

The role of semi-natural grasslands and livestock in sustaining dung beetle communities (Coleoptera, Scarabaeoidea) in sub-Mediterranean areas of Slovenia

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Abstract

The role of semi-natural grasslands and livestock in sustaining dung beetle communities (Coleoptera, Scarabaeoidea) in sub-Mediterranean areas of Slovenia. We studied the richness and structure of the coprophagous Scarabaeoidea community in two pastures (Hrastovlje and Zazid) in sub-Mediterranean Slovenia. In each pasture, we examined three habitat patches characterised by different levels of grazing (S1, the active part of the pasture; S2, the overgrown part of the pasture, mainly spiny shrubs; S3, a meadow with some overgrown patches of shrubs outside the fenced pasture). The main results were as follows: (1) 29 species were sampled, corresponding to about three quarters of the species presumably present at the two study sites; (2) species richness and abundance in Zazid were similar in all three patches; (3) the species richness and abundance in Hrastovlje (in total, and separately for dwellers and tunnelers) were highest in S2. In Hrastovlje, dwellers were most abundant in S1. As the two different habitat patches were shown to positively influence the dung beetle community, we recommend maintaining a traditionally-managed mosaic landscape.

Key words: Karst pasture/meadow, Species biodiversity, Microhabitat, Bait, Pitfall traps

Resumen

La importancia de los pastizales seminaturales y la ganadería en el mantenimiento de las comunidades de coleópteros coprófagos (Coleoptera, Scarabaeidae) en las zonas submediterráneas de Eslovenia. Estudiamos la riqueza y la estructura de la comunidad de escarabeoideos coprófagos en dos pastizales (Hrastovlje y Zazid) en la zona submediterránea de Eslovenia. En cada pastizal, analizamos tres fragmentos caracterizados por diferentes grados de pastoreo (S1, la zona activa de pastoreo; S2, la zona de crecimiento del pasto, principalmente arbustos espinosos; y S3, una pradera con algunos fragmentos arbustivos con crecimiento fuera del pastizal vallado). Los resultados principales fueron los siguientes: (1) se muestrearon 29 especies que correspondían aproximadamente a tres cuartas partes de las especies previsiblemente presentes en los dos sitios de estudio; (2) la riqueza y la abundancia de especies en Zazid fueron parecidas en los tres fragmentos; y (3) la riqueza y la abundancia de especies en Hrastovlje (en total y los residentes y los cavadores por separado) fueron más elevadas en S2. En Hrastovlje, los residentes fueron más abundantes en S1. Como se constató que ambos fragmentos de hábitat influían positivamente en la comunidad de coleópteros coprófagos, recomendamos mantener un territorio en mosaico gestionado de forma tradicional.

Palabras clave: Pasto y pradera cársticos, Biodiversidad de especies, Microhábitat, Cebo, Trampas de caída

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Introduction

Within the topographically diverse Mediterranean Basin (S Europe) lying at the intersection of Europe, Asia and Africa (cf. Blondel, 2006; Blondel et al., 2010; Christodolou et al., 2016), grasslands (e.g. meadows, pastures) and shrublands support exceptionally high biodiversity (Lumaret and Kirk, 1991; Verdú et al., 2000; Allen, 2003). Karst meadows belonging to the class *Festuco–Brometea*, for example, are regarded as species-rich habitats of national and European importance, and are among the most species-rich environments within the semi-natural habitat types (Jugovic et al., 2013a). Two main associations can be found there: the association *Carici–Centaureetum* in pastures and the association *Dianthonio–Scorzeneretum* in meadows (Kaligarič, 2005). These grasslands are the result of past human activities (Kaligarič, 2005; Stergaršek, 2009) that strongly influenced the layout and biodiversity of the landscape. Many turned into overgrown areas (shrublands and later pioneer forests: Jugovic et al., 2013a) after traditional extensive agricultural practices were abandoned (Zeiler, 2000; Stefanescu et al., 2004). In the Mediterranean, the maintenance of open (meadows, pastures) and semi-open (shrubland) habitats ceased with the abandonment of traditional agricultural practices (extensive grazing and occasional extensive mowing: see Jogan et al., 2004; Kaligarič, 2005). The consequent fragmentation of grasslands decreased the size of habitat patches and their connectivity (Polus et al., 2007). However, a dense network of suitable habitats is crucial to maintain metapopulations and enable dispersal of animals inhabiting the remaining open spaces (cf. Anthes et al., 2003; Bergman and Landin, 2001; Mousson et al., 1999; Polus et al., 2007; Thomas et al., 1992).

