

PATTERNS IN HABITAT TYPE, SPECIES RICHNESS AND COMMUNITY COMPOSITION AT AVDAT LTER, ISRAEL

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ABSTRACT

The EBONE (European Biodiversity Observation Network project) asked the Israel Nature and Parks Authority to test methodology correlating patterns of species distribution with habitat in arid regions. A test of this methodology was conducted at the Avdat LTER site in the Negev Desert. Four square kilometers were mapped using the EBONE system of structural habitat mapping. Samples of vegetation, reptile and arthropod communities were taken using stratified random sampling of the mapped habitat polygons. Habitat type correlated poorly with species richness, but correlated well with community composition across all the taxonomic groups. We also found that the correlation of species composition to habitat type coincided with a gradient of substrate texture, from fine silt, sand, gravel and stones to large boulders and bedrock outcrops.

Key words: habitat differentiation, species richness, community composition, desert

INTRODUCTION

Monitoring trends and identifying changes in species abundance and distribution are high priority tasks for conservation biologists everywhere (Rosenzweig 1995; UNEP 1992; Millennium Ecosystem Assessment 2005; Halada et al. 2009), yet few countries have the resources to adequately sample even major taxonomic groups directly on a nationwide basis (Danielsen et al. 2000). In recent years, the idea of monitoring species through their correlation with habitat variables or remote sensing data gained ground as an alternative to intensive *in-situ* sampling of species (Franklin 1993; Pereira and Cooper 2006; Scholes et al. 2008)

In 2008, a European Union-sponsored project named EBONE (European Biodiversity Observation Network) was initiated to develop a system of biodiversity observation at regional, national and European levels, based on correlations between species and community parameters, structural habitat properties and remote sensing information

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(Halada et al. 2009). Most of the work in EBONE was specifically focused on Europe. As participants in EBONE, our team in Israel was asked to test whether this approach would work in landscapes which do not occur in Europe.

During 2008 and 2009 we used EBONE methodology in the Avdat National Park and LTER site (Shachak et al. 2008), a well-documented area within the northern Negev Highlands steppe desert (Danin 1983), to map habitat types and test the correlation of species richness and community composition with habitat type based on substrate.

We asked the following questions at this site:

- Which correlates better with habitat categories, species richness or community composition?
- If correlations exist, are they consistent across taxonomic groups?
- At what scale does species richness correlate best with habitat classes?
- What are the gradients of community composition versus habitats at this site?

SITE DESCRIPTION

The Avdat Farm LTER site ("30°47'N, 34°45'E") consists of arid shrub steppe on rocky limestone slopes and loessal ephemeral streambeds. Ancient agricultural terraces (Nabatean and Byzantine, roughly 4th century BCE to 5th century CE) occur in most of the streambeds and still function to retain some rainwater, resulting in a rich ephemeral flora. Sparse perennial vegetation is dominated by dwarf shrubs (*Haloxylon scoparium* on loessal plains, and *Artemisia sieberi* and *Zygophyllum dumosum* on rocky slopes. Mean maximum summer temperature is 32°C; mean minimum winter temperature is 5°C.

The site was established for research in 1958 by the Hebrew University of Jerusalem, and is since 1978 part of the Blaustein Institutes for Desert Research of the Ben-Gurion University of the Negev. It is currently part of the Israeli Long-Term Ecological Research site network (Ma'arag) (Shachak et al. 2008). Livestock grazing has taken place in the area for thousands of years. Remains of ancient Nabatean runoff agriculture (ca. 0-300 CE) in the form of terraces are still evident. Currently Bedouin inhabitants practice sedentary pastoralism with goats, sheep and camels. Livestock grazing has been excluded from parts of the site.

The area has long been a research site for topics including ancient surface runoff agriculture, hydrology of runoff, dryland agroforestry, population and community ecology of herbaceous plants and arthropods, biodiversity and ecosystem management, ecosystem engineering and patch dynamics, food-web dynamics, watershed modeling, and soil fauna dynamics (Evenari et al. 1982).

METHODS

Habitat classification

Habitat in the EBONE system was generally defined by dominant growth form structure in the vegetation (Bunce et al. 2005, 2010), in polygons not less than 400 m² in total area. Terrestrial habitats with less than 30% vegetation cover were classified in the system as a single category – TER. However, in desert landscapes the perennial vegetation cover is generally less than 10%. Clearly the system devised for Europe needed modification for desert habitats.

As a result of our habitat mapping at Avdat, a change was made in the EBONE habitat categorisation system to define desert habitat categories by parameters other than vegetation. This change for sparse vegetation was later added to the field manual (Bunce et al. 2005, 2010).

