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e Manejo da Vida Silvestre

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Besouros rola-bostas (Coleoptera: Scarabaeidae: Scarabaeinae) e suas funções ecológicas ao longo de um gradiente altitudinal tropical

Belo Horizonte

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Dissertação apresentada ao programa de Pós-graduação em Ecologia Conservação e Manejo da Vida Silvestre do Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais como requisito parcial para a obtenção do título de Mestre em Ecologia.

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Dedico esta dissertação de Mestrado
aos meus pais (Netu e Ninha)!

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“... E a hora chegará quando você ver
que somos todos um,
E a vida flui com você e sem você"

George Harrison
The Beatles
Within You Without You

VISÃO GERAL DA DISSERTAÇÃO

Pretendo publicar os resultados da pesquisa realizada ao longo do meu mestrado em periódicos internacionais, em forma de artigos científicos. Para tanto, escrevi esta dissertação já em formato de artigo e a dividi em dois capítulos. Os dois capítulos estão escritos na língua inglesa e devidamente formatados conforme as regras dos periódicos nos quais pretendo publicá-los.

O primeiro capítulo trata da comunidade de besouros rola-bostas (família Scarabaeinae) e seus atributos como riqueza, abundância e diversidade funcional ao longo de uma montanha na cadeia do Espinhaço (Serra do Cipó). A biodiversidade pode ser subdividida em diversas facetas, como a diversidade taxonômica, funcional e filogenética. Recentemente, ecólogos vêm utilizando métricas que acessam essas várias facetas, para um melhor entendimento dos padrões de biodiversidade e os processos que os regulam. Além disso, a diversidade pode ser fragmentada em componentes espaciais que ajudam a entender a distribuição de espécies. Entretanto, estudos que misturam essas duas abordagens ainda são raros. Neste primeiro capítulo, o objetivo foi entender os processos que regulam a diferenciação entre comunidades de rola-bostas ao longo da altitude. Apesar de saber que a riqueza geralmente diminui com a altitude, não sabíamos a influência desta sobre a diversidade funcional. Nós conseguimos resultados que nos permitiram concluir que os filtros ambientais, no caso do nosso estudo, não agem igualmente sobre a diversidade taxonômica e funcional. Além disso, a divisão espacial da diversidade nos alertou sobre efeitos do aquecimento global em comunidades de rola-bostas de montanhas tropicais.

O segundo capítulo enfoca as funções dos rola-bostas ao longo do mesmo gradiente altitudinal. Ao longo das duas últimas décadas, tem sido grande a preocupação com a perda da biodiversidade causada pelos impactos humanos e seus desdobramentos no funcionamento dos ecossistemas. Diversas pesquisas foram realizadas tentando demonstrar a ligação entre a biodiversidade e o funcionamento do ecossistema. Entretanto, algumas incertezas ainda precisam ser resolvidas, como a influência de fatores ambientais na realização das funções ecológicas. Neste capítulo, nosso objetivo foi mostrar quais fatores influenciam a realização das funções ecológicas dos rola-bostas. Nós obtivemos a quantidade de três funções desempenhadas por esse grupo ao longo do gradiente altitudinal, que fornece grandes variações climáticas e ambientais.

Dessa forma, pudemos testar a influência do ambiente, assim como as características da comunidade na realização das funções. Até onde sabemos, este trabalho é pioneiro em mostrar a conexão entre biodiversidade, ambiente e funções ecológicas. De forma semelhante a que fizemos no primeiro capítulo, discutimos também a influência do aquecimento global no funcionamento dos ecossistemas.

A ordem de publicação desta dissertação será primeiramente o Capítulo 1 e posteriormente o Capítulo 2, já que parte deste depende da publicação do Capítulo 1. Para facilitar o entendimento do texto da dissertação, no Capítulo 2 haverá citações ao primeiro capítulo como “Article 1”. Assim que o Capítulo 1 for publicado ele será citado no segundo artigo como qualquer outra citação.

Após revisão de escopo de periódicos, a revista Ecology foi escolhida para a publicação do primeiro capítulo e a revista Journal of Ecology para o segundo capítulo. Algumas normas de redação de ambos os periódicos foram ignoradas, para facilitar o entendimento do texto. As exceções às regras são: as tabelas e figuras estão inseridas ao longo do texto; o texto está justificado às margens; o espaçamento entre linhas é de 1.5; as margens são 3 cm esquerda e direita e 2.5 cm acima e abaixo.

SUMÁRIO

Dung beetles along a tropical altitudinal gradient: environmental filtering on taxonomic and functional diversity

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ABSTRACT

Mountains provide an interesting scenario to study biodiversity responses to macroclimate, as environmental conditions change rapidly due to elevation over short spatial distances. Generally, biodiversity decreases with increasing altitude, following geophysical and climatic trends. Although there is lot of data on how taxonomic diversity responds to altitude, there is a lack of information on what happens to other facets of biodiversity like functional and phylogenetic diversity. Studies that merged the multifaceted concept of diversity with the spatial partition are very rare. Our goal was to understand what happens to dung beetles community along a tropical altitudinal mountain gradient, including the spatial partition of taxonomic and functional diversities instead of using only richness and abundance as proxies of biodiversity. This study was performed along a mountain in the Espinhaço's range, Southeast Brazil. The altitudinal gradient ranged from 800 up to 1400 m a.s.l. and we collected dung beetles every 100 m of altitude. We used the Rao quadratic entropy decomposition of diversity to calculate γ, α and β diversity for taxonomic and functional diversity of dung beetles. Further, climatic, soil and vegetation variables were used to explain variation on community's attributes along the altitudinal gradient. Dung beetles richness declined with altitude and it is related to climatic and vegetation variables, but functional diversity did not follow the same pattern. Over 50% of γ taxonomic diversity is caused by among altitudes diversity (β), but almost 100% of functional diversity is caused by α component. Contrasting β taxonomic with β functional diversity suggest that there is ecological redundancy among communities and environmental variables are filtering species in terms of Grinnellian niche, but not in terms of Eltonian niche. β taxonomic diversity is caused mainly by turnover components and it reinforces the idea that different environmental filters, provided by elevation, are selecting dung beetles species in terms of physiological niche. We think that in a global warming scenario, upslope range shifts, mountaintop and lowland extinctions will lead to even bigger loss of diversity than expected as taxonomic diversity among altitudes is high and proportioned mainly by turnover of species.

Keywords: Taxonomic Diversity, Functional Diversity, Alpha Diversity, Beta Diversity, Dung beetles, Scarabaeinae, Mountain, Altitudinal Gradient, Environmental Filtering.

INTRODUCTION

Mountains provide an interesting scenario to understand how living beings respond to macroclimate since they offer steep environmental gradients. As we ascend a mountain, environmental conditions change rapidly (von Humboldt and Bonpland 2009), favoring ecological and evolutionary studies over short spatial distances (Körner 2007). After decades of research, ecologists and biogeographers proposed that there is a pattern of species distribution along an altitudinal gradient: the decreasing of diversity with elevation (Rahbek 2005, Grytnes and McCain 2007, McCain 2009). In humid tropical mountains species richness usually decreases monotonically with increasing altitude (McCain 2009, 2010). The general geophysical and climatic trends with altitude are: (i) decline of land area; (ii) decreasing total atmospheric pressure as well as partial pressure of O_2 e CO_2; (iii) reduction of air temperature; and (iv) increasing in solar radiation (Körner 2007). Other factors can be associated with an altitudinal gradient, such as relative humidity, precipitation, wind velocity, geological substrates, nitrogen deposition and soil pH but they are driven by regional variations (Körner 2007, Sundqvist et al. 2013). These are some of the mechanisms that will influence the plants and animals species distribution in different mountains. As the abundance, diversity and functional traits of plants change along an altitudinal gradient, the primary production is affected, and this can also affects animal distribution (Sundqvist et al. 2013).

Biodiversity is a concept that includes not only species diversity (taxonomic) but also functional and phylogenetic diversity (Pavoine and Bonsall 2011). Functional diversity is one of the most important components of biodiversity that affects ecosystem functioning, and calculating it can help us in nature conservation (Díaz et al. 2007, Devictor et al. 2010a). Furthermore, studying both taxonomic diversity (TD) and functional diversity (FD), can improve the understanding of biodiversity patterns since they capture different aspects of species ecological roles, resources' use and habitat requirements. Thus this can be helpful in understanding how environmental and biotic factors acts as filters to species and their traits along a gradient (Villéger et al. 2012, de Bello et al. 2013). Although there are a lot of papers focusing species richness patterns along altitudinal gradients, there is a lack of information on what happens with the other facets of diversity (but see de Bello et al. 2005, 2013, Dainese et al. 2014, in press).

Beyond this multi-faceted concept, biodiversity can be partitioned into different spatial components and this is crucial to understand processes influencing species distribution (Jankowski et al. 2009). Regional diversity (called γ-diversity) can be decomposed into within local community diversity (α-diversity) and among communities diversity (β-diversity) (Veech et al. 2002, Crist et al. 2003). Recently, the partition of diversity have been extended to the other facets of diversity, such as FD (de Bello et al. 2009, Villéger et al. 2012, Swenson et al. 2012, Carmona et al. 2012). As shown by Baselga 2010, β diversity (both TD and FD) can be decomposed into two main components: turnover (species replacement between communities) and nestedness (species loss or gain between communities). Studies that merged the multifaceted concept of diversity with the spatial partition along environmental gradients are very rare (but see Meynard et al. 2011 and Devictor et al. 2010a) and as far as we know there is only one study along altitudinal gradients (Dehling et al. 2014). In addition, the decomposition of both β TD and β FD also is very scarce in the literature (but see Villéger et al. 2013), especially in tropical ecosystems.

Dung beetles are members of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae), a diverse and abundant group of insects. They have been used as bioindicators due to their sensibility to environmental changes and because they perform various ecological functions such as soil fertilization and aeration, increasing nutrient cycling and secondary seeds dispersal (Andresen 2005, Spector 2006, Nichols et al. 2008, Slade et al. 2011, Almeida et al. 2011, Braga et al. 2013). Several studies in Europe, North America, Southeast Asia, South Africa and in South America reveled a consistent decrease in the number of species of dung beetles with increasing altitude (Lobo and Halffter 2000, Escobar et al. 2005, 2007, Larsen 2012, Herzog et al. 2013). However, we could not find any study of dung beetles functional diversity along altitudinal gradients.

In this study, we tried to understand what happens to the dung beetles community along a tropical altitudinal gradient, but differently from other studies, we included the spatial partition of TD and FD, instead of using only richness and abundance as proxies of biodiversity. We tested the hypothesis that environmental factors may control the differentiation in biodiversity. We expected a decrease in species richness with the altitude (Lobo and Halffter 2000) and as a consequence, also a decrease in FD. Further, since the altitudinal gradient can provide different filters, we expected both β TD and β FD would be high for the whole gradient. We also expected that β TD and β FD of each class of altitude diminishes along the altitudinal gradient, because total diversity and habitat heterogeneity decreases with elevation. By partitioning β diversity we tested if mountaintop communities are sub-sets of lowland communities. Moreover, we tested a practical issue: how including relative abundances to calculate diversity alter our understanding of biodiversity responding to environmental variables.

MATERIALS AND METHODS

Study site

The study was conducted on cerrado and rupestrian fields areas located on the south of the Espinhaço mountain range, in Minas Gerais State, Brazil (19°10' and 19°22' S, 43°29' and 43°36' W) during December 2013. The region, called Serra do Cipó, presents a highland tropical Cwb Köppen climate with a rainy season between November and February and mean annual temperature and rainfall of 20°C and 1,500 mm, respectively (Madeira and Fernandes 1999). The Espinhaço range is a quartzite mountain chain that crosses the Southeast and part of Northeast of Brazil and separates the Atlantic Forest and Cerrado biomes (Giulietti et al. 1987, Kamino et al. 2008). At the study location, altitude vary from 750 up to 1670 m a.s.l. and soil and vegetation are very heterogeneous, varying from five principal habitats: peat bogs, sandy bogs, quartz gravel fields (rupestrian fields), rocky outcrops and cerrado (de Carvalho et al. 2014). Serra do Cipó is well known by its high plant and animal biodiversity and a large number of endemic species (Giulietti et al. 1987, Rapini et al. 2008, Vasconcelos et al. 2008, Freitas et al. 2012).

