Climatic variables drive temporal patterns of α and β diversities of dung beetles

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Abstract

Understanding the mechanisms underpinning spatiotemporal diversity patterns of biological communities is a major goal of ecology. We aimed to test two ecological hypotheses: (i) temporal patterns of β-diversity will mostly be driven by nestedness, with a loss of species from summer to winter, and (ii) nestedness values will correlate with climatic variables instead of turnover values, indicating either a loss of species during winter or a gain of species during summer. We sampled dung beetles using standardized sampling protocols along a year in four Atlantic forest sites: two at the northwest and two at the central region of Rio Grande do Sul state, southern Brazil. We partitioned temporal patterns of β-diversity into turnover and nestedness in order to investigate if community changes are driven by species substitution or gain/loss across time. Our results highlighted five main findings: (i) dung beetle composition varied more with sites than site geographic position; (ii) there was almost one and a half 'true' dung beetle assemblages regarding the spatial distribution of species weighed by abundance; (iii) we found a positive influence of mean temperature and a negative influence of relative humidity on both species richness and abundance; (iv) both spatial and temporal dissimilarity among sites were dominated by species replacement, while the relative importance of nestedness was higher in temporal than spatial patterns; (v) there was an effect of precipitation and relative humidity on temporal patterns of β-diversity components, but these effects were site-dependent. Contrary to our expectations, the β-diversity component of turnover dominated both spatial and temporal patterns in dung beetle dissimilarity among sites and months. Distinct climatic variables affected differently the α-diversity and β-diversity components of dung beetle assemblages. Partitioning β-diversity into temporal components is a promising approach to unveil patterns of the community dynamics and to produce insights on mechanisms underlying such patterns.

Keywords: Atlantic Forest, nestedness, Scarabaeinae, species replacement, turnover

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Introduction

Understanding the mechanisms underpinning spatio-temporal diversity patterns of biological communities is a

major goal of ecology, with practical and theoretical applications in conservation (Jost *et al.*, 2010). The species diversity of a given region (i.e. γ-diversity) can be partitioned into within- and between- components, the so-called α- and β-diversity. The β-diversity was firstly used to describe spatial changes in species identities among sites (Whittaker, 1960, 1972), but it can also be used to describe temporal changes in community patterns (Legendre & Gauthier, 2014). In addition, β-diversity can be partitioned into two process-related components: species replacement (turnover) and gain/loss (nestedness) among sites or times (Baselga, 2010, 2012).

In a meta-analysis, Soininen *et al.* (2018) found that spatial species substitution is the main mechanism driving β-diversity patterns across different organisms and ecosystems. These authors also found that turnover and total β-diversity increased with spatial extent, whereas nestedness was unrelated to scale. It means there is a species substitution related to the geographic distance among sites, in which dispersal limitation and/or environmental filtering may be important drivers (Qian *et al.*, 2005). In addition, passively dispersed organisms had lower turnover and total β-diversity than flying organisms, an unexpected result (Soininen *et al.*, 2018).

Unlike spatial patterns, temporal patterns in β-diversity components are a little-explored topic (Baselga *et al.*, 2015; Shimadzu *et al.*, 2015). Temporal changes in species composition can be related to both substitution of species from time to time (temporal turnover) and gain or loss of species forming nested subsets from time to time (nestedness-resultant dissimilarity) (Baselga *et al.*, 2015). Changes in species composition from time to time are expected to occur due to variation in climatic and environmental conditions, and resource availability. For instance, winter assemblages are expected to be a sub-sample of the summer assemblage in subtropical regions (Hernández & Vaz-de-Mello, 2009; da Silva *et al.*, 2013). However, there is no way to predict whether there will be a substitution or gain/loss of species over time since the response can be context- and organism-dependent. We, however, can hypothesize mechanisms causing those changes and try to relate them to the components of β-diversity.

Dung beetles (Coleoptera: Scarabaeinae) are a diverse and widely distributed insect group that perform several ecological functions, such as bioturbation, nutrient recycling, secondary seed dispersal, control of dung-dependent parasites, and pollination (Nichols *et al.*, 2008). Several authors have argued about the usefulness of dung beetles in studying theoretical and applied ecological issues (Halffter & Favila, 1993; Spector, 2006; Nichols *et al.*, 2007; Simmons & Ridsdill-Smith, 2011). These beetles show qualitative and quantitative responses to both natural and human-driven environmental changes, being used as good ecological and biodiversity indicators (Barlow *et al.*, 2007; Gardner *et al.*, 2008; Culot *et al.*, 2013; Audino *et al.*, 2014; Beiroz *et al.*, 2014; Campos & Hernández, 2015). In addition, temperature and precipitation influence dung beetle species richness and abundance in temperate and tropical regions, respectively (Davis, 1994; Hernández & Vaz-de-Mello, 2009; da Silva *et al.*, 2013; Batista *et al.*, 2016). However, there is a lack of information about the relation between temporal patterns of β-diversity components and climatic variables. In fact, this lack of information can be generalized for several groups and systems.

