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Linking Biodiversity, the Environment and Ecosystem Functioning: Ecological Functions of Dung Beetles Along a Tropical Elevational Gradient

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ABSTRACT

Biodiversity loss and anthropogenic environmental changes are known to impact ecosystem functions and services. However, there are still some uncertainties such as confounding environmental factors other than community attributes that affect ecosystem functioning. Our goal was to understand what factors influence the performance of Scarabaeinae dung beetle functions, testing the hypothesis that both community attributes and environmental variables influence the performance. Toward this aim, we collected dung beetles along an elevational gradient (800–1400 m a.s.l.) in the Espinhaço mountain range (Brazil) and quantified dung beetle functions, that is, dung removal, soil excavation and secondary seed dispersal. We recorded data on environmental factors related to climate, soil and vegetation and evaluated their effects on dung beetle functions. Dung beetle ecological functions declined with elevation and the decrease was more pronounced than richness, indicating that there are other factors involved in functions performance besides diversity of beetles. Indeed, we found that the ecological functions measured were dependent on both dung beetle community attributes and environmental factors. Climate, soil and vegetation influenced dung beetle function performance as much as richness, abundance and body size. Dung beetle functional diversity did not explain any of the

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Author's contributions CAN, RFB, FMR and GWF conceived the ideas and designed study; CAN and RFB collected the data; CAN, RFB and JECF analyzed the data; CAN, RFB, FMR, FSN, GWF and JECF wrote the paper. All authors contributed critically to the drafts and gave final approval for publication.

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functions measured. Our study demonstrates that ecological functions are directly influenced by both community attributes and environmental variables and confirms the link between biodiversity, environment and ecosystem functioning.

Key words: altitude; diversity; dung removal; functional diversity; scarabaeinae; secondary seed dispersal; soil excavation.

INTRODUCTION

Over the last 20 years, intensive research has focused on how the loss of biodiversity and anthropogenic environmental alterations impact ecosystem functions and services (Hooper and others 2005, 2012; Cardinale and others 2012; Naeem and others 2012). Despite all the advances in linking biodiversity to ecosystem functioning (BEF), there remain uncertainties to be addressed. Some of them are: (1) the simultaneous effects of different components of diversity (richness, composition, functional diversity); (2) confounding environmental factors that affect ecosystem functioning; and (3) context-dependent patterns (Balvanera and others 2014). Measuring ecological functions is often difficult, but is extremely important to understand how the components of biodiversity affect ecosystem functioning (Braga and others 2012, 2013; Korasaki and others 2013). Furthermore, it is also important to show how environmental factors (for example, climate and soil characteristics), in addition to biological communities, can influence ecological functions (Steudel and others 2012).

A strategy to better understand how environmental factors influence ecological functions is to perform studies in regions that possess great environmental variation. As first highlighted by von Humboldt and Bonpland (1805), mountains provide interesting environmental gradients with conditions that change rapidly over short spatial scales, and which affect species distributions. Decreasing land area, total atmospheric pressure and air temperature, and increasing solar radiation are some of geophysical and climatic trends associated with increasing elevation (Körner 2007). Moreover, relative humidity, precipitation, geological substrates, nitrogen deposition and soil pH are other factors that can be associated with an elevational gradient, although they are driven by regional conditions (Körner 2007; Sundqvist and others 2013). Because most communities experience a loss of diversity with increasing elevation (Fernandes and Price 1988; Rahbek 2005; Grytnes and McCain 2007; McCain 2009, 2010), ecosystem functioning might also change with elevation. Measuring ecological functions, besides community attributes, along an elevational gradient can help to better understand the link between biodiversity, the environment, ecosystem functions and even ecosystem services.

