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Article

Elevational Patterns of Generic Diversity in the Tenebrionid Beetles (Coleoptera Tenebrionidae) of Latium (Central Italy)

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Abstract: The concept of generic diversity expresses the ‘diversification’ of species into genera in a community. Since niche overlap is assumed to be higher in congeneric species, competition should increase generic diversity. On the other hand, generic diversity might be lower in highly selective environments, where only species with similar adaptations can survive. We used the distribution of tenebrionid beetles in Central Italy to investigate how generic diversity varies with elevation from sea level to 2400 m altitude. Generic diversity of geophilous tenebrionids decreased sharply with elevation, whereas the generic diversity of xylophilous tenebrionids showed similarly high values across the gradient. These results suggest that geophilous species are more sensitive to variation in environmental factors, and that the advantages of close relationships (similar adaptations to harsh conditions) are greater than the possible drawbacks (competition). This is consistent with the fact that geophilous tenebrionids are mostly generalist detritivores, and hence weakly affected by competition for resources. By contrast, xylophilous species are more protected from harsh/selective conditions, but more limited by competition for microhabitats and food. Our results support the environmental filtering hypothesis for the species composition of tenebrionid beetles along an elevational gradient.

Keywords: altitude; mountain; elevational gradient; darkling beetles; Mediterranean; Apennines; competition; environmental filtering; species richness

1. Introduction

Elevational variations in biodiversity are among the most investigated patterns in biogeography [1,2]. Many environmental characteristics (including climate, land use, soil composition, and geological settings), as well as species richness, beta-diversity, functional diversity, biogeographical composition, and several aspects of community structure, vary markedly with altitude, which makes elevational gradients ideal to investigate patterns of variation in biodiversity in response to environmental factors [3–16].

The concept of generic diversity has been introduced to express the ‘diversification’ of species into genera [17], as the inverse of the probability that two species selected at random from a community belong to the same genus. Despite its simplicity, this measure has important ecological implications. In general, it is assumed that morphological distance between species is associated with ecological similarity [18–21]. As congeneric species are expected to be morphologically more similar than non-congeners, they should also have more overlapping niches than species belonging to different

genera. This concept has been originally formulated by Elton, who concluded that there is “a strong tendency for the species of any genus to be . . . unable to coexist permanently on the same area of the same habitat” [22]. This idea represented a major step in the history of ecology, leading to the development of a variety of approaches to investigate the possible role of competition from patterns of species co-occurrence [23–30]. Although competition may occur between non-congeners, and congeners may not significantly compete, in general, taxonomically closely related species are also ecologically similar, and hence subject to higher competition [31–37]. If competition is stronger between congeneric species, species belonging to different genera will co-occur in the same habitats more often than congeneric species, thus increasing generic diversity (because species are less concentrated into genera). On the other hand, in virtue of their morphological similarity, congeneric species are also expected to share similar adaptations [21]. Thus, especially in highly selective environments, generic diversity might be high because only species with similar adaptations (and hence probably belonging to the same genera) can survive [38]. Therefore, a low generic diversity indicates that the advantages of a close relationship, as expressed by belonging to the same genus, might largely compensate for any associated drawbacks. The balance between the two contrasting selective forces exerted by competition and habitat requirements might lead generic diversity to increase with resource limitations, and to decrease with environmental severity. Although some papers investigated variations in generic diversity among beetle communities [34,39,40], to the best of our knowledge, no research has attempted to study how generic diversity can be influenced by elevation.

In this paper, we used the distribution of tenebrionid beetles in Latium (Central Italy) to investigate how generic diversity varies with elevation along a gradient from sea level to 2400 m altitude and in relation with species lifestyle. Tenebrionid beetles are a family of beetles, which exhibit an extraordinarily wide range of ecological diversity, occurring from deserts to boreal forests. Most species are saprophagous, feeding on humus, leaf litter, decaying wood, windblown detritus, carrion, and dung. However, some tenebrionids are predators or semipredators, and many others feed on fungi and lichens. The vast majority of tenebrionids can be divided into two groups according to the adult main lifestyle: (1) those that occur in the soil (geophilous species), and (2) those associated with wood (xylophilous species) [41].

