The effect of local environmental heterogeneity on species diversity of alpine dung beetles (Coleoptera: Scarabaeidae)

The effect of local environmental heterogeneity on alpine dung beetle diversity: a case study from the Ferret valley (Italian side of Monte Bianco)

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ABSTRACT

Through an appropriate sampling design, we tested the relative effects of two components of mountain environmental heterogeneity, i.e. altitudinal levels (1500, 1700 and 2000 m a.s.l.) and habitat types (pastures, coniferous forests, wet meadows, shrubbery and anthropogenic woods) on the dung beetle diversity of an Italian alpine valley**.** The analysis of additive gamma diversity showed that differences among habitat types (β_H) were always smaller than those between altitudinal levels (β_A), irrespectively of the metrics considered; it also showed that the contribution of β_A to γ-diversity was higher than expected by chance for all the metrics, whereas the contribution of β_H was significantly higher in the case of one metric only. Generalized linear models confirmed that altitude was the most important controller of local diversity, with all diversity parameters considered progressively and significantly increasing with increasing altitude. Indicator species analyses revealed that dung beetle altitudinal and habitat diversity patterns depended on local choices of species, with preferences for altitudinal levels being more numerous and apparent than those for habitats. Despite the minor impact of habitat differences, by comparing a three-habitat scenario with a single-habitat one, we were able to demonstrate that greater habitat heterogeneity induces significantly greater dung beetle diversity.
This study suggests that preservation of local environmental heterogeneity through the maintenance of traditional pastoral activities should be encouraged for adequate dung beetle conservation in the Alps.

Key words: scarabeoid beetles, habitat heterogeneity, additive partitioning, Generalized Linear Models, IndVal.

INTRODUCTION

Alpine landscapes are some of the most diverse in Europe thanks to an ancient history of human settlement and the climatic constraints imposed by steep altitudinal gradients.

Among human activities, in particular, pastoral activities have been practiced for at least 6000 years (Lichtenberger 1994), thereby shaping the alpine environment: pre-existing forests were cleared or burned over large areas to increase the availability of open grasslands for livestock. Today, as a consequence, in most of the mountain belt (below the tree line), the alpine landscape consists of a mosaic of herbaceous, shrubby and forest habitats (Errouissi et al., 2004). The alpine distribution of habitats is also controlled by altitudinal gradients, with vegetation dramatically changing along these gradients, from mid-altitude coniferous forests to high-altitude prairies and pastures.

Several studies have shown that habitat heterogeneity may contribute to increase overall animal diversity (Beaufoy et al., 1994; Pain and Pienkowski, 1997; Laiolo et al., 2004; Negro et al., 2007; Zahn et al., 2007). These results are in keeping with the so called habitat heterogeneity hypothesis, which simply predicts that more animal species will occur where different forms and species of plants provide greater structural heterogeneity in the vegetation (Hart and Horwitz, 1991; Dennis et al., 1998). Thus, greater resources are available for the coexistence of more species within each trophic group (Moore and de Ruiter, 1997).

Dung beetles (Coleoptera, Scarabaeidae) are undoubtedly the most typical and ecologically relevant insects of alpine grazed habitats. By manipulating feces during the feeding process, they play important ecological functions in numerous ecological processes such as nutrient cycling, seed dispersal, bioturbation, and pollination, hence providing valuable ecological services such as biological pest control and soil fertilization (Nichols et al., 2008). According to the BEF (Biodiversity and Ecosystem Functioning) approach (Loreau et al., 2001; Hooper et al., 2005; O'Connor and Crowe, 2005), the decline or local extinction of these insects may have significant short and long term implications for the maintenance of ecosystem processes (Nichols et al., 2008).

Dung beetle species may show specific local habitat preferences (Barbero et al, 1999; Macagno and Palestrini, 2009) which may nevertheless change from area to area, suggesting a certain degree of ecological flexibility. Moreover, several studies conducted in Europe (Martín-Piera et al., 1992; Romero-Alcaraz and Ávila, 2000; Menéndez and Gutiérrez, 2004) have shown that habitat selection usually does not depend upon vegetation structure *per se*, but upon related microclimatic conditions (mainly temperature and humidity).

Change in land use by humans may be directly or indirectly responsible for the degree of local habitat heterogeneity. Pastoral abandonment, in particular, may significantly affect the local landscape. In such a situation, ungrazed (or undergrazed) grassland, through processes of ecological succession, gradually turns into shrubs and, ultimately, to forest. This may have consequences for dung beetles assemblages, since most Paleartic dung beetles are known to prefer open habitats (Galante et al., 1995; Jay-Robert et al., 2008).

Additionally, altitude strongly influences the distribution of dung beetle families and species, and produces zonation (Jay-Robert et al., 1997). In the Alps, in particular, assemblage compositions are determined in large part by elevation. Scarabeidae, which include many thermophilous species restricted to Mediterranean environments, colonize warmer and lower south-facing non-forest habitats (Lumaret and Kirk, 1991;

Lobo et al., 2002). Conversely, most Geotrupidae and Aphodiidae species tolerate a broad range of environmental conditions and are predominant in the colder north-facing alpine habitats at higher elevations (Hanski, 1991; Errouissi et al., 2004).
Jay Robert et al. (2008) analyzed a large assemblage of dung beetles from the southern Alps, and showed that elevation and vegetation type strongly influenced species composition, suggesting that alpine local diversity is primarily driven by environmental heterogeneity caused by habitat types and altitudinal gradients.
In this paper, we describe the effect of environmental heterogeneity (namely elevation and habitat type) on the dung beetle assemblages in an alpine valley on the Italian side of Monte Bianco. Through an appropriate sampling design we separately evaluated the relative effect of elevation and habitat type on local diversity. Moreover, assuming habitat diversity can be controlled though specific habitat managing choices, we tested whether the hypothetical disappearance of some local habitats would significantly affect diversity. Using different analytical methods (additive partition of diversity, richness estimation, generalized linear models and Indicator Species Analysis) we aimed to describe patterns and to unveil processes of local dung beetle diversity.