Grazing activity increases the extent of open areas (Lumaret, 1994), but it also strongly modifies the vegetation structure. Hence, grazing is often seen to have a negative impact on biodiversity (e.g. Jugovic et al., 2013a, 2014a, 2017), but some invertebrates, such as dung beetles (Coleoptera: Scarabaeoidea), rely on the presence of livestock, depending on their feces as a main source of nutrients (Verdú and Galante, 2004; Zamora et al., 2007). Such ephemeral habitats with prominent temporal instability (Finn, 2001) are subjected to succession that is short-termed (days or weeks, rarely months), and the organisms specialised in their exploitation compete with one another (e.g. Metazoa, Fungi; Sladecek et al., 2017). Different animal taxa can occupy different spatial compartments: while the community inhabiting the surface or outer rim of the excrement consist mainly of adult dipterans (Diptera), the internal community consists mainly of beetle (Coleoptera) adults and dipteran larvae (Sladecek et al., 2017; Mohr, 1943). Temporal segregation and use of the excrement has already been extensively studied, showing that copro- and necrophilous species are segregated along the successional gradient by their oviposition preferences (see Sladecek et al., 2017 for a review). Although not as highly specialised as co-

prophagous Scarabaeoidea, some other invertebrate taxa can also be consistently attracted to vertebrate excrement, either because it is a food source (coprophagous invertebrates such as dipterous larvae and earthworms) or because it contains their (e.g. Chilopoda, Scorpiones) prey species (Curry, 1994).

Coprophagous dung beetles (Scarabaeoidea) are an invertebrate group that is attracted to (predominantly) fresh herbivore and omnivore excrement; and many species have developed complex nesting behaviour that includes the use of dung as a food supply for their offspring (Cambefort and Hanski, 1991). Coprophagous dung beetles are a part of the diverse superfamily Scarabaeoidea, and members of three families, Aphodiidae, Geotrupidae and Scarabaeidae (Halffter and Matthews, 1966), share a coprophagous life style. Dung beetles fall into three basic nesting categories, rollers (telecoprids), tunnelers (paracoprids) and dwellers (endocoprids; cf. Errouissi et al., 2009). Rollers make a ball from the excrement and use it as a food source or as a brooding chamber. Tunnelers bury the dung wherever they find it, while dwellers neither roll nor burrow, but stay and live in the dung (Scholtz et al., 2009).

In a wide array of habitats in ecosystems, Coprophagous Scarabaeoidea play an important role in many processes, such as recycling of animal excreta, nutrient cycling, bioturbation, pollination, seed dispersal and primary production, and parasite suppression (Losey and Vaughan, 2006; Nichols et al., 2008; Hanski and Camberfort, 1991; Lobo et al., 2004). Through these roles, they help establish and sustain other ground living invertebrate communities. Coprophagous Scarabaeoidea may be used as bio-indicators (cf. Favila and Halffter, 1997; Lobo et al., 2002; Verdú et al., 2000) as they are susceptible to slight changes in their environment and compositionally respond to local changes (Nichols et al., 2008). They are therefore useful to detect small differences in habitat changes on a local scale. Moreover, significant differences in species presence, abundance and diversity indices can help conservation practitioners assess the relative importance of natural, semi-natural and highly transformed habitats (Davis et al., 2004). The transformation in habitat considered to be mainly responsible for the decrease in the dung beetles' species richness and abundance is the abandonment of pasturelands. Nevertheless, a variety of impacts on the dung beetle community during the succession that follows grazing abandonment have been proposed (e.g. Macagno and Palestrini, 2009; Negro et al., 2011; Verdú et al., 2000; Tonelli et al., 2017a).

In an attempt to highlight the differences in diversity of a dung beetle community at a local scale, we (i) present data on the species community of dung beetles from two study sites located in sub-Mediterranean dry grasslands of SW Slovenia, and (ii) test for possible differences in dung beetle species richness and abundance between three habitat patches within each site differing in their levels of grazing (S1, S2, S3: see section on study sites). We aimed to determine what level of grazing impact can support the highest dung beetle diversity.

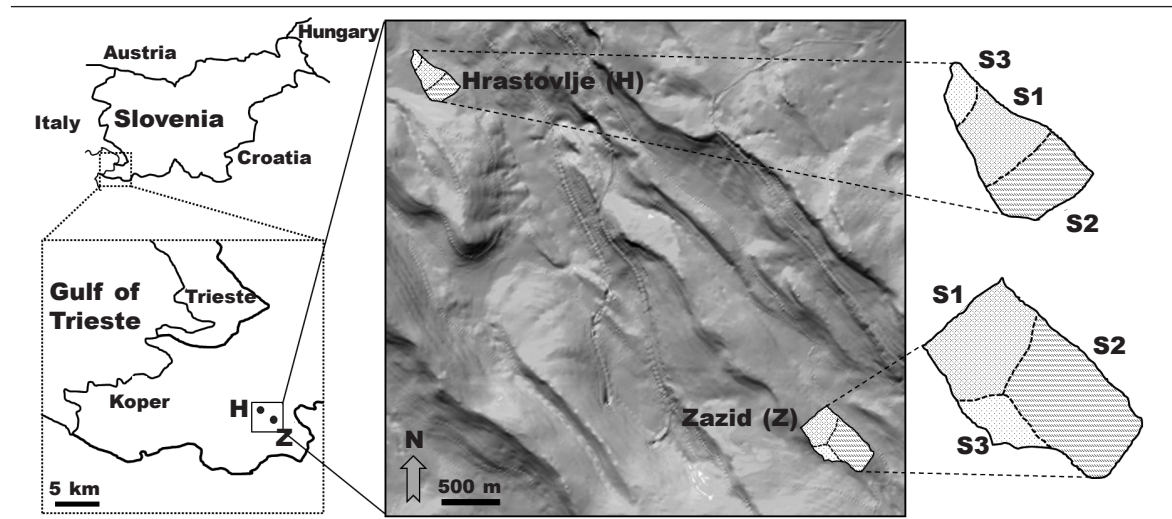


Fig. 1. Geographic position (inset) and habitat patches (S1, grazed part of the pasture; S2, overgrowth part of the pasture; S3, dry karst meadow) at two study sites (Hrastovlje and Zazid) in SW Slovenia.