We looked for ecological variables which we could use to classify sparsely vegetated areas into classes that can be recognized in the field, perhaps also by remote sensing methods, and that would correlate with species diversity. We decided to use the list of existing BioHab Qualifiers Substrate (Bunce et al. 2005) which defined the following substrate types:

- 5 = Bare rock Areas of continuous rock divided only by cracks, crevices or gullies
- 6 = Boulders Discrete elements of rock >20 cm
- 7 = Rocks Discrete elements of rock 5-20 cm
- 8 = Stones Discrete elements of rock 1-5 cm (specify if necessary in site qualifiers)
- 9 = Gravel/sand/silt/soil/peat (specify in site qualifiers)

For every mapped polygon the percentage coverage of every substrate category was recorded. These data were later used for additional classification of sparsely vegetated areas. The following proposed modifications were accepted and included in an improved version of the mapping manual (Bunce et al. 2010). The modified classification of substrate by particle size is as follows:

- ROC continuous bedrock divided by cracks, crevices or gullies
- **BOU** boulders over 0.20 m diameter
- STO rocks and stones 0.05-20 m diameter
- GRV gravel 0.01-0.05 m diameter
- SAN sand 0.001-0.01 m diameter
- EAR earth, mud, silt and bare soil below 0.001 m diameter

General Habitat Categories within sparsely vegetated habitats were defined according to the rules of BioHab/EBONE mapping procedure. If a single substrate type covered more than 70% of the area the GHC of the polygon was defined by this single substrate type code. For example, if a habitat is 20% ROC, 10% BOU and 70% EAR, it will be classified as EAR. If there was a mixture of substrates in which none covered at least 70%, the GHC of the polygon was defined by the combination of two most common substrates. For example, if a habitat was 20% ROC, 40% BOU and 40% EAR, it was classified as BOU/EAR. In the case of more than 2 substrate types having the same cover in a polygon, the habitat of the polygon was named according to the precedence following the list above. For example, if a habitat was 30% ROC, 30% BOU, 10% STO and 30% EAR, it was classified as ROC/BOU.

Habitat field mapping

Prior to the field work, we obtained and printed 1:5,500 orthophoto images of the squares to be mapped. Four 1-km² blocks were randomly selected from a 10 x 10 km² grid centered on the LTER area in Avdat (Figure 1).

For field mapping, each team was provided with a detailed orthophoto of the assigned square. Our teams sketched borders on the polygons visible in the orthophotos, following BioHab rules for a minimum area of 400 m^2 for a polygon. We mapped both aerial and linear/point features in this exercise.

Fig. 1: Orthophoto of the Avdat area with the EBONE sampling grid superimposed. Habitat polygons selected from the 1 x 1 sq. km. squares 42, 63 and 68 were used for collecting the species data in this study.

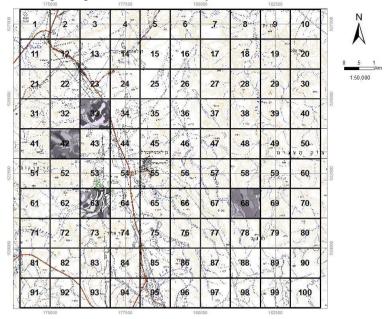
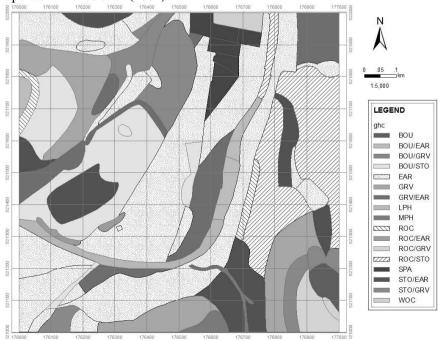


Fig. 2: An example of habitat mapping from orthophoto (1 x 1 sq km). Square 63 from the Avdat grid was mapped using BioHab/EBONE modified method reported in Bunce et al. (2002).



A team of six people field-mapped four squares in the Avdat area during February 2009. The BioHab survey methods (Bunce et al. 2005, 2010) were used. The hand-mapped squares were digitized on GIS using Arc View (Figure 2)

A total of 234 polygons and 96 line features were mapped to 30 general habitat categories, 15 of which were newly based on substrate properties and specially developed to allow ecologically sound mapping of large sparsely vegetated areas.

Species sampling design

Ten of the more common general habitat categories (GHC's) were sampled in Avdat. Only three of the five mapped square kilometer plots were used. Two were remote and difficult to access, so were discarded. For species sampling, polygons were randomly selected, stratified for habitat type, from the remaining three square kilometer plots.

We used species richness and community composition as relatively simple and easy parameters of species abundance and distribution. Direct and indirect ordinations were used to correlate species communities with habitat types.

Vascular plants

Vascular plants were sampled in three of the mapped square kilometers. We wanted to get a balanced representation of the available habitat types; thus 5 polygons were randomly selected for each of the GHC's.

