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Revisiting spatial and temporal patterns of dung beetles in Brazilian Pampa: the role of β-diversity process-related components

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Abstract. β-diversity is a key measure to understand biodiversity patterns across spatial and temporal scales. In this study, two published datasets on dung beetle (Coleoptera: Scarabaeinae) from Brazilian Pampa are re-analyzed aiming to investigate the role of β-diversity process-related components based on composition- and abundance-based approaches for both spatial (grassland-forest ecotone) and temporal (samplings along a year) scales. Dung beetles were sampled in a grassland-forest ecotone in October 2006 and in a grassland area monthly during an entire year (December 2006 to November 2007), using baited pitfall traps. β-diversity was decomposed into turnover and nestedness-resultant components based on Jaccard dissimilarity coefficient, and also into balanced variation in abundance and abundance gradients based on Bray-Curtis dissimilarity coefficient. Both environmental (spatial scale) and climatic (temporal scale) differences affected dung beetles similarly in terms of species replacement and nestedness patterns, and similarly in terms of variation in abundance and abundance gradients. For both spatial and temporal approach, the species turnover and the variation in species abundances were higher, while nestedness patterns and abundance gradients were of minor relative importance.

Keywords: turnover, nestedness, balanced variation in abundance, abundance gradients, Scarabaeinae.

Resumo. Revisitando padrões espaciais e temporais de escarabeíneos no Pampa Brasileiro: o papel dos componentes de diversidade β relacionados a processos. A diversidade β é uma medida chave para compreender os padrões de biodiversidade em escalas espaciais e temporais. Neste estudo, são reanalisados dois conjuntos de dados publicados sobre escarabeíneos (Coleoptera: Scarabaeinae) do Pampa Brasileiro, com o objetivo de investigar o papel dos componentes da diversidade β relacionados a processos com base em abordagens baseadas em composição e abundância, tanto para escala espaciais (ecótono campo-floresta) e temporais (amostragens ao longo de um ano). Os escarabeíneos foram amostrados em um ecótono de campo-floresta em outubro de 2006 e em uma área de campo mensalmente durante um ano inteiro (dezembro de 2006 a novembro de 2007), usando armadilhas de queda iscadas. A diversidade β foi decomposta em seus componentes de turnover e aninhamento com base no coeficiente de dissimilaridade de Jaccard e também em variação balanceada de abundância e gradientes de abundância com base no coeficiente de dissimilaridade de Bray-Curtis. As diferenças ambientais (escala espacial) e climáticas (escala temporal) afetaram os escarabeíneos similarmente em termos de substituição de espécies e padrões de aninhamento, e similarmente em termos de variação de abundância e gradientes de abundância. Tanto para a abordagem espacial quanto temporal, a substituição das espécies e a variação na abundância das espécies foram maiores, enquanto que os padrões de aninhamento e os gradientes de abundância foram de menor importância relativa.

Palavras-chave: substituição, aninhamento, variação balanceada na abundância, gradientes de abundância, Scarabaeinae.

INTRODUCTION

Understanding the processes driving the spatial and temporal variation in biodiversity is the main goal of community ecology (SIMBERLOFF, 2004). Beta (β) diversity is a key concept that has long been used to study biodiversity patterns (LEGENDRE & LEGENDRE, 1998; LEGENDRE *et al.*, 2005), since its introduction by WHITTAKER (1960). Several approaches have been proposed to study diversity patterns, including multivariate approaches (LEGENDRE *et al.*, 2005; TUOMISTO & RUOKOLAINEN, 2006; LEGENDRE, 2008; TUOMISTO, 2010a, 2010b; ANDERSON *et al.*, 2011; LEGENDRE & DE Cáceres, 2013), partitioning approaches (WHITTAKER, 1960, 1972; JOST, 2006, 2007; JOST *et al.*, 2010), and more recently, decomposition approaches (BASELGA, 2010, 2012, 2013; LEGENDRE, 2014) especially designed to decompose β-diversity into process-related components.

Among this 'diversity of measures', two main ways have long been used to investigate biodiversity variation across space and time: compositional (species presence-absence) and structural (mainly abundance) approaches. For this purpose, two families of dissimilarity coefficients have widely been used: (i) Jaccard or Sorensen for compositional approaches (BASELGA, 2010), and (ii) Bray-Curtis or Ruzicka for abundance-based approaches (BASELGA, 2013).

The composition-based indices can be decomposed into two process-related components: turnover and nestedness-related dissimilarity (BASELGA, 2010). Turnover occurs when some species are replaced by others as a consequence of environmental sorting or spatial and historical constraints (QIAN *et al.*, 2005). Nestedness occurs when communities of sites with smaller numbers of species are subsets of the communities at richer sites, reflecting a non-random process of species loss as a consequence of factors that promote the community disaggregation (GASTON & BLACKBURN, 2000).

The abundance-based indices can be decomposed into balanced variation in abundance and abundance gradients. Balanced variation in abundance occurs when individuals of some species in one site are substituted by the same number of individuals of different species in another site. Abundance gradients occurs when some individuals are lost from one site to the other (BASELGA, 2013). These approaches have recently been used to measure pairwise and multiple-site β-diversity components for both spatial and temporal scales, helping us to investigate biodiversity patterns and their underlying ecological processes.

