The role of habitat and daily activity patterns in explaining the diversity of mountain Neotropical dung beetle assemblages

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Abstract The interaction between land use and climate change is expected to strongly affect species distributions along high elevation landscapes. We aimed to test the effect of climatic variables on community metrics among five types of land use in a high elevation landscape. We described dung beetle spatial and temporal taxonomic and functional diversity patterns, and partitioned β-diversity into turnover and nestedness components. The interaction between land use and daily period of activity mostly drives abundance, functional richness and functional diversity, but not dung beetle species richness. Unlike Neotropical lowlands, species richness and abundance in open environments are similar to those existing in forests. Temperature is an important predictor of abundance and functional divergence. There is a higher spatial component of the taxonomic β-diversity, which is highly driven by species turnover. The temporal component of the taxonomic β-diversity was strongly driven by nestedness, where night assemblages are sub-sets, although not entirely, of diurnal assemblages. For functional diversity, the temporal β-diversity was much higher than the spatial β-diversity, but both were similarly represented by functional group turnover and nestedness. The composition of nocturnal and diurnal assemblages is clearly different, even more than the differences observed between habitats. However, taxonomic turnover is the dominant force between sampling sites while nestedness dominates the daily pattern. This means that forest habitats are unlikely to act as shelters for grassland species under a scenario of rising temperature.

Key words: functional diversity, Scarabaeinae, spatial pattern, taxonomic diversity, temporal pattern.

INTRODUCTION

Habitat changes such as conversion, degradation and habitat loss due to human activities are causing global biodiversity declines (Tittensor *et al.* 2014). However, the local response by biodiversity to these changes are less clear but can be very useful to predict global biodiversity responses. Although many of the main drivers of biodiversity loss are detected at the global scale, the most important pressure mechanisms generally act more locally (Brook *et al.* 2013).

Locally, the climate experienced by a species is a key determinant of population growth and an important variable of the fundamental niche space (Hutchinson 1957). Microclimates can differ markedly between different types of habitats (Geiger *et al.* 2003), where forest cover substantially reduces solar radiation at the soil and lowers the temperature compared to open environments (Oliver & Morecroft 2014). Moreover, there also is a buffering effect between ambient and soil temperatures; while surface temperature is cooler during temperature peaks, it is warmer at night in closed environments compared to grasslands (Suggitt *et al.* 2011). Changes in land use are also expected to be a major biodiversity driver near the tropics, while the temperature change is expected to have higher importance towards the poles (Jetz *et al.* 2007). Therefore, studies attempting to unveil the interacting effects of land use and temperature on biodiversity patterns are needed urgently (Oliver & Morecroft 2014) to understand the probable buffering capacity of habitat on temperature effects, especially in the current scenario of global warming (Frey *et al.* 2016).

Temperature has a strong impact on species distributions, especially in poikilothermic or heterothermic insects, such as dung beetles (Schowalter 2011). Dung beetles (Coleoptera: Scarabaeinae) comprise a diverse group of dung and detritus-feeding insects that play a key role in important ecological processes such as decomposition, secondary seed dispersal and nutrient recycling (Nichols *et al.* 2008). They have

long been used as good models to investigate applied and theoretical issues in ecology and conservation because their assemblages are negatively affected by both natural and anthropogenic environmental changes (Nichols *et al.* 2007). In tropical biomes, several scarabaeine beetles are forest-dependent and unable to extend their populations to open areas (Klein 1989), probably due to climatic and resource limitations. Both temperature and precipitation are also known to affect dung beetle distribution spatially and temporally (Hernández & Vaz-de-Mello 2009; Liberal *et al.* 2011; da Silva *et al.* 2013).

Nesting behaviour and body size have been acknowledged to affect dung beetle ecological functions (Slade *et al.* 2007). There is strong evidence of the negative impacts on ecosystem functioning due to the loss of some dung beetle traits in human-driven environments (Braga *et al.* 2013). Tropical primary forests host large dung beetles and body size decreases among individuals of different genera outside this habitat (Gardner *et al.* 2008). Daily activity can also be an important trait since climatic conditions can drive the daily and seasonal activity of dung beetles in environments with extreme climates, having a spatial and temporal effect on the diversity and distribution of species. Therefore, gathering relevant traits are needed for a better understanding of the mechanisms driving the spatiotemporal distribution of species.

As opposed to Palearctic temperate biomes (Hanski & Cambefort 1991; Lobo *et al.* 1998), there is a huge body of evidence that dung beetle diversity is higher in Neotropical forests than in open environments (either natural or artificial) (Scheffler 2005; Gardner *et al.* 2008). A decline in dung beetle ecosystem functions and services is also well documented along those habitat gradients (Braga *et al.* 2013; Batilani-Filho & Hernández 2017). However, there is little information specific to the dung beetle response to changes in human-driven land uses along high elevational Neotropical landscapes (Arellano *et al.* 2005; Aguilar-Amuchastegui & Henebry 2007). In these systems, there is a wide variation in daily and seasonal climatic conditions, which can have different effects on dung beetles depending on the type of land use. Dung beetles also seem capable of using incident radiation differently in order to gain the necessary body heat (Amore *et al.* 2017). Thus, unlike tropical lowlands, under the relatively cold conditions of tropical mountain areas, some species might prefer open environments to acquire the body temperature required for their activities.

Dung beetles can also show differential daily activity patterns (Landin 1968; Koskela 1979; Krell-Westerwalbesloh *et al.* 2004; Iannuzzi *et al.* 2016) probably linked with the capacity of thermoregulation and the management of body temperature (Verdú

et al. 2004; Gallego *et al.* 2018; Giménez-Gómez *et al.* 2018). Thus, it might be expected that night dung beetle assemblages may be a small sub-sample of day assemblages inhabiting temperate-cold conditions in the Neotropical region; i.e. assemblages composed of those species able to deal with low temperatures. However, it may also be possible that closed habitats (e.g. forests) could have buffered temperatures, and therefore, harbour higher species richness and abundance values than open environments (e.g. grasslands) at night, thus being able to act as thermal shelters harbouring species with different functional traits as those present in grasslands. For example, body size can be an essential trait to gain body heat, and roller dung beetles, which roll food-balls above the ground away from the resource, could be more affected by environmental conditions than tunneler species that are more related to soil conditions due to their nesting strategy.

In this study, we examine the differences in species richness, abundance and taxonomic or functional composition among five sites with different land uses along day-night sampling periods at a high elevation landscape in southern Brazil. Day and night dung beetle assemblages were sampled in five sites along a closed-open gradient: primary forest, secondary forest, agroforest, shrubland and grassland. The main purposes of these comparisons are to assess (i) if the general decreasing pattern in dung beetle diversity established for open habitats when compared to forests is maintained when these habitats are located in cold mountainous subtropical regions and (ii) how taxonomic and functional composition of dung beetle assemblages vary with the daily period depending of the habitat type. Additionally, since functional and compositional differences between habitats and daily periods can be due to the replacement (turnover) or gain/loss (nestedness) of species, we estimate the comparative relevance of these two patterns on spatial and temporal assemblage differences because they would have different implications for the shelter role played by forest under an increasing temperature scenario.

METHODS

Study area

The study was performed in a landscape composed of five different types of land uses (called sites from now on; Appendix S1) in the São Joaquim National Park, a Federal Conservation Unit located in the state of Santa Catarina, southern Brazil (28°05′–28°20′S, 49°21′–49°39′W). This conservation unit was created to preserve the *Araucaria angustifolia* forest (also called Mixed Ombrophilous Forest) and high-altitude grasslands located in the Serra Geral mountainous formation. Since the park is located at the top

of a mountainous region, there is a wide variation in temperature, ranging from negative temperatures in the winter to near 40°C in the summer.

The five sampled sites included primary forest, secondary forest, shrubland, agroforest and grassland. Primary and secondary forests were characterized by the presence of *A. angustifolia* with differences in timber harvesting, where the secondary forest suffered selective cutting and has been regenerating for 30–40 years. The shrubland is characterized by isolated trees (*A. angustifolia*) and a high density of *Baccharis uncinella* (Asteraceae), a phanerophyte and woody bush that can reach up to 2 m in height. The grassland consists of species such as *Andropogon lateralis* (Poaceae) and *Baccharis articulata* (Asteraceae), and no trees. Two horses were present in this site during the previous months. The agroforest was composed of both forest and grassland biotic components, with the presence of *A. angustifolia*. The understory is open and grasslands dominate the soil. During the previous months, the cattle herd consisted of about 10 cows and 5 horses. The grassland and agroforest were human-modified land uses, since both were previously *A. angustifolia* forests.