Fig. 1. Posición geográfica (recuadro) y fragmentos de hábitat (S1, zona activa de pastoreo; S2, zona de crecimiento del pasto; S3, pradera cárstica seca) en los dos sitios del estudio (Hrastovlje y Zazid), en el sudeste de Eslovenia.

Material and methods

Study sites

The study sites selected were two pastures and their surroundings with a total size of 22.5 ha, located in south-western Slovenia (45° 30' 40.55" N, 13° 54' 47.55" E). Study sites were between 90 and 450 m above sea level. Both sites lie on the predominately carbonate bedrock near the villages of Hrastovlje (study site H) and Zazid (study site Z) and are 4.3 km apart (measured centre to centre). Each study site consisted of three habitat patches that represent different levels of grazing impact (fig. 1). Within the fenced pasture, two habitat patches were present: (1) a grazed part of the pasture (stage S1: goats in H, and cattle in Z), and (2) an overgrown part of the pasture, mainly with some spiny shrubs, as a result of selective grazing (stage S2: in Z, *Prunus spinosa* Linnaeus, *Prunus mahaleb* Linnaeus, *Crataegus monogyna* Jacquin, *Cotinus coggygria* Scopoli, and in H: *Paliurus spina-christi* Miller; cf. Jugovic et al., 2013a, 2017; field observations). The shrubs were relatively evenly distributed across the patch and close to each other. Outside the fenced pasture, (3) abandoned and partly overgrown dry karst meadow ('islands' of predominantly *C. coggygria* or *C. monogyna*) grazed in the past made up the third patch (stage S3).

Sampling design

Sampling took place between 12 March 2012 and 7 November 2012. We used pitfall traps to capture

dung beetles at each habitat patch in the two study sites. Traps consisted of 500 ml plastic jars with a depth of 13 cm and a diameter of 10 cm. Traps were evenly distributed across the habitat patches, at least 50–100 m away from each other (Larsen and Forsyth, 2005; Silva and Hernández, 2015). The only exception was the smallest patches (S3 at both sites), where any given pair of two nearest traps could be closer, but still at least 20 m apart. Even then, such a pair consisted of one baited and one unbaited (control) trap. Four sampling traps were used per habitat type × study site, i.e.; 24 traps in total. On every occasion, two traps were used as a control (without bait). In the other two, we added a ball of fresh cow excrement (cca. 4–5 cm³) as bait to additionally attract the animals. The use of cow excrement for bait has shown to be highly effective for sampling Scarabaeoidea in Mediterranean regions (e.g. Martín-Pfiera and Lobo, 1996; Barbero et al., 1999; Dormont et al., 2007, 2010; Errouissi et al., 2004). The bait was wrapped in gauze and attached to a wire over the trap opening. Although some authors recommend larger amounts of bait (e.g. Errouissi et al., 2004), we found the baited traps to be highly effective in comparison with the control traps. Animals were collected 14 days after placement of traps. Traps were emptied a total of 15 times. Propylene glycole was used as a fixative.

Laboratory work

Dung beetles were separated from other trapped ground invertebrates. Each specimen was identified to species level (following Ballerio et al., 2010:

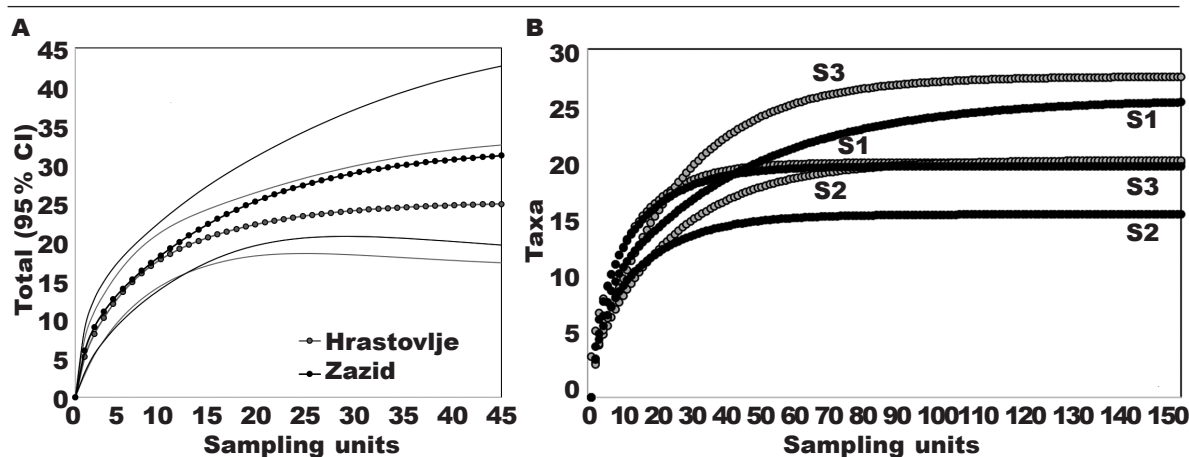


Fig. 2. A, species accumulation curves (dotted) for Scarabaeoidea from Hrastovlje (grey) and Zazid (black) with 95 % confidence interval (outer lines). The accumulation curve is extrapolated by the factor 3. B, species accumulation curves for Scarabaeoidea from three habitat patches (S1, S2, S3) from Hrastovlje (grey) and Zazid (black). The accumulation curve is extrapolated by the factor 10. Each sampling unit represents: A, twelve traps per locality; B, four traps per habitat patch. Traps were emptied 15 times, at 14-day intervals.

