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PENSOFT

Dung beetles (Coleoptera, Scarabaeinae) from high-altitude grasslands in São Joaquim National Park, Santa Catarina, southern Brazil

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Abstract

São Joaquim National Park (SJNP), in southern Brazil, covers large areas of high-altitude grasslands (HAG), which are a conspicuous ecosystem that belongs to the Atlantic Forest domain. Previous studies recorded 6 species of dung beetles (Coleoptera, Scarabaeinae) in SJNP. Dung beetles were sampled using a standardized protocol (baited pitfall traps) at 6 HAG sites in January 2016. In this paper, an annotated list of the dung beetle species sampled in SJNP is presented. This list includes previous literature records and ecological and distributional information of the species. Nine species of Scarabaeinae were collected, including 8 of them newly recorded from SJNP. The dung beetle assemblages were composed of species having diurnal habits and colorful bodies, and showing a similar proportion of roller–tunneller, and coprophagous–trophic generalist species. New studies could substantially increase the number of dung beetle species in the SJNP.

Key words

Campos de Altitude; Campos de Cima da Serra; Serra Geral; South Brazilian Plateau; Scarabaeidae; Atlantic Forest; species' inventory.

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Introduction

The Atlantic Forest is one of the richest Brazilian biomes. However, it also is one of the most threatened regarding conservation of its biodiversity (Myers et al. 2000, Tabarelli et al. 2010). The high levels of biodiversity and endemic species found in the Atlantic Forest have been attributed to the high environmental and climatic heterogeneity found in this biome (Ribeiro et al. 2009, Tabarelli et al. 2010), which comprises areas from Rio Grande do Norte to Rio Grande do Sul along the east coast of Brazil (ca 29° range in latitude), and also northern Argentina and southern Paraguay (Tabarelli et al. 2010).

The grasslands found at high altitudes in southern Brazil (*campos de altitude* or high-altitude grasslands) are a very conspicuous environment in the Atlantic Forest domain. High-altitude grasslands (HAG) are typical of montane and high montane areas with shrub and/or herbaceous structure, and usually occur on lithic mountaintops at high elevations, predominantly in subtropical and temperate climate (Brasil 1993). In southern Brazil, these grasslands are distributed from northern Rio Grande do Sul to Paraná states and form mosaics with forest formations. Despite increased research on the composition and ecology of these grasslands in recent decades, few studies have focused on the importance of biodiversity and conservation (Iganci et al. 2011, Barros et al. 2015, Overbeck et al. 2015).

In this region, fires occur naturally and the use of fire to clear grasslands in late winter was a traditional practice. These grasslands have tussock grasses that are more tolerant to fire, such as species of *Andropogon* L., *Schizachyrium* Ness, *Aristida* L., and *Baccharis* L. (Overbeck et al. 2015). Another important component in the evolution of old-growth grasslands is herbivory, especially cattle grazing (Veldman et al. 2015). Horses and cattle were introduced in the region by Jesuit missionaries in the 17th century (Pillar and Quadros 1997), and livestock became an important land use in southern Brazil and remains so today (Overbeck et al. 2007). However, species of deer, rhea, and rodents are natural herbivores in these environments, and there also is fossil evidence that large herbivorous Equidae, Camelidae, and Cervidae existed in the region until 8000 years before present (Pillar and Quadros 1997, and references therein). Due to the high altitudes and their geographic position at around 30° S latitude in southern South America, HAG faced severe climate regimes during their evolution (Overbeck et al. 2007). Nowadays, this region is in a tropical-temperate transition zone, with hot summers, cool winters, and no dry season (Overbeck et al. 2007). Thus, the biodiversity found in HAG is due to historical and biogeographical processes, and current land use adopted by landowners for centuries. Features such as fire, grazing, and soil characteristics limit tree growth in old-growth grasslands (Rehm and Feeley 2015, Veldman et al. 2015).

In southern Brazil, São Joaquim National Park (SJNP) is a protected area on the South Brazilian Plateau that covers large areas of HAG and other vegetation formations, such as nebular forest, dense and mixed ombrophilous forest (also called Araucaria forest) (Brasil 1961, Castilho et al. 2014, ICMBio 2016). The altitude varies between 350 and 1822 m above sea level and several grassland areas within the park that have not been expropriated continue to be grazed by livestock (ICMBio 2016). In southern Brazil, HAG show high levels of plant species richness and endemic plant species (ca 25% of their taxa) (Boldrini et al. 2009, Iganci et al. 2011), which are important for conservation and for studies on patterns of diversification in a subtropical transitional environment (Iganci et al. 2011, Barros et al. 2015). Despite being important for conservation, the park lacks a management plan and continuous biodiversity surveys (Vaz-de-Mello et al. 2014b).

The first inventory of scarabaeoidean beetles in the park was made by Vaz-de-Mello et al. (2014b), who found 14 species belonging to 4 families: Lucanidae (5 species), Melolonthidae (2 species), Scarabaeidae (6 species), and Trogidae (1 species). The low species richness of Scarabaeoidea was attributed to the low temperatures, and the data were considered insufficient for a robust assessment of the fauna of this group in the park (Vaz-de-Mello et al. 2014b). Thus, there is a need to better know the scarabaeoidean fauna (and coleopteran fauna as a whole) occurring in the park, with the aim of providing new information on biodiversity and the distribution of species.

Regarding the family Scarabaeidae, all species sampled by Vaz-de-Mello et al. (2014b) belonged to the subfamily Scarabaeinae, a taxonomic group that is popularly known as dung beetles. The term "dung beetle" is generally used to describe species of Scarabaeoidea with essentially coprophagous habits, such as Scarabaeinae, Aphodiinae, and Geotrupidae (considered Geotrupinae by some authors) (Lobo and Halffter 2000). In this study, "dung beetle" is used to refer only to the subfamily Scarabaeinae, which is the predominant group sampled using baited pitfall traps (Halffter and Favila 1993).

Dung beetles feed primarily on mammal feces, animal carcasses, and rotting plant matter. They have an important role in the decomposition of organic and nutrient cycling (Halffter and Matthews 1966, Halffter and Edmonds 1982, Hanski and Cambefort 1991). These beetles bury portions of food resources in the soil, making the nutrients in these materials available to the ecosystem once again, and also increasing aeration and water infiltration; they also can bury eggs of other organisms (such as parasites of cattle) and secondarily disperse fruit seeds consumed by mammals (Nichols et al. 2008, and references therein).

