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Relationships between herbaceous diversity and biomass in two habitats in arid Mediterranean rangeland

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ABSTRACT

Plant diversity patterns vary across the landscape. This study was conducted to answer the question: What is the pattern of species diversity (α and β) along an abstract productivity/cover gradient at two topographical positions (Wadi (a depression with overland flow) and hilltop) of a Mediterranean herbaceous plant community in Jordan? Results indicated that the less productive hilltop localities exhibited higher species richness than the more productive Wadi localities. Species richness exhibited a unimodal relationship with aboveground biomass within Wadis whereas a positive linear relationship was revealed for hilltops. Within Wadis, abundant species did not show a significant relationship with productivity while common and rare species showed a unimodal relationship. Within hilltops, abundant, common, and rare species showed a linear relationship with biomass. β -diversity, measured as species dissimilarity, showed significant negative relationship to biomass within hilltops, whereas a positive relationship was observed within Wadis. Wilson-Shmida index (β_T) had a unimodal function with increased differences in productivity whereas Morisita-Horn index (C_{mh}) showed a reverse unimodal relationship. Examination of the species richness-biomass relationship among species groups (abundant, common, and rare) suggested that abundant species maybe more important on low productivity sites whereas common and rare species maybe more important on high productivity sites.

KEY WORDS: biodiversity, ecotone, Jordanian, productivity, species richness

1. Introduction

The potential impact of global biodiversity loss due to climate change had accelerated the efforts to investigate the relationship between diversity and ecosystem properties and processes such as productivity, nutrient cycling, and resilience to disturbance (Walker 1995; Chapin et al. 1998; Peterson et al. 1998; Lavorel 1999; Loreau et al. 2001). Many researchers have studied the effect of increased productivity on plant diversity and suggested numerous models to relate diversity to productivity across different spatial scales. At the largest scale (i.e. among biomes), diversity often increases with increasing productivity (Waide et al. 1999; Mittelbach et al. 2001; Chase and Leibold 2002). At local scales (within communities), the pattern is more variable; positive, negative, and unimodal relationships exist (Waide et al. 1999; Gross et al. 2000; Mittelbach et al. 2001), with the unimodal model being the most common relationship between herbaceous species diversity and biomass (Grace 1999).

The different patterns for diversity-productivity relationship at different spatial scales suggest that either no universal pattern exists in the diversity-productivity relationship, or that complex or variable mechanisms are shaping the diversity-productivity relationship. Factors contributing to such complexity include the nature of plant species (Fox 2003), environmental growth conditions (Hector et al. 1999; Fridley 2002) and spatial scale (Waide et al. 1999; Gross et al. 2000; Whittaker et al. 2001; Chase and Leibold 2002; Stevens and Willig 2002). Chase and Leibold (2002) found a significant unimodal relationship for productivity–diversity relationship at the local scale (alpha diversity (α) among communities) and a significant positive linear relationship at the landscape scale (beta diversity (β) among watersheds). However, Chalcraft et al., (2004) found that richness-productivity relationship resembled a weak unimodal shape at local scale, but a strong unimodal relationship emerged between species turnover (β) and productivity.

Plant competition theory was the basis for explaining the unimodal productivity-diversity relationship. Grime (1973) proposed that species diversity is reduced under high and low productive habitats as compared to intermediately productive environments. High species diversity at intermediate environments was attributed to the reduced competition for nutrients. Grime's theory on resource competition was modified by Newman (1973), who concluded that competition for light rather than nutrients is the prime player in controlling species diversity, suggesting that species diversity is reduced under high competition for light, while diversity tends to be higher under low light competition and/or low nutrients supply (e.g. poor sites). Newman's modification was further supported by the resource ratio theory (Tilman 1980; Tilman 1985; Tilman 1988). Tilman hypothesized that competing species can coexist only if they show differential response to different limiting resources, where these resources are found under various levels of abundance. Tilman and Pacala's (1993) habitat heterogeneity model suggested that at low

productivity sites, growth is limited by soil resources, while where site productivity is high, growth is limited by light. At intermediate productivity, different micro-sites have different soil resource/light ratios. Therefore, mixture of different competitor species that suite each micro-site can coexist. Grytnes (2000) reported similar unimodal relationships between species richness and plant biomass and cover, suggesting that light can be an important factor in determining species diversity at local scale, whereas positive linear relationship prevailed at larger scales (Grytnes and Briks 2003).

Arid and semi-arid Mediterranean plant communities are characterized by high regional and local species richness. These communities have been influenced by wild and domestic animals grazing since prehistoric times (Perevolotsky and Seligman 1998). This diversity is the result of small-scale spatial heterogeneity in resources coupled with grazing pressure (Osem et al. 2002; Alhamad 2006; Alrababah and Alhamad 2007). This study focuses on changes in plant species diversity (α and β) along abstract resource gradients in a Mediterranean herbaceous plant community. Further, the relationship between biomass production and canopy cover on one hand and species richness on the other hand were investigated. In particular, this study addresses the question: What is the pattern of species diversity (α and β) along an abstract productivity/cover gradient at two topographical positions (Wadi (a depression with overland flow) and hilltop) of a Mediterranean herbaceous plant community? It was hypothesized that differences in community diversity between the two positions will be driven by different species within each position.

