Rarity of blister beetles (Coleoptera: Meloidae) in Southern Africa correlates with their phylogeny and trophic habits, but not body size

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Abstract. Ecologists have identified several correlates of biological rarity in animals. Among the various correlates identified so far, three are explored in this paper: (a) abundance is correlated with absolute body size in animals; (b) phylogenetically primitive taxa are overrepresented in samples of rare species; (c) more specialized species are rarer than less specialized species. Here we use Namibian blister beetles (Coleoptera: Meloidae) as a model system for exploring these issues. We used data from five field expeditions, which resulted in the identification of 891 beetles belonging to 76 species collected from 191 sites. 13% of the species accounted for over 50% of the individuals; 22% of all species were represented by singletons. Abundance patterns differed significantly among the different trophic categories, with non-pollinophagous (non-specialized) species being more abundant than weed-eaters and pollinophagous (specialized) species. Species of phylogenetically basal tribes were less abundant than those of more derived groups. Trophic category and phylogenesis did not have a synergic effect in determining the relative abundance of the species, and body size had no influence on their abundance.

INTRODUCTION

The biology of rarity has received tremendous attention over the past two decades (Schoener, 1987; Gaston, 1994; Blackburn & Gaston, 1997, 1999). Theoretical advances in the understanding of the biology of rarity has been due primarily to research on insects (Morse et al., 1988; Novotny, 1993; Price et al., 1995; Ulrich, 2001a, b), endothermic vertebrates (i.e., Cotgreave & Pagel, 1997; Yu & Dobson 2000; Harcourt et al., 2002), ectothermic vertebrates (Luiselli, 2006) as well as plants (Rabinowitz, 1981).

It has been demonstrated that, for example, there is a geographical bias in the distribution of animals (Schoener, 1987) with rare species more prevalent in the tropics than in temperate regions (Morse et al., 1988; Novotny, 1993; Stork et al., 1997). However, the above-mentioned patterns remain relatively controversial, with contrasting evidence from distinct datasets (e.g., Gaston, 1994). On the other hand, it is more evident that within each taxon large animals are usually scarcer than smaller ones (Cotgreave, 1993; Gaston, 1994; Blackburn & Gaston, 1997, 1999; Spencer, 2000). For instance, this pattern occurs consistently in both African tropical and Asian tropical snake assemblages (Luiselli et al., 2005; Rahman et al., 2013). However, this pattern is likely to occur more frequently in assemblages of predators (due to limited resource availability) than of phytophagous organisms (Luiselli, 2006). In addition, rare species are often characterized by narrow realized ecological niches and high degrees of specialization (Gaston, 1996; Gaston & Curnutt, 1998), and typically belong to phylogenetically old and/or primitive taxa

(Cotgreave & Pagel, 1997). However, these latter patterns are difficult to test rigorously because few of the groups so far studied show such a remarkable diversity in terms of phylogeny and life-history traits (Gaston, 1994). Thus, it is important to find suitable model organisms that are sufficiently diverse in phylogeny and life-history traits to test for the occurrence of the above-mentioned patterns. In this regard, the beetle family Meloidae may be an ideal study system, given that it fulfills all the biological characteristics mentioned above (Bologna, 1991; Bologna et al., 2008b; Bologna & Di Giulio, 2011). There has been no previous study on the biology of rarity in blister beetles.

Of the several hypotheses formulated to explain the biology of rarity we tested the following three key questions using data for Meloidae: (1) do abundance patterns correlate with absolute body size of animals, (2) are more specialized species (for instance, monophagous compared to polyphagous) rarer than less specialized species and (3) are some phylogenetically primitive taxa overrepresented among rare species? We tested these hypotheses by determining what aspects of the biology of beetles of the family Meloidae occurring in Namibia (Southern Africa) are correlated with their rarity. Meloid beetles are particularly suitable for this type of analysis because in tropical savannahs there are many species that are remarkably heterogeneous in terms of the parameters studied. In particular, Meloidae vary greatly in body size (3 to 70 mm; Bologna et al., 2010), in their phylogeny, with three subfamilies and 15 tribes (Bologna et al., 2010) and feeding habits of the larval and adult stages (larvae are obligate parasites of both Hymenoptera Aculeata and Orthoptera Caelifera, and

adults either pollinophagous, phyllophagous, or antophagous; Bologna, 1991; Bologna et al., 2010). In addition, in Namibia these species are active in open habitats over a relatively short period of time (from late January to early April), which minimizes any biases in collecting the different species due to differences in their phenology.

