Ben-Gurion University of the Negev Faculty of Natural Sciences Department of Life Sciences

The Effect of Landscape Patchiness and Heterogeneity on Beetle Species Diversity in the Southern Judea Lowland

Thesis submitted for the degree of Master of Sciences (M.Sc.)

By: Gal Yaacobi

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Summary

Ecological communities that inhabit heterogeneous landscapes are affected by local-scale as well as by landscape-scale processes. Understanding species-diversity patterns in heterogeneous landscapes requires comprehensive research on how these processes interact to determine community composition and structure. The semi-arid landscape of the Southern Judean Lowland (SJL), which currently undergoes intensive fragmentation, is highly heterogeneous, therefore requires the exploration of ecological processes at different spatial scales. It also requires a biodiversity management plan.

In this research I used two common ground-dwelling beetle families (Tenebrionidae, detrivors, and Carabidae, predators) to explore how different factors at both local and landscape scales determine community structure and diversity.

A beetle census was conducted by using uniformly-distributed pitfall traps, in 25 different-sized patches (500 m²- 40000 m²). I used Fisher's α and non-parametric extrapolators to estimate species diversity. Patch characteristics (vegetation species-diversity and cover, soil cover and stoniness degree) were measured in the field by random transects. In order to examine patch spatial arrangements, I used a spectral-based classification of high-resolution aerial photos. Thereafter, I created cellular maps in which every pixel represented a habitat type. An aggregation index (AI) was used to define patch spatial heterogeneity from the cellular maps. Spatial variables -- patch size, shape, physiognomy and connectivity -- were measured using GIS applications, with field GPS validations. In addition, I used GIS to define landscape characteristics at the landscape scale.

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A total number of 11125 beetles of 56 species were trapped. Both area-abundance relationships and species-area curves for the two beetle assemblages revealed no significant pattern. I found a significant difference between small patches and large patches. Both patch variables and landscape variables were found to affect beetle species diversity significantly. The results varied between the beetle families and among patch-size categories.

In order to evaluate the strength of interactions and to identify the major pathways determining species diversity patterns in the SJL system, I used path-analysis statistical models. My results showed that landscape variables had the strongest effect on species-diversity patterns of the Carabidae family in all patches. Tenebrionidae species responded differently to patch and landscape variables: in small patches both patch and landscape variables affected species diversity. However, in large patches, mainly patch variables affected species diversity.

Among patch variables, spatial heterogeneity and plant species diversity had the strongest effect on beetle species diversity. Among landscape variables, edge effect, contrast, and disturbance had the most significant effects on beetle species diversity. Most of the significant paths affected species diversity both directly and indirectly, uniting the effects of both patch variables and landscape variables.

Consequently, my main research conclusions are: 1) Biodiversity patterns in the heterogeneous, fragmented landscape of the Southern Judean Lowland show scaledependent response of beetle communities to patch and landscape-scale variables; 2) Species diversity patterns are designed by interactive effects of local patch and landscape variables; 3) Patch spatial heterogeneity has a major effect on species

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diversity at the local scale, while the contrast to the surrounding habitat and disturbance regime have the most significant influence at the landscape scale.

The potential complexity of the interaction between patch processes and landscape processes to affect species diversity pattern, suggests that we should take into consideration scale-dependence and processes synergism when we explore species diversity at large, heterogeneous landscapes.

Further investigation and experiments are needed to explain the exact mechanism creating the species diversity patterns found in the heterogeneous landscape of the Southern Judea lowland region.

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Introduction

One of the main issues in community ecology concerns species diversity and how it is determined (May 1986; Rosenzweig 1995). The number of species at a location is shown to be affected by several factors, on different scales. On a local scale (i.e. grain, single patch), processes such as demographic and environmental stochasticity, competition and predation operate. In addition, abiotic variables (e.g. percentage of rock and soil cover, precipitation) and biotic variables (e.g. percentage of vegetation cover, vegetation species diversity and composition) have direct and indirect influences on community structure.

Recently, it has been shown that environmental heterogeneity affects ecological processes at the landscape scale (Turner 1989; Holt 1992; Svensson 1999). On a regional scale, spatial processes such as migration, extinction, dispersal and the subsistence of a species pool operate (see Cornell and Karlson 1997). Patch variables at this level include productivity (e.g. Preston 1962; Rosenzweig and Abramsky 1993; Rosenzweig 1995), size (e.g. Arrhenius 1921; MacArthur and Wilson 1967), shape (e.g. Turner 1989; Farina 1998), isolation (e.g. MacArthur and Wilson 1967; Pulliam 1996; 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, habitat fragmentation, a human-induced spatial process, has received much attention from ecologists and conservation biologists (Haila et al. 1993; Fahrig and Merriam 1994; Murcia 1995; White at al. 1997). Reduction in total habitat area (i.e. habitat loss) is considered to be a major factor affecting population size (e.g., Fahrig and Paloheimo 1988; Andren 1994; McCoy and Mushinsky 1999). In addition, habitat fragmentation may lead to a breakdown of continuous populations

into isolated populations (Hanski and Gilpin 1991), or source-sink populations (Pulliam 1988).

In fact, community structure and species diversity patterns may be determined by the relative roles of local and regional processes (Ricklefs 1987; Cornell and Karlson 1997; Ziv, 1998; 2003). In order to plan management strategies for the conservation of such communities, we therefore need to identify which are the important factors to be controlled (Haila and Kouki 1994).

Drawing together the concepts mentioned above leads to the main research question of this study: How are community structure and species-diversity patterns affected by landscape patchiness and heterogeneity, and what importance do they have on the multi-scale system?

My research area is located in the Southern Judea Lowland region (hereafter known as the Bet-Govrin area). The area is characterized by natural-vegetation patches surrounded by agricultural fields, newly planted forests and other habitats subject to anthropogenic disturbance. Human have used this region since the late Bronze Age, approximately 5500 years ago (Ben-Yosef 1980). Consequently, this has produced a natural archipelago of vegetation that may have attracted a wide variety of organisms. The 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 landscape scale.

My research focuses on ground-dwelling beetles, mostly from the Tenebrionidae and Carabidae families, which inhabit the natural-habitat patches found at Bet-Govrin. These beetle assemblages were chosen for the following reasons: a) the large species diversity of beetles present in the study system may permit the study of ecological

processes at the community level; b) beetles play a major role in the functioning of the ecosystem; c) the life-history traits of beetles (e.g. size, life cycle, mobility) enable the use of a small heterogeneous area for examination of the impacts of spatial ecological processes on species diversity patterns.

Aim and hypotheses

My study has two main purposes: 1) To investigate the interaction between local scale (patch) and landscape scale variables that determine beetle species diversity patterns on both scales. 2) To study the role of human-induced habitat fragmentation and landscape heterogeneity in shaping the observed patterns in beetle community structure.

The random-sampling hypothesis (null model)

Passive sampling from the species pool may determine the number of beetle species. Larger areas provide larger samples than smaller ones and consequently, may contain a greater number of individuals (Connor and McCoy 1979; Andren 1994). Therefore, the number of species will rise in relation to the size of the sampled patches.