In this paper, we aimed to test two ecological hypotheses. First, different from turnover-dominated spatial patterns (Soininen *et al.*, 2018), (i) temporal patterns of β-diversity will mostly be driven by nestedness, with a loss of species from summer to winter. Very abundant dung beetle species occur throughout the year with a reduced number of individuals in winter, while some rare or thermal-sensitive species occur only at warm periods (Louzada & Lopes, 1997; Errouissi *et al.*, 2009; da Silva *et al.*, 2013). In addition, climatic features, especially temperature in subtropical and temperate regions, drive the temporal patterns in species richness and abundance of dung beetles, producing nested patterns of community assembly from summer to winter (Hernández & Vaz-de-Mello, 2009; da Silva *et al.*, 2013). Therefore, due to the increase of species richness in warm conditions, (ii) nestedness values will correlate with climatic variables instead of turnover values, indicating either a loss of species during winter or a gain of species during summer.

Material and methods

Study area

The study was carried out in Atlantic Forest sites in four localities, two of them located at the northwest and two at the central region of the Rio Grande do Sul state, southern Brazil (Supporting Information Figure S1). The sites at northwest region were the Turvo State Park (TSPK; Derrubadas municipality) and Moreno Fortes Biological Reserve (MFBR; Dois Irmãos das Missões municipality), two environmental protection areas with Seasonal Deciduous Forest. The sites at central region were isolated Seasonal Deciduous Forest fragments called 'Morro do Cerrito' (MOCE) in Santa Maria municipality and 'Val Feltrina' (VAFE) in the Silveira Martins municipality. Both regions (central and northwest) are classified as Cfa (subtropical climate, with hot summers and no rainy season), with an annual precipitation of 1500–1700 mm, and an average annual temperature of 18–19°C (range 0–39°C). Santa Maria and Silveira Martins municipalities belong to the ecotone region between Atlantic Forest and Pampa (grassland-dominated) biomes. The sites at the northwest and central regions are ~275 km apart; the sites at the northwest region are 55 km apart, while sites at the central region are 18 km apart. A detailed description of the sites sampled can be found in Supporting Information Appendix S1.

Dung beetle sampling

Dung beetles were sampled with the use of baited pitfall traps (see da Silva *et al.*, 2013 for a detailed trap description) since they are a standard sampling protocol for this group. We used ten traps per forest fragment, 100 m apart from each other along a linear transect (da Silva & Hernández, 2015a). Human feces (*ca.* 15 g) were used as bait to attract dung beetles because several studies have shown it is the most attractive bait for this insect group (Larsen *et al.*, 2006; Filgueiras *et al.*, 2009; da Silva *et al.*, 2012).

Except for TSPK, we sampled dung beetles monthly between May 2016 and July 2017, totaling 12 samples in each site. In TSPK, we were only able to perform seasonal samplings ($N = 4$, middle of summer, autumn, winter, and spring). Traps remained in the field during 48 h per sampling. We identified dung beetles using dichotomous keys (da Silva *et al.*, 2011; Vaz-de-Mello *et al.*, 2011) and vouchers were sent to an expert who confirmed beetle identification. Vouchers were deposited at the Universidade Federal de Santa Maria and Universidade Federal de Mato Grosso.

Climatic variables

Monthly historical values (last 30 years, i.e. 1987–2017) of mean temperature (°C), accumulated precipitation (mm), and relative humidity of air (%) were obtained from the Brazilian National Institute of Meteorology (INMET). We were able to obtain such values for Santa Maria and Dois Irmãos das Missões cities. Although fine scale measures can address micro-environmental and temporal variations in climatic variables truly experienced by organisms (Pincebourde *et al.*, 2016), in their absence, the use of historical variables has proved useful in investigating the mechanisms underpinning biological patterns (Silva *et al.*, 2017). Furthermore, historical data account for variations in climate conditions among years. Thus, only the data from both municipalities (i.e. Santa Maria and Dois Irmãos das Missões) were used to test the relationship between climatic variables and dung beetle assemblage metrics.

Data analysis

The sampling completeness of each site was estimated with the use of a coverage estimator in order to guarantee that compositional comparisons are based on reliable inventories (Chao & Jost, 2012). Sample coverage was calculated using the R package *iNEXT* with species abundance data (Hsieh *et al.*, 2016) in the R software (R Core Team, 2017).

The permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) was used to test the compositional differences among sites and regions ('northwest' and 'central'). To avoid bias due to differences in the number of samplings among sites, we performed the analysis using only incidence data (Jaccard coefficient). The *adonis* function of the R package *vegan* (Oksanen *et al.*, 2016) was used to perform the PERMANOVA analysis, with 999 permutations. We used the *betadisper* function of the R package *vegan* to test the multivariate homogeneity of group's dispersions (PERMDISP analysis) (Anderson *et al.*, 2006). The non-metric multidimensional scaling (NMDS) was used to represent graphically the PERMANOVA results.

We partitioned species diversity metrics using Hill numbers (Jost, 2006) into α, β, and γ in order to investigate species changes and the number of communities among sites sampled. We used the R package *entropart* (Marcon & Hérault, 2014) and multiplicative partitioning because it guarantees the independence (or unrelatedness) between α and β components (Chao *et al.*, 2012). We used Hill numbers of order 0 (^0D, species richness) and order 1 (^1D, exponential of Shannon entropy). ^0D is not sensitive to the abundance of species, giving too much weight to rare species (Jost, 2006). ^1D weighs each species according to their abundance in the community, without favoring rare or abundant species and can be interpreted as the number of common species in the community (Jost, 2007). β-diversity of Shannon entropy can be considered the effective number of different communities in a given landscape or region (Jost, 2007). β-diversity is lower when a community dominates the landscape and higher when all communities share the landscape equally (Jost, 2006, 2007). We weighed communities by their total abundance when using ^1D (Chao *et al.*, 2012).