Ecologically, Namibia consists of xeric or sub-xeric biomes, namely the Namib desert, exclusive to this country and a small area in southern Angola, the Succulent and Nama Karoo, both of which extend in South Africa, Savannah which extends in Botswana and South Africa, and salt Pan (restricted to the Etosha plain) (e.g. Irish, 1994; Rutherford & Westfall, 1994; Barnard, 1998). This area along with western South Africa is one of 25 hot spots of biodiversity recorded in the world (Myers et al., 2000). The great number of endemic taxa (especially species and genera) of plants and animals recorded there is the result of a long history of isolation and extreme ecological pressures of Namibian ecosystems (Jarvis & Robertson, 1997; Barnard, 1998; Maggs et al., 1998; Simmons et al., 1998).

Our study is the first on the beetle fauna associated with arid open ecosystems in the tropics and provides further generalizations about the biology of rarity. There are similar studies by Siemann et al. (1999) on North American non-tropical grassland communities of arthropods.

MATERIAL AND METHODS

Study area

Research was conducted throughout almost the whole of Namibia at a total of 191 sites (Fig. 1). There are five main biomes in Namibia, which include several types of vegetation (e.g. Giess, 1971; White, 1983; Rutherford, 1997), all of which were extensively covered in this study. Tree and shrub savannahs are the most extensive ecosystems, while Succulent Karoo is restricted to a narrow area in the south-west, close to the mouth of the Orange River. The Namib desert extends along the sea cost and the Nama Karoo is diagonally wedge shaped and progressively narrows from South Africa to the Angolan border (Fig. 1). The climate of Namibia is primarily xeric, except in the north-eastern Caprivi strip and it rains from January to April (uncommonly in May) in most of the country and in Winter (August–October) in south-western and southern central parts of the country or, occasionally, also in other areas (Tyson, 1986).

Taxonomic model

Meloidae is a family of phytophagous beetles, particularly rich in species in Afrotropical savannahs, which are characterized by hypermetabolic development and larval stages that parasitize Orthoptera Caelifera, Hymenoptera Apoidea and less frequently other Aculeata. Bologna (1991) and Bologna et al. (2008b) have studied the biology and phylogeny of this family and in particular the faunistics and taxonomy of the Namibian Meloidae were recently studied and updated by Bologna (2000, unpubl.).

Field study

Five expeditions, aimed at sampling most of the regions in this country were undertaken during the main rainy period (when host plants are in bloom) in 1997, 2001, 2003, 2004 and 2005. Each field expedition lasted on average 20 days. We know that this could potentially limit the value of this study as a few of the species (usually the most abundant ones: Bologna, unpublished database) may be occasionally active in other periods of the year
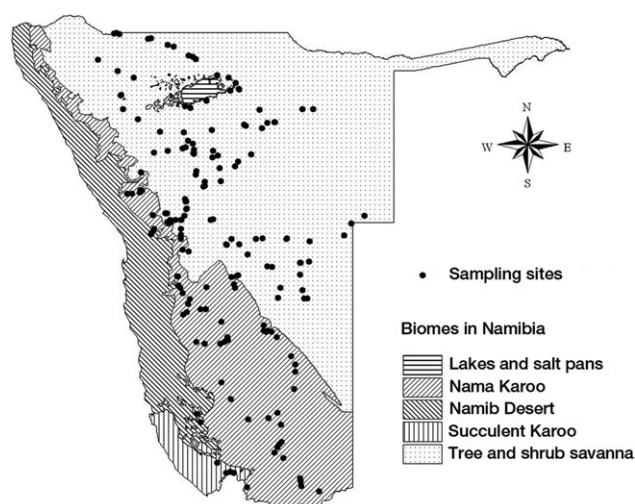
Fig. 1. Map of Namibia showing the distributions of the different biomes and location of the sites sampled.

and were therefore not sampled. However, it is unlikely that this greatly biased our results, because such occasional records are uncommon even among abundant species in the thousands of museums records for this country (Bologna et al., unpubl.). All the sites selected were within vegetation zones (Fig. 1) in which the habitat was extensively homogeneous. At each site, we standardized the field effort in order to minimize inter-site differences in the probability of capturing beetles. Hence, we spent 30 min collecting at each site, with three people actively patrolling flowering plants and collecting samples. As the three people walked at the same speed, approximately 1 km per hour, it is likely that the area surveyed at each site was nearly identical. All field collectors were experts on Namibian Meloidae and ecosystems (with over 10 years of field experience), which minimized sampling biases due to different catchabilities across sites and among species.

