


Turnover and nestedness in subtropical dung beetle assemblages along an elevational gradient

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Abstract

Aim: We investigated changes in dung beetle β -diversity components along a subtropical elevational gradient, to test whether turnover or nestedness-related processes drive the dissimilarity of assemblages at spatial and temporal scales.

Location: An elevational gradient (200–1,600 m a.s.l.) of the Atlantic Forest in southern Brazil.

Methods: We investigated the extent to which β -diversity varied along the elevational gradient (six elevations) at both spatial (among sites at different elevations) and temporal (different months at the same site) scales. We compared both the turnover and nestedness-related dissimilarity of species and genera using multiple-site or multiple-month measures and tested whether these measurements were different from random expectations.

Results: A mid-elevation peak in species richness along the elevational gradient was observed, and the lowest richness occurred at the highest elevations. We found two different groups of species, lowland and highland species, with a mixing of groups at intermediate elevations. The turnover component of β -diversity was significantly higher for both spatial (i.e. elevational) and temporal changes in species composition. However, when the data for genera by site were considered, the elevational turnover value decreased in relative importance. Nestedness-related processes are more important for temporal dissimilarity patterns at higher elevation sites.

Main conclusions: Spatial and temporal turnover of dung beetle species is the most important component of β -diversity along the elevational gradient. High-elevation assemblages are not subsets of assemblages that inhabit lower elevations, but this relationship ceases when β -diversity is measured at the generic level. Environmental changes across elevations may be the cause of the differential establishment of distinctive species, but these species typically belong to the same higher taxonomic rank. Conservation strategies should consider elevational gradients in case-specific scenarios as they may contain distinct species assemblages in lowlands vs. highlands.

KEYWORDS

Atlantic Forest, compositional differences, elevation patterns, Scarabaeinae, seasonality, vertical colonization

1 | INTRODUCTION

Understanding the variation in species composition among sites (β -diversity) along environmental, spatial or temporal gradients is a central question in ecology. Because β -diversity is related to the partitioning of environmental resources among species, it is also important to discern the mechanisms responsible for among-site variation (Kraft et al., 2011; Qian, Wang, & Zhang, 2012; Ricklefs, 2004). The interest in β -diversity has increased in the last decades with the recognition of its crucial role in identifying processes and mechanisms driving community diversity patterns at multiple spatial scales (Ricklefs, 2004; Soininen, Lennon, & Hillebrand, 2007). Furthermore, a better understanding of β -diversity will help us to address threats to biodiversity in a more effective way.

Generally defined as the variation in species composition among sites (Whittaker, 1960) or through time, β -diversity has long been used to investigate changes in patterns of composition and abundance of biological communities (Anderson et al., 2011). Understanding patterns of β -diversity is therefore essential to unveil how biodiversity varies spatially (Baselga, 2010b) and temporally (Korhonen, Soininen, & Hillebrand, 2010). Although important, the mechanisms of community assembly driving β -diversity remain poorly understood and open for investigation (Kraft et al., 2011; Qian et al., 2012). Several explanations have been proposed for the variation observed in β -diversity patterns along different gradients, including environmental heterogeneity, habitat specialization (niche-related processes) and dispersal limitation (neutral-related processes) (Legendre, Borcard, & Peres-Neto, 2005; Qian & Ricklefs, 2007). In the case of elevational gradients, some authors argue that β -diversity patterns are more likely to be driven by variations in γ diversity than by differences in community assembly mechanisms (Kraft et al., 2011, 2012). However, some authors argue the opposite; that is, that β -diversity patterns reflect variation in the strength of local community assembly mechanisms across spatial scales (or elevational gradients) (Bishop, Robertson, van Rensburg, & Parr, 2015; Tello et al., 2015).

Globally, β -diversity generally increases from temperate to tropical regions (Myers et al., 2013; Qian & Ricklefs, 2007) and from mainland to island ecosystems (Stuart, Losos, & Algar, 2012). Another frequently observed pattern is that local species richness (α -diversity), differences in species compositions among sites (β -diversity), and regional (γ -diversity) species pools generally decline with increasing elevation (Kraft et al., 2011; Rahbek, 2005). That said, patterns in α -diversity can differ markedly between taxa, geographic regions and elevational gradients. Indeed, studies report a range of relationships between species richness and elevation, which include no relationship, linear positive and negative relationships, and nonlinear declines in richness with increasing elevation (i.e. greater species richness at intermediate elevations) (Bertuzzo et al., 2016; Domínguez, Marín-Armijos, & Ruiz, 2015; Heaney, 2001; Liew, Schilthuizen, & Bin Lakim, 2010; Mori et al., 2013; Paknia & Rajaei, 2015; Smith, 2015; Smith, de Oca, Reeder, & Wiens, 2007). Understanding these patterns is crucial for predicting how

biodiversity will be affected by climate change, as some species are expected to change their geographic distributions to higher elevations and latitudes as temperatures increase (Menéndez, González-Megías, Jay-Robert, & Marquéz-Ferrando, 2014; Sheldon, Yang, & Tewksbury, 2011). Although it can be difficult to distinguish the mechanisms underlying these patterns, because several multi-scale processes may determine spatial variation in diversity (Ricklefs, 2004), studies that investigate these patterns represent one of the most promising areas of research to further our understanding of climate effects on species distribution (Menéndez et al., 2014; Qian & Ricklefs, 2007).

β -diversity can be partitioned into two process-related components: turnover (species replacement between communities) and dissimilarity due to nestedness (species gain or loss between communities) (Baselga, 2010b; Legendre, 2014). The turnover component may occur because of environmental filtering or spatial and historical constraints (Qian, Ricklefs, & White, 2005), but it will be independent of the differences in the number of species per site. The nestedness component of β -diversity is due to the fact that one assemblage is a subset of another. Nestedness may either reflect the quantity of niches available or occupied at different sites throughout the study area (Legendre, 2014) or be the result of extinctions in poor sites or colonizations in rich sites along gradients (Ulrich, Almeida-Neto, & Gotelli, 2009). Environmental filtering is also expected to produce nested patterns (Soininen, Heino, & Wang, 2018), when the environment filters only a subset of an assemblage along large spatial extents.