We also partitioned incidence-based β-diversity into its turnover and nestedness-related components (Baselga, 2010) in order to verify if temporal patterns of β-diversity are driven by species substitution or species gain/loss. The functions *beta.pair* and *beta.multi* of the R package *betapart* (Baselga & Orme, 2012) and Jaccard coefficient were used for this purpose. To calculate spatial patterns in β-diversity components, we pooled the data of each site to summarize them in one sample per site. Due to differences in the number of samplings among sites, we selected one sample per season in those sites with 12 samplings in order to make sites to be comparable with the TSPK site. We then selected four samples per site from similar months (i.e. January, April, June, and October).

Generalized linear models (GLM) were used to relate monthly climatic variables (i.e. mean temperature, precipitation, and relative humidity) and community metrics (i.e. richness and abundance). We also used GLM to relate β-diversity components of turnover and nestedness and differences of monthly climatic variables between consecutive months. The *beta.pair* function of the *betapart* R package was used to calculate β-diversity components between consecutive months. Differences in climatic variables between consecutive months were calculated by subtracting the value of the following month from the previous month. Positive values indicate there was a decrease in the climatic variable, while negative values indicate there was an increase in the climatic variable between consecutive months. Therefore, we had 11 samples for MOCE and MFRB, the unique sites with monthly climatic variables. We ran models searching for the best error distribution for each response variable and correcting for overdispersion or underdispersion when necessary. Therefore, we used quasi-Poisson distribution for species richness, Gaussian distribution for abundance (log10-transformed), and quasi-binomial for turnover and nestedness.

Results

We sampled 5533 dung beetles belonging to 45 species, ranging from 21 (VAFE) to 30 (MFBR) species (Supporting Information Table S1 and S2). *Canthidium* aff. *trinodosum* and *Canthon rutilans cyanescens* were the most abundant species in both MOCE and VAFE (central region), while *Scybalocanthon nigriceps* and *Eurysternus parallelus* were the most abundant ones in MFBR and TSPK, respectively. The total abundance ranged between 148 (2.7%; VAFE) and 2178 (39.4%; MOCE) individuals. Only 11 species (24.4%) occurred in all sites sampled, seven species (15.6%) occurred in at least three sites, while 13 species (28.9%) were restricted to one site. Despite having fewer samplings, the TSPK had the second highest total abundance ($N = 1901$). The sample coverage ranged between 0.967 and 0.999, indicating a good accuracy of inventories.

Dung beetle composition varied among sites (PERMANOVA: $R^2 = 16.5\%$; $F = 3.705$; P-value = 0.001; fig. 1) and between regions (PERMANOVA: $R^2 = 9.7\%$; $F = 4.348$; P-value = 0.001). No differences in the variances of groups were found (PERMDISP$_{(sites)}$: $F = 2.893$; P-value = 0.097; PERMDISP$_{(region)}$: $F = 1.486$; P-value = 0.231).

There was an opposite response pattern between results of the multiplicative partitioning of species richness (^0D) and Shannon diversity (^1D) (Table 1). The site with lower species richness (VAFE) had the highest Shannon diversity value, while the site with the second highest value of observed richness (TSPK) had the lowest Shannon diversity value. The Shannon β-diversity was 1.66, indicating there were almost one and a half 'true' dung beetle assemblages regarding the spatial distribution of species weighed by abundance.
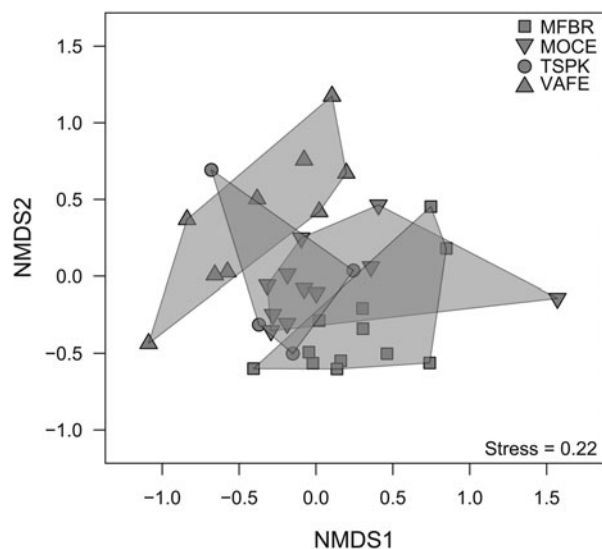
Fig. 1. Non-metric multidimensional scaling of dung beetle community composition (based on incidence) among sites sampled. MFBR, Moreno Fortes Biological Reserve; MOCE, Morro do Cerrito; TSPK, Turvo State Park; VAFE, Val Feltrina.

Table 1. Multiplicative partition of dung beetle diversity in the Atlantic Forest sites.

	Sites				Components of diversity		
	MOCE	VAFE	MFBR	TSPK	α	β	γ
^0D	26	21	30	29	27.84	1.62	45
^1D	8.38	10.10	9.03	7.73	8.34	1.66	13.83

MFBR, Moreno Fortes Biological Reserve; MOCE, Morro do Cerrito; TSPK, Turvo State Park; VAFE, Val Feltrina.