Fig. 2. A, curvas de acumulación de especies (punteadas) de la familia Scarabaeidae de Hrastovlje (gris) y Zazid (negro) con un intervalo de confianza del 95 % (líneas externas). La curva de acumulación se ha extrapolado por el factor 3. B, curvas de acumulación de especies de la familia Scarabaeidae de los tres fragmentos de hábitat (S1, S2 y S3) de Hrastovlje (gris) y Zazid (negro). La curva de acumulación se ha extrapolado por el factor 10. Cada unidad de muestreo representa: A, doce trampas por localidad; B, cuatro trampas por fragmento de hábitat, respectivamente. Las trampas se vaciaron 15 veces, a intervalos de 14 días.

when not identifiable by external morphology, genital structures were also inspected). Each animal was labelled and stored in the collection of the Department of Biodiversity, Faculty of Mathematics, Natural Sciences and Information Technologies, University of Primorska, for further studies. Numbers of specimens and taxa were counted per trap. For dung beetles, numbers of specimens and species were counted in total, and further subdivided into four groups from three guilds (cf. Jay–Robert et al., 2008a; Errouissi et al., 2009: Aphodiidae–dwellers, Scarabaeidae–tunnelers, Geotrupidae–tunnelers and Scarabaeidae–rollers).

Data analysis

We constructed species accumulation curves with 95% confidence intervals using the program EstimateS 9.1.0 (purl.oclc.org/estimates), separately (i) for each of the two study sites and (ii) for each of the three habitats (separately for the two study sites) to estimate inventory completeness. A single sampling unit (SU) consisted of the specimens collected per (i) locality and (ii) habitat patch over each 14-day interval (i.e. number of sampling occasions (= 15) correspond to number of SUs). At the locality level, each SU consisted of 12 pitfall traps, and at the habitat patch level, each SU consisted of 4 pitfall traps. Table 1 shows the complete list of collected species and individuals.

Diversity of taxa is represented by the number of species. The Shannon index (H' , here with \ln) was calculated for each study site and study site \times habitat patch. Mean Shannon values were then calculated using the data of the 24 traps. For these calculations, we used program PAST (Palaeontological Statistics: Hammer, 1999–2012). The mean Shannon index values between the two study sites (t -test, significance accepted at $p < 0.05$) and between the three habitat patches within each study site (ANOVA, at $p < 0.05$) were compared using the SPSS Statistical package ver. 20.0 (SPSS inc., 1989, 2011). Due to the deviations of data from the normal distribution (Kolmogorov–Smirnov test, $p < 0.05$), non-parametric statistical tests executed within SPSS Statistical package ver. 20.0 were used to test the following hypotheses. To test for possible differences in the number of species and specimens between the two study sites (data for all pitfall traps combined) we implemented a Mann–Whitney U-test of ranks, and accepted the difference to be significant at $p < 0.05$. We also tested for possible differences in abundance of species and specimens between the three habitat patches using a Kruskal–Wallis test of ranks ($p < 0.05$) and post-hoc pairwise comparisons with the Dunn–Bonferroni post-hoc method. Finally, to test for differences in species richness and abundance between the three patches, we treated the data at each study site separately in order to

Table 1. A list of Scarabaeoidea species collected in pitfall traps in three habitat patches (S1, S2, S3) at two study sites (Hrastovlje and Zazid) in SW Slovenia in 2012. Diversity indices (No. of species, H') are shown at the bottom of the table for the two study sites, and three habitat patches within each of them.

Tabla 1. Lista de especies de la familia Scarabaeidae recogidas en trampas de caída en tres fragmentos de hábitat (S1, S2 y S3) en los dos sitios del estudio (Zazid y Hrastovlje), situados en el sudeste de Eslovenia en 2012. Al final de la tabla se muestran los índices de diversidad (n° de especies y H') de los dos sitios del estudio y los tres fragmentos de hábitat en cada uno de ellos.

