations (maximum at 2650 m) than our

study. In addition, the conspicuous decrease in diversity starting from 2700 m asl may be related to changes in the composition and structure of tree vegetation and microclimate (Cuesta *et al* 2009), with the formation of structurally homogeneous forest habitat that harbors low diverse communities compared to habitats at lower elevations (Lobo & Halffter 2000). Also, harsh climatic conditions in the summit area allow only few specialists to succeed in this *Chusquea* sp.-dominated forest. Decline in diversity at high elevation has been attributed also to a decrease in the area of habitat and isolation than at low elevations, supporting a lower equilibrium number of species (MacArthur & Wilson 1967). However, habitat area is not expected to be a limiting factor in this study because in the Andes, at high elevation, mountains are convoluted and provide comparable habitat area than at low elevation (Brehm *et al* 2003), but isolation related to a low dispersal rate of individuals from adjacent forested habitats, due to their small size and short distance flights, may be possible. For insect communities, other explanations are the reduction of resource diversity and the reduction of primary productivity (Lawton *et al* 1987). Therefore, the higher heterogeneity in floral resources at low altitude areas favors a higher diversity of flower visitors. Besides, for plant communities, low diversity may be related to cooler temperatures, nutrient limitation and decreased rates of nitrification



**Fig 4** Species richness (estimated as Chao 2) of insect flower visitor and flowering plant communities **a** along the elevation gradient and **b** through 8 months.

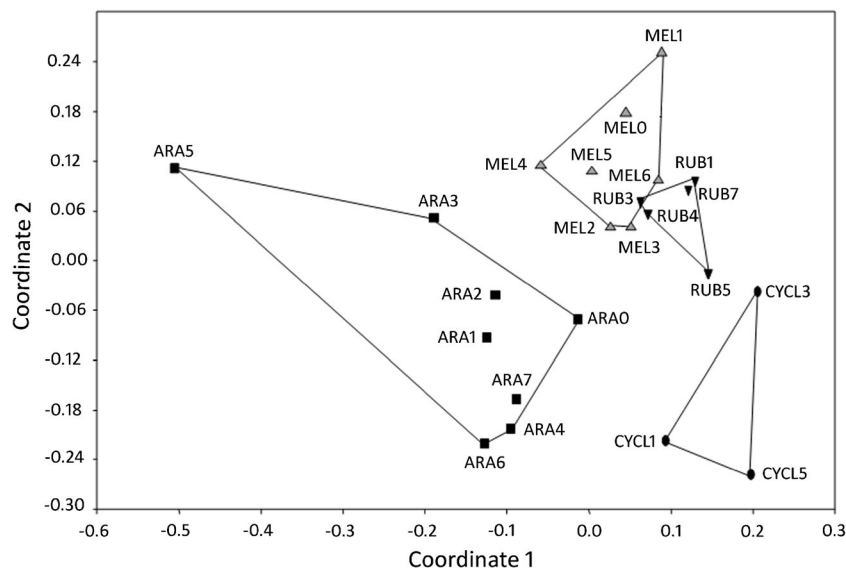


Fig 5 NMDS for species of flower visitors for four plant families: *ARA* Araceae, *CYCL* Cyclanthaceae, *MEL* Melastomataceae, *RUB* Rubiaceae. Stress=0.21. Each object is the community data of insects visiting flowering plants from each family at each elevation where it was recorded.

in mountain soils restraining plant growth rate at high elevations (Vásquez & Givnish 1998).

#### *Composition of communities along the elevation gradient and time*

In spite of the low number of species, composition of communities is very changing among elevations and time. The assemblages of insects change more slowly (~75%) than the assemblages of flowering plants (~89%), which suggests that flowering periods are short and some insects in the guild of visitors could share resources during brief periods of flowering overlap (Vilela *et al* 2014). Positive and significant correlations between dissimilarity index and distance in elevation and time reflect a prominent spatial and temporal turnover of species (i.e.,  $\beta$ -diversity) that was maintained along the entire gradient and the whole period of study. Besides, we did not detect greater dissimilarity levels in species composition at some particular elevations or between any pair of months, in spite of the observed changes in diversity at high elevation and dry months.

The exceptional high values of dissimilarity found indicate abrupt shifts in composition from one community to other at the studied spatial and temporal scales (100-m altitude and 1-month units). Variation in plant and insect assemblages has been described along altitudinal gradient and monthly (Fisher 1998, Basilio *et al* 2006, Petanidou *et al* 2008) although not as high as the observed in our system. This can be explained by the high proportion of altitudinal-restricted species (i.e., unique) that was recorded through the complete gradient for both plant and insect communities.

