

Article

The Role of Vegetation in Elevational Diversity Patterns of Tenebrionid Beetles in Central Italy

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Abstract: Vegetation tends to vary in a systematic fashion along elevational gradients, leading to the possibility of recognizing distinct vegetational belts, which are frequently used to describe and interpret elevational variations in biodiversity. However, anthropogenic changes can create landscapes dominated by secondary grasslands in areas formerly occupied by forests, thus altering the natural sequence of vegetation types. The present research illustrates how the distribution of tenebrionid beetles in central Italy is influenced by secondary vegetation. Classical schemes of vegetational belts were modified into a scheme of main vegetation types that include secondary vegetations. Tenebrionid species presence/absence in each vegetation type was then assessed. Species richness tended to decrease with elevation in both natural and secondary vegetations. Geophilous (ground-dwelling) species (which include many endemics) prevailed in natural and secondary grasslands, while xylophilous species (associated with trees) prevailed in the natural forests. Similarities in tenebrionid composition indicated the presence of two main groups: one associated with forests and the other with natural and secondary grasslands. Geophilous species prevailed among tenebrionids with Mediterranean distributions, whereas xylophilous species prevailed among species distributed mainly in Europe and the Palearctic. High values of richness, biogeographical complexity and proportion of endemics make secondary vegetations of high conservation concern.

Keywords: Apennines; biogeography; chorotypes; conservation; endemism; forests; grasslands; Latium; Mediterranean; mountains



Citation: Fattorini, S. The Role of Vegetation in Elevational Diversity Patterns of Tenebrionid Beetles in Central Italy. *Diversity* **2024**, *16*, 110. <https://doi.org/10.3390/d16020110>

Academic Editors: Michael Wink, Luc Legal and Michel Baguette

Received: 26 December 2023

Revised: 27 January 2024

Accepted: 6 February 2024

Published: 8 February 2024



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1. Introduction

Centuries or even millennia of low-intensity agricultural practices (especially mowing) and pastoralism (grazing) have profoundly altered European landscapes, turning natural forest vegetations into open areas represented by seminatural grasslands [1–3]. These landscapes, which are important biodiversity reservoirs [3–7], are now menaced by higher human pressures (e.g., intensification of agricultural practices and urbanization, afforestation, intensive grazing) and spontaneous succession towards woody vegetation after the abandonment of traditional land management [3,8–10].

Located in the middle of the Mediterranean global biodiversity hotspot [11–14], Italy occupies a prominent position for European biodiversity conservation due to its complex biogeographical history [15–18], being home for exceptionally high numbers of plant and animal species, many of which are endemic [19–23]. The Italian territory is also characterized by a huge variety of landscapes, with many resulting from transformations produced over millennia of human activities [24–27].

About 77% of the Italian territory is classified as montane (35%: areas occupied by relief higher than 600–700 m) or hilly (42%: areas with lower elevations, but not flat) [28]. In particular, the Italian territory is largely dominated by two main chains: the Alps in the north, and the Apennines along the peninsula [29]. Therefore, Italian landscapes are profoundly influenced by the mountainous nature of the territory [24–27], with vegetation

types that vary with elevation [26]. The systematic variation of vegetation along elevational gradients—one of the most universal ecological patterns—leads to the possibility of recognizing distinct vegetational belts that roughly parallel the latitudinal variation of biomes [30,31]. However, millennia of anthropogenic changes in the Apennines, such as agriculture and grazing [24,26,32], created landscapes dominated by grasslands at elevations which would be naturally occupied by forests [3]. Thus, Apennine landscapes offer the intriguing opportunity of investigating how secondary open vegetations influenced elevational patterns of biodiversity.

The aim of the present paper is to investigate how the presence of secondary vegetation influences the distribution of a group of insects, tenebrionid beetles (Coleoptera Tenebrionidae), along the whole elevational gradient of a region (Latium) of Central Apennines. Because of millenary human activities, e.g., [24–26,33–37], most of the lowland areas of Latium have been transformed into agricultural fields and grasslands, as have vegetations on mountains, with the current presence of secondary grasslands interspersed within more or less well-preserved natural vegetations through the whole elevational gradient. Previous research showed that tenebrionid diversity in Latium declines with elevation mainly because of the filtering effects of increasingly harsher conditions with increasing elevation [38–40], but the role of different types of vegetation in determining elevational patterns in tenebrionid diversity has been not investigated. Under the assumption of environmental filtering processes, we expect that insect species richness should decline with elevation in both natural and secondary vegetations, independently from their ecological preferences and biogeographical origin. However, because of the highly contrasting nature of open and forest vegetations, we expect that species assemblages that can be found in secondary vegetations within elevational belts that should be naturally occupied by forests are not a simplified version (i.e., remnants) of forest assemblages, but very different species assortments arising from natural open habitats occurring in other belts. Tenebrionids are particularly well suited to investigate this issue as they can be classified into two main ecological groups that can be distinctly associated with open and forest vegetations: geophilous (i.e., those associated with soil) and xylophilous (i.e., those associated with trees) [41]. Whereas geophilous species are expected to be more common in open vegetation, xylophilous are expected to be associated mainly with tree vegetations.

To test these hypotheses, we investigated here the elevational patterns of tenebrionid beetles in Latium with reference to the sequence of the main vegetation types along the elevational gradient, taking into account their association with forest and secondary open vegetations. Specifically, we tested the following predictions:

- (1) Prediction 1. If tenebrionid richness varies along the elevational gradient in response to a filtering process [39,40], declining patterns in species richness should be observed in both forest and secondary open vegetations. To test this prediction, richness was calculated separately for natural and secondary vegetations, and the respective elevational patterns compared.
- (2) Prediction 2. If tenebrionids of secondary open vegetations are not an impoverished version of the communities inhabiting former forests, but are composed of species associated with natural open vegetations, we expect a low similarity in species composition between tenebrionid of secondary and natural vegetations even within the same elevational belt, but a high similarity between secondary and open natural vegetations. Additionally, we expect a high relative abundance of geophilous species even at elevations in which xylophilous species should be more frequent. To test this prediction, similarities in species composition among vegetation types and levels of association between ecological groups (geophilous vs. xylophilous) and vegetation types were investigated.
- (3) Prediction 3. Previous research showed that biogeographical composition of tenebrionid beetles in Latium changed with elevation, with species mainly distributed in the Mediterranean basin declining with elevation, being less tolerant to decreasing temperatures [38]. As a result of this filtering process, it can be expected that their pro-

portion declines with elevation in both secondary and natural vegetations. Variation in the incidence of Mediterranean species in different vegetation types was analyzed for testing this prediction.