Family	Hrastovlje			Zazid		
	S1	S2	S3	S1	S2	S3
Aphodiidae—dwellers						
<i>Oxyomus sylvestris</i> (Scopoli, 1763)	2	0	3	0	12	0
<i>Sigorus porcus</i> (Fabricius, 1792)	2	4	8	0	0	0
<i>Loraphodius suarius</i> (Faldermann, 1836)	0	0	0	0	0	1
<i>Subrinus sturmi</i> (Harold, 1870)	1	0	0	0	0	0
<i>Aphodius fimetarius</i> (Linnaeus, 1758)	0	0	12	0	0	0
<i>Eurodalus paracoenosus</i> (Balthasar & Hrubant, 1960)	0	0	1	0	0	1
<i>Teuchestes fossor</i> (Linnaeus, 1758)	0	0	0	0	0	1
<i>Phalacrothous biguttatus</i> (Germar, 1824)	0	0	0	0	0	1
<i>Esymus pusillus</i> (Herbst, 1789)	0	0	0	1	0	0
<i>Colobopterus erraticus</i> (Linnaeus, 1758)	0	0	0	2	0	0
<i>Acrossus luridus</i> (Fabricius, 1775)	0	0	0	2	0	0
<i>Melinopterus prodromus</i> (Brahm, 1790)	3	0	0	0	0	0
Geotrupidae—tunnelers						
<i>Geotrupes spiniger</i> Marsham, 1802	0	0	0	3	0	2
<i>Trypocopris vernalis</i> (Linnaeus, 1758)	68	201	46	54	134	147
Scarabaeidae—tunnelers						
<i>Onthophagus grossepunctatus</i> Reitter, 1905	51	82	96	54	59	165
<i>Onthophagus verticicornis</i> (Laicharting, 1781)	0	7	2	26	21	52
<i>Onthophagus medius</i> (Kugelann, 1792)	3	0	0	19	2	20
<i>Onthophagus ruficapillus</i> Brullé, 1832	4	2	1	0	1	0
<i>Onthophagus coenobita</i> (Herbst, 1783)	0	2	0	0	0	12
<i>Onthophagus lemur</i> (Fabricius, 1781)	0	0	0	11	0	0
<i>Onthophagus ovatus</i> (Linnaeus, 1767)	3	4	3	7	6	7
<i>Onthophagus joannae</i> Goljan, 1953	4	5	4	5	6	18
<i>Onthophagus taurus</i> (Schreber, 1759)	10	3	1	1	1	3
<i>Onthophagus illyricus</i> (Scopoli, 1763)	2	0	1	0	0	5
<i>Onthophagus fracticornis</i> (Preyssler, 1790)	0	2	2	7	3	15
<i>Caccobius schreberi</i> (Linnaeus, 1767)	20	0	2	0	0	0
<i>Euoniticellus fulvus</i> (Goeze, 1777)	3	1	0	0	2	0
<i>Copris lunaris</i> (Linnaeus, 1758)	2	0	0	0	0	0
Scarabaeidae—rollers						
<i>Sisyphus schaefferi</i> (Linnaeus, 1758)	35	364	148	403	459	968
No. of species (study site × habitat patch)	16	12	15	14	12	16
No. of species (study site)		21			23	
No. of individuals (study site × habitat patch)	232	677	330	595	706	1,418
No. of individuals (study site)		1,220			2,719	
H' (study site × habitat patch)	1.91	1.18	1.51	1.25	1.13	1.16
H' (study site)		1.54			1.21	

Table 2. Comparisons of median values (Mann–Whitney U–test) in numbers of Scarabaeoidea species and specimens between the two study sites (H, Hrastovlje; Z, Zazid) for different datasets: All, whole dataset, and separately for dwellers, tunnelers and rollers; n/a, not applicable; ¹ rollers were omitted from the analysis as only one species was present in the samples (*Sisyphus schaefferi*); ² only two species of Geotrupidae–tunnelers were present in the samples, so the analyses were conducted on data pooled together for Scarabaeidae–tunnelers + Geotrupidae–tunnelers.

Tabla 2. Comparación de los valores medianos (prueba U de Mann–Whitney) de la cantidad de especies e individuos de la familia Scarabaeidae en los dos sitios del estudio (H, Hrastovlje; Z, Zazid) para diferentes conjuntos de datos: All, todo el conjunto de datos; y por separado para dwellers (residentes), tunnelers (cavadores) y rollers (rodadores); n/a: no aplicable. ¹ se omitió a los rodadores del análisis porque en las muestras solo se encontró una especie (*Sisyphus schaefferi*); ² solo se encontraron dos especies de la familia Geotrupidae–cavadores en las muestras, de tal forma que los análisis se realizaron con los datos agrupados de Scarabaeidae–cavadores + Geotrupidae–cavadores.

Compared groups	All		Dwellers		Tunellers ²		Rollers		
	Z	p	Z	p	Z	p	Z	p	
No. of species ¹	H:Z	–0.839	0.401	–1.099	0.272	–0.899	0.369	n/a	n/a
No. of individuals	H:Z	–0.58	0.562	–1.108	0.268	–0.974	0.330	–1.58	0.114

avoid the influence of geographic distance, altitudinal difference, and different livestock characteristics between the two sites.

Results

Species richness

In total, 3,939 Scarabaeoidea specimens (Hrastovlje: 1,220; Zazid: 2,719) were collected. Of these, we identified 29 species of Scarabaeoidea belonging to all four groups from the three guilds (Aphodiidae–dwellers: 12 species, Geotrupidae–tunnelers: 2 species, Scarabaeidae–tunnelers: 14 species, Scarabaeidae–rollers: 1 species). This corresponds to ca. 25% of known Slovenian species belonging to these three families (cf. Brelih et al., 2010). In Hrastovlje, we collected 21 species, i.e. 87% of species we would collect at doubled sample effort, or 84% of species at tripled effort. In Zazid, we collected 23 species, and the respective percentages were 79% and 74%. At higher sampling effort, the extrapolation line for Hrastovlje started to approach the maximum at 5–times greater effort (i.e. calculated maximum of 25 species: collected species represent 84%), whereas for Zazid, the extrapolation line reached its maximum at 9–times larger effort (i.e. calculated maximum of 32 species: collected species represent 72%). Both accumulation curves with their 95% confidence intervals overlapped (fig. 2A).