Materials and methods

2.1. Study area

The study was located within the Khanasri Range Reserve (36°3'57"E and 32°24'3"N) at altitudes ranging from 650–850 m. The reserve was established in 1958 covering an area of approximately 400 ha in the northern steppe rangeland of Jordan. Before establishment it was an open access rangeland grazed by sheep and goats. The study area is located within the north Jordan Basalt Plateau soil-mapping unit that is characterized by having calcids-aridisols and inceptisols (<http://alic.arid.arizona.edu/jordansoils/index.html>). Annual precipitation is highly variable (96 to 406 mm, with a mean of 190 mm) for the past 22 years. Most of the rainfall is received during December-March. During the 2003/2004 and 2004/2005 rain seasons, the reserve received an annual precipitation of 132 and 140 mm, respectively, representing dry years. The study area is a typical arid and semi arid Mediterranean area characterized by high spatial heterogeneity in soil moisture regimes (Yair and Danin 1980) and in turn in primary productivity, thus affecting species diversity and distributional pattern of plant communities (Noy-Meir 1973; Osem et al. 2004; Alhamad 2006).

This area is ecotonal, with species from Mediterranean, Irano-Turanian and Saharo-Arabian phytogeographical regions. The 5000 years of domestic livestock grazing in the Mediterranean region (Noy-Meir and Seligman 1979; Perevolotsky and Seligman 1998) had shaped the vegetation of these ecosystems. Herbaceous (annual and perennial grasses and forbs) species represent 87% of the reserve's flora (Alhamad 2006) and appear shortly after the first rain event and persist for two to five months, depending on the amount and distribution of rainfall.

2.2 Experimental design and field measurements

The study utilized 30 sites which were distributed across the landscape. Each site was randomly selected and consisted of Wadi and an adjacent hilltop. Wadis exhibited deeper colluvium soil and thus higher water holding capacity. In other words, Wadi sites reflected a higher growth potential and productivity as well as different species composition. This study focused on herbaceous species diversity as the study area is largely composed of herbaceous species (87% of the species) and shrubs are nearly absent at Wadi sites. Two 1 m² quadrats (one within each topographic position) were placed within each site for a total of 60 plots. For each quadrat, species were identified, counted, clipped at soil level, and weighed separately by life form, after drying for 72 hrs at 70 °C. The total herbaceous plant cover percentage was estimated visually within each quadrat.

2.3. Data analysis

Phytogeographical analysis of encountered plant taxa and species identification was based on the work of Zohary and Feinbrun-Dothan (1966–1986). Raunkiaer life-forms were used to provide insight into species composition (Raunkiaer 1934; Whittaker 1975). Local species diversity (α) of herbaceous plants was evaluated using richness (total number of species per quadrat), Shannon-Wiener's index, and Simpson's index (Barbour *et al.* 1987). Diversity indices (Shannon-Wiener's and Simpson's) were utilized to account for species abundance and evenness and provide sample-size independent estimates, and thus more comparable results. Relative species density (calculated as the percent contribution of one species to the total plant density; Rd) was utilized to assess the rareness or commonness of the species in the plant community. Species were classified based on their relative density (Rd) as abundant ($Rd > 5\%$), common ($Rd = 1-5\%$), or rare ($Rd < 1\%$) (Osem *et al.* 2002). Dividing the species into abundance classes allowed for the examination of the contribution of each class to the diversity pattern along gradients.

To estimate species diversity among topographical positions, species dissimilarity (measured as one minus Jaccard's similarity index) was utilized as a surrogate for β -diversity. According to Chase and Leibold (2002), dissimilarity allows for evaluating compositional differences without having the confounding effect of estimating local (α) and regional (γ) diversity. In addition, the dissimilarity measure is conceptually similar and highly correlated to β -diversity. Dissimilarity values were plotted against average productivity of the paired plots under consideration.

To allow for comparability, two additional indices of β -diversity were used to quantify differences in species composition between paired habitats (hilltop vs. Wadi) for each of the 30 plot pairs. The Wilson-Shmida index (β_T) quantifies differences in terms of species presence/absence only (Wilson and Shmida 1984) and is calculated as:

$$\beta_T = \frac{g(H) + l(H)}{2\bar{\alpha}} \quad (1)$$

where, $g(H)$ is the gain and $l(H)$ is the loss of species along a gradient and $\bar{\alpha}$ is the average species richness of the paired habitat (Magurran 1988). According to Wilson and Shmida (1984), β_T is a measure of species turnover that assumes a gradient structure and that is independent of sample size. However, Vellend (2001) demonstrated that β_T is independent of species distributions as well as spatial and environmental gradients, and thus does not reflect species turnover but variability in species composition among localities. The Morisita-Horn index (C_{mh}) allowed for the inclusion of species abundance in estimating species diversity among topographical positions (Magurran 1988; Cramer and Willig 2005) and is calculated as:

$$C_{mh} = \frac{2 \sum_{i=1}^s (n_{ai} * n_{bi})}{(da + db) * N_a * N_b} \quad (2)$$

where s is the total number of species encountered in the paired habitats, n_{ai} and n_{bi} represent the abundance of the i th species in habitat a (hilltop) and habitat b (Wadi), respectively. N_a and N_b represent the total number of individuals of all species at hilltops and Wadis, respectively. The term da represents the total number of individuals of the i th species in habitat a divided by the square of N_a and db represents the total number of individuals of the i th species in habitat b divided by the square of N_b . When paired habitats share no species, β_T is equal to zero, whereas β_T equals one when paired habitats have exactly the same set of species. In contrast, C_{mh} equals one when each habitat include the same species in equal proportions. Both indices were plotted against difference in productivity of the respective pair of plots of Wadi and hilltop locations.