Vaz-de-Mello (2000) compiled a list of the Scarabaeinae in Brazil and found 618 species cited in publications, but this number is greatly an underestimate due to the lack of surveys in several regions of Brazil and the need for taxonomic revisions of some groups. Nowadays, there are 726 valid species occurring in Brazil, with 62 endemic species (Vaz-de-Mello 2017). The Scarabaeinae present species with a wide range of sizes, colors, and body shapes. There are genera with species just a few millimeters long, such as in *Besourenga* Vaz-de-Mello, 2008, *Canthonella* Chapin, 1930, and *Degallieridium* Vaz-de-Mello, 2008 (Ratcliffe and Smith 1999, Vaz-de-Mello 2008) and species with about 5 cm, such as some species belonging to the genus *Coprophanaeus* Olsoufieff, 1924 (Edmonds and Zídek 2010). The body color in Scarabaeinae varies from opaque black to a range of metallic colors (Halffter and Matthews 1966), which can help prevent predation, allow intraspecific communication, or be related to activity period (Young 1984, Vulinec 1997, Hernández 2002). The body shape also varies, from oval (most species) to rectangular (such as *Eurysternus* Dalman, 1824 and *Dendropaemon* Perty, 1830) and represent body adaptations related to the food-handling and nesting behavior and to reduce competition (Hernández et al. 2011). The diversity and combinations of body traits found in Scarabaeinae beetles contribute to

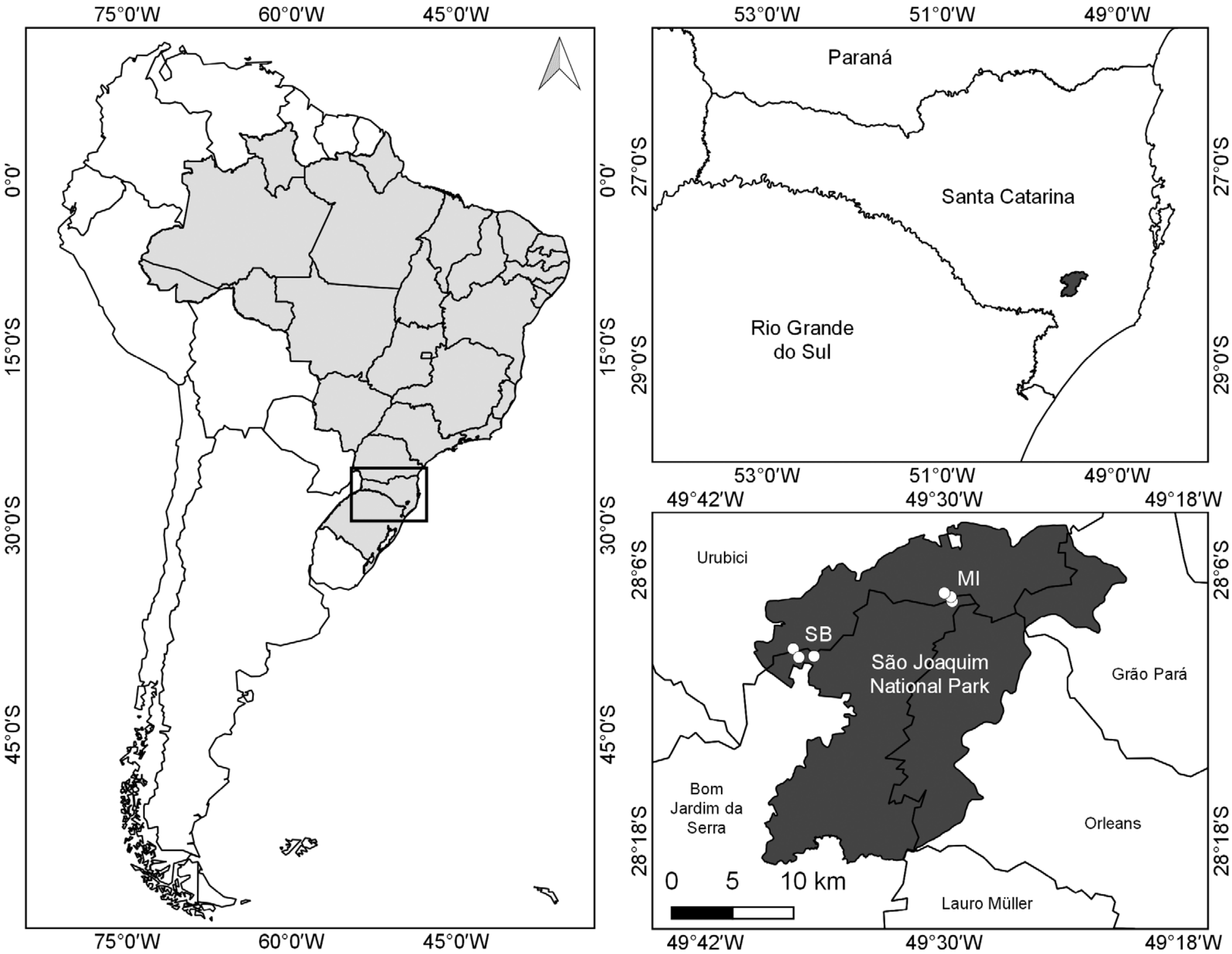

Figure 1. Location of the 6 high-altitude grasslands (white circles) in São Joaquim National Park, Santa Catarina, southern Brazil. Localities sampled: Morro da Igreja (MI) and Santa Bárbara (SB).

the high diversity of the group.

Dung beetles have been used as biological indicators because they are sensitive to natural or anthropogenic environmental changes (Halffter and Favila 1993, Nichols et al. 2007). Several studies have shown that assemblages from open and forest environments may be quite different (Klein 1989, Costa et al. 2013), and these differences may be greater or lesser depending on the predominant type of matrix. Open environments are expected to be occupied by specialized species that require more sunlight, a warmer temperature, and less humidity (Gossner 2009). However, species of the HAG face climatic conditions quite different from those living in open habitats near or at sea level. Due to historical and biogeographical processes, communities in HAG evolved to support extreme environmental and climatic conditions.

The aim of this study was to know the species composition of scarabaeine assemblages from HAG in the SJNP by using a standardized sampling protocol. I also aim to characterize the assemblages and their species using body traits and ecological characters. In the HAG of southern Brazilian, one would expect that scarabaeine assemblages would be composed of open-habitat specialists, with behavior, daily activity, and trophic preference adapted to survive in environments with extreme climatic conditions.

Methods

Study area. SJNP (Fig. 1) is a 49,300 ha protected area located on the South Brazilian Plateau in Santa Catarina state; the region is called the *Serra Geral*. The park is contained within 4 municipalities: Bom Jardim da Serra, Grão Pará, Orleans, and Urubici (Brasil 1961, ICMBio 2016). SJNP, which is located in the Atlantic Forest biome, covers extensive areas of high-altitude grasslands (in Portuguese, *Campos de Altitude*), Araucaria forest (*Araucaria angustifolia* (Bertol.) Kuntze), and also nebular forest and dense ombrophilous forest. The park as a range of altitude from 350 to 1822 m above sea level (ICMBio 2016). The highest point in the park is Morro da Igreja (MI) in the park's northeast region. At the center of the park, there are also areas above 1650 m that are named Campos de Santa Bárbara (SB). The climate in the high grasslands is humid subtropical, with hot summers, cool winters (with frequent frosts and snow), and without a pronounced dry season (Overbeck et al. 2007, 2015). Summers are cooler in the South Brazilian Plateau than summers at low altitudes, with the annual average temperature around 16–22 °C. The annual averages of precipitation and air relative humidity are 1400 mm and 85%, respectively. The geological formation of the park is composed of volcanic rocks (basalt), which together with sandstone formations, is permits the discharge and recharge of the Guarani Aquifer. Studies date the age of these formations as approximately 133 million years (ICMBio 2016).