MATERIAL AND METHODS

Study area and dung beetle sampling design

The study was carried out in the Ferret valley, an alpine valley on the Italian side of the Monte Bianco massif, at the top end of the Aosta valley (45°50’60” N; 7°01’00” E). The climate is continental with mean temperatures varying from 1,3°C in the coldest month (January) to 15,8°C in the warmest month (August). Annual rainfall (957 mm average) could be defined as "Mediterranean" with two peaks in May and October and two minima in July and December-January (Focarile, 1987). Because of the position of the Monte Bianco massif, which is a major barrier to the clouds coming from the Atlantic Ocean, this valley is less humid than those on the French side of the massif (Giglio, 1991).
The area has great conservation relevance due to the presence of several bird species listed in Annex 1 of Directive 79/409/EEC. For this reason, part of the Ferret valley has been recently declared a Special Protection Zone (SPZ) for birds (IT1204030). Moreover, the entire area on the left side of the valley has been declared a Site of Community Importance (S.C.I.) (IT1204010) with the main conservation aim of protecting the glacial and wet meadows of the Monte Bianco massif.
Despite the great conservation relevance of the area, over the last several decades the impact of human activities has increased, mainly due to increased tourism.
We investigated six habitat types: pastures (dominated by Gramineae grasses), coniferous forests (dominated by the larch *Larix decidua*), wet meadows (on a small waterlogged plateau, the remains of a large moraine lake now completely buried), shrubbery (alpen rose *Rhododendron ferrugineum* L. and bilberry *Vaccinium myrtillus* L.)] and anthropogenic woods for picnickers (groves of larch trees provided with wooden tables, cooking and parking facilities).

To evaluate the relative effect of elevation on local dung beetle diversity, we kept the habitat type constant by sampling the same habitat type (pastures) at different elevations (three sites set at 1500, 1700 and 2000 m a.s.l.). Conversely, to evaluate the

relative effect of habitat type, we kept the elevation constant by sampling different habitat types (five sites representative of pastures, coniferous forests, wet meadows, shrubbery and anthropogenic woods) at the same elevation (1700 m a.s.l.) (Table 1).
Dung beetle assemblages in sites located at the same elevation, but with different geographic exposures, can be significantly different (Errouissi et al., 2008). Hence, we selected sampling sites with the same exposure (north-northwest).
We used dung-baited pitfall traps of the hang-bait type, which are known to be one of the most efficient methods for sampling dung beetles in alpine environments (Palestrini et al., 2008; Macagno and Palestrini, 2009). Pitfall traps were 7.5 cm in mouth diameter and 9 cm deep; they were baited with 100 g of cattle dung and filled with 150 ml of a standard mixture of water, liquid soap and sodium chloride solution to preserve individuals.
Three dung-baited pitfall traps spaced 30 m apart were placed at each site. The exact location of traps was established by means of a Global Positioning System (GPS) Garmin eTrex1 Navigator. Traps were placed at the beginning of June 2007 and emptied every week until the end of October 2007; a total of 399 samples (three traps x seven sampling sites x nineteen sampling periods) were collected.
Dung beetles caught were sorted and identified to species using updated standard keys (Pesarini, 2004; Dellacasa and Dellacasa, 2006, Paulian and Baraud, 1982) or specialist works. Nomenclature follows Alonso-Zarazaga (2004).
All specimens trapped in this study are held at the Department of Animal and Human Biology, Turin, Italy.

Data analysis

Additive partitioning of gamma diversity

The total amount of diversity (γ) in the Ferret valley was additively decomposed into the components of mean diversity within samples (α) and diversity between samples (β) using the computer program PARTITION (Veech and Crist, 2007). Additive partitioning is based on the simple relationship that alpha and beta sum to gamma ($\gamma = \alpha + \beta$) and that species diversity can be partitioned at each level or scale of hierarchical sampling schemes in which samples at level j are nested within samples at level j + 1. Given the experimental design, the total amount of diversity (γ) was calculated separately for habitats and altitudes, using single traps as samples.
The three most widely used metrics of species diversity [i.e. species richness (R), Shannon-Wiener Index ($H' =- \Sigma\, p_i \times \ln p_i$ where p_i is the relative frequency of species i) and Simpson Index ($S = \Sigma\, p_i^2$)] were employed, in keeping with Lande (1996).
Total habitat diversity was decomposed into its average components, i.e. within (α_H) and among (β_H) habitat types so that $\gamma_H = \alpha_H + \beta_H$. To further investigate habitat diversity patterns, we decomposed the average within-habitat diversity parameters (α_H) into the within (α_P) and among pitfall-traps (β_P) components, $\alpha_H = \alpha_P + \beta_P$, so that, by substitution, the overall hierarchical partition becomes $\gamma_H = \alpha_P + \beta_P + \beta_H$ (Crist and Veech, 2006; Crist et al., 2003). The same procedure was used to decompose altitudinal γ-diversity (the model was $\gamma_A = \alpha_P + \beta_P + \beta_A$).
The sample-based randomization procedure in PARTITION was used to test whether the observed partitions of diversity could have been obtained by a random allocation of lower level samples nested among higher-level samples (Crist et al., 2003).