The vegetation sampling was done by using Whittaker plots (Shmida 1984; Barnett and Stohlgren 2003), which are replicated nested sample plots with multiples of 10 at 1 m^2 , 2 at 10 m^2 , 1 at 100 m^2 and 1 at 1,000 m^2 , thus giving an estimated nested species/area curve. The Whittaker plots were located in approximately the centre of the polygon. If the size of the polygon allowed, a 50 x 20 m plot was made. In some cases the layout had to be modified, making a plot of 100 x 10 m in order to get to the 1000 m^2 sample fitted into the habitat polygon. Because of time constraints, species occurrences were recorded, but not cover or abundance data.

Arthropods

The arthropod populations were sampled by use of pitfall traps on transects in randomly selected mapped habitat polygons. A total of 15 polygons were sampled, three for each of the five habitat categories. In each polygon were 10 pitfall traps on a transect of 45 m, leaving 5 meters between each pitfall trap. The transect direction was random, unless the polygon was located at a slope, in which case the transect was directed along the contour line (a level plane).

The traps themselves were small plastic cups (tapered, 6.5 cm top, 4 cm bottom, 9 cm high) put in the ground with the opening at ground level. Each trap contained two nested cups, so that with each visit only the top cup had to be taken out, emptied and replaced. The top was covered with a rock, so that the cup would be shaded but still accessible for arthropods.

Contents were examined, identified by species and released on the spot. If the species could not be determined in the field it was taken to the lab. Ants, spiders and caterpillars were not identified to species. Beetles were identified if possible. Scorpions were identified to species.

The sampling was done in two weeks (4-7 and 12-15 April) over four consecutive days. On the first day, clean traps were set. On the second day, the pitfall traps were checked in the morning following the same sequence. The pitfall traps in square 42 were utilised first, followed by the pitfall traps in square 63 during the second week of sampling.

Reptiles

Reptiles were sampled in some of the same polygons as arthropods, but also in terraces (which were particularly rich in reptiles). Reptiles were sampled on two days (31 March and 15 April) in 9 polygons in two of the squares closest to Avdat Park (squares 42 and 63). There were four habitat categories with 2 replications randomly selected from the map (Table 1). Sampling was done by observing the ground while walking a transect of 100 m length in each selected polygon, followed by checking under 100 rocks in each selected polygon.

Table 1: The ten General Habitat Categories (GHC's) used for species sampling

design in Avdat. The categories are discussed in Bunce et al. (2010).

GHC Code	Vegetation Vegetation	Reptile	Arthropod
	samples	Samples	Samples
ROC	5		
ROC/BOU	5		
ROC/STO	5		
BOU	5	2	3
BOU/STO	5		
STO	5	2	3
STO/GRV	5	3	3
STO/EAR	5		
GRV/EAR &	5		3
GRV			
EAR	5	2	3
TRC			
	ROC ROC/BOU ROC/STO BOU BOU/STO STO STO/GRV STO/EAR GRV/EAR & GRV EAR	samples ROC 5 ROC/BOU 5 ROC/STO 5 BOU 5 BOU/STO 5 STO 5 STO/GRV 5 STO/EAR 5 GRV/EAR & 5 5 GRV 5	samples Samples ROC 5 ROC/BOU 5 ROC/STO 5 BOU 5 2 BOU/STO 5 STO 5 2 STO/GRV 5 3 STO/EAR 5 3 GRV/EAR & 5 5 3 GRV 5 2

Data analysis

Species richness patterns were analyzed with SPSS Statistics 17.0 (IBM 2010), using the non-parametric Kruskal-Wallis Test (Sokal and Rohlf 1995). Differences in species number between habitat classes across sampling scales (1, 10, 100 and 1000 m²) were analysed by ANOVA for each scale, while the species-area curves were analysed using linear regression of species number against scale. Differences between the slopes were analysed using t-tests for slope differences (Zar 1999).

Direct ordination was done with the RDA and CCA options in Canoco (Jongman et al. 1987; Ter Braak and Šmilauer 2002) using General Habitat Categories (GHC's) as dummy environmental variables. This provided the percentage variance explained by different habitat types at different sampling scales, and tested for the significance of correlations between species gradients and habitat factors, using forward selection with Monte Carlo

testing of correlation significance (Jongman et al. 1995). In the analysis we opted for the down weighting of rare species option in RDA, in which the abundance of species is downweighted in proportion to their frequency (see Ter Braak and Šmilauer 2002, page 203). CVA (Canonical Variance Analysis, a form of MANOVA) was done using PAST (Hammer 2010) to maximize separation between groups of habitats by linear combinations of the species values (presence in 1 m² samples).

RESULTS

Habitat mapping

In four sample squares of 1 sq. km each, most of the mapped area was natural and very sparsely vegetated. Less than 2% of the total mapped area had vegetation cover exceeding 30%, as either natural vegetation (low and medium phanerophytes, chamaephytes) or planted vegetation (strips of trees). 3.5% of the total area was classified as agricultural land (an experimental farm) and about 9% as urban non-vegetated area (a Bedouin camp). The rest of the area was sparsely vegetated with plant cover less then 10%.