Using taxa that are important components of ecosystems and for which population size and ecological functions are easily estimated would facilitate investigations into the uncertainties that remain about BEF. Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are a diverse and abundant group of insects that have been used as bioindicators of habitat disturbance due to their sensitivity to environmental changes (Halffter and Favila 1993; Spector 2006; Almeida and others 2011; Bicknell and others 2014; Gómez-Cifuentes and others 2017). Because they feed and nest on decomposing matter, mostly vertebrate feces, they perform several important ecological functions including soil fertilization and aeration, increased nutrient cycling, secondary seed dispersal and biological control of pest flies and parasites (Nichols and others 2008; Slade and others 2011; Braga and others 2012, 2013; Santos-Heredia and Andresen 2014). Studies linking dung beetle diversity to their ecological functions are relatively common (for example, Braga and others 2013; Nervo and others 2014; Gregory and others 2015; Yoshihara and Sato 2015), but there is a lack of information on how environmental variables influence the functions performed by them (but see Griffiths and others 2015). Although information on dung beetle community responses to elevational gradients is easily found (for example, Lobo and Halffter 2000; Escobar and others 2005, 2007; Larsen 2012; Herzog and others 2013; Nunes and others 2016), studies evaluating dung beetle functions along elevation gradients are lacking.

Here, we aimed to understand which factors influence the ecological functions performed by dung beetles. Our hypothesis was that dung beetle community attributes and environmental factors influence together the ecological functions performance. To do this, we evaluated the effects of dung beetle community attributes (abundance, richness, mean biomass and functional diversity) and environmental variables (climate, soil and vegetation) along a tropical mountain on three main ecological functions they perform: dung removal, soil excavation and secondary seed dispersal. We expected a decrease in dung beetle ecological functions along the elevational gradient, following the commonly reported decline of their richness with elevation (Lobo and Halffter 2000; Escobar and others 2005; Herzog and others 2013; Nunes and others 2016). We also expected that environmental variables, such as temperature, humidity and soil features, would influence dung beetle functions. We discuss how dung beetle community attributes and environmental factors can alter dung beetle functions performance. Furthermore, we discuss some implications of global warming and anthropogenic alterations to ecosystem functioning.

Materials and Methods

Study Site

The study was conducted in Serra do Cipó (19°10′ and 19°22′ S, 43°29′ and 43°36′ W), in the southern part of the Cadeia do Espinhaço (Espinhaço Mountain Range), in the Brazilian state of Minas Gerais during December 2013 (Figure S1 in Supporting Information). The Cadeia do Espinhaço is a quartzitic mountain chain that extends for 1100 km across the states of Minas Gerais and Bahia in Brazil separating the Atlantic Forest and Cerrado biomes (Fernandes 2016). The region possesses a highland tropical Cwb Köppen climate with a rainy season between November and February, a mean annual temperature of 20 °C and mean annual rainfall of 1500 mm (Madeira and Fernandes 1999; Alvares and others 2013; Fernandes and others 2016). At the study area, the soil and vegetation are very heterogeneous, including five principal habitats: peat bogs, sandy grasslands, stony grasslands, rocky outcrops and Cerrado (Brazilian savanna) (de Carvalho and others 2012; Streher and others 2017).

Sampling Design and Environmental Variables

Because this study is part of a larger research project (LTER-PELD-Site 17 Serra do Cipó), we used its pre-established sampling sites to sample dung beetles and record their ecological functions. The sampling sites were located at approximately every 100 m of elevation. As the elevational gradient ranged from 800 to 1400 m a.s.l., a total of seven elevations were sampled. Each sampling site consisted of three transects, separated by at least 250 m, each having three traps separated by 100 m, to assure independence of sampled communities (da Silva and Hernández 2015). We calculated the mean for the data from the three pitfalls of each transect since the sampling unit was intended to be the transect. This resulted in a total sample size of 21: elevation sites = 7 X transects = 3; $n = 21$.

We used data on three main environmental factors that are known to influence dung beetles: climate, soil and vegetation (Lobo and Halffter 2000; Louzada and others 2010). We obtained climatic data from meteorological monitoring stations (Onset HOBO® U30 data logger) located in each sampling site (that is, seven meteorological monitoring stations) and recorded air temperature, air humidity, soil moisture, solar radiation and precipitation. Data loggers from meteorological stations recorded these data every 5 min and so the maximum, minimum, mean and variation of these parameters were recorded. We also used in our analysis data regarding the amount of organic matter and texture (percentage of sand, silt and clay) of the soil (Coutinho and others 2015) and the richness, abundance, height and basal area of plants (Silva Mota and others 2017) from the same sampling sites.