Elevational gradients reflect increasing stressful conditions [3,4,7,42–44], which are particularly severe at high altitudes, because of low temperatures, high radiation, strong winds, low soil nutrients, unstable substrates, and short plant growing seasons [5,45,46]. As a result, we expect that only few tenebrionid species will be able to survive at high altitudes, resulting in very low generic diversity because of the higher probability of belonging to the same genera. By contrast, at low altitudes, thanks to the presence of more favorable conditions, even species with very different morphological characteristics, and hence which are non-congeneric, may coexist, leading to higher values of generic diversity. Thus, we expect an overall pattern of decreasing generic diversity with elevation, and a different response between geophilous and xylophilous species. Competition is expected to be generally not important in geophilous species, since those are mainly omnivores and can easily find resting places under stones, but it might be relevant to xylophilous species, which depend on plants. Thus, we expect that generic diversity will be relatively high for xylophilous beetles, even at high elevation, if they compete for the same plant species as resting places or as food sources (dead wood, and/or associated fungi or lichens).

2. Materials and Methods

2.1. Study Area

Latium is an Italian region extending for 17,200 km² in the central part of the Italian peninsula. Most of the area is occupied by flat and hilly landscapes. However, the region also includes several mountain chains that can exceed 2000 m elevation. Coasts are mainly represented by sandy shores, whereas a large alluvial plain, corresponding to the course of the river Tevere, characterizes the

central part of the region. The city of Rome (which extends for 360 km² and hosts about 3 million inhabitants) is located in this alluvial plain. Most of the region presents a typical Mediterranean climate, with, however, obvious elevational variations. Whereas temperatures are high (9–10 °C in winter and 24–25 °C in summer) and annual rainfall scarce (700 mm) along the coasts, mountain areas are characterized by low temperatures (below 0 °C in winter) and abundant rainfall (1200 mm) [47].

2.2. Data Sources

We used the dataset assembled by Fattorini [12,48], which included 3,561 tenebrionid records, plus 526 new records, spanning from 1860 to 2015. Data were obtained from the examination of museum and private collections, publications, and unpublished lists for a total of 27,476 specimens. Overall, they form a random sample not affected by biases due to collector preferences for certain biotopes, sites, or species. Possible elevational shifts due to climate change occurring from 1860 to 2015 did not extend far enough to influence the overall patterns [12,49].

Sample sites were georeferenced (latitude and longitude decimal degrees) using digital topographic maps. Thanks to the high density of place names in study area, true collecting places were likely very close to the position of locality reported on the maps [50]. Elevation was taken as recorded by the collector (when available) or retrieved from topographic maps.

In total, we considered the vertical distribution of 84 native species and subspecies of Tenebrionidae. Recent morphological [51–54] and molecular [55–57] analyses showed that some tenebrionid populations traditionally classified as subspecies are evolutionarily significant units, usually demanding a species status. Thus, we considered both species and subspecies as terminal taxonomic units of equal rank. The term “species” will be used for simplicity. We omitted from the analysis the genus *Lagria* and the subfamily Alleculinae (formerly considered a separate family), because the ecology of many of these beetles is completely different from that of all other tenebrionids (many alleculines are flower-visiting insects) and their biology and distribution in the study area are poorly known. We also excluded synanthropic species associated with human food, and which became cosmopolitan or subcosmopolitan, and alien species introduced into Italy.

For each species, we established the main lifestyle of adults, coded as geophilous (i.e., beetles that occur in the soil, usually taking shelter under stones, or in the sand under debris) vs. xylophilous (e.g., beetles that occur in rotten wood or on living trees, usually into subcortical spaces) using information reported in Aliquò et al. [58] and personal observations of the first author.

Taxonomy follows Löbl and Smetana [59]. We recognize that the interpretation of genus boundaries can vary among taxonomists (e.g., some genera can be considered subgenera), and the monophyly of most tenebrionid genera remains untested. However, the vast majority of species here investigated have been unambiguously classified to the same genera by different researchers, and so genus boundaries are fairly stable.

2.3. Data Analysis

We divided the whole elevational gradient into 24 belts of 100 m (0–100, 101–200, 201–300 m, etc.). As commonly done in biodiversity studies on elevational gradients, we considered species as continuously distributed along the gradient from the lowest to the highest recorded belt, assuming possible gaps due to sampling incompleteness [60–62].