Studies with dung beetles have long been used to investigate theoretical and practical ecological issues (Nichols *et al.*, 2007; Gardner et al., 2008a), because they respond quickly to environmental and spatial restrictors (Audino *et al.*, 2014; da Silva & Hernández, 2014; Campos & Hernández, 2015; da Silva & Hernández, 2015; Bitencourt & da Silva, 2016; Bogoni *et al.*, 2016; da Silva & Hernández, 2016).

Taking these new available approaches on calculating and interpreting β-diversity measures, this paper revisit two published studies on spatial (da Silva *et al.*, 2008) and temporal (da Silva *et al.*, 2009) patterns of dung beetles (Coleoptera: Scarabaeinae) from Brazilian Pampa (southern Brazil), aiming to describe the β-diversity process-related components based on both composition- and abundance-based approaches. In doing so, a better understanding of the general patterns of Scarabaeinae fauna related to both spatial and temporal scales, which until then was fragmented due to the lack of satisfactory statistical approaches, is expected.

Material and Methods

Description of data studied

Both studies were carried out in Bagé (54º06'25"O, 31º19'51"S), Rio Grande do Sul state, southern Brazil, which belongs to the Pampa biome. According to the Köppen classification, this region has a subtropical mesothermal climate (Cfa) with four well-defined seasons. The mean annual precipitation varies around 1,350 mm a year and temperatures between -2 and 40°C, with frequent frost formation in winter and drought periods in summer. In general, the environmental characteristics of the region are the predominance of shallow soils and rock outcrops, strongly undulating relief (60 to 300 m) and vegetation composed of a mosaic of wide natural grassland areas with few native forests, mainly near water bodies (Gonçalves, 2000).

Briefly, da Silva *et al.* (2008) sampled dung beetles along a natural ecotone between grassland and forest (53°59'00"O, 31°16'51"S) during 15 days (four pooled samplings), and the data from this study was re-analyzed here as a spatial approach. In this study, dung beetles were sampled using pitfall traps baited with cattle dung and rotting flesh (cattle liver) along three parallel transects across the ecotone. da Silva *et al.* (2009) sampled dung beetles in a grassland area (54°00'49"O, 31°21'10"S) monthly between December 2006 and November 2007, using pitfall traps baited with human feces and rotting flesh (chicken heart). Pitfall traps were placed along two parallel transects, each one containing four traps baited with one bait type.

The data from this study was re-analyzed here as a temporal approach. Detailed information on sample area, sample design and results can be found elsewhere (da Silva *et al.*, 2008, 2009). Taxonomic and nomenclatural differences between original works and the present study are due to the recent revision of several dung beetle species groups. Areas of both studies were 8.5 km apart.

DATA ANALYSIS

General patterns for both dung beetle datasets were described according to their species richness, abundance and sample coverage using the *iNEXT* package (HSIEH *et al.*, 2016) of the software R (R CORE TEAM, 2017). For both spatial and temporal approaches, the β-diversity decomposition into its components was performed using the composition- and abundance-based approaches. The coefficients of Jaccard and Bray-Curtis were used, respectively. The Jaccard coefficient was decomposed into turnover and nestedness-related component following BASELGA (2010). The Bray-Curtis coefficient was decomposed into balanced variation in abundance and abundance gradients following BASELGA (2013). All formulae for both approaches can be found elsewhere (BASELGA, 2010, 2013). To decompose the β-diversity into its components, the package *betapart* (BASELGA & ORME, 2012) of the software R (R CORE TEAM, 2017) was used. The functions *beta.pair* and *beta.multi* were used to calculate pairwise and multiple-site measures. The function *beta.temp* was used to calculated composition-based β-diversity components between consecutive samplings (sampling 1 x sampling 2, …, sampling 11 x sampling 12) for the temporal approach (BASELGA & ORME, 2012).

For the spatial approach, the pooled data (of all traps per distance class) of each distance (15, 45 and 75 m) from the edge between the grassland and forest was used as sampling unit. For the temporal approach, the pooled data (all traps per month) of each sampling period (month) was used as sampling unit. Based on pairwise measures, clusters were constructed to graphically represent the relationship between sampling units. The unweighted pair group method using arithmetic averages was used for this purpose.

RESULTS

SPATIAL APPROACH

In total, 250 individuals belonging to 17 species of dung beetles were sampled along the grassland-forest ecotone (Table 1). Ten species (N=65) of dung beetles were found in transition between grassland-forest, 11 (N=51) in the grassland and 12 (N=134) in the forest. However, the traps in the forest at 75 m from edge sampled higher number of species and individuals (Figure 1a). Sample coverage ranged between 0.896 and 0.970 (Table 1).

The total dissimilarity among distance classes along the grassland-forest ecotone was 74.8%, and the turnover component (0.65) accounted for 87.1% of that dissimilarity. The nestedness-resultant component (0.09) accounted only for 12.9% of the dissimilarity between both habitats. However, the turnover was also high within each distance class for both habitats, while the nestedness-resultant component was

Table 1. Dung beetle data re-analyzed in the spatial decomposition of β-diversity (data from da Silva *et al.*, 2008) and sample coverage estimator. Samplings were performed in October 2007.