Dung Beetle Community Attributes

We used baited pitfall traps to capture dung beetles and quantify their species richness, abundance, biomass and functional diversity. Traps consisting of a plastic bowl (9 cm deep and 15 cm in diameter), containing 250 ml of a salt + detergent solution and baited with 25 g of fresh human dung, were left in the field for 48 h. The captured beetles were preserved and transported to the laboratory where they were identified to the lowest taxonomical level possible. We used the key of Vaz-de-Mello and others (2011), and its literature cited, to identify New World Scarabaeinae genera and subgenera and comparisons with voucher specimens to identify species. We assigned species to the following functional guilds based on their strategies for food allocation for reproduction (Halffter and Edmonds 1982): rollers (telecoprids)—that construct balls which they roll way from the original food source and deposit their eggs; tunnelers (paracoprids)—that dig tunnels directly beneath the food source where they store their food balls; and dwellers (endocoprids)—that live and reproduce inside the food source. We obtained the mean biomass of each species by drying all individuals at 45 °C until a constant weight was reached, and weighing the beetles with a 0.001 g precision balance.

To determine functional diversity (FD), we first calculated a species dissimilarity matrix based on mean biomass and functional guild of the dung beetle species, because these are considered the two main traits that affect the functions of dung beetles (Slade and others 2007; Braga and others 2013). We then calculated the Rao Index, which estimates FD considering species dissimilarities and abundances in each sampling point. (Details about the calculation of functional diversity are presented in Appendix S1 in Supporting Information.)

Permits for field research were provided by Ministério do Meio Ambiente (MMA); Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio); 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 Functions

Two days prior to the collection of dung beetles, we measured their ecological functions. To do this, we used ''function arenas,'' as adapted from Braga and others (2013), in each sampling point. 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. At the center of each arena, we placed 100 g of a mixture of fresh human and swine dung (proportion: 1–3). When we prepared this mixture, we added three sizes of plastic beads that have been used as seed mimics (from here onwards just seeds) in several studies because they have the advantage of not being removed by seed predators (Andresen 2003; Slade and others 2007; Braga and others 2013). In each experimental dung pile, we placed 50 small (3.5 mm diameter), 20 medium (8.6 mm diameter) and 10 large seed mimics (15.5 mm diameter). Function arenas were left in the field for 48 h, after which we measured three dung beetle ecological functions: dung removal, soil excavation and secondary seed dispersal (hereafter only seed dispersal). More details about the functions arenas can be found in Appendix S1 and in Braga and others (2013).

Data Analysis

To reduce the number of correlated variables, we first summarized the several environmental variables using principal component analysis (PCA). We performed three PCAs (one for climate, one for soil and one for vegetation variables) and obtained two axes for climatic variables, two axes for soil and one axis for vegetation (see details in Appendix S2 in Supporting Information). To analyze the effects of elevation on dung beetle ecological functions, we used generalized linear models (GLMs), with the ecological functions being response variables and elevation as the explanatory variable. We used *quasi-binomial* error distribution for dung removal and seed dispersal GLMs and *Gaussian* error distribution for soil excavation GLM. We calculated the mean elevation of each transect using the elevation of each trap. Since the three different seed sizes did not influence dispersal (Figure S3 in Supporting Information; $F = 0.17$, D.F. = 60, $p = 0.838$), we pooled all sizes to obtain a general rate of dispersal.

We also constructed GLMs to analyze the effects of environmental variables (summarized, that is, PCA axes) and dung beetle community attributes (abundance, richness, mean biomass and functional diversity) on the ecological functions (dung removal, soil excavation and seed dispersal). In specific cases of soil excavation and seed dispersal functions, we considered dung removal as an explanatory variable in the model. We used an information-theoretic approach based on the second-order Akaike's information criterion (AICc) to rank the models. We used the ''dredge'' function from the ''MuMIn'' package to test models defined by all possible variable combinations and ranked them by the AICs-based model weight. Because the models constructed for dung removal and seed dispersal best fit for the *quasi-binomial* family, we used the method proposed by Bolker (2016) for extracting the AICc for *quasi*-models. After all possible models were ranked, we considered only those models that had ΔAICc lower than two to be strongly supported.