Studies that analyse the variation in the two components of β -diversity along elevational gradients are still sparse (Bishop et al., 2015; Jacquemyn, Honnay, & Paillet, 2007; Nunes, Braga, Figueira, Siqueira-Neves, & Fernandes, 2016; Paknia & Rajaei, 2015). The available results suggest that species turnover may decrease and nestedness increase with elevation, but these patterns can differ depending on the geographical region (Paknia & Rajaei, 2015). On the other hand, some authors argue that β -diversity along elevational gradients is primarily caused by species turnover and suggest species sorting and abiotic changes as the main factors responsible for these elevational replacements (Nunes et al., 2016). Differences between nestedness and turnover components of β -diversity along elevational gradients can be related to the concepts of "vertical" and "horizontal" colonization proposed by Lobo and Halffter (2000). In a vertical colonization, high-elevation assemblages are composed by species phylogenetically related with those inhabiting lowlands, whereas in horizontal colonization highland assemblages consist of species with a different evolutionary history and origin from those occupying lowlands. Thus, with vertical colonization, one may expect that communities at higher elevations are subsets of those occurring at lower elevations with a lesser number of phylogenetically related species (nestedness-related pattern). In contrast, lowland and highland communities under horizontal colonization will be composed by species with different evolutionary histories, origins and thermal tolerances, what may or may not lead to a lower number of species (turnover-related pattern).

Recently, studies have started to investigate the partition of β -diversity into its process-related components along temporal gradients (Baselga, Bonthoux, & Balent, 2015; Wojciechowski, Heino, Bini, & Padiál, 2016). Coupling temporal and spatial approaches can also be useful to better understand the processes related to both spatial and temporal variations in assemblages along elevational gradients. In this study, we conducted an analysis of spatial (among sites at different elevations) and temporal (between months at the same site) β -diversity to disentangle its turnover and nestedness-resultant components along an elevational gradient. We used dung beetles (Coleoptera: Scarabaeinae) as a model species group because they are considered a cost-effective and responsive taxonomic group for assessing environmental changes (Bicknell et al., 2014; Campos & Hernández, 2015; Gardner et al., 2008; Slade, Mann, & Lewis, 2011). Furthermore, strong environmental filtering has shown to affect dung beetle β -diversity patterns at both local and regional scales (da Silva & Hernández, 2014, 2015a). In particular, we examined patterns of species richness, including species turnover and nestedness along

elevational and temporal gradients of an Atlantic Forest landscape in southern Brazil. We tested the following predictions: (1) species richness of dung beetles will decrease with increasing elevation as favourable environmental conditions decrease along elevational gradients and only a limited number of species are well adapted to the conditions found at the highest sites; and (2) as the study sites are relatively far from regions with cold-temperate conditions, it is expected that nestedness-related patterns and vertical colonization processes dominate β -diversity variation along the spatial gradient (among sites at different elevations). Finally, as lowland sites show clearly contrasted seasons (cold/warm), and the occurrence of unsuitable climatic conditions during the year for ectothermic species increases with elevation in these biomes, we also expected that temporal β -diversity should be maximized in more seasonal sites (Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017). Thus, we predicted that (3) the turnover-related component of dissimilarity would be the most important component of β -diversity along the temporal variation (between months at the same site) in lowland sites, while the

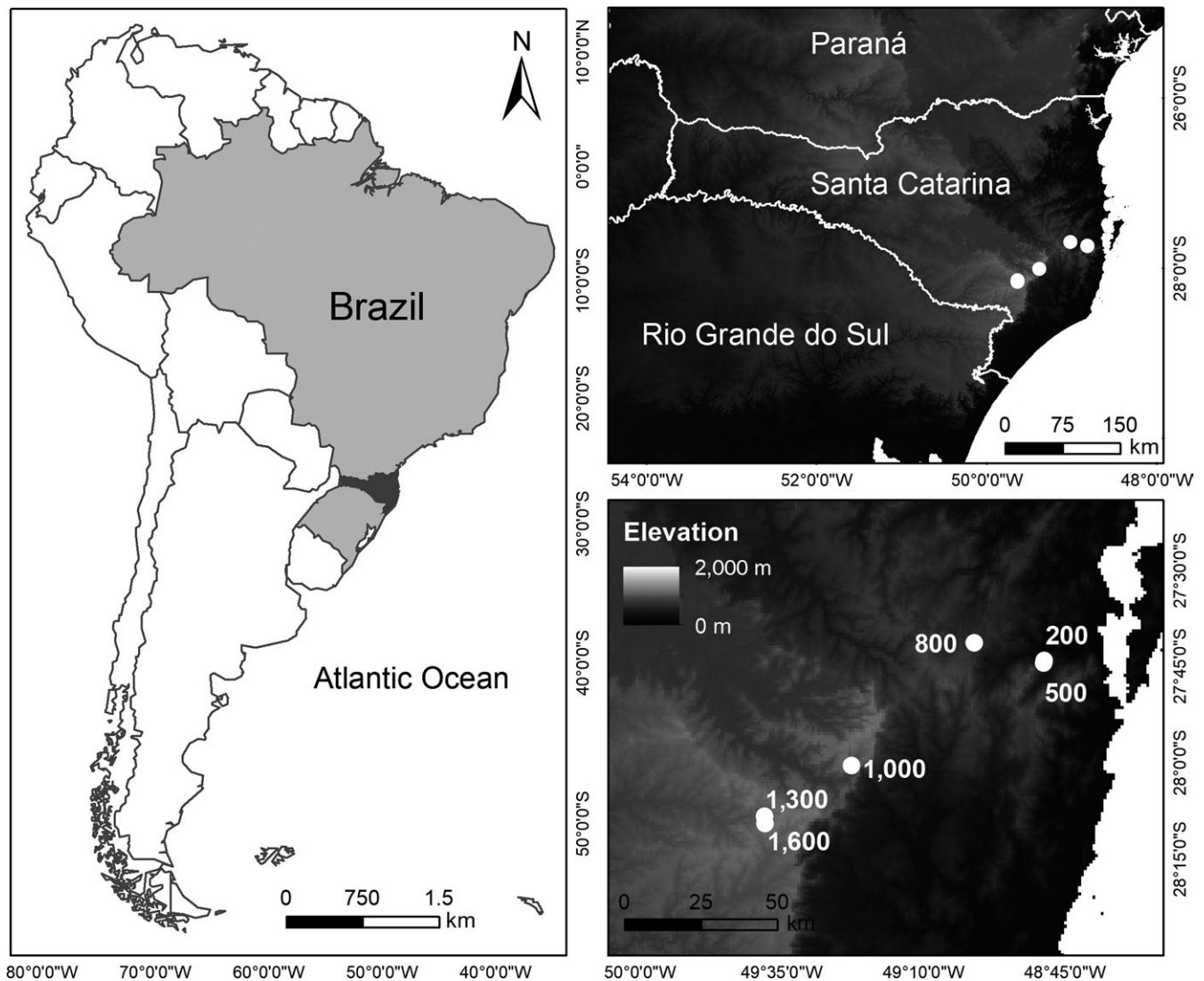


FIGURE 1 Geographic position of sites sampled in Santa Catarina, southern Brazil

temporal nestedness-related component should increase in importance at higher elevations.