- (4) Prediction 4. Not only tenebrionid species richness, but also biogeographical diversity declines with increasing elevation [38]. Under the filtering hypothesis, this decline in biogeographical diversity should be observed in both natural and secondary vegetations. To test this prediction, diversity profiles based on the biogeographical composition of tenebrionid assemblages were constructed for the different vegetation types.
- (5) Prediction 5. The proportion of tenebrionid endemic species is known to increase with elevation [38]. This may be explained by the fact that they are almost entirely represented by geophilous tenebrionids, which should be more associated with open habitats that naturally dominate the highest elevations. If this assumption is correct, endemics should also represent a conspicuous component of tenebrionid assemblages of secondary open vegetations at high elevations. For this prediction, frequencies of endemics were compared among vegetation types.

2. Materials and Methods

2.1. Study Area

The study was conducted in Latium (central Italy, Figure 1). This region extends for 17,242 km², of which 20% is flat, 54% hilly, and 26% mountainous [28]. In coastal areas, sandy beaches are the main type of habitat with also some remnants of dunes, while rocky shores are restricted to small areas in the southernmost part of the region. Coastal plains are largely occupied by cultivated fields, interspersed with remnants of natural vegetation mainly represented by Mediterranean shrublands and maquis, with rare fragments of hygrophilous woodlands. The mountainous territory of the region includes both pre-Apennine and Apennine mountains. The pre-Apennines include groups of mountains mainly occupied by mixed broadleaved forests, including typical evergreen broadleaves (*Quercus ilex* L. and *Quercus suber* L.) and chestnut woods (*Castanea sativa* L.). The Apennines of Latium are a continuation of the Apennines of Abruzzo, and are mainly characterized by the presence of deciduous oak woods (*Quercus cerris* L., *Quercus pubescens* Willd.) and beech woods (*Fagus sylvatica* L.). For further details on the vegetation of Latium, see, for example, [42,43]. Because of its complex topography (the highest peak is Mount Gorzano, with 2458 m, on the border with the Abruzzo region), the region shows a wide variety of climates, ranging from typically Mediterranean climates along the coasts (with average annual temperatures even around 17 °C, less than 1000 mm of annual precipitation, and a distinct period of summer aridity) to subalpine climates on the highest peaks (with average annual temperatures < 10 °C, about 1500 mm of annual precipitation, and a lack of a period of summer aridity) [44,45].

For the purposes of this research, classical schemes of vegetational belts used for Italian mountains [46–50] were modified into a scheme of main vegetation types that includes secondary open vegetations [51]:

1. Dunes (about sea level). This belt includes the vegetation of mobile and fixed dunes and extends inland to a very limited extent. Because of coastal exploitation, this habitat is now currently highly fragmented and under severe threats, including those posed by climate change [52,53]. It represents a natural open vegetation.
2. Mediterranean shrubland and maquis: holm-oak forests, cork oak forests, coastal pinewoods, Mediterranean maquis with xerophilic species (~0–800 m). This belt is represented by a mosaic of vegetation types, ranging from garrigues to Mediterranean forests. Coastal pinewoods were mostly planted centuries ago and are mixed with natural vegetation. This belt roughly corresponds to the Mediterranean belt of Pignatti [49]. It represents a natural and more or less closed (forest) vegetation.

3. Arid grasslands of lowlands and low hills (~0–800 m). This form of secondary open vegetation is the result of anthropic activities (low intensity agriculture and grazing) within the former belt.
4. Mixed forests (Turkey oaks and chestnuts) (~400–1000 m). This belt, which roughly corresponds to the Samnite belt of Pignatti [49], is characterized by mixed deciduous forests. The presence of large chestnut groves is anthropogenic, but ancient (for example, on the Abani Hills, they date back to the 17th century); currently they are managed as coppices or orchards for fruit production [54,55]. It represents a substantially natural closed vegetation.
5. Grasslands of medium and high hills (~400–1000 m). This form of secondary open vegetation is the result of anthropic activities (especially grazing) within the former belt.
6. Beech forests (~700–1800 m). This belt is characterized by pure or mixed forests of *Fagus sylvatica* and roughly corresponds to the sub-Atlantic belt of Pignatti [49]. In fact, in peninsular Italy, old-growth primary forest remnants can only be found at high elevation (say, >1600 m), whereas most beech forests are secondary old-growth forests, but occupy areas where they would be the natural vegetation anyway [56,57]. This vegetation represents a substantially natural closed vegetation.
7. Montane grasslands (~700–1800 m). This form of secondary open vegetation is the result of anthropic activities (especially grazing) within the former belt.
8. Pseudo-alpine grasslands (beyond the tree line) (~1600–2000 m). This belt is represented by the grassland vegetation above the tree line and corresponds to the Mediterraneo-altomontane belt of Pignatti [49]. It represents a substantially natural open vegetation.

For the purposes of this paper, vegetations 1, 2, 4, 6, and 8 are considered as natural (either open or forest) vegetations, although they were also subject to human influence, and 3, 5, 7 as secondary open vegetation. Examples of these vegetation types are illustrated in Figure 2.

Figure 1a illustrates the distribution of these vegetations deduced from Corine Land Cover (CLC) categories as given in [58]. CLCs (fourth and five level) falling in the same vegetation type were merged (e.g., CLCs 3.2.3, 3.1.1.1, 3.1.2.1, 3.1.3.1.1, and 3.1.3.2.1 were merged to obtain the distribution of Mediterranean shrubland and maquis) whereas the different types of secondary vegetations all corresponding to the same CLC 3.2.1 were distinguished on the basis of their elevation.