To express the actual distribution over genera of the species present in each elevational band (i.e., the generic diversity, GD), we used the method proposed by Williams [17] and based on Simpson’s index [63]. The total number of possible ways in which two species can be taken at random from any collection of N species, classified into genera, each with n_i species, respectively, is $N(N-1)/2$, whereas the total number of possible congeneric pairs is $\sum n_i(n_i-1)/2$. Hence, the chance that any two species picked independently and at random from the community will belong to the same genus is $\sum n_i(n_i-1)/N(N-1)$, by which $N(N-1)/\sum n_i(n_i-1)$ can be used as a measure of the “generic diversity” (GD) of N . GD is therefore a number that will increase with the number of genera over which the N

species are distributed. Simpson's index is an unbiased estimate of diversity when the sample size varies, provided no samples of size 0 or 1 are included. We calculated GD across elevational belts for all tenebrionids and for the two main ecological groups (geophilous vs. xylophilous).

To model elevational patterns for number of genera, number of species, and GD, we tested various functions (linear, semilogarithmic, power, polynomial, and exponential) [12,64] and selected the best fit model according to the goodness-of-fit (R^2) and Akaike Information Criterion (AIC). Curvilinear models were linearized by using \log_{10} -transformations. We used Analysis of Covariance (ANCOVA) to compare regression slopes. Since the species–elevation relationship may be an indirect effect of decreasing available area due to the basically conical shape of mountains [65], we also used here the procedure recommended by McCain [66] to control for variation in belt area. We first calculated the amount of land surface in each 100 m elevational belt using a digital elevational model. Then, assuming a power function $S = cA^z$ for the species area–relationship (where S is the number of species, A is area), we calculated the constant c ($c = S/A^z$), which is a measure of species density (i.e., number of species per area unit) and regressed c -values against elevation. The same approach was used for the genus–elevation relationship. In both cases, for the z -value we used the canonical value of Preston (0.25) [66,67].

Errors refer to standard errors and significance was set at $\alpha = 0.05$. Analyses were performed using R version 3.2.0 [68].

3. Results

Both the total number of species (species richness) and the total number of genera decreased with elevation according to a semilogarithmic function (Table 1, Figure 1a). The two curves showed significantly different slopes (ANCOVA: $F_{1,44} = 30.63$, $p < 0.0000001$), indicating a faster decline in species richness than in the number of genera. The same pattern was found for the geophilous species (Table 1, Figure 1b). Species richness declined with elevation faster than the number of genera here too (ANCOVA: $F_{1,44} = 46.68$, $p < 0.0000001$). In the case of the xylophilous species, both species richness and number of genera declined linearly with elevation (Table 1, Figure 1c). However, also in this case species richness declined with elevation faster than the number of genera (ANCOVA: $F_{1,44} = 14.44$, $p = 0.0004$). Use of number of species or number of genera per area unit (c -values) produced analogous results (see Supplementary Materials, Table S2). The slope of the curve for the number of species was higher than that for the number of genera (all species: ANCOVA: $F_{1,44} = 12.85$, $p = 0.0008$; the geophilous species: ANCOVA: $F_{1,44} = 8.845$, $p = 0.0048$, and xylophilous species: ANCOVA: $F_{1,44} = 6.701$, $p = 0.0130$).

Table 1. Results of OLS regression models for the number of tenebrionid species (S) and genera (G), and generic diversity (GD) as function of elevation (E). Errors refer to Standard Errors. R^2 = goodness-of-fit, t = Student's t value.

Tenebrionid Groupings	Response Variable	Model	Slope (b)	Intercept (a)	R^2	t	P
Total tenebrionids	Number of species	$S = a \times \log(E) + b$	-46.394 ± 1.985	159.630 ± 5.916	0.961	-23.369	<0.0000001
	Number of genera	$G = a \times \log(E) + b$	-31.491 ± 1.820	109.420 ± 5.422	0.932	-17.306	<0.0000001
	Generic diversity	$GD = a \times E + b$	-0.032 ± 0.003	65.375 ± 3.461	0.874	-11.798	<0.0000001
Geophilous tenebrionids	Number of species	$S = a \times \log(E) + b$	-28.661 ± 1.024	98.027 ± 3.052	0.973	-27.982	<0.0000001
	Number of genera	$G = a \times \log(E) + b$	-19.256 ± 0.920	65.638 ± 2.741	0.952	-20.937	<0.0000001
	Generic diversity	$GD = a \times \log(E) + b$	-27.15 ± 2.074	91.602 ± 6.102	0.896	-13.094	<0.0000001
Xylophilous tenebrionids	Number of species	$S = a \times E + b$	-0.010 ± 0.001	22.220 ± 0.858	0.933	-17.458	<0.0000001
	Number of genera	$G = a \times E + b$	-0.008 ± 0.000	17.491 ± 0.450	0.966	-25.098	<0.0000001