Insects were caught on host plants using a net or, at daybreak, also under house and petrol station lights, and afterwards identified to species at the laboratory in Rome, University 'Roma Tre'. Host plant was identified to family or genus (determined using keys, field guides and expert opinions of researchers associated with the National Museum of Windhoek), and the trophic category of each species was determined by direct observation of individuals in the field. The number of specimens collected for each species are the measures of species abundances used in this paper. Singletons are here defined as those species for which only a single individual was collected (see Gaston, 1994).

There are some shortcomings in this method of sampling, however, that should be taken into account when interpreting the emerging patterns. For instance, the plant species were not similarly abundant at all sites, which possibly introduced some biases, especially for the most specialized beetles. Moreover, differences in plant density at the different sites may have affected catchability and the estimates of insect abundance. However, a Kruskal-Wallis ANOVA revealed no significant differences in mean abundances of the various species across habitat types (χ^2 = 0.130, df = 3, p = 0.898), thus the results for the different sites were pooled in our analyses. In addition, we could not exclude that were fluctuations in population size from year to year in at least some species and at some sites.

Analyses

Each meloid species was assigned to a particular trophic category: (i) non-pollinophagous (feeding on every part of a flower, apart from pollen) (= non-specialized), (ii) pollinophagous (eat-

TABLE 1. List of the Meloidae beetles of Namibia studied, including details of the number of specimens collected, tribe, trophic category, phylogenetic score and body size. Endemic/subendemic species are asterisked.