The 6 HAG sites sampled are open environments, formed by herbaceous and/or shrubby vegetation structure, which is mainly represented by species of Poaceae, Asteraceae, and Cyperaceae (Pillar and Quadros 1997, Overbeck et al. 2007). These are humid or semi-humid grasslands (Zanin et al. 2009, Overbeck et al. 2015); the soil of all sites was always wet during the sampling period. This is due to the constant influence of fog and/or the high concentration of rainwater in shallow soils (Overbeck et al. 2015), which occur at top of mountains and plateaus.

Dung beetle sampling. Dung beetles were sampled in 6 HAG sites, 3 of them in MI and another 3 in SB (Table 1, Fig. 1). These 2 areas are 12 km from each other. In each area, individual sampling sites were on average 900 m from one other (range 300–1300 m). To sample dung beetles, baited pitfall traps, which consisted of 750 ml plastic containers (15 cm diameter, 20 cm depth) buried with their edge level with the ground. Above the traps, a rain guard was placed to prevent trap overflow and to support the bait. In each trap, a solution of water and neutral detergent (300 ml) was added to catch beetles. Human feces and rotting flesh (20 g) were used as bait to attract coprophagous and necrophagous species, respectively. Baits were wrapped in thin cloth and tied in the central portion of the rain guard.

In each site, 10 baited pitfall traps were distributed in pairs, with each pair spaced 100 m apart (da Silva and Hernández 2015b). Paired traps were spaced 5–10 m apart, and each one was baited with human feces or rotten flesh. Each pair of traps was considered a sampling unit. All traps remained in the field for 48 h. Similar sampling designs were previously in dung beetle studies in southern Brazil (da Silva and Hernández 2014, 2015a, 2016).

The study was carried out between 11–14 January 2016. In the first day, 10 baited pitfall traps were mounted in each of the 3 sites from SB. In the second day, the same for the 3 sites from MI. In the last 2 days, after 48 h sampling period for each site, dung beetles were collected. The accumulated rainfall was 14 mm (6 mm and 8 mm for the first and second days). The relative humidity ranged 60–82% during the sampling period. The minimum temperature varied between 14 °C and 16 °C, while maximum temperature was 25–27 °C (Climatempo 2016). Dung beetles were sampled in January (summer in the southern hemisphere) because this month has high temperatures and a high species richness and abundance of Scarabaeinae in southern Brazil (Hernández and Vaz-de-Mello 2009, da Silva et al. 2013).

Table 1. Details of the sample sites in high-altitude grasslands of São Joaquim National Park, Santa Catarina, southern Brazil.

Site	Area	Latitude (S)	Longitude (W)	Altitude (m)
1	Santa Bárbara	028°09′30″	049°37′37″	1685
2	Santa Bárbara	028°09′53″	049°37′21″	1716
3	Santa Bárbara	028°09′50″	049°36′35″	1697
4	Morro da Igreja	028°07′24″	049°29′38″	1769
5	Morro da Igreja	028°07′12″	049°29′43″	1751
6	Morro da Igreja	028°07′02″	049°30′02″	1738

All collected beetles were sorted, mounted on entomological pins, and dried in an oven (60 °C for 72 h). They were identified using dichotomous keys and species diagnoses (Harold 1867, 1868, 1869b, Schmidt 1922, Luederwaldt 1929, Boucomont 1932, Balthasar 1939, Pessôa and Lane 1941, Edmonds 2000, Edmonds and Zídek 2010, Vaz-de-Mello et al. 2011, Maldaner et al. 2015). A leading specialist in scarabaeine taxonomy, Dr Fernando Vaz de Mello (Universidade Federal de Mato Grosso, Cuiabá, Brazil) confirmed all identifications. In recent years, Dr Vaz de Mello had performed a broad study of the types of species of Neotropical Scarabaeinae deposited in European museums and, therefore, can assure the identity of the species in this study. The study did not involve protected species and all permits to collect dung beetles were granted prior to the study by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio, permit #49486-1). The voucher specimens are deposited in the Entomological Collection of the Centro de Ciências Biológicas in the Universidade Federal de Santa Catarina and in the Entomology Section of the Zoological Collection of the Universidade Federal de Mato Grosso, Cuiabá, Brazil. Voucher specimens sampled in this study were labeled with a number unique to each individual specimen.

Data analysis. Dung beetles were grouped in categories of food relocation behavior, trophic preference, and body color following the specialized literature (Halffter and Matthews 1966, Halffter and Edmonds 1982, Cambefort 1991, Hanski and Cambefort 1991, Hernández 2002, Campos et al. 2011, Lopes et al. 2011, Medina and Lopes 2014, da Silva and Hernández 2015a) and field observations. Species accumulation curves were used to verify the sampling sufficiency (Colwell et al. 2004) between the 2 sampling areas (MI and SB) and for the entire dataset, representing the assemblage of dung beetles found in SJNP. The curves were calculated using the 'specaccum' function and the method 'exact' of the Vegan package (Oksanen et al. 2016) in the program R 3.1.2 (R Core Team 2017). The Chao 1 species richness estimator (and its confidence interval), which is based on species abundance, was calculated using EstimateS 9.1 program (Colwell 2013). The Chi-square test was used to test for differences between the proportions of rollers and tunnellers found in the SJNP. Citations to the literature are not exhaustive because this work is neither a taxonomic study nor catalog of species. Only the main references to published synonymies and recent ecological and taxonomic data are included.

Results

In the SJNP, 152 individuals belonging to 9 species of Scarabaeinae were sampled (Table 2, Fig. 2). Three species, *Canthon (Francmonrosia) rutilans rutilans* Castelnau, 1840, *C. (Canthon) lividus seminitens* Harold, 1868, and *Onthophagus (Onthophagus)* aff. *hirculus* Mannerheim, 1829 were the most abundant, representing 87.5% of individuals sampled. The dung beetle assemblage at SJNP was composed of similar proportions of roller (45%) and tunneller species (55%) (χ^2 = 0.111, df = 1, *p*-value = 0.73). All sampled species had colorful bodies and were grouped as diurnal (Fig. 2).