2.2. Data Collection

The elevational distribution of 85 tenebrionid species and subspecies (hereafter species for simplicity, as the dividing line between species and subspecies, as applied to these insects, is arguably arbitrary [59–65]) from Latium was assessed using a database comprising about 4600 records spanning from 1860 to 2020 [38–40,66], plus new records. These data originated from a critical review of available literature and examination of material preserved in public and private collections, for a total of about 29,000 specimens. Species were collected using a variety of methods, including hand searching (on the ground, under stones and fallen trees, on trees, under bark, etc.), pitfall traps, light traps, aerial traps, soil examination (with sand and litter sieving), in both open and forest vegetations from sites distributed through the whole elevational gradient (Figure 1b). In particular, the use of pitfall traps, litter sieving and hand searching on the ground assures that geophilous species were adequately sampled also in forest habitats. Overall, because of the variety of sources used, they form a random sample not affected by biases due to collector preferences for certain areas, habitats, or species. The use of belts based on vegetation settings, instead of elevational limits, ensures that the results are not influenced by species elevational shifts due to climate changes, which were in fact too small to affect overall patterns [67].

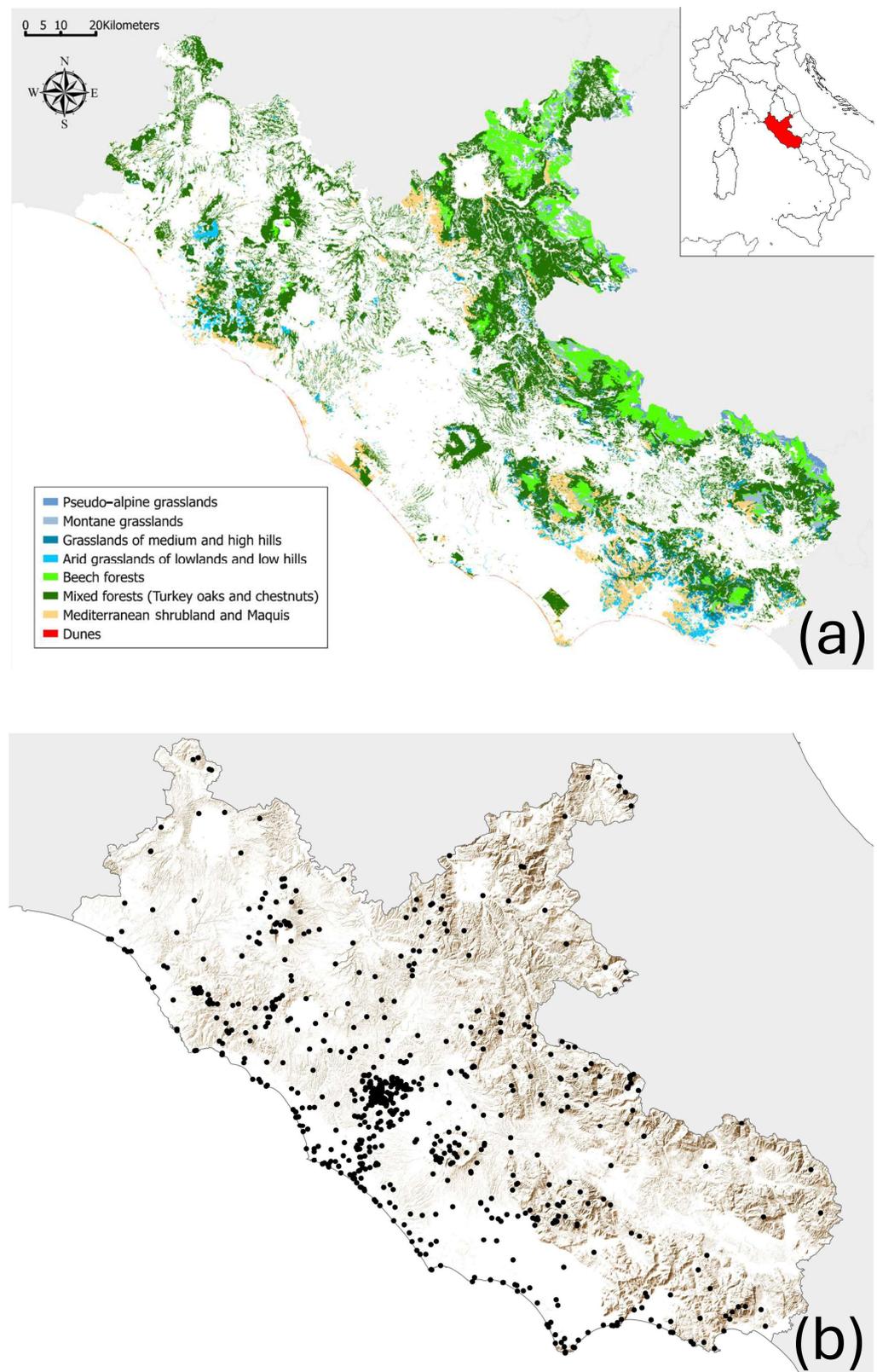


Figure 1. Study area (Latium, central Italy). (a): Distribution of main natural and secondary vegetation types. The inset shows the location of Latium (in red) within the Italian territory. (b): Distribution of tenebrionid records (each dot is a locality for which one or more records are available).