Differences between habitat types and altitudes

To estimate the expected species richness at each site, we used the abundance-based richness estimator (ACE). Inventory completeness for each site was measured as the percentage of the total number of species predicted by the estimator that we actually observed. The richness estimator was computed using EstimateS 8.0.0 (Colwell, 2006).

To test for differences in diversity between habitats and altitudes we considered individuals collected in each trap (i.e. single traps as samples) and calculated three metrics, i.e. abundance (N), species richness (R), and H' diversity (Shannon-Wiener index). Parametric tests (such as Two-way ANOVA) could not be properly employed because several assumptions were not met. In particular, variances of samples were not equal, hinting to the violation of homoscedasticity between the different populations considered, and error terms were not always normally distributed even after appropriate data-transformation [violations were assessed through the Levene's test and the Normal Probability plot, respectively (Sokal and Rohlf, 1995)]. Differences in mean species richness, abundance and Shannon-Wiener Index among habitat types and altitudes were first assessed by means of a descriptive statistical analysis. Generalized linear models (GLM) were then employed to obtain a quantitative description of the differences in mean species richness and abundance pertaining to the habitat types and altitudes considered. For each analysis we considered two categorical factors (habitat type or altitude and sampling period). Abundance and species richness attained a Poisson distribution; therefore a Poisson distribution of errors was assumed and the density of ground-dwelling arthropods was related to explanatory variables via a logarithmic link function (McIntyre and Lavorel). GLM were not employed to study the Shannon-Wiener Index since the corresponding data did not allow to choose a normal distribution for the errors. However from the preliminary descriptive analysis performed it was possible to infer that this Index behaved exactly in the same way as the species richness.

Tests for the significance of the effects in the models were performed by means of the Wald statistic (Dobson, 1990). Such statistics is based on the asymptotic normality property of maximum likelihood estimates and is computed as the generalized inner product of the parameter estimates with the respective variance-covariance matrix. Moreover, we explored the habitat and altitude factor estimates, their standard errors and individual statistical significance. Generalized linear models with categorical variables and Wald statistics were calculated using the STATISTICA 6.0 package (StatSoft Italia srl, 2001). According to this package, if one selects to use the sigma-restricted parameterization the last category that is specified for a categorical variable is the reference category (or level) and hence only pairwise comparisons between the effects of the remaining levels of the predictor variable on the response (dependent variable) are allowable. According to the parameterization chosen the estimation of each parameter refers to the additional effect on the dependent variable of a particular level of the considered predictor, depending on the link function chosen, with respect to the reference one and holding the other possible predictors at a constant level.

In the parameter estimation analysis, we used anthropogenic woods and intermediate altitudes (1700 m a.s.l.) as the reference categories for habitat and altitude, respectively.

Indicator Species Analysis (IndVal)

High specificity and fidelity of every dung beetle species within habitats and altitudes were explored by the IndVal (Indicator Value) procedure (Dufrêne and Legendre 1997). The indicator values are highest (100) when all individuals of a species are found in a single habitat (high specificity) and when the species occurs in all samples of that habitat (high fidelity). The statistical significance of the maximum indicator value was evaluated by a Monte Carlo randomization test (1000 runs). IndVal analyses were run using PC-Ord software (McCune and Mefford, 1999).

Testing the effect of habitat heterogeneity

To test whether greater habitat heterogeneity induces greater dung beetle diversity, we considered the same elevation (1700 m a.s.l.) and compared a three-habitat scenario (i.e. pastures, coniferous forests and wet meadows, i.e. the most extensive and characteristic habitats of the Ferret valley) with a single-habitat one (i.e. pastures, the typical, standard dung beetle habitat in the western Alps). For each period (n=19) we calculated abundance, species richness R and H' diversity (Shannon-Wiener index) for each site from a three-trap sample (i.e. using all beetles caught with the three traps as sample). In the case of the single habitat scenario, we considered all three traps placed in that habitat, whereas in the case of the three-habitat scenario we considered one trap at a time for each of the three habitats considered. There are 27 different possible combinations of three given traps, obtained by drawing one trap at a time from each of the three groups of three traps (i.e. $3^3 = 27$). Therefore, for each metric, differences between the one-habitat and the three-habitat samples (with 19 sampling units in either group) were tested 27 times (Wilcoxon signed-rank tests).

RESULTS

A total of 22 dung beetle species (corresponding to 11,583 individuals) were collected. The sampling effort was adequate to correctly describe local assemblages given that most of the expected species (ranging form 83 to 100 %) were caught in each sampling site (Table 2). The dung beetle assemblage was strongly dominated by Aphodiidae (92.1% of the sampled individuals), whereas Scarabaeidae and Geotrupidae were much less abundant (respectively 7.0 and 0.9%).

Additive partitioning of γ-diversity

Diversity within pitfall traps (α_P) gave the greatest contribution both to total habitat and altitude γ-diversity, irrespectively of the metrics employed (ranging from 69.5% to 92.4%), whereas diversity between pitfall traps (β_P) gave the lowest contribution (ranging from 0.49% to 12.73%).