The number of species was similar between the types of baited pitfall traps: 6 species found in traps baited with human feces and 5 in traps with rotten flesh. However, the number of individuals found in traps with human feces was almost double than that found in traps baited with rotten flesh. Among localities, the highest number of species (8) was found in SB (MI = 5 species). However, MI showed a greater number of individuals (*N* = 105) than SB (*N* = 47). Four species were sampled only in SB, with all being singletons.

None of the species accumulation curves, for each locality and for the whole park, tended to stability, demonstrating a high probability of encountering other dung beetle species in the SJNP (Fig. 3). The Chao 1 estimator also corroborated these results, especially for SB and the whole Park, where only 44.5% and 60% of the estimated numbers of species were sampled, respectively (Fig. 3).

List of species

Phylum Arthropoda
Class Insecta
Order Coleoptera
Superfamily Scarabaeoidea
Family Scarabaeidae
Subfamily Scarabaeinae

Canthidium* (*Canthidium*) *chabanaudi Boucomont, 1928; Figure 2a

Canthidium chabanaudi Boucomont 1928: 202—Blackwelder 1944: 205.

Canthidium (*Canthidium*) *chabanaudi*—Martínez and Halffter 1986: 27; da Silva et al. 2008b: 145; Garcia et al. 2016: 149.

Material examined. Table 2.

Species diagnosis. Boucomont (1928).

Canthon* (*Canthon*) *curvipes Harold, 1868; Figure 2b

Canthon curvipes Harold 1868: 33—Harold 1869a: 990; Burmeister 1874: 121; Bruch 1911: 183; Luederwaldt 1911: 421; Blackwelder 1944: 199; Schmidt 1922: 69; Balthasar 1939: 211; Pessôa and Lane 1941: 417; Martínez 1959: 31; Vulcano and Pereira 1964: 608.

Coprobius curvipes Burmeister 1874: 121.

Canthon (*Canthon*) *curvipes*—Halffter and Martínez 1977: 90; Silva and Carvalho 2000: 201; Vaz-de-Mello 2000: 191; Audino et al. 2007: 75; da Silva 2008: 25; da Silva et al. 2008b: 145; Almeida and Mise 2009: 236; da Silva et al. 2009a: 64; Audino et al. 2011: 123; da Silva 2011: 550; da Silva et al. 2012a: 249; Almeida et al. 2015: 277.

Material examined. Table 2.

Species diagnosis. Harold (1868).

Canthon* (*Canthon*) *lividus Blanchard, 1846; Figure 2c

Canthon lividus Blanchard 1846: 164—Bruch 1911: 184; Gillet 1911: 31; Schmidt 1922: 77; Balthasar 1939: 213; Blackwelder 1944: 200; Lange 1947: 306; Martínez 1959: 36; Vulcano and Pereira 1964: 618.

Canthon cupricollis Harold 1868: 44—Harold 1869a: 990.

Table 2. Details on dung beetles sampled in high-altitude grasslands of São Joaquim National Park, Santa Catarina, southern Brazil. Abbreviation: SU = sex undetermined.

Species	Color	Behavior	Bait		Localities		Total	Material examined
			RT	HF	MI	SB		
Canthidium chabanaudi Boucomont, 1928	Green	Tunneller		1		1	1	ECUFSC (drawer SJNP) 010 (1 ♂)
Canthon curvipes Harold, 1868	Green	Roller	1			1	1	ECUFSC (drawer SJNP) 033 (1 SU)
Canthon lividus Blanchard, 1846	Red pronotum, black elytra	Roller	1			1	1	ECUFSC (drawer SJNP) 050 (1 ♀)
Canthon seminitens Harold, 1868	Green or blue	Roller	41	2	42	1	43	ECUFSC (drawer SJNP) 034, 055, 059, 060, 066, 074, 075, 085, 087, 092-095, 107-121, 127-129, 135, 137, 152-160, 167 (41 SU, 2 ♂)
Canthon rutilans rutilans Castelnau, 1840	Red	Roller	12	60	53	19	72	ECUFSC (drawer SJNP) 001-005, 009, 011, 015, 017, 019-023, 032, 040, 041, 046, 051, 053, 054, 056, 057, 061, 062, 065, 067-069, 071-073, 076, 077, 079-084, 086, 088-091, 096-103, 124, 125, 130, 131, 136, 138-148, 163-165 (1 ♂, 71 SU)
Coprophanaeus saphirinus (Sturm, 1826)	Green	Tunneller	1			1	1	ECUFSC (drawer SJNP) 168 (1 ♀)
Dichotomius opalescens (Felsche, 1910)	Green or blue	Tunneller		6	6		6	ECUFSC (drawer SJNP) 104, 132-134, 149, 150 (1 ♂, 1 ♀, 4 SU)
Onthophagus aff. *hirculus* Mannerheim, 1829	Green pronotum, brown elytra	Tunneller		18	3	15	18	ECUFSC (drawer SJNP) 006-008, 012, 025-027, 035-039, 042, 043, 052, 058, 105, 106 (1 ♂, 17 SU)
Sulcophanaeus menelas (Castelnau, 1840)	Green	Tunneller		9	1	8	9	ECUFSC (drawer SJNP) 018, 024, 028-031, 044, 047, 126 (1 ♂, 1 ♀, 7 SU)
Number of individuals			**56**	**96**	**105**	**47**	**152**	
Number of species			**5**	**6**	**5**	**8**	**9**	