Regression analysis between species richness and diversity indices (α and β) on one hand and herbaceous biomass and canopy cover on the other hand was performed using the curve estimation procedure in SPSS version 11.0.1 (SPSS, Inc. 2001). One-way analysis of variance was utilized to test for significant differences between Wadis and hilltops in terms of herbaceous biomass production (g m^{-2}), overall plant density, density of abundant, common, and rare species, species richness, and Simpson's and Shannon-Weiner's values.

3. Results

3.1. Flora, productivity, and diversity

In total, 53 (46 herbaceous and 6 semi-shrub) species were observed in the study area, with 44 species at hilltops, and 29 species found at Wadis (Table 1). Species from all four phytogeographical regions (chorotypes) were observed in the study area. Species were identified based on Raunkiaer life-forms as phanerophytes, chamaephytes, hemicryptophytes, geophytes, and therophytes with 1, 6, 4, 8, and 34 species, respectively (Table 1).

Wadis had significantly ($P < 0.01$) greater herbaceous biomass ($188.9 \text{ g m}^{-2} \pm 17.4$) and common species richness (3.6 ± 0.4) than that for hilltops with $103.3 \text{ g m}^{-2} \pm 11.6$ and 2.3 ± 0.4 , respectively. Hilltops had significantly greater overall species richness (9.1 ± 1.1), abundant species richness (3.1 ± 0.3), rare species richness (3.8 ± 0.6), and Shannon-Wiener's index values (1.6 ± 0.1) than that for Wadis with 6.7 ± 0.5 , 1.6 ± 0.2 , 1.6 ± 0.2 , 1.4 ± 0.1 , respectively. Numbers in parenthesis represent means and standard errors. Simpson's index values and overall plant density were not significantly different between Wadis and hilltops.

Although Simpson's diversity index and overall plant density did not differ significantly between habitats, the two parameters reflected variability within habitats.

3.2. Alpha diversity and productivity

Regression analysis indicated, a significant ($R^2=0.47$, $P<0.001$) positive linear relationship between biomass and species richness for hilltop localities (Fig. 1a) whereas a significant ($R^2= 0.58$, $P<0.001$) unimodal model explained the relationship for Wadi localities (Fig. 1b). A significant ($R^2= 0.40$, $P<0.001$) unimodal model also explained the diversity-productivity relationship at the landscape level (Fig. 1c). Maximum species richness corresponded to a biomass production of 200-300 g m⁻².

A significant positive linear relationship was revealed between abundant, common, and rare species richness and biomass for hilltop localities (Fig. 2a), with the abundant species showing the strongest relationship ($R^2=0.86$, $P<0.001$). For Wadi localities, a non significant ($P=0.38$) linear relationship was revealed between abundant species richness and biomass whereas a significant unimodal relationship was revealed between common ($R^2 =0.48$, $P<0.001$) and rare ($R^2 =0.29$, $P<0.01$) species richness and biomass (Fig. 2b). Common species richness peaked at 200-300 g m⁻² production whereas rare species richness peaked at values of biomass production closer to 200 g m⁻² (Fig. 2b). At the landscape level, a unimodal pattern was observed for abundant, common, and rare species richness in relation to productivity (Fig.2c).

3.3. Alpha diversity and cover

The relationship between herbaceous cover and species richness varied between Wadi and hilltop localities. For hilltops, species richness had a significant ($R^2 = 0.58$, $P<0.001$) positive linear relationship with herbaceous cover (Fig. 3a) while a significant unimodal relationship was revealed for Wadi localities and at the landscape level (Fig. 3b and 3c). Maximum species richness values corresponded to intermediate values of herbaceous cover (75-85%) for Wadi localities and at the landscape level.

3.4. Beta diversity and productivity

Species dissimilarity among hilltop plots significantly decreased with increasing productivity ($R^2 = 0.60$, $P<0.001$) (Fig. 4a) whereas a weaker but positive linear relationship was observed among Wadi plots ($R^2 = 0.36$, $P<0.001$) (Fig. 4b). At the landscape level, a significant reverse unimodal relationship was observed ($R^2 = 0.32$, $P<0.001$). Thus, β -diversity is lowest at intermediate levels of productivity (Fig. 4c). The two indices of β -diversity showed contrasting responses to increasing site productivity (Fig. 5). β_T showed a significant unimodal response ($R^2 = 0.32$, $P<0.03$) to increasing differences among site productivities (Fig.5a). On the other hand, C_{mh} showed a significant reverse unimodal relationship ($R^2 = 0.41$, $P<0.01$) (Fig. 5b).