Habitat classification

Habitat types identified by new EBONE rules (Bunce et al. 2010) ranged from solid rock, through boulders, stones, gravel and earth, and included mixtures of these components as well. These habitat types were spatially related to topography and resulted from erosion and sedimentation processes. Wide wadis were mainly covered by fine grain substrate (loess) and were classified as EAR. This type of habitat covered more than 12% of total mapped area. Coarser substrate (stones and boulders) occurred mainly on slope (result of erosion) and in some parts of wadis, with faster water flow. 12% of the mapped area was classified as covered by stones alone (STO) and additional 13% as a combination of stones with gravel (STO/GRV) or with earth (STO/EAR). Only 2% of the mapped area was classified as covered by boulders (BOU) and additional 14% as combination of boulders with other substrate types (BOU/EAR, BOU/GRV, and BOU/STO). A small portion of the area (0.2%) was covered by solid rock (ROC) and an additional 11% by the combination of rock and boulders (ROC/BOU). This combination appears usually as small eroded cliffs on the slopes, whereas a solid rock covers parts of hilltops and narrow wadis.

SPECIES RICHNESS

Plants

Histograms of species richness at different scales in the different GHC's did not show interpretable trends. Neither did a non-parametric Kruskal-Wallis test show significant differences among habitats. However, species-area curves for the different GHC's were more interpretable (Figure 3). There is a monotonous log-linear increase in species richness for larger sampling scales, which is highly significant (all slopes P<0.01). Although the differences in species richness between the various habitat classes at all sampling scales were not significant, there is a tendency of slightly greater species richness for stony habitats than for those with boulders and rock outcrops, while gravel and earth were intermediate.

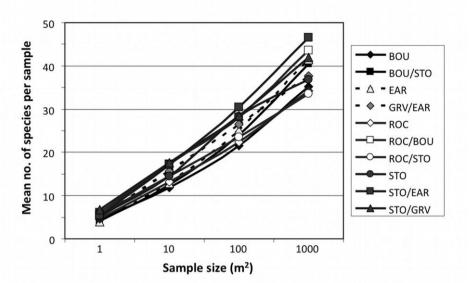


Fig. 3: Plant species-area curves for GHC's at Avdat.

The same trend emerges from comparing the log-linear regression coefficients for the habitat classes at increasing scale (Zar 1999). The slopes are steepest for STO/EAR, ROC/BOU and STO/GRV (between 14.33 and 15.55) and lowest for ROC, BOU and ROC/STO habitats (between 11.46 and 11.61). The difference is statistically significant (df= 42, t= 2.0106 > t[0.05,2-tailed,42]= 0.9604), but not for the slopes in between. This implies that species accumulation is greatest in mixed medium-textured (mainly STO) and lowest in coarse substrates (BOU and ROC), with the fine-textured substrates (GRV, EAR) at intermediate values.

This trend may be related to the relatively low spatial heterogeneity of the coarse habitats, or with the tendency of zones with bedrock outcrops or boulders to cause runoff water accumulation in adjacent fine-textured patches during rainfall. It is a well-known pattern in the Negev Highlands that these water-enriched zones contain more species, many of them with more mesic requirements (Olsvig-Whittaker et al. 1983; Boeken et al. 1995; Gutterman 2002). Therefore, enlarging the sample scale will add fewer species than in intermediate and finer substrates with no additional runoff water. On the other hand, the intermediate substrates (BOU and STO) have less microsite heterogeneity than the finer-textured GRV and EAR.

1. Reptiles

The numbers of individual reptiles obtained in the sampling were inadequate for statistical analysis. Nevertheless, there was a trend of increasing species richness from rocky habitats to earth (Figure 4). This may be an artifact of visibility, as reptiles can be spotted more easily in exposed habitat (EAR).

2. Arthropods

In a Kruskal-Wallis test, the only two habitat categories which differ significantly from each other are boulder (BOU) and earth (EAR).

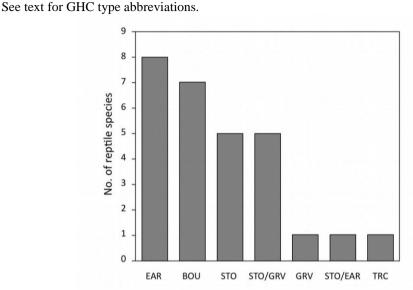


Fig. 4: Reptile species richness by GHC habitat.