#### *Effect of diversity of flowering plants on insect diversity*

The diversity of anthophyllous insects significantly depended on the diversity of flowering plants through time. It is interesting that this relationship is diluted when the patterns of diversity are evaluated along the altitudinal gradient, suggesting that local conditions affect plants more strongly than insects, due to plants are sessile, in contrast to insects which are mobile, and consequently, effects are expressed at smaller spatial scale in plants than in insects (Hoffman 2005). In the tropics, local climate changes over few hundred meters along the elevation gradient influencing the exact location of the “climatic optimum” (Rahbeck 1995), shaping the patterns of flowering regionally and locally. At the same time, flowering seems to be highly dependent on precipitation and as a result, flowering communities are more distinctive temporally than spatially. High availability of flower resources during rainy periods which promote an increase on insect diversity in our system due to the presence/absence of food resources influences the nature of the associations between visitor assemblages and flowers (Bachman *et al* 2004, Novotny *et al* 2006, Rico-gray *et al* 2012).

In summary, the complete system of flowering plant–flower visitor interaction in this mountain forest consists of small functional units. These units are delimited first for the amount of precipitation (rainy or dry) which influences the number of flowering plant species every month (i.e., phenology) and subsequently determines the diversity of associated flower visitor assemblages. This pattern is simultaneously affected for altitude in a threshold fashion. Furthermore, flower visitor communities exhibit segregation at even



smaller scale that in our case is the family of the flowering plant they visit. There is a differential use of floral resources by different assemblages of insects, implying that flowering plants might function as “hard boundaries” for ranges of specific flower visitors (Condon *et al* 2008) and that perhaps a process of adaptation of the insect life to the reproductive cycle to the flowering period might come about (Faegri & Van Der Pijl 1979). This variation in the use of floral resources suggests that a certain level of specialization (i.e., at plant family level) takes place within the insect community, sharing limited resources, reducing interspecific competition, and facilitating species coexistence by partitioning niche space (Dyer *et al* 2007), which is a very plausible process due to floral resources are very scarce in the understory of this forest. Furthermore, it is possible that sequential flowering of different species decreases the competence for pollinators and increases the efficiency in the dispersal of pollen (Carranza-Quiceno & Estévez-Varón 2008).

This study is an initial insight into the effect of biotic and abiotic factors on the diversity of interacting guilds, showing that their effects are expressed in diverse ways (linear vs. threshold, respectively). Our analysis on the patterns of diversity of flowering plants and insect visiting flowers along a gradient of elevation and time showed that in spite of great fluctuations of diversity, some patterns emerged. First, the diversity of flower visitors and plants decreased significantly at high elevations and dry months. Second, species richness of the flower visitor assemblages depends on species richness of flowering plants through time. Third, local insect communities are functionally divided depending on the floral resource they use (i.e., plant family). Thus, the diversity of floral resources, precipitation, and elevation are factors that explain in a great proportion the visiting insect diversity on tropical mountain forest.

Although with low numbers of species, communities showed rapid turnover of species of both interacting guilds at the scale of this study, indicating that each of these Neotropical communities are singular and distinctive. Additionally, a great fraction of the insects (21%) and of plant (31%) species we recorded was found at only one elevation and may have very limited ranges. It follows that conservation strategies for this mountain forest should involve protection of forest cover at the whole elevation gradient, in order to preserve common and exclusive components of diversity at each elevation level, and simultaneously, empowering the local ecological processes which are adjusted on an evolutionary time.

Finally, we consider that the low proportion of insect taxa identified to genera and species reflects the current state of taxonomy of mountain forest insects in the Neotropical Region. The proportion of undescribed species from tropical samples of several groups of small and inconspicuous insects is high compared to well-known groups such as birds or

vascular plants (Brehm *et al* 2005). It is likely that an important fraction of species sampled are new to science. Indeed, from our sampling, six species of Curculionidae have recently been described as new (Cardona-Duque *et al* 2011). This scenario constitutes an argument to empower research on taxonomy of insects and beyond, to understand the evolutionary consequences of the spatial, temporal, and functional segregation of insect assemblages on plant populations in tropical mountain environments.

**Acknowledgments** Thanks to The Hummingbird Conservancy and Gustavo Suárez for the logistic support. We are greatly indebted to Martha Wolff (Colección Entomológica de Antioquia) for the assistance with identification of insects, Felipe Cardona and Alvaro Idarraga for the assistance with identification of plants (Herbario Universidad de Antioquia), and Liliana Ramírez and local assistants from Family Rondón-Agudelo for the field job. This work was supported by grant Comité para el Desarrollo de la Investigación CODI-Universidad de Antioquia CPT-0915.

**Electronic supplementary material** The online version of this article (doi:10.1007/s13744-014-0265-2) contains supplementary material, which is available to authorized users.