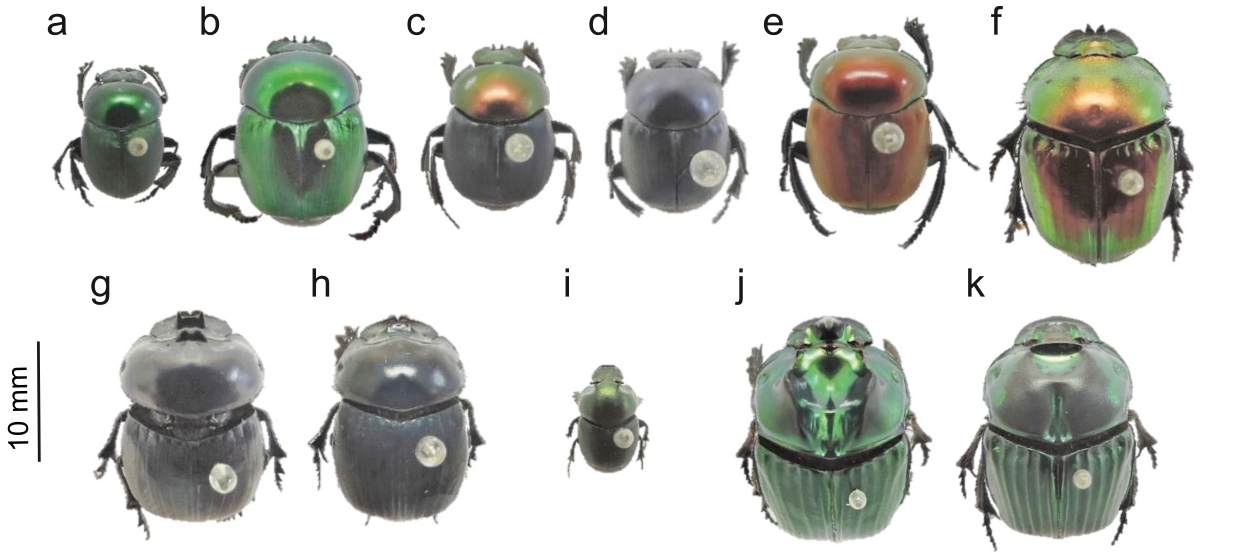

Figure 2. Species of Scarabaeinae sampled at São Joaquim National Park, Santa Catarina, southern Brazil. **a.** *Canthidium (Canthidium) chabanaudi*. **b.** *Canthon (Canthon) curvipes*. **c.** *Canthon (C.) lividus*. **d.** *Canthon (C.) seminitens*. **e.** *Canthon (Francmonrosia) rutilans rutilans*. **f.** *Coprophanaeus (Metallophanaeus) saphirinus*. **g.** *Dichotomius (Luederwaldtinia) opalescens* (male). **h.** *Dichotomius (L.) opalescens* (female). **i.** *Onthophagus (Onthophagus)* aff. *hirculus*, **j.** *Sulcophanaeus menelas* (male). **k.** *S. menelas* (female).

Coprobius semicupreus Burmeister 1873: 413.
Coprobius cupricollis—Burmeister 1874: 122.
Canthon (*Canthon*) *lividus lividus*—Halffter and Martínez 1977: 89.
Canthon (Canthon) *lividus*—Vaz-de-Mello 2000: 191; Audino et al. 2007: 75; da Silva 2008: 25; da Silva et al. 2008b: 145; da Silva et al. 2009a: 64; da Silva et al. 2009b: 35; da Silva 2011: 550; da Silva and Di Mare 2012: 199; da Silva et al. 2012a: 249; da Silva et al. 2012b: 433; Campos and Hernández 2013: 51; da Silva et al. 2013: 684; Costa-Silva et al. 2014: 67; da Silva and Bogoni 2014: 340; Lima et al. 2015: 396; Garcia et al. 2016: 149.

Material examined. Table 2.

Species diagnosis. Balthasar (1939).

Canthon (*Canthon*) *seminitens* Harold, 1868; Figure 2d

Canthon seminitens Harold 1868: 68—Burmeister 1874: 122; Bruch 1911: 185; Gillet 1911: 37; Schmidt 1922: 80; Balthasar 1939: 213; Blackwelder 1944: 201; Lange 1947: 207; Martínez 1949: 187; Martínez 1959: 41; Pereira and Martínez 1960: 41; Vulcano and Pereira 1964: 628.
Coprobius seminitens—Burmeister 1874: 122.
Canthon (*Canthon*) *lividus seminitens*—Halffter and Martínez 1977: 89.
Canthon (*Canthon*) *seminitens*—Vaz-de-Mello 2000: 191; da Silva 2008: 25; da Silva et al. 2008b: 145; da Silva 2011: 550; da Silva et al. 2012a: 249; Campos and Hernández 2015a: 220.

Material examined. Table 2.

Species diagnosis. Harold (1868) and Balthasar (1939).

Canthon (*Francmonrosia*) *rutilans rutilans* Castelnau, 1840; Figure 2e

Canthon rutilans Castelnau 1840: 69—Burmeister 1874: 122; Bruch 1911: 185; Gillet 1911: 33; Luederwaldt 1911: 425; Schmidt 1922: 80; Pessôa and Lane 1941: 416; Blackwelder 1944: 201; Pereira 1944: 88; Lange 1947: 307; Martínez 1959: 40.
Coprobius rutilans—Burmeister 1874: 122.
Francmonrosia rutilans—Pereira and Martínez 1959: 181; Vulcano and Pereira 1964: 601.
Canthon (*Francmonrosia*) *rutilans rutilans*—Halffter and Martínez 1977: 86; Vaz-de-Mello 2000: 191; da Silva 2008: 25; da Silva et al. 2008b: 145; da Silva et al. 2009a: 64; da Silva et al. 2009b: 35; Hernández and Vaz-de-Mello 2009: 611; Hernández et al. 2011: 7; Medina and Campos 2013: 447; Costa-Silva et al. 2014: 67; Lima et al. 2015: 396; Almeida et al. 2015: 277; Garcia et al. 2016: 149; Amore et al. 2017: 5; Tissiani et al. 2017: 405.

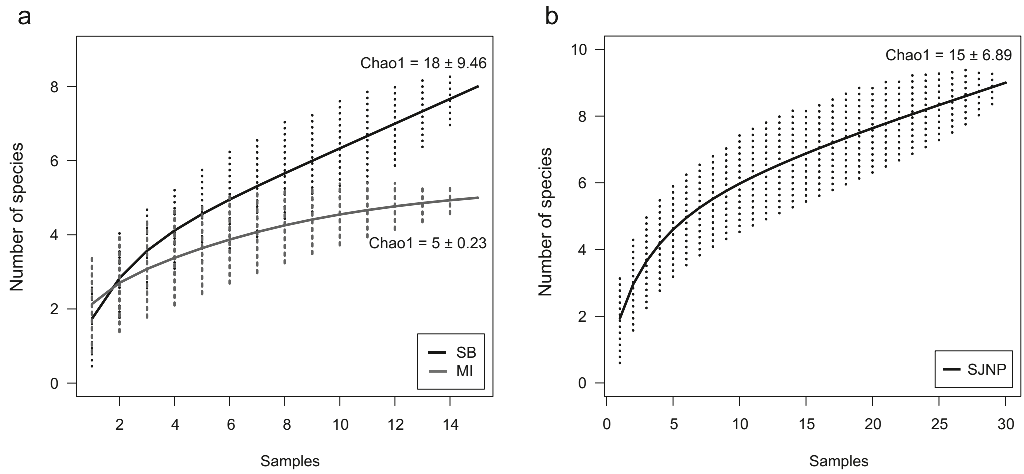

Figure 3. Species accumulation curves for each area (**a**) and for total dataset (**b**) of dung beetles in São Joaquim National Park, Santa Catarina, southern Brazil. MI = Morro da Igreja. SB = Santa Bárbara.

Material examined. Table 2.
Species diagnosis. Harold (1868) and Balthasar (1939).

Coprophanaeus* (*Metallophanaeus*) *saphirinus (Sturm, 1826); Figure 2f

Copris saphirina Sturm 1826: 65.

Phanaeus sapphirinus—Dejean 1833: 140; Dejean 1836: 155; Nevinson 1892: 7; Gillet 1911: 86.