Differences between habitat types (β_H) were always smaller than those between altitudes (β_A), irrespectively of the metrics considered (Fig.1A, B). A randomization procedure showed that the contribution of α_P and β_P to γ-diversity was never significantly different from that expected by chance. Vice-versa, the contribution of β_A to γ-diversity was higher than that expected by chance ($P < 0.001$) for all the

metrics, whereas the contribution of β_H was significantly higher in the case of Simpson diversity index only.

Differences between habitat types and altitudes

Total abundance and species richness significantly changed among habitat types (Table 3, Fig. 2), altitudes (Table 3, Fig. 3) and periods. Habitat estimates showed that all the parameters pertaining to the abundance and species richness indexes associated with anthropogenic woods were significantly lower than those associated with wet meadows and (especially for species richness) higher than those associated with shrubbery (Table 4). In the case of the species richness index, for example, considering that a Poisson response variable with a log link has been chosen for the GLM, it can be argued that the ratio between the mean species richnesses pertaining to wet meadow and shrubbery respectively is exp(0.331-(-0.349))=1.973. Altitude estimates depicted a well-defined trend, with both diversity parameters considered progressively and significantly increasing with increasing altitude (Table 5).

Indicator Species Analysis

The analysis of indicator species by IndVal showed that eleven species did not show a clear preference for a particular habitat (Table 6). The other species were evenly distributed among natural habitat types: three species preferred pastures (*Acrossus rufipes*, *Onthophagus baraudi*, *Otophorus haemorhoidalis*), two shrubbery (*Anoplotrus stercorosus*, *Oromus alpinus*), two wet meadows (*Amidorus obscurus*, *Colobopterus erraticus*) and three coniferous forests (*Onthophagus fracticornis*, *Parammoecius corvinus*, *Planolinus fasciatus*) (Table 6). No species positively selected anthropogenic woods.

Altitudinal choices depicted a rather clear altitudinal pattern, with four distinct groups: (Table 7): 1) species of low elevations, which were found mainly at the 1500 m. a.s.l. sampling site (*Esymus pusillus*, *Onthophagus fracticornis*, *Parammoecius corvinus*; 2) species of medium elevations, which were found mainly at the 1700 m. a.s.l. sampling site (*Acrossus rufipes*, *Anoplotrus stercorosus*, *Aphodius fimetarius*, *Bodilopsis rufa*, *Geotrupes stercorarius*, *Onthophagus baraudi*, *Otophorus haemorhoidalis*); 3) species of high elevations, which were found mainly at the 2000 m. a.s.l. sampling site (*Agoliinus satyrus*, *Agolius abdominalis*, *Amidorus immaturus*, *Amidorus obscurus*, *Oromus alpinus*, *Planolinus fasciatus*) and 4) species with no elevation preferences, which occurred at all altitudes.

Testing the effect of habitat heterogeneity

Median values of the Shannon-Wiener index and species richness of the three-habitat scenario were significantly greater than that of the single-habitat scenario in all instances, that is, irrespectively of the combinations of traps used (n=27). Conversely, median values of abundance were significantly higher in 10 instances out of 27 only; given that the proportion of significant differences (10/27= 0.37) was higher than 0.05, we considered abundance as not being significantly affected by habitat heterogeneity.

DISCUSSION

Dung beetles have been repeatedly proposed as a very useful group for biodiversity inventories and monitoring because they posses all the characteristics of an ideal focal taxon: amenable to standardized sampling, taxonomically well known, broad geographic distribution, ecological and economic importance, correlation with other taxa, and a wide range of responses to environmental changes or human disturbance (Spector, 2006).

Recently, they have been widely used in several ecological studies aiming to evaluate the impact of grazing (including overgrazing, undergrazing, and the complete elimination of grazing) (Lobo et al., 2006; Verdú et al., 2007; Jay-Robert et al., 2008), logging (Davis et al., 2001; Horgan, 2005) and habitat fragmentation (Roslin and Koivunen, 2001; Quintero and Roslin, 2005).

Local dung beetle diversity is generated and maintained by a range of factors such as ecosystem productivity and age, climatic variability, predation, intra- and inter-specific competition, latitude, altitude, and habitat heterogeneity (Romero-Alcaraz and Avila, 2000). In the Alps, in particular, elevation and habitat type greatly influence assemblage composition (Jay-Robert et al., 2008).

Our results on additive partitioning suggest that differences in altitude may have an important effect on β diversity, irrespectively of the metrics considered. The observed partition differs from the expected one, mostly due to differences in the β diversity at the highest level (β_A). Presumably, differences between observed and expected diversity components are due to ecological processes that lead to a non-random dispersion of individuals along the altitudinal gradient, giving rise to a very apparent altitude selection (Veech et al., 2002). This result is in keeping with previous works that showed elevation is an important factor influencing community parameters (Lumaret and Stiernet, 1991; Martín-Piera et al., 1992; Menéndez and Gutiérrez, 1996).

GLM analyses showed that abundance and species richness were significantly and positively correlated with altitude. This trend is likely due to the preponderance of Aphodiidae, which are known to colonize high elevation and cold temperate habitats (Errouissi et al., 2004; Jay-Robert et al., 2008).

