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Variation in dung beetle (Coleoptera: Scarabaeoidea) assemblages with altitude in the Bulgarian Rhodopes Mountains: A comparison

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Abstract. Variation with altitude in the composition of dung beetle assemblages and species richness was measured by sampling in spring, summer and autumn, both manually and with pitfall traps at twelve localities in the western Rhodopes Mountains. Non-parametric estimates indicate that most of the regional species pool was collected, some 73% of all taxa previously recorded in the entire region. The rate of species richness decrease with altitude is around 11 species per km, with an evident altitudinal change in the incidence of two main dung beetle functional groups in which Aphodiinae species begin to dominate Rhodopes assemblages at around 1400–1500 m. Species richness of dung pats is dominated by Scarabaeinae in spite of the fact that the number of Aphodiinae species is highest at each locality. Thus, Aphodiinae species are the main contributors to both local and regional pool richness and to species turnover between localities. These characteristics are similar to those observed in the assemblages from another European mountain range, also located near the Mediterranean-Eurosiberian boundary, the Iberian Central System. These results suggest that eastern European dung beetle assemblages are similar in compositional turnover and species richness variation with altitude to that observed in western Europe and North America.

INTRODUCTION

Biogeographers, long ago described the species richness and composition changes that occur with altitude (Humboldt, 1805; Merriam, 1894), and it is now widely recognized that both environmental conditions and historical factors play an important role in explaining such variation (Brown & Lomolino, 1998). In the case of Holarctic dung beetle assemblages, the variation in species richness and composition turnover with altitude seems to be related to replacement of one dung beetle lineage by another. Geotrupinae – but mainly Aphodiinae – species generally dominate in north-temperate regions and at high altitudes, while Scarabaeinae species dominate in the Mediterranean region and in the lowlands (see Hanski, 1986; Martin-Piera et al., 1992; Halffter et al., 1995; Jay-Robert et al., 1997; Lobo, 2000; Lobo & Halffter, 2000; Errouissi et al., 2004; Escobar et al., 2005, 2006). This may be the consequence of the colonization of the south by northern lineages, favoured by the climate changes that occurred in the Pleistocene (Jay-Robert et al., 1997; Lobo & Halffter, 2000; Escobar et al., 2006). Unfortunately, data on the distribution of dung beetles with altitude in the Palaearctic are only for some western European regions (France and the Iberian Peninsula); there is no reliable, standardized data from the eastern European mountains. This study of the variation with altitude in faunistic composition and species richness in the western Rhodopes Mountains, near the oriental Euromediterranean region, aims to: corroborate patterns established for other western European mountain assemblages; discuss the general characteristics of these mountain assemblages; and determine the altitudinal variation in species richness, abundance and composition of the main dung beetle groups.

METHODS

Studied region

The Western Rhodopes, in south-central Bulgaria, occupy an area of more than 8,000 square kilometres. The western and eastern peaks of the massif (the highest is Golyam Perelik, 2191 m), are separated by the Vucha River valley. Its complex relief and broad surface, together with its connection to the highest massif of the Balkan Peninsula and its proximity to the Mediterranean Sea, determine its diverse climate. In the middle and high mountain regions, which include most of the area, the average annual temperature is 5–9°C. Maximum precipitation is evenly distributed, in May–June and November. Highly diverse habitats (e.g. forest, meadow, riverside, limestone, sandy, stony, gravel, as well as various types of ecotones) coexist in the region. Four main vegetation formations are distributed along an altitude gradient: (i) xero-mesophilous, broad-leaved woodlands and shrubs of Submediterranean type; (ii) mesophilous, broad-leaved woodlands of Nemoral type; (iii) mesophilous, coniferous forest of Boreal type; and (iv) open, high-mountain mesophilous pastures of Alpine type. A local peculiarity is the predominance of mesophilous, coniferous forests of Boreal type, between 800 and 1800 m; to a large extent they have displaced the second formation, which occurs between 1000 and 1600 m in other Bulgarian mountains.