All sites were located at *ca.* 1300 m a.s.l. and with a mean distance of 280 (±103 SD) m between each other. The small distance between the sampling sites is characteristic of the studied landscape. This distance does not limit the colonization and dispersion of the species between sampling sites and, at the same time, is enough to ensure their independence character during the period of study (see da Silva & Hernández 2015b). Since the objective of this study was not to obtain results which can be extrapolated to a particular situation (i.e. grasslands *vs.* forests) we did not include replicates of each habitat type (Peyras *et al.* 2013). Instead, as our objective was to explore the response of species and assemblages to daily periods in series of contrasting habitats, we decided to maximize the number of different habitat in the landscape instead of replicating particular sites (Peyras *et al.* 2013).

Sampling design

Dung beetles were sampled using baited pitfall traps. These traps were made with plastic containers (15 cm diameter × 20 cm depth) buried with the top edge at ground level, a rain protector and a mixture (300 mL) of water and neutral detergent to prevent the escape of beetles. As bait, human faeces and rotting flesh (aged in plastic containers at room temperature 3 days prior to sampling) were used separately (*ca.* 20 g of each) to attract copronecrophagous dung beetles.

Each sampling site contained five pairs of traps spaced 5–10 m apart. Each pair contained both kinds of bait and was considered a sampling unit (the data from each pair were pooled and considered as a sampling unit). The pairs were spaced 100 m apart assuming that this distance is enough to promote independence independently of the vegetation structure (da Silva & Hernández 2015b). The traps remained in the field for a total of 48 h (da Silva & Hernández 2014). The study was conducted in January 2017, which is summer in the region, a period of high richness and abundance of dung beetles

in southern Brazil (Hernández & Vaz-de-Mello 2009; da Silva *et al.* 2013).

We obtained four samples during the study period to characterize diurnal and nocturnal dung beetle assemblages. On day one, we installed the traps in all sampling sites between 6.00–7.30 hours in the morning. All beetles sampled during the day were removed between 18.30–20.00 hours. The next morning, between 6.00–7.30 hours, all beetles sampled during the night were removed and the baits renewed. The same was done for day two, totalling two samples of diurnal and two samples of nocturnal dung beetles in each sampling site. Thus, in total, we managed information coming from 100 samplings units (5 sampling units × 5 sites × 2 days × 2 periods). The beetles collected were sorted, identified and conserved in 70% alcohol. An expert, Dr. Fernando Vaz-de-Mello (Universidade Federal de Mato Grosso, Brazil), confirmed species identifications. The beetles were deposited in the Entomological Collection of the Universidade Federal de Santa Catarina and the Zoological Collection of the Universidade Federal de Mato Grosso, Brazil.

Dung beetle attributes

In order to characterize dung beetle functional attributes, all species were grouped according to their nesting behaviour (tunneler, roller or dweller), daily activity (diurnal, nocturnal or diurnal-nocturnal) and body size (small and large-sized). Nesting behaviour was attributed according to the literature (Halffter & Edmonds 1982; da Silva & Hernández 2015a). Daily activity (diurnal or nocturnal species) was attributed following the criteria of ≥95% of individuals sampled in one daily period of activity. Species with a similar number sampled in both periods were grouped as diurnal-nocturnal species. Data from literature were also consulted for species with less than 10 individuals to corroborate the species grouping (Hernández 2002; Lopes *et al.* 2011; da Silva & Hernández 2015a). Species with less than 1 cm in length were grouped as small-sized, while species with a length ≥1 cm were grouped as large-sized (Escobar *et al.* 2008).

Climatic predictors

To characterize the climatic conditions experienced by dung beetles during day and night, we used data loggers to record measurements of temperature at 15 min intervals during the samplings. We installed two data loggers at the third sampling point in each site, the first at 1 m above the soil (in a shaded location) and the other buried in the soil (5 cm). In additional, we installed a pluviometer to record the rain during the samplings.

Using the temperature measurements, we calculated mean, minimum, maximum and range of temperature for each sampling period (two days and two nights separately), for both ambient and soil. After standardization of all these climatic variables to eliminate the effect of measurement scale differences (to a mean of zero and standard deviation of one), they were subjected to a Principal Component Analysis to select those uncorrelated. Three uncorrelated

components with eigenvalues higher than one were obtained and together were able to explain 91.4% of the total variability (50.7%, 24.7% and 16.0%, respectively). Three variables with the highest factor loadings (fl) were selected for each of the components: minimum ambient temperature for the first PCA component (fl = 0.946), maximum soil temperature for the second PCA component (fl = 0.900) and precipitation for the third PCA component (fl = −0.875). These three climatic predictors were selected as co-variables in order to assess the differences in biodiversity measurements between sampling sites (primary forest, secondary forest, agroforest, shrubland and grassland) and daily period of activity (day or night) when the effect of these climatic predictors was controlled (see Appendix S2).

Statistical analyses

We first estimate the completeness of the obtained assemblages by calculating the final slope (coverage) of the species accumulation curves relating the increase in the number of species with the addition of individuals. To do that, the function 'iNEXT' of the R package 'iNEXT' was used (Hsieh *et al*. 2016). In additional, the Chao1 non-parametric estimator (Chao 1984) was also calculated to estimate the 'true' number of species in each site taking into account the number of species represented by just one or two individuals (singletons and doubletons). These calculations were conducted with the sole aim of assuring that the comparison of the obtained assemblages is not excessively biased.

Besides species richness and abundance of dung beetles, we used two metrics able to represent different aspects of functional diversity: functional richness (*FRic*) and functional divergence measured by using the Rao quadratic entropy (*Rao's Q*). *FRic* represents simply the number of unique trait combinations (Villéger *et al*. 2008), while *Rao's Q* characterizes the dispersion of species in the trait space weighted by their relative abundance (Laliberté & Legendre 2010). The complementary use of these two functional metrics allow us to examine the between-site differences in the number of functional attributes that the collected species possess, but also to compare the degree of functional variability present in each site. *FRic* was measured for each period using all sampling sites and the 'dbFD' function of the R package 'FD' (Laliberté *et al*. 2014). To estimate *Rao's Q* a species dissimilarity matrix was first created based on the formerly described functional attributes by using the 'Gower approach' from the 'trova' function (see de Bello *et al*. (2013) for details) for R software on the data of each sampling period and sampling site. We used the 'Rao' R function (de Bello *et al*. 2009) that calculates the Rao quadratic entropy taking into account Jost's correction (Jost 2007). This metric represents the number of equivalent species (in terms of abundance) sharing no functional traits (minimum value = 1) and is maximal when all species in a sampling unit are maximally dissimilar and have equal abundances (Nunes *et al*. 2016). *FRic* and *Rao's Q* are not correlated (Pearson's correlation = 0.32, $t = 1.427$, $P = 0.170$).

Generalized Linear Mixed Models (GLMMs) were used to estimate whether the four response variables (species richness, abundance (in Log), *FRic* and *Rao's Q*) significantly vary between the five sampling sites (spatial scale) and the two daily periods of activity (temporal scale). The effect of these two categorical factors on these response variables was evaluated, including the interaction between them (sampling sites × daily periods), as well as the three formerly selected climatic variables as covariates. Since we did not have replicates of sites, we used the traps as sample units repeatedly sampled over two days and two nights at the same site. We, therefore, included traps and sampling periods as random factors to account for pseudoreplication. The GLMMs were ran using the function 'glmer', 'glmer.nb' and 'lmer' of the R package 'lme4' (Bates *et al*. 2015) for *Rao's Q* (Gaussian distribution), abundance (negative binomial distribution) and species and functional richness (both using Poisson distribution), respectively.

As two sites can have similar species richness, abundances and functional diversity values, but may differ in their faunistic compositions, additional analyses were carried out to examine the compositional changes between sampling sites and daily periods ($N = 20$). This has been done by calculating a permutational multivariate analysis of variance (PERMANOVA; (Anderson 2001); a non-parametric multivariate statistical test used to analyse differences between two or more groups or factors (and their possible interactions) based on any distance or similarity measure. The Jaccard coefficient was used to perform the similarity matrix and the 'adonis' function of the 'vegan' R package (Oksanen *et al*. 2016) used to carry out calculate PERMANOVA tests. The so obtained results were graphically depicted by using a non-metric multidimensional scaling (NMDS) representation.