Before we ranked the GLMS, we tested them for multicollinearity among the variables to prevent variance inflation factors using ''vif'' function found in ''car'' R package (Fox and Weisberg 2011). We removed abundance from dung removal and soil excavation models and vegetation from seed dispersal and soil excavation models due to multicollinearity. All GLMs were checked with residual analyses to evaluate the adequacy of the error distribution. We performed all analyses using the software R (R Core Team 2013).

RESULTS

The three dung beetle ecological functions evaluated declined with elevation (Figure 1). Dung removal: $F = 25.72$, D.F. = 19, $R^2 = 0.562$,

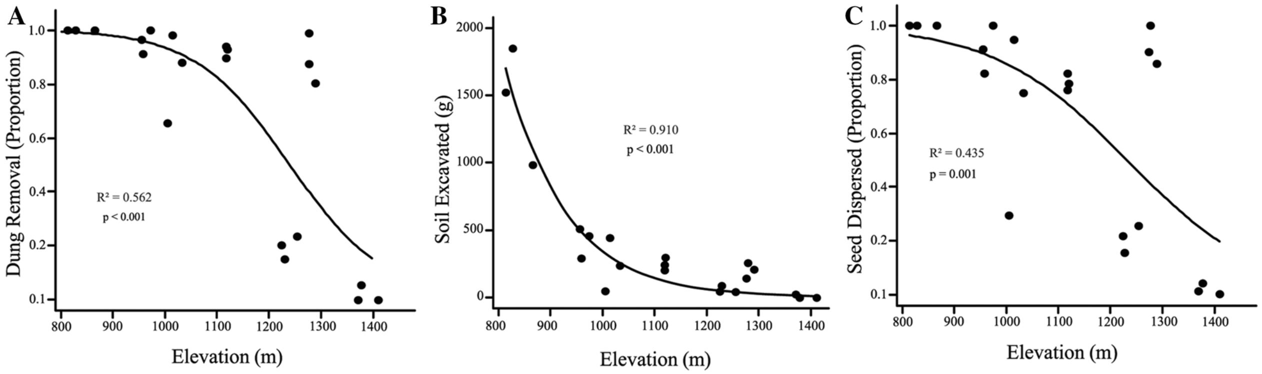

Figure 1. Dung beetle ecological functions along an elevational gradient at Serra do Cipó, state of Minas Gerais, Brazil: **A** dung removal; **B** soil excavation; **C** seed dispersal

