BIOLOGICAL SCIENCES

Altitudinal variation in butterfly community associated with climate and vegetation

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Abstract: Elevation creates a variety of physical conditions in a relatively short distance, which makes mountains suitable for studying the effects of climate change on biodiversity. We investigated the importance of climate and vegetation for the distribution of butterflies from 800 to 1400 m elevation. We sampled butterflies, and woody and rosette plants and measured air temperature and humidity, wind speed and gust, and solar radiation. We partitioned diversity to assess the processes underlying community shifts across altitudes – species loss versus replacement. We assessed the strength of the association among butterfly, vegetation, and climate. Butterfly richness and abundance decreased with altitude, and species composition changed along the elevation. Changes in butterfly composition with altitude were mainly through species replacement and by abundance increases in some species being compensated by decreases in others. Since the floristic diversity decreased with altitude due to soil conditions, and butterflies are closely related to their host plants, this could explain species replacement with altitude. Overall, we found a stronger association of butterfly community with vegetation than climate, but plant community and climate were also strongly associated between them. Butterfly richness was more strongly associated with plant richness than with temperature, while the reverse was true for butterfly abundance, which was more strongly associated with temperature than with plant richness. We must consider the complementary roles of resource and conditions in species distribution.

Key words: altitudinal gradient, biodiversity, distribution, grasslands, Lepidoptera, mountains.

INTRODUCTION

Mountains represent around a quarter of all terrestrial surface and more than half of the human population depends on the services and goods provided by these ecosystems (Kapos et al. 2000, Körner 2004), such as recreation and tourism, the capture, storage and purification of freshwater, wildlife products, and many others services (for an extensive list see Grêt-Regamey et al. 2012). Ecosystem functioning and all sorts of ecosystem services are sustained by a great

diversity of plants, vertebrates, invertebrates, and microorganisms found in mountains, which, in turn, is the consequence of an equally rich variety of microhabitats (Körner 2004, Egoh et al. 2009, Callisto et al. 2019, Silveira et al. 2019). These ecosystems are hotspots of biodiversity and present a high degree of endemism, especially at the top (Körner & Spehn 2002). Thus, the major conservationist concern about mountain habitats is the serious threat of climate change

to endemic biodiversity at mountaintops (La Sorte & Jetz 2010, Fernandes 2016).

Mountain ecosystems also provide a unique scenario to evaluate the influence of geophysical forces modulating species distribution since they show a great variety of physical conditions in a relatively short distance, and elevation can be used as a proxy for the latitudinal gradient (Fernandes & Price 1988, Körner 2007). Thus, mountains are perfect natural laboratories for the investigation of the effects of climate change on biodiversity (e.g., Silveira et al. 2019). Most organisms show a hump-shaped distribution across altitudinal gradients, with a higher diversity found at intermediate altitudes, although this pattern changes depending on taxa and mountain conditions (Rahbek 1995, Grytnes & McCain 2007). The great diversity of species in mountains is partially due to their distribution into climatic zones or habitats along the elevation, which allows the coexistence of many distinct species within a relatively small area. The species segregation along the altitudes is driven by a series of evolutionary adaptations to abiotic and biotic constraints (Rull 2014, Merckx et al. 2015). For instance, the climate tolerance of organisms can restrict the number of species at different altitudes (Grytnes & McCain 2007). Thus, understanding the processes underlying changes in communities with altitude is essential to predict the effects of climate change on biodiversity.