In accordance with the random-sampling hypothesis, I predict that the number of individuals will increase linearly with patch size (Andren 1994; 1999). As a result, any increase in number of species with patch size will be correlated to the increase in the number of individuals. At the same time, beetle diversity will not be significantly correlated with intra-patch variables (see below, "the intra-patch effect hypothesis") or with inter-patch variables (see below, "the landscape effect hypothesis").

The intra-patch effect hypothesis

A larger variety of habitats (i.e. greater heterogeneity) may increase the number of species, since different species may occupy different niches (Hutchinson 1959; Anderson 1978; Begon et al. 1996; Ziv, 2003). The presence of more habitats may also create more opportunities for species coexistence (Rosenzweig 1991; Rosenzweig 1995). Intra-patch biotic variables (e.g. percentage of vegetation cover, plant species diversity and composition) and abiotic variables (e.g. percentage of rock and soil cover, climatic variables) may promote habitat diversity and hence, affect community patterns. Patch size and/or patch quality may affect species diversity via effects on population size and the extinction probability mechanism (e.g. MacArthur and Wilson 1963; Pimm et al. 1988; Robinson and Quinn 1988). This hypothesis assumes that every population has some carrying capacity in each patch. Therefore, smaller populations may have a higher probability of going extinct due to both stochastic and deterministic mechanisms (Pimm et al. 1988).

In keeping with the intra-patch effect hypothesis, I predict that beetle species diversity will be significantly correlated to patch habitat diversity and structure. This includes the following variables: percentage of vegetation cover, plant species diversity, quantity of exposed soil, stoniness, and patch spatial heterogeneity. In addition, I predict that beetle diversity will not be significantly correlated with any landscape factor (see below, the "landscape effect hypothesis"). Significant correlation between intra-patch variables and beetle diversity is predicted to result either from using a local station within a patch (i.e., a grid of pitfall traps, see methods) or from using different patches as independent data points.

The landscape effect hypothesis

Recent advances in ecology have emphasized the importance of landscape-scale processes to explain population distribution and species diversity patterns (Hanski 1998; Ziv, 1998). Theoretical metapopulation models, with the reality of heterogeneous landscape structure (i.e. landscape physiognomy), have revealed a new ecological paradigm (Wiens 1997). Consequently, the relationship between patches in the landscape has an important meaning in determining the ecological processes that shape species diversity patterns. Spatial variables such as patch size (e.g. Arrhenius 1921; MacArthur and Wilson 1967), shape and contrast (e.g. Turner 1989; Farina 1998), and isolation and connectivity (e.g. MacArthur and Wilson 1967; Hanski and Gilpin 1997; Tischendorf and Fahrig 2000) may affect ecological processes such as dispersal and extinction, thus determining community structure and species diversity in a given patch.

According to the landscape effect hypothesis, I predict that the following landscape variables will influence patch species diversity: a) patch shape. Patches with a higher area to perimeter ratio will have more species than patches with smaller proportions due to the edge-effect mechanism. b) Patch isolation. The isolation and connectivity degree of a patch are predicted to affect the existence of species: a high proximity to other patches will increase patch species diversity. c) Patch contrast. The contrast between an examined patch and the adjacent land will affect species diversity. Irrigated neighboring land will increase patch isolation. Seasonally untreated field boundaries may change the patch edges and increase them. d) Species composition. I predict that the number and composition of patch species will reflect regional regime of disturbance and the level of influence exerted by landscape variables.

The multiple-scale effect hypothesis

It is expected that both habitat variables within a patch and landscape factors will act simultaneously to determine species diversity patterns and community structure (Davies et al. 2001; Ziv 2003). For example, resource diversity, which may be the result of within-patch plant diversity, can affect beetle abundance and species diversity. However, the identity of the species occupying that patch may be determined by the dispersal ability of particular beetles from an adjacent patch with a specific quality, size and shape. Similarly, many combined effects are possible. Hence, any joint combination (within-patch effect and landscape-scale effect) affecting species diversity to a statistically significant extent will be considered to support the multi-scale effect hypothesis.

In order to support the multi-scale effect hypothesis, the observed speciesdiversity patterns should be correlated with at least one patch variable and one landscape variable. Multivariate statistical models (Sokal and Rohlf 1981; Sall and Lehman 1996; Scheiner and Gurevitch 2001) are used to investigate the effect of interaction between variables.

This study strives to describe the unified effect of intra-patch and landscape factors on species diversity patterns at three trophic levels: plants, detritivorous beetles and predatory beetles. In the Methods section, I describe advanced GIS and remote-sensing techniques used to assess spatial heterogeneity and landscape characteristics, as well as the field sampling routine for estimating species diversity and measuring patch characteristics. Using statistical path analysis, in the Results and Discussion sections, I show the scale-dependent response of beetle communities to patch and landscape variables in a heterogeneous, fragmented region of the Southern Judea Lowland.

Methods

Study site

The research area is located in the Southern Judea Lowland region (Fig 1). Its boundaries include the Gat – Galon line (latitude $31^{\circ}40$) in the north and the Adoraim wadi (latitude $31^{\circ}25$) in the south. The eastern border of the area is the Beer Sheva – Kiryat Gat road, while the Hebron mountainside marks the western border.

The region is a semi-arid climatic zone, characterized by Mediterranean vegetation, with an average annual precipitation of 350 mm. Between May and October there is almost no rain, while solar radiation is very high (Israel Meteorological Service data, with permission). The dominant rock formation is a soft limestone (chalk) covered with Nari (a thin, strong, calcium-based layer), and the dominant soil is 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 assemblage is formed from *Ceratonia siliqua – Pistacia lentiscus – Rhamnus palaestinus*, with *Gramineae* and *Sarcopoterium spinosum* as leading plants in the southern area (Zohary 1982; Waizel 1984).

Thousands of years of human development and interference since the late Bronze Age (approximately 5500 years ago) have further added to the patchy configuration of the landscape. In the past, humans used the plain loessal valleys for agriculture (Ben-Yosef 1980), while the rocky patches remained uncultivated. Modern methods of cultivating now facilitate utilization of the rocky patches for agriculture, making the surviving natural habitat patches even smaller and more isolated.

I 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 m^2), 7 small (1000-5000 m²), 7 medium (5000-10,000 m²) and 1 large (40,000

 m^2). The selected patches represented the area's plant composition, soil type and rock formation, but varied in patch spatial attributes (e.g., shape) and location in the matrix (e.g., isolation degree, contrast with surrounding habitat).

Study species

Arthropods are often selected as study organisms for large-scale research (e.g. Simberloff 1974; Davies et al. 2001). The main advantage of using beetles is the high species diversity found within each family. This enables us to study an assemblage of species and to have a large sample size, hence increasing statistical confidence.

The beetle species occupying the research area are mainly from the Tenebrionidae and Carabidae families (Insecta: Coleoptera). Both families are ground-dwelling and contain a large number of species (ca. 400 in each family in Israel, ca. 25,000 in the world). 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; Ellsbury, Powell et al. 1998; Petit and Usher 1998). The larvae of both families hatch underground. The carabid larvae usually live above ground while tenbrionid larvae mostly live underground. Both families' larvae develop into pupae underground. The majority of species in both families are flightless. Some of the species are nocturnal (Parmenter and Macmahon 1988). There is a high variation in body size in both families, ranging from 2 mm to 40 mm in the research area (G. Yaacobi; V. Chikatunov, personal observation).