4. Discussion and Conclusions

The significantly greater herbaceous biomass at Wadi localities, as compared to hilltops, is a mere reflection of the greater growth potential and productivity of those sites. The greater growth potential may be attributed to the deeper colluvium soils and thus greater water holding capacity for those sites. However, grazing differential between hilltop and Wadi localities may have attributed to the observed differences. Although hilltop and Wadi localities were sampled across the landscape to fully account for the variation between and within those localities, the impact of long-term grazing could not be separated from the inherent productivity of those localities.

Greater α -diversity for the less productive hilltop localities, as compared to the more productive Wadi localities, may only assert the lack of a causal relationship between ecosystem function and species diversity (Grime 1997). Greater abundant and rare species richness but lower common species richness for hilltops may support the notion that functional characteristics of component species (functional types) are more important in ecosystem function than simply high species diversity.

Within hilltops, high species richness corresponded to high biomass and thus reflected a positive linear relationship (Fig. 1a) which is in agreement with that of Aronson and Shmida (1992). Within Wadi localities, species richness showed a different response to increasing productivity reflecting the more commonly reported unimodal pattern (Fig. 1b) and thus indicating that species richness peaked at intermediate levels of productivity (Garcia 1993). It is important to emphasize here, that what was considered intermediate levels of productivity at Wadi localities was equivalent to the greatest levels of productivity at hilltops. This suggests that the relationship between observed species richness and productivity is dependent upon the magnitude of change or width of the underlying gradient (Maranon and Garcia 1997; Guo and Berry 1998). The emerged unimodal relationship, when Wadi and hilltop localities were combined, (Fig. 1c) had been reported for some semiarid plant communities with comparable ranges of productivity in the Mediterranean region (Kutiel and Danin 1987; Puerto et al. 1990). The non significant relationship between abundant species richness and biomass within Wadi localities and the weak linear relationships for common and rare species of hilltop localities (Fig. 2) indicate that abundant species are important contributors to changes in species richness with productivity within hilltops, while common and rare species are most important in relating productivity with diversity within Wadi localities.

The observed pattern of α -diversity as a function of herbaceous cover (Fig. 3) was similar to that with biomass. This pattern is in agreement with Grytnes (2000) and Casado et al. (2004) findings and Newman's theory, which states that competition for light is a key factor in reduced species diversity at high productivity sites. Further, cover showed a stronger relationship with species richness as compared to biomass.

The contrasting pattern of β -diversity between hilltop and Wadi localities reflects again the importance of the magnitude of the underlying gradient (Fig. 4). Within hilltop localities, relatively short gradients resulted in a negative pattern (Fig. 4a) indicating that similar species composition among plot-pairs was associated with higher biomass values. On the other hand, similar species composition among plot-pairs was associated with lower biomass values within Wadi localities (Fig. 4b), which is in agreement with the notion that β -diversity increases with increasing productivity (Chase and Leibold 2002; Chalcraft et al. 2004; Chase and Ryberg 2004; Harrison et al. 2006). This contrasting pattern of diversity between localities also emphasizes the uniqueness of each locality in reflecting the relationship between diversity and biomass production and may hint to the importance of functional characteristics of component species. The reverse unimodal pattern that emerged when Wadi and hilltop localities were combined (Fig. 4c) indicates that species dissimilarity reached a minimum at intermediate levels of biomass. This stresses the scale issue previously discussed by Chase and Leibold (2002) and confirms the manifestation of unimodal relationships when different habitats are encompassed in the sample area (Gough et al. 1994; Guo and Berry 1998). It is important to emphasize, here, that the use of dissimilarity as a surrogate for β -diversity does not imply a measure of species turnover but rather a measure of unstructured heterogeneity in species composition among plots since that no physical or environmental distances were measured between plot-pairs (Vellend 2001).

β -diversity indices also showed unimodal relationships to differences in biomass production (Fig. 5). However, C_{mh} showed a reverse unimodal relationship similar to that observed using dissimilarity (Fig. 5b). The reverse model may be attributed to the inclusion of species abundance as a measure of evenness in calculating C_{mh} . It is apparent, however, that the unimodal relationship is an inherent attribute of the spatially heterogeneous habitats. Although β -diversity may increase with increasing biomass differences within a locality (Fig. 4b), when viewed across topographies, microhabitats, or localities β -diversity may exhibit unimodal response to increasing biomass differences.

Although many causative mechanisms were suggested to explain the unimodal diversity-biomass relationship (Grime 1973; Newman 1973; Tilman 1980), the common denominator seems to be competition. The use of soil seed bank micro communities as experimental systems (Palmer and Hussain 1997) seems promising to provide an insight into the underlying mechanisms of the unimodal diversity-biomass/cover relationship.

