

Effects of interactive scale-dependent variables on beetle diversity patterns in a semi-arid agricultural landscape

Gal Yaacobi · Yaron Ziv ·
Michael L. Rosenzweig

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Abstract Understanding species-diversity patterns in heterogeneous landscapes invites comprehensive research on how scale-dependent processes interact across scales. We used two common beetle families (Tenebrionidae, detritivores; Carabidae, predators) to conduct such a study in the heterogeneous semi-arid landscape of the Southern Judean Lowland (SJL) of Israel, currently undergoing intensive fragmentation. Beetles were censused in 25 different-sized patches (500–40,000 m²). We used Fisher's α and non-parametric extrapolators to estimate species diversity from 11,125 individuals belonging to 56 species. Patch characteristics (plant species diversity and cover, soil cover and degree of stoniness) were measured by field transects. Spatial variables (patch size, shape, physiognomy and connectivity) and landscape characteristics were analyzed by GIS and remote-sensing applications. Both patch-scale and landscape-scale variables affected beetle species diversity. Path-analysis models showed that landscape-scale variables had the strongest effect on carabid diversity in all patches. The

tenebrionids responded differently: both patch-scale and landscape-scale variables affected species diversity in small patches, while mainly patch-scale variables affected species diversity in large patches. Most of the paths affected species diversity both directly and indirectly, combining the effects of both patch-scale and landscape-scale variables. These results match the biology of the two beetle families: Tenebrionidae, the less mobile and more site-attached family, responded to the environment in a fine-grained manner, while the highly dispersed Carabidae responded to the environment in a coarse-grained manner. We suggest that understanding abiotic and biotic variable interactions across scales has important consequences for our knowledge of community structure and species diversity patterns at large spatial scales.

Keywords Carabidae · Fragmentation · GIS · Habitat variability · Landscape heterogeneity · Patch size · Path analysis · Remote sensing · Species diversity · Tenebrionidae

G. Yaacobi (✉) · Y. Ziv
Department of Life Sciences, Ben-Gurion University
of the Negev, Beer-Sheva 84105, Israel
e-mail: yaacobi@bgu.ac.il

M. L. Rosenzweig
Department of Ecology and Evolutionary Biology,
University of Arizona, Tucson, AZ 85721, USA

Introduction

The number of species at a given location is affected by several factors that may operate at different spatial scales. Such spatial scales are mainly defined by the organism's mobility and the

connectivity between its populations. On a local scale (i.e., grain, single patch; Turner 1989), processes such as demographic stochasticity and competition may operate (Ziv 1998). Such processes are highly affected, directly and indirectly, by both abiotic (e.g. percentage of rock and soil cover) and biotic (e.g. percentage of vegetation cover and diversity) variables.

On a landscape scale, environmental heterogeneity, through the patchy structure of the landscape, has a major role in determining ecological processes (Turner 1989; Svensson 1999). At this scale, processes such as dispersal of individuals between distinct populations and extinction may operate (see Cornell and Karlson 1997). These processes are mostly influenced by patch-related variables, including patch productivity (e.g. Preston 1962; Rosenzweig and Abramsky 1993), patch size (e.g. MacArthur and Wilson 1967), patch shape (e.g. Turner 1989; Farina 1998), isolation (e.g. MacArthur and Wilson 1967; Hanski and Gilpin 1997), proximity to other patches, and contrast with the surrounding habitat (e.g. Turner 1989; Farina 1998).

Over the last two decades, human-induced habitat fragmentation has contributed to habitat loss and decreased sizes of plant and animal populations (e.g. Andren 1994; Fahrig 2003), as well as causing a breakdown of continuous populations into isolated (Hanski and Gilpin 1997) or source-sink (Pulliam 1988) populations. As a result, studying the relative roles of local and landscape processes (Cornell and Karlson 1997; Ziv 1998, 2003) and their corresponding variables in a fragmented landscape may have both theoretical and practical uses. However, studies that explore how scale-dependent variables interact in determining species diversity and community structure are scarce. It is likely that the complexity of scaling and the difficulty of studying heterogeneous landscapes deter ecologists from pursuing this direction. In this study we take up the challenge of exploring complex interactions between variables operating at different scales by combining field data, spatial analysis using GIS data and path analysis statistics.

In particular, we suggest four mutually-exclusive hypotheses regarding local-scale and landscape-scale effects that differ in their focus on the

scale at which particular variables are effective: the random-placement hypothesis (null hypothesis), the patch effect hypothesis, the landscape effect hypothesis, and the multiple-scale effect hypothesis.

The random-placement hypothesis states that passive sampling from a species pool (i.e., all the available species in the study area and its surroundings) will determine the number of species at a site (e.g. Andren 1994; Hubbell 2001). Note that although Andren (1994) used the term ‘sampling’, Turner and Tjorve (2005) suggest that the term ‘placement’ represents more accurately the underlying process). Larger areas provide larger targets than smaller ones and, consequently, may contain a greater number of individuals (Andren 1994; 1996; 1999). Therefore, the number of species rises in relation to the size of the sampled patches. Simultaneously, species diversity will not be significantly correlated with patch-scale variables (see below, “the patch effect hypothesis”) or with landscape-scale variables (see below, “the landscape effect hypothesis”). Since the random-placement hypothesis explicitly refers to a randomly, process-independent phenomenon we consider it as our null model (Crist et al. 2003; Turner and Tjorve 2005).

The patch effect hypothesis suggests that within-patch biotic variables (e.g. percentage of vegetation cover) and abiotic variables (e.g. percentage of rock and soil cover) increase habitat diversity and niche opportunities. In addition, variables such as patch size and/or patch quality may affect species diversity via effects on population size and extinction-probability mechanisms (e.g. Pimm et al. 1988; Robinson and Quinn 1988). Consequently, a larger variety of habitats (i.e., greater heterogeneity) should increase the number of species (e.g. Hutchinson 1959; Ziv 2003) a higher abundance of individuals may increase species diversity due to decreasing stochastic and deterministic effects (Pimm et al. 1988). Hence, this hypothesis predicts that species diversity should be significantly correlated to patch variables, including percentage of vegetation cover, plant species diversity, quantity of exposed soil, stoniness, and patch spatial heterogeneity. However, species diversity should not be significantly correlated with any landscape-oriented variable.

Alternatively, *the landscape effect hypothesis* suggests that spatial variables can affect ecological processes such as dispersal and extinction, thus determining community structure and species diversity in a given patch. Such variables may include patch shape, edge effect, patch isolation, patch contrast and disturbance. However, species diversity should not be significantly correlated with any within-patch oriented variable.