The results for the three habitat patches from Hrastovlje and Zazid (fig. 2B) were: 16 and 14 collected species in S1 (corresponding to 79% and 55% of expected maximum number of species [H: 20 species, Z: 26 species] at 7 and 19–times larger sampling effort), 12 species in S2 from each of the

two localities (corresponding to 59% and 76% of expected maximum number of species [H: 20, Z: 16] at 11– and 8–times larger sampling effort), and 15 and 16 collected species in S3 (corresponding to 54% and 80% of expected maximum number of species [H: 28, Z: 20] at 11– and 8–times larger sampling effort). There was an evident overlap among the 95% confidence intervals for all six accumulation curves.

In total, six species (Aphodiidae–dwellers: *Aphodius fimetarius* (Linnaeus, 1758), *Aphodius prodromus* (Brahn, 1790), *Sigorus porcus* (Fabricius, 1792), *Subrinus sturmi* (Harold, 1870); Scarabaeidae–tunellers: *Copris lunaris* (Linnaeus, 1758), *Caccobius schreberi* (Linnaeus, 1767)) were present exclusively at the study site in Hrastovlje, and eight species (Aphodiidae–dwellers: *Acrossus luridus* (Fabricius, 1775), *Colobopterus erraticus* (Linnaeus, 1758), *Esymus pusillus* (Herbst, 1789), *Loraphodius suarius* (Faldermann, 1836), *Phalacro-nothus biguttatus* (Germar, 1824), *Teuchestes fossor* (Linnaeus, 1758); Geotrupidae–tunellers: *Geotrupes spiniger* Marsham, 1802; Scarabaeidae–tunellers: *Onthophagus lemur* (Fabricius, 1781)) were found only in Zazid. The rest of the species were collected at both study sites (table 1).

Diversity and factors influencing species richness and structure

Diversity index values showed no statistically significant differences between Hrastovlje ($H' = 1.54$) and Zazid ($H' = 1.21$) (t–test, $p > 0.05$; table 1). The most abundant species, *Sisyphus schaefferi* (Linnaeus, 1758), represented 44.8% and 67.3% of the Scarabaeoidea community in Hrastovlje and Zazid, respectively. The Shannon index was highest

Table 3. Comparison of median values of the number of species and specimens of Scarabaeoidea among the three habitat patches (S1, S2, S3) (KW, Kruskal–Wallis test) and post-hoc pairwise comparisons (PC, Dunn–Bonferroni) from two study sites (SS: H, Hrastovlje; Z, Zazid) in SW Slovenia: STS, standardised test statistic; n/a, not applicable; ¹ rollers were omitted from the analysis as only one species was present in the samples (*Sisyphus schaefferi*); ² only two species of Geotrupidae–tunnelers were present in the samples, so the analyses were conducted on data pooled together for Scarabaeidae–tunnelers + Geotrupidae–tunnelers.

Tabla 3. Comparación de los valores medianos de la cantidad de especies e individuos de la familia Scarabaeidae en los tres fragmentos de hábitat (S1, S2, S3) (KW, prueba de Kruskal–Wallis) y comparación por pares a posteriori (PC, Dunn–Bonferroni) de los dos sitios del estudio (SS: H, Hrastovlje; Z, Zazid), situados en el sudeste de Eslovenia: STS, prueba estadística estandarizada; n/a: no aplicable; ¹ se omitió a los rodadores del análisis porque en las muestras solo se encontró una especie (*Sisyphus schaefferi*); ² solo se encontraron dos especies de la familia Geotrupidae–cavadores en las muestras, de tal forma que los análisis se realizaron con los datos agrupados de Scarabaeidae–cavadores + Geotrupidae–cavadores.

SS	Compared groups	Test	All		Dwellers		Tunellers ²		Rollers	
			χ^2 /STS	<i>p</i>	χ^2 /STS	<i>p</i>	χ^2 /STS	<i>p</i>	χ^2 /STS	<i>p</i>
Number of species ¹										
H	S1, S2, S3 (df = 2)	KW	9.743	0.008	2.069	0.355	6.283	0.043	n/a	n/a
H	S1 : S2	PC	-2.309	0.063	n/a	n/a	-1.972	0.146	n/a	n/a
H	S1 : S3	PC	0.664	1.000	n/a	n/a	0.355	1.000	n/a	n/a
H	S2 : S3	PC	2.973	0.009	n/a	n/a	2.326	0.060	n/a	n/a
Z	S1, S2, S3 (df = 2)	KW	2.306	0.316	1.003	0.606	5.156	0.076	n/a	n/a
Number of specimens										
H	S1, S2, S3 (df = 2)	KW	11.154	0.004	9.502	0.009	8.098	0.017	13.120	0.001
H	S1 : S2	PC	-2.641	0.025	2.889	0.012	-2.332	0.059	-3.334	0.003
H	S1 : S3	PC	0.450	1.000	0.514	1.000	-0.246	1.000	-0.442	1.000
H	S2 : S3	PC	3.091	0.006	-2.375	0.053	2.578	0.030	2.892	0.011
Z	S1, S2, S3 (df = 2)	KW	2.031	0.362	0.884	0.643	5.910	0.052	1.366	0.505

in habitat patch S1 and lowest in S2 (both study sites; table 1). However, no significant differences were detected between the three patches, either within or between the two study sites (ANOVA, $p > 0.05$).