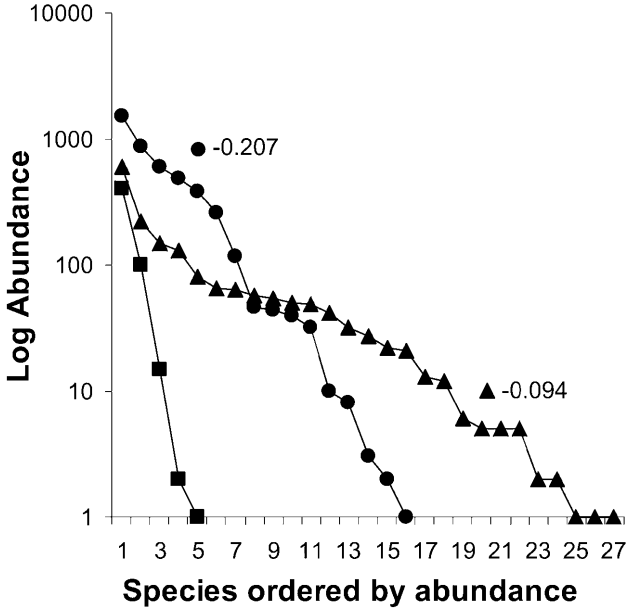

Fig. 1. Scarabaeinae (circles), Aphodiinae (triangles) and Geotrupinae (squares) species abundance relationships with the species ordered according to their decreasing abundance on the abscissa. Linear slopes of these relationships for the two main families are shown.

Sampling methods

Dung beetles were trapped over three periods: 10–19 May 2004 (spring); 14–21 October 2004 (autumn); 15–21 July 2006 (summer), at twelve localities (Fig. 1). These constituted a transect of the altitude gradient in the region. At five localities along this gradient baited pitfall traps, each a plastic basin 100 mm in diameter containing water, were buried to the rim in the soil. Fresh cattle dung (*c.* 250 g) was placed on a grill wire on top of the basin. All the pitfall traps were exposed only once during the trapping period and remained attractive for 48 h. Ten pitfall traps at each locality and season were separated by a mean distance of around 10 m. A total of 150 baited pitfall traps were set, although three were destroyed by wild animals. At the other seven localities beetles were sampled, comparably, by three people collecting all the beetles found within and beneath cattle, sheep or horse excrement, over a period of 45 min.

Data analysis

Due to the great ability of dung beetles to colonize highly patchy and ephemeral resources, baited pitfall traps may be used to collect species representative of a locality (see Lobo et al., 1988; Veiga et al., 1989). Previous studies show that the samples collected from ten dung-baited pitfall traps accurately represent the structure and composition of local dung beetle assemblages (Lobo et al., 1998). Non-parametric richness estimators ACE (abundance-based coverage estimator) and Chao1 (see Colwell & Coddington, 1994 or Colwell, 2005) were used to determine how representative trapped species were of the true species richness. To avoid misinterpretations of gradients in species richness with altitude two different analyses were carried out: one using baited pitfall traps data and another using manual sampling. Between-site richness was compared using the actual number of collected species, the ACE and Chao1 richness estimates and also an estimate of the expected number of species in a random sample of 100 individuals (1000 iterations). The rarefaction scores were obtained using EcoSim 7.70 software (Gotelli & Entsminger, 2001).

A triangular similarity matrix of localities was computed from the rectangular matrix of species abundance (log transformed) at each locality using the recommended Chord distance (Ludwig & Reynolds, 1988), a Euclidean distance measure, with sample vectors normalized to unit length. Hierarchical agglomerative cluster analysis of the triangular similarity matrix yielded groups of localities with similar faunistic composition. The Cluster Analysis used the Ward method, or error sums of squares clustering strategy, to detect clusters that are relatively homogeneous with respect to all variables (Legendre & Legendre, 1998).

The Mann-Whitney (MW), Kruskal-Wallis ANOVA (KW) and Spearman rank correlation coefficient (*rs*) non-parametric tests were used for both abundance and species richness comparisons as well as for correlations.

TABLE 1. Total number of species collected at each site (S_{TOT}), total number of individuals (N_{TOT}), and mean number of individuals and species per pitfall trap (N_{MEAN} and S_{MEAN}, respectively ± SD). Two non-parametric richness estimators (ACE and Chao1) were also calculated (see Colwell, 2005), together with the Shannon index of diversity (H'). The median value of rarefaction, the expected number of species in a random sample of 100 individuals (1000 iterations), were calculated indicating the 95% confidence intervals (in parenthesis).

Site	altitude	type of sampling	S_{TOT}	N_{TOT}	N_{MEAN}	S_{MEAN}	ACE	Chao1	H'	Rarefaction
1	662	Manual	31	432	–	–	33	35	2.72	21 (17–24)
2	991	Manual	19	240	–	–	25	25	2.24	16 (13–18)
3	1274	Manual	22	278	–	–	34	34	2.01	14 (11–17)
4	1510	Manual	18	223	–	–	18	19	2.38	16 (13–18)
5	1712	Manual	15	257	–	–	16	16	2.11	13 (11–15)
6	1771	Manual	16	172	–	–	16	17	2.15	15 (13–16)
7	2014	Manual	14	104	–	–	17	22	2.09	14 (13–14)
8	985	Pifall traps	30	1974	68 ± 65	8.9 ± 3.8	31	32	2.33	15 (12–19)
9	1307	Pifall traps	22	1166	39 ± 25	5.5 ± 1.9	23	24	1.96	11 (8–14)
10	1403	Pifall traps	17	369	13 ± 10	3.6 ± 2.2	19	22	1.93	13 (11–16)
11	1780	Pifall traps	21	1258	42 ± 50	5.9 ± 4.3	29	26	2.11	13 (11–16)
12	2016	Pifall traps	16	230	8 ± 7	2.9 ± 1.9	20	20	1.95	13 (10–15)