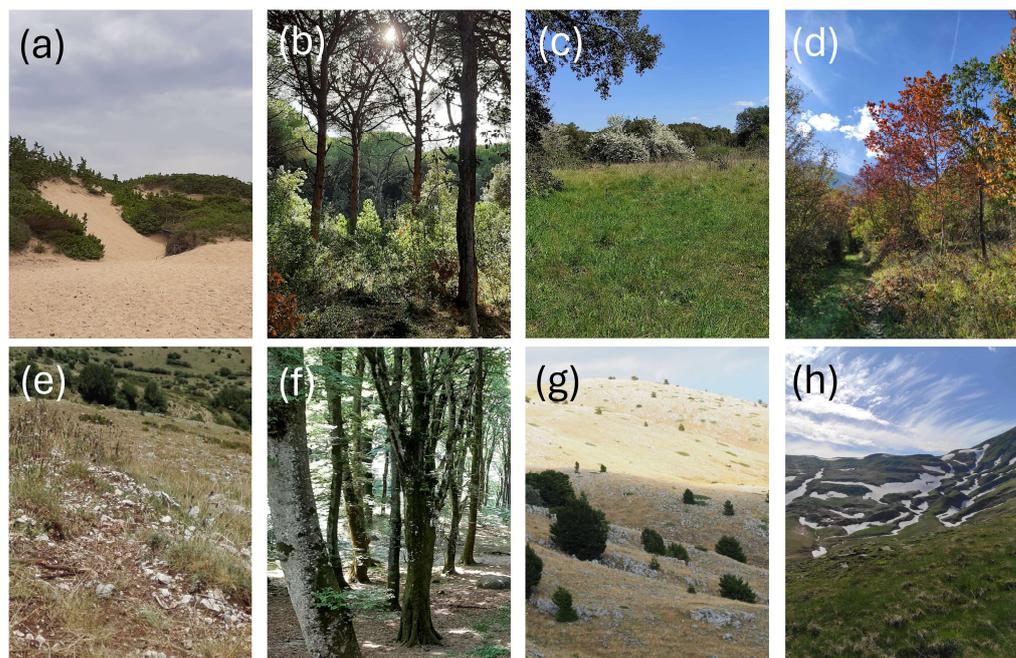


Figure 2. Examples of natural and secondary vegetations occurring along the elevational gradient in the Apennines of central Italy. (a): Dunes; (b): Mediterranean shrubland and maquis; (c): Arid grasslands of lowlands and low hills; (d): Mixed forests; (e): Grasslands of medium and high hills; (f): Beech forests; (g): Montane grasslands; (h): Pseudo-alpine grasslands. Photos (a,b,f) by S. Fattorini; photos (c–e,h) by L. Di Biase; photo (g) by A. Di Giulio.

Species presence/absence in each vegetation type was based on species distribution, species ecological preferences resulting from literature, e.g., [68–71] and personal observations conducted in Latium during the last 30 years in all the aforementioned vegetation types. The genus *Lagria* (traditionally regarded as a member of a separate family, Lagriidae) and the subfamily Alleculinae (traditionally regarded as a distinct family, Alleculidae) were excluded, as their ecological characteristics are very different from that other tenebrionids (both are mainly flower-visiting insects), and faunal and ecological information on these beetles are still scant. Introduced and synanthropic species associated with human food were also not considered. Nomenclature followed Iwan and Löbl [72]. The validity of *Leptoderis italicus* Solier 2015 [73] and *Pachychila italica* Ferrer, 2018 [74] should be confirmed, and, for the present, they are listed as *Pachychila frioli* Solier, 1835 and *Leptoderis collaris* (Linnaeus, 1767), respectively.

On the basis of their biology, tenebrionids were divided into two broad ecological categories [41]: geophilous (i.e., ground-dwelling species, with larvae living on or in the soil, and adults usually found under stones, or in the sand) and xylophilous (i.e., species associated with plants, especially trees, whose larvae usually develop in rotten wood and adults occupy subcortical spaces). For a few species that can occupy both habitats, the preferred habitat was considered.

Tenebrionids were classified biogeographically by using chorotypes. Chorotypes are groups of generalized distributional patterns based on inductive methods: individual species distributions are mapped and species with similar distributions are grouped together to define chorotypes as recurrent patterns [75–77]. Once a chorotype is defined, any additional species exhibiting a similar distribution can be ascribed to that chorotype. Species assigned to the same chorotype can be members of entirely different taxonomic or ecological groups. Analyzing the chorotype composition of local species assemblages might help to identify the ecological and historical reasons that have produced these assemblages, since species with comparable distributions should also have similar macroecological demands [78]. Chorotypes used in this paper followed Vigna Taglianti et al. [79] and

were subsequently grouped into fewer groups of wider meaning, as follows: European (Centraleuropean, European, and S-European chorotypes: 32%), Palearctic (Centralasiatic-Europeo-Mediterranean, Holarctic, Sibero-European, Turano-Europeo-Mediterranean, and Turano-Mediterranean chorotypes: 14%), and Mediterranean (Mediterranean, N-African, W-Mediterranean, and E-Mediterranean chorotypes: 38%). Species that occur only within the Italian territory were classified as endemic (16%). All data (species classification as either geophilous or xylophilous, chorotype, general distribution, and occurrence in the various vegetations) are provided in Table S1.

2.3. Data Analysis

To test Prediction 1, elevational variation in species richness was investigated for native and secondary vegetations separately.

To test Prediction 2, similarity in species composition between vegetation types was investigated by using two coefficients of dissimilarity (β -diversity): the Dice–Sørensen coefficient (β_{sor} , which expresses the total β -diversity) and the Simpson coefficient (β_{sim} , which expresses the pure turnover component, i.e., the compositional differences after removing the effect of nestedness, that is the compositional change caused by ordered species loss) [80,81]. Distance matrices of β_{sor} and β_{sim} were then subject to non-metric multidimensional scaling (NMDS) with Procrustes analysis. NMDS is a multivariate ordination technique that is very useful to disclose multiple biotic relationships [17,18,82]. In NMDS the first two dimensions were retained for visualization, in which the axis with the highest variance was standardized between 0 and 1, and the other axis was rescaled according to the first one. Additionally, chi-square tests were used to test differences in the proportional distribution of geophilous and xylophilous species among vegetation types at different elevations.

To test Prediction 3, chi-square tests were used to test differences in the proportional distribution of main biogeographical groups among vegetation types. Chi-square tests were also used to investigate the association between ecological and biogeographical groups and association between endemics and vegetation types.

To test Prediction 4, tenebrionid assemblages were compared by constructing diversity profiles on the basis of the frequencies of chorotypes. To this end, we used Hill numbers qD [83–87]. Hill numbers are a mathematically unified family of diversity indices which differ among themselves only by the exponent q (which is the diversity order): as q can assume any value, it is possible to calculate, for a given assemblage of species, a diversity profile plotting qD versus q [85]. Although Hill numbers are typically used to express diversity with reference to the number of individuals belonging to the different species, they can be applied to any category (see, for example, their use for chemical diversity [87]), and in the case of the present research they were calculated using the number of species belonging to the different chorotypes, thus expressing the biogeographical diversity. Hill numbers are gaining increasing favor in community ecology [84–86], since they are all expressed in units of effective numbers, that is, the number of equally abundant categories (chorotypes in our case) required to obtain the same value of diversity. Therefore, they are perfectly comparable [84,86]. Hill numbers include three widely used diversity measures as special cases: richness (for $q = 0$), the exponential version of Shannon diversity (when $q = 1$ as the limiting case, since the equation for Hill numbers is undefined for $q = 1$) and Simpson diversity ($q = 2$) [84,86]. Since the parameter q controls the sensitivity of the measure to the relative abundances of the categories, for $q = 0$ the measure strongly reflects the contribution of rare categories; for $q = 1$, categories are weighed in proportion to their abundance; for $q > 1$, more weight is put on abundant categories, and the index can be roughly read as the effective number of the dominant categories in the assemblage, being more influenced by the most abundant categories [84,85,87]. We constructed diversity profiles by plotting qD versus q from $q = 0$ to $q = 4$ (as beyond $q = 3$ or 4 there is little variation, whereas values of diversity with $q < 0$ are not used, as they are dominated by the abundances of rare species and have poor statistical sampling properties) [85].