Butterflies are excellent focal organisms, as they play important roles in many ecosystem functions (Arroyo et al. 1982). For instance, at higher elevations, their pollination efficiency is higher than that of bees and they represent c.a. 75% of floral visitors of Asteraceae, one of the most representative plant families in mountainous rupestrian grasslands in Brazil (Giulietti et al. 1987, Mani & Saravanan 1999, Mota et al. 2016). Butterflies and moths are also

very sensitive to environmental conditions, such as temperature, humidity, rainfall, and wind speed (Brown & Freitas 2000, Brehm et al. 2003, Stefanescu et al. 2004, Bhardwaj et al. 2012), which can influence their distribution across the environmental gradients found in mountain regions. Lepidoptera also have an intimate relationship with the vegetation used as a food source and shelter against predators, especially in the immature phases (Dennis et al. 2004, Marquis et al. 2002, Ferrer-Paris et al. 2013). The adults can feed on flower nectar and for that reason can be less specialized to their host plant than the larvae. Thus, butterfly species distribution can also be closely related to plant structure and community composition (Sawchik et al. 2003, Axmacher et al. 2009, Carneiro et al. 2014).

Many studies report a higher diversity of butterflies at intermediate altitudes - hump-shaped distribution - due to optimal productivity, temperature, and rainfall conditions in these habitats (Gutiérrez 1997, Illán et al. 2010, Abrahamczyk et al. 2011, Stefanescu et al. 2004). Another commonly reported pattern is a linear decrease in species richness with altitude (Chettri 2010, Bhardwaj et al. 2012, Carneiro et al. 2014). One of the most accepted hypothesis to explain this second pattern is that the tolerance of organisms to the harsher climatic conditions at the top would limit the number of species (Grytnes & McCain 2007), leading to community subsets along the altitudinal gradient. Thus, a higher degree of community nestedness and population reduction with the increase in altitude should be expected due to environmental filters getting harsher - although it may also be due to other factors such as the small-area effect or resource scarcity. On the other hand, plant species composition also changes across altitudes (Mota et al. 2016, 2018), and given the intimate relationship between

butterfly and plant communities we could also expect a higher degree of species replacement (turnover) across altitudinal zones.

Recent studies have focused on understanding the role and relative importance of the environment (condition) and vegetation (resource) as drivers of butterfly distribution (Axmacher et al. 2009, Carneiro et al. 2014). Here, we investigated the effects of altitude on nectarivorous butterfly communities and what would be the relative importance of environmental conditions (climate) and feeding resources (plant community) for butterfly variation across the altitudinal gradient. More specifically, we addressed the following questions: i) How does altitude affect the composition, abundance, and richness of the studied butterfly community? ii) What are the processes underlying the possible shifts in butterfly community – species loss (nested communities), caused by the environmental filter, or species replacement (species turnover), following changes in plant community?

MATERIALS AND METHODS

Study site

This study was conducted in Serra do Cipó, in Minas Gerais state, southeast Brazil (19°10' - 19°22' S and 43°29' - 43°36' W, Fig. 1). This region is in the southern portion of the Espinhaço Mountain Range (800 - 2100 m elevation), in the Cerrado biome and is characterized by quartzitic soils covered by rupestrian grasslands, with the predominance of herbs and shrubs (Fernandes 2016). Predominantly, it has a Cwb Köppen climate type, with dry winters and rainy summers. The average temperature varies from 15.1 to 20.7°C and the average annual rainfall is between 1250 and 1550 mm, with a rainy season from November to January, a dry season from May to September, and transitional periods of reduced

rainfall in between (Madeira & Fernandes 1999). The study sites were located along an altitudinal gradient varying from ca 800 to 1400 m elevation (Fig. 1), which covers most of the total elevation range of Serra do Cipó (800 – 1700 m elevation).

Data sampling

We installed weather stations equipped with the Onset HOBO® U30 data logger in seven sites evenly distributed between 800 and 1400m elevation in Serra do Cipó – one every 98 ± 28 m elevation (Fig. 1). The following climatic parameters were monitored in this study: air temperature (annual mean, minimum, maximum, and range), air humidity, wind speed, wind gust, and solar radiation. We used plant community data (richness, abundance, and height) from previous studies in the same area (Mota et al. 2016, 2018), including woody species (shrubs and trees) as well as rosette plants, which is a very frequent life form in the rupestrian grassland (e.g., Velloziaceae, Eriocaulaceae). In each of the same sites, the authors from the previous study set up 13 plots of 100 m² (10 × 10m), where all woody and rosette plant individuals with a diameter at soil height (DSH) ≥ 1cm were sampled. Plant species were processed following standard herbarium techniques and deposited at the Montes Claros Herbarium (MCMG), State University of Montes Claros (UNIMONTES), Montes Claros, Brazil (for details see Mota et al. 2016).