Sampling Design and Environmental Variables

This study is a part of a larger research project ("Projeto Ecológico de Longa Duração – PELD – Sítio Serra do Cipó") and we used its pre-established sampling sites. Transects were distributed every 100 m, from 800 to 1400 m a.s.l., with a minimum geographic distance of 2 km, totaling seven sampling areas. In each of these areas we used three transects separated by at least 250 m, each consisting of three sampling points in turn separated by 100 m. At each altitude, a meteorological monitoring tower (equipped with the Onset HOBO® U30 data-logger) registered the mean, maximum, minimum and the variation of the following climatic parameters: air temperature; air humidity; soil humidity; solar radiation; and precipitation. Furthermore, because the project has multiple research lines, we could also access the grain size of the soil (Coutinho 2012) and the richness, abundance, height and basal area of plants (Mota 2012).

Dung Beetle Community Attributes

To quantify the dung beetles species richness, abundance and biomass we used baited pitfall traps. Traps were 9 cm deep and 15 cm in diameter, containing 250 ml of a salt + detergent solution, and were baited with 25 g of fresh human dung. Each trap was left in the field for 48 h, and then beetles were collected, preserved and transported to the laboratory where all individuals were identified. We used the Vaz-de-Mello et al. 2011 key to genera and subgenera identification, and its basic taxonomic literature cited on Scarabaeinae's species identification. All individuals were identified to species level and counted. Further, the species were assigned to a functional guild based on their food allocation strategies for reproduction (Halffter and Edmonds 1982): rollers (telecoprids), that construct balls where they will deposit their eggs and roll it apart from the original food source (dung); tunnelers (paracoprids), that dig tunnels directly beneath the food source, where they will storage their dung balls; and dwellers (endocoprids), that live and reproduce inside the food source. To obtain the biomass of the beetles, all individuals were dried at 45°C to constant weight and weighted in a 0.001 g precision balance. Then, we calculated the mean biomass of each species. All necessary permits were obtained for the described field studies. Responsible for the authorization: Ministério do Meio Ambiente (MMA); Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA); and Sistema de Autorização e Informação em Biodiversidade (SISBIO); license number 38952-1, date 02/05/2013, authentication code: 47946752; http://www.icmbio.gov.br/sisbio/verificar-autenticidade.

Data Analysis

Taxonomical and Functional Diversities

Dung beetle taxonomic diversity (TD) was measured by species richness and by Simpson Index, because we asked what happened when we considerate abundance for estimating TD as it is generally for FD. To obtain the functional diversity (FD), we first calculated a species dissimilarity matrix based on multiple traits using the "Gower approach" from the "*trova*" R function (see Lepš et al. 2006 for more details). We used mean biomass and functional guild of the dung beetles species for the matrix construction, because they are considered the two main traits that affects dung beetles functions (Slade et al. 2007, Braga et al. 2013). Since we had the dissimilarities, we calculated the Rao Index, which estimates the FD considering the species dissimilarities and its abundances in each sampling point. de Bello et al. 2010, proposed a R function “Rao”, that calculate both Simpson and Rao index taking into account the Jost’s correction (Jost 2007) with equivalent numbers for partition of diversity. With these function, it is possible to partition both TD and FD into α, β and γ components, thus, providing “a standardized methodology applicable to compare the partition of different facets of diversity”.

α diversity is calculated by weighting each pair of species functional distances by their relative abundances:

$$\alpha_{\mathrm{Rao}} = \sum d_{ij} p_i p_j$$

where d_{ij} is functional distance between two species, and p_i and p_j are species relative abundance. If we consider $d_{ij} = 1$, which means: all species are different, the Rao Index becomes equivalent to Simpson Index. γ diversity is calculated by the same formula, but pooling all local samples in one regional. β diversity is the mean difference between regional and local communities. Applying Jost correction with equivalent numbers, we get β diversity independent of α. Using additive partitioning with equivalent numbers the formulas are:

$$\alpha_{\mathrm{corrected}} = 1/(1 - \alpha_{\mathrm{Rao}});\ \gamma_{\mathrm{corrected}} = 1/(1 - \gamma_{\mathrm{Rao}});\ \beta_{\mathrm{corrected}} = \gamma_{\mathrm{corrected}} - \alpha_{\mathrm{corrected}}$$

In this case, α TD means: number of equivalent species in a local community (minimum value = 1). Note that if all species have the same relative abundance in a sampling unit the Jost-corrected Simpson diversity equals the number of species. The same way, α FD means the number of equivalent species (in terms of abundance) sharing no functionally traits (minimum value = 1). Jost-corrected Rao Index is maximal when all species in a sampling unit are maximally dissimilar and have equal abundances. β diversity will be the average difference between local and regional diversity. To turn β TD and β FD comparable, we expressed β as a percentage of γ diversity (to more details on TD and FD partition see de Bello et al. 2010).

To do the partition of the taxonomical and functional β we used the “beta.multi” function from “betapart” package (Baselga and Orme 2012) (index used: Sørensen). We obtained β diversity and its components for the whole gradient and for each altitude.

Statistical Analysis

We summarized the various environmental variables using principal component analysis (PCA) on PAST 2.17 program (Hammer et al. 2001) and obtained two axes for climatic variables, two axes for soil and one axis for vegetation (see details on Appendix A). To analyze the effects of altitude and the environmental variables (summarized) on dung beetles abundance, richness, α TD and α FD, we used generalized linear models (GLMs) on R program (R Core Team 2013). The data from the three pitfalls of each transect were pooled (addition), so that transects were the sampling unit (three transects in each altitude, seven altitudes, n=21). We calculated the mean altitude of each transect using the altitude of each sampling point. All GLMs were checked with residual analyses to evaluate the adequacy of the error distribution and we accept the minimal significant model.

As we did with α components, β TD and β FD and its components were analyzed with altitude, but in this case the we used one value per altitude (n=7). Because the n was too low, we could not perform GLMs for the environmental variables, so we used Hierarchical Partitioning. This analysis provides a measure of the effect of each variable that is largely independent from effects of other variables and by randomizations it is possible to evaluate competing models. Hierarchical partitioning and associated randomization tests were made using the “hier.part” R package.

We made a supplementary analysis of dung beetles community along the altitudinal gradient, using the Permutational Multivariate Analysis of Variance (PERMANOVA). To do this, we used the “adonis” function available on the R package “vegan 2.0-7” (Oksanen et al. 2013) using Jaccard index as dissimilarity measure and performing 999 permutations. As the other analysis, we construct models with altitude and the environmental factors as explicative variables for the variation on dung beetle community composition.

RESULTS

2100 individuals representing 50 species were collected. Paracoprids were 76% of all species (38 species), telecoprids 14% (7 species) and endocoprids 10% (5 species) (details on Appendix B).

Dung beetle richness declined with the increasing in altitude (χ^2=6.809, p<0.01), whereas the gradient did not influence abundance (F=0.0357, p>0.05) (Fig. 1a e 1b), even when we used the environmental factors as explicative variables (F=2.668, p>0.05). Climatic variables such as temperature, radiation and humidity are the main factors, followed by vegetation variables, driving the loss of species (climatic PCA axis 1 and vegetation PCA axis in a minimal model) (F=8.781, p<0.005). Climatic axis 1 can be interpreted as a thermal-humidity axis that is negatively correlated with altitude, as well as the vegetation axis (Appendix A). Dung beetle richness declines with decreasing temperatures and increasing humidity. Further, it is bigger when vegetation richness and abundance are bigger.

Despite richness declines with increasing altitude, α Simpson TD variation was not explicated by the altitude (F=0.007, p>0.05) (Fig. 1c), but by temperature, radiation, air humidity, precipitation and soil humidity (climatic axis 1 and 2; minimal model F=62.754, p<0.001). In the same way, altitude did not explicate α Rao FD variation (F=0.249, p>0.05), but neither environmental variables (F=1.675 , p>0.05) (Fig. 1d).

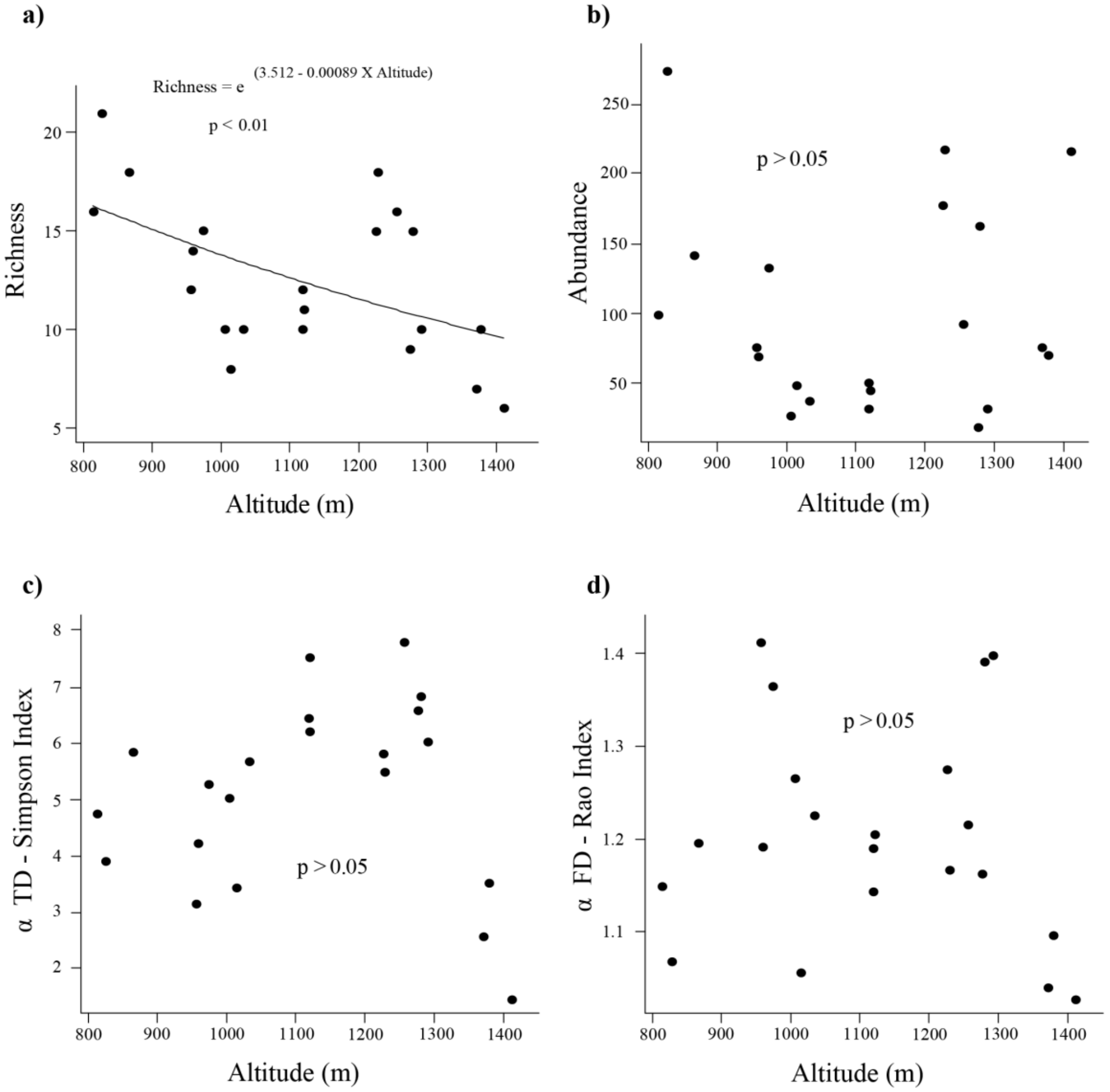

FIG. 1. Dung beetles a) richness, b) abundance, c) α Simpson TD and d) α Rao FD along an altitudinal gradient at Serra do Cipó, Minas Gerais State, Brazil.