All calculations were performed in R 4.1.3 software [88]. Chi-square tests were performed with the stats package. Analyses based on Hill numbers were conducted using the package SpadeR version 0.1.1 [89]. β -diversity and NMDS analyses were performed using vegan 2.6–2 [90] and recluster 2.9 [91] packages. Figure 1a,b were constructed in ArcGis Pro 3.1.3 [92]. Figure 1b was realized with the function Hillshade using data from TINITALY [93].

3. Results

Species richness varied among vegetations, with the highest richness recorded in the Mediterranean shrubland and maquis vegetation, where about 45% of the total fauna occurred (Figure 3). In general, except for the first belt (represented by the sandy shore vegetation) species richness decreased with elevation, both for natural vegetation (Mediterranean shrubland and maquis: 38 species > Mixed forests: 31 species > Beech forests: 15 species > Pseudo-alpine grasslands: 4 species) and for secondary vegetation (Arid grasslands of lowlands and low hills: 28 species > Grasslands of medium and high hills: 11 species > Montane grasslands: 8 species), as expected according to Prediction 1.

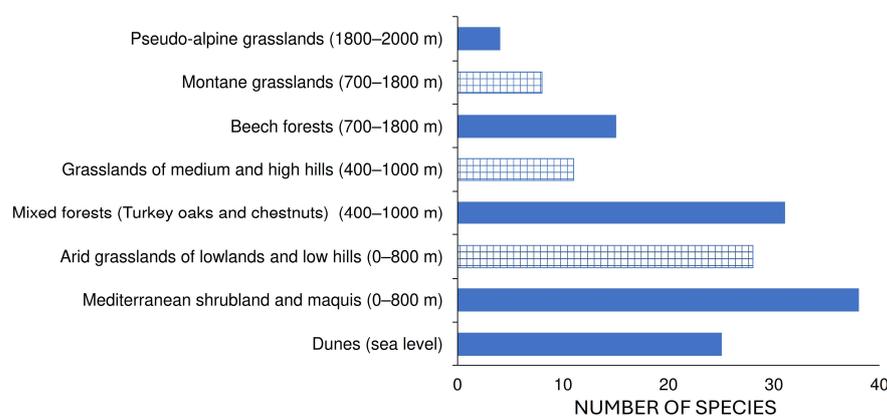


Figure 3. Number of tenebrionid species recorded from different vegetations along the elevational gradient in Latium (central Italy). Grid patterns identify secondary vegetations.

The study fauna included much more geophilous species than xylophilous species (geophilous species: 55 species, 65%; xylophilous species: 30 species, 35%; $\chi^2 = 7.353$, $df = 1$, $p = 0.007$). The proportion of geophilous and xylophilous species varied among vegetation types ($\chi^2 = 64.021$, $df = 7$, $p < 0.000001$), with geophilous species being prevalent in coastal, secondary, and natural high elevation vegetations, and xylophilous species in natural forests (Figure 4). These results indicate that geophilous species are associated with open vegetations (both secondary and natural), as expected according to Prediction 2.

The study fauna included 14 species (about 16%) endemic to Italy. The remaining, non-endemic species (71 species) belong to 12 chorotypes (Table S1). If chorotypes are grouped into groups of broader meaning, it appears that vegetations of lower elevations were characterized by relatively high proportions of Mediterranean species (37–68%), whereas at higher elevations European and Palearctic species accounted for 70–100% of the species ($\chi^2 = 58.460$, $df = 21$, $p < 0.00001$) (Figure 5), thus supporting Prediction 3.

Diversity profiles based on chorotypes (Figure 6) indicated that: (1) grasslands of medium and high hills, montane grasslands, and pseudo-alpine grasslands are the vegetation types with the lowest chorotypological diversity for the whole range of q -values; (2) Mediterranean shrubland and maquis, arid grasslands of lowlands and hills, mixed forests, and beech forests are the vegetation types with the highest chorotypological diversity for the whole range of q -values; (3) dunes occupy an intermediate position. Overall, diversity profiles indicate no difference at low elevations between natural and secondary vegetations (Mediterranean shrubland and maquis, and arid grasslands of lowlands and low hills), while a clear difference exists in diversity for medium to high belts (between

mixed and beech forests on one hand, and grasslands of medium and high hills on the other hand). These results support Prediction 4. A clear decline in diversity is seen in the open habitats independently of the naturalness (with the exception of dunes, that are less diversified than arid grasslands of lowlands and low hills), as expected according to Prediction 1.

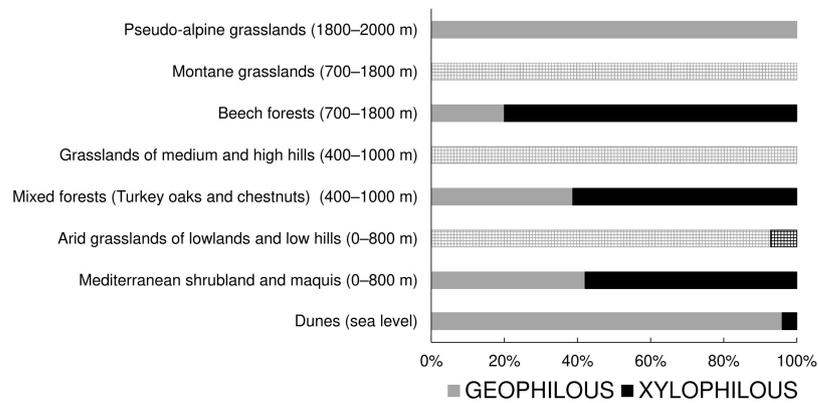


Figure 4. Percentage of geophilous and xylophilous tenebrionid species in different vegetations along the elevational gradient in Latium (central Italy). Grid patterns identify secondary vegetations.