The Indicator Species Analysis provided further evidence that the distribution of dung beetles in Ferret valley was mainly driven by elevation through local species-specific selection processes. Most species (all belonging to the family Aphodiidae) tended to select intermediate and high elevations. Five species (*Agoliinus satyrus*, *Amidorus immaturus*, *Amidorus obscurus*, *Oromus alpinus* and *Planolinus fasciatus*) can be considered high altitude specialists, ($P < 0.001$, Monte Carlo randomization test). Additive partitioning analysis suggested that habitat was less important than altitude in structuring dung beetles assemblages, given that the observed β diversity values, with the only exception of the Simpson Index, did not differ statistically from those expected. Differences between habitats, however, did exist. Dung beetle assemblages were more abundant and diversified in wet meadows than in other habitats. This habitat type, peculiar to the Ferret valley, has been recently included in a Site of Community Importance (SCI) (IT1204010) in order to protect it from ecological decay stemming from increased tourism. Our results clearly demonstrated that shrubbery is a suboptimal habitat for dung beetles, in keeping with findings in several Mediterranean ecosystems of southern Europe (Lumaret and Kirk, 1987; Verdú et al., 2000). Dung beetles are probably negatively affected by shrub cover because of lower

resource density; vice-versa, where shrubbery becomes open and grazed, its attractiveness to dung beetles is likely to increase (Jay-Robert et al., 2008). IndVal analyses showed that most species did not prefer any particular habitat type, thus confirming the secondary role played by habitat in comparison with altitude and indicating, at the same time, that species-specific choices (or lack thereof) are responsible for the diversity patterns observed. Nevertheless, each natural (or semi-natural) undisturbed habitat type (i.e. pastures, coniferous forests, shrubbery, and wet meadows) accounted for two/three indicator species. These results suggest that each undisturbed habitat of the Ferret valley may play a role for the conservation of certain dung beetle species. This is in keeping with the idea that dissimilarity of structure in high complexity habitats may support more potential niches for a functionally diverse suite of species, and is likely to support a greater range of food webs than less complex habitats (Klopfer and MacArthur, 1960; Lassau et al., 2005). Tests conducted comparing a three-habitat scenario with a single-habitat scenario confirmed that the presence of numerous habitats significantly increases local dung beetle diversity.

A notable exception to this habitat selection pattern was represented by habitats subject to human disturbance (anthropogenic woods), which did not account for any indicator species. Tourism and related infrastructure (mainly access roads and shelters) is known to negatively affect coprophagous beetle assemblages (Lobo et al., 2001).

Therefore, habitat heterogeneity may play a useful role in preserving alpine dung beetle diversity if it is driven by natural processes or ecologically-sustainable human activities (such as pastoral activities). Land use may drive habitat heterogeneity and, therefore, affect dung beetle diversity. The abandonment of certain rural areas, especially after the Second World War, through processes of natural succession, has allowed forest regeneration which, in the long term, may produce habitat homogeneity. Reforestation is often associated with colonization on the part of wild ungulates (such as red deer *Cervus elaphus*, roe deer *Capreolus capreolus* and wild boar *Sus scrofa*), whose excrements are used by dung beetles (Barbero et al., 1999). However, it has been shown that wild ungulate manure is not enough to ensure the conservation of the regional dung beetle species pool (Jay-Robert et al., 2008). The contribution of pastoral activities with the presence of livestock herds (such as cows, goats and sheep) is therefore essential.

In light of this, we conclude that preservation of environmental heterogeneity should be encouraged for adequately conserving dung beetles in the Alps. The maintenance of traditional pastoral activities, in particular, may significantly help preserve habitat heterogeneity and, consequently, dung beetle diversity.

		HABITAT TYPE				
		Pasture	Forest	Wet meadow	Shrubbery	Anthropogenic wood
ALTITUDE (m a.s.l.)	about 1500	Pontpailler				
	about 1700	Greuvettaz	Bois de Frebouge	Ferrachet	Arnouva	Lavachey
	about 2000	Pré de Bard				

Table 1 List of the sampling sites in relation to altitude and habitat type. We evaluated the effect of altitude by keeping the habitat type (pasture) constant, and vice-versa we evaluated the effect of habitat by keeping the altitude constant (1700 m a.s.l.).