Contrasting patterns of α and β -diversity along abstract productivity and cover gradients were observed between Wadi and hilltop localities of this Mediterranean herbaceous plant community. Within hilltops, a linear pattern of α and β -diversity was revealed, while within Wadis, a unimodal pattern of α but a linear pattern of β -diversity was revealed. When combined, a unimodal pattern of α and β -diversity emerged. Variation in diversity pattern between localities emphasizes scale-dependence of both levels of

diversity and stresses the dependence of the pattern upon the magnitude of change or width of the underlying gradient. Examination of the species richness-biomass relationship among species groups (abundant, common, and rare) suggested that abundant species maybe more important contributors in the diversity-productivity relationship on low productivity sites whereas common and rare species maybe more important on high productivity sites.

The lack of research in this region of the world as to diversity and productivity is compounded by centuries of passive management through domesticated grazing. The results reported in this manuscript utilize both alpha and beta diversity measures, and found that while wadi and hilltop communities are uniquely diverse, the relationship for the entire region is driven by the more productive sites, producing a unimodel relationship.

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Figure legends

Fig. 1 The relationship between herbaceous biomass (g m^{-2}) and species richness (species m^2) under two localities: A) hilltop (low productivity); B) Wadi (high productivity); and C) Landscape (hilltop and Wadi sites combined)

Fig. 2 The relationship between herbaceous biomass (g m^{-2}) and number of abundant, common, and rare species within two localities: A) hilltop (low productivity); B) Wadi (high productivity); and C) landscape (hilltop and Wadi sites combined)

Fig. 3 The relationship between herbaceous cover (%) and species richness in: A) hilltop (low productivity); B) Wadi (high productivity); and C) Landscape (hilltop and Wadi sites combined)

Fig. 4 The dissimilarity (calculated as 1-Jaccard's index of similarity) in species composition among local plots within: (A) hilltop; (B) Wadi; and (C) Landscape localities

Fig. 5 The relationship between differences in productivity (g m^{-2}) between hilltop and Wadi localities and β -diversity; (A) Wilson-Shmida index (β_T), and (B) Morisita-Horn index (C_{mh})

Herbaceous diversity

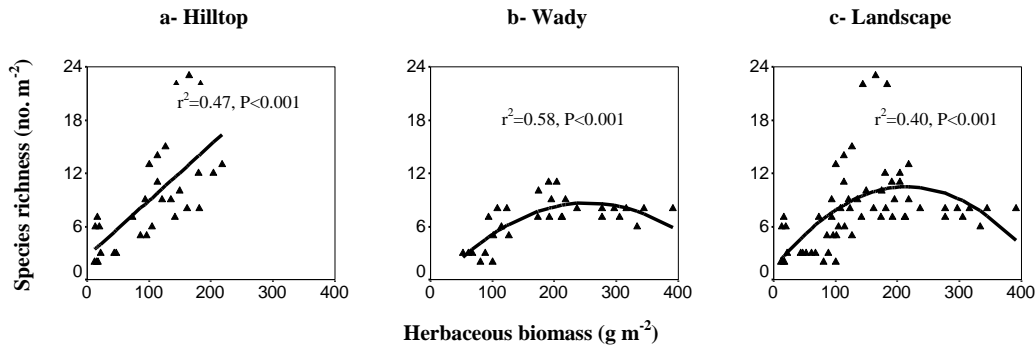


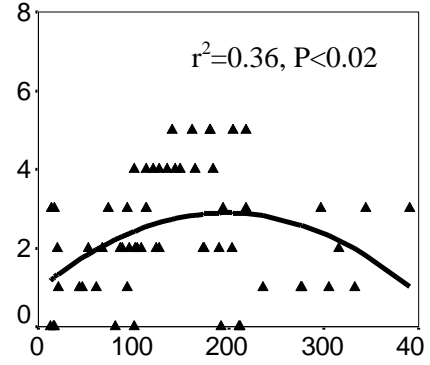
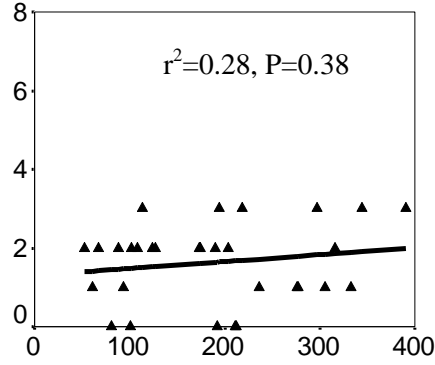
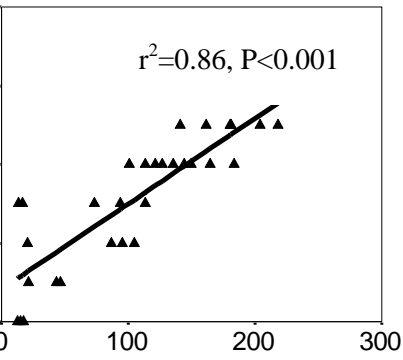
Fig. 1 The relationship between herbaceous biomass (g m⁻²) and species richness (species m⁻²), under two localities: A) hilltop (low productivity); B) Wadi (high productivity); and C) Landscape (hilltop and Wadi sites combined).