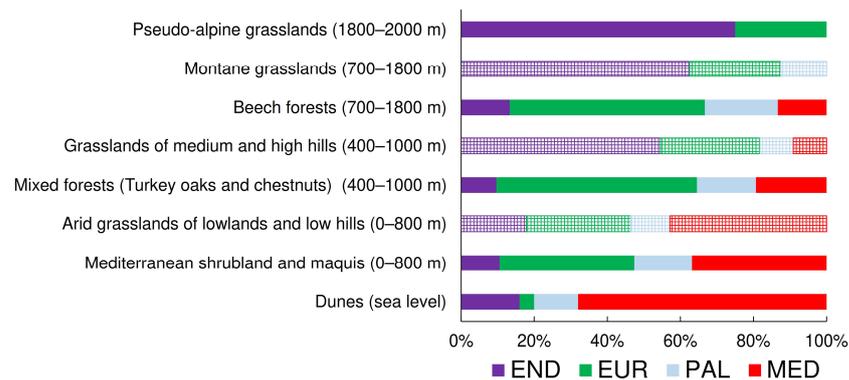


Figure 5. Biogeographical composition of tenebrionid species in different vegetations in Latium (Central Italy). END: Endemic; EUR: European, PAL: Palearctic; MED: Mediterranean. Grid patterns identify secondary vegetations.

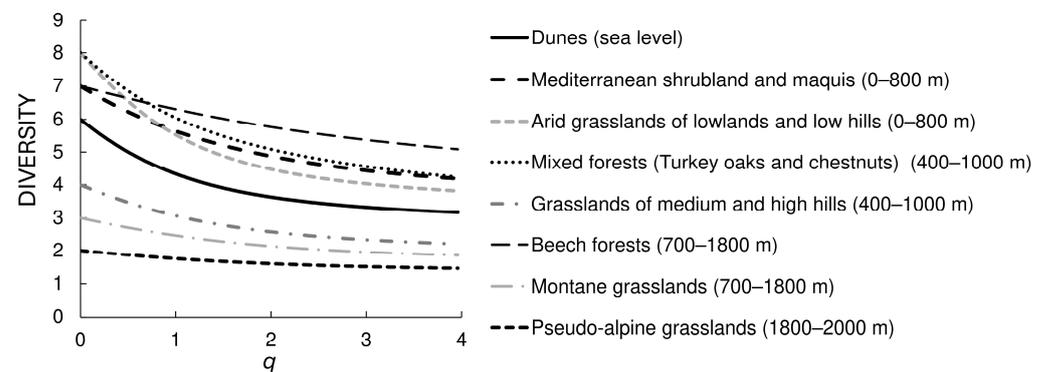


Figure 6. Biogeographical diversity profiles for tenebrionid species in different vegetations along the elevational gradient in Latium (central Italy). Black lines indicate natural vegetations, grey lines indicate secondary vegetations.

Proportion of geophilous and xylophilous species varied among the main biogeographical groups ($\chi^2 = 18.273$, $df = 3$, $p = 0.0004$), with a disproportionate presence of geophilous species among endemics (93%, thus supporting Prediction 5) and Mediterranean species

(81%); by contrast, xylophilous species were only slightly more abundant than geophilous ones among European (59%) and Palearctic species (58%).

Proportion of endemics varied among vegetation types (Figure 7, $\chi^2 = 29.741$, $df = 7$, $p = 0.0001$), with endemic species being highly associated with some open habitats such as montane grasslands (63%) and pseudo-alpine grasslands (75%) (Prediction 5).

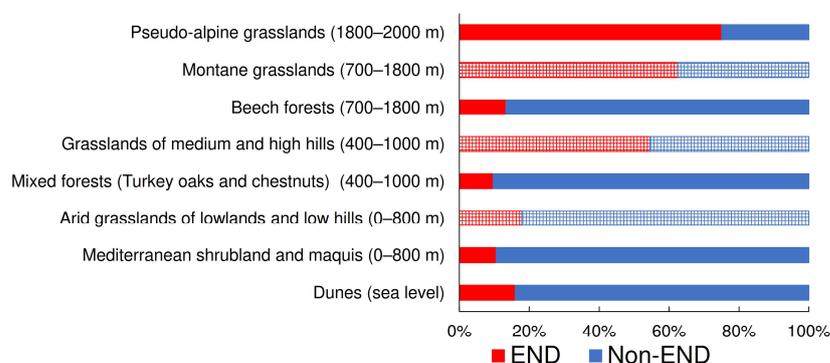


Figure 7. Percentages of endemic (END) and non-endemic (Non-END) tenebrionid species from different vegetations in Latium (central Italy). Grid patterns identify secondary vegetations.

Relationships between vegetation types outlined by overall similarities (β_{sor}) in tenebrionid composition indicated the presence of two main groups (Figure 8a): one including forest vegetations (vegetations 2, 4, and 6) and the other including natural and secondary grasslands (vegetations 5, 7, and 8); dunes (vegetation 1) are well distinct and arid pastures of lowlands and low hills (vegetation 3) occupy an intermediate position. When only the pure turnover is considered (β_{sim} , Figure 8b), arid pastures of lowlands and low hills appear to be more similar to vegetation 5 (grasslands of medium and high hills), which suggests that the higher distance obtained with β_{sor} was due to the influence of nestedness on β -diversity pairwise relationships. In both ordinations, mixed forests (vegetation 4) occupy an intermediate position between Mediterranean shrubland and maquis (vegetation 2) and beech forests (vegetation 6), which indicates that the fauna found in mixed forests comprises species of both Mediterranean shrubland and maquis and beech forests. Specifically, about 23% of the species recorded in the mixed forests were also found in both the Mediterranean shrubland and maquis and the beech forests, about 45% were shared with the Mediterranean shrubland and maquis (but not with the beech forest), and about 16% with the beech forests (but not with the Mediterranean shrubland and maquis). Similarly, grasslands of medium and high hills (vegetation 5) showed an intermediate position between arid grasslands of lowlands and low hills (vegetation 3) and montane grasslands (vegetation 7). Specifically, about 27% of the species recorded in the grasslands of medium and high hills were also found in both the arid grasslands of lowlands and low hills and the montane grasslands, about 55% were shared with the arid grasslands of lowlands and low hills (but not with the montane grasslands), and about 18% with the montane grasslands (but not with the arid grasslands of lowlands and low hills). All species of the pseudo-alpine grasslands can be found in the montane grasslands. Thus, the communities of mixed forests share a large fraction (about 84%) of their species with those of the maquis and/or the beech forests, whereas those of the grasslands of medium and high hills share all of their species with those of the arid grasslands of lowlands and low hills and/or montane grasslands. These results support Prediction 2.