The total spatial dissimilarity was 67.4% among all sites sampled. The turnover component accounted for 90% of the dissimilarity, while nestedness accounted only for 10%. The average seasonal dissimilarity was 77% (±0.06 SD; range 71.3–85.5%) and turnover had higher values (74.8% ± 0.1 SD; range 60.9–85.1%) than nestedness (25.2% ± 0.1 SD; range 14.9–39.1%).

GLM between monthly species richness and abundance of dung beetles and climatic variables revealed a strong influence of mean temperature and relative humidity on species richness and abundance (Table 2). For MOCE and MFBR, there was a positive relationship between community metrics and mean temperature and a negative relationship between community metrics and relative humidity (fig. 2). Precipitation did not affect temporal patterns of dung beetle richness and abundance.

The difference in precipitation and relative humidity values between consecutive months influenced the temporal patterns of turnover and nestedness of dung beetles (Table 3). However, temporal patterns were not consistent between MFRB and MOCE. In MRFB, the turnover increased and nestedness decreased when there was a decrease in precipitation (i.e. positive values) between consecutive months (fig. 3b, e). In MOCE, the turnover decreased with a negative increase (i.e. positive values) in relative humidity between consecutive

Table 2. Generalized linear models between dung beetle community metrics (species richness and abundance) and climatic variables (mean temperature, precipitation, and relative humidity).

	F	DF	P-value
Dois Irmãos das Missões city			
Richness × Mean temperature	14.966	1, 10	**0.003**
Richness × Precipitation	3.989	1, 10	0.077
Richness × Relative humidity	5.659	1, 10	**0.038**
Abundance × Mean temperature	7.665	1, 10	**0.020**
Abundance × Precipitation	0.148	1, 10	0.709
Abundance × Relative humidity	13.200	1, 10	**0.005**
Santa Maria city			
Richness × Mean temperature	10.579	1, 10	**0.008**
Richness × Precipitation	0.152	1, 10	0.705
Richness × Relative humidity	11.542	1, 10	**0.007**
Abundance × Mean temperature	6.455	1, 10	**0.029**
Abundance × Precipitation	0.248	1, 10	0.629
Abundance × Relative humidity	8.776	1, 10	**0.014**

F, test value; DF, degrees of freedom.
P-values <0.05 are in bold.

months. Higher values of turnover were found when there was an increase in relative humidity between consecutive months (fig. 3c). Changes in relative humidity did not affect patterns in nestedness in this site (fig. 3f).

Discussion

Our results highlighted five main findings. First, dung beetle composition varied more among sites than among site geographic position. There were almost one and a half 'true' dung beetle assemblages regarding the spatial distribution of species weighed by their abundance. We found a positive influence of mean temperature and a negative influence of relative humidity on both species richness and abundance. Both spatial and temporal dissimilarity among sites were dominated by species replacement; the relative importance of nestedness was higher in temporal than spatial patterns. Finally, there was an effect of precipitation and relative humidity on temporal patterns of β-diversity components, but these effects were site-dependent.