Some complementary analyses have been carried out in order to discriminate the comparative role of the two studied scales (spatial or daily) in explaining the taxonomic and functional composition of the complete regional dung beetle assemblage. To do this, an analysis of additive partitioning of diversity (β = γ–α) was used. The taxonomic alpha diversity (α) represents species richness by sampling site per daily period of activity, while the functional α diversity represents the number of equivalent species (in terms of abundance) sharing no functional traits (minimum value = 1). The taxonomic beta diversity (β) represents the composition differences between sampling site per daily period, while functional β diversity represents the addition of new functional diversity when pooling different communities together. Finally, the taxonomic gamma diversity (γ) represents the total species richness of all sites sampled, while the functional γ diversity represents the total functional diversity of all sites sampled. Therefore, we will have two α, β and γ diversity values, one representing the spatial scale ($\beta_S = \gamma_S–\alpha_S$) and the second representing the daily activity scale ($\beta_T = \gamma_T–\alpha_T$). For taxonomic diversity, we used the function 'adipart' of the 'vegan' R package (Oksanen *et al*. 2016), performing 999 permutations to test for statistical differences between observed and expected values of α, β (spatial and temporal) and γ diversity at random. The *Rao's Q* function described earlier also provides the partition of α, β and γ functional diversity components, which provides standardized results to compare the partition of different facets of diversity (i.e. taxonomic and functional) (de Bello *et al*. 2009). Using the hierarchical null model test,

performed by the 'hiersimu' function of the 'vegan' R package, we used the same levels as the 'adipart' R function to test the functional diversity partitioning among spatial and temporal scales with 999 permutations. It allowed us to test for statistical differences between observed and expected values of α, β (spatial and temporal) and γ functional diversity at random.

Finally, the difference in diversity (both taxonomic and functional) between sampling sites (spatial β) or along the daily periods of activity (temporal β) can be due to species turnover (species replacement) or nestedness (species gain or loss) (Baselga 2010). An analysis of β diversity partitioning was performed to test if the spatial and temporal β diversities are a result of species substitution or gain/loss, using the 'beta.multi' function for taxonomic diversity and 'functional.beta.multi' for functional diversity from the 'betapart' R package (Baselga & Orme 2012) and the Jaccard coefficient for both diversities. For functional diversity, we first performed a principal coordinate analysis (PCoA) on a Gower dissimilarity matrix of species traits, using the 'pcoa' function of the 'ape' R package with the 'Lingoes' correction for negative values (Legendre & Legendre 2012). The PCoA eigenvectors were then used to calculate functional turnover and nestedness since this transformation preserves the original distance among objects. As the proximity between the sampling sites may be affecting these calculations, we calculated Euclidean distances among sample units and used Mantel tests (with 999 permutations) to correlate β diversity metrics and geographic distance. To do that, the 'beta.pair' function of the 'betapart' package was used calculating pairwise Jaccard dissimilarity (1-similarity), turnover, and nestedness values among samples to test if there is a spatial autocorrelation because of the relatively small distance among sampling sites.

RESULTS

We sampled 1428 individuals belonging to 19 species (Appendix S3). The values of sample coverage for the five sites were high, ranging between 0.992 and 1.000, except in the case of the grassland site (0.988) (Appendix S3). Thus, the probable total number of species hardly differs from the one observed for most

sites, except in the case of grassland where eight more species could be expected according to Chao1 estimator (Appendix S3). Species richness ranged between 10 and 15 species, while abundance ranged between 202 and 377 individuals by sampling site. A total of 18 species (94.7%) were sampled during the day, while only nine species (47.4%) were sampled during the night. We sampled 7.3 times more individuals ($N = 1257$) during the day than at night ($N = 171$). Among sampling sites, we sampled between 5 and 13 species (mean 8.6 ± 2.8 SD) during the day, but only between 1 and 4 species (mean 2.9 ± 1.3 SD) during the night. From all the species, only one (0.1%) was a doubleton, while four (21.1%) were found in all sampled sites.

Species richness, abundance and functional differences

The statistically significant interaction between sampling sites and daily activity period was important to explain dung beetle abundance, functional richness and functional divergence (Rao's Q), but not species richness (Table 1). Species richness differed significantly only between daily periods, with three times more individuals sampled per trap during the day, on average (Fig. 1). There were more individuals sampled during the day for open grassland and secondary forest (Fig. 2). Functional richness was lower in grassland and agroforest sites (predominance of diurnal, small-sized rollers and tunnelers) and does not differ between day and night except for the secondary forest site (Fig. 2). However, functional divergence seems to be low in open sites but high in the forest at night, where a slightly opposed pattern appears in the case of diurnal assemblages (Fig. 2). This pattern is found because of the occurrence of the large-sized roller and both small- and large-sized tunneler species in the primary forest site at night. The significant role of minimum ambient temperature reveals that a

Table 1. Effect of site, daily period, their interaction and climatic variables on each dung beetle response variable (richness, abundance, functional richness [FRic] and functional divergence [Rao's Q]). Results are based on generalized linear mixed models using repeated measures of traps along daily periods in each site. The chi-square tests were used for richness, abundance and functional richness, while the F test was used for Rao's Q. The climatic variables of minimum ambient temperature (T^a_Mamb), maximum soil temperature (T^a_Msoil) and precipitation are used as co-variables. *$P < 0.01$, **$P < 0.001$, ***$P < 0.0001$; NS, Non Significance

	Site df(4, 87)	Period df(1, 87)	Site*Period df(4, 87)	T^a_Mamb df(1, 87)	T^a_Msoil df(1, 87)	Precipitation df(1, 87)
Richness	5.771[NS]	4.489*	7.458[NS]	2.636[NS]	0.194[NS]	0.219[NS]
Abundance	14.272*	3.399[NS]	49.057***	12.483**	0.593[NS]	0.087[NS]
FRic	21.972***	0.014[NS]	13.348**	0.700[NS]	0.039[NS]	1.035[NS]
Rao's Q	45.891***	6.724[NS]	211.149***	67.597***	0.266[NS]	2.201[NS]
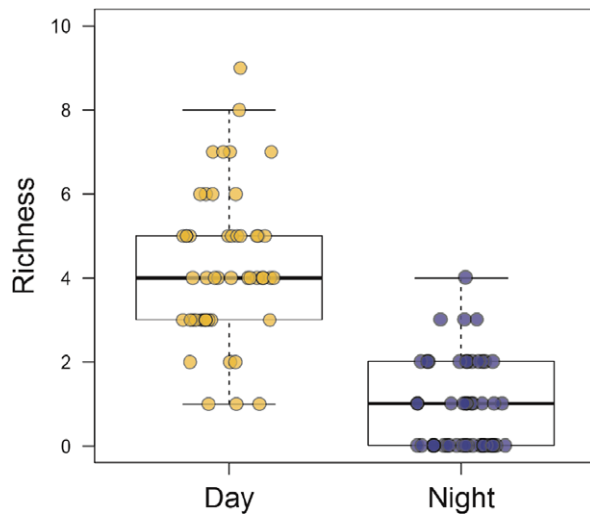
Fig. 1. Richness (median and quartiles) of dung beetles by daily periods. Dots represent species richness for each trap regardless of the site (see Table 1). [Colour figure can be viewed at wileyonlinelibrary.com]

higher abundance and functional divergence can be obtained when the temperature increases (Table 1). Maximum soil temperature and precipitation did not affect any of the dung beetle metrics.

Compositional differences

The interaction between sampling site and daily period did not significantly influence the community composition of dung beetles in the studied system (PERMANOVA $F = 1.602$, $P = 0.095$). However, dung beetle composition changed between sampling sites (PERMANOVA $F = 3.138$, $P = 0.003$, $R^2 = 25.9\%$; Fig. 3), but mainly between daily periods (PERMANOVA $F = 19.554$, $P = 0.001$, $R^2 = 40.3\%$). No differences in the variances of the groups were found by sampling site (PERMDISP $F = 0.345$, $P = 0.843$) or daily period (PERMDISP $F = 4.137$, $P = 0.056$).