Habitat			**Edge**				
	Grassland			**Forest**			**Total**
Distance from edge	**75**	**45**	**15**	**15**	**45**	**75**	
Species							
Ateuchus robustus (Harold, 1868)	2	2	2	12	7	8	33
Canthidium moestum Harold, 1867		2				2	4
Canthidium sp.						1	1
Canthon aff. *chalybaeus*	2						2
Canthon aff. *heyrovskyi*		1					1
Canthon curvipes Harold, 1868	2	2	4		1	5	14
Canthon lividus lividus Blanchard, 1843	2		4	5	11	7	29
Canthon rutilans rutilans Castelnau, 1840	21	5	18	5	17	65	131
Deltochilum elevatum (Castelnau, 1840)	5		1			3	9
Deltochilum sculpturatum Felsche, 1907	1		1	1		2	5
Eurysternus aeneus Génier, 2009						1	1
Eurysternus navajasi Martínez, 1988				2			2
Ontherus sulcator (Fabricius, 1775)	1	2	2	2		2	9
Onthophagus aff. *hirculus*			3	2		1	6
Sulcophanaeus menelas (Castelnau, 1840)		1					1
Uroxys dilaticollis Blanchard, 1843					1		1

Table 1. Continuation.

Uroxys sp.					1			1
Species richness	**8**	**7**	**8**		**8**	**5**	**11**	**17**
Abundance	**36**	**15**	**35**		**30**	**37**	**97**	**250**
Sample coverage	**0.950**	**0.896**	**0.946**		**0.940**	**0.946**	**0.970**	

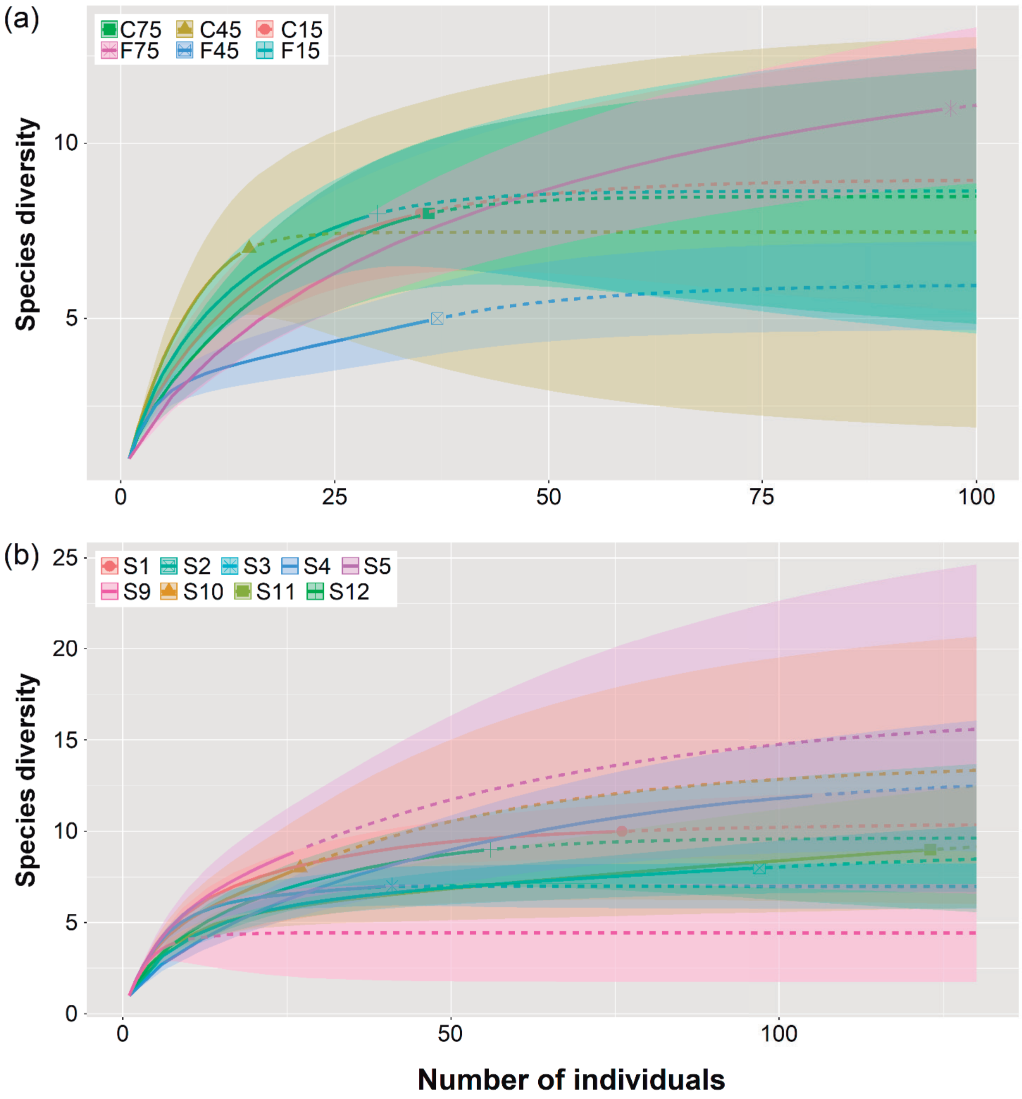

Figure 1. Extrapolated rarefaction curves for both spatial (a) and temporal (b) approaches. Curves for samplings (S) 6 to 8 were not calculated because the low number of individuals.

always low (Figure 2a). There was no evident pattern of increase or decrease of β-diversity components based on species composition from the edge to the interior of habitats. In addition, pairwise measures of β-diversity components did not show any edge-interior pattern (Figure 3a,b). In other words, the longest distances in both habitats (75 m) did not show higher turnover values.