System characterizing techniques

My research combines advanced spatial-analysis technology with a field survey (Fig. 2). The selected patches were characterized according to spatial attributes (e.g., size, shape, location in matrix, distance from other patches and type of disturbed habitat surroundings); geological parameters (rock and soil); and biological parameters (i.e., vegetation attributes, such as percentage cover, diversity and composition). In order to estimate the influence of these variables, random line transects were used in which vegetation cover, plant species diversity, exposed soil and stoniness were measured in each patch.

In order to analyze the spatial attributes of patches, I used ArcInfoTM (ESRI) Geographical Information System (GIS) tools. Raster-based methods (e.g. Haines-Young et al 1993; ESRI 1997) enabled intersection and analysis of patch characteristics. In addition, I used the ERDAS IMAGINE[®] (Leica Geosystems) remote sensing application to assess patch heterogeneity. Such a technique can reveal the type of vegetation, amount of vegetation cover, soil cover and exposed rock according to spectral reflections.

Geographic Information Systems and spatial characteristics

I used an advanced GIS methodology to characterize patch spatial attributes and landscape physiognomy (Haines-Young et al 1993; Turner, Gardner et al. 2001). High resolution (1×1 m pixel) and standardized color aerial photos were used as the basic layer for all of the GIS procedures. All patches in the study system were digitized with field validation by differential GPS. I used ArcInfoTM (ESRI) as the main GIS platform for spatial analysis and presentation. The patch spatial variables examined in the research were: size, shape (corrected ratio of area to perimeter; see

appendix 1) (Farina 1998, Turner et al 2001), patch edge portion (see appendix 1) (Farina 1998), isolation degree (distance to other patches; the nearest neighbor method) (Krebs 1999) and location in matrix (juxtaposition to road, planted wood, different field types) (Turner et al 2001). The use of VLATE vector-based landscape analysis tools extension; (Lang and Tiede 2003) enabled calculation of the fractal dimension of patch border (appendix 1) (Farina 1998). I also used GIS coverages of soil and vegetation association (by permission of the JNF) to characterize landscape extent.

Assessing heterogeneity index

In order to evaluate patch heterogeneity I used ERDAS-Imagine[™], remote sensing and image analysis software, and developed a model that differentiates between four variables: stoniness, soil, perennial plants and annual plants.

I scanned a 35,000 feet, color aerial photo with a geodetic scanner (20 micron) to receive a sub-meter pixel size resolution. In order to minimize errors in pixel values, I classified the image before any geometric correction (Richards and Jia 1999). The classified image subsets were exported to FRAGSTATS[©] (landscape pattern metrics software; McGarigal and Marks 1995), and analyzed in turn to achieve heterogeneity assessments.

• Classification:

Three different classification methods were tested and evaluated: RGB advanced clustering, user supervised classification and isodata unsupervised classification. The supervised classification method was found to be more accurate and suitable for the patch heterogeneity assessing procedure (Yaacobi and Blumberg, in preparation).

Using supervised classification, four groups were identified (bush, weed, soil and stone) using 200 spectral signatures (11000 pixels) from all relevant research areas. These specific groups were chosen for several reasons: the ability to distinguish precisely between the large elements in the image; previous knowledge from the field; and the spectral distance between the groups. Due to pixel size, it was not possible to identify or distinguish soil crust from soil; likewise some families of weeds (e.g., Gramineae and Cruciferae) or specific bushes (*Pistacia lentiscus* and *Rhamnus palaestinus*).

• Pattern analysis:

Texture measures were used to analyze patterns of brightness variation within an image (Musick and Grover 1991). The spatial co-occurrence probability $P(i,j,d,\theta)$ is the probability that a pixel or cell of type *i* is separated by a pixel or cell of type *j* by distance *d* according to an angle direction θ , which may be 0° horizontal, 45° right diagonal, 90° vertical or 135° left diagonal. The comparison involves two reciprocal co-occurrences, which produce a symmetrical matrix. Figure 3 presents examples of co-occurrence analysis.

In this study, I exported 25 classified raster subsets to FRAGSTATS[©] software (McGarigal and Marks 1995). FRAGSTAT[©] uses a wide variety of matrices and algorithms to analyze different spatial aspects on 3 scales: patch, cluster and landscape. Here, I present only relevant models and manipulations that were used to assess spatial heterogeneity based on texture analysis.

The classified raster was examined using cluster and landscape scales (the patch scale deals only with the pixel unit). FRAGSTAT determines a cluster as an aggregate of similar pixels. Landscape was defined as a whole mosaic. In this work,

the relevant procedure for quantifying heterogeneity used the aggregation index algorithm (*AI*).

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):

$$AI_i = \frac{e_{i,i}}{\max e_{i,i}} \tag{1}$$

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 $e_{i,j}$, the total edges shared by class *i* itself. The shared edges are counted only once in *AI*, and currently only four neighbors are considered.

AI is related to the shape index ($SI = 0.25 P\sqrt{A}$) and the contagion index (see appendix) but, according to He et al. (2000), it calculates aggregation more precisely.

For the overall landscape, a landscape aggregation index (AI_L) can be calculated by summarizing AI_L that is weighed by the percentage of AIi:

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

where *n* is the total number of classes present in the landscape, and Ai% 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 measured for different maps or layers may be compared as long as it was measured using comparable spatial resolutions.

Measuring biotic and abiotic attributes of a patch

I measured plant species diversity, vegetation cover, exposed soil and degree of stoniness using line transects (10 m each). Up to 24 such transects were laid in each of the studied patches, proportional to patch size. Each transect was placed in a

random position, but never overlapping with other transects to avoid pseudoreplication. One cm was used as the minimal measuring unit.

Transect data was 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 to 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 all patches as part of a disturbance index.

Census of beetle species diversity

Pitfall traps were dug in each of the sampled patches in order to collect grounddwelling beetles. These 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. The specific positioning of the PVC sleeve ensured that trapped animals were collected efficiently without the need to pour away the fluid every time a census took place. A PVC ring (15 cm in diameter) was positioned around the entrance to each pitfall trap at ground level. This specific design prevented small rodents and reptiles that entered the trap from being caught (A. Tsairi and 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 about ground beetle home ranges (Gotelli 1995; McIntyre 1997; Raworth and Choi 2001) and an attempt was made to sample all micro-habitats in a patch with a fixed design. The number of traps per patch was derived from the patch size class

(i.e. 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). Beetles were collected during the highly active season (Rickard et al 1965; Parmenter and Macmahon 1988), at the same time for all traps. The use of ethylene glycol as a preserving medium in the traps enabled a long collecting period. The traps were open continuously from April to July and the contents were collected every two weeks. Classification and identification of the samples were done in the laboratory using an existing beetle collection for comparison.