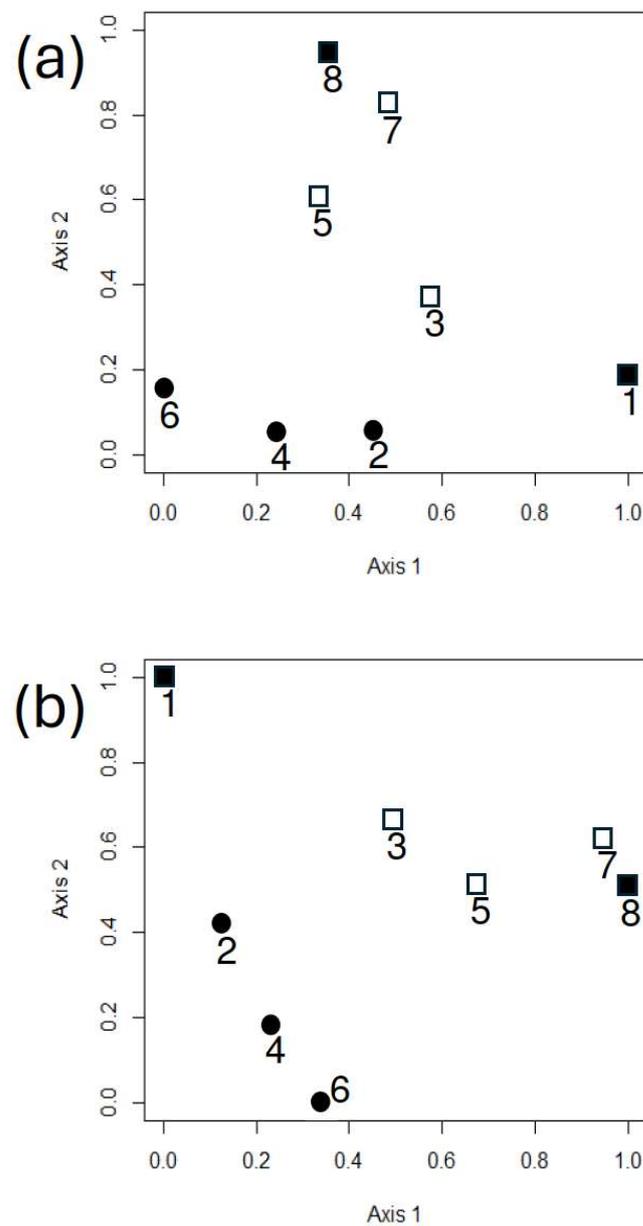


Figure 8. Non-metric multidimensional scaling plots showing β -diversity distances between vegetation types for tenebrionid species composition along the elevational gradient in Latium (central Italy). (a) Results obtained using Dice-Sørensen coefficient (Stress: <0.0001); (b) Results obtained using Simpson coefficient (Stress: 0.017). Numbers identify vegetation types as follows: 1. Dunes; 2. Mediterranean shrubland and maquis; 3. Arid grasslands of lowlands and low hills; 4. Mixed forests (Turkey oaks and chestnuts); 5. Grasslands of medium and high hills; 6. Beech forests; 7. Montane grasslands; 8. Pseudo-alpine grasslands (beyond the tree line). Black symbols: natural vegetations; white symbols: secondary vegetations. Squares: open vegetations; circles: forest vegetations.

4. Discussion

Overall, the considered fauna represents about 25% of the entire Italian fauna (about 334 species/subspecies if *Lagriina* and *Alleculinae* are excluded; estimate based on [73,74,94–100]). This high diversity can be related to the relatively large surface of the region, its position in the center of the Italian peninsula and the variety of landscapes [66,67,94].

The landscapes of Latium region (central Italy) have been profoundly modified by human presence, leading to a mosaic of natural, seminatural and artificial landscapes, with open areas of secondary vegetation interspersed within belts naturally characterized

by forest vegetation [24–27]. Given the different preferences of animals for biotopes with different types of vegetation [68,69], species associated with open areas might infiltrate belts where forest is the expected vegetation if anthropogenic transformations produced open areas. Results obtained in this research are in accordance with the hypothesis that species richness declines with elevation in both natural and secondary vegetations because of environmental filtering processes, and this pattern is independent from species' ecological preferences and biogeographical origin. Additionally, as hypothesized on the basis of species preferences for open and tree vegetations, species assemblages of open vegetations within elevational belts that should be naturally occupied by forests are not subsets of those of forest assemblages, but are more similar to those of natural open habitats occurring in other belts.

Consistent with results obtained in previous studies in which there was no distinction among vegetation types [38–40], the current study shows that, in general, tenebrionid species richness decreases upwards, in both natural and secondary vegetation (Prediction 1), which suggests that the drivers of such elevational decline in tenebrionid diversity (possibly represented by increasing harsher conditions) are more important and likely different from changes in vegetation. However, it is important to note that the lowest belt, represented by sandy shore vegetation, has fewer species than the following belt, occupied by the Mediterranean maquis. This is clearly a reflection of the harsh conditions of coastal environments (e.g., high temperatures, especially on the ground in summer, low water availability, low productivity, low vegetation diversity), where tenebrionid communities are mainly represented by few, highly adapted species [101,102]. Although this decline in diversity might be influenced by the fact that, with increasing elevation, available area also decreases, previous research indicated that decrease in species richness of tenebrionids along the elevational gradient of Latium can be observed also after controlling for available area [39,40].