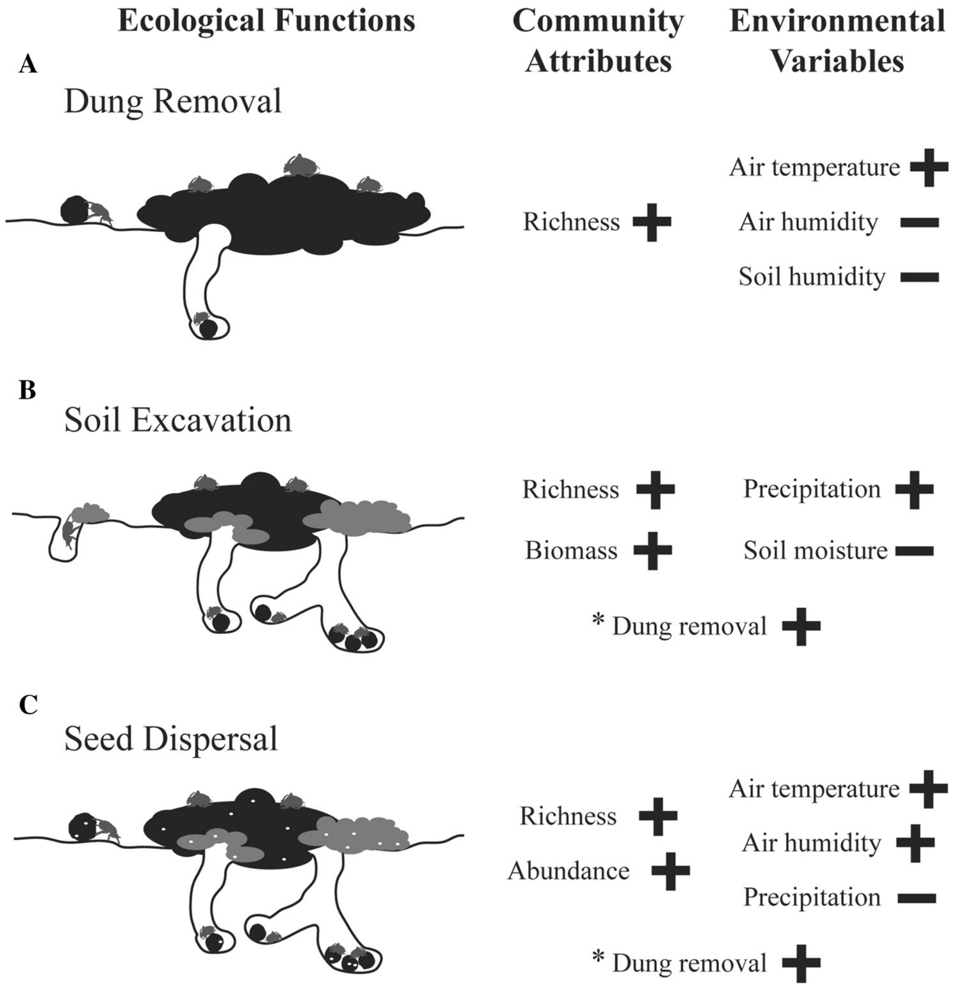

Figure 2. Community attributes and environmental variables that influence three dung beetle ecological functions measured: **A** dung removal; **B** soil excavation; **C** seed dispersal. The plus signal represents a positive relation, and the negative signal represents a negative relation between the variable and the ecological function. In the models of soil excavation and seed dispersal, dung removal entered as an explanatory variable

$p < 0.001$; soil excavation: $F = 193.22$, D.F. = 19, $R^2 = 0.910$, $p < 0.001$; seed dispersal: $F = 15.07$, D.F. = 19, $R^2 = 0.435$, $p = 0.001$. Dung removal was dependent on both dung beetle community and environmental variables (best models, $\omega_{\text{accumulated}}$: 0.682, Figure 2). Dung removal was

Table 1. Results of (Q)AICc-Based Model Selection for the Three Dung Beetle Ecological Functions Recorded—Dung Removal, Seed Dispersal and Soil Excavation

Model ranks	Model	D.F.	QAICc	Δ	ω	Cumulative ω	% DE
Dung removal							
1	C1 + C2 + V	4	31.517	0	0.382	0.382	0.81
2	S + C1 + C2 + V	5	31.999	0.481	0.300	0.682	0.86
3	FD + C1 + C2 + V	5	35.217	3.699	0.060		
Seed dispersal							
1	DR + A + S + C1 + C2	6	60.670	0	0.147	0.147	0.96
2	DR + S + C1	4	60.805	0.134	0.137	0.285	0.94
3	DR + A + S + C1	5	60.944	0.274	0.128	0.414	0.95
4	DR + S + C1 + C2	5	61.806	1.135	0.083	0.497	0.94
5	DR + A + S + C1 + So1	6	62.943	2.272	0.047		

	Model	D.F.	AICc	Δ	ω	Cumulative ω	% DE
Soil excavation							
1	DR + B + C2 + So2	6	250.91	0	0.413	0.413	0.98
2	DR + FD + B + C2 + So2	7	252.94	2.035	0.149		

We show the models with Δ QAICc lower than 2 and the next model in the rank. D.F.: degrees of freedom used; QAICc: AICc calculated for quasi-correction; Δ: QAICc differences; Akaike weights (ω); and %DE: percentage of deviance explained by the model. Error distribution of models was quasi-binomial (except for soil excavation, which had a Gaussian error distribution).