TABLE 2. Species richness (S) and abundance (N) of the taxonomic groups collected in this study, and the mean richness (S_{LOC}) or mean abundance (N_{LOC}) (± SD) between localities, and between pitfall traps (S_{PT} and N_{PT}). MW are the results of a Mann-Whitney test of the respective scores for Scarabaeinae and Aphodiinae.

	S	N	S_{LOC}	N_{LOC}	S_{PT}	N_{PT}
Scarabaeinae	16	4466	6.9 ± 3.9	372 ± 469	2.6 ± 2.3	23 ± 34
Aphodiinae	28	1723	11.6 ± 1.9	144 ± 93	2.1 ± 1.5	6 ± 7
Geotrupinae	5	523	1.6 ± 1.2	42 ± 98	0.4 ± 0.7	3 ± 10
MW			2.97, p = 0.001	0.75, ns	0.98, ns	3.46, p < 00.1

RESULTS

Sampling completeness

A total of 6712 specimens belonging to 48 species were collected, of which five were represented by only one individual and four by two individuals. The non-parametric estimates of total species richness are 50 species for ACE and 51 species for Chao1, indicating that most of the regional species pool was collected (around 94%). Both richness estimates for each locality were very similar to the observed scores (Table 1). The mean percentage of completeness (number of species collected/estimated) is 83%. Mean percentages of completeness at localities sampled both by pitfall traps and manually were similar (82% and 85%; minimum-maximum: 64–96% and 79–94%, respectively), although completeness at three manually sampled localities was lower than 80% (Table 1). ACE and Chao 1 percentages of completeness are not significantly correlated with the altitude of the locality (*rs* = 0.21 and *rs* = –0.05, respectively), so no altitude bias is assumed in richness estimates.

The regional pool

Of the 48 species recorded in this study, 56% are Aphodiinae, 33% are Scarabaeinae and the remaining 10% are Geotrupinae. In the case of abundance, most specimens collected (67%) are Scarabaeinae; only 26% of all individuals belong to the Aphodiinae (Table 2), although Aphodiinae dominate regional species richness. The steep slope in the Scarabaeinae species-abundance relationship shows that most dominant species belong to this family (Fig. 2). The dominance of the Scarabaeinae is illustrated by the Scarabaeinae-Aphodiinae abundance ratio (2.6) for the whole region. This ratio is similar when the mean abundance per locality of the two groups is considered, but is greater when the mean abundance per pitfall trap (3.8) is used because these scores significantly differ between the groups (Table 2). This pattern of change with scale in the dominance of both taxonomic groups is also observed in the variation in species richness detected in this study. Scarabaeinae/Aphodiinae ratios based on both total species richness and mean richness per locality are 0.6, with mean richness per locality differing significantly between the two groups. However, a similar ratio is obtained when the mean richness per trap is used (1.2; see also Table 2).

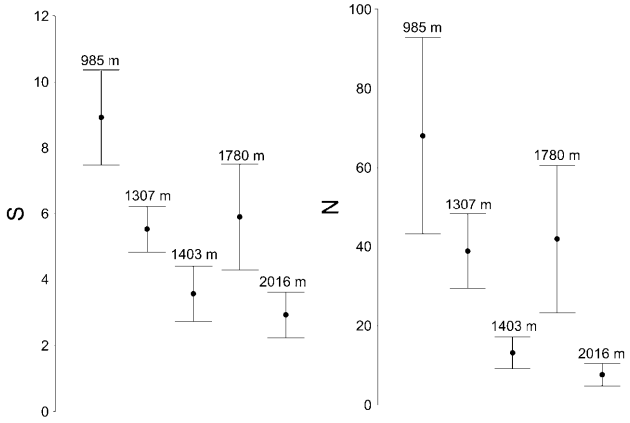

Fig. 2. Mean species richness and mean abundance per pitfall trap (± 95% confidence interval) at each of the five localities sampled using pitfall traps.