The number of collected species or specimens (total or subdivided by guilds) did not differ significantly between the two study sites ($p > 0.10$; table 2).

Except for two datasets from Hrastovlje (all traps combined: $p = 0.008$, tunnelers: $p = 0.043$), there were no significant differences in the number of species between the three habitat patches (Kruskal–Wallis test: $p > 0.05$; table 3) in either of the two study sites (see also figure 3 for Hrastovlje—all traps combined). Furthermore, we found significant differences in the numbers of specimens only in Hrastovlje (Kruskal–Wallis test: $p < 0.02$; table 3). However, differences were found for the whole dataset as well as for each of the three guilds. Further post-hoc pairwise comparisons of habitat patches in Hrastovlje revealed that more species at S2 than at S3 (the whole dataset; $p = 0.009$); however, no differences were found between S1 and S3, and S1

and S2 ($p > 0.05$). There was a higher abundance of specimens at S2 than at S1 or S3 in Hrastovlje in most cases ($p < 0.05$), and no significant differences between S1 and S3 (see figure 3 for pooled dataset), whereas in Zazid, no statistically significant differences were found between the pairs of habitat patches (Kruskal–Wallis test: $p > 0.36$).

Discussion

Species richness

We report the community richness and structure of Scarabaeoidea dung beetles from dry karst grasslands with different habitat types (pastures under different impact of livestock, and dry karst meadows) in southwestern Slovenia. Although the use of pitfall traps alone rarely reflects the majority of species present in a given study area (Barbero et al., 1999), the sampling throughout 2012 with many pitfall traps and additional baits provided a high proportion of

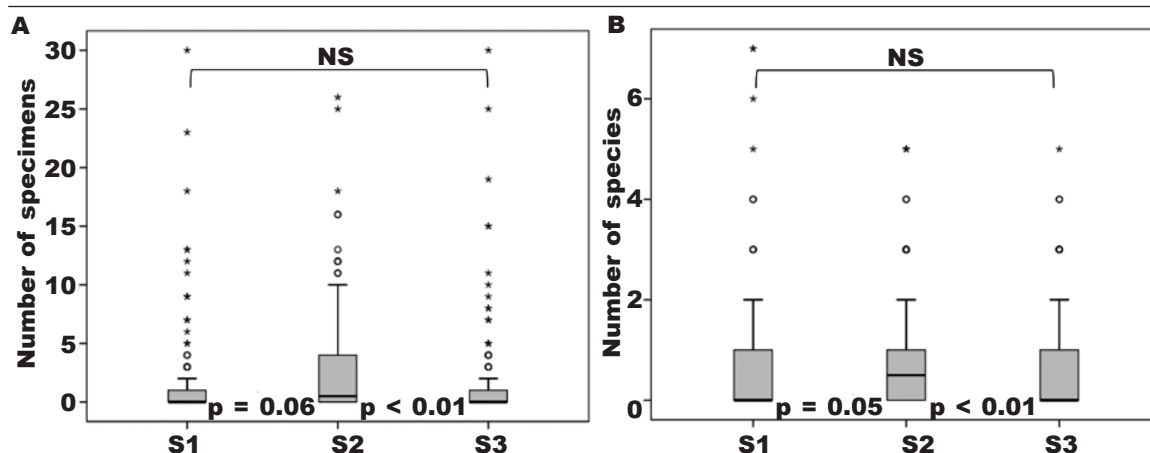


Fig. 3. Comparisons of numbers of specimens (A) and species (B) of Scarabaeoidea among the three habitat patches in Hrastovlje: NS, non-significant (significance p-values added).

Fig. 3. Comparación de las cifras de individuos (A) y especies (B) de la familia Scarabaeidae entre los tres fragmentos de hábitat en Hrastovlje: NS, no significativo (valores p de significación añadidos).

species that are presumably present in the area, and exceeded at least 70 % of species presumably present at any of the two sampling sites. Some species that were not trapped, however, were additionally collected manually (*Onthophagus vacca* (Linnaeus, 1767), *Coprimorphus scrutator* (Herbst, 1783)) during our field trips (cf. Koprivnikar, 2012). Lobo et al. (1998) determined the number of traps needed to collect a certain proportion of species at local and regional scales; they suggest the use of five, seven and ten baited traps to successfully trap over 70 %, 78 % and 89 % of species at local level, respectively. Although we did not follow all their recommendations (i.e. we used six baited traps plus six control traps/site) their estimated proportions (1998) are in line with the outcome of our study. At the habitat patch level, however, our success was expectedly lower as we used only four traps (two baited plus two control traps/habitat patch). Our trapping success ranged between 54 % (Hrastovlje, S3) and 80 % (Zazid, S3) and corresponded to the use of two to seven traps, respectively (cf. Lobo et al., 1998).