2 | METHODS

2.1 | Study area

The study was performed at six sites comprising a cross-elevational transect extending northeast-southwest from latitude 27°44'S to 28°9'S and longitude 48°48'W to 49°37'W, in two Atlantic Forest formations in Santa Catarina, southern Brazil (Figure 1). The cross-elevational transect includes sites at 200, 500, 800, 1,000, 1,300 and 1,600 m a.s.l. (see Appendix S1: Table S1.1 for a detailed description). We only sampled dung beetles within natural forest sites. The vegetation formations found in our study were dense ombrophilous forest and mixed ombrophilous forest. Dense ombrophilous forests occur between sea level and around 800 m a.s.l., while mixed ombrophilous forests are found mainly between 800 and 1,700 m a.s.l. The climate in southern Brazil is subtropical, with regular rainfall and relatively well-defined seasons: Winter is usually cold, with frequent frosts due to the influence of elevation. Temperatures range from below zero in winter to 30°C in summer (IBGE, 1992).

2.2 | Dung beetle sampling

Dung beetle samplings were carried out once a month between June 2015 and June 2016 (totalling 13 samplings). We used baited pitfall traps to sample dung beetles. A detailed description of the traps can be found in da Silva and Hernández (2014, 2015a). Human faeces and rotting flesh (ca. 10 g) were used to attract dung beetles (i.e. coprophagous and necrophagous species, respectively). Each of the six sites was sampled using 10 baited pitfall traps, distributed in pairs (5–10 m distant) along a linear transect, with each pair spaced 100 m apart (da Silva & Hernández, 2015b). Each pair of traps contained both types of bait separately (data from both traps were pooled). Traps remained in the field for 48 h per month. There were three occasions when we were not able to perform sampling due to road obstruction (flooding): July 2015 for the site at 1,300 m, and September 2015 and March 2016 for the site at 1,000 m. Beetles were identified at the species level, and voucher specimens were deposited in institutional collections (Universidade Federal de Santa Catarina and Universidade Federal de Mato Grosso, Brazil). In each site, we also recorded temperature values (every 15 min) using data-loggers installed at 1.5 m above ground. These temperature values were used only for discussing species distribution patterns along the elevation gradient.

2.3 | Data analysis

The sampling completeness of each site ($n = 6$) and sampling month ($n = 13$ months per site) was assessed to guarantee that compositional comparisons were based on reliable inventories. Sampling completeness was estimated taking into account the values of

abundance coverage estimator (ACE), calculated separately for each site (spatial approach comprising all months for each site) and time (temporal approach comprising all sites for each month) as the percentage of observed species against estimated richness. The software ESTIMATES 9.1 was used for these analyses (Colwell, 2013). Sample coverage and species accumulation curves for both spatial and temporal approaches were also calculated using the "INEXT" R package (Hsieh, Ma, Chao, & McInerney, 2016). Sample coverage is estimated as the final slope of the plot relating the increase in number of species with number of samples, and only inventories with similar high coverage values can be compared from the perspective of their composition (Chao & Jost, 2012).

The Pearson correlation coefficient as well as linear and curvilinear (quadratic functions) regressions were used to assess whether species richness and abundance at each site were related to elevation. These analyses were carried out only to estimate the explanatory capacity of elevation. We used average elevation values obtained from geographic coordinates of each one of the sampling points in each site (i.e. among the five pairs of traps). We first tested the variables to verify the normality of data using the Shapiro-Wilk test. Abundance was transformed into natural logarithms.

We used Mantel tests and partial Mantel tests to disentangle the effect of geographic distance and elevation on the compositional similarity of dung beetle assemblages. Three distance matrices were constructed: (1) a dissimilarity matrix of species composition by site using the Jaccard coefficient; (2) a Euclidean distance matrix accounting for differences in elevation; and (3) a Euclidean distance matrix representing the geographical distances between sites corrected by their elevations. We performed Mantel tests between dung beetle composition and elevation, and between dung beetle composition and geographic distance separately. We also conducted partial Mantel tests between dung beetle composition and both distance matrices, conditioning elevation by geographic distance and vice versa. The Pearson correlation method and 9,999 permutations were used by means of the "VEGAN" R package (Oksanen et al., 2016).

Differences in species composition among elevations and between lowland (200–800 m) and highland (1,000–1,600 m) assemblages were tested using permutational multivariate analysis of variance using distance matrices (PERMANOVA) (Anderson & Walsh, 2013). The Jaccard coefficient was used to calculate the dissimilarity in R software (R Core Team, 2017).

Patterns of species turnover and nestedness-resultant components were examined using the β -diversity partitioning method (Baselga, 2010a,b) calculated with multiple-site or multiple-month dissimilarity metrics of the Jaccard dissimilarity coefficient (Baselga, 2013; Legendre, 2014). β -diversity partitioning allows the total Jaccard dissimilarity coefficient (β -diversity; β_{JAC}) to be partitioned into components of dissimilarity due to turnover and nestedness, following equations provided by Baselga (2012). We examined whether both turnover and nestedness components differed according to spatial (among sites located at different elevations) and temporal (between months for each site) variations. For spatial gradient, we estimated turnover and nestedness components using two

different sets of data: species by site and genera by site. If turnover and nestedness measurements were similar when using these two taxonomic ranks, this would suggest that segregation (turnover) or decay (nestedness) patterns involved not only different species but also probable different clades with a higher likelihood of having experienced distinctive evolutionary histories. However, if “vertical colonization” processes dominated, we expected to find highland assemblages composed by species from the same genera of those inhabiting lowlands.

In the case of the temporal gradient, we investigated patterns of turnover and nestedness at each site using the 13 sampling periods, both for species by site and genera by site. We used the function “beta.multi” of the “BETAPART” R package to calculate multiple-site dissimilarities (Baselga, 2012), as average values derived from pairwise comparisons are different from those values calculated using multiple-site comparisons. The function “beta.pair” of the “BETAPART” R package was also used to calculate pairwise measurements of Jaccard dissimilarity, which was partitioned into turnover and nestedness-related dissimilarity to graphically represent the pair-to-pair pattern of dissimilarity between sites via Cluster Analysis.