Estimating species diversity

In order to estimate beetle species diversity, two independent methods were applied: 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 index relies on the log-series abundance fitting assumption, solving the classic problem of sample size sensitivity (Rosenzweig 1995; Rosenzweig, Turner et al. 2003), which other common indices such as rarefaction curves (Sanders 1968) or Simpson's index (Simpson 1949; Magurran 1988), do not. However, Fisher's index for species diversity does not enable transformation for estimating the number of species itself (Rosenzweig, Turner et al. 2003). To estimate species number in a location, I chose the 'BO' technique.

The 'BO' technique (Burnham and Overton 1978; Burnham and Overton 1979; Smith and Van Belle 1984), also known as the step-by-step jackknife estimator, is a non-parametric method to estimate the finite number of species in a quadrate sample

(Colwell and Coddington 1994; Krebs 1999; Brose and Martinez 2004). This estimate is distribution-free, and based on the observed frequency of rare species in the community. To calculate 'BO' through all five jackknifes orders, I used the Ws2m software package (Turner et al. 2000).

Statistical methods

The complexity of the Bet-Govrin system required a multivariate analysis method in order to distinguish between factors and identify processes. The use of multiple regression is requested in such analysis, but variable multi co-linearity and contradictory trends do not allow the use of such a method (Wootton 1994; Sall and Lehman 1996; Smith et al. 1997).

I used the path-analysis statistical model (Wright 1934; 1960a; 1960b) to evaluate the strength of interactions (Wootton 1994; Scheiner and Gurevitch 2001) and to identify the major pathways of variables affecting species diversity in the Bet-Govrin system.

By definition, path analysis places a set of correlations into assume 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 taking part, by the use of regression coefficients (Wright 1960a; 1960b; 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. The statistical analyses in this work were performed using JMP[®] software (SAS).

Similarity and cluster analysis

In order to compare species similarity between the patches and their surroundings, I used the Bray-Curtis similarity index (Bray and Curtis 1957; Clarke 1994; Krebs 1999). This index compares species composition by using species abundances; rare species are therefore not equal to dominant species, but 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 increase the influence of the rare ones (Clarke 1994). In addition, sample size was standardized. Without this, the Bray-Curtis coefficient reflects differences between unequal samples due to both community composition and total abundance in a sample (Clarke 1994).

Similarity analysis was followed by cluster analysis (Jongman et al. 1995; Krebs 1999) for all patches. The multivariate analysis of species composition was performed with PRIMER-E [®] software (Clarke 2001).

Results

The ground beetle and darkling beetle assemblages

A total number of 11,125 beetles of 56 species were trapped (Table1). The darkling beetle assemblage was represented by 24 species and 4809 individuals; the ground beetle 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 (Fig 4). A one-way ANOVA test (Sokal and Rohlf 1981) was used to examine whether there is any difference in species-area relations between patch categories. This statistical test differentiates only between the smallest patch group and the other three groups (Tenebrionidae: F = 9.7, n = 24, p < 0.001. Carabidae: F = 17.2, n = 25, p < 0.01). According to the statistical test, my results show that the patch system can be divided into two main size categories: 15 large patches ($5000 \text{ m}^2 - 40,000 \text{ m}^2$) and 10 small patches ($200 \text{ m}^2 - 5000 \text{ m}^2$).

The effect of patch-scale variables

I 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 categories (large and small patches). Table 2 summarizes all variables and correlations.

I found a significant relationship between tenebrionid species diversity and patch spatial heterogeneity (AI) in both patch categories. However, the patterns differed in the direction of their polynomial regression line (Fig 5a, b). Contradictory, the carabid species diversity was correlated to patch spatial heterogeneity (AI) in the small patch categories.

I found no significant correlation between plant cover (perennials and annuals) and beetle species diversity, except for the Carabidae in the small patch-size category $(R^2 = 0.71, p = 0.024)$.

Patch soil cover and degree of stoniness did not differ significantly when correlated with beetle species diversity in both patch-size categories. Such a result is unexpected in an agro-ecosystem because both families rely on undisturbed soil patches during their larval and pupal stages, and during hibernation (Burel and Baudry 1995; McIntyre 2000; Fournier and Loreau 2001; Bilde and Topping 2004). A suggested explanation for this occurrence relates beetle diversity to low exposure of soil cover and homogeneity of soil types (Petit and Usher 1998).

Plant species diversity was correlated significantly to tenebrionid diversity both in the small patches ($R^2 = 0.45$, p = 0.067) and in the large patches ($R^2 = 0.38$,

p = 0.013). I found a higher equitability of the plant community as well as smaller number of rare plant species in the large patches than in the small patches, even 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 variables

Patch shape significantly affected species diversity directly only in small patches. The Carabidae ($R^2 = 0.52$, p = 0.027; Fig 6) showed a linear decrease with a changing shape from circle to narrow ellipsoid.

No significant correlation between tenebrionid diversity and patch edge effect was found, while there was a decreasing correlation between patch edge effect and the carabid assemblage (Fig 8, see below: The effect of scale-invariant variables).

The location of patches in the matrix was expressed in the study by the use of patch-proximity measurements using the nearest-neighbor method, as well as by contrast to the surrounding fields (based on dissimilarity in species composition between different field habitats and patches). The results showed no effect of patch adjacencies to other natural habitats on species diversity of the two beetle assemblages. Similarity analysis of patches and the adjacent fields showed different species compositions for the two habitats, as expected, but not any gradient that correlated dissimilarity with species diversity except for the tenebrionid assemblage in small patches ($R^2 = 0.62$, p = 0.02).

Patch disturbance regime (an aggregate of five environmental variables: agricultural pressure, tourism influence, distance from road, presence of invasive plant species and dissimilarity in species composition) affected both beetle assemblages in the small patch group. Both carabid and tenebrionid species diversity responded positively to increasing disturbance ($R^2 = 0.56$, p = 0.01 and $R^2 = 0.63$, p = 0.01, respectively).

Scale-invariant relationships

My research results showed a scale-dependent response of beetle species diversity to most of the tested variables. In addition, some of the variables were found to affect beetle diversity at all scales, expressing the same trends without patch-size variation. A decreasing regression line expresses the relationship between carabid species diversity and patch edge effect at all scales (combined small and large patches), as presented in Fig 8. Similar patterns were found when plant species diversity was correlated with area, spatial heterogeneity, patch shape and degree of disturbance (see below "plant species diversity").

These observed results clarify the difference in response to patch and landscape scales between the three different trophic level organisms: plants, ground beetles and darkling beetles (see Discussion).

Beetles species similarity

Similarity analysis using a transformed Bray-Curtis index was followed by cluster analysis (Jongman et al. 1995; Krebs 1999) for all patches. Different patterns of species similarity were found between scales and taxa: the Tenebrionidae showed high similarity of species in the small patches (8 out of 10 patches were clustered together; Fig. 10). The rest of the patches were clustered in two large groups, sharing high similarity (up to 80%), except for one patch, which may be considered an outlier, having only 1 species. Testing similarity between different field crops (e.g., wheat, watermelon) showed a similarity of 87% in species composition and abundance. This supports my 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. 11). Moreover, similarity between fields was not much different from other patch combinations (even though they clustered together with 72% similarity). These results support the landscape-effect hypothesis for this group.