Figure 2a shows the contribution of α and β to the taxonomic and functional γ diversity and figure 2b shows the contribution of nestedness and turnover to the β TD and β FD of the whole gradient. The FD is caused practically only by α component (98.8%), showing that there are little differences in FD between the communities from different altitudes. In the other hand, 55% of TD diversity is caused by β2 component, which means that there are different community compositions along the altitudinal gradient. Furthermore, β TD is caused almost completely by the turnover component (93.8%), while the practically insignificant β FD (1.2%) appears more due to nestedness component (Fig. 2b).

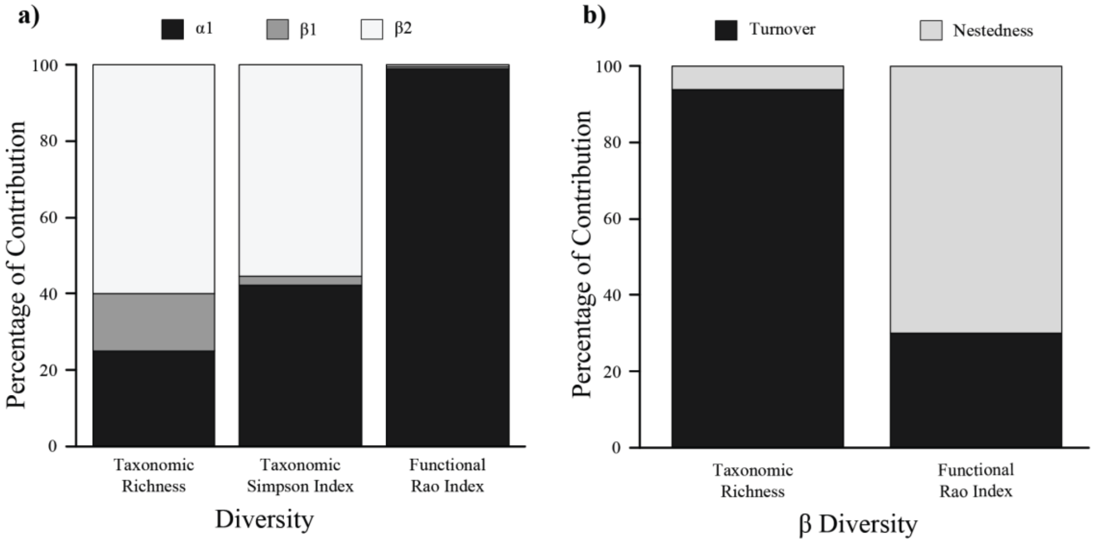

FIG. 2. a) Contribution of α1, β1 and β2 to γ taxonomic and functional diversity. α1 is transects diversity, β1 is the among transects diversity and β2 is the among altitudes diversity; b) Contribution of turnover and nestedness to β taxonomic and functional diversity.

Corroborating the result of the diversity partitioning, PERMANOVA shows that dung beetle community composition vary along the altitudinal gradient and its variation is explicated by climatic, soil and vegetation variables (environment) (Table 1).

Taxonomic (both richness and Simpson) and functional β contribution to γ diversity did not change due to altitude (Fig. 3a, 3b and 3c) (F and P values on Appendix C). However, hierarchical partitioning showed that soil variables are correlated with β TD (richness and Simpson), although β TD did not follow the same pattern (Fig. 4a, 4b, 4c). The altitude did not explicate the variation on the contribution of turnover component to β TD too (Fig. 3d), but soil variables did (Fig. 4d). We did not perform this last analysis with FD, because the beta component was almost zero (Fig. 2a).

The results of all GLMs and hierarchical partitioning realized in this study are summarized in Appendix C.

TABLE 1. Results of PERMANOVA with dung beetles communities along an altitudinal gradient at Serra do Cipó, Minas Gerais State, Brazil. df = Degrees of Freedom; SS = Sums of Squares; MS = Mean Squares; F value; R^2; and p values.

Variables	df	SS	MS	F value	R^2	p value
Model 1 – with Altitude only						
Altitude	1	1.0223	1.02231	3.2408	0.14571	< 0.001
Residuals	19	5.9935	0.31545	0.85429		
Total	20	7.0158			1	
Variables	df	SS	MS	F value	R^2	p value
Model 2 – with environmental variables						
Climatic 1	1	1.1325	1.13253	4.9622	0.16142	< 0.001
Climatic 2	1	0.6666	0.6666	2.9207	0.09501	< 0.001
Soil 1	1	0.4584	0.45835	2.0083	0.06533	< 0.01
Soil 2	1	0.6367	0.63674	2.7899	0.09076	< 0.01
Vegetation	1	0.6981	0.69813	3.0589	0.09951	< 0.001
Residuals	15	3.4235	0.22823	0.48797		
Total	20	7.0158			1	

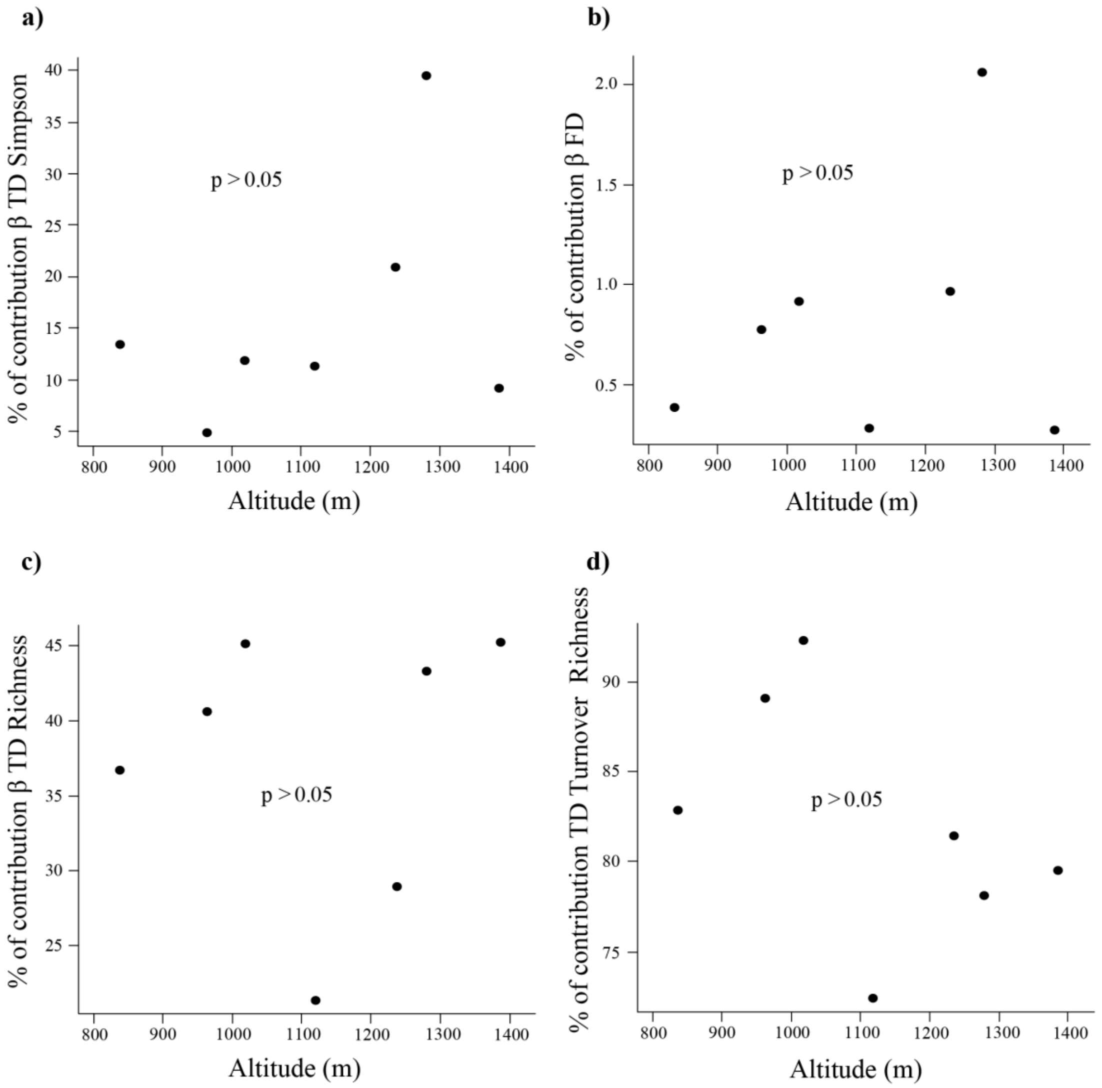

FIG. 3. a), b) and c) shows the percentage of contribution of β component to γ TD and γ FD in each altitude along the gradient. d) Presents the percentage of contribution of turnover component to β TD based on richness in each altitude along the gradient.

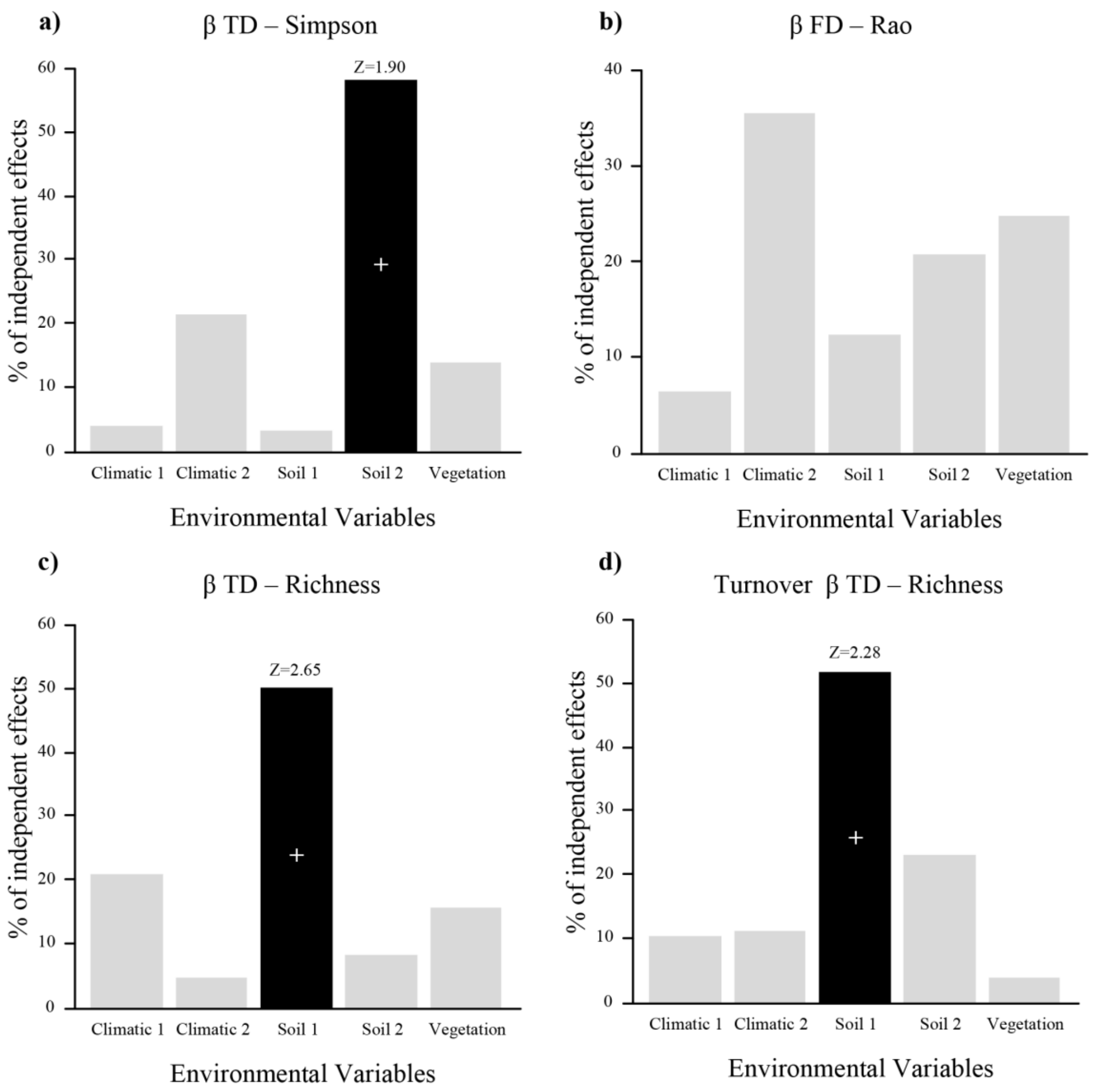

FIG. 4. Hierarchical partitioning analysis. Distribution of the percentage of independent effects of environmental variables on the a) β TD – Simpson, b) β FD – Rao, c) β TD – Richness and d) Turnover β TD – Richness. Black bars represent significant effects ($p<0.05$) as determined by randomization tests. += Positive relationship.