We constructed null models to test whether the observed turnover and nestedness values were different from those expected by chance. We used the “oecosimu” function ($n = 9,999$ simulations) of the “VEGAN” R package with a presence-absence matrix of species per site, and a non-sequential algorithm for binary matrices that maintains site (row) frequencies and uses squared column sums as probabilities to select species (Wright, Patterson, Mikkelsen, Cutler, & Atmar, 1997). This null model was selected to generate random assemblages in which both the number of species at each site and the distribution range of the species were restricted to the values found, assuming that they constitute biological and environmental constraints. Both turnover and nestedness values were transformed to percentages of total dissimilarity.

3 | RESULTS

3.1 | Patterns of species richness and abundance

We collected a total of 6,676 dung beetles from 41 species and 13 genera (see Appendix S2: Table S2.1). Completeness analyses indicated that an average of 88% (ranging from 66% to 97%) of the estimated total number of species present was collected at each site (see Appendix S2: Table S2.2). Sample coverage values suggest even better completeness estimates, which were always >0.99 (range: 0.991–1.000) for the spatial approach and higher than 0.90 (range: 0.901–0.997) for the temporal approach (see Appendix S2: Table S2.2). In addition, species accumulation curves tended towards stability for both spatial and temporal approaches (see Appendix S3: Figure S3.1).

The total number of collected species varied curvilinearly with elevation, and as expected, the lowest species richness was found at high elevations (1,000–1,600 m) (Figure 2). Thus, there was no linear decline in species richness with increasing elevation (Pearson's

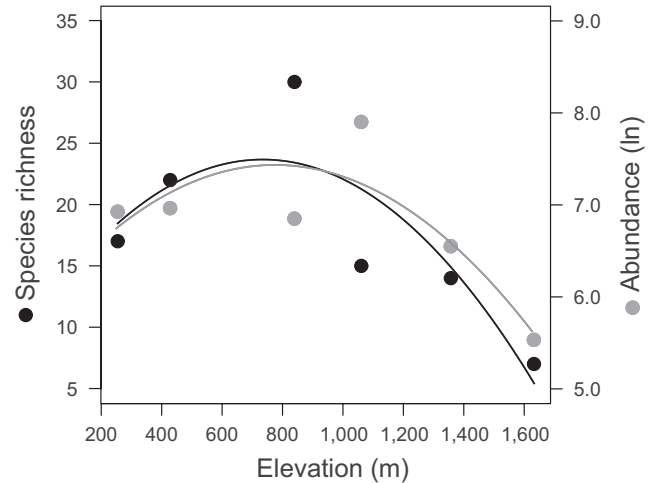


FIGURE 2 Observed species richness and abundance (in natural logarithms) of dung beetles along an elevational gradient in southern Brazil. The lines represent the adjustment to a quadratic function

correlation = $-.59$, $p = .212$), as the highest number of species was found in the site at 800 m ($S = 30$). A linear regression accounted for 34% of variability in species richness ($R^2 \times 100$), while a quadratic function explains 70%. A very similar pattern was found for abundance, which also showed no linear correlation with elevation (Pearson's correlation = $-.210$, p -value = $.688$) as the highest abundance ($n = 2,702$) occurred in the site located at 1,000 m, while the sites at 1,300 and 1,600 m showed the lowest values (Figure 2). A quadratic function accounted for 39% of variability in total abundance variation whereas linear regression barely explained 5%. When the data for genera by site were considered, a similar pattern was found to that considering species by site (see Appendix S3: Figure S3.2). A higher number of genera were found at 800 m, while a lower number of genera were found at 1,600 m. Only the genus *Paracanthion* Balthasar was not sampled at 800 m. A quadratic function accounted for 20% of variability in genera variation whereas linear regression barely explained 3%.

Dung beetles were sampled throughout the year at all sites, with higher total numbers of species and individuals at the beginning of summer (December 2015), considering all sites together (see Appendix S2: Table S2.2) and each site separately (Figure 3; see Appendix S2: Table S2.3). Only the site located at the highest elevation (1,600 m) showed a different seasonal pattern with a high number of species and individuals during late summer (February 2016).

Mantel tests between dung beetle composition and elevation, and between dung beetle composition and geographic distance are both statistically significant (Mantel r : $.584$, p -value = $.001$, and Mantel r : $.188$, p -value = $.001$, respectively). However, only the partial Mantel test between dung beetle composition and elevation was statistically significant when elevation was conditioned by geographic distance (Mantel r : $.564$, p -value = $.001$). When dung beetle composition was correlated with geographic distance conditioned on elevation, we found no significant correlation (Mantel