Finally, our *multiple-scale effect hypothesis* states that both within-patch and landscape variables will act interactively to determine species diversity and community structure patterns (Davies et al. 2001; Ziv 2003). For example, resource diversity, which may be the result of within-patch plant diversity, can affect species abundance and diversity. However, the identity of the species occupying that patch may be determined by the dispersal ability of particular species from an adjacent patch with a specific quality, size and shape. Hence, any joint combination affecting species diversity to a statistically significant extent will be considered to support the multiple-scale effect hypothesis.

The Southern Judean Lowland area (hereafter, Bet-Govrin Area; BGA) in Israel is characterized by natural vegetation patches surrounded by agricultural fields, newly planted forests and other habitats subject to anthropogenic disturbance. Humans have used this region since the late Bronze Age, approximately 5,500 years ago (Ben-Yosef 1980), producing as a result a natural archipelago of vegetation attracting a wide variety of organisms, among them a diversity of beetle species. The latter may be strongly affected by both local (within a patch) and landscape (between patches) variables. Therefore, this fragmented landscape, together with its semi-arid Mediterranean characteristics, forms an appropriate model for investigating how environmental heterogeneity and patchiness affect species diversity and community structure at the local and landscape scales. At this landscape we focus on species diversity patterns at three trophic levels: plants, detritivorous beetles and predatory beetles.

Methods

Study site

The Bet-Govrin Area (BGA) is located in the Southern Judean Lowland region (Fig. 1) of Israel, which forms part of the semi-arid climatic zone with an average annual precipitation of 350 mm during a short winter season (October–March). The landscape is characterized by a patchy arrangement of exposed rocks (soft limestone covered with a strong calcium-based layer) inbetween areas of soil cover (brown Rendzina; haploxerolls) (Ben-Yosef 1980; Waizel 1984). Vegetation in this area varies from scrubland and garrigue to batha (or phrygana to scrub). The dominant plant association is formed by *Ceratonia siliqua*—*Pistacia lentiscus*—*Rhamnus palaestinus*, with Gramineae and *Sarcopoterium spinosum* as leading plants in the southern area (Zohary 1982; Waizel 1984).

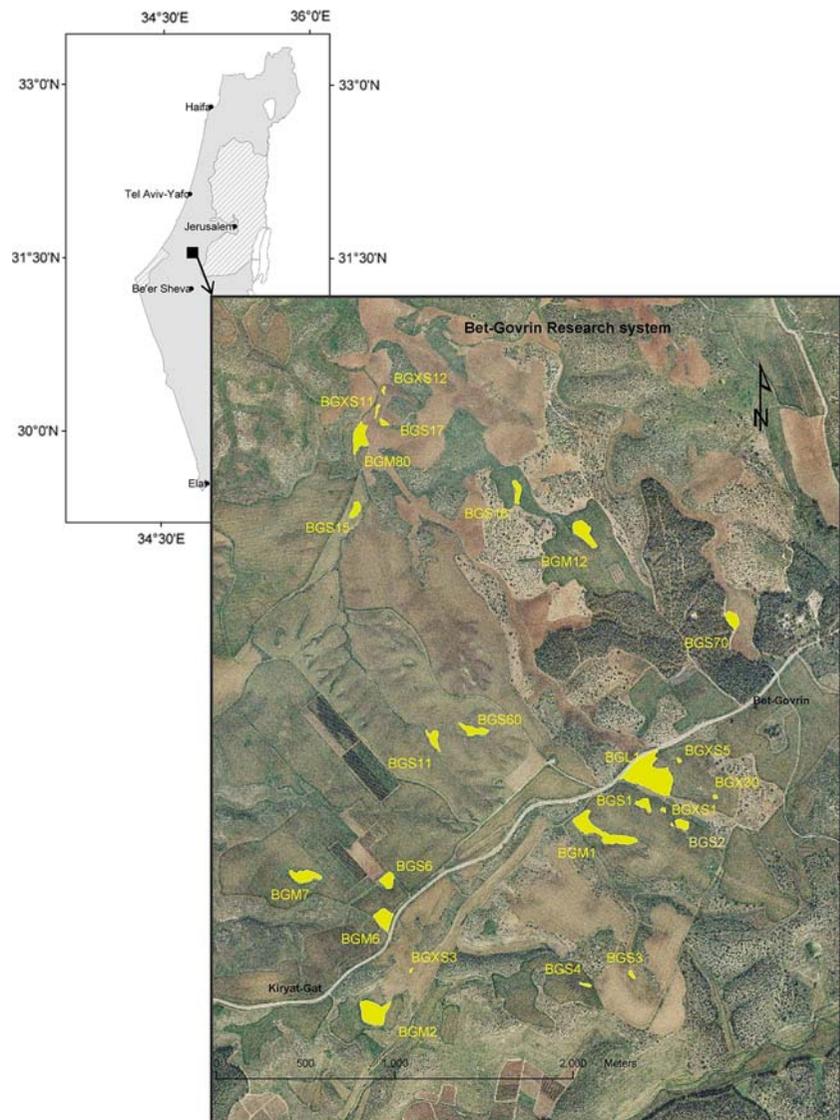
More than five thousands years of human development and interference since the late Bronze Age have further added to the patchy configuration of the landscape. While in the past, humans mainly used the plain loessal valleys for agriculture (Ben-Yosef 1980), modern cultivation methods allow for utilization of some of the rocky patches for agriculture, making the surviving natural-habitat patches even smaller and more isolated.

We selected 25 natural habitat patches surrounded by an agricultural field matrix (Fig. 1). These patches were classified into four size groups: 10 extra small (up to 1000 m²), 7 small (1000–5000 m²), 7 medium (5000–20,000 m²) and 1 large (40,000 m²). The selected patches represented the plant composition, soil type and rock formation of the area, but varied in their patch spatial attributes (e.g. shape) and location in the matrix (e.g. degree of isolation and contrast with surrounding habitats).