A abundance of dung beetles, S species richness of dung beetles, B biomass of dung beetles, FD functional diversity of dung beetles, C1 climatic axis 1 of PCA, C2 climatic axis 2 of PCA, V vegetation axis of PCA, So1 soil axis 1 of PCA, So2 soil axis 2 of PCA, DR dung removal—by dung beetles.

higher where both richness of dung beetles and air temperature were higher and where humidity of air and soil was lower (climatic axis of PCA 1 and 2). Also, dung removal was negatively correlated with the vegetation PCA axis, which means that where there was more diverse and abundant vegetation there was less dung removal (Table 1, Table S1 in Supporting Information, Figure 2).

As expected, seed dispersal and soil excavation were both dependent on dung removal. Seed dispersal was best explained by dung removal, dung beetle species richness and abundance, and the environmental variables of climate (Table 1; best models, $\omega_{\text{accumulated}}$: 0.497, Figure 2). Seed dispersal was higher where dung beetle communities were more diverse and abundant and was negatively correlated with temperature, radiation and precipitation (climatic axis 1 and 2 of PCA, Table 1, Table S1). Soil excavation was best explained by dung removal rate, dung beetle mean biomass and climate and soil (Table 1; best model, ω: 0.42, Figure 2). Soil excavation was higher where mean biomass of dung beetle communities was higher and where there was higher precipitation and lower soil moisture (climatic axis 2 and Soil axis 2 of PCA, Table 1, Table S1).

The rates of seed dispersal of different sizes were statistically similar along the elevational gradient (Figure S3, $F = 0.17$, D.F. = 60, $p = 0.838$), that is, although elevation influenced seed dispersal (dispersal declined with elevation), it did not differentially affect the dispersion of large, medium or small seeds.

DISCUSSION

The three measured ecological functions of dung beetles (dung removal, soil excavation and secondary seed dispersal) declined with elevation and were explained by both community attributes and environmental variables. Although dung beetle richness also declined with increasing elevation (see Nunes and others 2016 and Figure S2 in Supporting Information), the rates of decline of ecological functions were more pronounced than of richness (Figure 1 and Figure S2). Dung removal and seed dispersal by dung beetles varied from 100% at low elevations to almost 0% at high elevations, while soil excavation varied in parallel from a mean of 1500 g of loose soil at low elevations to approximately 0 g at the highest elevation. This result demonstrates that although dung beetle richness is linked with their functions (Slade and others 2007, 2011; Braga and others 2013), there are other factors involved, as we discuss below.

Ecological Functions and Community Attributes

In this study, we corroborate the link between biodiversity and ecological functions found in other studies on dung beetles (Slade and others 2007; Braga and others 2013; Yoshihara and Sato 2015). However, of all community attributes measured only species richness was related to dung removal. Body size (mean biomass), which is usually related to the amount of dung buried by dung beetles (Andresen 2002; Nervo and others 2014; Gregory and others 2015), was not present in the best models in our study. Abundance, which is also known to influence function performance, was present in only one model (seed dispersal). This could be due to the influence of environmental variables that mask or inhibit the effects of these community attributes on the performance of ecological functions.

Surprisingly, dung beetle functional diversity did not appear in any of the best models of ecological functions measured in our study. Although functional diversity did not decrease with elevation, functions themselves did drastically. We can draw two main conclusions from this: (1) ecological functions might depend substantially on environmental factors to be performed; and (2) although functional diversity indices predict ecosystem functioning better than species richness (Petchey and Gaston 2006; Gagic and others 2015), they may fail due to context-dependent and environmental effects. There is a difference in measuring functional diversity and the functions themselves. As functional diversity is based on the characteristics of species and their abundances, it can be very helpful in studies of species resource use and niche (Villéger and others 2012; de Bello and others 2013). Functional diversity is a community attribute that theoretically is linked with species ecological function performance. However, ecological function also depends on environmental variables (for example, Griffiths and others 2015). This leads to a practical issue: how much of ecosystem functioning is really predicted by a community's metric? Because these metrics are frequently used to measure human impacts on ecosystems, we may be underestimating the effects on ecosystem functioning. For example, we can have an agroforest with fewer species of dung beetles than a primary forest, but with similar functional diversity 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 argue that measuring functions themselves can provide much more information on ecosystem functioning than just measuring community attributes.