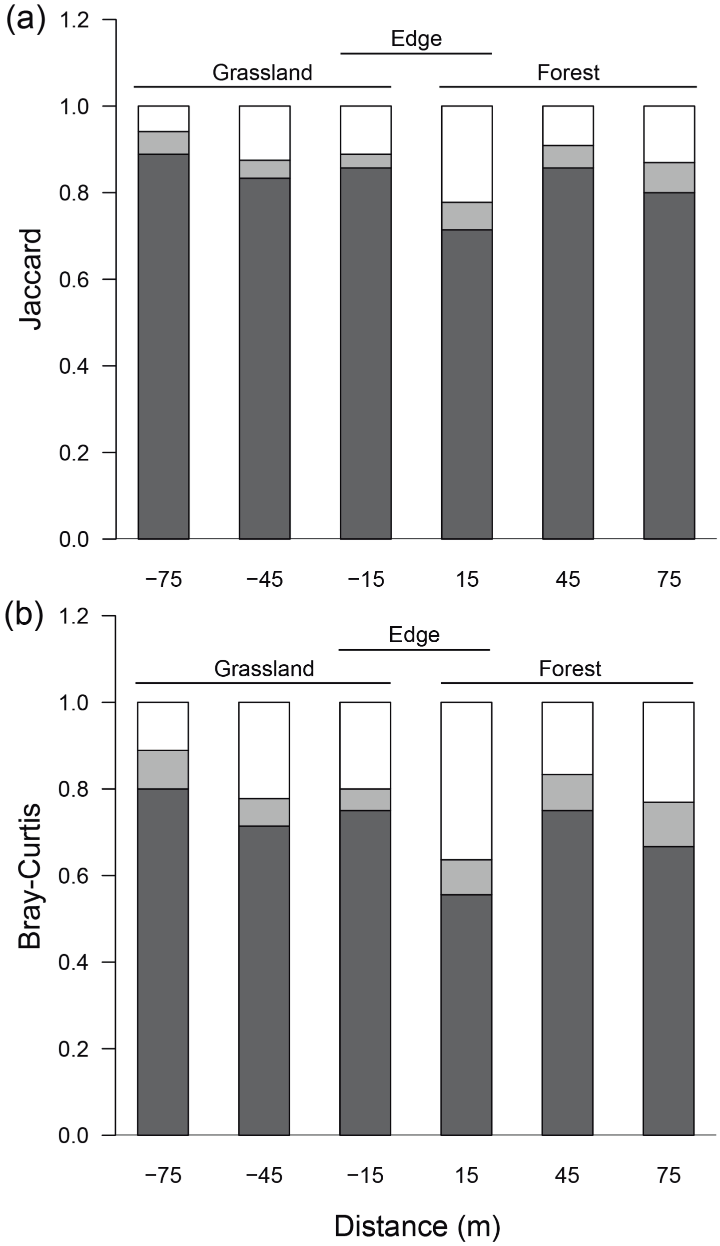

Figure 2. β-diversity decomposition into turnover (dark gray) and nestedness-related (gray) component (a), and into balanced variation in abundance (dark gray) and abundance gradients (gray) (b) for each distance class (spatial approach). White portions in each bar represent similarity.