Study species

We chose to test the four hypotheses using beetles from the Tenebrionidae and Carabidae families, which inhabit the natural-habitat patches found at BGA, due to their relatively large species

Fig. 1 An orthophoto image of the Bet-Govrin research area, Israel. Yellow polygons are the studied patches. The third letter(s) of each patch name—either XS, S, M, or L—indicate either extra-small, small, medium or large patch, respectively



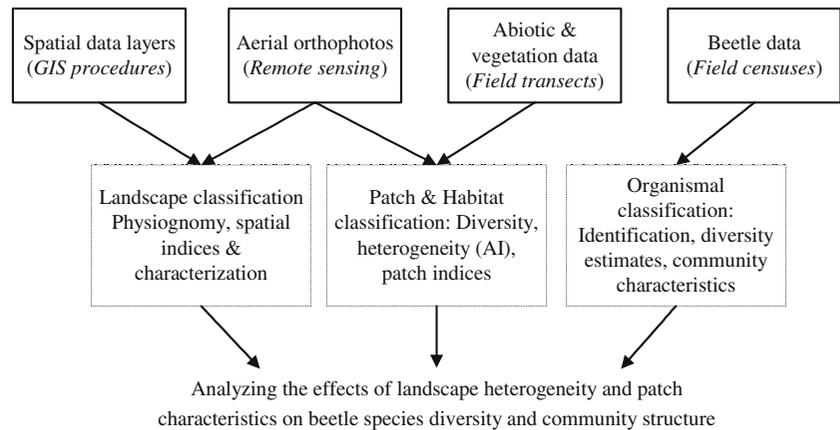
diversity, their known role in ecosystem functioning, and their life-history traits (e.g. size, life cycle and mobility). This enabled the use of a small heterogeneous area for studying scale-dependent species diversity patterns.

Both families are ground-dwelling and contain a large number of species (ca. 400 in each family in Israel). In general, the Tenebrionidae are detritivorous, feeding on available dead organic matter (Rickard and Haverfield 1965; Allsopp 1980). The Carabidae mostly feed on insects, snails, earthworms and other small invertebrates (Burel 1989; Ellsburly et al. 1998; Petit and Usher 1998). The larvae of both families hatch and

develop into pupae underground. The majority of species of both families are flightless. Both families display high variation in body size, ranging from 2 mm to 40 mm in the research area (G. Yaacobi; V. Chikatunov, personal observation).

System characterizing techniques: GIS and spatial characteristics

We combined advanced spatial-analysis technology with a field survey (Fig. 2). The selected patches were characterized according to spatial attributes (size, shape, location in matrix, distance

Fig. 2 The research analysis flowchart

from other patches and type of disturbed habitat surroundings), geological variables (rock and soil), and biological variables (percentage vegetation cover, diversity and composition).

We used ArcInfoTM (ESRI) Geographical Information Systems (GIS) tools and raster-based methodology to characterize patch spatial attributes and landscape physiognomy (Haines-Young and Green 1993; Turner et al. 2001). High resolution (89 × 89 cm pixel) and standardized color aerial photos were analyzed using ERDAS IMAGINE[®] (Leica Geosystems) remote-sensing application as the basic layer for all the GIS procedures, as well as for assessing patch heterogeneity (see below). We also used ArcInfoTM (ESRI) as the main GIS platform for spatial analysis and presentation. The patch spatial variables examined were: size, shape (corrected ratio of area to perimeter; Turner et al. 2001), patch edge portion (Farina 1998), degree of isolation (distance to other patches using the nearest neighbor method; Krebs 1999) and location in matrix (juxtaposition to road, planted wood, different field types; Turner et al. 2001). We calculated patch spatial heterogeneity by developing an image analysis-based model that differentiates between four variables: stoniness, soil, perennial plants and annual plants. We scanned a 35,000 feet, color aerial photo with a 20-micron geodetic scanner to receive a sub-meter pixel size resolution (Richards and Jia 1999).

Using the supervised classification method (Richards and Jia 1999), four groups were identified (bush, weed, soil and stone) with 200

spectral signatures (11,000 pixels) from all relevant research areas. These specific groups were chosen due to the ability to distinguish precisely between the large elements in the image, previous knowledge from the field, and the spectral distance between the groups.

We exported 25 classified raster subsets to FRAGSTATS[®] software (McGarigal and Marks 1995), in order to assess spatial heterogeneity based on image texture analysis (Musick and Grover 1991). The classified rasters were examined using cluster and landscape scales.

The aggregation index algorithm (AI) was used to quantify heterogeneity:

$$AI_i = \frac{e_{i,i}}{\max e_{i,i}} \quad (1)$$

where $e_{i,j}$ represents total edges of class i adjacent to class j ; for class i of area A_i , the aggregation index measures $e_{i,i}$, the total edges shared by class i itself. The AI algorithm (He et al. 2000) assumes that a class with the highest level of aggregation ($AI = 1$) is comprised of pixels sharing the most possible edges. A class whose pixels share no edges has the lowest level of aggregation ($AI = 0$). The shared edges are counted only once in AI, and currently only four neighbors are considered. For the overall landscape, a landscape aggregation index (AI_L) can be calculated by summarizing AI_L that is weighed by the percentage of AI_i :

$$AI_L = \sum_{i=1}^n AI_i \times A_i\% \quad (2)$$

where n is the total number of classes present in the landscape, and $A_i\%$ is the percentage of the landscape of AI_i .

Both AI_i and AI_L are sensitive to spatial resolution, since $e_{i,j}$ varies with spatial resolution. AI_i values measured for different maps or layers may be compared as long as they were measured using comparable spatial resolutions.

Field measurements of patch biotic and abiotic attributes

We measured plant species diversity, vegetation cover, exposed soil and degree of stoniness using random positioned 10 m line transects. Proportional to patch size, up to 24 such transects were conducted in each of the studied patches. Transect data were collected at the end of April in all patches. Information was recorded on: plant species identity, percentage of vegetative cover of each plant (including perennials and annuals), percentage of exposed soil, and the degree of stoniness (ranging from 0–5). In addition, environmental disturbance (e.g. vehicle tracks, agricultural effects such as herbicide marks and nutrient traces, presence of invasive species in a patch and sheep grazing) was evaluated in each patch.

Beetle census and estimating beetle species diversity

Pitfall traps were placed in each of the sampled patches. Traps consisted of a cut plastic bottle containing a 17 cm PVC sleeve (5 cm in diameter) blocked by a meshed net. Commercial ethylene glycol was used as a preserving medium for arthropods falling into the trap. A PVC ring (15 cm in diameter) was positioned around the entrance to each pitfall trap at ground level to prevent small rodents and reptiles from being caught (A. Tsairi; G. Yaacobi, personal observation).

Traps were placed uniformly in all patches, ensuring that most of the patch was sampled. An equal distance of 10 meters between traps was chosen, based on knowledge of ground beetle home ranges (e.g. McIntyre 2000; Raworth and Choi 2001) and an attempt was made to sample

all microhabitats in a patch with a fixed design. The number of traps per patch was derived from the patch size class (extra small, small, medium and large) in proportion to patch area. In addition, we plotted saturation curves for traps and species from a preliminary census, to make sure that the sample size was satisfactory (Gotelli and Colwell 2001). The traps were open continuously from April to July (the highly active season), during which the contents were collected every two weeks. Beetle classification and identification were performed with the help of the late Dr. Cabir Argaman, PPIS—Volcani Center and Prof. Vladimir Chikatunov, Tel-Aviv University.

