

## Ground spider communities in experimentally disturbed Mediterranean woodland habitats

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**Abstract:** The protected Mediterranean woodland habitats in Israel are undergoing tree encroachment, resulting in loss of open patches with herbaceous vegetation. We suggested that this process results in a ground spider community dominated by shade-loving species. At three Mediterranean woodland sites located along a rainfall gradient, we examined the effects on the ground-spider community of experimental removal of the woody vegetation in 1000 m<sup>2</sup> plots by cutting and overall plant biomass reduction by grazing and browsing by livestock. Pitfall traps were placed in replicated plots of four treatments (control, cutting, grazing/browsing, and cutting together with grazing/browsing) and in two different habitat patch types (open, woody). ANOVA and multivariate analyses were performed on family abundance by treatment and habitat patch type. Tree-cutting reduced the number of families in plots at two of the three sites. Grazing did not have a significant effect on the number of families or on the ground spider community composition. The spider community of cut-woody patches was more similar to that of open patches than to that of uncut woody patches. Most spider families separated along an axis of open versus woody patches, with woody habitat families predominating at all sites. Families typical of open habitats were positively associated with cut-woody patches as well. The overall effect on ground spider diversity of such manipulations may depend on the scale of habitat changes.

**Key words:** diversity, family composition, ordination, patchiness, similarity

Patterns of diversity and community structure are the consequence of a large number of factors operating at small and large scales. These effects of different factors may be deduced by investigating the naturally occurring patterns over a range of sites (e.g. OXBROUGH et al. 2005, DE MAS et al. 2009). However, this is a static approach and differences among sites may result from historical as well as current factors. Large-scale habitat manipulation experiments provide an opportunity to examine changes in communities over time at multiple levels of organization and in different groups of organisms (BROWN et al. 2001). Large-scale controlled manipulations will change habitat features in such a way as to provide insight into how specific changes affect communities (SHACHAK et al. 2008). In the present study, we use such an experimental approach to examine effects of a manipulation at the landscape scale on the composition of spider communities at the habitat scale in a Mediterranean ecosystem.

Mediterranean landscapes are patchy, with patches consisting mostly of two habitat types: woody patches that are occupied by shrubs or trees, and contrasting

open patches that are devoid of woody plants (NAVEH 1982, GABAY et al. 2008). In protected Mediterranean woodland areas in Israel, the proportion of area covered by woody patches increases along a climatic gradient from south to north with increasing annual precipitation and productivity (KADMON & DANIN 1997). Open patches are mostly covered by herbaceous vegetation that is green in the winter and spring months (January–April) and otherwise dry. Mediterranean woodlands in Israel have been exposed to regimes of grazing and forest cutting for thousands of years (NAVEH & DAN 1973). The combined effect of disturbance from intensive grazing and browsing by livestock, and removal of woody vegetation for firewood, has maintained the mosaic of open and woody patches in the Mediterranean landscape. With the establishment of nature reserves in the Mediterranean region of Israel, grazing and tree-cutting were largely eliminated; consequently the woodland became more closed and with reduced cover of grasses and annual plants (PEREVOLOTSKY 2006). Such changes could have positive and negative effects on biodiversity of different groups of organisms owing to a number of different processes that may act in different ways. For example, the increased structural diversity of trees may create more niches for arboreal arthropods, while increased shade may lower annual plant productivity and reduce arthropod abundance in the understory.

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The effect of encroachment of the woodland and subsequent re-opening by cutting and grazing on the diversity of a range of organisms was the aim of a multi-year investigation of biological diversity in three Mediterranean woodland sites along a precipitation gradient in Israel (SHACHAK et al. 2008). In this study, we tracked the changes in community composition of ground-active spiders in woody and open patches following two large-scale manipulations of the landscape: 1) tree cutting and removal of the woody vegetation canopy and 2) grazing and browsing. The structure of the habitat is well-known to influence habitat selection by spiders (e.g., UETZ 1991, LANGELLOTTO & DENNO 2004, MALLIS & HURD 2005) and thus was expected to affect community composition following the manipulation. We report on the changes following the manipulations, concentrating on effects of cutting and woody vegetation removal on the spider community found in the two habitat patch types. Our working hypothesis was that creating large open areas in the landscape by removal of woody canopy will change the spider community composition from predominantly shade-loving taxa to a community dominated by taxa typical of open habitats, and that this change will be accompanied by a loss of shade-loving taxa.