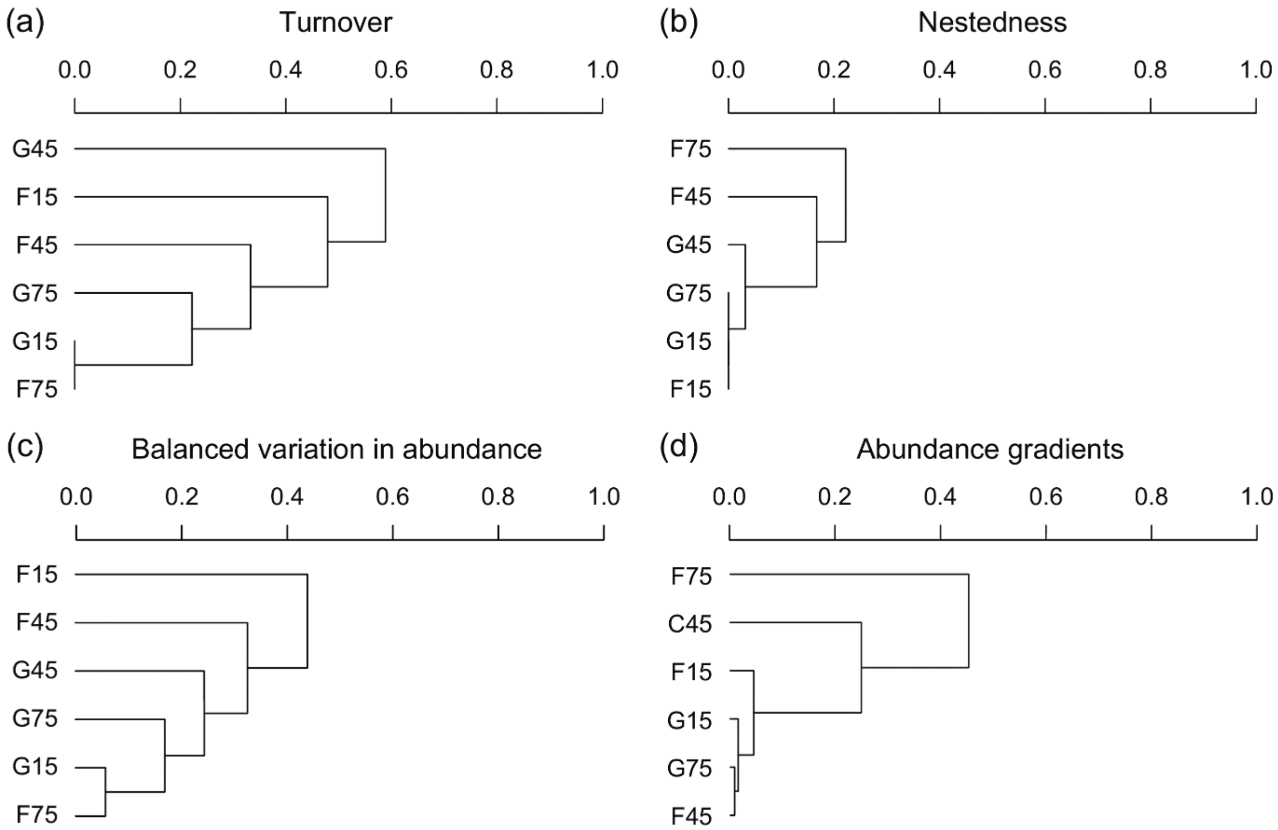

Figure 3. Pairwise measures of β-diversity components among distances for grassland (G) and forest (F) habitats for both composition-based approach (a-b) and abundance-based approach (c-d). Distance classes: 15, 45 and 75 m from the edge for each habitat.

Taking into account the abundance-based approach, the total dissimilarity between both habitats was 71.8%, and the balanced variation in abundance (0.47) accounted for 66.7% of that dissimilarity. The abundance gradients (0.23) accounted only for 33.3% of the dissimilarity between both habitats. There is a lack of edge-interior patterns for both abundance-based β-diversity components (Figure 3c,d). However, the most similar distances (G15, F75 and G75, which showed lowest turnover values; see Figure 3 for details) also showed lower variation in abundance (Figure 3c). For abundance gradients, sites with similar abundance values were clustered together, and the site with high abundance value (F75) showed higher values of abundance gradients (Figure 3d).

TEMPORAL APPROACH

In total, 565 individuals belonging to 17 species of dung beetles were sampled along the year in a grassland area (Table 2). High numbers of species were found at the beginning and end of summer, while high number of individuals were found at the beginning of spring (Figure 1b). June and July, both months of cold temperatures,

Table 2. Dung beetle data re-analyzed in the temporal decomposition of β-diversity (data from da Silva *et al.*, 2009) and sample coverage estimator. Samplings were performed between December 2006 and November 2007.

Species	**Samplings**												**Total**
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	
Ateuchus robustus (Harold, 1868)	0	0	0	1	1	0	0	0	1	0	0	0	3
Canthidium breve (Germar, 1824)	1	0	0	1	1	0	0	0	0	0	0	0	3
Canthidium moestum Harold, 1867	9	3	3	11	2	0	0	0	3	7	22	7	67
Canthon aff. *chalybaeus*	0	0	0	0	1	0	0	0	0	0	1	1	3
Canthon bispinus (Germar, 1824)	9	7	0	0	0	0	0	0	0	1	0	2	19
Canthon lividus lividus Blanchard, 1843	0	1	8	3	1	0	0	0	3	3	13	7	39
Canthon mutabilis Lucas, 1859	0	0	0	1	0	0	0	0	0	0	0	1	2
Canthon ornatus bipunctatus (Burmeister, 1873)	3	54	10	6	3	0	0	0	0	5	0	2	83
Canthon podagricus Harold, 1868	16	11	1	0	4	0	0	0	0	0	1	0	33
Canthon rutilans rutilans Castelnau, 1840	11	0	0	2	0	0	0	0	0	0	0	0	13
Coprophanaeus milon (Blanchard, 1843)	3	1	6	2	0	0	0	0	0	0	1	0	13
Deltochilum sculpturatum Felsche, 1907	19	11	7	2	0	0	0	0	0	1	9	4	53

Table 2. Continuation.