In order to estimate beetle species diversity, we used two independent methods: Fisher's alpha diversity index (Fisher et al. 1943) and Burnham & Overton's (hereafter: 'BO') extrapolator (Burnham and Overton 1979). For both algorithms, we used the total number of species and individuals collected during the trapping period. Fisher's alpha relies on the log-series species-abundance fitting assumption, eliminating the classic problem of sample size bias (Fisher et al. 1943; see Rosenzweig 1995; Rosenzweig et al. 2003), from which other common indices such as rarefaction curves (Sanders 1968) or Simpson's index (Simpson 1949) may suffer (Magurran 1988). However, Fisher's index for species diversity provides a relative value rather than the estimated number of species itself (Rosenzweig et al. 2003).

To estimate species number in a location, we chose the BO technique (the step-by-step jackknife estimator; Burnham and Overton 1979; Smith and Van Belle 1984). This is a non-parametric method that estimates the finite number of species in a quadrat sample (Colwell and Coddington 1994; Brose and Martinez 2004). This estimate is distribution-free and is based on the observed frequency of rare species in the community. To calculate BO through all five jackknife orders, we used the Ws2m software package (Turner et al. 2000).

Statistical methods

Studying the effects of scale-dependent variables in accordance with our hypotheses requires a multivariate analysis. However, the use of

multiple-regression analysis as well as ANOVAs is quite limited in this system due to the existence of multiple co-linearity and contradictory trends (Wootton 1994; Smith et al. 1997). We therefore used the path-analysis statistical model (Wright 1934; 1960) to evaluate the strength of interactions (Wootton 1994; Scheiner and Gurevitch 2001) and to identify the major variable pathways affecting species diversity in BGA. By definition, path analysis places a set of correlations into an assumed cause-and-effect flow-chart. The technique helps to define direct and indirect effects, and to make assumptions on the importance of the different traits involved, by the use of regression coefficients (Wright 1960; Scheiner and Gurevitch 2001). Path analysis is restricted to the use of linear regression between variables; therefore, some of the non-linear regressions found for several interactions were not used in this analysis.

In order to compare species similarity between the patches and their surroundings, we used the Bray-Curtis similarity index (Bray and Curtis 1957; Clarke and Warwick 1994; Krebs 1999). This index compares species composition using species abundances, so that rare species are not equal to dominant species, but are still considered. A $\log(1+y)$ data transformation was used before each calculation in order to down-play the importance of the very abundant species and to increase the influence of the rare ones (Clarke and Warwick 1994). In addition, sample size was standardized to prevent the Bray-Curtis coefficient from reflecting differences between unequal samples (Clarke and Warwick 1994).

Similarity analysis was followed by cluster analysis (Jongman et al. 1995) for all patches. Multivariate analysis of species composition was performed using PRIMER-E® software (Clarke and Warwick 2001).

Results

Tenebrionid and carabid assemblages

We censused a total number of 11,125 beetles belonging to 56 species (Appendix Table 3): the tenebrionid assemblage was represented by 24

species and 4809 individuals and the carabid assemblage was represented by 32 species and 6316 individuals.

Species-area curves (MacArthur and Wilson 1967) for the two beetle assemblages revealed no significant pattern when using Fisher's α (see Rosenzweig 1995). However, a one-way ANOVA (Sokal and Rohlf 1981) revealed a significant difference in species-area relations between the smallest patch category and the other three categories (Tenebrionidae: $F_{1,24} = 9.7$, $P < 0.001$; Carabidae: $F_{1,25} = 17.2$, $P < 0.01$). Consequently, we separated our next analyses into two main size categories—15 large patches (3000 m²–40,000 m²) and 10 small patches (200 m²–1000 m²)—to avoid area-size bias.

The effect of patch-scale variables

We tested the effect of the patch-scale variables—patch spatial heterogeneity, patch area, plant cover, plant species diversity, stoniness and soil cover—on beetle species diversity in the two patch-size categories (Table 1). We found a significant relationship between tenebrionid species diversity and patch spatial heterogeneity (AI) only in the large patch-size category. In contrast, carabid species diversity was correlated to patch spatial heterogeneity (AI) only in the small patch-size category. We found no significant correlation between plant cover (perennials and annuals) and beetle species diversity, except for the Carabidae in the small patch-size category ($R^2 = 0.71$, $P = 0.024$).

Beetle species diversity in both patch-size categories was not significantly correlated with patch soil cover and degree of stoniness. Although such a result is unexpected, it is possible that the low exposure of soil cover and homogeneity of soil types does not allow us to relate beetle diversity to these variables (Petit and Usher 1998).

Plant species diversity was significantly correlated to tenebrionid diversity both in the small and the large patches ($R^2 = 0.45$, $P = 0.067$; and $R^2 = 0.38$, $P = 0.013$, respectively). We found a higher equitability of the plant community as well as a smaller number of rare plant species in the large patches than in the small patches, even

Table 1 The effect of patch and landscape variables on species diversity of the Tenebrionidae and Carabidae families in small (a) and large (b) patches

Variable	Tenebrionidae diversity	Trend	Carabidae diversity	Trend
(a) Small patches				
<i>Patch scale</i>				
Area	Not significant		$R^2 = 0.4, P = 0.046$	↑
Heterogeneity	Not significant		$R^2 = 0.71, P = 0.02$	∩
Plant cover	Not significant		$R^2 = 0.71, P = 0.024$	∩
Plant diversity	$R^2 = 0.45, P = 0.067$	↓	Not significant	
Shape	Not significant		$R^2 = 0.52, P = 0.027$	↓
<i>Landscape</i>				
Isolation	Not significant		Not significant	
Edge effect	Not significant		$R^2 = 0.74, P = 0.003$	↓
Contrast	$R^2 = 0.62, P = 0.02$	↓	Not significant	
Disturbances	$R^2 = 0.63, P = 0.01$	↑	$R^2 = 0.56, P = 0.023$	↑
(b) Large patches				
<i>Patch scale</i>				
Area	Not significant		Not significant	
Heterogeneity	$R^2 = 0.32, P < 0.1$	∩	Not significant	
Plant cover	Not significant		Not significant	
Plant diversity	$R^2 = 0.38, P = 0.01$	↑	Not significant	
Shape	Not significant		Not significant	
<i>Landscape</i>				
Isolation	Not significant		Not significant	
Edge effect	Not significant		$R^2 = 0.26, P = 0.05$	↓
Contrast	Not significant		$R^2 = 0.44, P = 0.006$	↑
Disturbances	Not significant		Not significant	

The symbols in the trend column indicate: ↑ = positive relationship; ↓ = negative relationship; ∩ = unimodal relationship

though an abundance-based estimator was used (Scheiner and Gurevitch 2001). These results may explain the difference in correlations between patch-size categories and plant species diversity.