For the sampling of butterflies, three transects of 250m spaced 500m apart were established at each of the seven altitudes, thus comprising a sample unit (General Protocol of RedeLep, C.A. Iserhard & O.J. Marini-Filho, pers. comm.). The only butterfly sampling method that we used was the direct collection of flying butterflies. Each transect was searched by two samplers for two hours and the individuals found were captured with an entomological

Figure 1. Map of the study sites along an altitudinal gradient in Serra do Cipó, Minas Gerais, Brazil. (a) Location of rupestrian grasslands along the Espinhaço Mountains (gray area) in Minas Gerais State, Brazil. (b) Sampling sites (white circles = weather stations) at each altitude.

net. Three periods were set for sampling, from 08:00 to 10:00, from 11:00 to 13:00, and from 14:00 to 16:00. The samplings took place once a month in January, April, July and October of 2012, and January, May, August and October of 2013, therefore comprising distinct periods of the year. Only nectarivorous butterflies were included in this study.

Whenever possible, the sampled butterflies were identified in the field with the aid of guides and then released. Otherwise, specimens were mounted and sent for identification by specialist taxonomists. All material is deposited in different Brazilian institutions: Laboratório de Ecologia Evolutiva e Biodiversidade, Universidade Federal de Minas Gerais (LEEB-UFMG), Museu de Zoologia da Universidade de São Paulo (MZUSP), and Coleção Entomológica Padre Jesus Santiago Moure, Universidade Federal do Paraná (UFPR).

Data analysis

All analyses were performed in R environment (R Core Team 2017). For all analyses, we used the cumulative values of abundance and species richness of all transects in each altitude. To evaluate the effect of altitude on species composition, we built a Distance-based Linear Model (DistLM) in which the response variable was the Bray-Curtis dissimilarity matrix based on the log-transformed values of species abundance in each altitude. Subsequently, we ran a permutational analysis of variance (PERMANOVA) to verify the significance of altitude as the explanatory variable, using the *vegan* package (Oksanen et al. 2017). The effect of altitude on both butterfly species abundance and richness was determined by Generalized Linear Models (hereafter, GLM) based on negative binomial and quasi-Poisson error-distribution, respectively (O'Hara & Kotze 2010). We ran a z and t test to evaluate whether the explanatory

variable (altitude) significantly affected the abundance and richness, respectively.

We assessed the components of community variation along the altitudinal gradient through the values of Bray-Curtis dissimilarities (based on species abundance) and β -diversity (based on species occurrence). Additionally, we partitioned the Bray-Curtis dissimilarity into: i) balanced variation in abundance, which represents the replacement of individuals of some species by a similar number of individuals of different species in another sample, and ii) abundance gradient, which represents the components related to the equal loss of individuals among all species (Baselga 2017). We also considered the following components of β -diversity: i) species turnover, which indicates the proportion of species replacement, and ii) nestedness, representing the loss of species with no replacement (Baselga 2010). All values were calculated for the whole study site and also between each altitude and the next one up using the *betapart* package (Baselga & Orme 2012).