## References

- Alves-Silva E, Barônio GJ, Torezan-Silingardi HM, Del-Claro K (2013) Foraging behavior of *Brachygastra lecheguana* (Hymenoptera: Vespidae) on *Banisteriopsis malifolia* (Malpighiaceae): extrafloral nectar consumption and herbivore predation in a tending ant system. *Entomol Sci* 16:162–169
- Arnott SE, Vanni MJ (1993) Zooplankton assemblages in fishless bog lakes: influence of biotic and abiotic factors. *Ecology* 74:2361–2380
- Arroyo MTK, Primack R, Armesto JJ (1982) Community studies in pollination ecology in the high temperate Andes of Central Chile. I. Pollination mechanisms and altitudinal variation. *Am J Bot* 69:82–97
- Bachman S, Baker WJ, Brummit N, Dransfield J, Moat J (2004) Elevational gradients, area and tropical island diversity: an example from the palms of New Guinea. *Ecography* 27:299–310
- Basilio AM, Medan D, Torretta JP, Bartoloni NJ (2006) A year-long plant–pollinator network. *Austral Ecol* 31:975–983
- Basset Y (2001) Invertebrates in the canopy of tropical rain forests—how much do we know? *Plant Ecol* 153:87–107
- Brehm G, Süßenbach D, Fiedler K (2003) Unique elevational patterns of geometrid moths in an Andean montane rainforest. *Ecography* 26:456–466
- Brehm G, Pitkin LM, Hilt N, Fiedler K (2005) Montane Andean rain forests are a global diversity hotspot of geometrid moths. *J Biogeogr* 32:1621–1627
- Callejas R, Idarraga A (2011) Flora de Antioquia. Catálogo de las plantas vasculares, vol I, Introducción. D’Vinni, Bogotá
- Cardona-Duque J, Gómez-Murillo L, Franz NM (2011) Phylogenetic reassessment of *Cyclanthura*, a Neotropical genus of Acalyptini associated with arum and cyclanth inflorescences (Coleoptera: Curculionidae: Curculioninae). Annual Meeting of the Entomological Society of America, Reno NV, XI-14-2011
- Carranza-Quiceno JA, Estévez-Varón JV (2008) Ecología de la polinización de Bromeliaceae en el dosel de los bosques neotropicales