The percentage of explanation of the compositional dissimilarity among sites was higher than that found among regions. The diversity partitioning into spatial scales (α, β, and γ) revealed one and a half 'true' dung beetle assemblages, even though both pairs of sites (at the northwest and central regions) were more than 275 km apart. Therefore, there is a set of species shared by all sites, while the remaining dissimilarity is mainly due to species replacement. These results suggest that differences in environmental conditions or resource availability between sites are more important driving the distribution of dung beetle species than spatial effects, even in large spatial extensions (da Silva, 2014; da Silva & Hernández, 2014, 2015b). Due to high fragmentation and habitat loss of the Atlantic Forest in southern Brazil (Ribeiro et al., 2009), only a small part of the dung beetle assemblage remains in all sites sampled. Our results reveal that less than 25% of the species occur in all sites and several studies highlighted similar patterns (da Silva & Hernández, 2014; Bitencourt & da Silva, 2016; da Silva & Hernández, 2016). Since the investigation of the factors underlying the spatial distribution of dung beetles is not the scope of this study, this topic remains
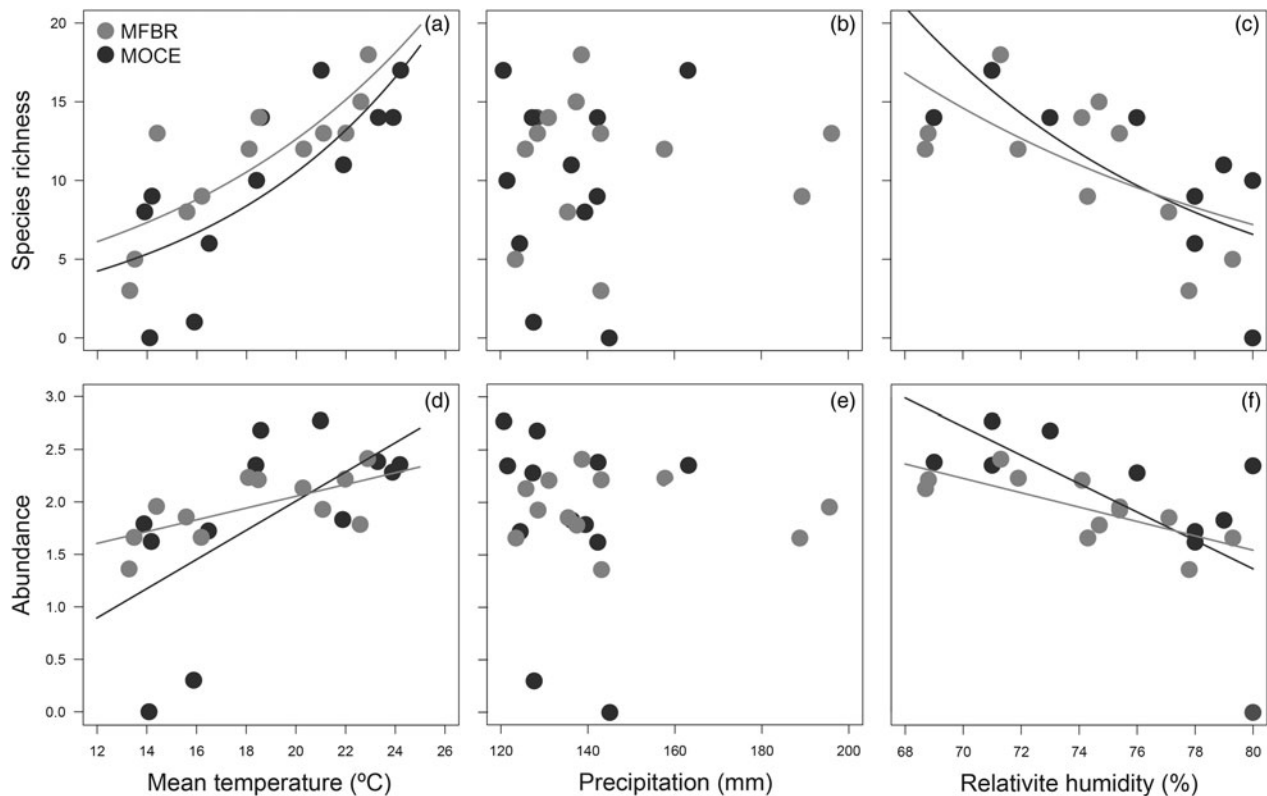
Fig. 2. Relationship between monthly dung beetle community metrics (species richness and abundance) and climatic variables [mean temperature (a, d), precipitation (b, e), and relative humidity (c, f)]. MFBR, Moreno Fortes Biological Reserve; MOCE, Morro do Cerrito.

Table 3. Generalized linear models between temporal patterns in turnover and nestedness and differences in climatic variable values (mean temperature, precipitation, and relative humidity) between consecutive months.

	F	DF	P-value
Dois Irmãos das Missões city			
Turnover × Mean temperature	0.004	1, 9	0.950
Turnover × Precipitation	11.410	1, 9	**0.008**
Turnover × Relative humidity	0.082	1, 9	0.781
Nestedness × Mean temperature	0.004	1, 9	0.950
Nestedness × Precipitation	11.410	1, 9	**0.008**
Nestedness × Relative humidity	0.082	1, 9	0.781
Santa Maria city			
Turnover × Mean temperature	0.022	1, 9	0.885
Turnover × Precipitation	1.986	1, 9	0.192
Turnover × Relative humidity	5.716	1, 9	**0.041**
Nestedness × Mean temperature	0.053	1, 9	0.823
Nestedness × Precipitation	1.918	1, 9	0.200
Nestedness × Relative humidity	2.247	1, 9	0.168

F, test value; DF, degrees of freedom.
The analysis was performed only for MOCE and MFRB.
P-values <0.05 are in bold.

important to be inquired to elucidate the high spatial substitution of species even at relatively close sites.

Climatic conditions play a major role in driving the spatiotemporal distribution of dung beetles. Several studies have found strong correlations between dung beetle community metrics and both temperature and relative humidity (Hernández & Vaz-de-Mello, 2009; da Silva *et al.*, 2013; Nunes *et al.*, 2016). Temporal changes in temperature are associated with vegetation structure changes and resource availability, and its effects are especially stronger in poikilo-thermic and heterothermic insects, such as dung beetles (Schowalter, 2011). Very low temperatures (<10°C) impair dung beetle flight and activity since several species require a minimum temperature for the flight of around 25°C (Verdú *et al.*, 2006). On the other hand, the negative relationship found between relative humidity and both species richness and abundance is explained by the negative correlation of this variable with temperature. In subtropical regions such as our study area, higher values of relative humidity are found during winter (mean 78.6 ± 1.5%; summer: mean 71.8 ± 0.3%).