a-Hilltop

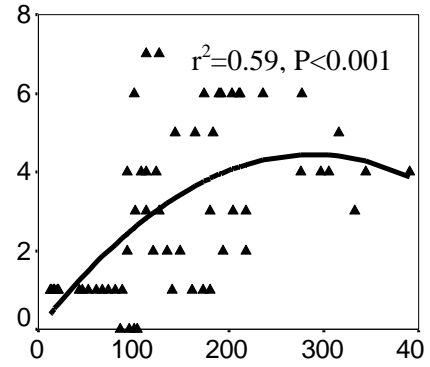
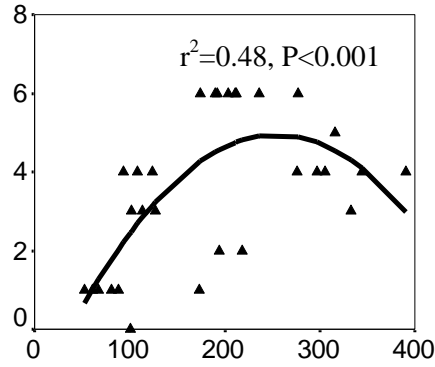
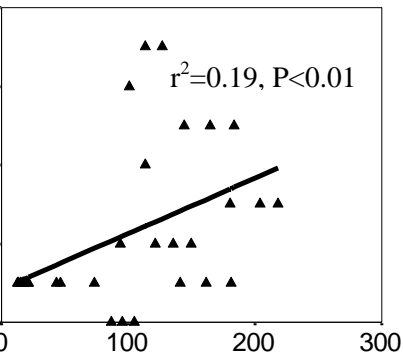
b-Wady

c- Landscape

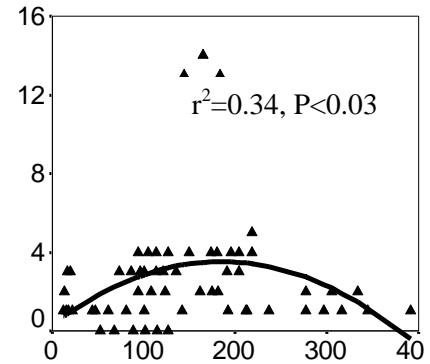
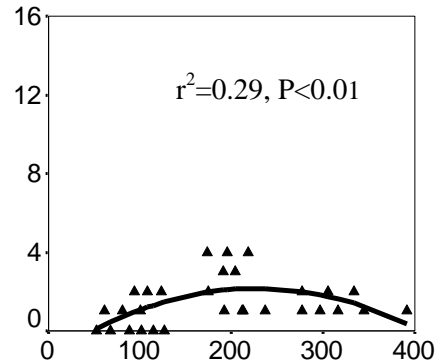
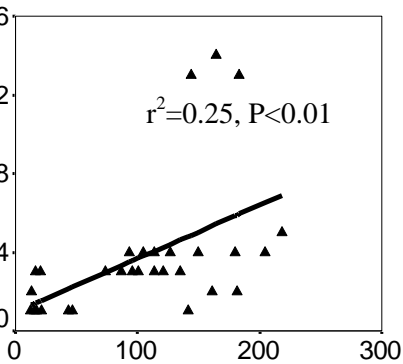
Abundant species



Common species



Rare species



Herbaceous biomass (g m^{-2})

Herbaceous diversity

Fig. 2 The relationship between herbaceous biomass (g m^{-2}) and number of abundant, common, and rare species within two localities: A) hilltop (low productivity); B) Wadi (high productivity); and C) landscape (hilltop and Wadi sites combined).

Herbaceous diversity

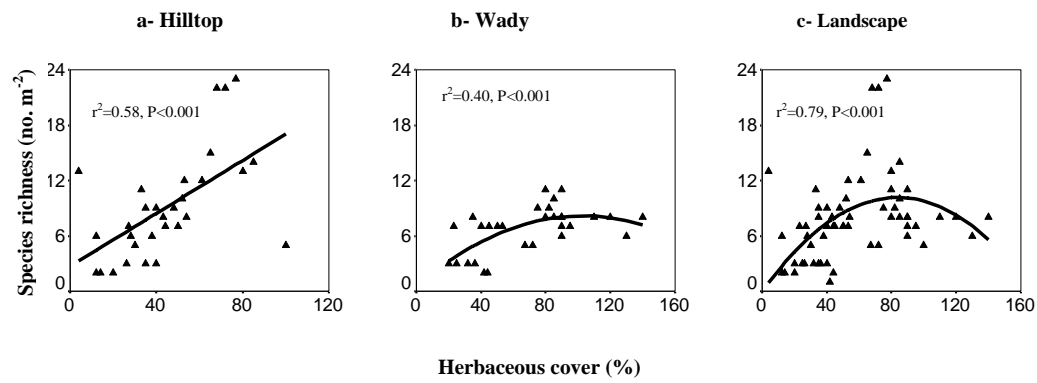


Fig. 3 The relationship between herbaceous cover (%) and species richness in: A) hilltop (low productivity); B) Wadi (high productivity); and C) Landscape (hilltop and Wadi sites combined)