The effect of landscape-scale variables

Patch shape was significantly correlated to species diversity only in small patches ($R^2 = 0.52, P = 0.027$). The carabids showed a linear decrease with changing patch shape from circular to narrow ellipsoid.

We found a non-significant correlation between tenebrionid estimated diversity and patch edge effect, while there was a negative correlation between patch edge effect and carabid assemblage (see below: “Scale-invariant relationships”).

The effect of the position of the patches in the landscape matrix was analyzed by using both the nearest-neighbor method and the similarity in species identity between the patches and their surrounding fields (i.e., contrast). We found no

effect of patch adjacencies to other natural habitats on species diversity of the two beetle assemblages. As expected, similarity analysis between patches and their adjacent fields showed different species compositions for these two categories (Figs. 3 and 4).

Patch disturbance regime (an aggregate of five environmental variables: agricultural pressure, tourism influence, distance from road(s), presence of invasive plant species and dissimilarity in species composition) was significantly and positively correlated to beetle assemblages in the small patch-size category ($R^2 = 0.56, P = 0.01$ for carabids and $R^2 = 0.63, p = 0.01$ for tenebrionids).

Scale-invariant relationships

Our results above showed a scale-dependent response of beetle species diversity to most of the tested variables. However, some of the variables were found to affect beetle diversity at all scales, presenting the same trends regardless of

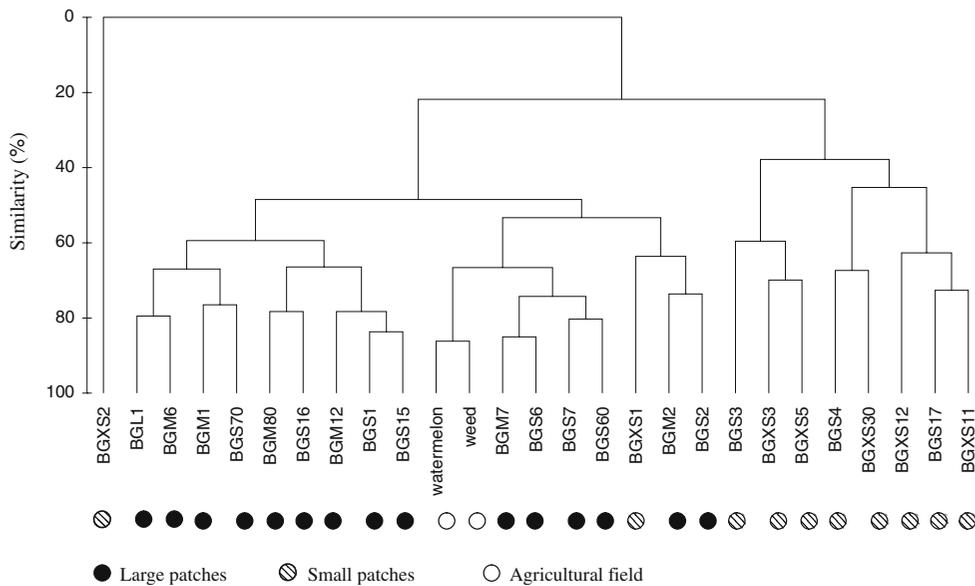


Fig. 3 Patch cluster analysis for the Tenebrionidae species similarity

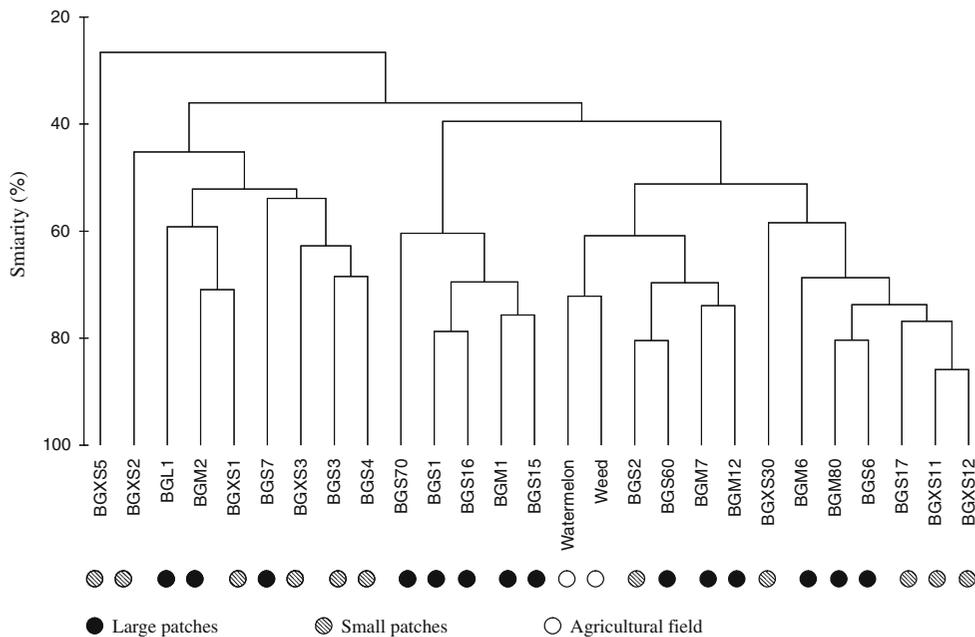


Fig. 4 Patch cluster analysis for the Carabidae species similarity

the patch-size category. Carabid estimated diversity decreased with patch edge effect similarly in both patch-size categories. Similar patterns were found when plant species diversity was correlated to area, spatial heterogeneity, patch shape and degree of disturbance (see below: “Plant species diversity responses”).

Beetles species similarity

A transformed Bray–Curtis index, followed by cluster analysis (Jongman et al. 1995) revealed different patterns of species similarity between scales and taxa. The tenebrionids showed high similarity of species in the small patches (8 out of

10 patches were clustered together; Fig. 3). The rest of the patches were clustered in two large groups, sharing high similarity (up to 80%), except for one patch, which only had a single species. Testing similarity between different field crops (e.g. wheat and watermelon) showed a similarity of 87% in species composition and abundance. Importantly, the high dissimilarity between the cultivated fields and the natural patches shown in Fig. 3 supports our assumption that the surrounding cultivated fields are hostile in some degree to the beetle communities of the natural patches.

In contrast, the carabid assemblage showed no unique patch clustering according to species composition (Fig. 4). Moreover, similarity between fields was not that different from other patch combinations (even though they clustered together with 72% similarity).