DISCUSSION

Dung beetles richness decreases with altitude, as expected based on literature (Escobar et al. 2007, Larsen 2012, Herzog et al. 2013). Richness declines with decreasing in temperature and increasing in humidity, suggesting that there are fewer species that can survive in colder and very humid highlands. This can be due to two main factors: first, because Scarabaeinae is a monophyletic group comprised of warm-adapted species (Lobo and Halffter 2000); second, because as dung beetles feed mostly on mammals dung, and mammals richness also diminish with elevation (McCain 2005, 2007), there is a reduction in food availability with increasing altitude. Beetles species richness is also positively correlated with abundance, richness and basal area of plants. Vegetation parameters, which decline with altitude, can affect dung beetles directly, by acting as regulator of microclimatic condition, or indirectly affecting vertebrate fauna and consequently food availability (Nichols et al. 2009, Louzada et al. 2010).

When we use Simpson Index, so including abundance, to get α TD, the pattern of decreasing diversity with elevation disappear, because abundance did not decline with altitude. This result was not the expected, but we think this can be due to the presence of dominant species well adapted to each altitude which have attained higher population sizes. In the contrary of what was expected too, α FD did not diminish with altitude and its variation neither was explained by environmental factors. Actually, the low values of α FD deserve a little attention (all very close to 1, minimum possible value). Rao’s Index is maximal when all the species have the same relative abundance and thus maximally functionally dissimilar to each other (de Bello et al. 2010). So, the low values found here means that the most abundant species in a plot are functionally close. Villéger et al. (2012) found similar results with estuarine fish communities, and in that case there were functionally close generalists fishes dominating each plot.

We found high contribution of β TD (using abundance or not) for γ TD of the whole altitudinal gradient (Fig. 2a). Over 50% of γ diversity is caused by differences among dung beetles communities, influenced by climatic, soil and vegetation of the altitudinal gradient, corroborating the hypotheses of environmental filtering (Cottenie 2005, Jankowski et al. 2009). The insignificant contribution of β FD for γ FD and the contrast between β TD and β FD showed small differences in FD among communities, suggesting ecological redundancy (de Bello et al. 2009, Villéger et al. 2012). In other words, there are different species doing the same “job” (having the same functional traits) along the gradient. In this case, environmental variables are filtering species in terms of Grinnellian niche, but not in terms of Eltonian niche (Devictor et al. 2010). This result is corroborated by the correlation between environmental variables and TD despite no correlation between the same variables and FD. The scale of environmental filter in this study has different impacts on different facets of diversity, when local filter is important for TD and has no impact on FD (de Bello et al. 2013). Our results reinforces the importance of measuring different facets of diversity to understanding biodiversity patterns along environmental gradients (Meynard et al. 2011, Pavoine and Bonsall 2011).

Turnover was the main component of β TD with 94% of contribution (Fig. 2b). It means that highland communities are not a sub-set of lowlands communities but communities with different species composition. This supports even more the idea that different environmental filters, provided by elevation, selects species in terms of physiological niche (Grinnellian Specialization) (Devictor et al. 2010). This also suggest that specialization for surviving in high altitudes result in loss of competition power in lowland areas (Escobar et al. 2007, Larsen 2012, Herzog et al. 2013).

Contribution of β TD and β FD to γ diversity did not decrease with altitude as we expected (Fig. 3a, 3b and 3c). Further, β TD was correlated with soil variables, suggesting that β diversity within the same altitude is caused by habitat heterogeneity (Jankowski et al. 2009, Meynard et al. 2011). The Serra do Cipó is well known by its landscape heterogeneity, and even in the same altitude we can find at least five types of habitats associated to different soils (de Carvalho et al. 2012, 2014). Apparently there are different non-nested sub-communities of dung beetles at the same altitudes as turnover is the main component of β TD among transects (Fig. 3d).

In this study we used Rao Index, which has the advantage of weighting species functional distances by their relative abundances. This weighting is very relevant to understand how communities respond to environmental variables in cases where dominant species are close functionally as it is in the case of our study (Villéger et al. 2012). Additionally, Rao decomposition is useful to compare taxonomic and functional facets of diversity at different spatial scales (de Bello et al. 2010, Meynard et al. 2011).

Some considerations on climatic change and dung beetles communities deserve a little attention. Tropical insects are particularly sensitive to climatic changes (Deutsch et al. 2008) and mountain insects are very vulnerable to global warming (Laurance et al. 2011). Responding to global warming, many species of plants and animals are shifting their geographic range upslope (Parmesan and Yohe 2003, Colwell et al. 2008, Sundqvist et al. 2013). This upslope displacement will lead to serious conservation problems like mountaintop species extinctions (Raxworthy et al. 2008) and lowland biotic attrition as lowland species will go upslope (Colwell et al. 2008). As shown by Larsen 2012, Andean dung beetles species occurred farther upslope in a hotter deforested landscape than in a forested landscape, when the temperature difference between forested and deforested sites was equivalent to 60– 100 yr of predicted global warming. This means that dung beetles may respond the same way as other animals and plants to global climatic change. Our study showed that over than 50% of the mountain diversity is due to the differences among communities of different altitudes (β TD) and these differences are due to almost completely different communities compositions (high β TD Turnover). Upslope range shifts, mountaintop and lowland extinctions will lead to even greater loss of taxonomic diversity than expected as diversity among altitudes is high. Although functional diversity did not change with altitude, we do not know how displacement of species will affect directly the dung beetles functions.

CONCLUSIONS

Our study showed that accessing multiple facets of diversity is very informative on how environment affects communities. Furthermore, partitioning diversity into its spatial components improve our understanding on species distribution and merging these two approaches allowed us to understand the scale of environmental filtering on taxonomic and functional diversity. We showed that there is an ecological redundancy among communities of dung beetles in our altitudinal gradient and environmental variables are filtering species in terms of Grinnellian niche, but not in terms of Eltonian niche. Besides richness declines with altitude, α FD did not showed this pattern. We found low values of α FD, meaning that the most abundant species in a plot are functionally close. Here, the use of different metrics of diversity led to different results, so, it's important to know which metric to use to answer specific questions. For example: if one wants to understand dominance of some functional group, abundance has to be considered. The use of Rao index and its decomposition has been shown very useful to compare taxonomic and functional facets of diversity at different spatial scales. Our findings showed that global warming can bring even bigger loss of diversity than was expected, as diversity among altitudes is responsible for at least 50% of regional diversity.

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APPENDIX A. Detailed description of principal component analysis

Principal component analysis (PCA) on PAST 2.17 program (Hammer et al. 2001) to summarize environmental variables. For all analysis we used the Correlation method to do the PCA.

A.1 Climatic variables

We use ten variables from the meteorological monitoring tower (equipped with the Onset HOBO® U30 data-logger) to get the climatic scenario of each altitude (all from December 2013 only). They were: means of air temperature, air humidity, soil humidity and photosynthetically active radiation (PAR); variation of air temperature and air humidity; maximum of air temperature; minimum of air temperature and air humidity; and sum of precipitation (Table A1). The variation of air temperature and air humidity was calculated with the Coefficient of Variation (C_v), which is the standard deviation/mean. All calculations were implemented in Microsoft Excel.

TABLE A1. Climatic variables used in PCA. Units: Altitude: m a.s.l.; Air Temperature: °C; Air Humidity: relative %; Soil Humidity: m^3/m^3; PAR:µE; Precipitation: mm.

Altitude	Mean Temperature	Mean Air Humidity	Mean Soil Humidity	Mean PAR	Temperature variation
800	23.02	83.98	0.154	448.51	0.144
900	22.53	83.10	0.162	422.11	0.133
1000	22.11	83.57	0.357	426.65	0.130
1100	21.33	85.53	0.125	413.36	0.139
1200	20.92	87.07	0.376	409.71	0.135
1300	20.07	89.31	0.171	410.70	0.130
1400	18.95	94.60	0.129	330.26	0.103

Altitude	Air Humidity Variation	Maximum Temperature	Minimum Temperature	Minimum Air Humidity	Precipitation
800	0.162	33.89	17.06	39.7	529.72
900	0.148	33.08	17.23	40.0	391.13
1000	0.143	32.43	17.23	39.1	426.69
1100	0.144	32.23	16.96	39.5	399.85
1200	0.136	31.33	16.25	40.6	447.91
1300	0.124	30.14	15.63	45.9	405.99
1400	0.067	23.71	16.03	73.5	578.63

Results of the PCA using the climatic variables are summarized in Table A2 and Fig. A1.

TABLE A2. PCA result with the Eigenvalue and % of variance of each axis (PC).

PC	Eigenvalue	% variance
1	7.51487	75.149
2	1.13053	11.305
3	0.80519	8.0512
4	0.49162	4.9162
5	0.04444	0.4446
6	0.01347	0.1341

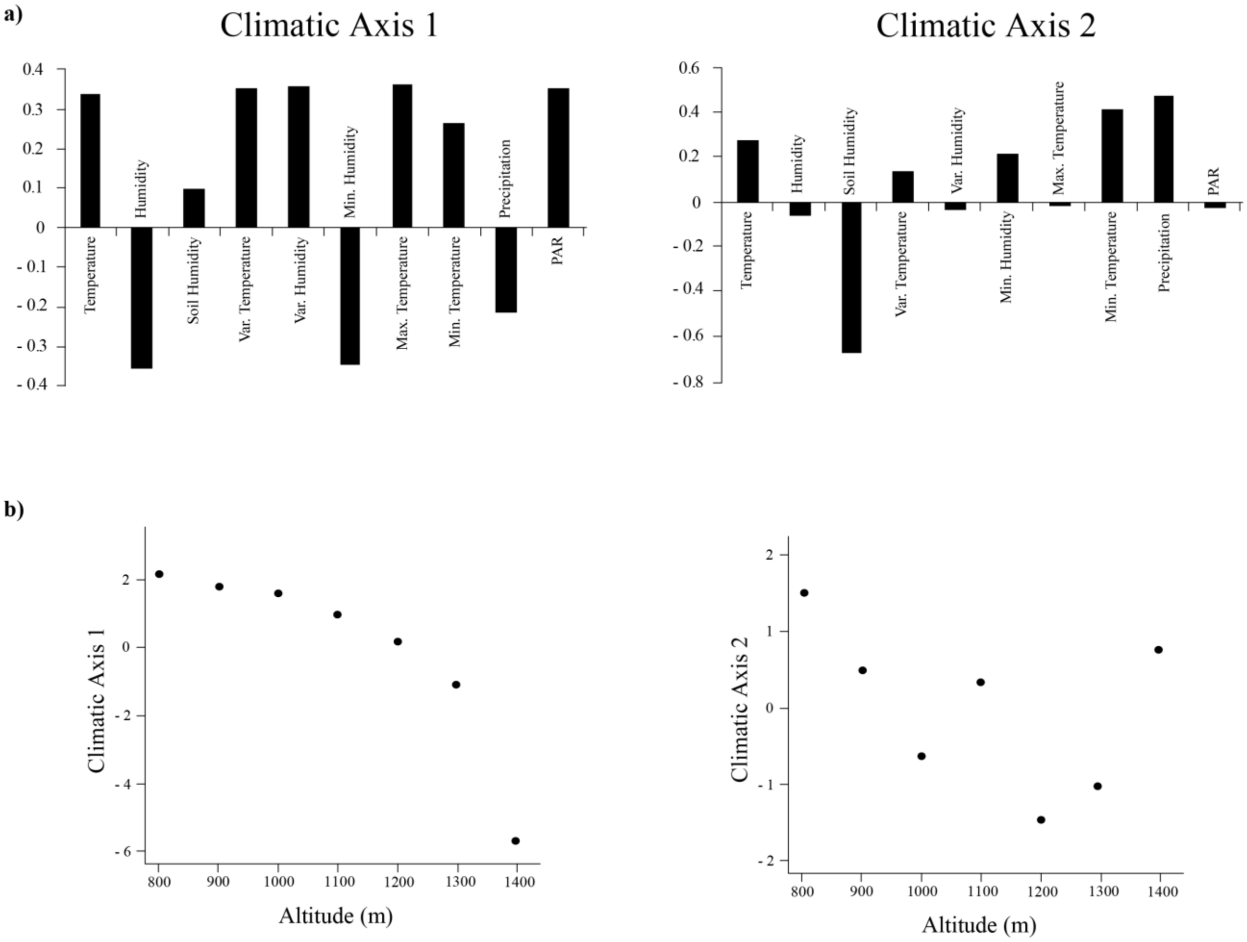

FIG. A1. a) Loadings of climatic axes 1 and 2. b) Climatic axes values in each altitude.