As expected, ecological preferences influenced species association with vegetation (Prediction 2): geophilous (ground-dwelling) and xylophilous (arboreal) species showed different proportions among vegetation types, with geophilous species prevailing in open vegetations, and xylophilous species in natural forests, independently from their elevation. Despite the higher proportion of the geophilous species in the study fauna, secondary open vegetations have fewer species than the corresponding natural (forest) vegetation found at the same elevations. These results stress the conservation importance of forests for tenebrionid beetles, especially for saproxylic species, some of which are imperiled [71,103]. Replacement of forests with secondary open habitats would impact dramatically on the diversity of tenebrionids at elevations that would be naturally occupied by forests. Additionally, the tenebrionids inhabiting secondary (open) vegetations are not subsets of those found in the corresponding natural (forest) vegetation, as shown by their low similarity in species composition (Prediction 2). This indicates that the assemblages of secondary vegetations are not impoverished versions of those associated with the original forest vegetation. If, on the one hand, this implies that secondary vegetation types cannot retain original communities of elevational belts naturally occupied by forests, on the other hand it suggests that they might serve as a habitat extension for some species found in natural vegetation at a different elevations, which supports the importance of secondary vegetation for certain species [68,69]. Moreover, endemics represent a conspicuous proportion (more than 50% of the species) of the tenebrionid assemblages of high-elevation open habitats, included those occupied by secondary vegetation. In general, the study area is home to a large number of endemics (at least 14 taxa), which account for about 10% of the total number of species/subspecies endemic to Italy (about 137 species/subspecies; estimate based on [74,94–100]). These results further support the importance of secondary (semi-natural) vegetations for biodiversity conservation in the Apennines [68,69]. Interestingly, endemics occur almost exclusively among geophilous species, which can be explained by the low dispersal capabilities of most ground-dwelling tenebrionids, which are flightless. In general, the study area shows a predominance of geophilous species, which reflects both

their prevalence in the whole Italian fauna (more than 75%) [41] and the prevalence of open areas in the study area (with less of 40% of the surface occupied by forests) [104].

Biogeographically, the study fauna is characterized by a relatively high proportion of species mainly distributed in the Mediterranean basin. This obviously reflects the geographical position of the study area, in the middle of the Mediterranean basin. However, Mediterranean species represent a conspicuous fraction (~40–70%) of the species assemblages in the three lowest vegetations (Prediction 3), whereas they are a minority of species in the mixed forests, in the grasslands of medium and high hills, and in the beech forests, being finally absent in the montane and pseudo-alpine grasslands. This reduction in the Mediterranean species is associated with an increase in European and Palearctic species. Differently from Mediterranean species, which are typically thermophilic species, these non-Mediterranean species are associated with colder climates, and their presence in the study area (in many cases limited to middle-high elevations) increases its biogeographical diversity, especially at low and intermediate elevations (Prediction 4). This is especially illustrated by the high biogeographical diversity (diversity profiles based on Hill numbers) shown by mixed forests and beech forests. Although arid grasslands of lowlands and hills are an anthropogenic vegetation, they host a biogeographical diversity even higher than that of Mediterranean shrubland and maquis, when the role of rare chorotypes is emphasized (Hill numbers with low q -values), thus highlighting the importance of secondary vegetation for these insects. Overall, vegetations at intermediate elevations (beech forests, mixed forests, and arid grasslands of lowlands and hills) showed higher biogeographical diversity values, compared to those of higher (montane and pseudo-alpine grasslands) and lower (dunes and possibly Mediterranean shrubland and maquis) elevations (Prediction 4).

We found a strong association between chorotypes and lifestyle, which explain the high proportion of endemic species at high elevations. Geophilous species prevail among Mediterranean and endemic species, whereas xylophilous species are mainly associated with European and Palearctic distributions. As high elevations are dominated by open vegetation, this leads to a predominance of geophilous species, and hence favors a higher proportion of endemics (Prediction 5). By contrast, European and Palearctic species are mainly associated with tree vegetations, especially those that predominate in areas with colder climates, being therefore prevalent in the mixed and beech forests. These results further stress the importance of forest vegetation for tenebrionids.

Finally, as expected according to Prediction 2, tenebrionid assemblages of open vegetations, both natural and secondary, appear to be relatively similar in species composition, being distinctly separated from that of forest vegetation, both in terms of overall composition (Dice–Sørensen coefficient) and pure turnover (Simpson coefficient). In particular: (1) dunes are profoundly different in tenebrionid composition from all other vegetations; (2) Mediterranean shrubland, mixed forests and beech forests clustered apart; (3) grasslands of middle elevation, montane grasslands and pseudo-alpine grasslands form another group; (4) arid grasslands of low elevations show an intermediate position between the Mediterranean shrubland and the grasslands of middle elevations. These results demonstrate the importance of vegetation types in constraining tenebrionid distributions across the elevational gradient.

5. Conclusions

Grasslands of secondary vegetation may represent important habitats for tenebrionid beetles in central Italy. They are characterized by high levels of species richness, biogeographical diversity and endemism, but are not reservoirs of species that are associated with the forest vegetation that would naturally occur at certain elevations. Tenebrionid assemblages in these habitats are not impoverished versions of those recorded from the forests naturally occurring at the same elevations, but form very different species assortments. Because of increasing human pressures on these seminatural habitats, it is important that their importance is recognized and valued in conservation programs, to ensure they are not subject to further degradation processes. However, this should not divert conservation

efforts from protecting natural vegetation. If, on one hand, secondary vegetations can play a pivotal role for biological conservation in the Mediterranean biodiversity hotspots, it is also important that natural vegetations are adequately preserved, especially for the conservation of xylophilous species.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d16020110/s1>, Table S1: Tenebrionid species distribution (0 = absence, 1 = presence) in different vegetation types in Latium and their ecological and biogeographical characterization. Chorotypes: CEU: Centraleuropean, END: Endemic to Italy; EUR: European, SEU: S-European, MED: Mediterranean; NAF: N-African; WME: W-Mediterranean; EME: E-Mediterranean; CEM: Centralasiatic-European-Mediterranean; OLA: Holarctic; SIE: Sibero-European; TEM: Turano-European-Mediterranean; TUM: Turano-Mediterranean.

Funding: This research was partially funded by the University of L'Aquila, Department of Life, Health and Environmental Sciences, FFO 2023 "Struttura di comunità in ecosistemi di sky island".

Institutional Review Board Statement: Not applicable.

Data Availability Statement: Data supporting reported results are provided as Table S1.

Acknowledgments: I am grateful to Maria Laura Carranza and Letizia Di Biase for discussions about vegetation types, to Davide Bergamaschi for his help with Figure 1, and to three anonymous reviewers for their comments on a previous version of this paper. Thanks are due to Letizia Di Biase and Andrea Di Giulio for allowing me to use their photos in Figure 2.

Conflicts of Interest: The author declares no conflicts of interest.

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