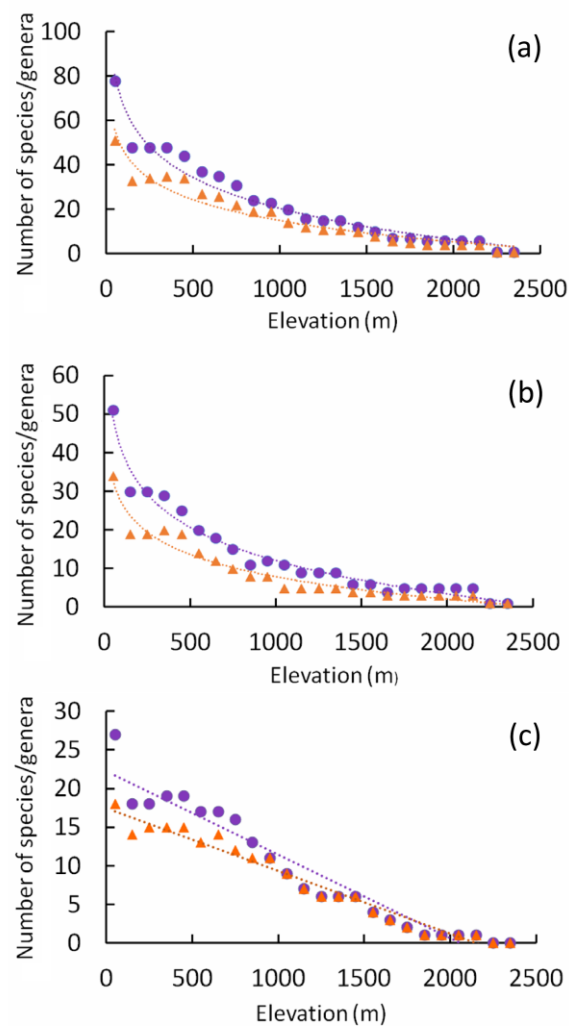


Figure 1. Relationships of number of tenebrionid species (purple circles) and genera (orange triangles) with elevation (in meters) calculated for all species (a), geophilous species (b), and xylophilous species (c). Dotted lines are regression lines. Regression models were semilog functions for panels (a,b), and linear functions for panel (c). Regression equations and goodness-of fit values are given in Table 1.

Overall GD declined linearly with elevation (Table 1, Figure 2a). When geophilous and xylophilous species were analyzed separately, we found that geophilous species followed a semilogarithmic model (Table 1, Figure 2b), whereas no trend was apparent for the xylophilous species. The slope of the GD equation for geophilous species did not differ significantly from that of geophilous species richness (ANCOVA: $F_{1,40} = 0.45$, $p = 0.506$), but was significantly higher than that observed for the number of geophilous genera (ANCOVA: $F_{1,40} = 12.89$, $p = 0.0009$).

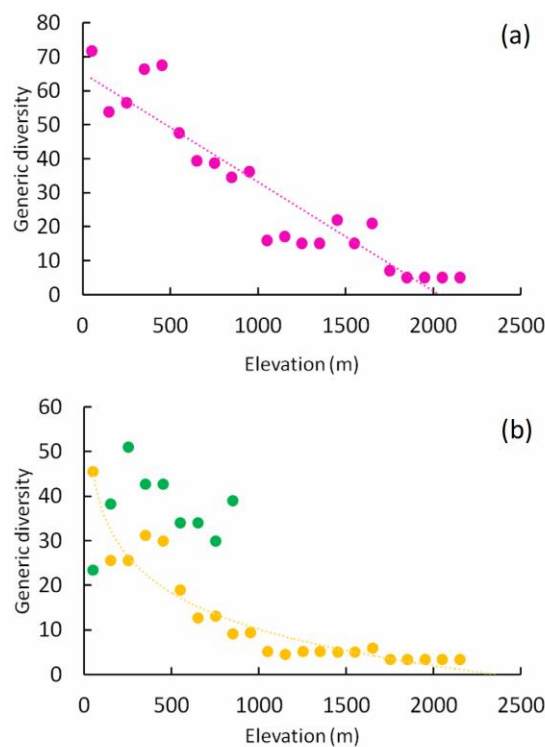


Figure 2. Relationships between generic diversity and elevation (in meters) for the total number of species (panel a, pink circles) and for geophilous (yellow circles) and xylophilous (green circles) species separately (panel b). Dotted lines are regression lines (linear function in panel a; semilog function in panel b). Regression equations and goodness-of fit values are given in Table 1.