Plant species diversity responses to patch and landscape variables

In order to understand the role of the plant diversity in the system, I 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 3). My results point out the similarity in diversity patterns across scales. Plant diversity, in contrast to the beetle assemblages, presents the same pattern in the variable sized patches along the research landscape (Fig 9).

Path analysis

An important characteristic of the Bet-Govrin research system is the complexity of traits affecting species diversity patterns. The three observed groups in the research (plants, darkling beetles and ground beetles) showed different multiple relations to the same measured variables, and varied also between patch-size categories. Therefore, the multiple relations of each group (Fig 12a, b and Fig 13a, b) were examined and evaluated statistically with multivariate path analysis.

Using path analysis, I found that the major paths affecting tenebrionid assemblage diversity in the large patches were plant species diversity with an indirect patch area

effect (coefficient value- 0.79) and spatial heterogeneity, both directly and indirectly through plant species diversity. In addition, two indirect paths affected the tenebrionid assemblage in the large patches: First was the patch shape – heterogeneity path. Second was the edge effect –plant species diversity path. Both paths were found by the model to have smaller affect (-0.56 for shape and -0.53 for edge effect) (Fig 12b).

However, different results were obtained for Tenebrionidae from the analysis of the small patch category (Fig 12a). Contrast with surrounding habitat (coefficient value -0.85) and disturbance regime (coefficient value 0.71) were the main variables affecting the tenebrionid diversity. Patch spatial heterogeneity had a significant effect, but did not play a role in the model due to the non-linear correlation type (first order polynomial, see Fig 12). Among the affecting variables, plant species diversity received the lowest rank (coefficient value -0.65).

Different paths affected the carabid assemblage in the large patches (Fig 13b): the strongest path was contrast with the surrounding habitat (coefficient value of 0.66); second powerful path was patch edge effect (coefficient value of -0.56). The model evaluated the indirect area effect (through edge effect) as the weakest path.

Landscape variables mostly affected the carabid assemblage in the small patches (Fig 13a). The edge effect was found to be the most important variable (coefficient value of -0.86), followed by patch shape and disturbance regime (coefficient values of -0.72, 0.71, respectively). The model placed the area variable last (coefficient of 0.64), together with spatial heterogeneity and plant cover variables (first order polynomial correlations).

Discussion

My analysis addressed two fundamental goals: the first was to investigate the interaction between local-scale (patch) and landscape-scale variables determining beetle species diversity patterns at both scales. The second was to study the role of human-induced habitat fragmentation and landscape heterogeneity in shaping the observed patterns in beetle community structure. In this section I will discuses my research results according to the research questions and hypotheses.

Rejecting the null hypothesis

The null hypothesis (the random sampling hypothesis; Andren 1994) was rejected 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 and landscape variables (see above, "The intra-patch effect hypothesis" and "The landscape effect hypothesis"), indicating that biological processes dictate the observed species diversity patterns.

Beetle responses to patch variables

Unexpectedly, direct variables of patch scale, such as soil cover (Parmenter and Macmahon 1988; Petit and Usher 1998) and degree of stoniness (Krasnov et al. 1996), did not play a role in determining species diversity at the Southern Judea Lowland (SJL) system. Also, the percentage of plant cover in a patch was not correlated to species diversity patterns, except for the Carabidae in small patches.

Patch area affected tenebrionid species diversity indirectly through plant-species diversity and edge effect. The area-edge effect relationship is known to exist (e.g.

Forman and Godron 1981) through the mechanism of relative increase in surface area of smaller objects. Therefore the indirect effect of area on Tenebrionidae is not surprising. The indirect effect of area on tenebrionid diversity through plant-species diversity is not so obvious, especially since I found no correlation between the diversity of the detritivorous beetles and the degree of plant cover (annuals, perennials, or both). In contrast to other studies (e.g., Parmenter and Macmahon 1988; Rogers et al. 1988), my results showed that in Bet-Govrin area, the density of plants as a food resource does not limit the diversity of Tenebrionidae. Rogers et al. (1988) investigated the diet of darkling beetles and found food partitioning within the community, but with high overlap. This means that different species prefer different food items, but will use other food sources if necessary. In that case, what is the functionality of plant diversity in the system? The answer might be found in the heterogeneity of plant functional groups, as suggested by Symstad et al. (2000). Many other studies have linked the spatial structure of plants to arthropod diversity (Hunter and Price 1992; Siemann et al. 1998; Atauri and de Lucio 2001; Tews et al. 2004). The spatial structure of a patch is determined by the arrangement of shrubs, weeds, soil, crust and stones. The diversity of these elements (e.g. type of soil, variation in soil depth, plant species diversity) plays a major role in this arrangement. In addition, plant diversity determines a third dimension of patches: a vertical structure.

The Carabidae showed low responses in species diversity pattern to local patch variables. Plant cover, spatial heterogeneity and area in small patches were significantly correlated to carabid species diversity, but with a low strength (Fig. 13). A possible explanation for this response might lie in the carabid habitat grain size and patch usage. Ground beetles in an agro-ecosystem use uncultivated areas such as

hedgerows (Burel 1989; Fournier and Loreau 2001; Thomas et al. 2001) or wood and scrub fragments (Ellsbury et al. 1998; Petit and Usher 1998; Fournier and Loreau 2001; Bilde and Topping 2004) for hibernation and larvae development. As generalist predators, carabid beetles seek food in the entire matrix, including the cultivated field (Ellsbury 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 daily if needed. The pattern of movement is defined usually as a random walk (Bilde and Topping 2004), which supports the carabid foraging mode. Consequently, ground beetles in the Southern Judea Lowland might use natural patches for temporary shelter and not as a limited food resource. During late spring through 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, increase carabid community similarity (Fig. 11) between fields and patches, and blurs the difference between these habitats from their surrounding background.

Beetle responses to landscape variables

The Tenebrionidae responded to landscape variables, such as contrast and disturbance, only in the small patches. A possible explanation for this phenomenon may be hidden in patch area size. Smaller patches are characterized by a high area-to-perimeter ratio which increases edge effect processes (e.g. Andren 1994; Gotelli 1995; Begon et al. 1996; Shochat 1999) and decreases populations resistant to environmental disturbance (Pimm et al. 1988; Murcia 1995). In addition, small patches in the SJL area are characterized by low spatial heterogeneity (Yaacobi and Blumberg, in preparation). Low habitat variation decreases a population's tolerance

to environmental catastrophe and reduces species diversity (Rosenzweig 1995 and references therein).

Landscape variables had the strongest effect on species diversity patterns of the Carabidae family in both patch size categories. Among landscape variables, the edge effect affected beetle species diversity in all patch sizes (Fig .13). two variables -- shape (Fig .6) and disturbance (Fig .7) -- significantly affected carabid species diversity only in small patches, while in the large patches beetle diversity was found to be affected by the contrast between patches and surrounding fields (Fig 13).

The effect of landscape variables on ground beetle diversity supports the assumption regarding patch and matrix usage. Their foraging behavior (based on movement pattern) and life history traits may be the explanation for the strong landscape effect on these beetles.

The carabid assemblage did not show unique patch clustering according to species composition (Fig 11). Moreover, similarity between fields was not much different from other patch combinations (even though they clustered together with 72% similarity). These results may support the landscape effect hypothesis for this group.