Axis 1 can be interpreted as a thermal-humidity axis where temperature variables are positively correlated and humidity variables negatively correlated. Furthermore, there is a negative correlation between Axis 1 and altitude, showing that temperature variables decrease and humidity variables increase with elevation. Axis 2 can be interpreted most as a soil humidity axis but the precipitation and minimum temperature also influences it.

A.2 Soil variables

We used one chemical and four physical soil variables from Coutinho (2012), which is part of "Projeto Ecológico de Longa Duração – Sítio Serra do Cipó" as well as this study. They were: chemical: organic matter; physicals: coarse sand, fine sand, silt and clay (Table A3).

TABLE A3. Soil variables used in PCA. Units: altitude: m a.s.l; all others: dag/Kg.

Altitude	Organic matter	Coarse Sand	Fine Sand	Silt	Clay
800	3.510	17.846	62.769	11.538	7.846
900	5.038	4.176	72.592	12.461	10.769
1000	3.574	17.653	67.115	8.153	7.076
1100	5.593	4.876	81.123	5.538	8.461
1200	6.899	12.800	75.661	6.000	5.538
1300	3.555	18.141	73.691	5.000	3.166
1400	6.901	9.353	78.492	7.846	4.307

Results of the PCA using the soil variables are summarized in Table A4 and Fig. A2.

TABLE A4. PCA result with the Eigenvalue and % of variance of each axis (PC).

PC	Eigenvalue	% variance
1	2.49068	49.814
2	1.95573	39.115
3	0.427345	8.5469
4	0.126244	2.5249
5	1.11E-13	2.22E-12

Axis 1 represents soils that have high values of organic matter and fine sand but little values of coarse sand, silt and clay (sandy soils). In the contrary, Axis 2 represents soils that have high values of silt and clay (clayey soils). The composition of soils can change the soil retention capacity and in this case, Axis 2 can be interpreted as soils that retain much water.

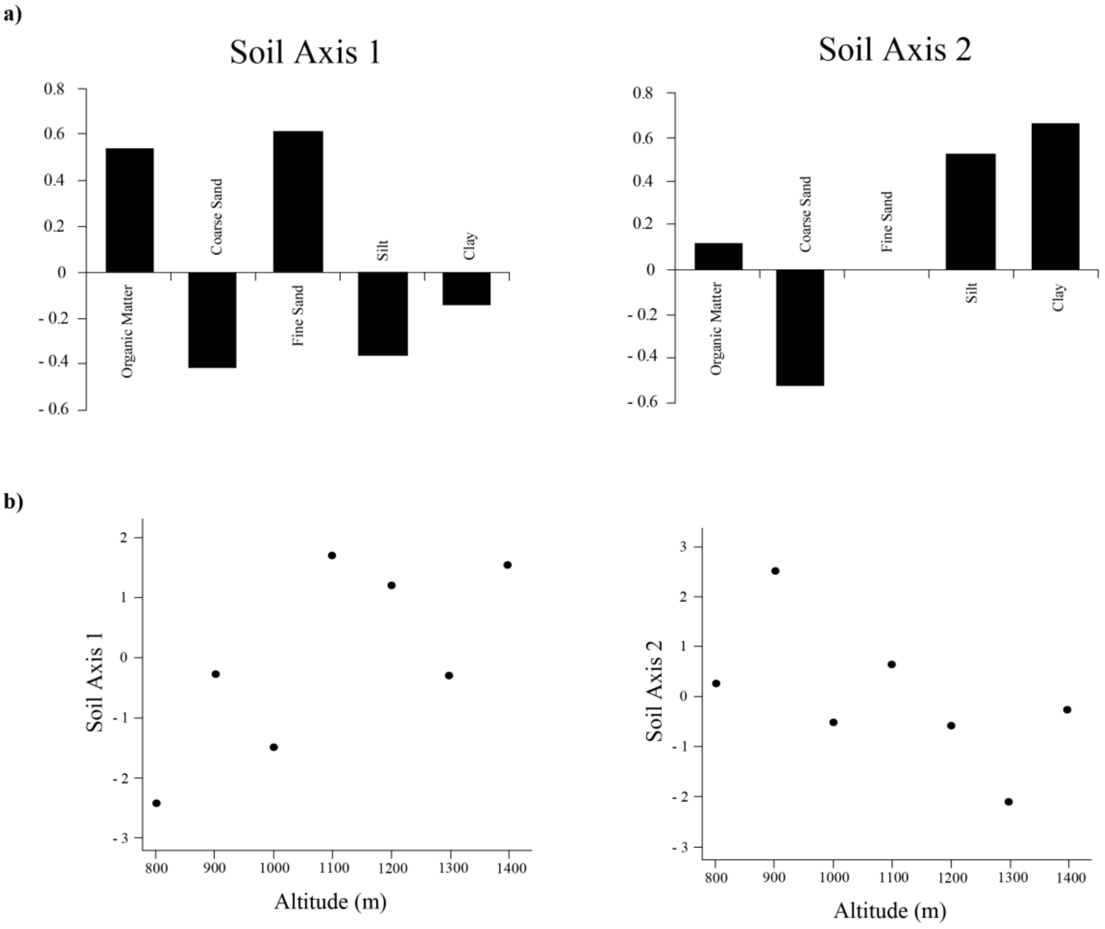

FIG. A2. a) Loadings of soil axes 1 and 2. b) Soil axes values in each altitude.

A.3 Vegetation variables

We used four vegetation variables from Mota (2012), which is also part of "Projeto Ecológico de Longa Duração – Sítio Serra do Cipó". They were: abundance, richness, height and basal area of plants (Table A5). Abundance, richness and basal area were obtained by adding all sampling plots of each altitude and height was the mean value of each altitude. The sampling points totaled 1300 m² per altitude (Mota 2012).

TABLE A5. Vegetation variables used in PCA. Units: altitude: a.s.l.; height: cm; basal area: m²/ha.

Altitude	Abundance	Richness	Height	Basal Area
800	1683	117	117.3	6.98
900	1422	119	110.3	2.79
1000	1201	78	81.79	2.51
1100	1456	84	71.46	3.5
1200	1479	94	60.95	2.63
1300	1110	48	23.81	3.09
1400	1421	29	20.51	4.11

Results of the PCA using the vegetation variables are summarized in Table A6 and Fig. A3.

TABLE A6. PCA result with the Eigenvalue and % of variance of each axis (PC).

PC	Eigenvalue	% variance
1	2.68465	67.116
2	1.01608	25.402
3	0.258679	6.467
4	0.040593	1.0148

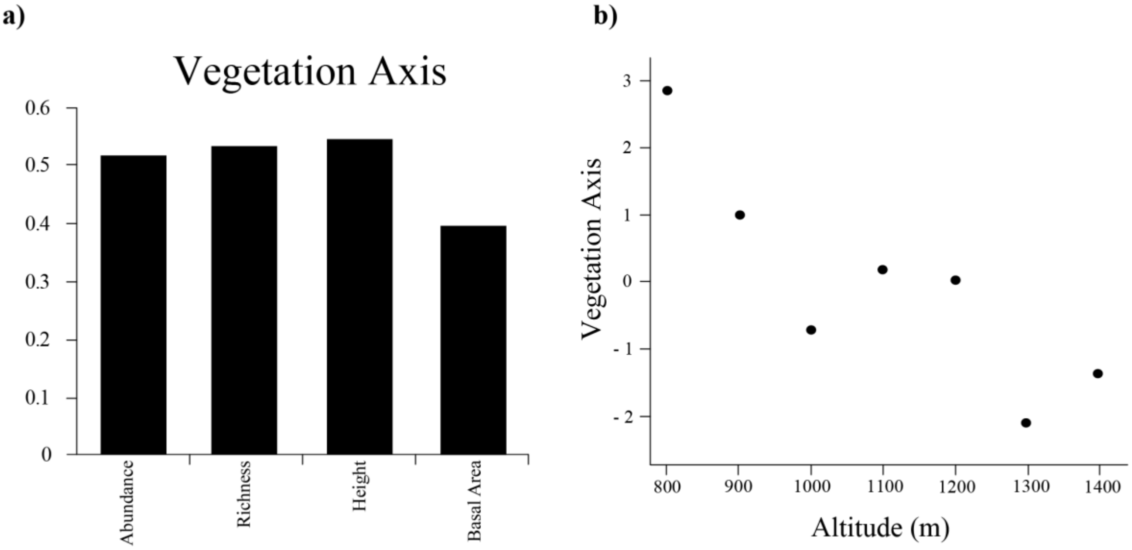

FIG. A3. a) Loadings of vegetation axis. b) Vegetation axis values in each altitude.

All variables are positively correlated with the vegetation axis. The axis presents a positive correlation with the altitude, so, consequently vegetation variables decrease with elevation.

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APPENDIX B. List of species and their abundance, functional guild and mean biomass captured in all sampling points.

TABLE B1. Total number of individuals, by species, captured in all sampling points.

Species	**Individuals**	**Functional Guild**	**Mean Biomass (mg)**
Agamopus unguicularis	1	Paracoprid	6.00
Agamopus viridis	8	Paracoprid	3.00
Anomiopus virescens	1	Paracoprid	20.00
Ateuchus vividus	6	Paracoprid	14.83
Canthidium aff barbacenicum	9	Paracoprid	7.56
Canthidium sp 1	121	Paracoprid	6.32
Canthidium sp 2	66	Paracoprid	8.20
Canthidium sp 3	1	Paracoprid	7.00
Canthidium sp 4	5	Paracoprid	8.20
Canthidium sp 5	8	Paracoprid	7.50
Canthidium sp 6	31	Paracoprid	12.94
Canthidium sp 7	20	Paracoprid	5.41
Canthon aff lamproderes	11	Telecoprid	82.36
Canthon sp 1	71	Telecoprid	4.70
Canthon sp 2	1	Telecoprid	6.00
Canthon unicolor	3	Telecoprid	73.67
Coprophanaeus ensifer	1	Paracoprid	2050.00
Coprophanaeus milon magnoi	9	Paracoprid	751.00
Deltochilum inaequale	6	Telecoprid	214.67
Deltochilum komareki	5	Telecoprid	95.80
Deltochilum pseudoicarus	34	Telecoprid	501.47
Dichotomius bos	6	Paracoprid	347.67
Dichotomius depressicollis	4	Paracoprid	338.25
Dichotomius glaucus	322	Paracoprid	289.03
Dichotomius luctuosus	15	Paracoprid	191.00
Dichotomius nisus	6	Paracoprid	362.00
Digitonthophagus gazella	1	Paracoprid	20.00
Eurysternus nigrovirens	40	Endocoprid	8.80
Genieridium bidens	4	Endocoprid	6.50
Genieridium cryptops	1	Endocoprid	6.00
Homocopris sp 1	13	Paracoprid	74.42
Homocopris sp 2	7	Paracoprid	40.43
Homocopris sp 3	4	Paracoprid	69.00
Ontherus (Caelontherus) sp	1	Paracoprid	26.00
Ontherus appendiculatus	14	Paracoprid	62.86
Ontherus aff carinifrons	12	Paracoprid	41.33
Onthophagus aff buculus	8	Paracoprid	11.67
Onthophagus aff hirculus	391	Paracoprid	9.93
Oxysternon palaemon	216	Paracoprid	276.72
Phanaeus dzidoi	1	Paracoprid	135.00

Phanaeus kirbyi ledezmai	1	Paracoprid	202.00
Phanaeus palaeno	12	Paracoprid	212.92
Sulcophanaeus menelas	99	Paracoprid	414.85
Trichillum sp 1	132	Endocoprid	0.54
Trichillum sp 2	7	Endocoprid	0.86
Uroxys sp 1	196	Paracoprid	0.50
Uroxys sp 2	154	Paracoprid	0.50
Uroxys sp 3	12	Paracoprid	0.67
Uroxys sp 4	2	Paracoprid	1.00
Uroxys sp 5	1	Paracoprid	12.00

APPENDIX C. Detailed results of all General Linear Models and Hierarchical Partitioning realized in the study.