Gromphas inermis Harold, 1869	0	0	0	0	0	0	0	0	0	1	0	0	1
Ontherus sulcator (Fabricius, 1775)	2	0	0	2	0	0	0	0	0	0	20	2	26
Onthophagus aff. *hirculus*	3	9	6	72	8	3	0	0	0	8	54	30	193
Onthophagus aff. *tristis*	0	0	0	0	0	0	0	0	0	1	0	0	1
Sulcophanaeus menelas (Castelnau, 1840)	0	0	0	3	6	0	0	0	2	0	2	0	13
Species richness	**10**	**8**	**7**	**12**	**9**	**1**	**0**	**0**	**4**	**8**	**9**	**9**	**17**
Abundance	**76**	**97**	**41**	**106**	**27**	**3**	**0**	**0**	**9**	**27**	**123**	**56**	**565**
Sample coverage	**0.987**	**0.979**	**0.976**	**0.972**	**0.855**	**-**	**-**	**-**	**0.911**	**0.852**	**0.976**	**0.966**	

did not record any species (Table 2). Sample coverage ranged between 0.852 and 0.987. Sample coverage estimator did not calculate values for 6th to 8th samplings because the low number of individuals.

The total dissimilarity between samplings was 83.8%, and the turnover component (0.72) accounted for 86.2% of that dissimilarity. The nestedness-resultant component (0.11) accounted only for 13.8% of the dissimilarity between samplings. Based on the composition-based approach, the temporal turnover of consecutive samplings showed increased values in samplings performed mainly during the spring season (samplings 10 to 12; Figure 4). The 6th sampling (May 2007) was entirely composed by turnover when compared with the next sampling, in that case, the 9th sampling (August 2007), because 7th and 8th samplings (June and July 2007; winter season) showed no individuals. It is explained by the absence of *Onthophagus* aff. *hirculus* in 9th sampling, since it was the unique species found in 6th sampling, and was also found in all other samplings, excluding 7th and 8th samplings (Table 2). Compositional nestedness-patterns were more frequent in samplings performed between the end of summer and end of autumn (Figure 4).

When pairwise measures of the composition-based approach were calculated, it is pos-

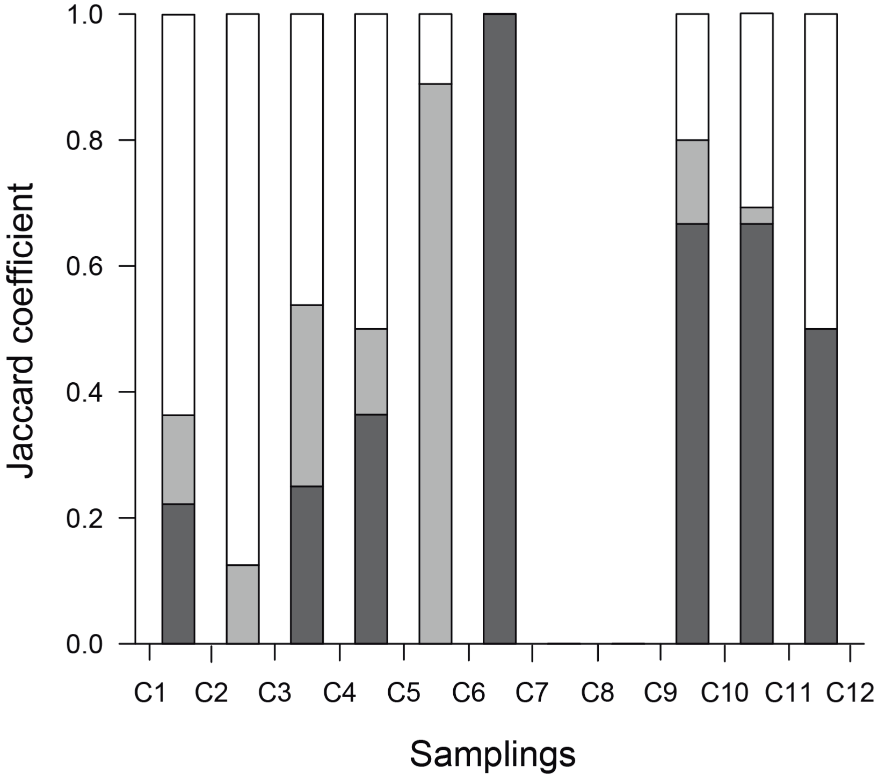

Figure 4. Pair-to-pair measures for consecutive samplings (C1-C12) of turnover (dark grey) and nestedness-resultant (grey) component of β-diversity based on Jaccard coefficient. White portions in each bar represent similarity.

sible to find two distinct groups with almost 50% of temporal turnover (Figure 5a). The first group was composed by 4th, 5th and 9th samplings, and the second group by all other samplings (excluding samplings 7 and 8). There was no temporal turnover between 4th and 9th samplings, 1st and 6th samplings, and 2nd and 3rd samplings (Figure 5a). The dissimilarity due to nestedness patterns was higher between 6th and 9th samplings, which formed one group, and all other samplings (excluding 7th and 8th samplings) with average values higher than 55% (Figure 5b).