Plant species diversity responses to patch-scale and landscape-scale variables

In order to understand the role of plant diversity in the system, we examined the effects of patch and landscape variables on this group. The following variables: patch area, patch shape, heterogeneity, edge effect and disturbance, were found to affect plant species diversity (Table 2, Appendix Table 3). Our results highlight the similarity in plant diversity patterns across scales. In contrast to the categorical size effect shown for the beetle assemblages, plant diversity changed non-linearly with patch size.

Path analysis

In the previous paragraphs we have shown that both patch-scale and landscape-scale variables affected both the tenebrionid and carabid assemblages, though in different directions and trends. In order to identify the combined effect of patch-scale and landscape-scale variables on each beetle assemblage, we used the path-analysis method to statistically characterize the way in which possible direct and indirect paths affect species diversity. Furthermore, due to the already known categorical effect of patch size (see above), we subdivided our path analysis into 4 separate schemes:

Table 2 The effect of patch and landscape variables on plant species diversity

Variable	Trend	Plant species diversity
Area	↑	$R^2 = 0.62, P < 0.001$
Shape	↑	$R^2 = 0.27, P = 0.01$
Heterogeneity	↑	$R^2 = 0.31, P = 0.005$
Isolation		Not significant
Edge effect	↓	$R^2 = 0.42, P = 0.001$
Disturbances	↓	$R^2 = 0.32, P < 0.01$

The symbols in the trend column indicate: ↑ = positive relationship; ↓ = negative relationship

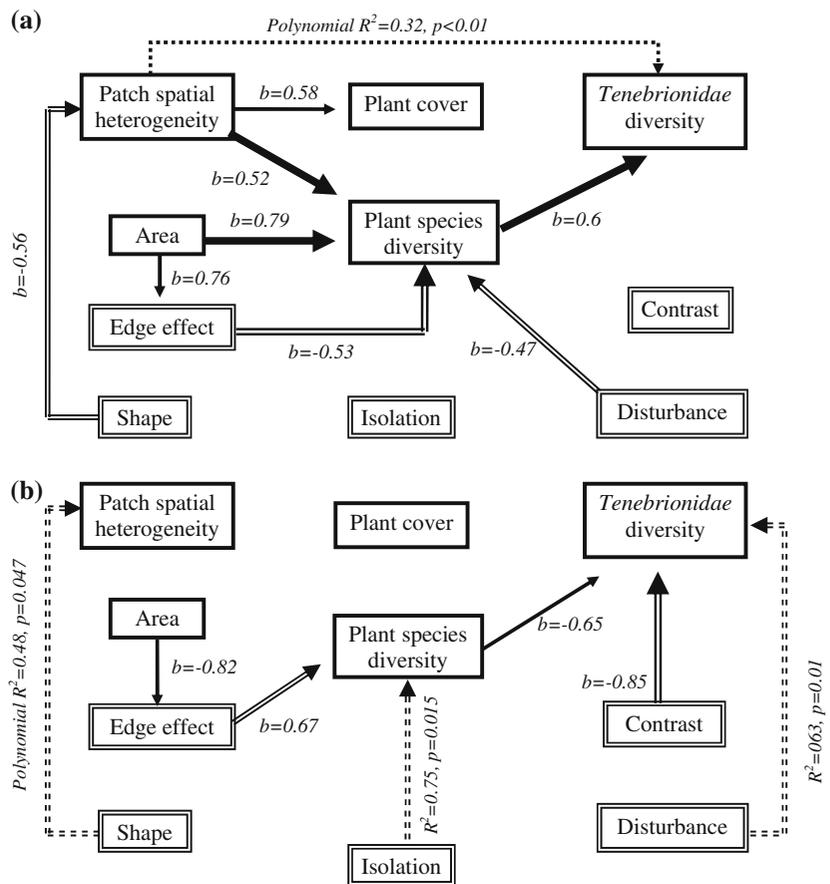
Tenebrionidae in large (Fig. 5a) and small (Fig. 5b) patches and Carabidae in large (Fig. 6a) and small (Fig. 6b) patches.

With respect to the major paths of Tenebrionidae in large patches, ‘Plant species diversity’ directly affected tenebrionid diversity, with ‘Area’ (weighted coefficient value = 0.47) and ‘Spatial heterogeneity’ (weighted coefficient value = 0.31) indirectly affecting beetle diversity through ‘Plant species diversity’ (Fig. 5a). In addition, ‘Edge effect’, ‘Shape’, and ‘Disturbance’ also indirectly affected tenebrionid diversity through ‘Plant species diversity’, but at lower intensities (weighted coefficient value = -0.32, -0.18 and -0.28, respectively; Fig. 5a).

The tenebrionid assemblage in the small-patch category (Fig. 5b) showed different patterns. Directly, ‘Contrast’ with a surrounding habitat (coefficient value = -0.85) had the most significant effect on tenebrionid diversity. In addition, at a lower intensity ‘Plant species diversity’ (coefficient value = -0.65) directly affected beetle diversity, with ‘Area’ (weighted coefficient value = -0.36) and ‘Edge effect’ (weighted coefficient value = -0.44) indirectly affecting beetle diversity through ‘Plant species diversity’ in the small patches. However, it is important to note that ‘Area’ and ‘Edge effect’ are highly autocorrelated, such that considering each separately may be misleading.

Different paths affected the carabid assemblage in the large patches (Fig. 6a). The strongest path was ‘Contrast’ with the surrounding habitat (coefficient value = 0.66), while the second strongest path was the ‘Edge effect’ (coefficient

Fig. 5 Path analysis diagram for Tenebrionidae in large (a) and small (b) patches. The width of the arrows indicates the strength of the path relative to the other paths (i.e., thick line for a strong effect; narrow line for a light effect). Dotted line indicates a non-linear relation. Solid and double-line frames present patch and landscape variables, respectively. Path coefficient is written beside each arrow



value = -0.56). Indirectly, the path ‘Area’—‘Edge effect’ affected carabid diversity in large patches at the lowest intensity (weighted coefficient value = -0.43).

Three landscape variables directly affected the carabid assemblage in the small patches (Fig. 6b). ‘Edge effect’ was the most influential variable (coefficient value = -0.86), followed by ‘Shape’ and ‘Disturbance’ regime (coefficient value = -0.72 and 0.71 , respectively). In addition, ‘Area’ affected the carabid assemblage in the small patches both directly (coefficient value = -0.64) and indirectly through ‘Edge effect’ (weighted coefficient value = 0.7).