4. Discussion

Overall, we found that both the number of species and the number of genera declined sharply with elevation. This pattern is consistent with a monotonic decrease in species richness with elevation in response to variation in abiotic and biotic factors observed for various animal groups and in a variety of contexts [1,69–71].

In general, elevational patterns in species richness tend to follow one of the following trends [9]: (1) monotonic decreasing richness with increasing elevation (as in our analyses); (2) plateaus in richness across low elevations, then decreasing, with or (3) without a mid-elevation peak; and (4) a hump-shaped pattern with a mid-elevational peak. The monotonic pattern was the second most common in Rahbek's reviews [72,73] (about 20% of studies analyzed). A monotonic decrease, however, can follow different models. The best fit model, in our case, was a semilog function, which indicates that the number of species declines very sharply from lowland to medium altitudes, and then continues to decline, but at a decreasing rate. Patterns of species richness and number of genera found in our study are similar to the decline in mammal species richness with increasing elevation in Europe [74], but with a substantial difference. In the case of mammals, the decrease of species richness with elevation was uniformly smooth from above 400 m up to about 3000 m, but there was a lower number of species at 0–150 m than at 200–250 m. This peak has been interpreted as a consequence of a depressive effect on species richness at very low elevations due to massive habitat alteration (such as extensive agriculture and urbanization) [74]. In our case, the highest number of species was found in the 0–100 m belt. This can be explained by two not mutually exclusive reasons. First, tenebrionid beetles include several groups adapted to arid conditions and associated with coastal environments, such as sand dunes [39,49,58]. Thus, tenebrionid are speciose also in lowland areas where mammals are poorly diversified. Second, tenebrionids can be less negatively affected by landscape changes than mammals. Although animal response to habitat loss and fragmentation is species-specific, mammals seem to be

more sensitive than other groups [75], and the tenebrionids of Latium include many species that can survive profound landscape alteration, including urbanization. Although urbanization also negatively affects tenebrionids [76,77], these animals form rich communities even in small green areas within the largest city (Rome) present in the study area [78,79].

The pattern found for the number of genera was similar to that modelled for species richness, but characterized by a lower slope, which indicates that the number of species decreased with increasing elevation faster than the number of genera. This suggests that the factors depressing tenebrionid diversity along the altitude tend to prune more severely the number of species than the number of genera, which means that species tend to be more concentrated in fewer genera at higher altitudes as a result of a filtering process. This is clearly shown by the pattern of generic diversity. We found that, in general, generic diversity decreased with elevation, thus paralleling the decrease in species richness. While the monotonic decrease in species richness with elevation is a widely recognized and well investigated pattern, our study is the first research showing a monotonic decrease for generic diversity. This decline of generic diversity with increasing elevation suggests that environmental conditions become progressively less favorable to most species; most genera are progressively eliminated, and the remaining species tend to belong to few genera that include the few species adapted to cope with increasing challenging conditions.

Many studies have shown that natural communities are not only assembled through neutral processes (e.g., dispersal and stochastic events), but are also driven by environmental conditions [80–83]. A widely accepted ecological hypothesis suggests that such environmental drivers act as hierarchical ‘filters’ constraining the assemblage of communities, i.e., progressively selecting species [84–86]. Our results support the environmental filtering hypothesis for the species composition of tenebrionid beetles along an elevational gradient, indicating that the harsh conditions of high altitude environments allow the persistence of species belonging to few genera adapted to cope with high temperatures and lack of water. An analysis based on climatic data gathered from 29 meteorological stations distributed along this elevational gradient revealed strong negative correlations between elevation and the following climatic measures: annual maximum, minimum and average temperatures, and Mitrakos’ summer drought stress and year drought stress [12]. These decreases in temperatures and aridity with altitude may act as an important factor driving species impoverishment by filtering thermophilic and xerophilic species. On the other hand, Mitrakos’ winter cold stress and year cold stress increased with altitude [12], which also supports the possible role of factors associated with elevation (such as temperature, humidity, or radiation) as filtering factors for thermo-xerophilic species.