The role of site and daily periods in explaining the diversity

The mean taxonomic α diversity sampled for the daily period of activity at each site was 7.3 species, which was lower than expected by chance. The taxonomic β diversity among sampling sites (spatial scale) was higher than among daily periods (temporal scale). The spatial component of taxonomic β diversity was 2.3 times higher than expected by chance, while the temporal component was similar to that expected by chance (Fig. 4a). At the spatial scale, the dissimilarity among sampling sites was 64.4%, mostly represented by species turnover, which accounted for 87.7% of the value. The nestedness-related component only accounted for 12.3% of the spatial β diversity. However, at the temporal scale taxonomic β diversity was 57.9%, mostly represented by species nestedness, which accounted for 65.5% of the dissimilarity between day and night assemblages. The turnover component represented only 34.5% of the
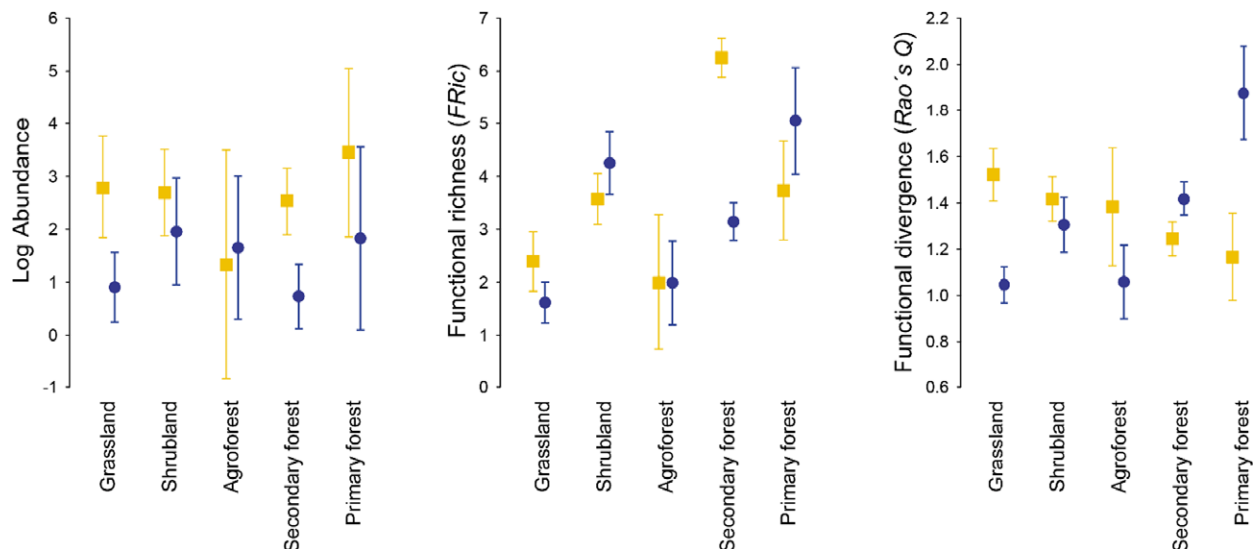
Fig. 2. Results of GLMM models showing the adjusted means (± 95% CI) of the response variables for which the interaction term 'sampling sites × daily periods' is statistically significant (see Table 1). Adjusted means derived from GLMM models controlling for the effects of the selected climatic variables. Night = circles, Day = squares. [Colour figure can be viewed at wileyonlinelibrary.com]
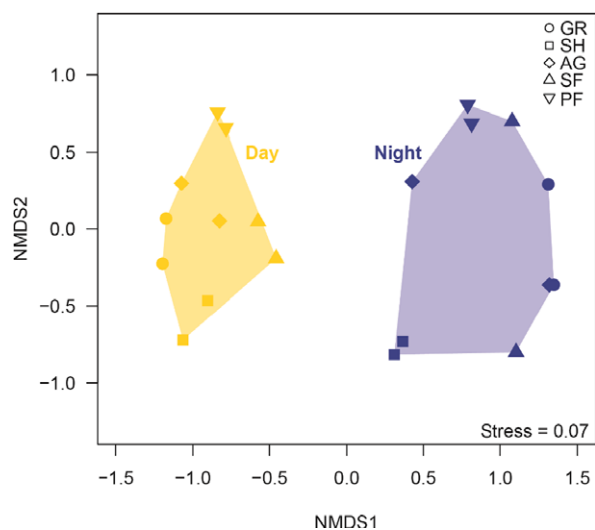
Fig. 3. Dung beetle composition among the five sampling sites during the day and night periods. Sites: AG, agroforest; GR, grassland; PF, primary forest; SF, secondary forest; SH, shrubland. [Colour figure can be viewed at wileyonlinelibrary.com]

temporal β diversity (Fig. 4b). There was no correlation between the geographic distance among sampling sites and Jaccard dissimilarity (Mantel $r = 0.072$, $P = 0.114$), species turnover (Mantel $r = 0.073$, $P = 0.164$) and the nestedness-related component of β diversity (Mantel $r = -0.044$, $P = 0.730$) (Appendix S4).

The functional γ diversity was mostly composed of the temporal β diversity of functional groups, which was 4.6 times higher than the spatial β diversity of functional groups (Fig. 4c). All diversity components were different from what was expected by chance. Functional α diversity was lower than the expected value, while both β diversities were 17.8 and 38.5 times higher than the expected values for temporal and spatial functional β diversities. Spatially, β diversity was composed equally of functional turnover and nestedness among sampling sites. Temporally, the functional turnover was slightly higher than functional nestedness, accounting for 58.6% of the functional β diversity in the day and night assemblages (Fig. 4d).

DISCUSSION

Our results revealed that (i) there is no decreasing pattern in dung beetle richness and abundance in open habitats when compared to forests in a cold mountainous subtropical region. In addition, (ii) the interaction between habitat and daily period of activity mostly drives abundance, functional richness and functional diversity, but not dung beetle species richness. (iii) There is a decrease in functional divergence along the open-closed gradient during the day

and an opposed pattern during the night. (iv) For taxonomic diversity, there is a high species turnover spatially, and a nested pattern temporally, where night assemblages are sub-sets, although not entirely, of daytime diurnal assemblages. (v) For functional diversity, the temporal β-diversity was much higher than the spatial β-diversity, but both were similarly represented by functional group turnover and nestedness. Finally, (vi) the composition of nocturnal and diurnal assemblages is clearly different, even more than the differences observed between habitats.

Of course, all these results may be dependent on the characteristics of the survey design carried out, specifically due to the apparent short sampling period used to collect the handled data (48 h pitfall traps placed during two days in a summer month). However, recent results demonstrate (da Silva *et al*. 2018) that the surveyed period is the one in which a higher species richness and abundance of dung beetles can be collected in this locality; around 71.4% of the total annual species richness can be collected in a short-term survey like the one carried out. Therefore, dung beetle data coming from short-term samplings are used to provide strongly supported results (e.g. Gardner *et al*. 2008; Solar *et al*. 2015). Nevertheless, further studies may allow to corroborate the detected patterns and to determine the role played by seasonal variations in these patterns.

Dung beetle diversity in Neotropical grasslands may depend on elevation

Unlike Neotropical lowlands (Klein 1989; Scheffler 2005), dung beetle species richness and abundance in open environments located in the sampled tropical mountain are not significantly lower than those existing in closed and forest habitats, as previously expected (Hanski & Cambefort 1991; Lobo *et al*. 1998). Moreover, taking into account the estimated richness (Chao1), it is possible that human-driven grasslands have a high number of undetected species according to the accomplished survey effort. In São Joaquim National Park, there are records of several other dung beetle species not sampled in our study that can be found in high elevation grasslands located above 1600 m a.s.l. (Vaz-de-Mello *et al*. 2014; da Silva 2017). Therefore, the expected richness in open environments in this mountainous landscape may be quite higher than in closed forests. Thus, Neotropical open habitats would act as temperate ones facilitating an increase in taxonomic and functional diversity of dung beetles, perhaps for historical reasons related to the relationship between high elevation grasslands and Pampas biome (a grassland-dominated ecosystem found in southern Brazil, Uruguay and eastern Argentina; see below) and/or evolutionary causes. Lowland
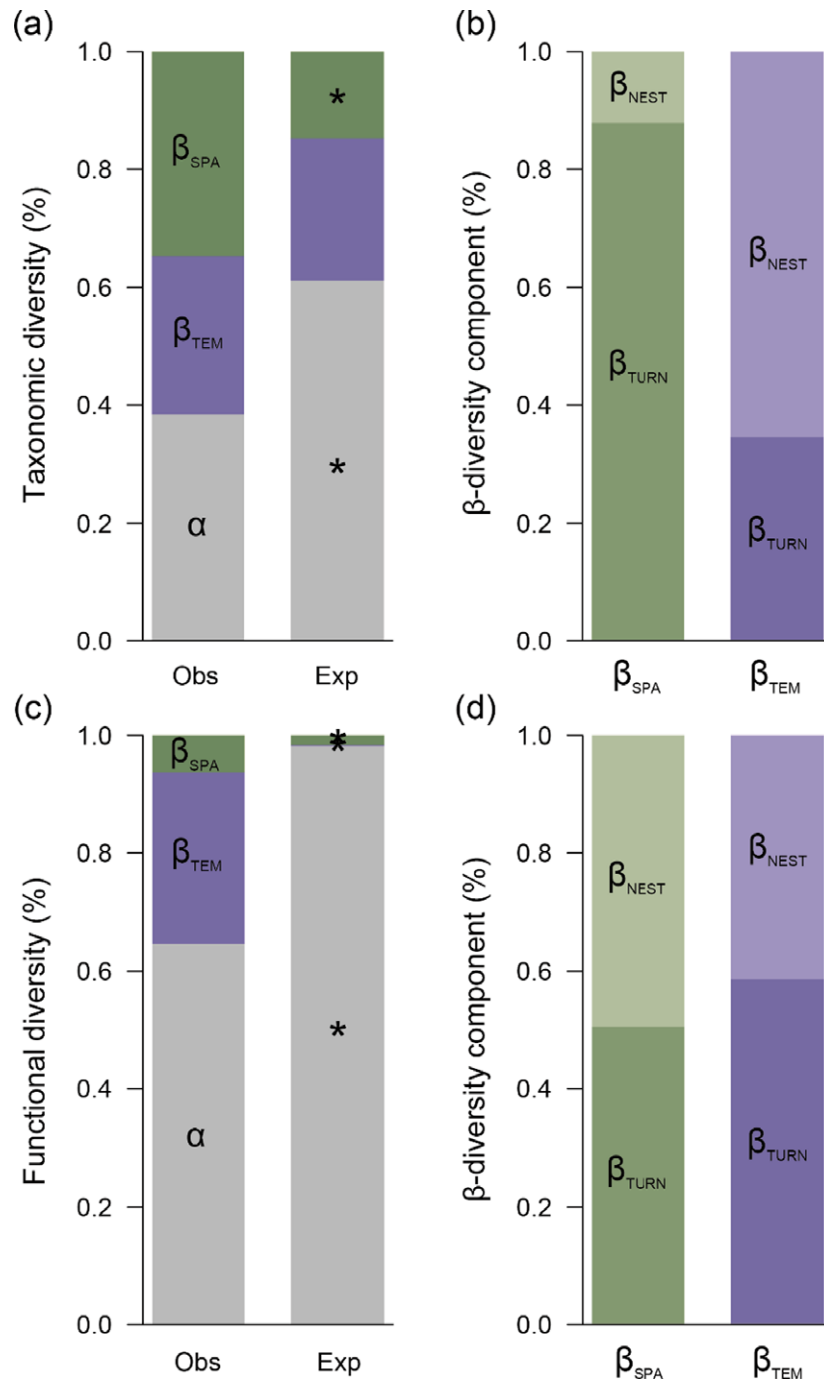
Fig. 4. Taxonomic (a-b) and functional (c-d) diversity partitioning (α, β, γ) among spatial (land uses; SPA) and temporal (sampling periods; TEM) scales (a,c), and β diversity partitioning into its turnover (turn) and nestedness-related (nest) components (b,d). Asterisks indicate statistical differences between observed (Obs) and expected (Exp) values. Taxonomic and functional β diversities were partitioned into turnover and nestedness components spatially and temporally. [Colour figure can be viewed at wileyonlinelibrary.com]