Species richness and altitude

The total number of species collected at each locality is negatively correlated with altitude (*rs* = –0.93, p = 0.003 in the case of manually sampled sites, and *rs* = –0.90, p = 0.04 for sites sampled using pitfall traps), with linear regression slopes of –0.011 in both cases (a decrease of approximately eleven species per kilometre). This statistically significant pattern of a decrease in species richness with altitude does not always occur when ACE of Chao1 estimates are considered: ACE estimates; *rs* = –0.77, p = 0.04 for manually sampled sites, and *rs* = –0.50, p = 0.39 for sites sampled using pitfall traps; Chao1 estimates; *rs* = –0.71, p = 0.07 for manually sampled sites, and *rs* = –0.70, p = 0.19 for sites sampled using pitfall traps. Neither the Shannon diversity index (*rs* = –0.54, p = 0.21 for manually sampled sites, and *rs* = –0.50, p = 0.3 for sites sampled using pitfall traps) or the number of species estimated by rarefaction (*rs* = –0.50, p = 0.32 for manually sampled sites, and *rs* = –0.22, p = 0.40 for sites sampled using pitfall traps) are significantly correlated with altitude.

There is no well-established pattern in the mean richness and mean abundance per trap at those localities sampled only using pitfall traps (Table 2). Although both abundance and species richness differ significantly between localities (KW = 47.8, p < 0.0001 and KW = 49.4; p < 0.0001; respectively), the only apparent altitudinal pattern is the greater diversity of the lowest-altitude assemblages and a slight impoverishment at the highest locality (Fig. 3).

Variation in richness variation with altitude shows up more clearly when each of three main taxonomic-functional groups is considered separately. Scarabaeinae and Geotrupinae richness per trap differs significantly