Investigating the dung beetle seasonality in subtropical Brazil, da Silva *et al.* (2013) also found no effect of precipitation on dung beetle community metrics. However, decreasing precipitation between consecutive months was an important driver of β-diversity components. Although there is no marked dry season in subtropical Brazil, months of heavy rainfall can be followed by months with very low rainfall and vice-versa, regardless of the season. The month-to-month decrease in rainfall causes a high pattern of species replacement, which occurred at the beginning of spring in our region. Contrary, increased values of month-to-month rainfall occurred during winter when there is a poor and nested dung beetle assemblage from winter to spring. The precipitation
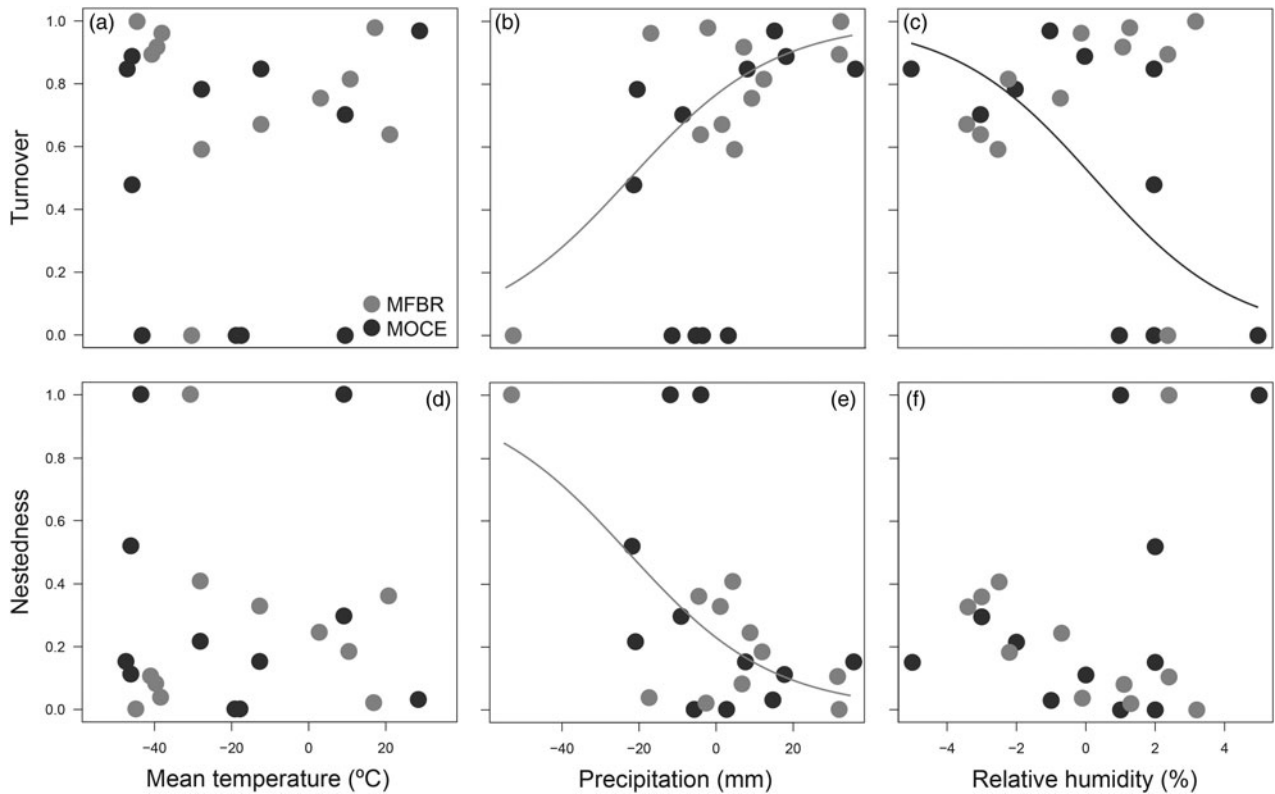
Fig. 3. Relationship between temporal patterns in turnover (upper panels) and nestedness (lower panels) of dung beetles and differences in values of mean temperature (a, d), precipitation (b, e), and relative humidity (c, f). MFBR, Moreno Fortes Biological Reserve; MOCE, Morro do Cerrito. Positive values indicate there was a decrease in the climatic variable, while negative values indicate there was an increase in the climatic variable between consecutive months.

indeed plays a major role driving the variation in species richness in tropical regions due to the existence of two marked seasons, dry and rainy (Andresen, 2005; Neves *et al.*, 2010). In subtropical regions, there is no marked dry season. Therefore, there is a change in the relative importance of temperature and precipitation with increasing latitude driving dung beetle community patterns.

Contrary to our hypothesis, the turnover component played a major role than nestedness driving the temporal dung beetle dissimilarity. We expected that most dung beetle species would occur throughout the year, with a nested subsample of summer species occurring during winter. However, on average, there is a high species substitution among seasons than species gain/loss. Our results, therefore, corroborate the findings of Soininen *et al.* (2018), who have proved that species replacement is the main component of spatial β-diversity. It seems that temporal patterns in β-diversity components are mostly driven by species substitution as well (da Silva, 2018).

Temporal values of turnover and nestedness were influenced by differences in climatic variables from consecutive months, contrary to our second hypothesis. In addition, there was no general pattern of the effect of climatic variables in β-diversity components among sites over time. Although the results obtained with the use of historical climatic variables instead of *in situ* climatic measures should be taken with caution, these results revealed that monthly differences in values of these variables affect the temporal pattern of β-diversity

components. Our results indicate when there is a successional increase in relative humidity, almost no species substitution occurs. When there is a successional decrease in relative humidity, there is an increase in species replacement. For precipitation, there is an opposite pattern; the species substitution is higher when rainfall increases from month to month, while the nestedness pattern decreases in these conditions. When rainfall is decreasing from month to month, there is a strong nested loss of species. The lack of a general pattern in these results may indicate that the effects of climatic variables on components of β-diversity are context-dependent. Our results suggest that such effects exist and this ecological issue deserves further investigation in future studies on mechanisms driving the temporal patterns of β-diversity.