Species composition

1. Plant communities

All direct ordinations, both RDA and CCA, showed a correlation of vegetation species composition with habitat. However, first axis correlations were somewhat lower at (a) smaller scale, (b) with no down weighting of rare species and (c) with annuals included. All of these parameter changes would increase the level of unaccounted variance in the data. RDA ordination of perennial plants was more explainable than that of annual plants, which is not surprising, given the unpredictability of annuals in desert conditions (Danin 1983). In this case the correlation of perennial plant species composition in tenth hectare samples was p = 0.0020 with a total of 25 % of variance explained, mostly by EAR (loessal earth) as the most important factor, followed by STO/GRV (stone and gravel, e.g. streambeds).

GHC type

In the Canonical Variates Analysis (Figure 5) both axes are significant (Wilk's λ = 0.1267; df = 4, 561 and 498; F = 2.223, P(same) < 0.00001; Pillai trace = 1.59; df = 4, 561, 509; F = 2.181; P(same) < 0.00001), with proportional eigenvalues of 0.402 and 0.236. The analysis differentiated between broad habitat classes (by primary descriptor) based on linear species combinations. ROC, BOU, GRV and EAR were similar, but significantly different from STO, except EAR. The species contributing mostly to the differentiation were Stipa capensis, Artemisia sieberi and Euphorbia falcata in STO habitats, Astagalus tribuloides, Reichardia tingitana in BOU, Schismus arabicus, Gymnarrhena micrantha and Bromus fasciculatus in ROC and GRV, and Hordeum glaucum and Anchusa milleri in EAR habitats. Interestingly, all differentiating species except Artemisia sieberi were annuals, some very common grasses. They appeared to respond mainly to the coarseness of the soil cover elements from large rock outcrops via large boulders, medium-sized stones, and finer-grained gravel to mainly earth cover. Using species data at the larger scales, CVA only differentiated between EAR and all other habitats. Both scales highlight high turnover of plant species in this desert landscape between exposed soils and those covered with stony elements.

Fig. 5: Canonical Variates Analysis (singletons removed) of all annual and perennial plant species against broad GHC types.

Species names shown represent species contributing most to the habitat differentiation. See text for abbreviations of GHC types and Table 3 for species names.

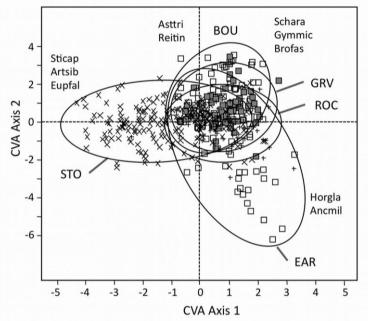
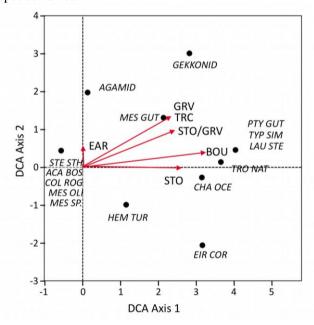


Fig. 6: Species biplot from DCA ordination of reptile species. The eigenvalue of the first axis = 0.731, and of the second axis = 0.105. See text for abbreviations of GHC types and and Table 3 for species names.



2. Reptile Communities

When the entire reptile community was considered in a DCA ordination, two distinct groups emerge, one centered on rocky substrates and one centered on earth (Figure 6), essentially similar to the habitat differentiation of plants (Figure 5). The numbers of reptile species in the two groups were about the same; EAR habitats were not more diverse in this analysis, although also for reptiles, the exposed habitats were quite distinct from rocky ones.

3. Arthropod communities

In RDA ordination the arthropods correlated significantly with earth habitat (p = 0.02), but no other habitat type had a significant correlation (Figure 7). For this group as well, the main differentiation is between largely exposed habitats and all others.

Fig. 7: Species biplot from RDA ordination of arthropod data against GHC types (as dummy variables).

Taxa were not always identified to species level; several are at genus level or higher. The eigenvalue of Axis 1 = 0.220, and of Axis 2 = 0.064. See text for abbreviations of GHC types and Table 3 for taxon names.

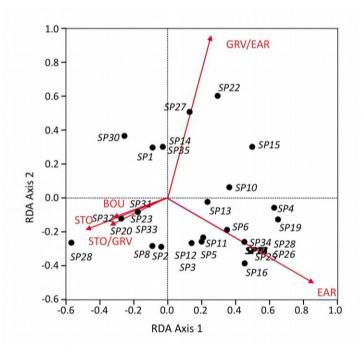


Table 3: List of taxon abbreviations used in this study. (Note arthropods were identified by taxon as possible, usually not to species level)