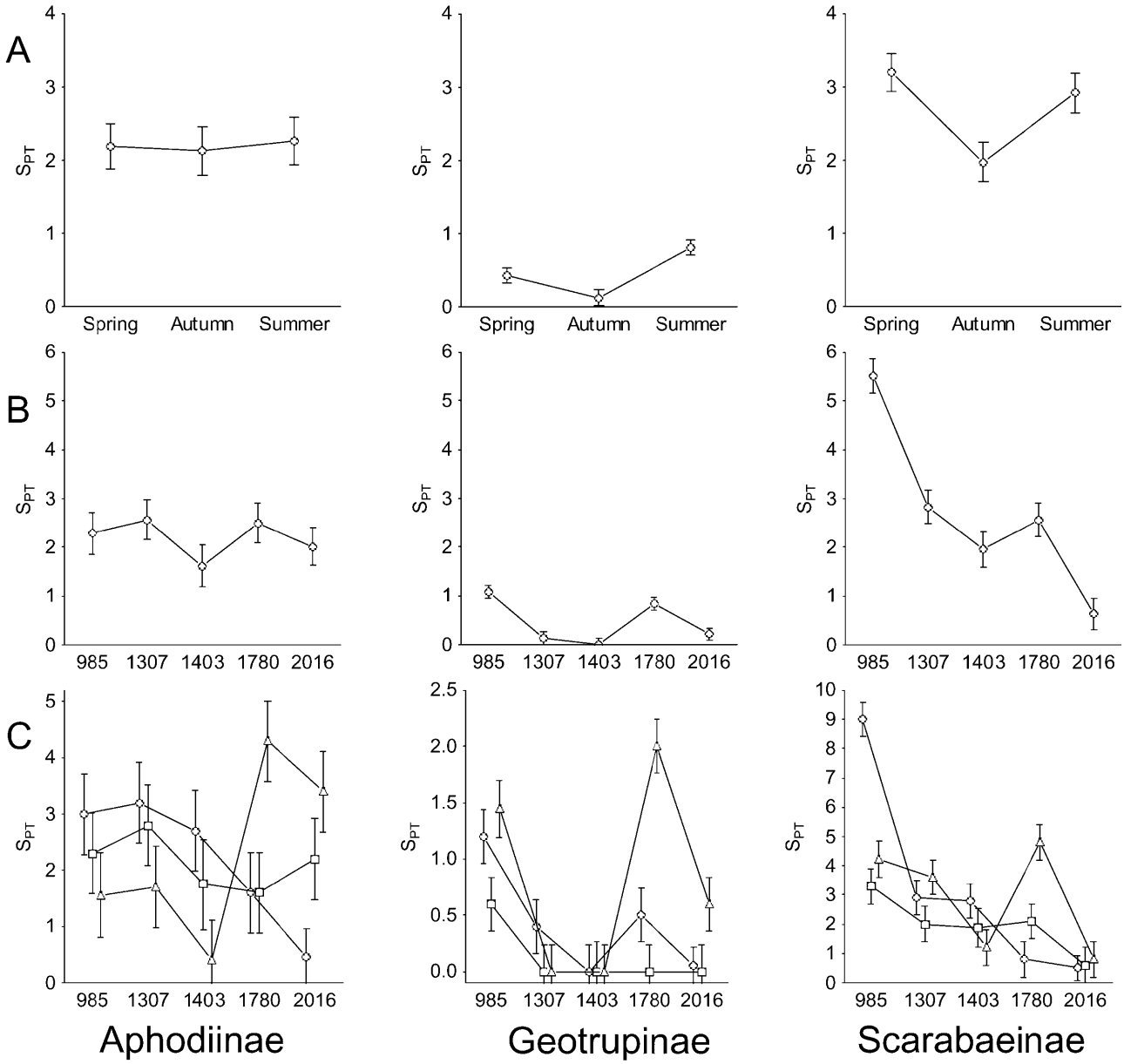

Fig. 3. Seasonal (A) and locality (B) variation in the mean species richness per pitfall trap (S_{PT} ± 95% confidence interval), and for the three dung beetle families (C): spring = circles, summer = triangles, autumn = squares.

between localities (KW = 81.96, $p < 0.0001$ and KW = 57.04, $p < 0.0001$; respectively). Scarabaeinae richness decreases generally with altitude, stabilizing between approximately 1300 and 1800 m (Fig. 3), while Aphodiinae richness per trap is almost invariable with altitude (KW = 11.78, $p = 0.02$) and season (KW = 2.98, ns), with only a slight decrease in the richness of localities at intermediate altitudes (Fig. 3). However, there is a clear dependence of altitudinal variation on season insofar as Scarabaeinae species richness is significantly greater at the lowest locality during spring, but greater during summer at 1780 m (Fig. 3). For the Aphodiinae the most outstanding pattern is the increment in richness at the highest localities during autumn and, principally, during summer (Fig. 3).

Faunistic composition

Cluster analysis for the composition identifies two main locality groupings (A and B), which can each be subdivided into two groups (Fig 4). These four groupings are clearly ordered according to altitude, with a major cluster separation border at around 1600 m, and two minor borders around 1900 and 1100 m. The pattern of similarity between localities is preserved when pitfall-trap or manually sampled localities are considered separately (Fig 4). The total number of species in each of these four altitudinal groups decreases with altitude for all three taxonomic groups, but less so for Aphodiinae (Fig 4). A species present in at least three of the four locality composition groupings is considered an altitude generalist (56% of Aphodiinae, 44% of Scarabaeinae and 40% of Geotrupinae), while those occurring in only one of the

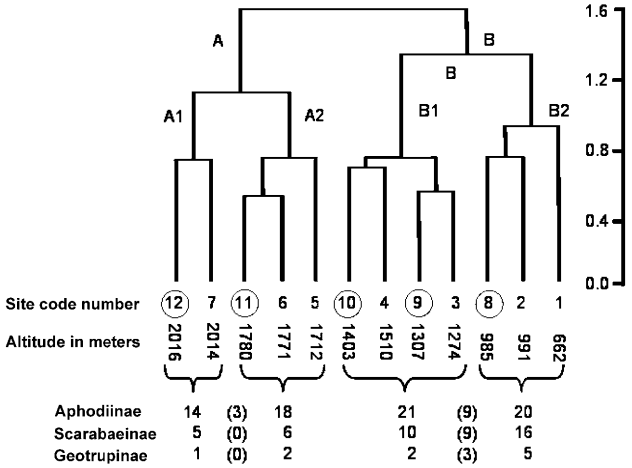

Fig. 4. Locality (12) cluster analysis using the Ward method as linkage rule and Chord distance as a measure of similarity. Locality numbers and altitudes as in Table 1. Localities cluster in two altitude groups (A and B), which in turn are subdivided into two subgroups (A1, A2, B1 and B2). For each group, the number of exclusive species of the three families is included (in brackets) as well as the number of species in each subgroup. Localities sampled using pitfall-traps are included within a circle.

two main locality groupings (A or B) are considered altitude specialists. In the higher locality groupings there are only three Aphodiinae specialist, two of them were only occasionally collected: *Aphodius distinctus* (n = 1) and *Aphodius consputus* (n = 1). Only *Euheptaulacus carinatus* (n = 64) can be considered as a representative species of higher altitude localities. In contrast, 21 species are specific to locality groupings at lower altitudes (Fig. 4). Lowland specialist species of which more than two specimens were collected: *Euoniticellus fulvus* (n = 40); *Copris lunaris* (n = 32); *Onthophagus lemur* (n = 10); *Euonthophagus gibbosus* (n = 3); *Aphodius obliteratus* (n = 22); and *A. thermicola* (n = 21) occur only in low altitude locality groupings (B2). The remaining lowland specialist species are all Aphodiinae: *A. fossor* (n = 13), *A. scrutator* (n = 12), *Oxyomus sylvestris* (n = 6) and *A. luridus* (n = 5).