Ecological Functions and Environmental Variables

We found that climatic and vegetation variables were related to dung removal by dung beetles, confirming an environment-ecological functions link. Climatic variables, mainly temperature, can affect dung beetle adult activity, egg laying and larval survival, thus influencing their feeding and breeding behavior (Lobo and others 1998; Chown 2001). Consequently, different temperatures could even lead to equivalent communities (in terms of species composition) removing different proportions of dung in the field. In the present study, much more dung was removed at areas at low elevations, where mean temperatures are higher (Appendix S2, Fernandes and others 2016). Characteristics of soil, like texture and moisture can be both crucial to dung beetle reproduction and influence dung removal. In excessively wet soils, soil excavation is impaired and, if dung beetles dig anyway, larvae mortality may be increased, thus explaining why moist soil are avoided by reproducing beetles and during dung burying (Sowig 1995, 1996; Nichols and others 2008). In a function arena located at 1400 m a.s.l., we found an almost intact experimental dung pile with dung beetles just beside it, failing to bury themselves due to soil moisture (Figure S4 in Supporting Information). This means that there were beetles present to do the ''job,'' but environmental factors impaired them from doing so. Vegetation was also present in the models that best explained variation in dung removal, and we argue that this may be due to the microclimates that plants can provide and their influence on dung beetle species composition. Where there is higher plant density, more shadowing is available, so soil temperature tends to be lower, whereas moisture tends to be higher than in a plant-poor area, and in this case, negatively affecting dung removal (Braga and others 2013).

Our results also show that soil excavation and seed dispersal are dependent not only on dung removal, but also on community attributes and some environmental variables. Thus, dung beetle species richness, abundance and body size can influence the performance of these functions, even after dung is removed. For soil excavation, we found that the only community attribute related to this ecological function was mean biomass of dung beetle communities. Large beetles, for example, dig deeper and consequently move more soil from deep layers to the surface (Braga and others 2013;

Gregory and others 2015). We also recorded less soil excavation by dung beetles in humid soils and suggest that this could be due to the difficulty for dung beetles to bury themselves in wet soils. Furthermore, secondary seed dispersal by dung beetles has been demonstrated to be dependent on beetle species richness and abundance (Andresen 2002; Braga and others 2013). However, we also found that climatic variables such as air temperature and radiation were positively related to seed dispersal. The same logic used to explain the influence of climate on dung removal could be applied here: temperature, radiation and air humidity affect dung beetle activity and breeding behavior and for this reason influence dung removal and seed dispersal.

Implications of Global Changes on Ecosystem Functioning in Mountains

Tropical insects are particularly sensitive to climatic change (Deutsch and others 2008), and global changes could lead to great loss of biodiversity (Colwell and others 2008; Raxworthy and others 2008; Larsen 2012). The impact on ecosystem functions should be even greater (Cardinale and others 2012; Hooper and others 2012). Environmental variables can alter ecological functions as much as biodiversity. Although dung beetles could survive under warmer conditions and maintain some functional diversity, 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 to climatic change (Parmesan and Yohe 2003; Sundqvist and others 2013), ecosystem functioning can change even more drastically as conditions vary rapidly with elevation. Nunes and others (2016) discuss the effects of global warming on mountain dung beetle communities and suggest that upslope range shifts, and mountaintop and lowland extinctions would lead to even greater loss of diversity than expected, as diversity among elevations (β diversity) is very high. Although functional diversity could be maintained, environmental factors can impede function performance.

It is not easy to measure ecological functions and even more difficult to link them to environmental factors. Here we suggest a good bioindicator taxon that performs important functions in an ecosystem and which community attributes and functions can be easily measured. The elevational gradient played an important role in our conclusion as it provides different conditions along surprisingly short distances. Although we worked with a specific taxon in a specific location and did not considered biogeographical aspects, our findings that community attributes and environmental factors directly influence ecological functions could be extrapolated to community assembly and its role on ecosystem properties in general. This way, we should start considering that ecological functions may be directly influenced both by community attributes and environmental variables and so the existence of the link between biodiversity, the environment and ecosystem functioning.

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Compliance with Ethical Standard

Conflict of interest The authors declare that they have no conflict of interest.

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