PLANTS	PLANTS	PLANTS	PLANTS
Species name	abbreviation	Species name	abbreviation
Achillea fragrantissima	Achfra	Onovis viscosa	Onovis
Adonis dentata	Adoden	Ornithogalum narbonense	Ornnar
Aizoon hispanicum	Aizhis	Ornithogalum neurostegium	Ornneu
Allium negevense	Allneg	Ornithogalum trigophyllum	Orntri
Allium rothii	Allrot	Pallenis spinosa	Palspi
Allysum simplex	Alysim	Peganum harmala	Peghar
Ammochloa palaestina	Ammpal	Phalaris minor	Phamin
Anabasis articulata	Anaart	Phagnalon rupestre	Pharup
Anagallis arvensis	Anaarv	Picris longirostris	Piclon
Anabasis setifera	Anaset	Plantago albicans	Plaalb
Anchusa milleri	Ancmil	Plantago coronopus	Placor
Anthemis pseudocotula	Antpse	Plantago notata	Planot
Arnebia decumbens	Arndec	Plantago ovata	Plaova
Artemisia siberii	Artsib	Plantago phaeostoma	Plapha
Asparagus horridus	Asphor	Poa bulbosa	Poabul
Aspodelus ramosus	Aspram	Pterocephalus brevis	Ptebre
Aspodelus tenuifolius	Aspten	Pteranthus dichotomus	Ptedic
Astragalus amalecitanus	Astama	Pulicaria incisa	Pulinc
Astragalus asterias	Astast	Ranunculus asiaticus	Ranasi
Astragalus hamosus	Astham	Reaumuria hirtella	Reahir
Asteriscus hierochunticus	Asthie	Reaumuria negevensis	Reaneg
Astragalus sanctus	Astsan	Reichardia tingitana	Reitin
Astragalus spinosus	Astspi	Reseda decursiva	Resdec
Astragalus tribuloides	Asttri	Reseda muricata	Resmur
Atriplex halimus	Atrhal	Reseda stenostachys	Resste
Atractylis phaelopis	Atrpha	Retama raetam	Retrae
Atriplex prostrata	Atrpro	Roemeria hybrida	Roehyb
Avena barbata	Avebar	Rostraria cristata	Roscri
Ballota undulata	Balund	Rumex cyprius	Rumcyp
Bellevalia desertorum	Beldes	Salvia dominica	Saldom
Bellevalia eigii	Beleig	Salvia lanigera	Sallan
Bromus fascuculatus	Brofas	Schismus arabicus	Schara
Bromus rubens	Brorub	Scorzonera judaica	Scojud
Buglossoides tenuiflorum	Bugten	Scorzonera papposa	Scopap
Calendula arvensis	Calarv	Scrophularia deserti	Scrdes
Carex pachystilis	Calcul	Senecio glaucus	Sengla

Cascuta species	Carpac2	Silene apetala	Silape
Centaurea aegyptiaca	Cenaeg	Sonchus oleraceus	Sonela
Centaurea pallescens	Cenpal	Spergularia diandra	Spedia
Chaetosciadium trichospermum	Chatri	Stachys aegyptiaca	Staaeg
Chiliadenus iphionoides	Chiiph	Stipa capensis	Sticap
Colchicum tunicatum	Coltun	Suaeda fruticosa	Suafru
Crepis aspera	Creasp	Thymus bovei	Thybov
Cuscuta species	Cussp.	Thymmelaea hirsuta	Thyhir
Cutandia dicotylon	Cutdic	Trigonella arabica	Triara
Cyonodon dactylis	Cyndac	Trifolium stellatum	Triste
Deverra tortuosus	Devtor	Tulipa systola	Tulsys
Dianthus strictus	Diastr	Umbillicus intermedius	Umbint
Diplotaxis harra	Diphar	Urginea maritima	Urgmar
Echinops polyceras	Echpol	Urginea undulata	Urgund
Emex spinosa	Emespi	Urospermum picroides	Uropic
Ephedra aphylla	Ephaph	Verbascum eremobium	Verere
Erodium arborescens	Eroarb	Zygophyllum dumosum	Zygdum
Erodium ciconium	Erocic		
Erodium crassifolium	Erocra	REPTILES	
Erodium glaucophyllum	Erogla	Species name	Abbreviation
Erodium gruinum	Erogru	Acanthodactylus boskianus	ACA BOS
Erodium laciniatum	Erolac	Agamidae	AGAMID
Erucaria microcarpa	Erumic	Chalcides ocellatus	CHA OCE
Eryngium creticum	Erycre	Coluber rogersi	COL ROG
Eryngium glomerata	Eryglo	Eirenis coronelloides	EIR COR
Euphorbia falcata	Eupfal	Gekkonidae	GEKKONID
Euphorbia ramanenis	Eupram	Hemidactylus turcicus	HEM TUR
Fagonia arabica	Fagara	Laudakia stellio brachydactyla	LAU STE
Ferula biverticillata	Ferbiv	Lytorhynchus diadema	LYT DIA
Ferula blanchei	Ferbla	Mesalina guttulata	MES GUT
Filago contracta	Filcon	Mesalina olivieri	MES OLI
Filago desertorum	Fildes	Mesalina sp.	MES SP.
Foeniculum vulgare	Foevul	Ptyodactylus guttatus	PTY GUT
Gagea reticulata	Gagret	Stenodactylus sthenodactylus	STE STH
Gastrocotyle hispida	Gashis	Tropiocolotes naterreri	TRO NAT
Geranium tuberosum	Gertub	Typhlops simoni	TYP SIM
Gymnocarpos decandra	Gymdec		
Gymnarrhena microcarpa	Gymmic	ARTHROPODS	
Gynandriris sisyrinchium	Gynsis	Taxon	code
Hammada scoparia	Hamsco	Buthus judiacus	SP1