The unified effect of patch and landscape variables and processes

The diversity pattern within the Southern Judea Lowland ecosystem is the result of a complex hierarchy of local and regional processes that change across scales and with time. In this research, three trophic levels were examined: 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 and landscape variables simultaneously. Although there has been little research on ground

invertebrates in fragmented Mediterranean scrub, some research dealing with grounddwelling beetles in grassland and agro-ecosystems may shed some light on important traits in this group, such as foraging (translated as movement, Crist and Wiens 1995; Hoffman and Wiens 2004) and the role of vertebrate predation in a mosaic landscape (Parmenter and Mcmahon1988; Brose 2003).

The structure of the environment was shown to have a strong influence on the movement of organisms. Ground-dwelling beetles are known to be sensitive to micro-habitat and landscape structure (e.g., Wiens and Milne 1989; McIntyre 1997; 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 followed by many researchers (e.g. den Boer 1970; Baars 1979; Firle et al. 1998) and defined as a correlated random walk. As mentioned above, the movement pattern of the two beetle families (Tenebrionidae remain in scrub patches; Carabidae forage throughout the matrix) are consistent with my observed species diversity patterns.

Another process determining beetle distribution 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, there is a variety of shelters and a variety of predators. 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 should be noted that, although the research area is defined as 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 I measured only 52% plant cover. This pattern reduces the possibility of bird predation as a major factor determining beetle distribution in arid zones as suggested by Ayal and Merkl (1994). Of course this reduction of bird predation does not include ploughed fields or nondense crops such as watermelons or chick-peas.

In this study, field observation and multivariate analysis link habitat scale variables and landscape scale variables to species diversity in a heterogeneous space. The use of path analysis enabled me to identify the major pathways determining species diversity patterns in the Southern Judea Lowland system. As I have shown, many of the variables affect species diversity both directly and indirectly, uniting the effects of both patch and landscape variables. Further investigation and experiments are needed to explain the exact mechanisms creating the species diversity patterns found in the heterogeneous landscape of the Southern Judea Lowland region.

The natural scrub archipelago of the Southern Judea Lowland agricultural area is a unique landscape in Israel. The results of this research are highly valuable for the conservation of this fragmented area, providing crucial information needed for producing a management plan for this region. Any possible plans for this area, such as the JNF biodiversity management plan, should consider the interactive effects of local and landscape variables on species diversity at different spatial scales.

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Carabidae Species	abundance	Tenerionidae Species	abundance		
Detomus semicylinreus	2296	Tentyria tessulata	2476		
Carterus cribratus	934	Zophosis puncata	1599		
Pterostichus barbarus	697	Cabirus simonies	153		
Harpalus smyrnensis	464	Microtelus careniceps	124		
Scarites nespericus	401	Gonocephalum setulosum	98		
Bembidion luridicorn	242	Stenosis fulvipes	66		
Detomus capito	242	Adesmia cancelata	61		
Platyderus ruficollis	184	Eutotagnia syriaca	58		
Carabus impressus	161	Tentyria herculeana	48		
Detomus clypeatus	130	Blaps cribarosa	33		
Broscus laerigatus	118	Pachyscelis rotundata	29		
Carabidae sp.	88	Scleron bodenheimeri	18		
Siagona fuscipes	77	Sceleron orientale	12		
Microlestes sp.	71	Omophlus syriacus	9		
Harpalus caiphus	69	Cossyphus rugulosus	8		
Sphodrus leucophtalmus	29	Catomus fulvipes	8		
Daptus vittatus	28	Laena syriaca	6		
Siagona europa	18	Brachyceris junix	5		
Pterostichus nigritus	11	Opatroides judaicus	4		
Dixus eremite	10	Belopus syriacus	2		
Notiophilus pussillus	10	Blaps indigator	2		
Carterus rufipes	6	Tenebrionid sp.	1		
Pseoduph Griseus	3	Pimelia bajula	1		
Cymindoidea gracilis	3	Dendarus crassiusculus	1		
Mettophonus israelita	3				
Ophonus franzinii	1				
Ophonus diffinis	1				
Siagona fuscipes	1				
Amblystomus metallescens	1				
Egadroma marginata	1				
Dasytiscus flaveolus	1				
Laemostenus cordicollis	1				
Calosoma maderae	1				

Table 1. Carabidae and Tenebrionidae beetles found in Bet-Govrin research area.

Table 2. The effect of patch and landscape variable on small (a) and large patches (b).

a. Small patches:

	Variable	Tenebrionidae diversity	Trend	Carabidae diversity	Trend			
le	Area	Not significant		$R^2 = 0.4, p = 0.046$	+			
scal	Heterogeneity	$R^2 = 0.66, p = 0.02$	Humped shape	$R^2 = 0.71, p = 0.02$	Humped shape			
atch	Plant cover	Not significant		$R^2 = 0.71, p = 0.024$ Humped shap				
Ч	Plant diversity	$R^2 = 0.45, p = 0.067$	_	Not significant				
	Shape	pe Not significant		$R^2 = 0.52, p = 0.027$	-			
ape	Isolation	Not significant		Not significant				
Landsc	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 scale:

	Variable	Tenebrionidae diversity	Trend	Carabidae diversity	Trend
le	Area	Not significant		Not significant	
sca	Heterogeneity	$R^2 = 0.32, p < 0.1$	Humped shape	Not significant	
atch	Plant cover	Not significant		Not significant	
d.	Plant diversity	$R^2 = 0.38, p = 0.01$	+	Not significant	
	Shape	Not significant		Not significant	
ape	Isolation	Not significant		Not significant	
Landsc	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	

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	-	$R^2 = 0.32, p < 0.01$

Table 3. The effect of patch and landscape variables on plant species diversity.

Fig 1. Bet-Govrin research area.





Fig 2. Research flow chart.

Fig 3. Co-occurrence analysis. (a) The co-occurrence have been measured

only along horizontal axis (θ =0°); (b) in all directions (θ =0°, 45°, 90°,

135°) at distance d=1







Figure 4a. Carabidae species number and diversity vs. patch area.

Figure 4b. Tenebrionidae species number and diversity vs. patch area.





large (a) and small (b) patches.



Power test with alpha = 0.05: >0.85



Fig 6. The effect of patch shape on *Carabidae* species diversity in small patches.

Fig 7. The effect of environmental Disturbance on Carabidae in small





Fig 8. The effect of edge effect on Carabidae species diversity in small (a) and



in all (b) patches





Fig 9. The effect of patch area on plant species diversity, in all patches.

Fig 10. Patch cluster analysis for Tenebrionidae species similarity.



Similarity (%)

Fig 11. Patch cluster analysis for Carabidae species similarity.



Similarity (%)



Fig. 12. Path analysis diagram for Tenebrionidae in small (a) and large patches (b).



Fig. 13. Path analysis diagram for Carabidae in small (a) and large patches (b).

Appendix

Edge portion (L/S):

The perimeter of each patch is divided by its area: where L= perimeter and S= area. This index varies according to the size of the patch even when the shape is constant (McGarigal and Marks 1995; Farina 1998).