DISCUSSION

A general description of assemblage richness and compositional variation in the oriental part of the Western Rhodopes Mountains was obtained with a moderate sampling effort. Of course, further sampling could provide improved faunistic information, but the inventory obtained from this first systematic sampling in this mountain zone does include a large percentage of the species previously recorded in this region. A compilation of the previously available faunistic data (Ioakimov, 1904; Nedelkov, 1905, 1909; Stolfa, 1938; Pittioni, 1940; Mikšić, 1957, 1959; Angelov, 1965; Zacharieva, 1965a,b; Zacharieva & Dimova, 1975; Král & Malý, 1993; Bunalski, 2001a,b; Rossner, 2005) cites 66 dung beetle species in the Western Rhodopes at altitudes above 600 m. Even though many of the previously surveyed localities are in the occidental part of the Western Rhodopes, the present study added six new records: *Aphodius* (*Chilothorax*) *distinctus* (Müller); *A.* (*Agrilinus*) *ater* (De Geer); *A.* (*Esymus*) *pusillus* (Herbst); *A.* (*Nimbus*) *contaminatus* (Herbst); *A.* (*Nimbus*) *obliteratus* Panzer; and *Geotrupes stercorarius* (L.), and collected 73% of all taxa previously recorded in the entire region. This is an impressively large percentage, given the many low-altitude localities and the small area sampled (approximately 50 km^2), less than 1% of the entire area (around 8000 km^2) (see Fig 1).

According to the estimators, around 50 species occur in the sampling zone. A previous comparison of six European mountain zones (Jay-Robert et al., 1997) indicate that Rhodopes dung beetle assemblages are rich in species. In the Alps a similar survey from 600 m and above collected 31 species, while in the Cantabric Mountains or Sierra Nevada, respectively in the north and south of the Iberian Peninsula, an annual survey collected 31 and 33 species, respectively, over the same range of altitude. The only comparable species richness occurs in the Iberian Central System, where 45 species were collected within a similar area between 1200 and 2000 m (Jay-Robert et al., 1997 and references therein). However, the percentage of endemicity seems to differ between these regions; in the Iberian Central System 13% of all dung beetle species are Iberian endemics, while none of the species collected in the Rhodopes are endemic to the Balkan region, and all have wide distributions (not shown). This remarkable difference could be due to the lack of isolation of this mountain chain, and its location at the crossroads between Europe and Asia. As are the Rhodopes, the Iberian Central System mountain chain is also located very close to the boundary between the Eurosiberian and Mediterranean regions. The separation of these two mountain chains in the eastern and western extremes of Europe, the relevance of the Balkan and Iberian peninsulas as refuge centres during Pleistocene climatic cycles (Bennett et al., 1991; Hewitt, 1996; Taberlet et al., 1998), and differences in the range size of their species indicate that a more exhaustive comparative study of both regions is needed in order to describe the differences in taxonomy and diversity, as well as the degree of convergence in regional and local species richness and composition.

The rate of decrease in number of species with altitude, of around 11 species per kilometre, is similar to that observed in the other European mountain zones for which data is available (11–15 species per km; see Jay-Robert et al., 1997). From our results altitudinal patterns in the eastern part of Western Rhodopes are similar to those in the mountains of central Spain. Aphodiinae species begin to dominate Rhodopes assemblages at around 1400–1500 m, which is similar to the species turnover altitude boundary of 1300 m in the Iberian Central System. The same species turnover takes place in other European mountain zones at: 900 m in the Northern Alps; 1000 m in the Southern Alps; 1700 m in the Sierra Nevada. Another similarity is the Scarabaeinae/Aphodiinae ratio (0.60) in the Rhodopes mountains (where Aphodiinae make up more than half of the regional species pool), and

that observed in the Iberian Central System (0.76), which differ from the ratios for the Alps (0.17 and 0.25), Cantabric Mountains (0.38) or Sierra Nevada (0.87). Like the Iberian Central System dung beetle assemblages, the dung pat species richness in the Rhodopes is dominated by Scarabaeinae in spite of the fact that the number of Aphodiinae that occur at each locality is higher. This is probably because the more abundant species of Scarabaeinae species are able to colonize a larger number of dung pats at each locality than the generally rare Aphodiinae. In the Iberian Peninsula, Aphodiinae, which are probably more sensitive to environmental heterogeneity, contribute more to both regional and local species richness, while the Scarabaeinae are more numerous in dung pats (Lobo & Martín-Piera, 1999; Hortal et al., 2000). The same pattern occurs in Rhodopes dung beetle assemblages: the richness of a single dung pat is rather more a function of the between-dropping mobility of Scarabaeinae, while Aphodiinae contribute more to local and regional pool richness and between-site species turnover.