TABLE C1. Results of GLM's with abundance, richness and α TD and α FD indices. Each Response Variable in the table represents a model with Quasipoisson error distribution (except for Richness ~ Altitude that is Poisson error distribution). For the significant variables are presented values of the minimum model and for the non-significant variables, values of the maximum model. D.F.= Degrees of Freedom; Dev.= Deviance; Res. D.F.= Residual Degrees of Freedom; Res. Dev.= Residual Deviance; F= F values.

Response Variable	**Explanatory Variables**	**D.F.**	**Dev.**	**Res. D.F.**	**Res. Dev.**	**F**	**P-value**
Abundance	Altitude	1	1.991	19	995.03	0.035	0.852
Abundance	Climatic Axis 1	1	5.04	19	991.98	0.134	0.719
	Climatic Axis 2	1	26.57	18	965.41	0.705	0.413
	Soil Axis 1	1	11.23	17	954.18	0.298	0.593
	Soil Axis 2	1	0.14	16	954.04	0.003	0.951
	Vegetation Axis	1	459.3	15	494.7	12.202	0.003
	Null			20	997.02	2.668	0.064
Richness	**Altitude**	**1**	**6.809**	**19**	**18.549**	**χ^2=6.80**	**0.009**
Richness	**Climatic Axis 1**	**1**	**8.305**	**19**	**17.054**	**11.405**	**0.003**
	Vegetation Axis	**1**	**4.483**	**18**	**12.57**	**6.157**	**0.023**
	Null			20	25.359	8.781	**0.002**
α TD – Simpson	Altitude	1	0.022	19	55.03	0.007	0.931
α TD – Simpson	**Climatic Axis 1**	**1**	**2.097**	**19**	**9.81**	**5.495**	**0.030**
	Climatic Axis 2	**1**	**2.647**	**18**	**7.16**	**6.937**	**0.016**
	Null			20	55.05	62.754	**7.6e-09**
α FD – Rao	Altitude	1	0.003	19	0.26	0.249	0.623
α FD – Rao	Climatic Axis 1	1	0.036	19	0.23	3.151	0.096
	Climatic Axis 2	1	0.036	18	0.19	3.157	0.095
	Soil Axis 1	1	1.9e-05	17	0.19	0.001	0.968
	Soil Axis 2	1	0.012	16	0.18	1.112	0.308
	Vegetation Axis	1	0.011	15	0.17	0.952	0.344
	Null			20	0.27	1.675	0.201

TABLE C2. Results of GLM's with β TD, β FD and TD Turnover. Each Response Variable in the table represents a model with Gaussian error distribution. D.F.= Degrees of Freedom; Dev.= Deviance; Res. D.F.= Residual Degrees of Freedom; Res. Dev.= Residual Deviance; F= F values.

Response Variable	**Explanatory Variables**	**D.F.**	**Dev.**	**Res. D.F.**	**Res. Dev.**	**F**	**P-value**
β TD – Simpson	Altitude	1	131.24	5	659.07	0.995	0.364
β FD – Rao	Altitude	1	0.162	5	2.18	0.372	0.568
β TD – Richness	Altitude	1	4e-04	5	0.048	0.041	0.846
Turnover β TD – Richness	Altitude	1	0.006	5	0.02	1.518	0.272

TABLE C3. Results of hierarchical partitioning with β TD, β FD and TD Turnover. Each Response Variable in the table represents hierarchical partition test with 500 randomizations. I Obs. = independent contribution towards explained variance in a multivariate dataset; Z = Z-scores for the generated distribution of randomized Is; P-value = statistical significance is based on upper 0.95 confidence limit, when Z ≥ 1.65).

Response Variable	**Explanatory Variables**	**I Obs.**	**Z**	**P-value**
β TD – Simpson	Climatic Axis 1	0.03	-0.83	> 0.05
	Climatic Axis 2	0.16	0.09	> 0.05
	Soil Axis 1	0.02	-1.05	> 0.05
	Soil Axis 2	**0.43**	**1.90**	**< 0.05**
	Vegetation Axis	0.10	-0.39	> 0.05
β FD – Rao	Climatic Axis 1	0.05	-0.72	> 0.05
	Climatic Axis 2	0.26	0.78	> 0.05
	Soil Axis 1	0.09	-0.55	> 0.05
	Soil Axis 2	0.15	-0.08	> 0.05
	Vegetation Axis	0.18	0.03	> 0.05
β TD – Richness	Climatic Axis 1	0.21	0.31	> 0.05
	Climatic Axis 2	0.05	-0.88	> 0.05
	Soil Axis 1	**0.50**	**2.65**	**< 0.05**
	Soil Axis 2	0.08	-0.59	> 0.05
	Vegetation Axis	0.16	-0.04	> 0.05
Turnover β TD – Richness	Climatic Axis 1	0.09	-0.55	> 0.05
	Climatic Axis 2	0.10	-0.49	> 0.05
	Soil Axis 1	**0.47**	**2.28**	**< 0.05**
	Soil Axis 2	0.21	0.27	> 0.05
	Vegetation Axis	0.03	-0.89	> 0.05

Linking biodiversity, environment and ecosystem functioning: dung beetles ecological functions along a tropical altitudinal gradient

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Summary

Over the past 20 years intensive research has focused on how loss of biodiversity and anthropogenic environmental changes impacts ecosystem functions and services. However, there is still some uncertainty like confounding environmental factors other than community attributes that contribute to effects on ecosystem functioning. It is very important to link biodiversity to ecosystem functioning (BEF), but it is also urgent to show how environmental factors, besides biological communities, can influence ecological functions. In this study we used Scarabaeinae dung beetles to access community attributes and ecological functions along an environmental gradient. Mountains can be very useful for testing environmental linked hypothesis as their conditions change rapidly over short spatial distances. Our goal was to understand what factors influence dung beetles functions, including community and environmental variables. To do this we collected dung beetles along an altitudinal gradient in the Espinhaço’s range, Southeast of Brazil. We also quantified dung beetles functions using a function arena and got the values of dung removal, soil excavation and secondary seeds dispersal. Dung beetles richness declined with altitude, as well as their ecological functions measured. However, inclination of curves of functions were much more pronounced than richness, indicating that there are other factors involved in ecological functions performance besides richness. Indeed, we found that dung removal was dependent both on communities attributes and environmental factors. Climate, soil and vegetation influenced dung removal as much as richness, abundance and body size of dung beetles. Although seeds dispersal and soil excavation were dependent on dung removal as a consequence of this last, community attributes and environmental variables also explicated the residual variance of these functions. Here, we demonstrate the link between biodiversity, environment and ecosystem functioning. We discuss some implications of direct effects of environmental variables on functions performance. As we usually evaluate ecosystem health using communities attributes we ignore environmental factors that can alter the ecological functions.

Key-words: altitudinal gradient; BEF; diversity; dung removal; scarabaeinae; secondary seeds dispersal; soil excavation.

Introduction

Over the past 20 years intensive research has focused on how loss of biodiversity and anthropogenic environmental changes impacts on ecosystem functions and services (Hooper *et al.* 2005, 2012; Cardinale *et al.* 2012; Naeem, Duffy & Zavaleta 2012). Concerned by the loss of biodiversity and ecosystem services, governments of the United Nations created the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) in 2012 (www.ipbes.net). Despite all advances in linking biodiversity to ecosystem functioning (BEF), there is still some uncertainty like: simultaneous effects of different components of diversity (richness, composition, functional diversity); confounding environmental factors, other than richness, that contribute to effects on ecosystem functioning; and context-dependent patters (Balvanera *et al.* 2014). Measuring ecological functions is often difficult but is extremely important to understand how the components of biodiversity affects ecosystem functioning (Korasaki *et al.* 2013; Braga *et al.* 2013). Nevertheless, it is also important to show how environmental factors, besides biological communities, can influence ecological functions (Steudel *et al.* 2012).

Mountains provide interesting environmental gradients as conditions change rapidly over short spatial distances (Körner 2007), affecting species distribution. Decline of land area, decreasing total atmospheric pressure, reduction of air temperature and increasing in solar radiation are some of are some geophysical and climatic trends with increasing altitude (Körner 2007). Moreover, relative humidity, precipitation, geological substrates, nitrogen deposition and soil pH are other factors that can be associated with an altitudinal gradient, but they are driven by regional conditions (Körner 2007; Sundqvist, Sanders & Wardle 2013). Since communities respond to altitude mostly with loss of diversity (Rahbek 2005; Grytnes & McCain 2007; McCain 2009, 2010), ecosystem functioning might change along elevation. Measuring ecological functions, besides species richness, in an altitudinal gradient can improve the understanding of the link between biodiversity, environmental and ecological functioning.

Using taxa that are important components of ecosystems and have easy estimations methods not only for the individuals, but also for their ecological functions is an advantage that might help us to solve the uncertainties about BEF. A diverse and abundant group of insects have been used as general bioindicators: the Scarabaeinae dung beetles (Coleoptera: Scarabaeidae). Studies focusing on habitat disturbance usually use dung beetles due to their sensibility to environmental changes (Spector 2006; Almeida *et al.* 2011; Bicknell *et al.* 2014). Since they feed on decomposing matter, mostly on vertebrates feces, they provide several important ecological functions such as soil fertilization and aeration, increasing nutrient cycling, secondary seeds dispersal and biological control of pest flies and parasites (Nichols *et al.* 2008; Slade, Mann & Lewis 2011; Braga *et al.* 2012, 2013; Santos-Heredia & Andresen 2014). Studies linking dung beetles diversity to their ecological functions are easy to found (Braga *et al.* 2013; Gregory *et al.* 2014; Nervo *et al.* 2014; Yoshihara & Sato 2015), but there is a lack of information on how environmental variables affects their functions too. Information on dung beetles communities responses to altitudinal gradients can also be found (Lobo & Halffter 2000; Escobar, Lobo & Halffter 2005; Escobar, Halffter & Arellano 2007; Larsen 2012; Herzog *et al.* 2013), but apparently, studies evaluating dung beetles functions along elevation gradients are lacking.

Here, we aimed to understand which factors influence dung beetles functions. To do this we used dung beetles community attributes and environmental variables along a tropical mountain as explanatory variables to three main ecological functions performed by dung beetles: dung removal, soil excavation and secondary seeds dispersal. Since dung beetles richness decline with altitude, we expected a decrease in their ecological functions. Further, we expected that soil excavation and seeds dispersal were more related to dung removal than to the community and environmental variables as they are a consequence of these last. We discuss how community and environmental factors can alter dung beetles functions. Because this is the first work that includes ecological functions measurement in altitudinal gradients we discuss some implications of global warming and anthropogenic changes on ecosystem functioning on mountains.