Shape index (CPA):

$$CPA = \frac{(0.282 \times L)}{\sqrt{S}}$$

The corrected perimeter-are index varies between 0, a perfect circle, and infinity for an infinitely long and narrow shape (McGarigal and Marks 1995; Farina 1998).

Contagion index (CI):

$$CI=2H\ln H+\sum\sum Q_{ij}\ln Q_{ij}$$

This index derives from the information theoretical measures (Shanon and Weaver, 1962) and measures the degree of cells clumping. Where H is the number of cells, Q_{ij} is the probability of adjacency between cells of type *i* and cell *j*. High index value represents aggregation and contiguous in space (O'Neill et al., 1988, Li and Reynolds, 1993).

Fractal dimension (*FD*):

$$P \approx \sqrt{A^{D}}$$

The complexity of a polygon is expressed by relationship $\log P \approx \frac{1}{2} D \log A$, where *P* is the perimeter and A the area. For simple polygons such as circles and rectangles $P \approx \sqrt{A}$ and D = 1. For irregular and complex shapes of polygons the perimeter tends to fill the plane and $P \approx A$ with $D \rightarrow 2$ (McGarigal and Marks 1995; Farina 1998).

	Tenebrioni	dae family		Carabidae family						
Patch	S	Ν	Fisher's a	S (est.)	S	Ν	Fisher's a	S (est.)		
BGL1	13	820	2.194	14.98	22	619	4.452	26.07		
BGM1	9	287	1.766	10.12	17	463	3.468	20.08		
BGM2	10	407	1.853	10.2	15	149	4.160	20.55		
BGM6	12	440	2.278	15.01	18	233	4.551	21.03		
BGM7	10	414	1.846	11.03	15	135	4.318	23.32		
BGM12	13	414	2.551	17.26	17	618	3.233	20.28		
BGM80	14	255	3.185	17.09	17	445	3.504	18.14		
BGS1	8	106	2.007	10.25	16	340	3.485	18.03		
BGS2	10	81	3.001	13.4	20	687	3.855	25.92		
BGS3	5	37	1.558	6.58	13	85	4.279	18.31		
BGS4	4	45	1.061	5.15	9	80	2.603	12.17		
BGS6	6	313	1.053	6.07	14	141	3.863	16.98		
BGS7	9	223	1.881	12.48	18	674	3.400	19.98		
BGS15	8	156	1.785	8.94	14	252	3.196	17		
BGS16	10	157	2.378	12.1	12	219	2.729	18.04		
BGS17	7	52	2.178	13.16	16	148	4.557	21.03		
BGS60	7	177	1.456	23.67	17	185	4.561	21.07		
BGS70	10	191	2.244	11.27	12	133	3.199	27.31		
BGXS1	5	25	1.879	8.11	12	44	5.435	15.12		
BGXS2	1	1	1.240	1	7	16	4.745	9.52		
BGXS3	6	30	2.553	7.66	13	48	5.861	18.58		
BGXS5	8	17	5.898	12.26	10	333	1.942	13.8		
BGXS11	9	123	2.236	12.23	12	176	2.915	15.5		
BGXS12	4	28	1.277	5.92	12	63	4.396	15.95		
BGXS30	3	8	1.743	4.96	8	30	3.570	10.79		

Appendix 2. Species / abundance summery of ground beetles in Bet-Govrin patches, 2003.

S – Cumulative number of species in a patch; S (est.) – estimate number of species using 'BO'

extrapolator algorithm.

Patch	Area (m ²)	СРА	L/S	AI (%)	NNd (m)	Disturbance (%)	Contrast (%)	Plant SD	%Plant Cover	%Annuals	%Perennials	% stoniness	% Exposed Soil
BGL1	38166	1.4189	0.0257	66.886	18.430	38.800	45.80	2.248	87.607	29.148	58.458	7.108	5.283
BGM1	19665	1.9405	0.0490	65.000	17.540	56.800	36.00	1.801	92.928	59.390	33.537	1.876	5.195
BGM2	15671	1.2795	0.0362	79.727	38.820	48.000	36.40	0.883	99.681	66.143	33.537	1.700	2.094
BGM6	8205	1.1394	0.0446	74.566	9.160	52.000	48.70	1.408	88.128	56.759	31.368	5.977	5.894
BGM7	8185	1.4213	0.0557	79.883	80.520	67.300	33.40	0.775	91.961	69.224	22.737	2.628	5.409
BGM12	9660	1.3513	0.0487	75.188	59.720	52.000	32.90	0.883	94.750	85.062	9.687	0.637	4.612
BGM80	9046	1.4409	0.0537	77.594	57.720	65.000	31.35	1.262	88.275	78.587	9.687	9.656	2.068
BGS1	3673	1.2888	0.0754	76.904	51.042	59.000	29.55	0.570	90.962	65.587	25.375	1.500	7.537
BGS2	3277	1.1083	0.0686	73.083	18.186	52.000	37.10	0.825	99.343	77.218	22.125	0	0.656
BGS3	956	1.2403	0.1422	71.694	35.620	56.560	47.20	0.591	91.879	47.762	44.116	2.050	6.070
BGS4	792	1.5331	0.1931	66.002	28.110	55.560	42.20	0.859	95.983	61.816	34.166	1.183	2.833
BGS6	4902	1.1156	0.0565	79.537	113.380	65.000	29.50	0.318	98.312	94.687	3.625	0.187	1.500
BGS7	4270	1.6312	0.0885	64.518	123.870	64.340	28.30	0.710	82.234	32.059	50.175	0.609	17.156
BGS15	3403	1.2327	0.0749	68.900	75.850	44.000	30.20	0.893	86.662	71.175	15.487	8.500	4.837
BGS16	3713	1.5179	0.0883	69.153	9.800	54.474	27.63	0.886	91.781	64.156	27.625	3.562	4.656
BGS17	1216	1.1806	0.1200	77.710	5.440	59.000	31.25	0.203	92.384	86.471	5.912	2.600	5.015
BGS60	5513	1.5875	0.0758	67.296	123.870	60.932	25.34	1.406	87.631	72.468	15.162	1.212	11.156
BGS70	5071	1.1563	0.0575	70.033	124.670	54.000	41.70	1.113	90.093	50.031	40.062	8.812	1.093
BGXS1	489	1.1222	0.1799	78.140	52.792	54.000	38.30	0.240	99.500	75.500	24.000	0.500	0
BGXS2	204	1.1056	0.2745	75.630	18.187	44.000	83.00	0.150	95.000	5.000	90.000	0	5.000
BGXS3	296	1.3276	0.2736	74.989	59.600	64.000	35.70	0.242	92.000	59.000	33.000	8.000	0
BGXS5	498	1.0235	0.1626	81.498	60.292	54.000	46.97	0.243	98.611	65.277	33.333	0	1.388
BGXS11	870	1.7782	0.2137	79.076	25.735	58.986	31.89	0.768	94.537	24.112	70.425	1.306	4.156
BGXS12	540	1.3591	0.2074	75.175	41.230	64.000	35.07	1.073	92.606	44.806	47.800	2.362	5.031
BGXS30	296	1.3276	0.2736	58.432	55.930	54.000	42.70	0.263	51.650	31.650	20.000	26.500	21.85

Appendix 3. Summery table of Bet- Govrin patches characteristics; data was collected during the years 2002-2003.