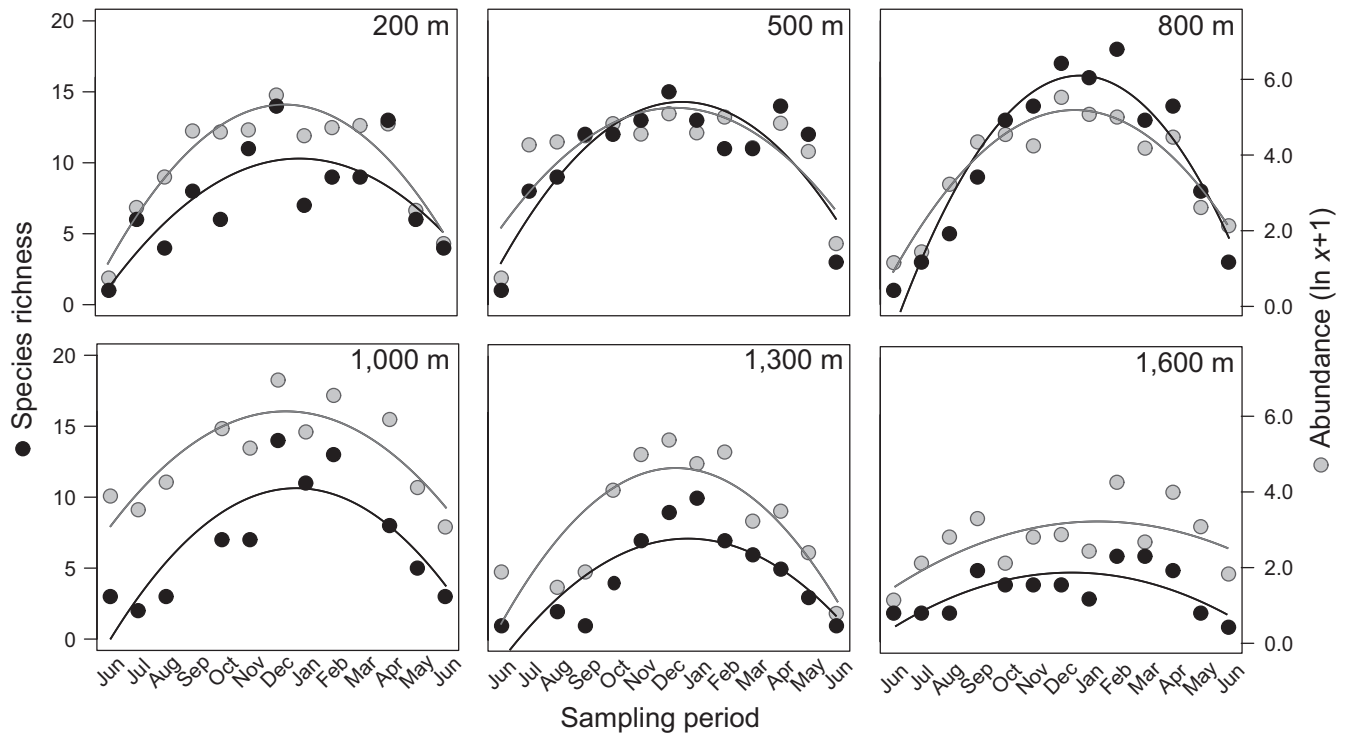


FIGURE 3 Monthly observed species richness and abundance (in natural logarithms; $\ln x+1$) of dung beetles in each site. The lines represent the adjustment to a quadratic function

$r = .048$, p -value = .081). Therefore, elevation plays a more important role than geographic distance driving dung beetle assemblage similarities.

3.2 | Spatial pattern of β -diversity

The proportion of shared species ranged from 4%, between the sites located at lower elevations (200 and 500 m) and the site located at 1,600 m, to 77% between the two sites located at lower elevations (200 and 500 m) (Table 1). This high proportion of shared species occurred because all species sampled at the site at 200 m were also found at 500 m (see Appendix S2: Table S2.1). Similarly, all species sampled at 1,600 m were also found in the sites located at 800 m and 1,000 m. Similar results were found for proportions of shared species relating to the total γ -diversity ($S = 41$), where sites at the beginning and the end of the elevational gradient (200 and 1,600 m) shared just one species (Table 1).

The surveyed sites were grouped into two clusters according to pairwise Jaccard dissimilarity values (Figure 4): one group formed by sites located at 200, 500 and 800 m, and another group composed by sites located at 1,000, 1,300 and 1,600 m, with an average dissimilarity higher than 80% (Figure 4). PERMANOVA results showed statistical differences in species composition among all sites ($F = 4.511$, $R^2 = .151$, p -value = .001) and between lowland (200–800 m) and highland (1,000–1,600 m) assemblages ($F = 32.110$, $R^2 = .269$, p -value = .001). *Canthidium* Erichson, *Canthon* Hoffmannsegg, *Dichotomius* Hope and *Onthophagus* Latreille showed different species restricted to lower and higher elevations (see Appendix S2: Table S2.1). Except for

TABLE 1 Matrix describing number and percentages (in parenthesis) of species shared between sites related to total γ -diversity and pair-to-pair comparisons

	200	500	800	1,000	1,300
Proportion of γ -diversity					
500 m	17 (44)				
800 m	14 (36)	17 (44)			
1,000 m	4 (10)	5 (13)	11 (28)		
1,300 m	3 (8)	4 (10)	10 (26)	10 (26)	
1,600 m	1 (3)	1 (3)	7 (18)	7 (18)	6 (15)
Proportion pair-to-pair					
500 m	17 (77)				
800 m	14 (42)	17 (49)			
1,000 m	4 (14)	5 (16)	11 (32)		
1,300 m	3 (11)	4 (13)	10 (29)	10 (53)	
1,600 m	1 (4)	1 (4)	7 (23)	7 (47)	6 (40)

Deltochilum brasiliense (Castelnau), which was the only species found in all sites, the remaining species of *Deltochilum* Eschscholtz occurred only between sites at 200–800 m. The species of *Eurysternus* Dalman and *Phanaeus* MacLeay showed the same distribution pattern, while *Homocopris* Burmeister occurred only between 800 and 1,600 m.

The complete multiple-site dissimilarity in species composition along the studied elevational gradient was high (82%), being dominated by the turnover component, which represented 85.5% of the spatial dissimilarity (Table 2). The turnover component was lower

than that expected by chance, while the value of the nestedness-related component was higher (14.5%) than expected by chance.

When the data for genera by site were considered, the turnover value was lower (57.7%) than the value found using the species by site approach and did not differ from that expected by chance (Table 2). The nestedness-related component was almost three times higher (42.3%) than that found using the species by site approach, although it did not differ from that expected by chance as well (Table 2).

3.3 | Temporal pattern of β -diversity

The temporal multiple-month dissimilarity at each site ranged from 83% to 89% and did not relate to site elevation (Pearson's correlation = -0.46 , p -value = $.677$). Turnover was the main component of β -diversity for all sites (Table 3). Higher values of temporal turnover ($>83%$) were found in sites at lower elevations (200–800 m), which were also lower and different from those expected by chance (Table 3). The turnover component

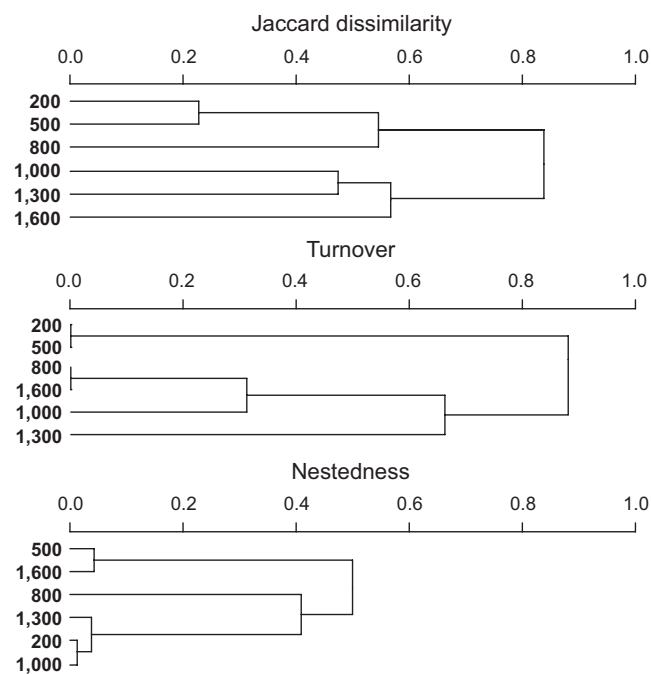


FIGURE 4 Mean Jaccard dissimilarity, turnover and nestedness. Values of turnover and nestedness are represented in percentages of total dissimilarity