| Species	Tribe	Number of specimens	Trophic categories	Phylogenetic score	Body size in cm (category)
Actenodia chrysomelina	Mylabrini	40	non-pollinophagous	5	1.1 (1)
*Australytta rubrolineata**	Lyttini	1	weed-eater	4	1.9 (2)
Australytta szekessyi	Lyttini	4	weed-eater	4	1.3 (1)
Ceroctis amphibia	Mylabrini	12	non-pollinophagous	5	1.2 (1)
Ceroctis angolensis	Mylabrini	57	non-pollinophagous	5	1.1 (1)
Ceroctis braunsiana	Mylabrini	7	non-pollinophagous	5	1.2 (1)
Ceroctis exclamationis	Mylabrini	1	non-pollinophagous	5	1.1 (1)
Ceroctis aliena	Mylabrini	13	non-pollinophagous	5	1.9 (2)
Ceroctis karroensis	Mylabrini	8	non-pollinophagous	5	1.1 (1)
Ceroctis korana	Mylabrini	9	non-pollinophagous	5	1.4 (1)
Ceroctis peringueyi	Mylabrini	9	non-pollinophagous	5	1.6 (2)
Ceroctis spuria	Mylabrini	2	non-pollinophagous	5	1.3 (1)
*Ceroctis trifasciata**	Mylabrini	40	non-pollinophagous	5	1.7 (2)
Cyaneolytta depressicornis	Epicautini	1	weed-eater	3	2.4 (2)
Cyaneolytta granulipennis	Epicautini	2	weed-eater	3	2.6 (3)
Cyaneolytta maculifrons	Epicautini	1	weed-eater	3	2.7 (3)
Cyaneolytta resplendens	Epicautini	1	weed-eater	3	2.3 (2)
Epicauta designata	Epicautini	3	weed-eater	3	1.4 (1)
*Epicauta ovampoa**	Epicautini	2	weed-eater	3	1.7 (2)
Epicauta velata	Epicautini	1	weed-eater	3	1.3 (1)
Hycleus amoenus	Mylabrini	1	non-pollinophagous	5	0.7 (0)
Hycleus basibicinctus	Mylabrini	4	non-pollinophagous	5	1.4 (1)
*Hycleus benguellanus**	Mylabrini	9	non-pollinophagous	5	1.1 (1)
Hycleus bifucatus	Mylabrini	5	non-pollinophagous	5	1.7 (2)
Hycleus bissexguttatus	Mylabrini	5	non-pollinophagous	5	1.5 (1)
Hycleus brincki	Mylabrini	2	non-pollinophagous	5	1.2 (1)
Hycleus buqueti	Mylabrini	11	non-pollinophagous	5	3 (3)
Hycleus burmeisteri	Mylabrini	25	non-pollinophagous	5	1.7 (2)
*Hycleus bushmanicus**	Mylabrini	9	non-pollinophagous	5	0.7 (0)
*Hycleus damarensis**	Mylabrini	8	non-pollinophagous	5	1.3 (1)
Hycleus decoratus	Mylabrini	39	non-pollinophagous	5	1.1 (1)
Hycleus dentatus	Mylabrini	42	non-pollinophagous	5	1.3 (1)
Hycleus derosus	Mylabrini	1	non-pollinophagous	5	2 (2)
Hycleus deserticolus	Mylabrini	45	non-pollinophagous	5	1.1 (1)
*Hycleus devylderi**	Mylabrini	21	non-pollinophagous	5	0.7 (0)
*Hycleus hilaris**	Mylabrini	4	non-pollinophagous	5	1.3 (1)
Hycleus hybridus	Mylabrini	34	non-pollinophagous	5	1.7 (2)
Hycleus jucundus	Mylabrini	15	non-pollinophagous	5	1.1 (1)
*Hycleus kochi**	Mylabrini	14	non-pollinophagous	5	0.7 (0)
Hycleus matabele	Mylabrini	14	non-pollinophagous	5	1.5 (1)
Hycleus peringueyi	Mylabrini	4	non-pollinophagous	5	1 (0)
Hycleus pilosus	Mylabrini	10	non-pollinophagous	5	1.3 (1)
*Hycleus politus**	Mylabrini	3	non-pollinophagous	5	0.5 (0)
*Hycleus scalaris**	Mylabrini	13	non-pollinophagous	5	3 (3)
Hycleus sp. n.*	Mylabrini	1	non-pollinophagous	5	3.8 (3)
Hycleus surcoufi	Mylabrini	2	non-pollinophagous	5	1.1 (1)
*Hycleus svakopinus**	Mylabrini	64	non-pollinophagous	5	1 (0)
Hycleus tinctus	Mylabrini	49	non-pollinophagous	5	2.1 (2)
Hycleus transvaalicus	Mylabrini	8	non-pollinophagous	5	1.3 (1)
Hycleus tricolor	Mylabrini	13	non-pollinophagous	5	2.4 (2)
Hycleus villosus	Mylabrini	1	non-pollinophagous	5	1.4 (1)
*Hycleus windhoekanus**	Mylabrini	12	non-pollinophagous	5	1.1 (1)
*Iselma hobohmi**	Derideini	1	pollinophagous	0	0.7 (0)
*Iselma penrithae**	Derideini	3	pollinophagous	0	1 (0)
Lydomorphus bisignatus	Lyttini	33	non-pollinophagous	4	1.9 (2)
*Lydomorphus karibibensis**	Lyttini	12	non-pollinophagous	4	2.3 (2)
"*Lydomorphus*" *mesembryanthemi**	Lyttini	5	non-pollinophagous	4	1.3 (1)
*Lydomorphus mimus**	Lyttini	9	non-pollinophagous	4	1.7 (2)
Lydomorphus optatus	Lyttini	1	non-pollinophagous	4	1.6 (2)
Lydomorphus strangulatus	Lyttini	3	non-pollinophagous	4	1.7 (2)
Lydomorphus thoracicus	Lyttini	55	non-pollinophagous	4	1.9 (2)
*Lydomorphus tibialis**	Lyttini	7	non-pollinophagous	4	2.2 (2)
"*Lytta*" *elegantula**	Eleticini	4	non-pollinophagous	1	1.2 (1)
Mimesthes maculicollis	Mylabrini	5	non-pollinophagous	5	1.2 (1)
Nemognatha vansoni	Nemognathini	5	pollinophagous	2	0.8 (0)
*Paractenodia glabra**	Mylabrini	2	non-pollinophagous	5	0.5 (0)
*Paractenodia namaquensis**	Mylabrini	10	non-pollinophagous	5	0.6 (0)
Paractenodia parva	Mylabrini	1	non-pollinophagous	5	0.9 (0)
Prionotolytta binotata	Lyttini	6	non-pollinophagous	4	1 (0)
*Prionotolytta hajekae**	Lyttini	2	non-pollinophagous	4	1 (0)
Prionotolytta melanura	Lyttini	17	non-pollinophagous	4	0.9 (0)
Prionotolytta streyi	Lyttini	1	non-pollinophagous	4	1.1 (1)
*Prolytta namibensis**	Lyttini	3	non-pollinophagous	4	1.5 (1)
*Zonitis notaticollis**	Nemognathini	2	pollinophagous	2	1.2 (1)
Zonitodema viridipennis	Nemognathini	1	pollinophagous	2	1 (0)
*Zonitomorpha costata**	Nemognathini	1	pollinophagous	2	1.5 (1)
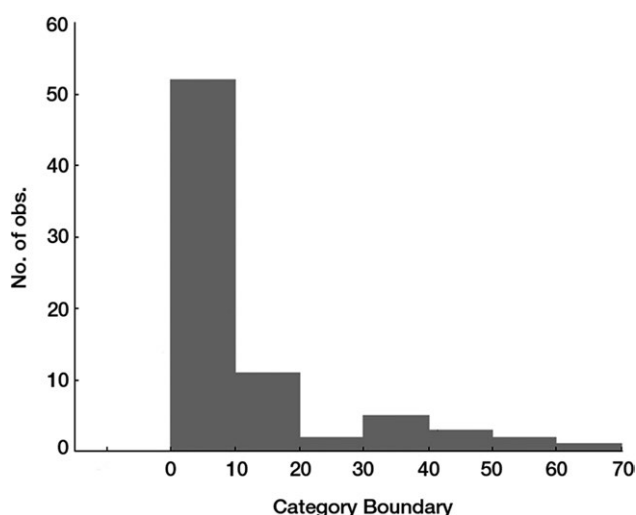
Fig. 2. Distribution of the numbers of individuals of species beetles belonging to the family Meloidae recorded in Namibia.
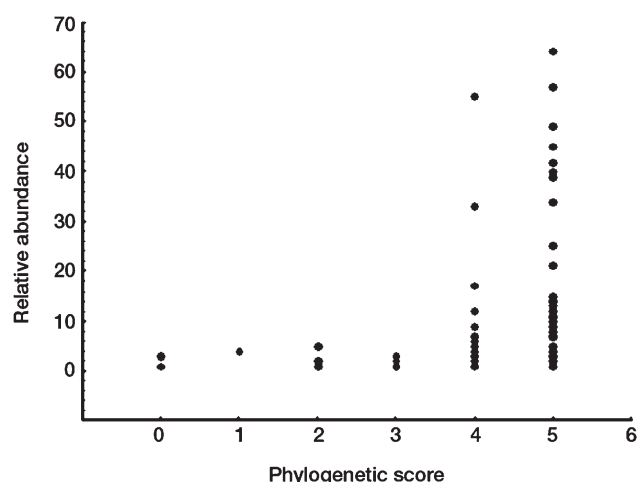