Phanaeus saphirinus—Klug 1841: 210; Sturm 1843: 106; Harold 1869a: 1019; Harold 1869c: 65; Harold 1875: 42 (misidentification of *Coprophanaeus machadoi* (Pereira & d'Andretta, 1955); see Cupello and Vaz-de-Mello 2014); Waterhouse 1891a: 129; Ohaus 1909: 28; Kolbe 1905: 529; Bruch 1911: 190; d'Olsoufieff 1924: 9; Arnaud 2002: 55; Almeida and Mise 2009: 238; Edmonds and Zídek 2010: 29.

Phaenaeus saphirinus—Moura et al. 1997: 271.

Phanaeus chabrillacii Thomson 1857: 117.

Phanaeus chabrillaci—Harold 1869a: 1017; Harold 1869c: 65; Edmonds and Zídek 2010: 69.

Phanaeus saphirinus var. *chabrillaci*—Gillet 1911: 86.

Phanaeus (*Metallophanaeus*) *saphirinus* var. *chabrillaci*—d'Olsoufieff 1924: 28; Pessôa 1934: 293; Pessôa and Lane 1941: 478.

Phanaeus (*Metallophanaeus*) *saphirinus*—d'Olsoufieff 1924: 15; Pessôa 1934: 34; Pessôa and Lane 1941: 478; Pereira 1949: 218; Pereira and d'Andretta 1955:260; Martínez 1959: 102; Halffter and Matthews 1966: 30; Edmonds 1967: 97 (probably in reference to *C. machadoi*; see Cupello and Vaz-de-Mello 2014).

Metallophanaeus sapphirinus—Blackwelder 1944: 209.

Metallophanaeus sapphirinus var. *chabrillaci*—Blackwelder 1944: 209.

Phanaeus (*Metallophanaeus*) *saphyrinus*—Redtenbacher 1868: 56; Lange 1947: 313.

Phanaeus (*Metallophanaeus*) *saphirinus chabrillacei*—Pereira 1949: 222; Pereira and d'Andretta 1955: 260.

Coprophanaeus (*Metallophanaeus*) *saphirinus*—Edmonds 1972: 842; Medri and Lopes 2001: 138; Edmonds and Zídek 2010: 34; Arnaud 2002: 55; Cáceres and Monteiro-Filho 2006: 1191; Almeida and Mise 2009: 232; Almeida and Louzada 2009: 36; Hernández and Vaz-de-Mello 2009: 608; Edmonds and Zídek 2010: 2; Hernández et al. 2011: 5; da Silva et al. 2011: 334; Vaz-de-Mello et al. 2011: 54; da Silva and Di Mare 2012: 199; da Silva et al. 2012b: 433; Campos and Hernández 2013: 51; Culot et al. 2013: 85; Korasaki et al. 2013: 396; da Silva et al. 2013: 684; da Silva and Bogoni 2014: 340; da Silva and Hernández 2014: 5; Viegas et al. 2014: 707; Almeida et al. 2015: 278; Campos and Hernández 2015a: 220; da Silva and Hernández 2015b: 7; Lima et al. 2015: 396; Bitencourt and da Silva 2016: 859; da Silva and Hernández 2015a: 9; da Silva and Hernández 2016: 76; Amore et al. 2017: 5; Santos et al. 2017: 42; Tissiani et al. 2017: 405.

Coprophanaeus (*Metallophanaeus*) *saphirinus saphirinus*—Arnaud 2002: 55.

Coprophanaeus (*Metallophanaeus*) *saphirinus* var. *chabrillacei*—Vaz-de-Mello 2000: 192.

Coprophanaeus (*Metallophanaeus*) *saphirinus chabrillacii*—Arnaud 2002: 56.

Material examined. Table 2.
Species diagnosis. Edmonds and Zídek (2010).

Dichotomius* (*Luederwaldtinia*) *opalescens (Felsche, 1910); Figure 2g (♂) and Figure 2h (♀)

Pinotus speciosus Waterhouse 1891b: 362 (pro part)—Felsche 1901: 145 (misidentification, see Maldaner et al. 2015).

Pinotus opalescens Felsche 1910: 342.—Gillet 1911: 61; Blackwelder 1944: 207.

Dichotomius (*Luederwaldtinia*) *bucki* Pereira 1953: 290.—Vaz-de-Mello 2000: 193.

Dichotomius (*Luederwaldtinia*) *opalescens*—Vaz-de-Mello 2000: 193; Maldaner et al. 2015: 553; Amore et al. 2017: 5.

Material examined. Table 2.
Species diagnosis. Maldaner et al. (2015).

Onthophagus* (*Onthophagus*) aff. *hirculus Mannerheim, 1829; Figure 2i

Onthophagus (*Onthophagus*) aff. *hirculus*—da Silva 2008: 25; da Silva et al. 2008b: 145; da Silva and Audino 2011: 244; da Silva 2011: 550; da Silva and Di Mare 2012: 199; da Silva et al. 2012a: 249; Campos and Hernández 2013: 51.

Material examined. Table 2.
Species diagnosis. Boucomont (1932).
Taxonomic note. This was the only species we could not identify because the group is under taxonomic revision. Thus, citations of the species in bibliographies and catalogs were omitted (see Discussion).

Sulcophanaeus menelas (Castelnau, 1840); Figure 2j (♂), Figure 2k (♀)

Phanaeus menelas Castelnau 1840: 82.

Phanaeus splendidulus (Fabricius, 1781)—Blanchard 1846: 175 (misidentification, see Edmonds 1994); Burmeister 1874: 132 (misidentification, see Edmonds 1994); Fabre 1899: 71 (misidentification, see Edmonds 1994); Judulien 1899: 371 (misidentification, see Edmonds 1994); Bruch 1911: 190 (misidentification, see Edmonds 1994); Gillet 1911: 86 (misidentification, see Edmonds 1994); Pessôa and Lane 1937: 482 (misidentification, see Edmonds 1994); Blackwelder 1944: 210 (misidentification, see Edmonds 1994).

Phanaeus (*Phanaeus*) *splendidulus*—d'Olsoufieff 1924: 35 (misidentification, see Edmonds 1994); Pessôa 1934: 29 (misidentification, see Edmonds 1994).

Phanaeus (*Phanaeus*) *menelas*—Martínez 1959: 105.

Sulcophanaeus menelas—Edmonds 2000: 42; Morelli et al. 1996: 11; Morelli and González-Vainer 1997: 197; Noriega-alvarado 2002: 68; Morelli et al. 2002: 54; Hamel-Leigue et al. 2006: 18; Audino et al. 2007: 75; da Silva et al. 2008a: 78; Almeida and Louzada 2009: 36; da Silva et al. 2009b: 35; Louzada and Carvalho e Silva 2009: 48; Audino et al. 2011: 123; Lopes et al. 2011: 74; Mariategui et al. 2006: 121; da Silva et al. 2012a: 249; Sánchez et al. 2012: 55; Campos and Hernández 2013: 51; Viegas et al. 2014: 707; Campos and Hernández 2015a: 220; Lima et al. 2015: 396; Garcia et al. 2016: 149; Tissiani et al. 2017: 405; Vaz-de-Mello et al. 2017: 4.