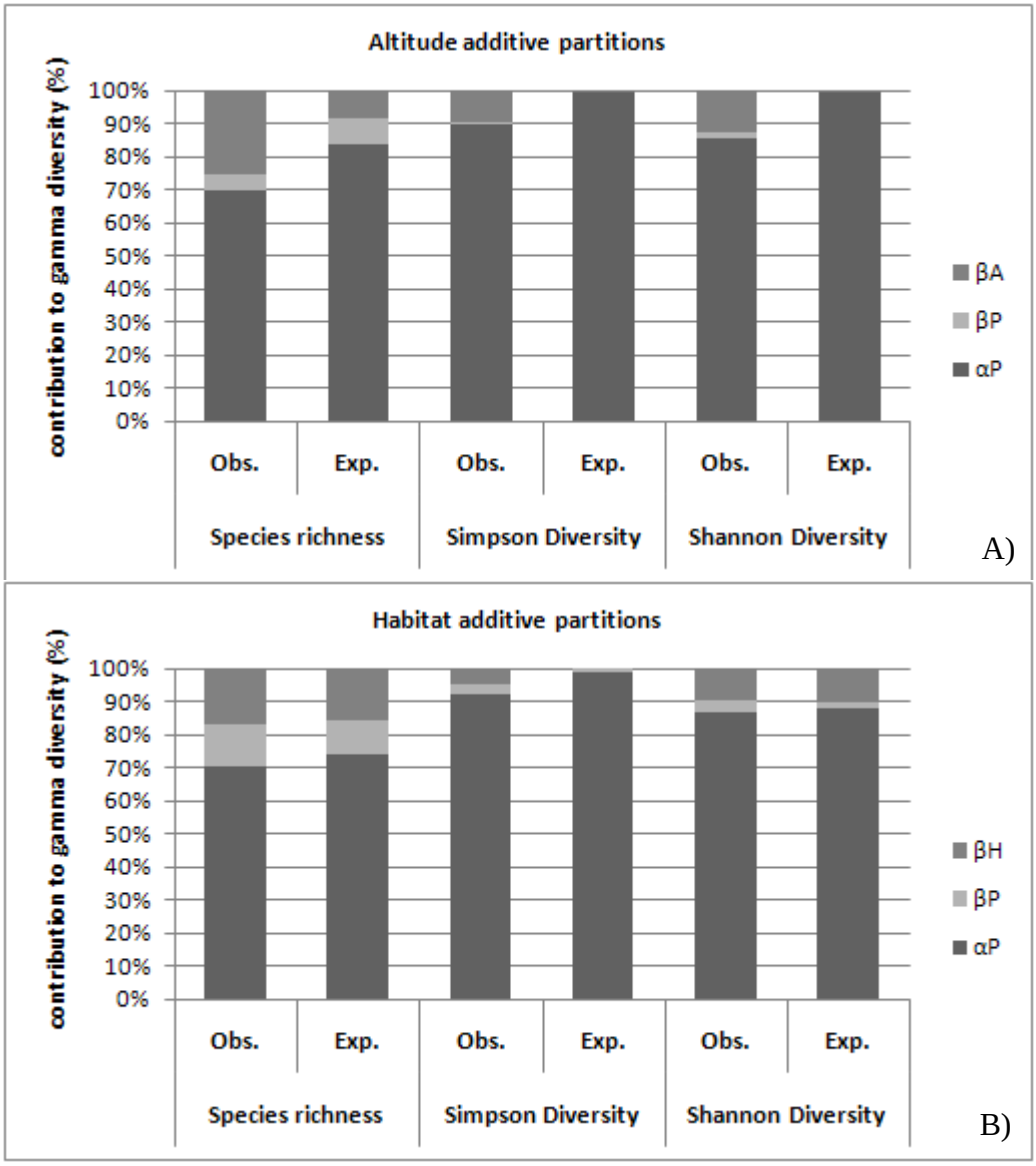

Fig.1 Additive partition of three metrics of species diversity (species richness, Simpson index and Shannon index) across five habitat types (A) and across three altitudinal levels (B). Values are expressed as the percentage of the total gamma diversity (γ) explained by each hierarchical level. The observed partitions are compared to expected values from individual-based randomization. α_P, β_P = pitfall traps; β_H = habitat types; β_A = altitudes.

Habitat type	Shrubbery	Wet meadow	Forest	Anthropogenic wood	Pasture	Pasture	Pasture	Total
Altitude	**1700**	**1700**	**1700**	**1700**	**1700**	**2000**	**1500**	
Aphodiidae								
Acrossus depressus	512	211	283	268	374	273	68	1989
Acrossus rufipes	134	45	229	192	983	580	1	2164
Agoliinus satyrus	148	103	201	78	55	207	0	792
Agolius abdominalis	2	2	0	0	8	14	0	26
Amidorus immaturus	1	2	1	1	0	14	0	19
Amidorus obscurus	91	273	28	4	154	702	9	1261
Aphodius fimetarius	4	13	11	4	17	4	1	54
Bodilopsis rufa	38	53	131	129	107	15	9	482
Colobopterus erraticus	7	153	10	3	41	25	25	264
Esymus pusillus	0	2	6	6	0	0	25	39
Euheptaulacus carinatus	0	0	1	0	1	0	0	2
Limarus zenkeri	0	0	0	0	0	0	3	3
Oromus alpinus	354	125	21	13	134	1533	7	2187
Otophorus haemorhoidalis	4	15	4	0	54	2	2	81
Parammoecius corvinus	10	1	195	68	0	0	7	281
Planolinus fasciatus	66	201	342	119	40	156	5	929
Rhodaphodius foetens	0	1	1	1	0	0	0	3
Teuchestes fossor	4	21	16	1	33	12	5	92
Scarabaeidae								
Onthophagus baraudi	0	1	6	0	7	0	0	14
Onthophagus fracticornis	83	132	194	80	98	43	169	799
Geotrupidae								
Anoplotrus stercorosus	31	20	1	0	11	3	2	68
Geotrupes stercorarius	2	11	3	4	10	3	1	34
Diversity (H')	1.93	2.30	2.16	1.99	1.86	1.67	1.69	2.25
Total number (N)	1491	1385	1684	971	2127	3586	339	11583
Observed richness (S)	17	20	20	16	17	16	16	22
ACE (A)	17.51	23.00	24.10	17.80	17.37	16.00	17.80	22.00
Completeness (%)	97	87	83	90	98	100	90	100

Table 2 Number of individuals and dung beetle species collected at seven sampling sites. Diversity (H'), total number (N), observed richness (S) and expected richness (A) according to ACE estimator were provided for each sampling site (each represented by a unique combination of habitat type and altitude). Inventory completeness is observed richness as a percentage of total expected richness.