Materials and methods

STUDY SITE

The study was conducted on Serra do Cipó, south of the Espinhaço Range, in the Brazilian state of Minas Gerais (19°10’ and 19°22’ S, 43°29’ and 43°36’ W) during December 2013. The Espinhaço Range is a quartzite mountain chain that crosses the southeast and part of northeast of Brazil and separates the Atlantic Forest and Cerrado biomes (Giulietti *et al.* 1987; Kamino, Oliveira-Filho & Stehmann 2008). The region presents a highland tropical Cwb Köppen climate with a rainy season between November and February and mean annual temperature of 20° C and rainfall of 1,500 mm (Madeira & Fernandes 1999). At the location of this study the altitude vary from 750 up to 1670 m a.s.l. and soil and vegetation are very heterogeneous, varying from five principal habitats: peat bogs, sandy bogs, quartz gravel fields, rocky outcrops and cerrado (de Carvalho *et al.* 2014).

SAMPLING DESIGN AND ENVIRONMENTAL VARIABLES

As this study is part of a larger research project (“Projeto Ecológico de Longa Duração – PELD – Sítio Serra Cipó”) we used its pre-established sampling sites. The altitudinal gradient ranges from 800 up to 1400 m a.s.l. and transects were distributed every 100 m of altitude with a minimum geographic distance of 2 km, totaling seven sampling areas. In each of these areas we used three transects separated by at least 250 m, each consisting of three sampling points in turn separated by 100 m (sampling unit = transect; n=21). Furthermore, the project has one meteorological monitoring tower (equipped with the Onset HOBO® U30 data-logger) in each sampling area that allowed us to have access to some climatic paramaters: air temperature; air humidity; soil humidity; solar radiation; and precipitation. Since the project has multiple research lines, we could access the data of the grain size of soil (Coutinho 2012) and the richness, abundance, height and basal area of plants (Mota 2012).

DUNG BEETLE COMMUNITY ATTRIBUTES

We used baited pitfall traps to capture the dung beetles and quantify species richness, abundance and biomass. Traps were 9 cm deep and 15 cm in diameter, containing 250 ml of a salt + detergent solution, and were baited with 25 g of fresh human dung. Each trap was left in the field for 48 h, and then beetles were collected, preserved and transported to the laboratory where all individuals were identified. We use Vaz-de-Mello et al. 2011 key to genera and subgenera identification, and its basic taxonomic literature cited on Scarabaeinae's species identification. To obtain the biomass of the beetles, all individuals were dried at 45°C to constant weight and weighted in a 0.001 g precision balance. Then, we calculated the mean biomass of each species. All necessary permits were obtained for the described field studies. Responsible for the authorization: Ministério do Meio Ambiente (MMA); Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA); and Sistema de Autorização e Informação em Biodiversidade (SISBIO); license number 38952-1, date 02/05/2013, authentication code: 47946752; http://www.icmbio.gov.br/sisbio/verificar-autenticidade.

DUNG BEETLE COMMUNITY FUNCTIONS

Two days before dung beetles were sampled, we measured their ecological functions. To do this, we used "functions arenas" adapted from Braga et al., 2013 in each sampling point (Fig. 1). Functions arenas consisted of a circular plot, 1 m in diameter, bordered by a fence (15 cm high) which limited the horizontal movement of dung beetles. We built the fence using a nylon net with a mesh size of 0.08 mm, which was held in place by bamboo sticks. We cleared the soil surface of each arena of vegetation to facilitate the measurement of ecological functions.

In the center of each arena we placed 100 g of a mixture of fresh human and swine dung (proportion: 1 to 3). When we prepared this mixture, we added plastic beads, used as seed mimics, in order to estimate the function of secondary seeds dispersal. Plastic beads have been used as seed mimics in several studies and have the advantage of not being removed by seed predators (Andresen 2003; Slade *et al.* 2007; Braga *et al.* 2013). In each experimental dung pile, we placed 50 small seeds (3.5 mm diameter), 20 medium seeds (8.6 mm diameter) and 10 large seeds (15.5 mm diameter). We put a plastic plate above the dung pile, to protect it from direct rain. Functions arenas were left in the field for 48 h and after, we measured three dung beetles ecological functions: dung removal, soil excavation, and secondary seeds dispersal. To quantify the dung removal function we weighed the dung remaining on the soil surface. All seed mimics present in the remaining dung were counted and weighed and their weights were subtracted from the dung weight, allowing calculate the amount of dung removed by beetles. To quantify the amount of soil excavated (i.e. soil moved from deep layers onto the surface as a consequence of tunnel building), loose soil indentified on the surface was collected with spatulas and then dried at 100º C in laboratory until reaching a constant weight. To quantify seed dispersal, all seed mimics not found in the dung remaining on functions arena were assumed to have been removed by dung beetles. Thus, the proportion of seeds dispersed was obtained dividing the number of seed mimics disappeared from the number of seed mimics originally put in the dung pile.

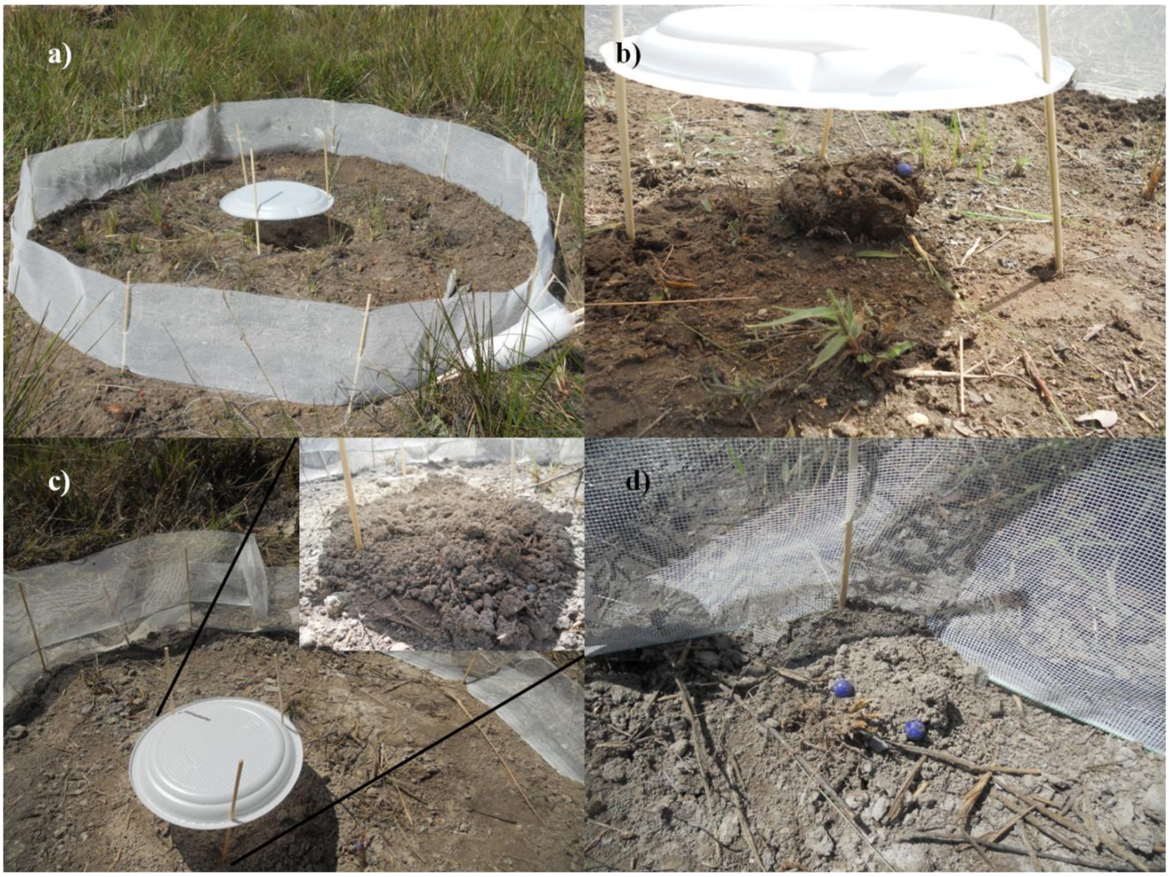

Fig. 1. a) function arena; b) experimental dung pile; c) function arena after dung beetles functions performance; d) dispersed seed

DATA ANALYSIS

We first summarized the various environmental variables using principal component analysis (PCA) on PAST 2.17 program (Hammer, Harper & Ryan 2001) and obtained two axes for climatic variables, two axes for soil and one axis for vegetation (see details in Appendix A from Article 1). To analyze the effects of altitude, environmental variables (summarized) and dung beetles community attributes on the ecological functions, we used generalized linear models (GLMs) on R program (R Core

Team 2013). In specific cases of soil excavation and seeds dispersal functions, we put dung removal as explanatory variable in the logistic model, as these functions are a consequence of the last. We tested seeds dispersal first with the three different sizes, and then pooling all sizes to obtain a general rate of dispersal. The data from the three pitfalls of each transect was pooled (mean), because the sampling unit was transects (three transects in each altitude, seven altitudes, n=21). We calculated the mean altitude of each transect using the altitude of each sampling point. We tested all GLMs for multicollinearity between the variables to prevent variance inflation factors with “spj.vif” found in sjPlot R package (Lüdecke 2014). All GLMs were checked with residual analyses to evaluate the adequacy of the error distribution and we accept the minimal significant model.

Results

Dung beetles richness decline with the altitude (χ^2=6.809, $p<0.01$) and climatic and vegetation variables explained its variation (F=8.781, $p<0.005$) (see Article 1 for more details).

The three dung beetles ecological functions measured here declined with altitude (F=11.147, $p<0.001$; F=133.39, $p<0.001$; F=76.771, $p<0.001$) (Fig. 2). Dung removal was dependent both on community and environmental variables (R^2= 0.88) (Table 1): summarizing, it is bigger where richness and mean biomass of dung beetles are higher and where temperature is higher, soil is poor and clayey and vegetation is more diverse. As expected, soil excavation and seeds dispersal are dependent on dung removal. Besides, soil excavation residual variation is explained by the three dung beetles community variables (abundance, richness and biomass), as well as seeds dispersal, but these last also were explained by soil and climatic variables (R^2= 0.97 and R^2= 0.96) (Table 1).