Discussion

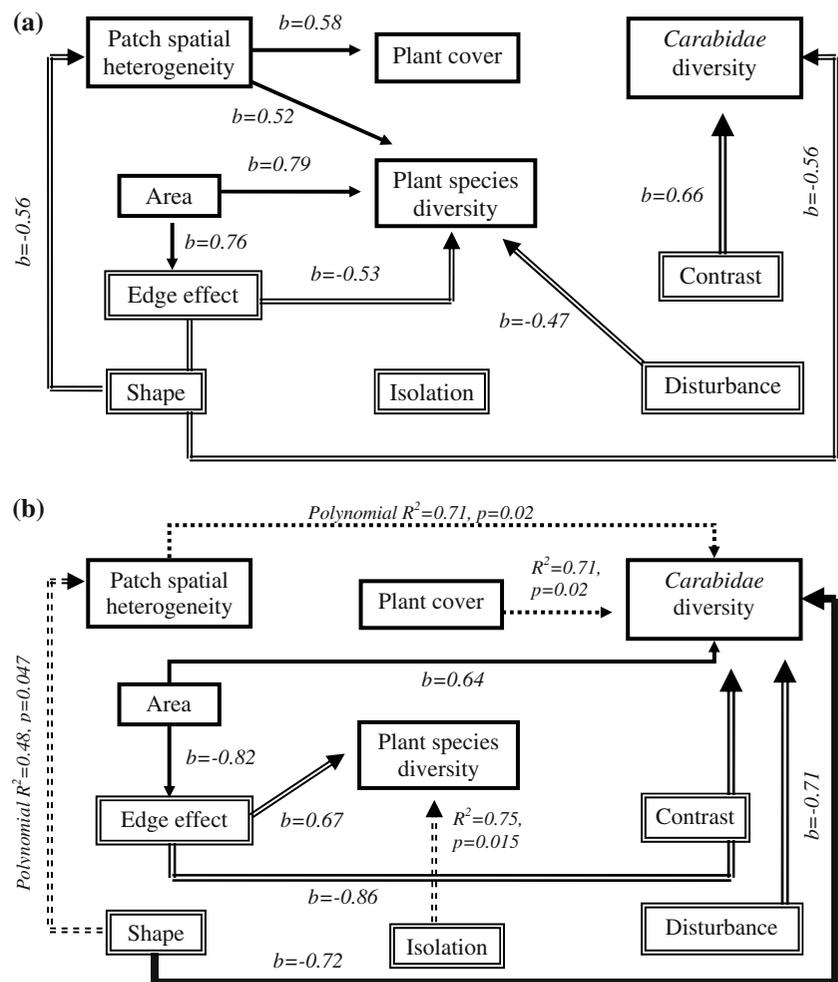
In line with one of the main challenges currently faced by spatial ecologists, our research tested

whether variables characterizing different scales affected species diversity patterns and community composition in beetles. Our results reject the null hypothesis that species diversity patterns are solely obtained from non-biological mechanisms (the random-placement hypothesis; Andren 1994) for two reasons. Firstly, no correlation was found between the sampled areas and the number of individuals in both observed beetle groups ($R^2 = 0.05, P = 0.27$). Secondly, significant correlations were found between beetle species diversity and patch-scale and landscape-scale variables, indicating that biological processes dictate the observed species diversity patterns.

Beetle responses to patch-scale variables

Plant species diversity affected the tenebrionid diversity in both the small and large patches, while not showing any correlation with carabid

Fig. 6 Path analysis diagram for Carabidae in large (a) and small (b) patches. The width of the arrows indicates the strength of the path relative to the other paths (i.e., thick line for a strong effect; narrow line for a light effect). Dotted line indicates a non-linear relation. Solid and double-line frames present patch and landscape variables, respectively. Path coefficient is written beside each arrow



diversity. It is important to note that the effect of plant species diversity on the tenebrionids does not necessarily mean that food resource *per-se* plays a role as a limiting factor, because plant cover did not affect tenebrionid species diversity. Indeed, previous studies of food selection by similar groups suggest that unvarying food (Rogers et al. 1988) does not limit darkling beetle diversity. Alternatively, as suggested by Symstad et al. (2000), it is likely that plant diversity reflects heterogeneity of plant functional groups, such that more beetle species can coexist on the basis of resource partitioning. Furthermore, the effect of spatial heterogeneity on both groups in both the small and large patches, either directly or indirectly, supports the idea that the presence of both biotic and abiotic diversity allows for increased species diversity of the studied groups.

Many other studies have linked the spatial structure of plants to arthropod diversity (e.g. Hunter and Price 1992; Siemann et al. 1998; Tews et al. 2004). In our study, the spatial structure of a patch is determined by the arrangement of shrubs, weeds, soil, crust and stones, and therefore the diversity of each of these components may play a major role in resource and habitat partitioning, and consequently higher species diversity.

The Carabidae showed low responses in their species diversity patterns to local patch variables (Fig. 6a and b). Plant cover, spatial heterogeneity and area in small patches were significantly, but weakly, correlated to carabid species diversity. A possible explanation for this response may lie in the carabids' habitat grain size and patch use. Ground beetles in agro-ecosystems have shown to

use uncultivated areas, such as hedgerows (Burel 1989; Fournier and Loreau 2001; Thomas et al. 2001) or wood and scrub fragments (Ellsbery et al. 1998; Petit and Usher 1998; Fournier and Loreau 2001; Bilde and Topping 2004), for hibernation and larvae development. As generalist predators, carabids seek food over large ranges, including cultivated fields (Ellsbery et al. 1998). Their high mobility (Tischendorf and Fahrig 2000; Raworth and Choi 2001) enables these beetles to move up to a few hundred meters a day if necessary (Bilde and Topping 2004). Consequently, ground beetles in the Southern Judean Lowland might use natural patches for temporary shelter and not as a limited food resource. From late spring to early summer the contrast between natural patches and cultivated fields is decreased due to the high pre-harvest vegetation cover. This phenomenon, together with the beetle movement pattern, increases carabid community similarity between fields and patches (Fig. 4), and blurs the difference between these habitats from their surrounding background.

Beetle responses to landscape-scale variables

The Tenebrionidae responded to landscape-scale variables, such as contrast and disturbance, only in the small patches. Smaller patches are characterized by a high area-to-perimeter ratio, which increases edge effect processes (see Ries et al. 2004) and therefore may decrease populations resistant to environmental disturbance (Pimm et al. 1988; Ries et al. 2004).

Landscape-scale variables had the strongest effect on species diversity patterns of the Carabidae in both patch size categories. Among those variables, edge effect affected beetle species diversity in all patch sizes (Fig. 6a and b). Edge effect is known to have an effect on diversity (Ries et al. 2004) through the mechanism of amplifying both biotic and physical disturbances due to a relatively high perimeter-surface.