dung beetle lineages could have evolved to inhabit cold conditions existing in tropical high elevation biomes by acquiring appropriate physiological mechanisms to manage their body temperature mainly under diurnal situations (the so-called 'vertical' colonization proposed by Lobo and Halffter (2000)).

The role of daily activity patterns

Species richness is substantially different between day and night, and there is a significantly high number of individuals collected during the day in the grassland compared to closed habitats. The grassland had the

highest values of average temperature and temperature range between day and night among all habitats, including temperatures below 15°C during the summer nights (Appendix S2), which is considered a temperature where several dung beetle species are unable to warm their flight muscles (Verdú *et al.* 2006). Furthermore, the maximum temperature in some open sites reached 40–42°C (Appendix S2), a maximum tolerated temperature that generates strong physiological flight constraints (Verdú *et al.* 2006). The maximum temperature did not exceed 25–30°C in primary and secondary forests (Appendix S2), a temperature range needed for successful and physiologically unconstrained flights in endothermic dung beetles (Verdú *et al.* 2006). Three species dominated and accounted for 91.1% of the day assemblages in grasslands: *Dichotomius opalescens* (44.4%), *Canthon seminitens* (23.7%) and *Canthon rutilans rutilans* (23.1%). These species are all colourful beetles (see Appendix S3), and therefore, are expected to be diurnal (Hernández 2002), which our results corroborated. In laboratory conditions, Amore *et al.* (2017) found that *C. rutilans rutilans* and *D. opalescens* had low heating rates compared to lowland species, regardless the source of radiation (infrared or simulated sun radiation). In addition, the heating rates of those species did not differ from that found in *Homocopris* sp., a nocturnal, black-coloured dung beetle that inhabits primarily high elevation forests (Amore *et al.* 2017). These results suggest that, in similar climatic conditions along the open-closed habitat gradient, both coloured and black dung beetle species are able to reach similar internal temperatures and heating rates. However, our results showed that temperature has different extreme values between open and closed habitats considering day-night conditions. Therefore, due to the differences in extreme temperature values among sites, dung beetle species may require climate-driven conditions that occur during different daily periods along the open-closed habitat gradient.

High abundances in open habitats during the day were also found by Iannuzzi *et al.* (2016), who evaluated the daily activity of dung beetles in a northern tropical Atlantic Forest. However, our results for forest habitats diverge from those found by these authors, who sampled lower abundance in diurnal periods. Dung beetles tend to exhibit adaptations that favour the occupation of both cooler and warmer periods of the day (Hernández 2002; Scholtz *et al.* 2009; Amore *et al.* 2017), especially in landscapes with harsh climatic conditions, such as mountainous regions. Since most dung beetles are poikilothermic, their small body size assists in thermoregulation during the day, favouring both the gain (in cooler periods, such as mornings) and exchange (in warmer periods, such as midday) of heat with the

environment (Feer & Pincebourde 2005; Scholtz *et al.* 2009). In addition, rollers are expected to exploit the resource more quickly than tunnelers to avoid strong competition and predation; thus, they can overcome wind, luminosity and temperature constraints in open environments (Krell *et al.* 2003). The predominance of distinct functional groups among habitats increases the landscape γ diversity.

There was an increase in day-night functional richness along the extremes of the open-closed gradient (two nocturnal, tunneler species found in the grassland and five roller and tunneler species of small and large body size found in the forest at night). A similar pattern was also found by Gómez-Cifuentes *et al.* (2017), who evaluated four types of land uses in relation to dung beetle functional richness and diversity in a northern Argentinean Atlantic Forest. However, this pattern was maintained only for night assemblages when using Rao functional divergence index. Our findings contradict those found by Barragan *et al.* (2011), who evaluated the functional diversity of dung beetles under different conditions of land use in three Mexican biosphere reserves, including pastures, forest fragments and continuous rainforest. The values of functional measurements seem to be much more directly related to factors representing day-night and site variations than climatic predictors. This is also reflected by the high temporal functional β diversity, where temporal and site characteristics exercise a strong influence on the functional diversity of dung beetle assemblages. Therefore, dung beetle functional response may vary depending on the daily period of activity but is independent of functional group richness for diurnal assemblages.

Spatial and daily complementarity of dung beetles assemblages

The faunistic composition of diurnal and nocturnal assemblages is clearly different, more so than the differences observed between sites. However, faunistic turnover is the dominant force between sampling sites while nestedness dominates the daily period of activity. Thus, although there are no differences in richness, there are different assemblages inhabiting each habitat. For example, only five species were shared between grassland and primary forest, with high contrasting patterns of abundance between these habitats (Appendix S3). Given the high contribution of species replacement among sites, our expectation that forest sites would be thermal shelters for grasslands species was not corroborated (see below) because each site have their own particular species. However, the relevance of nestedness patterns in daily variations indicates that there is a loss of species between day and night, where nocturnal assemblages

are a fraction of diurnal assemblages, except in the case of *Homocopris* sp. and *Uroxys terminalis*, which seem to be almost exclusively nocturnal species (but related to forested sites). This change in species according to the daily activity does not have the same effect on all functional groups. With the exception of *Deltochilum brasiliense*, all other rollers are small-sized diurnal species. In nocturnal assemblages, there is a loss of both small-sized rollers and small-sized tunnelers, represented by all species of *Canthon* and most species of *Canthidium*. Another pattern found in our study is that the few species that inhabit forests are functionally singular, while in pastures there are several redundant species. This finding is contrary to Barragan *et al.* (2011), who found that in fragments and continuous forests most species were redundant, with functional uniqueness found in pastures. Functional nestedness was the main pattern among dung beetle assemblages along an elevational gradient in southeast Brazil (Nunes *et al.* 2016), implying that there is a loss of functional diversity from lowlands to highlands. Moreover, we show that both turnover and nestedness of functional diversity of dung beetles similarly drive the daily pattern of these insects, with contrasting responses among open and closed habitats. Dung beetles are a diverse dung and detritus-feeding insect group that exhibits strong competitive behaviour for ephemeral food resources, and therefore evolved different feeding and nesting strategies to avoid intraspecific and interspecific competition and predation (Halffter & Edmonds 1982; Hanski & Cambefort 1991). In addition, dung beetles perform their activities during different periods of the day and year due to factors such as temperature and precipitation (Hanski & Cambefort 1991). The combination of spatial and temporal segregation and the complementarity of their respective assemblages is attributed as one of the main factors driving the γ diversity of this group.