## Methods

### Research sites and experimental design

The study was conducted in three Long-term Ecological Research sites in the Mediterranean region of Israel, listed from south to north: Adulam – in the Adulam Nature Reserve near Bet Guvrin (31°40' N, 34°50' E, 200 m elevation, ca. 400 mm annual rainfall), Ramat Hanadiv – in the southern Carmel mountains near Zichron Ya'acov (32°30' N, 34°55' E, 120 m elevation, ca. 600 mm annual rainfall), and Meron – on the slopes of Mt. Meron in the Upper Galilee (33°15' N, 35°25' E, 850 m elevation, ca. 900 mm annual rainfall). All of these sites have a canopy of small trees (3–5 m height) and woody shrubs, dominated by *Quercus calliprinos* and *Pistacia palaestina* at Meron (ZOHARY 1973), *Phillyrea media*, *Pistacia lentiscus* and *Sarcopoterium spinosum* at Ramat Hanadiv (BAR MASSADA et al. 2008) and *Phillyrea media* and *Pistacia lentiscus* at Adulam (MILMAN 2007).

At each site, 5–6 blocks were marked and within each block we established four plots of 1000 m<sup>2</sup> each. Each plot within a block received a different treatment, such that the treatments were replicated across the blocks. The treatments were: 1) control (no

manipulation of the habitat), 2) grazing and browsing, 3) cutting and removal of the woody vegetation from the plot, and 4) cutting and woody plant removal together with grazing and browsing. Grazing and browsing by livestock was introduced into the plots in the late spring (May–June) after the arthropod sampling. Livestock used were typical of the region, sheep at Adulam, goats at Ramat Hanadiv and cows at Meron. Grazing pressure was moderate and typical of the area, with the exception of Ramat Hanadiv where grazing was more intensive. Cutting and removal of the woody vegetation was done in the late autumn. The trees and woody shrubs were cut at the base and the above-ground parts were removed from the plot. Each site was cut twice during the four-year study, once in the first year and repeated in the second year, with the exception of Adulam, where cutting was repeated after a 2-year interval.

We measured ground spider activity-density using pitfall traps, which were set for 5 days in the late spring of 2006 (April–May), the season in the Mediterranean ecosystem when many plants are flowering and there is new growth of herbaceous vegetation. Flowering in spring begins in the south and progresses northward, such that the peak of flowering at the northernmost site (Meron) is about one month later than at the southern site (Adulam). Pitfall trapping was timed at each site to the local flowering period. At each site, dry pitfall traps consisting of two plastic cups (10 cm diameter at the top x 10 cm height) placed one inside the other were dug into the ground such that the rim was flush with the surface. In each plot there were 18 traps: three traps in each of three patches beneath trees or woody shrubs and, similarly, three traps in each of three open patches with herbaceous vegetation cover. In cut plots, traps were placed in former woody patches; these were easily distinguished by the remaining base of the tree or shrub and an area of leaf litter surrounding it. The samples from the three traps in each patch were combined. Thus, the samples in all analyses represent three replicates per patch type per plot. The traps were positioned and kept closed 1–2 weeks before the trapping began to allow the ground to settle around the traps. The traps were checked every morning for 5 days and each day all spiders were collected and transferred to 70 % alcohol for later identification.

All spiders were identified to family level (individuals of unknown family were removed from the data set), and for some families adults were identified to species. The analyses below were performed at the

family level in order to take advantage of the full data set. Classification by family is somewhat arbitrary, as species may be shifted from one family to another. Nevertheless, we justify this approach here because 1) species identification was possible for only some of the families, 2) juveniles constituted 16–40 % of the individuals and could not be reliably identified to species, and 3) creating morpho-species, especially with large numbers of juveniles, would artificially augment the number of species. Species in a family often belong to a single foraging guild and thus analysis by family can provide an indication of composition in relation to the diversity of habitat use and foraging strategies. Finally, we are cautious about inferring species-level processes from those observed at the family level. CARDOSO et al. (2004), for example, showed a significant correlation between numbers of species and families at sites in Portugal, but nonetheless found that species richness could not be inferred from family richness.

### Statistical analysis

Factorial ANOVA was performed on the total number of families at each site, with grazing and tree removal as factors and plots as sample replicates. The effect of the different blocks was not significant in any of the analyses and thus this was not entered as a factor.

In order to test for differences in the spider community composition we used multivariate analyses. The analyses were performed on the matrix of family abundance (fourth-root transformed) with plots as the sample replicates and block as a covariable. The environmental variables were the treatments (control, grazing, cutting, cutting and grazing combined) and habitat patch type (open and woody patches).