Two variables—shape and disturbance (Fig. 6b)—significantly affected carabid species diversity only in small patches, while contrast between patches and surrounding fields had the strongest effect on the carabids in the large

patches (Fig. 6a). In general, the effect of landscape-scale variables on ground beetle diversity can be explained by their foraging behavior (based on movement pattern) and life history traits, which allow them to cross-large areas, and therefore be affected by differences in landscape-dependent variables. Indeed, in accordance with the ability of carabids to cross-large areas, the carabid assemblage did not show unique patch clustering according to species composition (Fig. 4). Moreover, similarity between agricultural fields was not very different from other patch combinations (even though they clustered together with 72% similarity).

The unified effect of patch-scale and landscape-scale variables and processes

Our results suggest that the diversity pattern within the Southern Judean Lowland ecosystem should be considered as a complex hierarchy of local and regional processes that change across scales. In this research, we examined three groups, each belonging to a different trophic level: primary producers (plants), detritivores (tenebrionid beetles), and predators (carabid beetles). Species diversity of all the tested groups was found to be affected to some degree by patch-scale and landscape-scale variables simultaneously.

Previous studies on the fragmented Mediterranean scrub, such as on foraging range (or movement: Crist and Wiens 1995; Hoffman and Wiens 2004) and on the role of vertebrate predation in a mosaic landscape (Parmenter and Macmahon 1988; Brose 2003), demonstrated that the structure of this environment has a strong influence on the movement of organisms. Ground-dwelling beetles are sensitive to micro-habitat and landscape structure (e.g. Wiens and Milne 1989; Wiens et al. 1997; McIntyre and Wiens 1999; McIntyre 2000). Johnson et al. (1992) found that darkling beetles changed the fractal dimension of their movement pattern when moving from one grass patch to another. Crist and Wiens (1995) found that darkling beetles spent less time moving when crossing patches of bare soil between patches than when

moving inside a patch. Carabid beetle movement has been found by many researchers to be a correlated random walk (e.g. den Boer 1970; Baars 1979; Firlle et al. 1998). Indeed, our observed diversity patterns are consistent with the known movement patterns of the two beetle families: tenebrionids remain in scrub patches; carabids forage across patches.

Another process known to affect beetle distribution and movement between patches is predation. Ground-dwelling beetles are an important part of the diet of small vertebrates such as rodents (Bar et al. 1984; Parmenter and Macmahon 1988), lizards (Perez-Mellado et al. 1991) and shrews (Mendelssohn and Yom-Tov 1988). Beetle distribution may be influenced by variations in predation pressure according to location. In a heterogeneous patch, a variety of shelters and predators exist. In wheat and barley fields, small vertebrates may have the advantage of being able to move while avoiding bird predation; in non-dense crops such as watermelon fields, birds may have the predation advantage (preying on beetles and small vertebrates). It is important to note that although our research area is semi-arid, the total amount of patch plant cover in spring-time starts at 82% for the least covered patch and reaches 99% in the most covered patch, except for one single small patch, where we measured only 52% plant cover. This pattern reduces the possibility of bird predation as a major factor in determining beetle distribution in arid zones as suggested by Ayal and Merkl (1994). However, this reduction in bird predation

does not include ploughed fields or non-dense crops such as watermelons or chick-peas.

In this study, we used field observations and multivariate analysis to link variables operating at different scales in order to explore species diversity patterns in a heterogeneous space. The use of path analysis enabled us to identify major pathways determining these species diversity patterns in the Southern Judean Lowland system. Clearly, many of the variables affect species diversity both directly and indirectly, uniting the effects of both patch-scale and landscape-scale variables. Further investigations and experiments are needed to explain the exact mechanisms responsible for the species diversity patterns found in the heterogeneous landscape of the Southern Judean Lowland region. Regardless, we believe that any possible plans for this area, such as the Jewish National Fund biodiversity management plan, should consider the interactive effects of local and landscape variables on species diversity at different spatial scales.

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Appendix

Table 3 Carabidae and Tenebrionidae found in Bet-Govrin research area

Carabidae species	Abundance	Tenerionidae species	Abundance
<i>Detomus semicylinreus</i>	2296	<i>Dailognatha crenata</i>	2476
<i>Carterus cribratus</i>	934	<i>Zophosis punctata</i>	1599
<i>Pterostichus barbarus</i>	697	<i>Cabirus simonies</i>	153
<i>Harpalus smyrnensis</i>	464	<i>Microtelus careniceps</i>	124
<i>Scarites nespericus</i>	401	<i>Gonocephalum setulosum</i>	98
<i>Bembidion luridicorn</i>	242	<i>Stenosis fulvipes</i>	66
<i>Detomus capito</i>	242	<i>Adesmia cancelata</i>	61
<i>Platyderus ruficollis</i>	184	<i>Eutotagnia syriaca</i>	58
<i>Carabus impressus</i>	161	<i>Tentyria herculeana</i>	48

Table 3 continued

Carabidae species	Abundance	Tenerionidae species	Abundance
<i>Detomus clypeatus</i>	130	<i>Blaps cribarosa</i>	33
<i>Brosicus laerigatus</i>	118	<i>Pachyscelis rotundata</i>	29
<i>Carabidae</i> sp.	88	<i>Scleron bodenheimeri</i>	18
<i>Stagona fuscipes</i>	77	<i>Sccleron orientale</i>	12
<i>Microlestes</i> sp.	71	<i>Omophlus syriacus</i>	9
<i>Harpalus caiphus</i>	69	<i>Cossyphus rugulosus</i>	8
<i>Sphodrus leucophthalmus</i>	29	<i>Catomus fulvipes</i>	8
<i>Daptus vittatus</i>	28	<i>Laena syriaca</i>	6
<i>Stagona europa</i>	18	<i>Brachyceris junix</i>	5
<i>Pterostichus nigrinus</i>	11	<i>Opatroides judaicus</i>	4
<i>Dixus eremite</i>	10	<i>Belopus syriacus</i>	2
<i>Notiophilus pussillus</i>	10	<i>Blaps indigator</i>	2
<i>Carterus rufipes</i>	6	<i>Tenebrionid</i> sp.	1
<i>Pseudoph Griseus</i>	3	<i>Pimelia bajula</i>	1
<i>Cymindoidea gracilis</i>	3	<i>Dendarus crassiusculus</i>	1
<i>Mettophonus israelita</i>	3		
<i>Ophonus franzinii</i>	1		
<i>Ophonus diffinis</i>	1		
<i>Stagona fuscipes</i>	1		
<i>Amblystomus metallescens</i>	1		
<i>Egadroma marginata</i>	1		
<i>Dasytiscus flaveolus</i>	1		
<i>Laemostenus cordicollis</i>	1		
<i>Calosoma maderae</i>	1		

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