For the abundance approach, the total dissimilarity among samplings was 85.1%, and the balanced variation in abundance (0.67) accounted for 79.3% of that dissimilarity. The abundance gradients component (0.17) accounted for only 20.7% of the dissimilarity among samplings. Pairwise measures corroborated the high relative importance of the abundance gradients component (Figure 5d), which formed two groups with values higher than 60% in average. The 6th and 9th samplings showed the lowest abundance values, and then they formed one group, which was different from other samplings. For balanced variation in abundance, two groups were formed as well (Figure 5d). Because 4th and 9th samplings, and 1st and 6th samplings showed no species

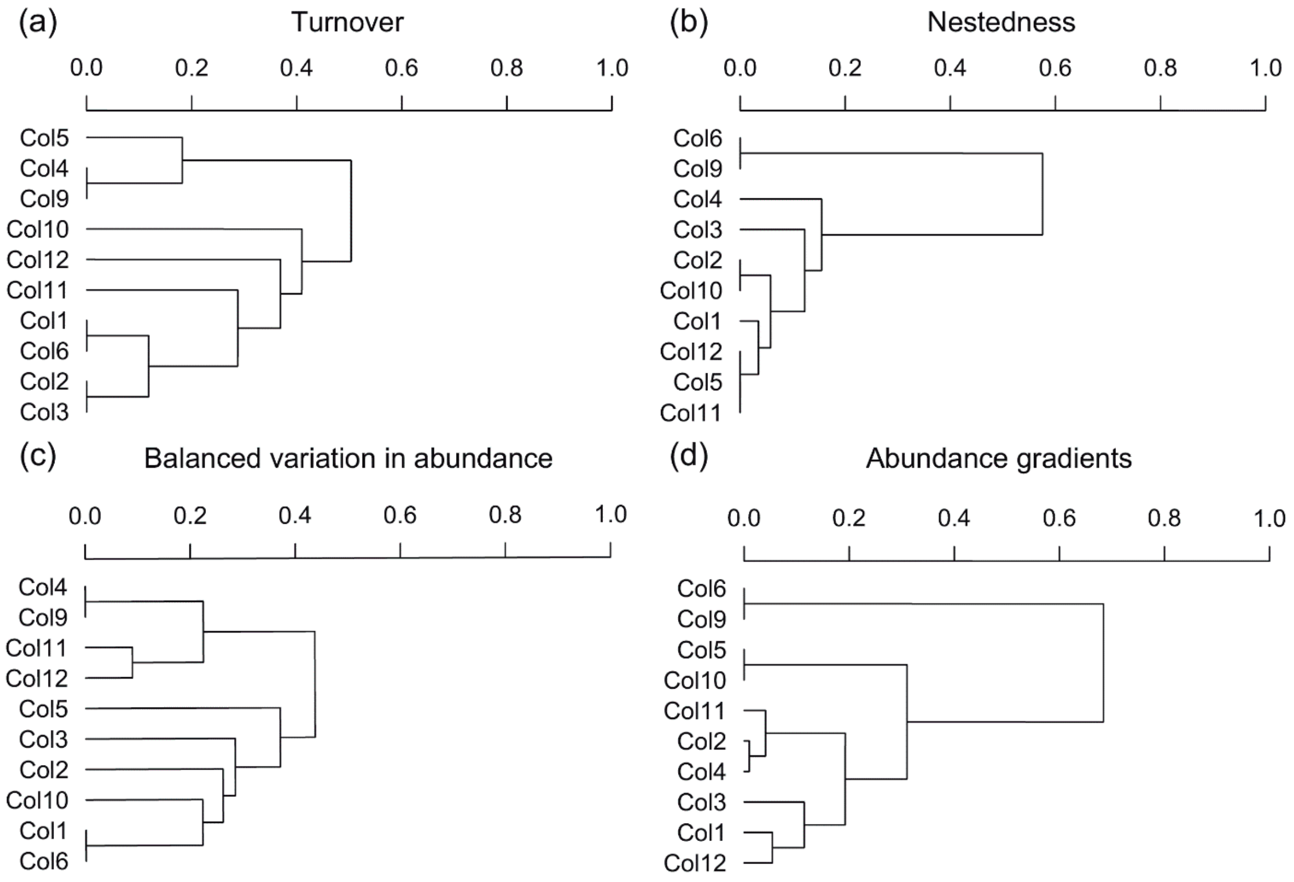

Figure 5. Pairwise measures of β-diversity components among samplings (Col) performed along a year (December 2006 to November 2007) for both composition-based approach (a-b) and abundance-based approach (c-d). Samplings 7 and 8 (June and July 2007) were omitted because they had no individuals.

turnover, they also showed no balanced variation in abundance. Those paired samplings were different from 2nd and 3rd samplings, which also showed no species turnover, but showed differences in abundance of some shared species.

DISCUSSION

This study revisited two published dung beetle datasets from southern Brazilian Pampa and demonstrated the role of β-diversity components using both composition- and abundance-based approaches for spatial and temporal scales. The turnover was the most important composition-based β-diversity component, while balanced variation in abundance was the most important abundance-based β-diversity component for both spatial and temporal approaches.