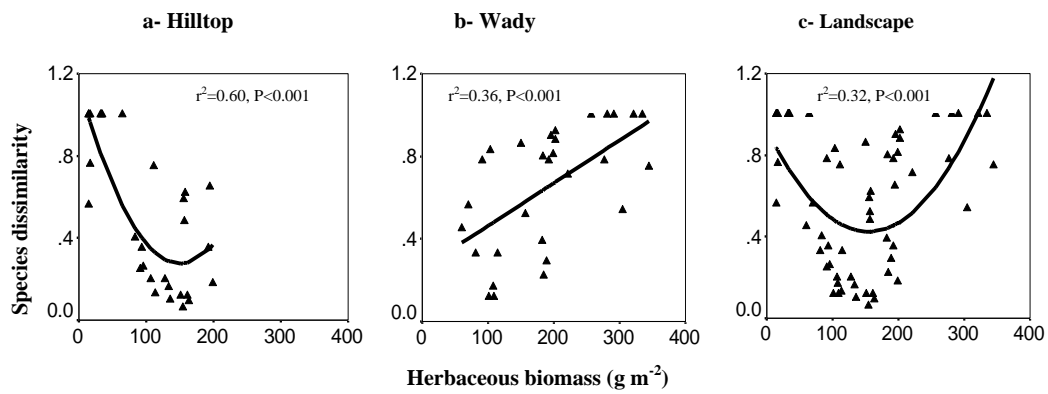


Fig. 4 The dissimilarity (calculated as 1-Jaccard's index of similarity) in species composition among local plots within: (A) hilltop; (B) Wadi; and (C) Landscape localities.

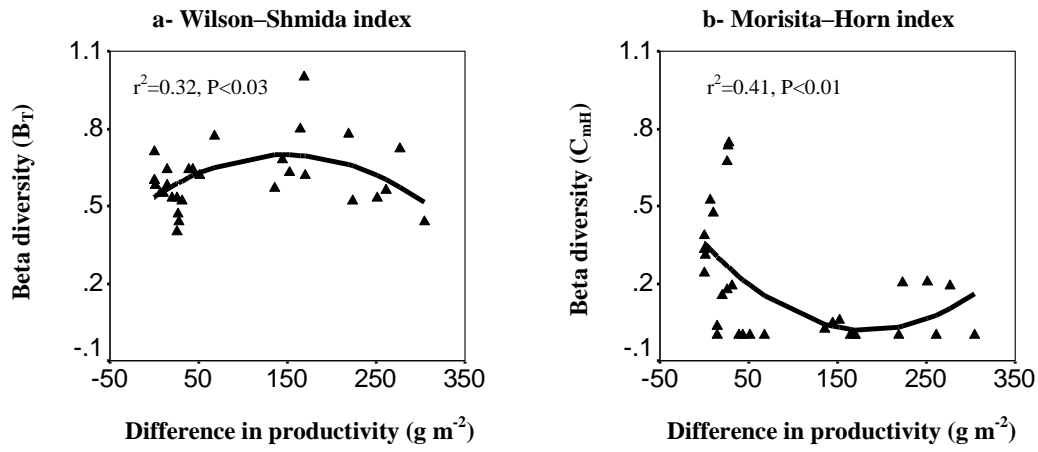


Fig. 5 The relationship between differences in productivity (g m⁻²) between hilltop and Wadi localities and β -diversity; (A) Wilson-Shmida index (β_T), and (B) Morisita-Horn index (C_{mh})

Table 1. Phytogeographical analysis and Life form of encountered plant taxa at hilltops (H) and Wadis (W). Identification of plant taxa followed Zohary and Feibrun-Dothan (1966-1986).

Species	Family	Habitat	Chorotype	Life form
<i>Thymus iva</i> (L.) Schreb.	Labiatae	H	Mediterranean	Chamaephyte
<i>Primula nagallis arvensis</i> L.	Primulaceae	H	Euro-Siberian-Med-Irano-Turanian	Therophyte
<i>Thymus palestina</i> Boiss	Compositae	H	Mediterranean	Therophyte
<i>Thymus herba_alba</i> Asso	Compositae	H	Irano-Turanian	Chamaephyte
<i>Medicago cruciatus</i> Link.	Fabaceae	H	Saharo-Arabian	Therophyte
<i>Thymus undulate</i> (Sieber ex Fresen.) Benth	Labiatae	H	Mediterranean	Chamaephyte
<i>Thymus australis</i> L.f.	Compositae	H	Irano-Turanian	Therophyte
<i>Thymus iberica</i> Spreng.	Compositae	H	Med-Irano-Turanian	Therophyte
<i>Crepis aspera</i> L.	Compositae	H	Mediterranean	Therophyte
<i>Stachytaraxis glomerata</i> L.	Gramineae	H	Euro-Siberian- Med-Irano-Turanian	Hemicryptophyte
<i>Thymus contracta</i> (Boiss.) Chrték & Holub	Compositae	H	Irano-Turanian	Therophyte
<i>Androsace sisyrinchium</i> (L.) Parl	Iridaceae	H	Europe-Mediterranean	Geophyte
<i>Androsace ledifolium</i> (L.) Mill.	Cistaceae	H	Mediterranean	Therophyte
<i>Androsace bulbosum</i> L.	Gramineae	H	Med-Irano-Turanian	Hemicryptophyte
<i>Androsace iberica</i> (M.Bieb.) Fisch. & C.A.Mey.	Labiatae	H	Irano-Turanian	Therophyte
<i>Androsace raetam</i> (Forssk.) Webb	Fabaceae	H	Saharo-Arabian	Phanerophyte
<i>Androsace stellatus</i> (L.) Gaertn.	Compositae	H	Med-Irano-Turanian	Therophyte
<i>Androsace palaestina</i> L.	Dipsacaceae	H	Mediterranean	Chamaephyte
<i>Androsace pallidum</i> M.B.	Crassulaceae	H	Mediterranean	Therophyte