- de montaña. Boletín Científico Centro de Museos. Museo de Historia Natural 12:38–47
- Clarke KR (1993) Non-parametric multivariate analysis of changes in community structure. *Austral J Ecol* 18:117–143
- Cowell RK (2009) EstimateS: statistical estimation of species richness and shared species from samples, version 8.2 (<http://purl.oclc.org/estimates>)
- Cowell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. *Phil Trans R Soc B* 345:101–118
- Condon MA, Scheffer SA, Lewis ML, Swensen SM (2008) Hidden Neotropical diversity: greater than the sum of its parts. *Science* 320:928–931
- Cuesta F, Peralvo M, Valarezo N (2009) Los bosques montanos de los Andes Tropicales: una evaluación regional de su estado de conservación y de su vulnerabilidad a efectos del cambio climático. Imprenta Mariscal, Quito
- Devoto M, Medan D, Montaldo NH (2005) Patterns of interaction between plants and pollinators along an environmental gradient. *Oikos* 109:461–472
- Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol Evol* 16:646–655
- Dyer LA, Singer MS, Lill JT, Stireman JO, Gentry GL, Marquis RJ, Ricklefs RE, Greeney HF, Wagner DL, Morais HC, Diniz IR, Kursar TA, Coley PD (2007) Host specificity of Lepidoptera in tropical and temperate forests. *Nature* 448:696
- Escobar F, Lobo JM, Halffter G (2005) Altitudinal variation of dung beetle (Scarabaeidae: Scarabaeinae) assemblages in the Colombian Andes. *Glob Ecol Biogeogr* 14:327–337
- Faegri K, Van Der Pijl L (1979) The principles of pollination ecology, 3rd edn. Pergamon, London
- Fisher BL (1998) Ant diversity along an elevational gradient in the Réserve Spéciale d'Anjanaharibe-Sud and on the western Masoala Peninsula, Madagascar. *Fieldiana Zool* 90:39–67
- Guisande-González C, Vaamonde A, Barreiro A (2011) Tratamiento de datos con R, Estadística y SPSS. FER Fotocomposición, España
- Hammer Ø (2011) PAlaeontological STatistics PAST. Version 2.12. Natural History Museum. University of Oslo, Norway
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978
- Hodkinson ID (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. *Biol Rev* 80:489–513
- Hoffman F (2005) Biodiversity and pollination. Flowering plants and flower-visiting insects in agricultural and semi-natural landscapes. PhD. Thesis, University of Groningen. Groningen, Netherlands, p 224
- Kearns CA, Inouye DW (1997) Pollinators, flowering plants, and conservation biology. *Bioscience* 47:297–307
- Kelly CK, Southwood TRE (1999) Species richness and resource availability: a phylogenetic analysis of insects associated with trees. *Proc Natl Acad Sci U S A* 96:8013–8016
- Kessler M (2000) Altitudinal zonation of Andean cryptogam communities. *J Biogeogr* 21:275–282
- Kessler M, Kromer T (2000) Patterns and ecological correlates of pollination modes among bromeliad communities of Andean forest in Bolivia. *Plant Biol* 2:659–669
- Korner C (2007) The use of 'altitude' in ecological research. *Trends Ecol Evol* 22:569–574
- Krömer T, Kessler M, Herzog SK (2006) Distribution and flowering ecology of bromeliads along two climatically contrasting elevational transects in the Bolivian Andes. *Biotropica* 38:183–195
- Lawton JH, MacGarvin M, Heads PA (1987) Effects of altitude on the abundance and species richness of insect herbivores on bracken. *J Anim Ecol* 56:147–160
- Ledesma-Castañeda EA (2011) Plan de manejo Reserva Natural La Mesenia-Paramillo. BSc Thesis. Servicio Nacional de Aprendizaje SENA, Caldas, Antioquia, Colombia
- Lobo JM, Halffter G (2000) Biogeographical and ecological factors affecting the altitudinal variation of mountainous communities of coprophagous beetles (Coleoptera, Scarabaeoidea): a comparative study. *Ann Entomol Soc Am* 93:115–126
- Lomolino MV (2001) Elevation gradients of species–density: historical and prospective views. *Glob Ecol Biogeogr* 10:3–13
- MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton
- Magurran AE (1988) Ecological diversity and its measurement. Princeton University Press, Princeton
- Malo JE, Baonza J (2002) Are there predictable clines in plant–pollinator interactions along altitudinal gradients? The example of *Cytisus scoparius* (L.) link in the Sierra de Guadarrama (Central Spain). *Divers Distrib* 8:365–371
- Manly BFJ (1991) Randomization and Monte Carlo methods in biology. Chapman and Hall, London
- Novotny V, Drozd P, Miller SE, Kulfan M, Janda M, Basset Y, Weiblen GD (2006) Why are there so many species of herbivorous insects in tropical rainforests? *Science* 313:1115–1118
- Petanidou T, Kallimanis AS, Tzanopoulos JS, Gardeli SP, Pantis JD (2008) Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecol Lett* 11:564–575
- Pinheiro F, Diniz IR, Coelho D, Bandeira MPS (2002) Seasonal pattern of insect abundance in the Brazilian Cerrado. *Austral Ecol* 27:132–136
- Power ME, Stout RJ, Cushing CE, Harper PP, Hauer FR, Matthew WJ, Moyle PB, Statzner B, Wais de Badgen IR (1988) Biotic and abiotic controls in river and stream communities. *J N Am Benthol* 7:456–479
- Pyrce TW, Wojtusiak J (2002) The vertical distribution of pronophiline butterflies (Nymphalidae, Satyrinae) along an elevational transect in Monte Zepa (Cordillera de Mérida, Venezuela) with remarks on their diversity and parapatric distribution. *Glob Ecol Biogeogr* 11:211–221
- Rahbeck C (1995) The elevational gradient of species richness: a uniform pattern? *Ecography* 18:200–205
- Rico-Gray V, Díaz-Castelazo C, Ramírez-Hernández A, Guimarães PR Jr, Holland JN (2012) Abiotic factors shape temporal variation in the structure of an ant–plant network. *Arthropod Plant Interact* 6:289–295
- Suárez YR, Junior MP, Catella AC (2004) Factors regulating diversity and abundance of fish communities in Pantanal lagoons, Brazil. *Fish Manag Ecol* 11:45–50
- Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300–1302
- Vásquez JA, Givnish TJ (1998) Altitudinal gradients in tropical forest composition, structure and diversity in the Sierra de Manatlán. *J Ecol* 86:999–1020
- Vilela AA, Torezan-Silingardi HM, Del-Claro K (2014) Conditional outcomes in ant-plant-herbivore interactions influenced by sequential flowering. *Flora*. doi:10.1016/j.flora.2014.04.004
- Wolda H (1987) Altitude, habitat and tropical insect diversity. *Biol J Linn Soc* 30:313–323
- Zak JC, Willig MR, Moorhead DL, Wildman HG (1994) Functional diversity of microbial communities: a quantitative approach. *Soil Biol Biochem* 26:1101–1108