Fig. 3. Relationship between the relative abundances and phylogenetic scores of 76 species of Namibian Meloidae. The phylogenetic score varies from 0 to 5, with the value increasing from basal to more derived taxa. For statistical details, see the text.

ing only pollen) or (iii) weed-eaters (feeding only on Poaceae) (both specialized). The assignment of each species to a particular trophic category was done using Bologna (2000, 2003), Bologna et al. (2001, 2008a), Bologna & Di Giulio (2002), Amore (2005), Pitzalis & Bologna (2008) and Marco A. Bologna's unpublished dataset. All nominal species listed belong to a single and distinct taxon and not to species complexes (Bologna, 2000). The species listed as *Hycleus* sp. n. is currently being described (Bologna, unpubl.).

The phylogenetic position of each species was defined based on Bologna et al. (2008b), which is a revision of this beetle family based on both morphological and molecular characters. We defined a "phylogenetic score" for each taxon, which increased in value from the base to the tips of the branches of the tree based on both Bayesian and Maximum Likelihood Tree analyses, which are strongly supported (see phylogeny in Bologna et al., 2008b). Unfortunately, it was not possible to extend this analysis to include the relationships between genera and species because the available information on phylogeny of Meloidae in Southern Africa is still rudimentary except for the genera *Actenodia* (Bologna et al., 2008a) and *Iselma* (Pitzalis & Bologna, 2010). The basal taxa are those showing more symplesiomorphic conditions of molecular, morphological and biological traits (Hennig, 1967). All species belonging to the same tribe received an identical phylogenetic score: Derideini = 0, Eleticini = 1, Nemognathini = 2, Epicautini = 3, Lyttini = 4, Mylabrini = 5. Eupomphini, the sister group of Mylabrini (i.e. the last clade in the phylogenetic sequence) does not occur in Namibia, is a North American endemic taxon and therefore was not taken into consideration when determining the "phylogenetic score".