Diversity and factors influencing species richness and structure

Species that were exclusively recorded at a single study site may be related to the specific type of livestock present at those sites (cattle in Zazid and goats in Hrastovlje). The dung source has shown to be an important factor influencing species richness and abundance of Scarabaeoidea (e.g. Carpaneto et al., 2005; Lobo et al., 2006), and this factor may be the most important of all (e.g. Carpaneto et al., 2005). Lumaret et al. (1992) showed that changes in resources from sheep to cattle grazing resulted

in a two to three-fold increase in beetle numbers and biomass over a five-year period. However, we could not relate the species' exclusiveness on one site with the preference for a specific type of excrement or habitat type (Lobo et al., 2006) alone. Other unknown factors could influence their presence, as could the altitudinal difference (Lobo et al., 2006; Negro et al., 2011; Tocco et al., 2013) of over 300 m between the two sites.

The Shannon index showed an insignificantly higher value in Hrastovlje (goats) than in Zazid (cattle). However, the abundance of dung beetles at the former site was lower. Barbero et al. (1999) reported that higher diversity is more common for pastures with cattle than for those with sheep and goats because the former habitats can support not only generalists but also more specialist species. It is true that our results deviate somewhat from this conclusion as we recorded two more species on pasture with goats, but it should also be noted that cattle excrement was used as bait. Nevertheless, the number of present species alone is only a rough estimate for species diversity. The lowest Shannon index was shown in habitat patch S2 (the overgrown part of the pasture); however, this patch supported the highest numbers of species and specimens of Scarabaeoidea. The numbers at S2 may be higher because the shadowed areas of the pasture provide a preferred microclimate for many ground living invertebrates (i.e. higher relative humidity, shade, and cooler temperatures during hot summers), and the difference then favoured S2 in comparison with any other patch (all datasets except for dwellers exclusively in Hrastovlje) or there was no difference (all datasets from Zazid).

In Hrastovlje, fewer specimens of tunnelers (abundance mostly on account of *O. grossepunctatus*)

and rollers were present in S3 than in S2, indicating their preference towards the shrubby areas and simultaneous requirement for availability of herbivore excrements nearby. The existence of such shrub patches within pastures is always a result of selective grazing (Stergaršek, 2009), when usually inedible and/or spiny plants (see Material and methods) are left intact. These plants can therefore serve as a temporary shelter for ground living invertebrates, as the microclimate (cool, shady and humid during the spring and early summer) is more appropriate for invertebrates. A lower abundance of animals and species of dung beetles in shrubby areas (as in our case S3) has previously been noted for the Mediterranean (e.g. Numa et al., 2009). Thus, the complete abandonment of grazing activity can consequentially lead to lower species richness and abundance of the dung beetles. A decrease in alpha diversity and biomass density in dung beetles has been shown after the pasture abandonment (Tonelli et al., 2017a, 2017b), while long-term grazing continuity and size of the pastures both have a positive effect on species richness (Buse et al., 2015). Nevertheless, Numa et al. (2009) pointed out that in homogeneous conditions of trophic resources and climate, the landscape structure is more important in determining the dung beetle assemblage than the characteristics of a given habitat patch.

Synthesis and implications for conservation

Recurring disturbance to agro-ecosystems is human influenced (management) and usually has a negative effect on biodiversity. Scalerio et al. (2007) reported that in the case of butterflies and moths, semi-natural habitat patches can support a higher diversity than highly transformed patches. Furthermore, species' communities in agricultural areas have high proportions of migrant species, and although some specialist species are found in these highly changed environments, it is assumed these patches primarily act only as stepping stones for species looking for permanent habitats. Although grazing and overgrowth both have a negative impact (in relation to open karst meadows) on some taxa (cf. Jugovic et al., 2013a, 2013b, 2014a, 2014b, 2017), the coprophagous dung beetle community can to some extent benefit from the presence of livestock in pastures (e.g. Lobo et al., 2006; Jay-Robert et al., 2008b). Despite some possible negative effects, extensive pastures with different types of livestock are important, especially when wild, large herbivores are absent (Zamora et al., 2007). Coprophagous animals at such places are thus commonly present because of the abundance of food (excrement; see Koprivnikar, 2012). Since the inter- and intra-guild competition of dung beetles (and some other coprophagous animals) is well expressed and can be avoided by temporal and spatial segregation (cf. Errouissi et al., 2009; Jugovic et al., 2015; Sladecek et al., 2017), we suggest that mosaic landscapes consisting of various open- to semi-open habitats for different species should be maintained for them to be able to find suitable (micro)

habitats. In such systems, distances between patches should not overlook the movement abilities of different taxa (e.g. Jugovic et al., 2017). Mosaic landscape is consistently mentioned among the richest and most temporally heterogeneous habitats, and should be further maintained through traditional human activities (e.g. extensive grazing, only occasional and late extensive mowing; cf. Jugovic et al., 2017; Barbero et al., 1999). This landscape is human-shaped and has been managed in a way that reflects the high spatio-temporal changes (Allen, 2003), where changes in agricultural, stockbreeding activities, and abandonment or intensification can lead to the loss of biodiversity (review in Zamora et al., 2007).

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