To test the relationship between the butterfly communities and the resource (vegetation), and condition (climate), we used the co-inertia analysis (hereafter, COIA). This analysis is a general and flexible method that measures the concordance (i.e. co-structure) between two multivariate datasets that share the same objects (in this case, altitudinal units, Dray et al. 2003). This approach was applied to quantify and test the association between three pairs of matrices: i) butterfly communities (131 species) and climate (8 variables), ii) butterfly and plant communities (349 species), and iii) plant communities and climate (see Fig. 3). The COIA provides a correlation coefficient (RV) that measures the strength of the association between matrices. This coefficient is bounded between zero (i.e. no association) and one

(i.e. maximum association), with significance (p -value) accessed by a Monte Carlo test with 100,000 permutations. To implement the COIA, a centred PCA was performed for both community matrices (butterfly and plant) based on the log-transformed absolute number of individuals, and another PCA was performed with the centred and standardized values of climate variables (mean zero and standard deviation one). The COIA analysis was carried out using the *ade4* package (Dray & Dufour 2007).

We also evaluated the relative influence of specific climatic conditions and plant community parameters on butterflies across the altitudinal gradient. We used Pearson's correlation to select the variables that are most correlated with altitude – but also biologically significant. The selected variables were average temperature ($r = -0.99$, $p < 0.001$) and plant species richness ($r = -0.89$, $p = 0.007$) as they were highly correlated to altitude and are directly associated with butterfly thermal requirement for flight and diversity of feeding resources, respectively (see Supplementary Material - Table S1 for all correlation results). Then, we built GLMs for butterfly abundance and richness, using temperature and plant richness as explanatory variables, followed by the same statistical test previously described for altitude. We considered the statistical z -values of each explanatory variable as a proxy for the strength of their influence on butterfly abundance, richness, and composition.

RESULTS

In total, we sampled 1033 individuals of butterflies from six families and 14 subfamilies, identified as 120 species and 11 morphospecies (identified to genus level) (see Supplementary Material - Figure S1). HesperIIDae was the most

represented family (58 species), followed by Lycaenidae (28 spp.), Nymphalidae (13 spp.), Riodinidae (15 spp.), Pieridae (12 spp.), and Papilionidae (5 spp.).

We found strong negative effect of altitude on butterfly abundance ($z = -6.140$, $p < 0.001$, d.f. = 7,5) as well as butterfly richness ($t = -3.317$, $p = 0.021$, d.f. = 7,5, Fig. 2). Species composition was also strongly affected by the altitudinal gradient (pseudo- $F = 2.104$, $p < 0.001$, d.f. = 7,5).

Regarding the shifts in the butterfly community, we found high overall levels of Bray-Curtis dissimilarities (0.779) and β -diversity (0.774) for the studied site. The most important components of the community

Figure 2. Effect of altitude on (a) butterfly abundance and (b) richness in Serra do Cipó, Brazil. The solid lines represent the fitted model, the shaded areas the confidence intervals and the circles the observed values.

shift for Bray-Curtis was the balanced variation in abundance (91.2%), and for β -diversity was species turnover (92.2%). For the comparison between consecutive altitudes, we also observed the dominance of the components balanced variation in abundance and species turnover (Fig. 3). Additionally, there was a clear pattern of increasing the Bray-Curtis dissimilarity with altitude and a less evident but still considerable similar pattern for β -diversity (Fig. 3).

Even though the correlations were not statistically significant, the positive influence of average temperature on butterfly abundance ($z = 1.859$, $p = 0.063$, d.f. = 7,4) was stronger than that of plant richness ($z = 0.217$, $p = 0.828$, d.f. = 7,4), based on the z -value. On the other hand, plant richness was the most important variable for butterfly richness, and was also positive ($z = 1.906$, $p = 0.057$, d.f. = 7,4), while temperature showed a weaker and negative affect on butterfly richness ($z = -0.263$, $p = 0.792$, d.f. = 7,4). In addition, butterfly communities were strongly and significantly associated to plant communities ($RV = 0.882$, $p = 0.020$) and lesser to climate variables, but still very significantly ($RV = 0.796$, $p < 0.001$, Fig. 4). Plant community and climate were also strongly associated ($RV = 0.642$, $p = 0.036$, Fig. 4). The COIA main axes explained 57.7% of the association between butterflies and plants, 92.2% between butterflies and climate, and 86.8% between plants and climate (see Figures S1 and S2).