For each species, we determined the range in its body length (from apex of mandibles to apex of abdomen) by measuring a few thousand specimens in entomological collections (in particular: M.A. Bologna, Roma Tre University; National Museum of Namibia, Windhoek; Iziko South African Museum, Cape Town; Transvaal Museum, Pretoria; Museum für Naturkunde, Berlin). Each species was scored based on its body size as either: 0.5–1.5 cm = 1; 1.51–2.5 cm = 2 or > 2.50 cm = 3. In this context it should be taken into consideration that some species were in the past captured so rarely (e.g., 2 specimens of *Zonitis notaticollis* or *Paractenodia glabra,* for which only the types and the single individuals we collected are known; Bologna et al., unpubl. data) that it is likely the mean values differ in their accuracy.

All data were checked for homoscedasticity and normality prior to applying parametric tests. Lilliefors test was used to determine the normality of the data. Chi-square tests were used to analyse differences in frequencies of occurrence among distinct groups of categories; Spearman's rank correlation coefficient was used to test correlation between two variables; a non-parametric ANOVA was used to evaluate the effects of trophic category × phylogenetic score. Polynomial models (in the form of $y = ax^2 + bx + c$) were used to explore the relationships between abundance and mean body size of species, taking into account the AICc values of the linear and polynomial models. Alpha was set at 5%. All analyses were performed using Statistica 6.0 software.

RESULTS

In total, we collected 891 beetles belonging to 76 species. 35.5% of these species were endemic/subendemic (n = 27), i.e. occurring only in Namibia or marginally also in northern South African Namaqualand or in Angolan western Kaokaland. We included the results for the whole group of Meloidae (n = 76 species) in the analysis in order to increase the size of the samples and statistical power. The abundances recorded for all the species of blister beetles plus details of their feeding habits and phylogenetic position, are given in Table 1. Overall, the abundance distribution pattern was strongly uneven, with only 10 species (13% of total) accounting for over 50% of the individuals and 20 species for well over 60% (Fig. 2). Thus, the main pattern was that there were few abundant and many uncommon or even rare species in the field. Singletons accounted for 22% of the total number of species recorded.

The great majority of the 76 species recorded were non-pollinophagous (80.3%), with weed-eaters accounting for 11.8% and pollinophagous 7.9%. Abundance of the species in the different trophic categories differed significantly, with non-pollinophagous species more abundant than pollinophagous and weed-eaters ($\chi^2 = 17.73$, df = 2, p = 0.0001). There were 9 singletons among the non-pollinophagous species, 3 among pollinophagous and 5 among weed-eating species. The frequency of singletons differed
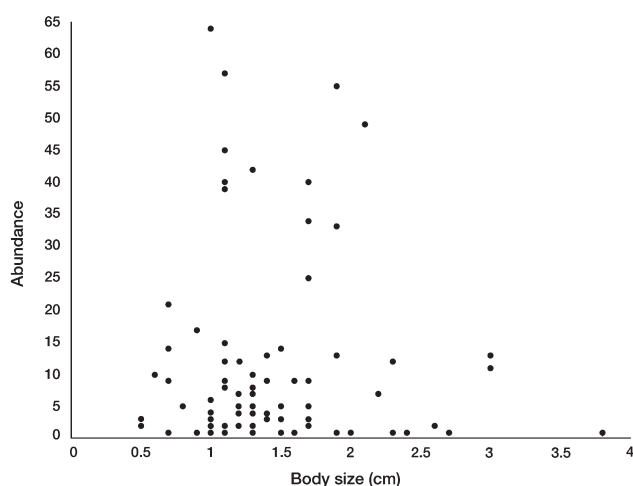
Fig. 4. Relationship between relative abundances and body sizes of beetles of the family Meloidae in Namibia.

significantly across the trophic categories ($\chi^2 = 16.33$, df = 2, p < 0.005), with significantly more singletons recorded among non-pollinophagous species (52.9% of total were singletons) and they accounted for 80.3% of all the species recorded. Thus, we conclude that the number of singletons did not depend on trophic category per se, but merely on the number of species included in each trophic category.