In our landscape, three species are forest-dependent, *Canthon* aff. *luctuosus*, *Deltochilum brasiliense*, and *Dichotomius* aff. *acuticornis*, occurring only in secondary and primary forests. All other species are matrix-tolerant species, but several of them are also related to natural open ecosystems, such as high elevation grasslands and the Pampas biome, as found by da Silva (2017). This author highlights that ~90% of the species found in high elevation grasslands in the São Joaquim National Park is shared with the Pampas. The high similarity found between these ecosystems is probably due to the biogeographic history of southern Brazil. Between 42–10 thousand years ago, cold, dry weather prevailed and the grassland formations dominated the region (Boldrini 2009). Between 10–4 thousand years ago, the temperatures increased, but the climate remained dry, thereby limiting the expansion of forest areas onto the grasslands. There

is evidence of more frequent fires, which also slowed the advance of tree species (Behling *et al.* 2004). Four thousand years ago, when the climate became wetter, the *Araucaria* and Semidecidual forests began a gradual process of expansion over the grasslands, which became more significant around a thousand years ago (Behling *et al.* 2004). Nowadays, dung beetle fauna from both high elevation grasslands and Pampas are spatially segregated. With the arrival of humans, both *Araucaria* logging, as well as the introduction of livestock into open areas changed the landscape of the mountains in southern Brazil to become mosaics of different types of land use (Mello & Peroni 2015).

Conservation implications

In the current scenario of global warming, the predicted future geographical distribution of the *Araucaria* forest based on a fundamental niche modelling (i.e. based on climate variables) shows a strong tendency to reduce their potential area in Brazil, especially in regions at lower latitudes and elevations (Wrege *et al.* 2017). The distribution of the *Araucaria* forest is strongly related to cooler temperatures and higher humidity in southern and southeast Brazil, covering areas up to 2400 m a.s.l. (Behling *et al.* 2004; Wrege *et al.* 2017). However, predicted scenarios of climate warming in South America suggest a great reduction in precipitation in the southeast of Brazil until 2100 (Chou *et al.* 2014). This scenario can severely affect the distribution of the *Araucaria* forest in our study region, where this forest formation does not surpass 1800 m a.s.l. (Behling *et al.* 2004). Although this forest has undergone advances and retractions in its area of occurrence over time, such changes have been relatively slow when compared to the current warming scenario (the predicted increase in air temperature from 1.8 to 6.3°C) (Wrege *et al.* 2016). Therefore, for long life-cycle species, such *A. angustifolia*, the process of adaptation should be much slower than expected (Hamrick 2004), and the loss of *Araucaria* forest can cause an irreversible loss of species of high conservation and functional importance.

In summary, both habitat type and daily period of activity drive dung beetle composition, abundance, functional richness and functional diversity. Average ambient temperatures also influence dung beetle abundance and functional divergence. There is an increase in functional richness along the open-closed gradient in the mountainous landscape, but the functional divergence is higher in open habitats during the day and in closed habitats at night. Spatially, there is high taxonomic species turnover, while nestedness predominates temporally. For functional

divergence, both turnover and nestedness are equally important. In the near future, microclimatic conditions may be affected as much by the change in land use as by climate change (Pyke 2004). Due to the probable increase in average temperatures because of climate warming in all environments including closed habitats, the prevalence of a high functional diversity assemblage of dung beetles at night, plus the buffering effect provided by closed habitats, forest-dependent species are expected to experience low effects due to climate warming per se. However, since changes in land use are driven by both socioeconomic and climatic factors (Oliver & Morecroft 2014), and the predicted future scenario of *Araucaria* forest is quite pessimistic (Wrege *et al.* 2017), the interaction between climate and human land use can cause pronounced negative effects in forest-dependent species inhabiting high elevation forests if their habitat is drastically changed or lost.

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REFERENCES

Aguilar-Amuchastegui N. & Henebry G. M. (2007) Assessing sustainability indicators for tropical forests: Spatio-temporal heterogeneity, logging intensity, and dung beetle communities. *For. Ecol. Manage.* **253,** 56–67.

Amore V., Hernández M. I. M., Carrascal L. M. *et al.* (2017) Exoskeleton may influence the internal body temperatures of Neotropical dung beetles (Col. Scarabaeinae). *PeerJ* **5,** e3349.

Anderson M. J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral. Ecol.* **26,** 32–46.

Arellano L., Favila M. E. & Huerta C. (2005) Diversity of dung and carrion beetles in a disturbed Mexican tropical montane cloud forest and on shade coffee plantations. *Biodivers. Conserv.* **14,** 601–15.

Barragan F., Moreno C. E., Escobar F. *et al.* (2011) Negative impacts of human land use on dung beetle functional diversity. *PLoS ONE* **6,** e17976.

Baselga A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* **19,** 134–43.

Baselga A. & Orme C. D. L. (2012) betapart: an R package for the study of beta diversity. *Methods Ecol. Evol.* **3,** 808–12.

Bates D., Maechler M., Bolker B. *et al.* (2015) Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67,** 1–48.

Batilani-Filho M. & Hernández M. I. M. (2017) Decline of ecological functions performed by dung beetles in areas of Atlantic Forest and contribution of rollers and tunnellers in organic matter removal. *Environ. Entomol.* **46,** 784–93.

Behling H., Pillar V. D., Orlóci L. *et al.* (2004) Late Quaternary Araucaria forest, grassland (Campos), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **203,** 277–97.

de Bello F., Lavergne S., Meynard C. N. *et al.* (2009) The partitioning of diversity: showing Theseus a way out of the labyrinth. *J. Veg. Sci.* **21,** 992–1000.

de Bello F., Carmona C. P., Mason N. W. H. *et al.* (2013) Which trait dissimilarity for functional diversity: trait means or trait overlap? *J. Veg. Sci.* **24,** 807–19.

Boldrini I. I. (2009) Introdução. In: *Biodiversidade dos campos do planalto das araucárias* (ed I. I. Boldrini) pp. 7–11. MMA, Brasília, DF.

Braga R. F., Korasaki V., Andresen E. *et al.* (2013) Dung beetle community and functions along a habitat-disturbance gradient in the Amazon: a rapid assessment of ecological functions associated to biodiversity. *PLoS ONE* **8,** e57786.

Brook B. W., Ellis E. C., Perring M. P. *et al.* (2013) Does the terrestrial biosphere have planetary tipping points?. *Trends Ecol. Evol.* **28,** 396–401.

Chao A. (1984) Nonparametric estimation of the number of classes in a population. *Scand. J. Stat.* **11,** 265–70.

Chou S. C., Lyra A., Mourão C. *et al.* (2014) Assessment of climate change over South America under RCP 4.5 and 8.5 downscaling scenarios. *Am. J. Clim. Change* **3,** 512–25.

Escobar F., Halffter G., Solís Á. *et al.* (2008) Temporal shifts in dung beetle community structure within a protected area of tropical wet forest: a 35-year study and its implications for long-term conservation. *J. Appl. Ecol.* **45,** 1584–92.

Feer F. & Pincebourde S. (2005) Diel flight activity and ecological segregation within an assemblage of tropical forest dung and carrion beetles. *J. Trop. Ecol.* **21,** 21–30.

Frey S. J. K., Hadley A. S., Johnson S. L. *et al.* (2016) Spatial models reveal the microclimatic buffering capacity of old-growth forests. *Sci. Adv.* **2,** e1501392.

Gallego B., Verdú J. R. & Lobo J. M. (2018) Comparative thermoregulation between different species of dung beetles (Coleoptera: Geotrupinae). *J. Therm. Biol* **74,** 84–91.

Gardner T. A., Hernández M. I. M., Barlow J. *et al.* (2008) Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. *J. Appl. Ecol.* **45,** 883–93.

Geiger R., Aron R. H. & Todhunter P. (2003) *The Climate Near the Ground*. Rowman & Littlefield Publishers, Lanham.

Giménez-Gómez V. C., Lomáscolo S. B., Zurita G. A. *et al.* (2018) Daily activity patterns and thermal tolerance of

three sympatric dung beetle species (Scarabaeidae: Scarabaeinae: Eucraniini) from the Monte Desert, Argentina. *Neotrop. Entomol.* **48,** 740–6.

Gómez-Cifuentes A., Munevar A., Gimenez V. C. *et al.* (2017) Influence of land use on the taxonomic and functional diversity of dung beetles (Coleoptera: Scarabaeinae) in the southern Atlantic forest of Argentina. *J. Insect Conserv.* **21,** 147–56.

Halffter G. & Edmonds W. D. (1982) *Nesting Behavior of Dung Beetles (Scarabaeinae).* Man and Biosphere Program - UNESCO, Mexico, D. F.

Hamrick J. L. (2004) Response of forest trees to global environmental changes. *For. Ecol. Manage.* **197,** 323–35.