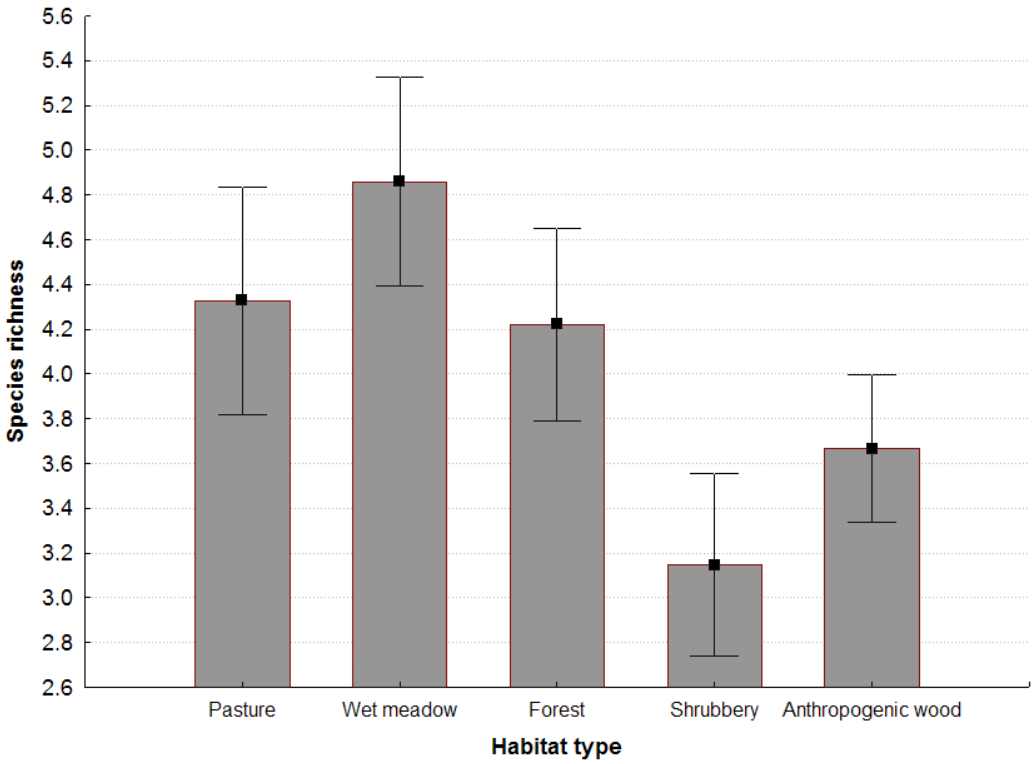

Fig.2 Mean values of species richness on five habitat types. Bars are ± standard errors.

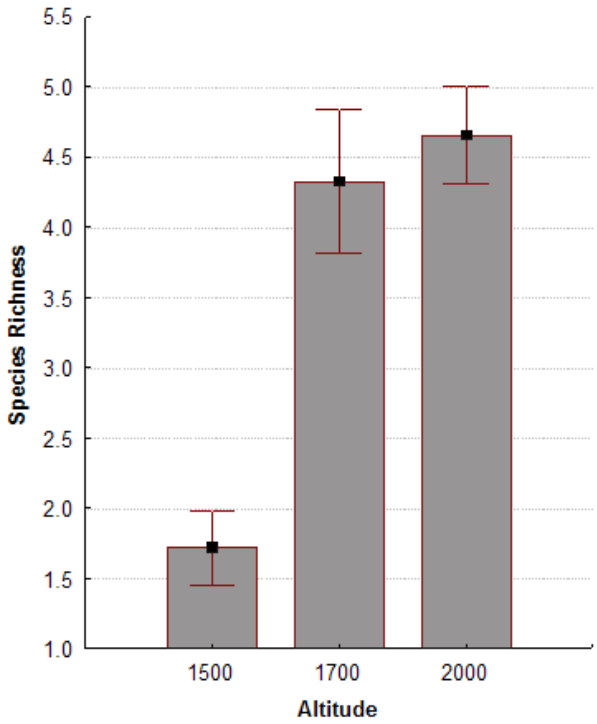

Fig.3 Mean values of species richness on three altitudinal levels. Bars are ± standard errors.

	Abundance Distribution: POISSON Link-function: LOG			Species richness Distribution: POISSON Link-function: LOG		
	DF	Wald Stat.	*p*	DF	Wald Stat.	*p*
Altitude	2	517.465	**0.000**	2	42.121	**0.000**
Sampling period	4	1020.514	**0.000**	4	112.245	**0.000**
Altitude*Sampling period	8	917.206	**0.000**	8	17.845	**0.022**
AIC	6260.07			572.79		

	Abundance Distribution: POISSON Link-function: LOG			Species richness Distribution: POISSON Link-function: LOG		
	DF	Wald Stat.	*p*	DF	Wald Stat.	*p*
Habitat	4	31.445	**0.000**	4	22.681	**0.000**
Sampling period	4	1249.280	**0.000**	4	121.670	**0.000**
Habitat*Sampling period	16	1696.952	**0.000**	16	105.879	**0.000**
AIC	8157.63			1123.44		

Table 3: Tests for the significance of the effects (habitat type/altitude and sampling period). Analyses were performed by means of the Wald statistic. The significant *p*-values are in bold type. Akaike's information criterion (AIC) was used to select the most appropriate models, i.e. the best fit to the available data set.