DISCUSSION

Our findings support the hypothesis that the studied butterfly community varies across the altitudinal gradient. There was a decrease in butterfly species richness and abundance with altitude as well as a change in species composition, corroborating previous studies

Figure 3. Results from the partitioning of butterfly community variation comparing consecutive altitudes in increasing order. In the Bray-Curtis dissimilarity (a), gray bars represent the proportion of *balanced variation in abundance* (replacement of individuals of some species by individuals of other species), while white bars indicate the proportion of *abundance gradient* (equal loss of individuals among all species; Baselga 2017). For β -diversity (b), gray bars represent the species *turnover* component of the community shifts, while the white bars indicate the *nestedness-resultant* component in each altitude comparison. Black dots represent overall values of (a) Bray-Curtis dissimilarity and (b) β -diversity.

with butterflies in other regions of the globe (Vargas-Fernandez et al. 1992, Camero & Calderón 2007, Carneiro et al. 2014). The changes in community composition were mainly through species replacement (β -diversity component: species turnover) across the altitudinal sites, and because abundance increases in some species were compensated by abundance decreases in other species (β -diversity component: balanced variation in abundance; Baselga 2017; Fig. 3). This would be the expected

scenario if the observed butterfly community shifts had a stronger association with changes in resource distribution (plant community) than with environmental filters (climate variables), which would have more likely been related to species loss (Grytnes & McCain 2007). Indeed, we found an overall stronger association of the butterfly communities with the plant communities than with the climatic variables, even though we used data on vegetation from previous years. Also, plant richness showed a stronger relationship with butterfly richness, whereas average temperature was more related to butterfly abundance. Conversely, a study by Hawkins & Porter (2003), at a much larger spatial scale, found that plant diversity did not directly influence butterfly diversity, even though plant and butterfly diversity were positively correlated. The association between butterfly diversity and vegetation composition and diversity can be indirect, mediated by an environmental parameter that affects both (e.g., temperature, humidity; Axmacher et al. 2009, Hawkins & Porter 2003). Thus, it may well be that it is a combination of various climatic and vegetation parameters that synergistically drive the shifts in butterfly communities along altitudinal gradients. The balance between the two drivers is likely dependent on spatial scale as well as on butterfly species specificity, which will determine their degree of dependence on vegetation structure, diversity and composition.

The climatic conditions at the top of Serra do Cipó are certainly more severe for most of the sampled species than at the lowlands, because of lower temperatures, higher rainfall during the summer, and more intense winter droughts (Fernandes & Price 1988, 1991). Our climate data indeed revealed a temperature reduction of 0.85°C per 100 m elevation (see Figure S3). This means that the temperature at the highest sampling site is about 5°C lower than at the

Figure 4. Results of co-inertia analysis (COIA) with the correlation coefficient (RV-value) between the variable matrices of climate, and plant and butterfly communities. The arrows represent the logical direction of the association between variable matrices. It shows climatic variables that are affected by altitude and have a strong influence on the plant and butterfly communities. Also, the butterfly communities are more strongly correlated to the plant communities (resource) than to the climate (condition). As a result, 'Balanced variation' (replacement of individuals of some species by individuals of other species) and 'Turnover' (species replacement) following the changes in plant community composition are more important components of community shifts than 'Abundance gradient' (the equal loss of individuals among all species) and 'Nestedness' (the nestedness-resultant component in each altitude comparison). 'Avg. temperature' = average temperature, 'Min. temperature' = minimum temperature, 'Max. temperature' = maximum temperature.