In general, low values of generic diversity may be a consequence of the preference of related species for similar habitats. It is expected for the habitats preferred by congeneric species to be more similar than those occupied by species of different genera; leading species that are ecologically closely related to frequently coexist in the same habitats, if interspecific interferences are not more important than possible intraspecific interferences [34,87]. Most insect communities seem to be not influenced by competition [87,88], and there is some evidence that, consistent with this general pattern, tenebrionid guilds are not regulated by competitive interactions [89–91], although the presence of different life strategies in lichen-feeding Helopini has been interpreted as a mechanism possibly reducing competition among species inhabiting the same tree or stone [92]. Additionally, even when insect interspecific competition has been reported, severe effects, such as competitive exclusion, were not demonstrated [87,93].

If tenebrionids are subdivided into two main ecological groups (geophilous and xylophilous) two distinct patterns emerge. Geophilous tenebrionids conform to the general pattern of decreasing generic diversity, whereas xylophilous species tend to maintain high values of generic diversity across the gradient. These results suggest that geophilous species are more sensitive to variation in environmental factors, and the advantages of close relationship (similar adaptations to harsh conditions) are on average greater than the drawbacks (competition). This is consistent with the fact that geophilous tenebrionids are mostly generalist detritivores, and hence competition for food is expected to be

low [94]. By contrast, xylophilous species, being associated with vegetation, may be less directly exposed to harsh conditions, but may be more subject to competition to find appropriate microhabitats and food. Xylophilous species are typically saproxylic species and competition has been frequently invoked to explain segregation patterns in saproxylic beetles, although the relative importance of competition in structuring saproxylic communities and how competition intensity varies are open questions [95].

Interestingly, above 1000 m, which typically marks the transition from the sclerophyll evergreen vegetation and heliophilic broadleaves dominated by the oak (*Quercus* spp.) to the sciaphilous broadleaves dominated by the beech *Fagus sylvatica* L. [96–98], generic diversity of xylophilous tenebrionids could not be calculated, because each genus was represented by only one species (e.g., *Helops caeruleus*, *Corticeus unicolor*, *Bolitophagus reticulatus*), which suggests a combination of competition and very harsh conditions. There is a long lasting debate whether changes in vegetational structure or composition along elevational gradients are abrupt, allowing the recognition of distinct vegetational belts, or gradual, making it impossible to identify clear separations between belts [2]. Our results support the notion that the boundary between oakwoods and beechwoods at around 1000 m is probably an abrupt transition, representing a strong discontinuity for the generic diversity of xylophilous tenebrionids.

We are aware that the use of genera can be problematic because of possible discrepancies in their delimitation by different taxonomists. For example, with reference to the fauna studied in this research, *Colpotus* is regarded as a true genus by most taxonomists, but it has been recently considered as a subgenus of *Pedinus* [99]. However, for the vast majority of the species considered in this paper, assignment to genera is not disputed, which makes our results robust. Recent phylogenetic reconstructions based on molecular data tend to support traditional tenebrionid taxonomy, at least for the major clades [100,101], but genus delimitations are still based on morphological similarities. The degree of morphological distance accepted by taxonomists to assign species to different genera varies among groups. For example, some tenebrionid genera are very heterogeneous, including a lot of species that exhibit a great morphological diversity (see, for example, the genus *Anomalipus* [102], which includes some 60 species and subspecies), whereas other groups, such as mammal taxa, typically include fewer and morphologically more similar species (for example, the entire family of Mustelidae includes some 65 species assigned to 23 genera [103]). The different criteria used for delimiting genera in different taxa may make it difficult cross-taxon comparisons in generic diversity patterns.

We are aware that our approach does not allow a direct test for the role of competition, mainly because there is no guarantee that species present in the same belt are really syntopic, i.e., that they co-occur in the same sites within the belt (and, in general, this is unlikely for some species). Thus, it would be interesting in the future to study within-belt co-occurrence patterns. However, our comparative analyses provide interesting insights into the role of species ecology into the possible relative effects of competition and adaptation.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1424-2818/12/2/47/s1>: Table S1. Tenebrionid species distribution across the elevational gradient in Latium (Central Italy). Table S2. Results obtained using area-corrected values of number of species and number of genera.

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