	Abundance Distribution: POISSON Link-function: LOG			
Habitat	Estimate	SE	Wald Stat.	*p*
Pasture	0.265	0.057	21.800	**0.000**
Wet meadow	0.153	0.055	7.866	**0.005**
Forest	-0.043	0.089	0.231	0.630
Shrubbery	-0.298	0.118	6.358	0.012

	Species richness Distribution: POISSON Link-function: LOG			
Habitat	Estimate	SE	Wald Stat.	*p*
Pasture	0.148	0.083	3.148	0.076
Wet meadow	0.331	0.076	19.101	**0.000**
Forest	-0.101	0.113	0.799	0.371
Shrubbery	-0.349	0.130	7.175	**0.007**

Table 4: Habitat factor estimates, their standard errors, and statistical significance. In this analysis anthropogenic habitat type is set as the reference category. Significant comparisons are in bold type.

	Abundance Distribution: POISSON Link-function: LOG			
Altitude (m a.s.l.)	Estimate	SE	Wald Stat.	*p*
2000	0.777	0.041	350.756	**0.000**
1500	-1.033	0.049	440.661	**0.000**

	Species richness Distribution: POISSON Link-function: LOG			
Altitude (m a.s.l.)	Estimate	SE	Wald Stat.	*p*
2000	0.330	0.075	19.356	**0.000**
1500	-0.572	0.089	41.595	**0.000**

Table 5: Altitude factor estimates, their standard errors, and statistical significance. In this analysis 1700 m a.s.l. is set as the reference category. Significant comparisons are in bold type.

	Observed Indicator Value (IV)	IV from randomized groups		p
		Mean	S.Dev	
No habitat selection				
Agolius abdominalis	1.3	2.4	1.22	N.S
Acrossus depressus	8.7	13	2.5	N.S
Aphodius fimetarius	5.1	4.8	1.58	N.S
Amidorus immaturus	0.5	1.9	1.1	N.S
Agoliinus satyrus	15.5	11.7	2.13	N.S
Bodilopsis rufa	10.7	10.7	2.22	N.S
Esymus pusillus	4.3	2.8	1.26	N.S
Euheptaulacus carinatus	0.9	1.5	1.07	N.S
Geotrupes stercorarius	5.6	4.2	1.45	N.S
Rhodaphodius foetens	0.6	1.7	1.14	N.S
Teuchestes fossor	7.2	5.2	1.69	N.S
Pasture				
Acrossus rufipes	31.5	14.9	3.52	**
Onthophagus baraudi	5.4	2.7	1.28	*
Otophorus haemorhoidalis	16.7	6.6	2.4	**
Shrubbery				
Anoplotrus stercorosus	9	4.8	1.58	*
Oromus alpinus	32	12.5	2.53	**
Wet meadow				
Amidorus obscurus	22.2	10.9	2.39	**
Colobopterus erraticus	33.5	7.5	1.96	**
Forest				
Onthophagus fracticornis	17.4	13.2	2.04	*
Parammoecius corvinus	34.3	8.5	2.33	**
Planolinus fasciatus	21	12	2.2	**

Table 6: Indicator Species Analysis (IndVal) calculated for five habitat types. Maximum observed value and mean expected (± SD) indicator value are given. Statistical significance obtained by Monte Carlo randomization test (1000 runs). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Note that no species selected anthropogenic woods.

	Observed Indicator Value (IV)	IV from randomized groups		p
		Mean	S.Dev	
No altitude selection				
Acrossus depressus	14.70	15.20	3.19	N.S.
Colobopterus erraticus	9.50	9.00	2.64	N.S.
Euheptaulacus carinatus	1.80	1.80	0.02	N.S.
Limarus zenkeri	5.30	2.30	1.26	N.S.
Teuchestes fossor	10.40	7.20	2.24	N.S.
1500 m a. s. l.				
Esymus pusillus	12.30	3.70	1.63	***
Onthophagus fracticornis	25.80	17.90	2.99	*
Parammoecius corvinus	10.50	3.20	1.44	**
1700 m a. s. l.				
Acrossus rufipes	30.90	17.30	3.82	**
Anoplotrus stercorosus	9.60	5.20	1.85	*
Aphodius fimetarius	10.80	5.30	1.93	*
Bodilopsis rufa	31.50	10.70	2.65	***
Geotrupes stercorarius	10.00	4.90	1.81	*
Onthophagus baraudi	10.50	3.20	1.47	*
Otophorus haemorhoidalis	21.20	7.50	2.64	***
2000 m a. s. l.				
Agoliinus satyrus	47.10	14.20	2.98	***
Agolius abdominalis	11.20	5.00	2.03	*
Amidorus immaturus	17.50	4.50	1.77	***
Amidorus obscurus	61.20	20.20	3.11	***
Oromus alpinus	62.70	20.70	4.19	***
Planolinus fasciatus	24.50	11.70	2.75	***

Table 7: Indicator Species Analysis (IndVal) calculated for three altitudes. Maximum observed value and mean expected (± SD) indicator value are given. Statistical significance obtained by Monte Carlo randomization test (1000 runs). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

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