In summary, we found that historical climatic variables (i.e. mean temperature, precipitation, and relative humidity) representing average climatic conditions of the sites sampled affected the monthly species richness, abundance and temporal β-diversity components of turnover and nestedness of subtropical dung beetle assemblages. Temperature and relative humidity drive dung beetle α-diversity, while precipitation and relative humidity drive β-diversity components temporally. Species substitution is the main driver of spatial and temporal β-diversity. Unlike static snapshots of community data (i.e. spatial comparisons based on one or very few temporal samplings), performing samplings over time enables the investigation of ecological processes underpinning the local extinction-colonization dynamics of metacommunities.

Therefore, the partitioning of β-diversity into temporal components is a promising approach to unveil patterns of the community dynamics and to produce insights on mechanisms underlying such patterns.

Supplementary material

The supplementary material for this article can be found at https://doi.org/10.1017/S0007485318000676.

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References

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

Anderson, M.J., Ellingsen, K.E. & McArdle, B.H. (2006) Multivariate dispersion as a measure of beta diversity. *Ecology Letters* **9**, 683–693.

Andresen, E. (2005) Effects of season and vegetation type on community organization of dung beetles in a tropical dry forest. *Biotropica* **37**, 291–300.

Audino, L.D., Louzada, J. & Comita, L. (2014) Dung beetles as indicators of tropical forest restoration success: is it possible to recover species and functional diversity? *Biological Conservation* **169**, 248–257.

Barlow, J., Gardner, T.A., Araujo, I.S., Avila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernández, M.I., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A., Miranda-Santos, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., Silva, M.N., Silva Motta, C. & Peres, C.A. (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 18555–18560.

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* **19**, 134–143.

Baselga, A. (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography* **21**, 1223–1232.

Baselga, A. & Orme, C.D.L. (2012) Betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution* **3**, 808–812.

Baselga, A., Bonthoux, S. & Balent, G. (2015) Temporal beta diversity of bird assemblages in agricultural landscapes: land cover change vs. stochastic processes. *PLoS ONE* **10**, e0127913.

Batista, M.C., Silva Lopes, G., Marques, L.J.P. & Teodoro, A.V. (2016) The dung beetle assemblage (Coleoptera: Scarabaeinae) is differently affected by land use and seasonality in northeastern Brazil. *Entomotropica* **31**, 95–104.

Beiroz, W., Audino, L.D., Queiroz, A.C.M., Rabello, A.M., Boratto, I.A., Silva, Z. & Ribas, C.R. (2014) Structure and composition of edaphic arthropod community and its use as bioindicators of environmental disturbance. *Applied Ecology and Environmental Research* **12**, 481–491.

Bitencourt, B.S. & da Silva, P.G. (2016) Forest regeneration affects dung beetle assemblages (Coleoptera: Scarabaeinae) in the southern Brazilian Atlantic Forest. *Journal of Insect Conservation* **20**, 855–866.

Campos, R.C. & Hernández, M.I.M. (2015) Changes in the dynamics of functional groups in communities of dung beetles in Atlantic forest fragments adjacent to transgenic maize crops. *Ecological Indicators* **49**, 216–227.

Chao, A. & Jost, L. (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* **93**, 2533–2547.

Chao, A., Chiu, C.H. & Hsieh, T.C. (2012) Proposing a resolution to debates on diversity partitioning. *Ecology* **93**, 2037–2051.

Culot, L., Bovy, E., Vaz-de-Mello, F.Z., Guevara, R. & Galetti, M. (2013) Selective defaunation affects dung beetle communities in continuous Atlantic rainforest. *Biological Conservation* **163**, 79–89.

da Silva, P.G. (2014) Efeitos espaciais e ambientais na composição das comunidades de Scarabaeinae no sul do Brasil. *Revista Congrega Urcamp* **8**, 1–16.

da Silva, P.G. (2018) Revisiting spatial and temporal patterns of dung beetles in Brazilian Pampa: the role of β-diversity process-related components. *Revista Brasileira de Zoociencias* **19**, 6–24.

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. (2015*a*) 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. & Hernández, M.I.M. (2015*b*) 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. (2016) Spatial variation of dung beetle assemblages associated with forest structure in remnants of southern Brazilian Atlantic Forest. *Revista Brasileira de Entomologia* **60**, 73–81.

da Silva, P.G., Vaz-de-Mello, F.Z. & Di Mare, R.A. (2011) Guia de identificação das espécies de Scarabaeinae (Coleoptera: Scarabaeidae) do município de Santa Maria, Rio Grande do Sul, Brasil. *Biota Neotropica* **11**, 329–345.

da Silva, P.G., Vaz-de-Mello, F.Z. & Di Mare, R.A. (2012) Attractiveness of different baits to Scarabaeinae (Coleoptera: Scarabaeidae) in forest fragments in the extreme south of Brazil. *Zoological Studies* **51**, 429–441.

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. *Anais da Academia Brasileira de Ciencias* **85**, 679–697.

Davis, A.L.V. (1994) Community organization in a South African, winter rainfall, dung beetle assemblage (Coleoptera: Scarabaeidae). *Acta Oecologica* **15**, 727–738.