Helianthemum salicifolium	Helsal	Lepidopteran larvae 1	SP2
Heliotropium sp.	Helsp.	Myriapoda	SP3
Helianthemum ventosum	Helven	Lepidopteran larvae 2	SP4
Helianthemum vesicarium	Helves	Gonocephalum perplexum	SP5
Herniaria hemistemon	Herhem	Coleoptera 1	SP6
Herniaria hirsuta	Herhir	,	SP7
		Hemilepistus reaumuri	_
Hippocrepis unisiliquosa	Hipuni	Coleoptera 2	SP8
Hordeum glaucum	Horgla	Coleoptera 3	SP9
Ifloga spicata	Iflspi	Lepidopteran larvae 3	SP10
Iris regis-uzziae	Irireg	Mesalina guttulata	SP11
Ixiolirion tataricum	Ixitat	Omophlus ocularis	SP12
Kickxia floribunda	Kicflo	Oxycara breviuscula	SP13
Koelpinia linearis	Koelin	Pimelia bottae	SP14
Lamarckia aurea	Lamaur	Pimelia grandis	SP15
Lappula spinocarpos	Lapspi	Sepidium tricuspidium	SP15
Lasiopogon muscoides	Lasmus	Coleoptera 4	SP17
Lathyrus species	Latsp.	unknown larvae	SP18
Launaea mucranata	Laumuc	Tentyria obiculata	SP19
Leontodon laciniatus	Leolac	Anacanthotermes ubachi Navas	SP20
Leopoldia longipes	Leolon	Buthus occitanus israelis	SP21
Linaria haelava	Linhae	Coccinellidae	SP22
Lomelosia porphyroneura	Lompor	Adelostoma grande	SP23
Malva aegyptia	Malaeg	Pimelia canescens	SP24
Malcolmia africana	Malafr	Mesalina guttulata (stripe)	SP25
Malva parviflora	Malpar	Mesalina guttala (stripe)	SP26
Marrubium alysson	Maraly	Lepidopteran larvae 4	SP27
Matricaria aurea	Mataur	Adesmia metallica	SP28
Matthiola livida	Matliv	Acanthadactylus	SP29
Medicago laciniata	Medlac	Glomerida	SP30
Medicago orbicularis	Medorb	Thysanura 1	SP31
Moricandia nitens	Mornit	Elateridae	SP32
Nasturiopsis coronopifolia	Nascor	Thysanura 2	SP33
Noaea mucranata	Noamuc	Chalcides ocellatus	SP34
Notobasis syriaca	Notsyr	Mesostoma punctata	SP35
		Coleoptera 5	SP36
		20.00ptora 0	J. 55

DISCUSSION

Adapting the EBONE mapping to desert

The first adaptation that had to be made to the classification of habitats in the desert was to move from reliance on vegetation structure to a reliance on substrate properties. When using traditional, vegetation-based classification system we were able to classify only 14% of the total mapped area. The remaining 86% fell in a single category of sparsely vegetated terrestrial (TER) in the mapping field manual of that time (Bunce et al. 2005).

Using substrate texture as a basis for habitat classification had several advantages. Different types of habitats could be recognised to some extent on high-resolution aerial photographs and this preliminary division was improved by field survey. The relative coverage of different substrate fractions could easily be estimated by amateur surveyors. The habitats defined by substrate proved to be well correlated with species composition in different systematic groups of organisms.

Since our study was performed in a relatively small and homogenous area (geology and rock types), we would suggest that these relations should be checked in additional regions, in different types of landscapes.

The correlation of GHC with species composition, as quantified in RDA ordination and CVA, was surprisingly good across taxonomic groups. In contrast, species richness and species area curves differentiated much less among habitats, and their variation did not correlate with any clear habitat gradient.

For all taxa, plants, arthropods and reptiles, substrate texture significantly explained the variation in composition. Important unmeasured drivers were probably related to substrate texture itself, such as shading, temperature and water availability, and possibly salinity (Olsvig-Whittaker et al. 1983; Shachak et al. 2008), as well as cover and protection against herbivory and predation.