Herbaceous diversity

<i>Sedum rubens</i> L	Crassulaceae	H	Med-Euro-Siberian	Therophyte
<i>Ilene arabica</i> Boiss	Caryophyllaceae	H	Saharo-Arabian	Therophyte
<i>Stipa tortilis</i> Desf.	Gramineae	H	Irano-Turanian-Saharo-Arabian	Therophyte
<i>Umbilicus intermedius</i> Boiss.	Crassulaceae	H	Med-Irano-Turanian	Geophyte
<i>Asclepias maritima</i> (L.) Baker	Liliaceae	H	Mediterranean	Geophyte

Table 1. Continued. Phytogeographical analysis and Life form of encountered plant taxa at hilltops (H) and Wadis (W).

Identification of plant taxa followed Zohary and Feibrun-Dothan (1966-1986).

Species	Family	Habitat	Chorortype	Life form
<i>Humulus lupulifolius</i> L.	Liliaceae	H, W	Med-Irano-Turanian	Geophyte
<i>Galium callichrous</i> Boiss	Fabaceae	H,W	Saharo-Arabian	Therophyte
<i>Geranium ciconium</i> (L.) L'Her	Geraniaceae	H,W	Med-Irano-Turanian	Therophyte
<i>Brassicaria hispanica</i> (L.) Druce	Cruciferae	H,W	Mediterranean	Therophyte
<i>Euphorbia peplus</i> L.	Euphorbiaceae	H,W	Euro-Siberian-Med-Irano-Turanian	Therophyte
<i>Argemone desertorum</i> Pomel	Compositae	H,W	Irano-Turanian-Saharo-Arabian	Therophyte
<i>Chamaecrista densiflora</i> DC.	Fumariaceae	H,W	Mediterranean	Therophyte
<i>Thermaria hirsute</i> L.	Caryophyllaceae	H,W	Euro-Siberian-Med-Irano-Turanian	Therophyte
<i>Ononis unisiliquosa</i> L.	Fabaceae	H,W	Mediterranean	Therophyte
<i>Stipa glaucum</i> Steud.	Gramineae	H,W	Med-Irano-Turanian	Therophyte
<i>Stipa spontaneum</i> K. Koch	Gramineae	H,W	Med-Irano-Turanian	Therophyte
<i>Quercus picta</i> (Sibth. & Sm.) Bornm	Caryophyllaceae	H,W	Irano-Turanian	Therophyte
<i>Isotriaena bicorne</i> (Aiton) Amo	Cruciferae	H,W	Saharo-Arabian	Therophyte
<i>Coronilla caput-galli</i> (L.) Lam	Fabaceae	H,W	Mediterranean	Therophyte
<i>Asperula narbonense</i> L.	Liliaceae	H,W	Med-Irano-Turanian	Geophyte
<i>Poa</i> spp.	Gramineae	H,W	Irano-Turanian	Hemicryptophyte
<i>Primula asiaticus</i> L.	Primulaceae	H,W	Mediterranean	Geophyte
<i>Papaver hybridum</i> (L.) DC.	Papaveraceae	H,W	Med-Irano-Turanian	Therophyte
<i>Delphinium coloratum</i> Poir	Caryophyllaceae	H,W	Mediterranean	Therophyte

Herbaceous diversity

<i>Stipa capensis</i> Thunb	Gramineae	H,W	Irano-Turanian-Saharo-Arabian	Therophyte
<i>Thymus fragrantissima</i> (Forssk.) Sch.Bip.	Compositae	W	Irano-Turanian-Saharo-Arabian	Hemicryptophyte
<i>Trigonotis deinacanthus</i> Boiss.	Fabaceae	W	Irano-Turanian	Chamaephyte
<i>Urtica eigii</i> Feinbrun	Liliaceae	W	Saharo-Arabian	Geophyte
<i>Valeriana nicaeensis</i> All.	Malvaceae	W	Med-Irano-Turanian	Therophyte
<i>Plantago indica</i> L.	Plantaginaceae	W	Irano-Turanian-Saharo-Arabian	Therophyte
<i>Achillea vermiculata</i> L.	Chenopodiaceae	W	Irano-Turanian-Saharo-Arabian	Chamaephyte
<i>Trisetum arabicum</i> Nees	Gramineae	W	Irano-Turanian-Saharo-Arabian	Therophyte
<i>Ononis stellata</i> Forssk.	Fabaceae	W	Mediterranean	Geophyte
<i>Vicia peregrina</i> L.	Fabaceae	W	Med-Irano-Turanian	Therophyte