Since the definition of β-diversity introduced by WHITTAKER (1960) as “the extent of change in community composition” among sites, only in the last decades it showed an increased interest and use by ecologists, especially due to the publication of theories that challenged the widely view that environmental factors and ecological-niche differences between species are the most important factors in determining species occurrence and their abundance (Tuomisto & Ruokolainen, 2008). However, it is not new that β-diversity may reflect two different phenomena: turnover and nestedness (Baselga *et al.*, 2007). Nestedness occurs when communities of sites with smaller numbers of species are strictly subsets of the communities at richer sites. Contrary to nestedness, the turnover implies the replacement of some species by others as a consequence of environmental sorting or spatial and historical constraints (Qian *et al.*, 2005).

For dung beetles, the turnover or species replacement has been proven be the most important β-diversity component in human-modified landscapes (Silva *et al.*, 2016), edge-affected landscapes (Filgueiras *et al.*, 2016), and altitudinal gradients (Nunes *et al.*, 2016), for example. In this study, the turnover was also important for both spatial and temporal scales. There is plenty evidence that dung beetles are very sensitive to environmental changes (Halffter & Favila, 1993; Nichols *et al.*, 2007), and open and forest habitats can host different assemblages (Audino *et al.*, 2011; da Silva *et al.*, 2012; Costa *et al.*, 2013), with a mix of species at edges (Spector & Ayzama, 2003; Durães *et al.*, 2005; da Silva *et al.*, 2008). Furthermore, differences in climatic conditions, mainly temperature and precipitation, along a year has been proven be strong restrictors for dung beetles (Hernández & Vaz-de-Mello, 2009; da Silva *et al.*, 2013), where several species only occur in humid and warmer conditions, which causes higher temporal turnover values.

Dissimilarity measures based on species abundances, such as Bray-Curtis coefficient, results from the summation of antithetic sources of dissimilarity: balanced variation in abundance and unidirectional abundance gradients (Baselga, 2013). Since these two dissimilarity components may show different patterns in different regions, decomposing β-diversity measures into its components can help us in identifying important differences between ecological systems (Baselga, 2013, 2017). Balanced variation in abundance occurs when individuals of some species in the first site are substituted by the same number of individuals of different species in the second site (Baselga, 2013).

It was the most abundance-based β-diversity component for both spatial and temporal approaches in this study. The increased number of individuals of several dung beetle species from grassland to forest [e.g., *Ateuchus robustus* (Harold, 1868), *Canthon lividus lividus* Blanchard, 1843, and *Canthon rutilans rutilans* Castelnau, 1840)], and the decreased number of individuals of several species from samplings performed during summer's beginning and end [(e.g., *Canthidium moestum* Harold, 1867, *Canthon ornatus bipunctatus* (Burmeister, 1873), *Canthon podagricus* Harold, 1868, *Deltochilum sculpturatum* Felsche, 1907, and *Ontherus sulcator* (Fabricius, 1775)] to those performed during other periods, especially during autumn and winter, and also the low number of singletons and restricted species sampled (occurring in only one site or sampling) may explain the high relative importance of the balanced variation in abundance component. In addition to species turnover, spatial and temporal variation in dung beetle abundance is also related to biotic and abiotic restrictors (Nichols *et al.*, 2007; Gardner et al., 2008b; Hernández & Vaz-de-Mello, 2009; da Silva *et al.*, 2013).

Although lower than balanced variation in abundance, the abundance gradients component was also important to describe dung beetle β-diversity for both spatial and temporal scales, especially in pairwise measures. Abundance gradients occurs when some individuals are lost from one site to the other or when all the species that change their abundance from one site to the other make it with the same sign (Baselga, 2013). In other words, it is equivalent to species nestedness in composition-based patterns, as some individuals are lost from one site to the other without any substitution. In this study, it represents both loss of dung beetle individuals among distance classes along the grassland-forest ecotone (spatial approach) and among monthly samplings along the year (temporal approach), meaning that most some samples are subsets of another in both approaches (Baselga, 2017).

The partition of dissimilarity measures, such as Jaccard and Bray-Curtis coefficients, into their process-related components has been proven be useful to assess biodiversity patterns and to explore their causes, as substitution and loss of species and individuals are patterns that can derive from completely different processes (Baselga, 2013). There also is an urgent need to model the response of biodiversity to human pressures and, thus, to estimate biodiversity changes across different scales (Hudson *et al.*, 2014; Hudson *et al.*, 2017), and then β-diversity decomposition into their process-related components can be a useful tool to achieve this important goal.

The results presented in this study show that for dung beetles in southern Brazilian Pampa, both environmental (spatial approach) and climatic (temporal approach) differences affected dung beetles similarly in terms of species replacement and nestedness patterns, and similarly in terms of variation in abundance and abundance gradients. For both spatial and temporal approach, the species turnover and the variation in species abundances were higher, while nestedness patterns and abundance gradients were of minor relative importance. These results also amplify the previous understanding of dung beetle patterns along a grassland-forest ecotone (da Silva *et al.*, 2008) and a monthly sampling during an entire year (da Silva *et al.*, 2009) in the southern Brazilian Pampa. Both studies highlighted that dung beetles were affected by both environmental (da Silva *et al.*, 2008) and climatic (da Silva *et al.*, 2009) changes. Now, it was possible understand that changes in dung beetle composition and structure cause higher substitution of species and individuals than patterns of nestedness and abundance gradients, spatially and temporally.

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