Material examined. Table 2.
Species diagnosis. Edmonds (2000).

Discussion

The number of species found in HAG was very low when compared with studies performed in similar open formations in southern Brazil. Using baited pitfall traps several authors found between 16–30 species of dung beetles in natural grasslands in the Brazilian Pampa (da Silva et al. 2008a, 2009b, 2012a). In the same region, even in a eucalyptus area in a matrix originally dominated by natural grasslands, Audino et al. (2011) found 28 species of dung beetles. However, the altitude in those areas was about 220 m above sea level. The low species richness of dung beetles is attributed to the severe climatic and associated environmental conditions found in SJNP, as previously stated by Vaz-de-Mello et al. (2014b). Based on sampling sufficiency curves, there is a great potential to find other species in the park, especially using longer sampling periods and/or other sampling methods.

From those species sampled in our study, only

Coprophanaeus (*Metallophanaeus*) *saphirinus* and *Dichotomius* (*Luederwaldtinia*) *opalescens* were not previously recorded in the southern Brazilian Pampa (see the discussion on species distribution below). The high similarity found between open grasslands in Brazilian Pampa and HAG in southern Brazil is due to the biogeographic history of these formations. Between 42,000 and 10,000 years before the present, cold and dry weather prevailed in the region, and the grassland formations dominated the region (Boldrini 2009). The forests were restricted to small patches in bottom valleys. Between 10,000 and 4000 years ago, temperatures increased, but the climate remained dry, thereby limiting the expansion of forest areas on the grasslands (Boldrini 2009). In addition, at the beginning of the Holocene (12,000–10,000 years ago), 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 Forest began a gradual process of expansion over the grasslands, which became more significant by about 1000 years ago (Behling 2002, Behling et al. 2004). Thus, open formations, now belonging to the Pampas and HAG, were connected by a long period allowing the widespread distribution of dung beetle species (and of other organisms) inhabiting those vegetation formations, despite the difference of altitude since both regions shared severe climatic and environmental conditions.

***Canthidium* Erichson (1847).** This genus is one of the most diverse among Neotropical dung beetles, comprising about 170 described species distributed in Neotropical forests and savannahs (Gill 1991, Audino et al. 2011, da Silva et al. 2011, 2014). It is divided into 2 subgenera, *Canthidium* s. str. Erichson, 1847 and *Eucanthidium* Martínez & Halffter, 1986 (Martínez and Halffter 1986, Vaz-de-Mello et al. 2011) and needs urgent revision, which may result in the establishment of new genera (França et al. 2016). Most species are attracted to dung- and carrion-baited pitfall traps, but there are records of species attracted to rotten fruit, rotten eggs, fungi, and dead insects (Falqueto et al. 2005, Halffter and Halffter 2009, da Silva and Audino 2011, da Silva and Bogoni 2014, Silva et al. 2014). *Canthidium* (*Canthidium*) *chabanaudi* Boucomont, 1928, attracted to human feces, was the only species of this genus found in SJNP. It was described from northern Argentina (Boucomont 1928, Martínez and Halffter 1986) and also has records from open formations that occur in extreme southern Brazil, Pampa biome (da Silva et al. 2008b).

***Canthon* Hoffmannsegg, 1817.** This genus comprises about 200 species distributed in 9 subgenera (*Boreocanthon* Halffter, 1958, *Canthon* s. str., *Francmonrosia* Pereira & Martínez, 1959, *Glaphyrocanthon* Martínez, 1948, *Goniocanthon* Pereira & Martínez, 1956, *Nesocanthon* Pereira & Martínez, 1956, *Peltecanthon* Pereira, 1953, *Pseudepilissus* Martínez, 1954, and *Trichocanthon* Pereira & Martínez, 1959), and a incertae sedis species-group (Vaz-de-Mello et al. 2011). It is an American genus, distributed from Canada to Argentina (Vaz-de-Mello et al. 2011), with mostly copro-necrophagous species. Some species, however, show other trophic habits feeding on fungi (Vaz-de-Mello 1999, Falqueto et al. 2005), rotten fruits (Halffter and Halffter 2009, Audino et al. 2011, da Silva et al. 2012a, 2012b, Lima et al. 2015), dead insects and millipedes (Villalobos et al. 1998), and also ant predation (Hertel and Colli 1998, Vaz-de-Mello et al. 1998, Silveira et al. 2006, Araújo et al. 2015). Four species/subspecies of *Canthon* were sampled in SJNP. *Canthon* (*C.*) *curvipes* was attracted to rotten flesh. It has been found in dung of large herbivores and human feces, as well as attracted to fish and other small dead animals; it is distributed for southeast region of South America, including open and forest formations (Luederwaldt 1911, Martínez 1959, da Silva et al. 2008a, Audino et al. 2011, da Silva et al. 2012a). Unlike the specimens found in the Brazilian Pampa, which are red, the individual found in SJNP is metallic green. Most individuals of *C.* (*C.*) *lividus* and *C.* (*C.*) *seminitens* were sampled in traps baited with rotten flesh in the SJNP. Both forms of this species have generalist trophic habits and also are distributed for southeast region of South America, including open and forest formations (Martínez 1959, Audino et al. 2011, da Silva et al. 2011, 2012b; da Silva and Di Mare 2012, Costa-Silva et al. 2014; da Silva and Bogoni 2014, Lima et al. 2015). *Canthon (Francmonrosia) rutilans rutilans* was attracted 5 times more to human feces than to rotten meat in SJNP. This species has also been attracted to fruit- and cattle dung-baited traps in grasslands, forests, and eucalyptus plantations in southern South America (Martínez 1959, da Silva et al. 2008a, 2009b, 2012a, Hernández and Vaz-de-Mello 2009, Audino et al. 2011, Medina and Campos 2013). The red or brown form of *C. rutilans* seems to be associated with cooler areas in its distribution range, both in forests and in open areas, while the green or blue form (i.e. *Canthon* (*F.*) *rutilans cyanescens* Harold, 1868) seems to be associated only with forests lower than 1000 m altitude (Campos and Hernández 2013, 2015a, 2015b, Bogoni and Hernández 2014, Costa-Silva et al. 2014, da Silva and Hernández 2014, da Silva and Hernández 2015a, 2015b, 2016). A taxonomic revision is currently underway to split the 2 subspecies into separate species (Vaz-de-Mello et al. 2014a).