Analysis of similarity (ANOSIM) was performed on a Bray–Curtis dissimilarity matrix of family abundance with Primer V5.2.2 (CLARKE & GORLEY 2006). ANOSIM was used first to compare family composition in plots of the different treatments (cutting, grazing) and then to compare between specific a priori combinations of treatment and habitat patch type.

To further explore the relationship between the spider family abundance and environmental variables of treatments and patch types we performed constrained ordinations. Detrended correspondence analysis (DCA) was performed to determine which ordination method to use. DCA showed that the length of the gradient was below 3 and therefore the axes were relatively short, implying that the response curves of the family scores were linear. Therefore, principal

components analysis (PCA) and redundancy analysis (RDA) are appropriate for these data. We used CANOCO software version 4.53 (TER BRAAK & ŠMILAUER 2004). The points in the two-dimensional PCA graphs represent sample scores of patch types per plot for the first two axes. Thus, the number of samples is equal to the number of plots in which the patch type appeared. In the PCA graphs, the closer the points are to each other, the more similar they are in their family composition.

Redundancy analysis (RDA), also performed in CANOCO (TER BRAAK & ŠMILAUER 2004), was used to determine the environmental variables (treatments and patch type) that best explain the family composition and to determine which families correlate best with the different treatments and patch types. RDA is a form of direct ordination in which axes are constrained by environmental variables and like PCA, it is based on linear correlation responses of the family scores curves (LEPŠ & ŠMILAUER 2003). We used reciprocal averaging of family abundances and site scores (representing the treatment and patch type variables) and manual forward selection with 499 Monte-Carlo permutations, to choose the set of environmental variables to include in the model, selecting only the significant variables. In order to compare among the three sites, we limited the RDA to the 10 most abundant families in each site (11 in Meron, due to a tie between the abundances; see Table 1). These families represent about 90 % of the total abundance in each site.

Finally, we quantified the contribution of the most abundant families to the differences in family composition between treatment and habitat patch type combinations, using the same Bray–Curtis dissimilarity matrix from the ANOSIM (see above). A similarity percentage analysis (SIMPER) was performed in PRIMER (v5.2.2) to calculate the average Bray–Curtis dissimilarity for each family, which is expressed as the average contribution of the family to the overall dissimilarity between pairs of treatment and patch-type combinations.

### Results

Sample sizes were small (Table 1), reflecting the relatively low productivity of a seasonal, semi-arid landscape and the short sampling period. The dominant families in all three sites were ground spiders (Gnaphosidae), jumping spiders (Salticidae), wolf spiders (Lycosidae) and ant-eating spiders (Zodariidae). These four families together constituted 78 %, 80 %

**Table 1:** Total numbers of individuals of the different families collected by pitfall trapping in Mediterranean woodland habitats at three sites in Israel (listed from south to north according to increasing rainfall). The abundances of the ten families used at each site (11 at Meron) for RDA are shown in bold.

| Family        | Adulam     | Ramat Hanadiv | Meron      |
|---------------|------------|---------------|------------|
| Agelenidae    | <b>13</b>  | <b>42</b>     | <b>10</b>  |
| Araneidae     | 4          | 6             | 3          |
| Cithaeronidae |            |               | 2          |
| Clubionidae   |            | 3             | 7          |
| Corinnidae    |            | 4             | 3          |
| Dictynidae    |            | 1             | 1          |
| Dysderidae    | <b>13</b>  | <b>25</b>     | <b>40</b>  |
| Eresidae      | 2          |               | 1          |
| Filistatidae  | 2          | <b>16</b>     | 3          |
| Gnaphosidae   | <b>187</b> | <b>190</b>    | <b>254</b> |
| Hahniidae     | 1          |               | 1          |
| Hersiliidae   | 7          |               | 4          |
| Linyphiidae   | <b>29</b>  | <b>25</b>     | <b>54</b>  |
| Liocranidae   | 2          |               | 3          |
| Lycosidae     | <b>145</b> | <b>307</b>    | <b>118</b> |
| Miturgidae    | 4          | 1             | <b>22</b>  |
| Nemesiidae    |            | 1             |            |
| Oecobiidae    | <b>20</b>  |               | 2          |
| Oonopidae     | 4          |               | 1          |
| Oxyopidae     | 3          |               | 2          |
| Palpimanidae  | 2          |               | 2          |
| Philodromidae | 6          |               | 5          |
| Pholcidae     |            | 3             |            |
| Pisauridae    | 4          | 2             | 6          |
| Salticidae    | <b>124</b> | <b>66</b>     | <b>91</b>  |
| Sicariidae    | 2          | 1             |            |
| Scytodidae    | 4          | <b>14</b>     | <b>13</b>  |
| Segestriidae  |            |               | 2          |
| Theraphosidae | 1          |               |            |
| Theridiidae   | 6          | <b>10</b>     | <b>14</b>  |
| Thomisidae    | <b>23</b>  | 3             | <b>10</b>  |
| Zodariidae    | <b>92</b>  | <b>65</b>     | <b>134</b> |
| Zoridae       |            | 1             |            |
| Totals        | 700        | 786           | 808        |

and 74 % of the total abundance in Adulam, Ramat Hanadiv and Meron respectively.