Lastly, our results suggest that eastern European dung beetle assemblages show a similar compositional turnover and variation in species richness with the altitude to that observed in western Europe and north America (Martin-Piera et al., 1992; Halffter et al., 1995; Jay-Robert et al., 1997; Lobo & Halffter, 2000; Errouissi et al., 2004). In the Rhodopes there is are also an obvious altitudinal substitution pattern between higher level taxa (Aphodiinae–Geotrupinae vs. Scarabaeinae) suggesting that east European mountain dung beetle assemblages are a consequence of a recent colonization process of elements coming from different latitudes (Lobo & Halffter, 2000).

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REFERENCES

ANGELOV P. 1965: Mistkäfer (Coprinae, Scarabaeidae) aus Bulgarien. *Trav. Sci. Ecole Norm. Super. Plovdiv (Biol.)* **3**: 95–109.

BENNETT K.D., TZEDAKIS P.C. & WILLIS K.J. 1991: Quaternary refugia of north European trees. *J. Biogeogr*. **18**: 103–115.

BROWN J.H. & LOMOLINO M.V. 1998: *Biogeography*. Sinauer Associates, Sunderland, 692 pp.

BUNALSKI M. 2001a: Checklist of Bulgarian Scarabaeoidea (Coleoptera) (Fourth contribution to the knowledge of Scarabaeoidea of Bulgaria). *Pol. Pis. Entomol.* **70**: 165–172.

BUNALSKI M. 2001b: Contributions to the knowledge Scarabaeoidea (Coleoptera) of Bulgaria. Part II. Species not recorded from Bulgaria before. *Wiad. Entomol.* **20**: 29–32.

COLWELL R.K. 2005: *EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples*. Version 7.5. http://viceroy.eeb.uconn.edu/EstimateS.

COLWELL R.K. & CODDINGTON J.A. 1994: Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. R. Soc. London. (B)* **345**: 101–118.

ERROUISSI F., JAY-ROBERT P., LUMARET J.P. & PIAU O. 2004: Composition and structure of dung beetle (Coleoptera: Aphodiidae, Geotrupidae, Scarabaeidae) assemblages in mountain grasslands of the Southern Alps. *Ann. Entomol. Soc. Am*. **97**: 701–709.

ESCOBAR F., LOBO J.M. & HALFFTER G. 2005: Altitudinal variation of dung beetle (Scarabaeidae: Scarabaeinae) assemblages in Colombian Andes. *Global Ecol. Biog*. **14**: 327–337.

ESCOBAR F., LOBO J.M. & HALFFTER G. 2006: Assessing the origin of Neotropical mountain dung beetle assemblages (Scarabaeidae: Scarabaeinae): the comparative influence of vertical and horizontal colonization. *J. Biogeogr*. **33**: 1793–1803.

GOTELLI N.J. & ENTSMINGER G.L. 2001: *EcoSim: Null Models Software for Ecology.* Version 7.0. Acquired Intelligence Inc. & Kesey-Bear. http://homepages.together.net/~gentsmin/ecosim.htm

HALFFTER G., FAVILA M.E. & ARELLANO L. 1995: Spatial distribution of three groups of Coleoptera along an altitudinal transect in the Mexican Transition Zone and its biogeographical implications. *Elytron* **9**: 151–185.

HANSKI I. 1986: Individual behaviour, population dynamics and community structure of Aphodius (Scarabaeidae) in Europe. *Acta Oecol*. **7**: 171–187.

HEWITT G.M. 1996: Some genetic consequences of ice ages, and their role in divergence and speciation. *Biol. J. Linn. Soc*. **58**: 247–276.

HORTAL J., MARTÍN-PIERA F. & LOBO J.M. 2000: Dung beetle geographic diversity variation along a western Iberian latitudinal transect (Col., Scarabaeidae). *Ann. Entomol. Soc. Am.* **93**: 235–243.

HUMBOLDT A. VON 1805: *Essai sur la Géographie des Plantes*. Schoel, Paris.

IOAKIMOV D. 1904: Contribution to the fauna of insects of Bulgaria. Insecta. I. Coleoptera. *Sbornik Nar. Umotvor. Nauka Knizhn.* **20**: 1–43.

JAY-ROBERT P., LOBO J.M. & LUMARET J.P. 1997: Elevational turnover and species richness variation in European montane dung beetles assemblages. *Arct. Alp. Res*. **29**: 196–205.

KRÁL D. & MALÝ V. 1993: New records of Scarabaeoidea (Coleoptera) from Bulgaria. *Acta Soc. Zool. Bohem*. **57**: 17–29.

LEGENDRE P. & LEGENDRE L. 1998: *Numerical Ecology*. Elsevier, Amsterdam, 853 pp.

LOBO J.M. 2000: Species diversity and composition of dung beetle (Coleoptera: Scarabaeoidea) assemblages in North America. *Can. Entomol*. **132**: 307–321.