Abundance of species in the different phylogenetic categories differed significantly, with Mylabrini species more abundant than those of other tribes ($\chi^2 = 17.62$, df = 5, p = 0.0035). There was a statistically significant correlation between abundance and phylogenetic position (Spearman's r= 0.441, n = 76, P < 0.00001), with the more basal tribes less abundant than those of more derived tribes (Fig. 3). In terms of the number of singletons, their frequency was significantly correlated with the number of species included in each phylogenetic category (Spearman's r = 0.943, n = 5, P = 0.0048).

A Kruskal-Wallis ANOVA revealed that neither the trophic category nor the phylogenetic score determined relative abundances of the species (trophic category: H = 0.553, P = 0.373; phylogenetic score: H = 0.196, P = 0.884).

Beetle body size did not affect the abundances recorded (equation: $y = 3.502x^2 + 12.08x + 2.899$; AICc = 17007; r^2 = 0.02; H = 0.664, P = 0.498) (Fig. 4).

DISCUSSION AND CONCLUSION

This study revealed several patterns. First, a few species dominated the samples and most of the other species were relatively less abundant. This pattern is quite general in the tropics (Lawton, 1991), recorded for snakes worldwide (Luiselli, 2006), amphibians in the Albertine Rift in East Africa (Behangana et al., 2009), arboreal beetles in Borneo (Morse et al., 1988), bugs in Indochina (Novotny, 1993) and canopy arthropods in general (Stork et al., 1997).

We also showed that non-pollinophagous species and those belonging to the tribe Mylabrini are more abundant than those of other trophic categories sampled. This undoubtedly is a consequence of an auto-correlation, given

that (i) the Mylabrini is the most speciose group of Meloidae (Bologna et al., 2010), (ii) all Mylabrini are non-pollinophagous (Bologna, 1991) and (iii) the majority of Namibian non-pollinophagous species belong to the tribe Mylabrini (Table 1). Why were the non-pollinophagous species in our samples more abundant than the pollinophagous species? We consider that this is because pollinophagy is a highly specialized way of feeding, which requires specialized mouthparts (Bologna, 1991). According to general theory, ecological specialists should be rarer than non-specialized organisms (Gaston, 1994, 1996; Gaston & Curnutt, 1998). Hence, it is not surprising that Derideini and Nemognathini (basal groups within Meloidae) were less frequently recorded in our samples. A greater incidence of rarity among specialist species is recorded for snakes (Luiselli, 2006). However, it is still possible that the abundance of non-pollinophagous species may simply reflect factors promoting diversity in Mylabrini that differ for pollinophagous species.

Singletons followed expected trends in abundance and diversity, that is, there were more singletons among non-pollinophagous species of Mylabrini. Hence, it is likely to be a by-product of chance (relative numbers of individuals in the samples) and does not merit further discussion. Novotny & Basset (2000) found a relationship between monophagous habits (host-specificity) and probability of the occurrence of singletons, a relationship not apparent in our results. For instance, all Mylabrini singletons in our samples were not strictly monophagous. In any case, recent studies also show that dispersal should be taken into account when interpreting the abundance of singletons in complex communities of organisms (Ulrich & Zalewski, 2006). Cotgreave & Pagel's (1997) hypothesis that rare species are mainly phylogenetically basal species was indeed confirmed by our analyses, whereas this was not indicated by some earlier studies on other types of organisms (e.g., Luiselli, 2006). Surprisingly, however, large species were not rarer in our samples, despite the prediction of general theory (Gaston, 1994; Blackburn & Gaston, 1997, 1999) and some evidence from other studies (e.g., snakes, see Luiselli, 2006).

Despite the distinct patterns in the correlates of abundance in Namibian blister beetles presented in this paper, nonetheless it should be noted that a major difficulty in evaluating rarity and abundance patterns is that there is no widely accepted definition of rarity and the issue is even controversial (Gaston, 1994; Kunin & Gaston, 1997; Ulrich, 2001a; Harcourt et al., 2002; Luiselli, 2006). For instance, the method of collecting used, behaviour of the species (not all the species are equally cryptic), time of sampling (i.e., season or time of day) and size of the species may affect their rate of capture and so result in a greater likelihood of one species being captured than another (Gaston, 1994; Luiselli, 2006). Hence, it is likely that the same problems may need to be taken into account when considering the data presented herein.

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