***Coprophanaeus* d'Olsoufieff, 1924.** This genus was revised by Edmonds and Zídek (2010) and comprises at least 43 valid species distributed among 3 subgenera (*Coprophanaeus* s. str. Olsoufieff, 1924, *Metallophanaeus* Olsoufieff, 1924, and *Megaphanaeus* Olsoufieff, 1924) in the New World (Cupello and Vaz-de-Mello 2014). The subgenus *Metallophanaeus* comprises 9 colorful species distributed from eastern Brazil (east of Amazonia) southward to northeastern Argentina (Edmonds and Zídek 2010). All species of this subgenus are diurnal and copronecrophagous. *Coprophanaeus* (*Metallophanaeus*) *saphirinus* is a very common species in forest habitats along the Paranaian subregion of the Neotropical region

(Edmonds and Zídek 2010). However, it is also found in open areas such as Chaco formations in northeastern Argentina (Edmonds and Zídek 2010). The only individual sampled in SJNP attracted to rotten meat is a red individual of *C.* (*M.*) *saphirinus*. In the southern portion of the species range, the red individuals occur more frequently in higher elevations than does blue or green ones, but they are also found at the sea level and in the northern portion of the species' range in sympatry with blue and green individuals (Cupello and Vaz-de-Mello 2014). *Coprophanaeus* (*M.*) *saphirinus* is attracted to herbivorous feces (Martínez 1959), humans feces, rotten meat, rotten fruit (Almeida and Louzada 2009, da Silva et al. 2011, 2012b, Lima et al. 2015), rotten fish (da Silva and Di Mare 2012), and rotten eggs (da Silva and Bogoni 2014).

***Dichotomius* Hope, 1838.** This genus, exclusive to the Americas, is comprised of about 170 species widely distributed in the Neotropical region (the USA to Argentina) (Vaz-de-Mello et al. 2011), especially in forest and grassland areas. It is divided into four subgenera, *Dichotomius s. str.*, *Homocanthonides* Luederwaldt, 1929, *Luederwaldtinia* Martínez, 1951, and *Selenocopris* Burmeister, 1846 (Martínez 1951; Vaz-de-Mello et al. 2011). The subgenus *Luederwaldtinia* has 65 valid species assigned to 13 species-groups (Nunes and Vaz-de-Mello 2013; Maldaner et al. 2015; Nunes et al. 2016). Some *Dichotomius* species show extremely restricted distributions (Nunes and Vaz-de-Mello 2013; Maldaner et al. 2015; Nunes et al. 2016). That is the case of *Dichotomius (Luederwaldtinia) opalescens* (Felsche, 1910), the only species of this genus sampled in the SJNP so far. This species belongs to the *D. (L.) speciosus* (Waterhouse, 1891) species group, which comprises four species restricted to areas above 1,000 m altitude in the Brazilian Atlantic Forest (Maldaner et al. 2015). *Dichotomius (L.) opalescens* is restricted to the Serra Geral mountain range (the northern Rio Grande do Sul and southern Santa Catarina states), and thus it is considered as Endangered (EN), according to the conservation status based on the extent of occurrence applied by the International Union for Conservation of Nature (IUCN) (Maldaner et al. 2015). However, its distribution covers at least three national conservation units in southern Brazil: São Joaquim National Park, Aparados da Serra National Park, and São Francisco de Paula National Forest (Maldaner et al. 2015). The biology of this species is poorly known. All individuals were sampled in traps baited with human feces, suggesting a coprophagous habit. This species has also been sampled in Araucaria forest and eucalyptus plantations (Maldaner et al. 2015), suggesting a generalist environmental distribution in the Serra Geral mountain range.

***Onthophagus* Latreille, 1802.** This genus is globally distributed and includes about 2000 species (Tarasov and Kabakov 2010), most considered coprophagous, with 160 species in the Americas (Rossini and Vaz-de-Mello 2016). In the Americas, the genus comprises species of two subgenera (*Onthophagus s. str.* Latreille, 1807 and *Palaeonthophagus* Zunino, 1979) and an *incertae sedis* species, including species introduced from African and Europe (Vaz-de-Mello et al. 2011). *Onthophagus (Onthophagus)* aff. *hirculus* Mannerheim, 1829 belongs to a group of species taxonomically close to *O. (O.) hirculus* and needs urgent taxonomic revision (França et al. 2016). Individuals of this species were sampled only in pitfall traps baited with human feces in the SJNP. However, this species-complex is distributed for a wide range of environments in the South America, being attracted by several kinds of baits (França et al. 2016, and references therein).

***Sulcophanaeus* d'Olsoufieff, 1924.** This genus was reviewed by Edmonds (2000) and comprises 14 species in five species groups distributed from Mexico to Argentina, and also Jamaica (Vaz-de-Mello et al. 2011). *Sulcophanaeus menelas* (Castelnau, 1840) has coprophagous habits and thus all individuals sampled were attracted to human feces in SJNP. It is attracted to human (Almeida and Louzada 2009; Audino et al. 2011; da Silva et al. 2012a) and also herbivorous feces (Martínez 1959). It is very common in open areas in southern Brazil (Edmonds 2000; Almeida and Louzada 2009; da Silva et al. 2009b; da Silva et al. 2012a), Uruguay (Edmonds 2000; Morelli et al. 2002), central and northeastern Argentina and eastern Paraguay (Martínez 1959; Edmonds 2000).

In addition to the previously mentioned species, Vaz-de-Mello et al. (2014b) found *Canthon (Canthon) angularis* Harold, 1868, *Canthon (Canthon) quadripunctatus* Redtenbacher, 1868, an unidentified species of *Canthon*, *Ateuchus hypocrita* Balthasar, 1939, an unidentified species of *Homocopris*, and also *D. (L.) opalescens* (Felsche, 1910) (cited as *Dichotomius bucki* Pereira, 1953). Those authors sampled Scarabaeoidea beetles using different methods in five sites, both in open and forest sites, in the MI, from 1,370 to 1,750 m a.s.l. *Ateuchus* Weber, 1801 has copro-necrophagous species inhabiting forest and grasslands in the Neotropical region (Vaz-de-Mello 1999). Some *Ateuchus* species are associated with ant nests (Vaz-de-Mello et al. 1998) or mammalian borrows (Génier 2015). *Homocopris* Burmeister, 1846 was recently reassigned as a valid genus, with few species under a reviewing process. Its species are generally found associated with altitude forests or open areas from Argentina, Chile, Colombia, Ecuador, and southern Brazil (Vaz-de-Mello et al. 2010). In Brazil, *Homocopris* species are associated with well-preserved Atlantic Forest sites with high altitudes (in general, above 1000 m).

The assemblages of dung beetles found in high altitude grasslands in the São Joaquim National Park were composed of diurnal species with colorful bodies (both small and large), with similar proportions of rollers and tunnellers, and coprophagous and/or generalist trophic habits. Due to the severe climatic conditions found in the Park, longer sampling periods should be performed aiming to achieve a more robust sampling sufficiency for dung beetle species (da Silva and Hernández 2015b). The importance of using Coleoptera in the development of public environmental strategies such as management plans and creation of protected areas is highlighted (Vaz-de-Mello et al. 2014b) since this order is the most diverse group in number of animal species.

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