LOBO J.M. & HALFFTER G. 2000: Biogeographical and ecological factors affecting the altitudinal variation of mountainous communities of coprophagous beetles (Coleoptera: Scarabaeoidea): a comparative study. *Ann. Entomol. Soc. Am*. **93**: 115–126.

LOBO J.M. & MARTÍN-PIERA F. 1999: Between-group differences in the Iberian dung beetle species-area relationship (Coleoptera: Scarabaeidae). *Acta Oecol.* **20**: 587–597.

LOBO J.M., MARTÍN-PIERA F. & VEIGA C.M. 1988: Las trampas pitfall con cebo, sus posibilidades en el estudio de las comunidades coprófagas de Scarabaeidae (Col.). I. Características determinantes de su capacidad de captura. *Rev. Écol. Biol. Sol* **25**: 77–100.

LOBO J.M., LUMARET J.P. & JAY-ROBERT P. 1998: Sampling dung beetles in the French Mediterranean area: effects of abiotic factors and farm practices. *Pedobiologie* **42**: 252–266.

LUDWIG J.A. & REYNOLDS J.F. 1988: *Statistical Ecology: A Primer on Methods*. John Wiley and Sons, New York, 337 pp.

MARTÍN-PIERA F., VEIGA C.M. & LOBO J.M. 1992: Ecology and biogeography of dung-beetle communities (Coleoptera, Scarabaeoidea) in an Iberian mountain range. *J. Biogeogr*. **19**: 677–691.

MERRIAM C.H. 1894: Laws of temperature control of the geographic distribution of terrestrial animals and plants. *Nat. Geog.* **6**: 229–238.

MIKŠIĆ R. 1957: Zweiter Nachtrag zur Fauna Insectorum Balcanica. Scarabaeidae. (Coleoptera, Lamellicornia). 24. Beitrag zur Kenntnis der Scarabaeidae. *Acta Mus. Maced. Sci. Nat.* **4**: 139–214.

MIKŠIĆ R. 1959: Dritter Nachtrag zur Fauna Insectorum Balcanica – Scarabaeidae. 30. Beitrag zur Kenntnis der Scarabaeiden). *Godišnjak Biol. Inst. Saraj.* **12**(1–2): 47–136.

NEDELKOV N. 1905: Contribution to the entomological fauna of Bulgaria. *Period. Spis. Bulg. Knizh. Druzh. (Sofia)* **66**: 404–439.

NEDELKOV N. 1909: Fifth contribution to the fauna of insects of Bulgaria. *Sbornik Nar. Umotvor. Nauka Knizhn.* **25**: 3–37.

PITTIONI B. 1940: Die Arten der Unterfamilie Coprinae (Scarabaeidae, Coleoptera) in der Sammlung des Kgl. Naturh. Museum in Sofia. *Mitt. Kgl. Naturw. Inst. Sofia* **13**: 211–213.

ROSSNER E. 2005: Die Verbreitung von Aphodius (Eurodalus) coenosus (Panzer, 1798) und Aphodius (Eurodalus) paracoenosus Balthasar & Hrubant, 1960 in Deutschland und Mittelung von Funddaten zu den Gesamtarealen beider Arten (Coleoptera: Scarabaeidae). *Entomol. Z.* **115**(2): 59–69.

STOLFA E. 1938: Revisione delle specie palearctiche del sottogenere Scarabaeus s. str. *Atti Mus. Civ. Stor. Nat. Trieste* **13**: 141–156.

TABERLET P., FUMAGALLI L., WUST-SCAUCY A.G. & COSSON J.F. 1998: Comparative phylogeography and postglacial colonization routes in Europe. *Mol. Ecol.* **7**: 453–464.

VEIGA C.M., LOBO J.M. & MARTÍN-PIERA F. 1989: Las trampas pitfall con cebo, sus posibilidades en el estudio de las comunidades coprófagas de Scarabaeidae (Col.). II. Análisis de efectividad. *Rev. Écol. Biol. Sol* **26**: 91–109.

ZACHARIEVA B. 1965a: Beitrag zur Erforschung der coprophagen Scarabaeoidae (Coleoptera) aus den Ostrhodopen. *Bull. Inst. Zool. Mus.* **19**: 129–134.

ZACHARIEVA B. 1965b: Scarabaeidae (Coleoptera) aus Thrakien. In Valkanov A.K. (ed.): *Die Fauna Thrakiens*. Sofia, pp. 229–254.

ZACHARIEVA B. & DIMOVA V. 1975: Faunistische Untersuchungen über die Scarabaeidae (Coleoptera) aus den Rhodopen. In Peshev G. (ed.): *La Faune des Rhodopes*. *Materiaux.* Bulg. Acad. Sci., Sofia, pp. 183–196.

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