Reptile and arthropod differentiation by substrate is already documented for this region. Species composition of Tenebrionid beetles in Maktesh Ramon differentiates between "sandy-gravel" and "clay" species (Krasnov and Shenbrot 1996). Ayal and Merkl (1994) also found different though overlapping sets of Tenebrionid species in the Central Negev, associated with soil compaction and exposure. The same trend was found for lizards, whose density and biomass were greatest but species richness was lowest in sand dune habitats compared to habitats with gravel and/or rock (Shenbrot and Krasnov 1997).

In general, these observations support our findings; that for all three taxa, habitat substrate is a main environmental factor which determines shelter, shade and food availability for detritivorous arthropods and reptiles (by accumulation of plant litter or cover for prey). For plants it also implies shelter and shade, as well as area available for establishment. The plant composition effects may also be related to the proportional area of soil available for establishment and growth, which decreases with coarseness of the ground cover by gravel, stones, boulders or bedrock outcrops.

When looking at species communities, we have found that changes in species composition are more consistent and explainable than species richness (number of species). There are differences between habitats in species richness along the species-area curves (Figure 3), but we still need to determine how consistent these patterns will be over time. Habitat differentiation of species composition has more predictive power, as it implies highest species richness in areas with high habitat diversity.

Table 2: Correlation of species with GHC's in direct ordinations at large and small scale sampling, with and without down-weighting of rare species.

RDA (1 versus 1000 m ²)				
dunam			1 m	
	1st axis	p = 0.0120	1st axis	p = 0.0380
	all axes	p = 0.0020	all axes	p = 0.0020
CCA (100	CCA (1000 m², with downweighting of rare species)			
no downw	eight		downweight	
	1st axis	p = 0.0300	1st axis	p = 0.0020
	all axes	p = 0.0020	all axes	p = 0.0020
CCA (1 m ² , with downweighting of rare species)				
no downw	no downweight downweight			
	1st axis	p = 0.0360	1st axis	p = 0.0180
	all axes	p = 0.0040	all axes	p = 0.0020
RDA (all species versus perennials per 1000 m²)				
all species	i.		perennials only	
	1st axis	0.012	1st axis	p = 0.002
	all axes	0.002	all axes	p = 0.002

1. Scale effects

Looking at the vegetation data (Table 2) sampled at different spatial scales, we see that when all species are included in RDA, CCA and CVA (Figure 5), the correlation between habitat and species composition seems better at small scales. This is partly a function of the unpredictable distribution of rare species, which mostly do not occur in the smaller samples. When rare species are downweighted in large area samples, correlation with habitat improves (Table 2). Similarly, when perennials are compared to annuals, the

correlation with habitat is better for perennials. Annuals possibly respond more favourably to unmeasured temporal factors, which have less importance for perennials.

2. Rare species

All of this suggests that rare species are less predictable in their distribution than more common species, which correlate better with habitat. Therefore, more common species can be studied collectively as a community, but rare species should be assessed individually. Rare plant species seem to be highly individual and unpredictable in their distribution, perhaps because there are many kinds of rarity (Rabinowitz 1981; Gaston 1994) and partly because important factors for rare species may be temporal or otherwise separate from habitat. Recent studies in a wide range of habitats in Greece (Mazaris et al. 2008) suggest that widespread, more common species contribute more to overall species richness, across all sampling scales and habitat types. If this is generally true, common species will be good predictors of species richness at the landscape level.

CONCLUSIONS

Originally EBONE had planned to mine existing species data for correlations with habitat. We tried this in the Mediterranean part of Israel without great success (Olsvig-Whittaker et al. 2010). The correlation of habitat and species was more significant and interpretable when the diversity samples were collected on the basis of the mapped habitats, as we did in Avdat. It seems that when the pre-existing species data do not match habitats in a statistically valid way, the noise will overwhelm pattern. This raises doubts about the usefulness of mining pre-existing species data.

Even if correlations exist between species richness and habitat, these are not always particularly interpretable or predictive. Community composition is often more useful, as particular habitat types or groups contain more or less predictable communities of common species.

From the conservation management perspective, the predictability of changes in community composition along environmental gradients is more useful information than patterns in species richness. Generally speaking we do not manage for species richness, but for habitats of known community composition which are likely to have many species. As a consequence of the habitat differentiation underlying the coenoclines, management that maximizes habitat diversity automatically maximizes species richness at the larger landscape scale.

Community composition, especially when restricted to the more common species, seems much more tractable. Common species usually correlate well with habitat, and are therefore predictable. This is not news for experienced field biologists. The news may be that community composition and species turnover can be regarded as useful measures of biodiversity (Huston 1994; European Environmental Agency 2007; Shachak et al. 2008).

Typically, biodiversity monitoring is restricted to a few taxonomic groups; plants, birds, butterflies, etc. However, if community composition of more common species would be used for monitoring, rather than species richness including the more rare species, then many more taxonomic groups may be readily sampled to show interpretable trends, as demonstrated by the reptiles and arthropods in this study. This may have useful implications for management purposes.

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