TABLE 2 Null model results of the multiple-site β -diversity components for species by site and genera by site approaches. β -diversity components are represented by percentage (%) of total dissimilarity

	Obs. (%)	Mean _(sim)	2.5%	50%	97.5%	$p_{(sim)}$
Species by site						
Turnover	0.855	0.961	0.926	0.963	0.985	.000
Nestedness	0.145	0.039	0.015	0.037	0.074	.000
Genera by site						
Turnover	0.577	0.714	0.428	0.767	0.884	.312
Nestedness	0.423	0.286	0.116	0.233	0.572	.312

Obs. (%)—percentage represented by β -diversity components of the total dissimilarity; Mean_(sim)—mean values of the 9,999 simulations; 2.5%, 50% and 97.5%—the amount of simulated values; $p_{(sim)}$ — p values.

of sites located at higher elevations (1,000–1,600 m) was lower, ranging from 56% to 74%, also differing from that expected by chance.

The nestedness-related component showed values ranging from 15.3% to 16.6% for the sites located at lower elevations, whereas this component increased in importance at high-elevation sites, ranging from 25.5% to 43.2% (Table 3). All values of the nestedness-related component differed from and were higher than those expected by chance.

These patterns are related to temperature variation across the year and the occurrence of low-temperature values in high-elevation sites (Table 3). As a consequence, several species along the elevational gradient seem to have a restricted seasonal occurrence. The number of species collected per month ranged from one (sites at 1,000 and 1,600 m) to 10 (site at 800 m) (see Appendix S2: Table S2.4). In addition, the proportion of species collected in 50% or less of the sampling units (i.e. species present in less than seven sampling units) ranged between 50.0% (site at 500 m) and 78.6% (site at 1,300 m) (200 m = 52.9%; 800 m = 66.7%; 1,000 m = 66.7%; 1,600 m = 57.1%). Furthermore, only *Homocopris* sp. was found in all sampling units of the site at 1,600 m. All remaining species were found in $<90%$ of the sampling units. These species were found mainly between the end of spring and the end of autumn (see Appendix S2: Table S2.4).

When data for genera by month were considered, the temporal multiple-month dissimilarity in each site ranged from 72% to 85% and did not seem to be related with site elevation as well (Pearson's correlation = 1.84 , p -value = $.144$). Turnover values were higher than nestedness values, except for the site located at 1,000 m, which showed a strong nestedness-related pattern (51.2%) (Table 3). In addition, sites at higher elevations showed similar nestedness values when compared to those values found using the species by site approach. The sites at low elevations showed nestedness values two to three times higher when compared to those values found using the species by site approach (Table 3). All nestedness values were higher than and different from those expected by chance.

4 | DISCUSSION

4.1 | Elevational variation in species richness

The occurrence of dung beetle species varied with elevation. Higher values for both richness and abundance of dung beetles were found

	Obs. (%)	Mean _(sim)	2.5%	50%	97.5%	p _(sim)	T _(range) (°C)
Species by site							
Turnover							
200 m	0.834	0.948	0.914	0.950	0.972	.000	3.7 to 32.3
500 m	0.847	0.945	0.911	0.946	0.971	.000	4.7 to 28.5
800 m	0.835	0.965	0.945	0.966	0.981	.000	4.7 to 28.4
1,000 m	0.568	0.928	0.875	0.930	0.965	.000	-1.3 to 24.4
1,300 m	0.745	0.941	0.897	0.942	0.973	.000	-2.3 to 37.3
1,600 m	0.580	0.845	0.712	0.853	0.935	.003	-1.2 to 33.5
Nestedness							
200 m	0.166	0.052	0.028	0.050	0.086	.000	3.7 to 32.3
500 m	0.153	0.055	0.029	0.054	0.090	.000	4.7 to 28.5
800 m	0.165	0.035	0.019	0.034	0.055	.000	4.7 to 28.4
1,000 m	0.432	0.072	0.035	0.070	0.125	.000	-1.3 to 24.4
1,300 m	0.255	0.059	0.027	0.058	0.103	.000	-2.3 to 37.3
1,600 m	0.420	0.155	0.065	0.147	0.288	.003	-1.2 to 33.5
Genera by site							
Turnover							
200 m	0.718	0.871	0.779	0.876	0.940	.005	3.7 to 32.3
500 m	0.515	0.830	0.709	0.842	0.917	.000	4.7 to 28.5
800 m	0.665	0.903	0.837	0.907	0.950	.000	4.7 to 28.4
1,000 m	0.488	0.881	0.787	0.886	0.946	.000	-1.3 to 24.4
1,300 m	0.754	0.902	0.820	0.906	0.956	.004	-2.3 to 37.3
1,600 m	0.580	0.845	0.712	0.853	0.935	.003	-1.2 to 33.5
Nestedness							
200 m	0.282	0.129	0.060	0.124	0.221	.005	3.7 to 32.3
500 m	0.485	0.170	0.083	0.158	0.291	.000	4.7 to 28.5
800 m	0.335	0.097	0.050	0.093	0.163	.000	4.7 to 28.4
1,000 m	0.512	0.119	0.054	0.114	0.213	.000	-1.3 to 24.4
1,300 m	0.246	0.098	0.044	0.094	0.180	.004	-2.3 to 37.3
1,600 m	0.420	0.155	0.065	0.147	0.288	.003	-1.2 to 33.5

Obs. (%)—percentage represented by β -diversity components of the total dissimilarity; Mean_(sim)—mean values of the 9,999 simulations; 2.5%, 50% and 97.5%—the amount of simulated values; p_(sim)—p values; T_(range) (°C)—range of temperature (minimum and maximum).

at intermediate elevations (hump-shaped pattern), but showed an overall decline with elevation. This supports our first hypothesis. Although the decline in species richness with increasing elevation is a widely documented pattern, mid-elevational peaks for species richness have been found for several groups in different biogeographic regions (Rahbek, 1995, 2005).