lowest site (Figure S3). Low temperature is known to negatively influence the number of butterfly species (Molina-Martinez et al. 2013), and here it seems to have been an important filter for butterfly abundance, which may also lead to smaller populations and, as a result, to lower species richness. However, climate is also an environmental filter for the plant community. In fact, in the present study, the climatic conditions were more related to the plant community than to the butterfly community. Thus, climatic variables are directly and indirectly associated with the distribution of nectarivorous butterflies as there is a clear and intimate relationship between butterfly and vegetation (Dennis et al. 2004, Marquis et al. 2002, Ferrer-Paris et al. 2013). Nonetheless, the lack of a direct relationship between plant and butterfly richness indicates that it is plant species composition that is more relevant to the butterfly communities. This is most likely due to butterfly species requiring specific host plant, particularly at their initial life stages (egg, larva, pupa). As shown by Mota et al. (2016), the floristic diversity decreases in the altitudinal gradient of Serra do Cipó, due to changes in soil conditions, reducing the amount of resource for butterflies (e.g., Brown & Freitas 2000, García-Barros 2000, Mota et al. 2018). Hence, more detailed studies on the interaction between butterfly species and their host plants can provide further information on the roles of condition and resource in butterfly species distribution.

Additionally, the community variation between pairs of sampling sites increased with altitude. Although α diversity decreased along the gradient, β diversity did not decrease, unlike previous studies (Kraft et al. 2011, Mori et al. 2013). Butterflies are very sensitive to environmental changes, which may be a barrier to their movement along the altitudinal gradient, making communities more homogeneous in

each altitudinal range. Some species show strong specificity to wetter, cooler, and windy conditions at higher altitudes and are typical butterfly species from mountain environments (Burns 1994, Carneiro et al. 2014). Although some species undergo large migratory events (Urquhar 1960, Baker 1969), other butterflies are sedentary or have little movement, spending much of their lives restricted to places where their host plants occur (Ehrlich & Raven 1964, Beirão et al. 2012), or limited by behavioural factors (Ehrlich 1961). As we found direct and indirect responses of butterfly community to plants diversity and environmental conditions, this study emphasises the importance of the conservation of mountainous environments for the maintenance of biodiversity, and consequently the ecological interactions supporting ecosystem services. Our study also sheds light on the likelihood of vertical displacement of butterfly species in response to climate change (Parmesan et al. 1999, Wilson et al. 2007, Colwell et al. 2008). Under the potential pressure of global warming or other climate changes (e.g., longer and severe droughts), species that are distributed at lower altitudes are expected to move to higher altitudes, while those restricted to mountaintops would be excluded (Parmesan & Yohe 2003, Molina-Martinez et al. 2016, Freeman et al. 2018). This process is likely to lead to low-altitude diversity impoverishment if not compensated by colonization, as corroborated by previous works (Wilson et al. 2007, Colwell et al. 2008, Inouye 2020). However, as we found that butterflies are more associated to plant community, their displacement is likely to depend on the host plants responses to environmental changes and vegetation shifts rather than climatic condition only.

This work represents an initial step and we hope that it will stimulate further investigations

on the interaction between butterflies and mountain environments. Studies on processes driving species distribution are fundamental to support species and habitat conservation plans, especially in threatened megadiverse tropical mountains. This study may also provide a basis for conservation strategies of endangered butterfly species, such as *Rhetus belphegor* (Westwood) (Riodinidae), with only three individuals collected at 1300 altitude (Figure S1), and classified as endangered on the IUCN list of threatened species (MMA 2014). The results here highlight the importance of more general and holistic views when planning areas for conservation. We show that the distribution of butterfly species is likely to be highly dependent on plant species distribution, but also on climatic conditions. We also stress that other factors potentially affecting plant communities, such as soil conditions, may also indirectly affect species distribution through their resources.

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SUPPLEMENTARY MATERIAL

Table S1. Figures S1, S2, S3.

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A.C.V.P., M.B., W.B. M.V.B. and G.W.F. wrote the paper. A.C.V.P., M.V.B. and F.A.L. did field sampling. O.J.M.F. contributed with text considerations. A.C.V.P., M.D. and O.H.H.M. were responsible for butterfly identification. Y.R.F.N. contributed with plant data. A.C.V.P., M.B., W.B. and D.N. did the data analysis.