Hanski I. & Cambefort Y. (1991) *Dung Beetle Ecology.* Princeton University Press, Princeton.

Hernández M. I. M. (2002) The night and day of dung beetles (Coleoptera, Scarabaeidae) in the Serra do Japi, Brazil: elytra colour related to daily activity. *Rev. Bras. Entomol.* **46,** 597–600.

Hernández M. I. M. & Vaz-de-Mello F. Z. (2009) Seasonal and spatial species richness variation of dung beetle (Coleoptera, Scarabaeidae *s. str.*) in the Atlantic Forest of southeastern Brazil. *Rev. Bras. Entomol.* **53,** 607–13.

Hsieh T. C., Ma K. H., Chao A. *et al.* (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol. Evol.* **7,** 1451–6.

Hutchinson G. E. (1957) Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* **22,** 415–27.

Iannuzzi L., Salomão R. P., Costa F. C. *et al.* (2016) Environmental patterns and daily activity of dung beetles (Coleoptera: Scarabaeidae) in the Atlantic Rainforest of Brazil. *Entomotropica* **31,** 196–207.

Jetz W., Wilcove D. S. & Dobson A. P. (2007) Projected Impacts of climate and land-use change on the global diversity of birds. *PLoS Biol.* **5,** e157.

Jost L. (2007) Partitioning diversity into independent alpha and beta components. *Ecology* **88,** 2427–39.

Klein B. C. (1989) Effects of forest fragmentation on dung and carrion beetle communities in Central Amazonia. *Ecology* **70,** 1715–25.

Koskela H. (1979) Patterns of diel flight activity in dung-inhabiting beetles: an ecological analysis. *Oikos* **33,** 419–39.

Krell F. T., Krell-Westerwalbesloh S., Weiß I. *et al.* (2003) Spatial separation of Afrotropical dung beetle guilds: a trade-off between competitive superiority and energetic constraints (Coleoptera: Scarabaeidae). *Ecography* **26,** 210–22.

Krell-Westerwalbesloh S., Krell F. T. & Linsenmair E. (2004) Diel separation of Afrotropical dung beetle guilds-avoiding competition and neglecting resources (Coleoptera: Scarabaeoidea). *J. Nat. Hist.* **38,** 2225–49.

Laliberté E. & Legendre P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91,** 299–305.

Laliberté E., Legendre P. & Shipley B. (2014) *FD: measuring functional diversity from multiple traits, and other tools for functional ecology.* R package version 1.0-12.

Landin B. O. (1968) *The Diel Flight Activity of Dung-Beetles (Coleoptera Scarabaeidae). A Study of the Influence of Environmental Factors, with Particular Reference to the Light.* Entomologiska Sällskapet, Lund.

Legendre P. & Legendre L. (2012) *Numerical Ecology.* Elsevier, Amsterdam.

Liberal C. N., Farias Â. M. I., Meiado M. V. *et al.* (2011) How habitat change and rainfall affect dung beetle diversity in Caatinga, a Brazilian semi-arid ecosystem. *J. Insect Sci.* **11,** 114.

Lobo J. M. & Halffter G. (2000) Biogeographical and ecological factors affecting the altitudinal variation of mountainous communities of coprophagous beetles (Coleoptera: Scarabaeoidea): a comparative study. *Ann. Entomol. Soc. Am.* **93,** 115–26.

Lobo J. M., Lumaret J. P. & Jay-Robert P. (1998) Sampling dung beetles in the French Mediterranean area: effects of abiotic factors and farm practices. *Pedobiologia* **42,** 252–66.

Lopes J., Korasaki V., Catelli L. L. *et al.* (2011) A comparison of dung beetle assemblage structure (Coleoptera: Scarabaeidae: Scarabaeinae) between an Atlantic forest fragment and adjacent abandoned pasture in Paraná, Brazil. *Zoologia* **28,** 72–9.

Mello A. J. M. & Peroni N. (2015) Cultural landscapes of the Araucaria Forests in the northern plateau of Santa Catarina, Brazil. *J. Ethnobiol. Ethnomed.* **11,** 51.

Nichols E., Larsen T., Spector S. *et al.* (2007) Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. *Biol. Conserv.* **137,** 1–19.

Nichols E., Spector S., Louzada J. *et al.* (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biol. Conserv.* **141,** 1461–74.

Nunes C. A., Braga R. F., Figueira J. E. *et al.* (2016) Dung beetles along a tropical altitudinal gradient: environmental filtering on taxonomic and functional diversity. *PLoS ONE* **11,** e0157442.

Oksanen J., Blanchet F. G., Friendly M. *et al.* (2016) Vegan: community ecology package. R package version 2.4-1.

Oliver T. H. & Morecroft M. D. (2014) Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. *WIREs Climate Change* **5,** 317–35.

Peyras M., Vespa N. I., Bellocq I. *et al.* (2013) Quantifying edge effects: the role of habitat contrast and species specialization. *J. Insect Conserv.* **17,** 807–20.

Pyke C. R. (2004) Habitat loss confounds climate change impacts. *Front. Ecol. Environ.* **2,** 178–82.

Scheffler P. Y. (2005) Dung beetle (Coleoptera: Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia. *J. Trop. Ecol.* **21,** 9–19.

Scholtz C. H., Davis A. L. V. & Kryger U. (2009) *Evolutionary Biology and Conservation of Dung Beetles.* Pensoft Publishers, Sofia.

Schowalter T. D. (2011) *Insect Ecology: An Ecosystem Approach.* Elsevier, Burlington.

da Silva P. G. (2017) Dung beetles (Coleoptera, Scarabaeinae) from high altitude grasslands in São Joaquim National Park, Santa Catarina, southern Brazil. *Check List* **13,** 817–30.

da Silva P. G. & Hernández M. I. M. (2014) Local and regional effects on community structure of dung beetles in a mainland-island scenario. *PLoS ONE* **9,** e111883.

da Silva P. G. & Hernández M. I. M. (2015a) Scale-dependence of processes structuring dung beetle metacommunities using functional diversity and community deconstruction approaches. *PLoS ONE* **10,** e0123030.

da Silva P. G. & Hernández M. I. M. (2015b) Spatial patterns of movement of dung beetle species in a tropical forest

suggest a new trap spacing for dung beetle biodiversity studies. *PLoS ONE* **10,** e0126112.

da Silva P. G., Vaz-de-Mello F. Z. & Di Mare R. A. (2013) Diversity and seasonality of Scarabaeinae (Coleoptera: Scarabaeidae) in forest fragments in Santa Maria, Rio Grande do Sul, Brazil. *An. Acad. Bras. Cienc.* **85,** 679–97.

da Silva P. G., Lobo J. M., Hensen M. C. *et al.* (2018) Turnover and nestedness in subtropical dung beetle assemblages along an elevational gradient. *Divers. Distrib.* **24,** 1277–90.

Slade E. M., Mann D. J., Villanueva J. F. *et al.* (2007) Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *J. Anim. Ecol.* **76,** 1094–104.

Solar R. R., Barlow J., Ferreira J. *et al.* (2015) How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecol. Lett.* **18,** 1108–18.

Suggitt A. J., Gillingham P. K., Hill J. K. *et al.* (2011) Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos* **120,** 1–8.

Tittensor D. P., Walpole M., Hill S. L. L. *et al.* (2014) A mid-term analysis of progress toward international biodiversity targets. *Science* **346,** 241–4.

Vaz-de-Mello F. Z., Leivas F. W. T. & Grossi P. C. (2014) Scarabaeoidea (Coleoptera: Polyphaga) do Parque Nacional de São Joaquim - PNSJ, Santa catarina, Brasil. In: *Parque Nacional de São Joaquim - Portal do Conhecimento* (eds P. V. Castilho, M. T. R. N. Omena & M. H. Tanivaki) pp. 115–34. Editora Santarém, Santarém, São Paulo.

Verdú J. R., Díaz A. & Galante E. (2004) Thermoregulatory strategies in two closely related sympatric *Scarabaeus* species (Coleoptera: Scarabaeinae). *Physiol. Entomol.* **29,** 32–8.

Verdú J. R., Arellano L. & Numa C. (2006) Thermoregulation in endothermic dung beetles (Coleoptera: Scarabaeidae):
effect of body size and ecophysiological constraints in flight. *J. Insect Physiol.* **52,** 854–60.

Villéger S., Mason N. W. H. & Mouillot D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89,** 2290–301.

Wrege M. S., Sousa V. A., Fritzsons E. *et al.* (2016) Predicting current and future geographical distribution of Araucaria niche modeling. *Environ. Ecol. Res.* **4,** 269–79.

Wrege M. S., Fritzsons E., Soares M. T. S. *et al.* (2017) Distribuição natural e habitat da araucária frente às mudanças climáticas globais. *Pesq. Flor. Bras.* **37,** 331–46.

SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Geographic coordinates and altitude of the sites sampled in the São Joaquim National Park, Santa Catarina State, southern Brazil.

Appendix S2. Distribution of temperature variables among land uses for ambient and soil.

Appendix S3. Dung beetle species sampled in five land uses for two days (D) and two nights (N) in the São Joaquim National Park, Brazil.

Appendix S4. Dissimilarity of Jaccard (a) and beta diversity partitioning into turnover (darker circles) and nestedness (lighter circles) (b) *versus* geographic distance among land uses.

Supporting information

The role of habitat and daily activity patterns in explaining the diversity of mountain Neotropical dung beetle assemblages

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Appendix S1. Geographic coordinates and altitude of the sites sampled in the São Joaquim National Park, Santa Catarina State, southern Brazil.

Local	Code	Latitude	Longitude	Altitude (m)	Area (ha)
Grassland	GR	28°08'29.31"S	49°38'10.43"W	1361	11.9
Shrubland	SH	28°08'33.07"S	49°38'04.00"W	1371	12.2
Agroforest	AG	28°08'29.08"S	49°38'12.82"W	1356	5.5
Secondary forest	SF	28°08'35.23"S	49°38'02.18"W	1386	111.9
Primary forest	PF	28°08'20.91"S	49°38'10.00"W	1360	611.1

Appendix S2. Distribution of temperature variables among land uses for ambient and soil. Land uses: grassland (GR), shrubland (SH), agroforest (AG), secondary forest (SF), and primary forest (PF). Since there is four measures for each land use, the day values are above the median, while the night values are below the median.
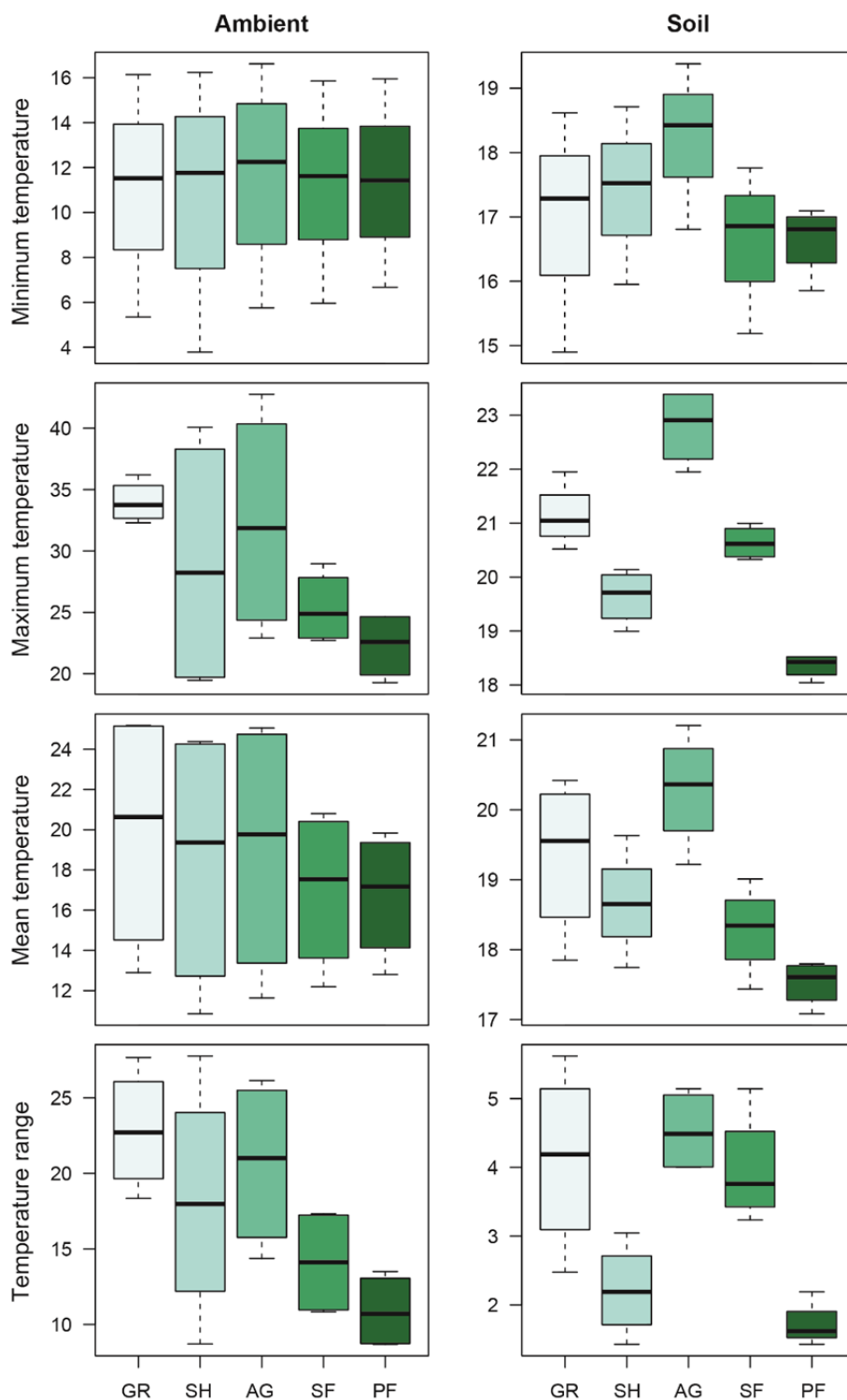
Appendix S3. Dung beetle species sampled in five sites or land uses for two days (D) and two nights (N) in the São Joaquim National Park, Brazil. Land uses: grassland (GR), shrubland (SH), agroforest (AG), secondary forest (SF), and primary forest (PF). T: Total; TG: total general. Sample coverage is the slope at the end of the accumulation curve relating the number of species with the addition of individuals, while Chao1 is a non-parametric estimator of the "true" number of species in each site taking into account the number of species represented by just one or two individuals (singletons and doubletons).

Species	GR		T	SH		T	AG		T	SF		T	PF		T	TG	Guild	Daily activity	Body size
	D	N		D	N		D	N		D	N		D	N					
Canthidium aff. *lucidum*													3		3	3	Tunneler	Diurnal	Small
Canthidium aff. *trinodosum* sp. 1				1	2	3				2	1	3				6	Tunneler	Both	Small
Canthidium aff. *trinodosum* sp. 2	1		1	16		16	3		3	2		2				22	Tunneler	Diurnal	Small
Canthidium moestum	8		8				2		2							10	Tunneler	Diurnal	Small
Canthon aff. *coeruleicollis*	2		2	64	3	67				1		1				70	Roller	Diurnal	Small
Canthon aff. *luctuosus*										4		4	1		1	5	Roller	Diurnal	Small
Canthon angularis obenbergeri	1		1	4		4	5		5	133		133	282	6	288	431	Roller	Diurnal	Small
Canthon lividus				3		3	2		2	2		2				7	Roller	Diurnal	Small
Canthon rutilans rutilans	78		78	55		55	46		46	9		9	2		2	190	Roller	Diurnal	Small
Canthon seminitens	80		80	7		7	43		43	10		10				140	Roller	Diurnal	Small
Canthon unicolor	1		1	1		1										2	Roller	Diurnal	Small
Coprophanaeus saphirinus	3		3	4		4	2		2	2		2				11	Tunneler	Diurnal	Large
Deltochilum brasiliense										3	1	4		3	3	7	Roller	Both	Large
Dichotomius aff. *acuticornis*										4	1	5		1	1	6	Tunneler	Both	Large
Dichotomius opalescens	150		150	71	2	73	29	1	30	10		10	54		54	317	Tunneler	Diurnal	Large
Homocopris sp.		1	1					2	2		2	2		12	12	17	Tunneler	Nocturnal	Large
Onthophagus aff. *hirculus*	11		11	1		1	2		2							14	Tunneler	Diurnal	Small
Onthophagus tristis	3		3				11	1	12	7		7	10		10	32	Tunneler	Diurnal	Small
Uroxys terminalis		10	10		21	21	1	95	96	5	3	8		3	3	138	Tunneler	Nocturnal	Small
Richness	**11**	**2**	**13**	**11**	**4**	**12**	**11**	**4**	**12**	**14**	**5**	**15**	**6**	**5**	**10**	**19**			
Abundance	**338**	**11**	**349**	**227**	**28**	**255**	**146**	**99**	**245**	**194**	**8**	**202**	**352**	**25**	**377**	**1428**			
Sample coverage			**0.988**			**0.992**			**1.000**			**0.995**			**0.995**				
Chao1			**21**			**12**			**12**			**15**			**12**				

Appendix S4. Dissimilarity of Jaccard (a) and beta diversity partitioning into turnover (darker circles) and nestedness (lighter circles) (b) versus geographic distance among land uses.