Errouissi, F., Labidi, I. & Nouira, S. (2009) Seasonal occurrence and local coexistence within scarabaeid dung beetle guilds (Coleoptera: Scarabaeoidea) in Tunisian pasture. *European Journal of Entomology* **106**, 85–94.

Filgueiras, B.K.C., Liberal, C.N., Aguiar, C.D.M., Hernández, M.I.M. & Iannuzzi, L. (2009) Attractivity of omnivore, carnivore and herbivore mammalian dung to Scarabaeinae

(Coleoptera, Scarabaeidae) in a tropical Atlantic rainforest remnant. *Revista Brasileira de Entomologia* **53**, 422–427.

Gardner, T.A., Hernández, M.I.M., Barlow, J. & Peres, C.A. (2008) Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. *Journal of Applied Ecology* **45**, 883–893.

Halffter, G. & Favila, M.E. (1993) The Scarabaeinae (Insecta: Coleoptera) an animal group for analysing, inventorying and monitoring biodiversity in Tropical Rainforest and modified landscapes. *Biology International* **27**, 15–21.

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. *Revista Brasileira de Entomologia* **53**, 607–613.

Hsieh, T.C., Ma, K.H., Chao, A. & McInerny, G. (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* **7**, 1451–1456.

Jost, L. (2006) Entropy and diversity. *Oikos* **113**, 363–375.

Jost, L. (2007) Partitioning diversity into independent alpha and beta components. *Ecology* **88**, 2427–2439.

Jost, L., DeVries, P., Walla, T., Greeney, H., Chao, A. & Ricotta, C. (2010) Partitioning diversity for conservation analyses. *Diversity and Distributions* **16**, 65–76.

Larsen, T., Lopera, A. & Forsyth, A. (2006) Extreme trophic and habitat specialization by Peruvian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *The Coleopterists Bulletin* **60**, 315–324.

Legendre, P. & Gauthier, O. (2014) Statistical methods for temporal and space-time analysis of community composition data. *Proceedings of the Royal Society Biological Sciences Series B* **281**, 20132728.

Louzada, J.N.C. & Lopes, F.S. (1997) A comunidade de Scarabaeidae copro-necrófagos (Coleoptera) de um fragmento de Mata Atlântica. *Revista Brasileira de Entomologia* **41**, 117–121.

Marcon, E. & Hérault, B. (2014) Entropart: an R Package to Measure and Partition Diversity. Version 1.4.5 pp. 72.

Neves, F.D.S., Oliveira, V.H.F., Espírito-Santo, M.M., Vaz-de-Mello, F.Z., Louzada, J., Sanchez-Azofeifa, A. & Fernandes, G.W. (2010) Successional and seasonal changes in a community of dung beetles (Coleoptera: Scarabaeinae) in a Brazilian tropical dry forest. *Natureza & Conservacao* **8**, 160–164.

Nichols, E., Larsen, T., Spector, S., Davis, A.L., Escobar, F., Favila, M. & Vulinec, K. and The Scarabaeinae Research Network (2007) Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. *Biological Conservation* **137**, 1–19.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S. & Favila, M.E. and The Scarabaeinae Research Network (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation* **141**, 1461–1474.

Nunes, C.A., Braga, R.F., Figueira, J.E., Siqueira-Neves, F. & Fernandes, G.W. (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., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymus, P., Stevens, M.H.H., Szoecs, E. & Wagner, H. (2016) Vegan: community ecology package, R package version 2.4-1.

Pincebourde, S., Murdock, C.C., Vickers, M. & Sears, M.W. (2016) Fine-scale microclimatic variation can shape the responses of organisms to global change in both natural and urban environments. *Integrative and Comparative Biology* **56**, 45–61.

Qian, H., Ricklefs, R.E. & White, P.S. (2005) Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters* **8**, 15–22.

R Core Team (2017) *R: A Language and Environment for Statistical Computing*. Vienna, R Foundation for Statistical Computing.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J. & Hirota, M.M. (2009) The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation* **142**, 1141–1153.

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

Shimadzu, H., Dornelas, M., Magurran, A.E. & O'Hara, R.B. (2015) Measuring temporal turnover in ecological communities. *Methods in Ecology and Evolution* **6**, 1384–1394.

Silva, L.F., Souza, R.M., Solar, R.R.C. & Neves, F.D.S. (2017) Ant diversity in Brazilian tropical dry forests across multiple vegetation domains. *Environmental Research Letters* **12**, 035002.

Simmons, L.W. & Ridsdill-Smith, T.J. (2011) *Ecology and Evolution of Dung Beetles*. Oxford, Blackwell Publishing.

Soininen, J., Heino, J. & Wang, J. (2018) A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography* **27**, 96–109.

Spector, S. (2006) Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. *The Coleopterists Bulletin Monograph Number* **5**, 71–83.

Vaz-de-Mello, F.Z., Edmonds, W.D., Ocampo, F.C. & Schoolmeesters, P. (2011) A multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the New World (Coleoptera: Scarabaeidae). *Zootaxa* **2854**, 1–73.

Verdú, J.R., Arellano, L. & Numa, C. (2006) Thermoregulation in endothermic dung beetles (Coleoptera: Scarabaeidae): effect of body size and ecophysiological constraints in flight. *Journal of Insect Physiology* **52**, 854–860.

Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* **30**, 279–338.

Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon* **21**, 213–251.