In the Neotropical region, there are relatively few studies describing elevational patterns of richness and composition of dung beetles. However, some examples include studies from the Mexican Transition Zone (Halffter, Favila, & Arellano, 1995; Lobo & Halffter, 2000; Martín-Piera & Lobo, 1993), Colombian Andes (Escobar, Lobo, & Halffter, 2005; Larsen, Escobar, & Armbrrecht, 2011), Ecuadorian Andes (Domínguez et al., 2015), Peruvian Andes (Larsen, 2012) and southern Brazil (Nunes et al., 2016; and the present study). From these studies and others conducted

TABLE 3 Null model results of the β -diversity components for multiple-month comparisons for each site using species by site and genera by site, and range of ambient temperature. β -diversity components are represented by percentage (%) of total dissimilarity

outside the Americas (e.g. Chamberlain et al., 2015; Hanski, 1983; Hanski & Krikken, 1991; Lumaret & Stiernet, 1991; Martín-Piera, Veiga, & Lobo, 1992; Menéndez et al., 2014), the main conclusion is that dung beetle richness is lower at higher elevations (Lobo & Halffter, 2000). Among these studies, species richness either declines monotonically or shows a mid-peak with increasing elevation. Similar to our study, a hump-shaped richness pattern was also found by Escobar et al. (2005) in the Colombian Andes. These authors attributed this result to the mixing at intermediate elevations of dung beetle assemblages that have different environmental adaptations and origins.

There are different hypotheses to explain the elevational patterns of species richness, which can be summarized into biological, ecological, climatic, geographic and historical hypotheses (Rahbek, 1995). Similar to latitude, elevation is a surrogate for one or more

factors spatially structured, which covary with elevations and are expected to directly influence species richness (Rahbek, 2005). With increasing elevation, there is a decrease in temperature, primary productivity and area availability for occupation. In addition, there may also be changes in habitat complexity, quantity of food resources, interspecific interactions, water balance, moisture and partial pressure of O₂ and CO₂, as well as a higher intensity of ultraviolet radiation (Körner, 2007; Rahbek, 1995). In our study, the contact and mixing of fauna with different tolerances, lineages and histories seem to occur at the 800 m site, where a mix of lowland and highland fauna appears together. Areas at intermediate elevations may also have experienced lower environmental and climatic variations than areas at lower and higher elevations that may have experienced flooding (due to rising sea levels) and glaciations, respectively, during warmer and colder periods in geological time. This may have allowed these areas to have more time to evolve their communities, as postulated by the hypothesis of effective evolutionary time (Rohde, 1992). All these factors, which are not exclusive but reinforcing, may limit, to some extent, the distribution and biology of species living across an elevational gradient (Romdal & Grytnes, 2007).

4.2 | Elevational variation in composition

Contradicting our second hypothesis, the results showed an evident division of species composition between sites at lower and higher elevations, strongly influenced by the turnover component of β -diversity. Like other studies that partition β -diversity into turnover and nestedness-related components (e.g. Nunes et al., 2016), spatial turnover was the main β -diversity component along the elevational gradient. This indicates that highland assemblages are not subsets of lowland assemblages. In fact, lowland and highland fauna formed two distinct groups with a dissimilarity >80% on average. These findings suggest that both environmental filters and/or dispersal limitations may have selected dung beetle species along the different elevational sites. One may consider that the effects of dispersal limitations may be minimal (or non-existent) at the studied scale, especially considering that this group is characterized by colonizing an ephemeral resource and, therefore, has a high dispersal capacity (Hanski & Cambefort, 1991). In fact, some dung beetle species have been documented to fly several hundreds of metres in just a few hours (Arellano, León-Cortés, & Ovaskainen, 2008; Peck & Forsyth, 1982; da Silva & Hernández, 2015b). Thus, it is likely that dung beetle species with marked spatial distributions along the gradient may have been filtered by climatic and/or biotic filters probably related to their thermal tolerance and competition ability.

Interestingly, the predominance of the species turnover component to explain the elevational changes in composition disappears when analyses are conducted at the taxonomic resolutions of genera. In other words, the environmental changes associated with elevation may cause the differential establishment of distinctive species, but these species belong to the same higher taxonomic group. This pattern would be in line with the so-called "vertical colonization" process proposed by Lobo and Halffter (2000). Highland assemblages

will be composed by a fewer number of species, but the likelihood that they have radiated from ancestral species occurring at lower elevations increases if these species belong to the same clade inhabiting lowlands. Therefore, mountains would be inhabited by elements coming from lowlands as a consequence of the acquisition of new environmental adaptations, and not from distant latitudes with similar environmental conditions (horizontal colonization). In line with other studies (Escobar et al., 2005; Lobo & Halffter, 2000; Nunes et al., 2016), our results suggest that the colonization of high mountains by lineages distributed at distant latitudes would have been very difficult. However, the slow evolutionary colonization of clades coming from lower elevations would have been possible. The occurrence of cold, temperate conditions such as those of the studied region within a tropical zone is a factor that promotes isolation and speciation. Hence, the allopatric speciation of mountain dung beetle species could have been facilitated by the ancient origin of Atlantic Forest assemblages and their long evolutionary history. The biotic interchanges with Amazonia during the Miocene (Fouquet et al., 2012), the isolation periods since the Pliocene (Joly, Metzger, & Tabarelli, 2014) or the grassland and climatic expansion/contraction cycles experienced during the Pleistocene (Jeske-Pieruschka, Pillar, De Oliveira, & Behling, 2013) could have also contributed to this pattern.