Patch shape – CPA, Area / Perimeter – L/S, Heterogeneity – AI (%), Nearest neighbor – NND, Plant species-diversity – Fisher's a, Contrast – Field Dissimilarity.

השפעת כתמיות והטרוגניות נופית על מגוון מיני חיפושיות בשפלת יהודה הדרומית מאת: גל יעקובי

(M.Sc.) חיבור לשם קבלת תואר מגיסטר במדעים 2004 אוניברסיטת בן גוריון בנגב אוקטובר

תקציר

חברות ביולוגיות המאכלסות נופים הטרוגנים מושפעות הן מתהליכים אקולוגים הפועלים בסקאלה מקומית והן מתהליכים אקולוגים הפועלים בסקאלת הנוף. תבניות מגוון מינים באזורים הטרוגנים, מצריכות מחקר מקיף הבוחן כיצד תהליכים אלו פועלים יחד וקובעים את הרכב ומבנה החברה. נופה המקוטע והצחיח-למחצה של שפלת יהודה הדרומית מתאפיין בהטרוגניות גבוהה, ולפיכך מצריך חקר תהליכים אקולוגים בסקאלות מרחביות שונות. כמו גם תוכנית ממשק לשימור המגוון הביולוגי בו.

במחקר זה השתמשתי בשתי משפחות מצויות של חיפושיות שוכנות-קרקע (שחרוריות -Tenebrionidae – דטריבוריות, רצות-Carabidae – טורפות) בכדי לבחון כיצד גורמים שונים בסקאלה מקומית ובסקאלה נופית קובעים את מגוון המינים ומבנה החברה.

איסוף החיפושיות התבצע תוך שימוש במערך אחיד של מלכודות נפילה, ב-25 כתמים בגדלים שונים (500 m²-40000 m²) ובמדדים לא-פרמטרים נוספים כדי לאמוד את Fisher's α ובמדדים לא-פרמטרים נוספים כדי לאמוד את מגוון המינים. מאפייני הכתם (מגוון מיני הצומח, כיסוי הצומח, כיסוי הקרקע ומידת האבניות) נמדדו מגוון המינים. מאפייני הכתם (מגוון מיני הצומח, כיסוי הצומח, כיסוי הקרקע ומידת האבניות) נמדדו בשדה תוך שימוש בחתכי צומח אקראיים. בכדי לבחון את הארגון המרחבי של הכתם, השתמשתי במיון ספקטרלי לתצלומי אויר באיכות גבוהה, אשר הותמרו לאחר מכן למפות דיגיטליות בהן כל פיקסל מייצג ספקטרלי לתצלומי אויר באיכות גבוהה, אשר הותמרו לאחר מכן למפות דיגיטליות בהן כל פיקסל מייצג בית גידול מסוים. המשתנים המרחביים -- שטח הכתם, צורת הכתם, מיקום במרחב ובידוד -- נמדדו בית גידול מסוים. המשתנים המרחביים -- שטח הכתם, צורת אימות GPS בשטח. בנוסף, השתמשתי במערכת-מערכת-גידע גיאוגרפית בכדי לאמוד משתנים בסקאלת הנוף.

בשטח המחקר נלכדו 11125 חיפושיות מ 56 מינים שונים. לא מצאתי דגמים מובהקים סטטיסטית בין שטח למס' פרטים, ובין שטח ושפע מינים בשתי משפחות החיפושיות. לעומת זאת, מגווני המינים נמצאו מושפעים באופן מובהק הן ממשתני הכתם והן משתני הנוף. התוצאות שהתקבלו נבדלות בין משפחות החיפושיות ומשתנות בהתאם לקטגוריית גודל הכתם.

על מנת לאמוד את עוצמת האינטראקציה בין המשתנים ולאתר את הנתיבים העיקריים הקובעים את מגוון המינים בדרום שפלת יהודה, השתמשתי במודל סטטיסטי של ניתוח נתיבים (Path analysis). תוצאותיי מראות כי משתנים נופיים השפיעו בצורה החזקה ביותר על דגם מגוון המינים של משפחת הרצות, בכל גדלי הכתמים. לעומת זאת, נבדלו דגמי מגוון מיני השחרוריות בהתאם לגודל הכתם: בכתמים גדולים הושפע מגוון מיני השחרוריות בעיקר על-ידי משתנים כתמיים, ואילו בכתמים קטנים הושפע המגוון ממשתנים כתמיים ומשתנים נופיים במשולב.

בקרב המשתנים הכתמיים, הטרוגניות מרחבית היוותה את המשתנה המשפיע ביותר על מגוון מיני החיפושיות. אפקט השוליים, מידת ההפרעה הסביבתית ומידת הניגוד לשדות נמצאו כמשתנים הנופיים המשפיעים ביותר על מגוון החיפושיות. רוב הנתיבים השפיעו על מגוון המינים הן בצורה ישירה והן עקיפה במשולב, ולפיכך מאחדים את השפעת המשתנים הכתמיים והנופיים.

מן המחקר עולות שלוש מסקנות עיקריות: 1) תבניות המגוון הביולוגי בנוף ההטרוגני והמקוטע של שפלת יהודה הדרומית, מראות תגובה תלוית-סקאלה של חברות החיפושיות למשתנים כתמיים ונופיים; 2) תבניות מגווני המינים מעוצבות במשולב ע"י משתנים כתמיים ונופיים; 3) להטרוגניות מרחבית חשיבות רבה כגורם משפיע בסקאלת הכתם, ואילו למידת הניגוד של הכתם לסביבתו, כמו גם למשטר ההפרעות הסביבתיות יש את ההשפעה הרבה ביותר בסקאלת הנוף.

מורכבות תצריף התהליכים הכתמיים והתהליכים הנופיים, מציעה כי יש להתחשב בפעולה משולבת של תהליכים תלויי סקאלות כאשר אנו חוקרים תבניות מגווני מינים בנופים גדולים והטרוגניים.

ניסויים ומחקר נוסף דרושים על מנת להסביר את המנגנון המדויק הקובע את תבניות מגוון המינים בנוף ההטרוגני והכתמי של דרום שפלת יהודה.

b

השפעת כתמיות והטרוגניות נופית על מגוון מיני חיפושיות

בשפלת יהודה הדרומית

(M.Sc) חיבור לשם קבלת התואר מגיסטר במדעים

בפקולטה למדעי הטבע

מאת: גל יעקובי

מנחה: ד"ר ירון זיו

המחלקה למדעי החיים

אוניברסיטת בן-גוריון בנגב

תאריך	חתימת המחבר
תאריך	אישור המנחה
תאריך	אישור יו"ר ועדה מחלקתית

אוניברסיטת בן-גוריון בנגב הפקולטה למדעי הטבע המחלקה למדעי החיים

השפעת כתמיות והטרוגניות נופית על מגוון מיני חיפושיות

בשפלת יהודה הדרומית

הטבע (M.Sc) היבור לשם קבלת תואר מגיסטר במדעים (M.Sc)

מאת

גל יעקובי

תשרי תשסייה

אוקטובר 2004

באר שבע