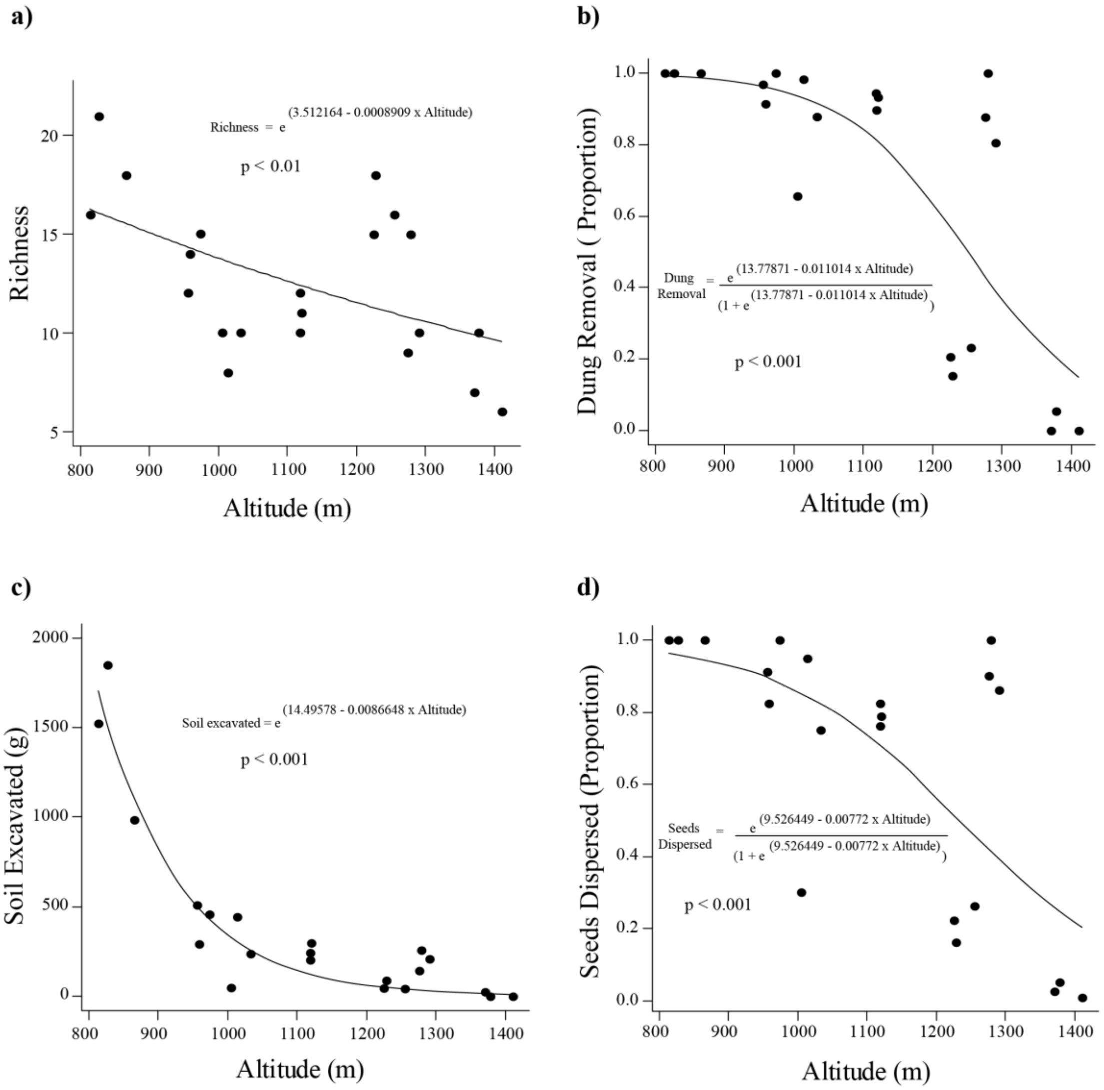

Fig. 2. Dung beetles richness a) and functions along the altitudinal gradient. b) dung removal; c) soil excavation; d) seeds dispersal

We found equal rates of dispersion of seeds of different sizes along the altitudinal gradient (Table 1) that is, although altitude influences seeds dispersal, it does not affect differently the dispersion of large, medium and small seeds.

Table 1. Results of GLM's with the three dung beetles ecological functions – Dung Removal, Soil Excavation and Seeds Dispersal. Each Response Variable in the table represents a model with Quasibinomial error distribution (except for Soil Excavation, which is Gaussian error distribution). All models presented are the minimum significant model. D.F.= Degrees of Freedom; Dev.= Deviance; Res. D.F.= Residual Degrees of Freedom; Res. Dev.= Residual Deviance; F= F values

Response Variable	Explanatory Variables	D.F.	Dev.	Res. D.F.	Res. Dev.	F	P-value
Dung Removal	**Altitude**	**1**	**913.64**	**19**	**712.22**	**25.706**	**6.8e-05**
Dung Removal	**Abundance**	**1**	**92.07**	**19**	**1533.56**	**4.997**	**0.0435**
	Richness	**1**	**385.3**	**18**	**1148.26**	**20.913**	**0.0005**
	Mean Biomass	**1**	**107.53**	**17**	**1040.73**	**5.836**	**0.0311**
	Soil Axis 1	**1**	**320.73**	**16**	**720.00**	**17.409**	**0.0010**
	Climatic Axis 1	**1**	**214.41**	**15**	**505.60**	**11.637**	**0.0046**
	Climatic Axis 2	**1**	**120.98**	**14**	**384.62**	**6.566**	**0.0236**
	Vegetation Axis	**1**	**196.51**	**13**	**188.11**	**10.666**	**0.0061**
	Null			20	1625.63	11.147	**0.0001**
Soil Excavation	**Altitude**	**1**	**4470599**	**19**	**439592**	**193.22**	**2.0e-11**
Soil Excavation	**Dung Removal**	**1**	**2879984**	**19**	**2030208**	**322.32**	**5.0e-12**
	Abundance	**1**	**616442**	**18**	**1413766**	**68.991**	**3.3e-07**
	Richness	**1**	**626887**	**17**	**786879**	**70.16**	**3.0e-07**
	Mean Biomass	**1**	**643931**	**16**	**142948**	**72.068**	**2.5e-07**
	Null			20	4910192	133.39	**4.5e-12**
Seeds Dispersal	Seeds Size	2	4.06	60	1196.76	0.177	0.8381
	Altitude	**1**	**516.18**	**59**	**680.59**	**45.045**	**9.6e-09**
	Size*Altitude	2	0.52	57	680.07	0.0228	0.9775
Seeds Dispersal	**Altitude**	**1**	**508.67**	**19**	**658.91**	**15.071**	**0.0010**
Seeds Dispersal	**Dung Removal**	**1**	**1011.04**	**19**	**156.55**	**412.67**	**8.7e-12**
	Abundance	**1**	**55.41**	**18**	**101.13**	**22.618**	**0.0003**
	Richness	**1**	**12.84**	**17**	**88.29**	**5.242**	**0.0380**
	Mean Biomass	**1**	**12.65**	**16**	**75.64**	**5.162**	**0.0393**
	Soil Axis 2	**1**	**24.42**	**15**	**51.23**	**9.966**	**0.0069**
	Climatic Axis 1	**1**	**12.15**	**14**	**39.07**	**4.96**	**0.042**
	Null			20	1167.59	76.771	**6.6e-10**

Discussion

As we expected based on decline of dung beetles richness (Article 1), the three ecological functions decrease with altitude. Inclination of curves of ecological functions deserves attention as they are much more pronounced than curve of richness (Fig. 2). Dung removal and seeds dispersal varied from 100 % on lowlands to almost 0 % in highlands, while soil excavation varied in parallel from a mean of 1500 g of loose soil on lowland to approximately 0 g in highest altitude. This result demonstrates that although dung beetles richness is linked with their functions, there are other factors involved (as we will show below), which explain curve shape differences.

Dung removal is dependent both on community's attributes and environmental variables (Table 1). Dung beetles richness, abundance and biomass were significant related with dung removal, confirming the link between biodiversity and ecological functions found in other studies (Slade *et al.* 2007; Braga *et al.* 2013; Yoshihara & Sato 2015). Body size is considered a variable with bigger effects on the quantity of dung beetles functions performed (Andresen 2002; Gregory *et al.* 2014; Nervo *et al.* 2014), since large beetles can remove and bury much more dung. We found that climatic, soil and vegetation variables were also related with dung removal, confirming the environment-ecological functions link. Climatic variables, mainly temperature, can affect dung beetles adult activity, egg laying and larval survival thus influencing their feed and breeding comportment (Lobo, Lumaret & Jay-Robert 1998; Chown 2001). Consequently, different temperatures could even lead equivalent communities to remove different portions of dung in the field. In the present study, much more dung was removed in lowland areas, where mean temperatures are higher, than in higher altitudes. Characteristics of soil, like granulometry and moisture can be either crucial for reproduction of dung beetles and also affects dung removal. When soil is very wet, dung beetles cannot dig, or if they dig, mortality of larvae is almost 100%, explaining why moist soil are avoided by beetles to reproduction and dung burying (Sowig 1995, 1996; Nichols *et al.* 2008). In a function arena located at 1400 m a.s.l, we found an almost intact experimental dung pile and dung beetles just beside trying to bury themselves, but stopping due to soil humidity (Fig. 3). This means that there were beetles to do the "job", but environmental factors impede them. Soil type also can influence dung beetles time budgets for nest construction, numbers of breed chambers and consequently the amount of dung removed (Sowig 1995, 1996; Nichols *et al.* 2008).

In this study, sandy soils presented less dung removal than clayey soils. Sandy soils demand more time for nest construction because they are more susceptible to landslide and loose humidity faster than clayey soils (Sowig 1995). Vegetation also explicated part of variation on dung removal and we think this can be due to the microclimate that plants can provide. Where shadow is more intense due to higher plant density, soil temperature, and radiation are lower, whereas moisture is higher than in a plant poor area, affecting dung removal (Braga *et al.* 2013).

Fig. 3. a) *Sulcophanaeus menelas* just beside an intact experimental dung pile (1400 m a.s.l); b) dung beetles unearthed in a flooded soil (1300 m a.s.l)

Our results show that soil excavation and seeds dispersal are dependent not only on dung removal, but also on community attributes and some environmental variables. Thus, beetles species richness, abundance and body size can make difference on these functions performance, even after dung is removed. Large beetles for example, dig deeper and consequently move more amounts of soil from deep layers to surface (Braga *et al.* 2013; Gregory *et al.* 2014). Furthermore, seeds dispersal has been demonstrated to be dependent on beetles size, guild (endocoprid, paracoprid and telecoprid) and abundance too (Andresen 2002; Braga *et al.* 2013).

As we showed in Article 1, in this tropical mountain, environmental filters seems to select species in terms of Grinellian niche, but not in terms of Eltonian niche as functional diversity does not vary with altitude. However, although functional diversity does not vary, functions themselves decrease drastically with elevation. We can draw two main conclusions from this: 1) as we showed, ecological functions might depend also on environmental factors to be performed; 2) although functional diversity indices predicts ecosystem functioning better than species richness (Petchey & Gaston

2006; Gagic *et al.* 2015), they can fail due to context dependent and environmental effects. There is a difference in measuring functional diversity and functions themselves. As functional diversity is based on characteristics of species and their abundances it can be very helpful in studies of species resource's use and niche (Villéger *et al.* 2012; de Bello *et al.* 2013). It reflects a community attribute that theoretically is linked with species ecological function performance. However, as we showed, ecological function also depends on environmental variables. This leads to a practical issue: how much of ecosystem functioning is really predicted by community's metrics? Since community's metrics are used to measure human impacts on ecosystem we can be underestimating the effects on ecosystem functioning. For example: we can have an agroforest with less species of dung beetles than a primary forest, but functionally similar and suggest that ecosystem functioning is going well. However, due to environmental differences the functions may not be the same in the two areas. We think that besides getting community's attributes, measuring functions themselves can provide much more information on ecosystem functioning.

It is not easy to measure ecological functions and even more difficult to link them to environmental factors. Here we showed a good alternative using a taxon that plays important functions in ecosystem and with easily estimated communities attributes and functions. The altitudinal gradient played an important role for our conclusions as it provide different conditions along short distances. With this study we prove that mountains can be very helpful in providing environmental gradients not only for studying ecology and evolution of biological groups, but also the links between biodiversity, environment and ecological functions.

Tropical insects are particularly sensitive to climatic changes (Deutsch *et al.* 2008). Thus, global warming and anthropogenic environmental changes would lead to great loss of biodiversity (Colwell *et al.* 2008; Raxworthy *et al.* 2008; Larsen 2012), and ecosystem functions can be affected more than we thought (Cardinale *et al.* 2012; Hooper *et al.* 2012). Here we demonstrate the link between biodiversity-environment-ecosystem functioning and the conclusion that environmental variables can alter ecological functions as much as biodiversity. For dung beetles we can imagine regions where some species could survive even in hotter conditions and maintain some functional diversity, but their ecological functions could be compromised by climatic, soil and vegetation changes due to global warming. Specifically in the case of mountains, where species and communities are expected to move upward in response of climatic change (Parmesan & Yohe 2003; Sundqvist *et al.* 2013), ecosystem functioning can change even more drastically as conditions change rapidly with elevation. We discuss in Article 1 the effects of global warming on dung beetles montane communities and showed that upslope range shifts, mountaintop and lowland extinctions would lead to even greater loss of diversity than expected, as diversity among altitudes were high. Although functional diversity could be maintained, we showed that environmental factors can impede functions performance.

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