The pattern of colonization of some dung beetle species in high elevations may be related to the ancient Austral-Antarctic-Andine floristic centre (Rambo, 1951). The high-elevation forests from southern Brazil, especially those represented by the *Araucaria* Forest (mixed ombrophilous forest present between 800 and 1,600 m along the gradient), have plant species with restricted geographical distribution, many of them of temperate origin and with an Andean dispersion centre (Safford, 2007). Some examples include species of *Araucaria* Juss., *Drimys* J.R. Forst. & G. Forst., *Fuchsia* L., *Griselinia* G. Forst., *Gunnera* L., *Podocarpus* L'Hér ex Pers. and *Weinmannia* L., which have strong affinities to environments with mild to cold temperatures and relatively high precipitation regimes, which became an integral part of the southern Cretaceous-Early Tertiary flora of Australia, Antarctica and southern South America (Safford, 2007). In southern Brazil, montane forests expanded their distribution with the contraction of high-elevation grasslands, following the Late Cenozoic climate change (Rambo, 1951; Safford, 1999). This distribution pattern of flora may have directly or indirectly influenced dung beetles via mammalian distributions, the main source of food resources for Scarabaeinae. In our study, *Homocopris* species occurred only between 800 and 1,600 m, while *Eurysternus* and *Phanaeus* occurred only between 200 and 800 m. *Homocopris* has been recently reassigned as a valid genus, with few species under a process of review (Vaz-de-Mello, Génier, & Smith, 2010). Its species were found generally associated with elevation forests or open areas from Argentina, Chile, Colombia, Ecuador and Brazil. In southern Brazil, *Homocopris* species were associated with well-preserved Atlantic Forest sites located at high elevations (in general, above 1,000 m) (Vaz-de-Mello et al., 2010) and perhaps constitute the only example of horizontal colonization within this assemblage. In addition, six

species belonging to *Canthidium*, *Canthon*, *Dichotomius*, *Onthophagus* and *Uroxys* Westwood were distributed only between 800 and 1,600 m, which may represent dung beetle lineages related to cold-humid environments. Furthermore, *Dichotomius opalescens* (Felsche) was collected only at 1,300 m. This species is restricted to the Serra Geral mountain range (northern Rio Grande do Sul and southern Santa Catarina) and is thus considered endangered (EN) according to the conservation status based on the extent of occurrence applied by International Union for Conservation of Nature (Maldaner, Nunes, & Vaz-de-Mello, 2015). The distribution of *D. opalescens* covers three national conservation units in southern Brazil: São Joaquim National Park (one of our study areas), Aparados da Serra National Park and São Francisco de Paula National Forest (Maldaner et al., 2015), all of them encompassing high-elevation environments in southern Brazil. Further molecular analysis may be useful to test the phylogenetic affinities of species present only in lower or higher sites and will help determine the age of these colonizations and/or vicariations.

4.3 | Seasonal variation in composition

Dung beetles were sampled over a complete year at all sites. As expected for a subtropical region, most sites (200–1,000 m) showed high species richness and abundance during the beginning of summer, while the site located at the highest elevation (1,600 m) showed higher species richness values at the end of summer (see Appendix S2: Table S2.3). Similar patterns have been found in other studies carried out in southern Brazil (Hernández & Vaz-de-Mello, 2009; da Silva, Vaz-de-Mello, & Di Mare, 2013), where dung beetle species show a marked seasonality, although occurring throughout the year. In regard to the spatial gradient, temperature is frequently acknowledged as the main factor driving the seasonal variation in dung beetle species richness in southern Brazil, unlike tropical regions, where precipitation is the main factor for the variation in species richness due to the existence of two marked seasons, dry and rainy (Andresen, 2005; Neves et al., 2010).

Our results showed that the turnover component of β -diversity predominates in driving the temporal dissimilarity at each site during the study period. Thus, despite the great difference in species richness between sites, there was a higher turnover of species throughout the year in all sites. However, the relative importance of this temporal turnover was higher for sites located at lower elevations, while sites at higher elevations showed a decrease in turnover importance and an increase in the nestedness-related component of β -diversity. Temperatures below 15°C reduced growth and development rates in insects (Gilbert & Raworth, 1996). Thus, unsuitable temperature conditions are more probable at higher elevation sites. This suggests that seasonal differences in climatic conditions of lowlands would be associated with compositional changes in dung beetle assemblages, and the existence of periods with unsuitable climatic conditions for ectothermic species in high-elevation sites will diminish the likelihood of these areas to be able to harbour low-elevation-adapted species. Additional physiological studies are needed to examine the thermal tolerance of these species, as well

as the relevance of factors other than temperature (e.g. insolation, precipitation, dung availability).

4.4 | Conservation implications

Due to the global warming, species are expected to change their distributions, habitat associations and phenology as the climate warms (Walther, 2010). There is a growing body of evidence showing changes in elevational distributions of species with the increasing warming. Specifically, Larsen (2012) showed that most dung beetle species in the Peruvian Andes occurred farther upslope in a hotter and drier deforested landscape than in a forested one, with the temperature difference (>2°C) between these sites equivalent to 60–100 years of predicted global warming. Menéndez et al. (2014) reported upslope range shifts for 63% and 90% of dung beetle species in two mountain regions in France and Spain, respectively. These range shifts were consistent with the level of warming experienced in each region. Thus, there is a need to improve our understanding of how shifts in species range will affect other species via interactions (e.g. competition, predation and parasitism) at the community level (Berg et al., 2010).

Temperature is acknowledged to be one of the most important environmental factors influencing the distribution of dung beetles, and thermal tolerance probably plays an important role determining their distribution (Gaston & Chown, 1999). For example, Escobar et al. (2005) found more range-restricted dung beetle species at lower elevations. Dung beetle species occurring at higher elevations show greater thermal tolerance ranges than species occurring at lower elevations (Gaston & Chown, 1999) because sites at higher elevations can experience more extreme seasonal and daily temperature variations. However, species living at higher elevations are expected to have a loss of competitive capacity when compared to those that inhabit lower elevations (Escobar, Halffter, & Arellano, 2007; Herzog et al., 2013). If true, changes in upslope range limits of lowland species can cause the local extinction of competitively inferior species at higher elevations, as they may have no escape routes or suitable habitats remaining (Raxworthy et al., 2008). Physiological studies able to estimate the thermal tolerance of species (Helmuth, Kingsolver, & Carrington, 2005) can help elucidate the possible effects of climate change on these assemblages and their capacity to generate elevation shifts and new interactions.

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DATA ACCESSIBILITY

All data used in this paper are included in Appendix S2.

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BIOSKETCH

Pedro G. da Silva conducted this work as part of his post-doctoral research at Universidade Federal de Santa Catarina. His research addresses determinants of community patterns and conservation biology of dung beetles, with emphasis on tropical and subtropical forests and grasslands. Specifically, he is exploring the ecological processes driving diversity patterns of dung beetles at different spatial and temporal scales.

Author contributions: J.M.L. and M.I.M.H. have conceived the manuscript objectives and written the manuscript; P.G.d.S., M.C.H. and M.I.M.H. have performed fieldwork; J.M.L. and P.G.d.S. have proceeded with data analysis and led the writing; F.Z.V.M. has identified the beetles and written the manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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