Tree cutting and removal reduced the number of families in Adulam ( $F_{1,20}=13.67$ ,  $p=0.0014$ ) and in Meron ( $F_{1,16}=26.45$ ,  $p=0.006$ ), but not in Ramat Hanadiv ( $F_{1,16}=5.0$ ,  $p>0.5$ ). The effect of grazing and the interaction between grazing and cutting were not significant at any of the sites (Fig. 1). The full

ANOVA models (cutting, grazing and the interaction between them) explained 41 % of the variance in number of families in Adulam ( $F_{1,20}=4.63$ ,  $p=0.012$ ) and 38.5 % in Meron ( $F_{1,16}=3.34$ ,  $p=0.046$ ), but only 17 % in Ramat Hanadiv ( $F_{1,16}=1.1$ , ns).

Analysis of similarity (ANOSIM) based on Bray-Curtis dissimilarity indices showed that family composition differed significantly between cut and uncut plots at all sites (Adulam, global  $R=0.09$ ,  $p<0.005$ ; Ramat Hanadiv, global  $R=0.06$ ,  $p=0.051$ ; Meron, global  $R=0.08$ ,  $p<0.05$ ) while grazing had no significant effect. When we segregated the cutting treatment according to open and woody patch types, ANOSIM showed that open patches did not differ from one another in family composition, regardless of cutting treatment (Table 2). As cut and uncut open patches did not differ from one another, for the principal components analysis we segregated the samples into three groups: open patches (cut and uncut combined), uncut-woody and cut-woody patches.

In the principal components analysis (PCA) there was no segregation along the first four axes according to grazing, and thus grazing is not shown in the PCA graphs (Fig. 2A, 2C, 2E; see RDA results below). The first principal components axis accounted for 27 % of the spider family variance at Adulam, 34 % at Ramat Hanadiv and 38 % at Meron (Appendix). In Adulam (Fig. 2A) and Meron (Fig. 2E), the first axis separated the samples from woody and open patches, with the cut-woody samples falling closer to the open patches. At these two sites, the variance in the second axis (12 % and 10 %, respectively) was not clearly associated with any treatment or patch-type gradient in the samples. At Ramat Hanadiv, the separation of woody and open samples was along the second axis, which accounted for 16 % of the variance (Fig. 2C). As in Adulam and Meron, the cut-woody samples were closer to the open samples, and indeed, intermixed with them along the second axis. The first axis could not be attributed to either cutting or to the patch type. Adding the grazing treatment did not show a clear pattern along this axis and thus, the first axis represents variation from other unmeasured factors.

In the redundancy analysis (RDA), the first two axes were correlated with the environmental variables of treatment and patch type (Figs. 2B, 2D, 2F; correlation coefficients: Adulam: 0.75 and 0.49 for axes 1 and 2 respectively, Ramat Hanadiv: 0.74 and 0.31, Meron: 0.78 and 0.62). However, the total variance in family composition explained by

**Table 2:** Analysis of similarity (ANOSIM) tables showing R (similarity index) for the comparison between pairs of treatment and patch type combinations at the three sites. The comparisons are arranged in decreasing order of R values. A high index of similarity ( $p < 0.05$ ; shown in *italics*) indicates that there was a significant difference in family composition between the two treatment-habitat types. Habitat patches in plots that were not cut are noted as 'woody' or 'open', while those in cut plots are noted as 'cut-woody' and 'cut-open'.

**A. Adulam**

| Treatment -patch type         | R            | Significance |
|-------------------------------|--------------|--------------|
| <i>cut-open vs. woody</i>     | <i>0.474</i> | <i>0.001</i> |
| <i>cut-woody vs. woody</i>    | <i>0.397</i> | <i>0.001</i> |
| <i>open vs. woody</i>         | <i>0.391</i> | <i>0.001</i> |
| <i>cut-open vs. cut-woody</i> | <i>0.098</i> | <i>0.03</i>  |
| cut-open vs. open             | 0.031        | 0.2          |
| cut-woody vs. open            | -0.034       | 0.8          |

**B. Ramat Hanadiv**

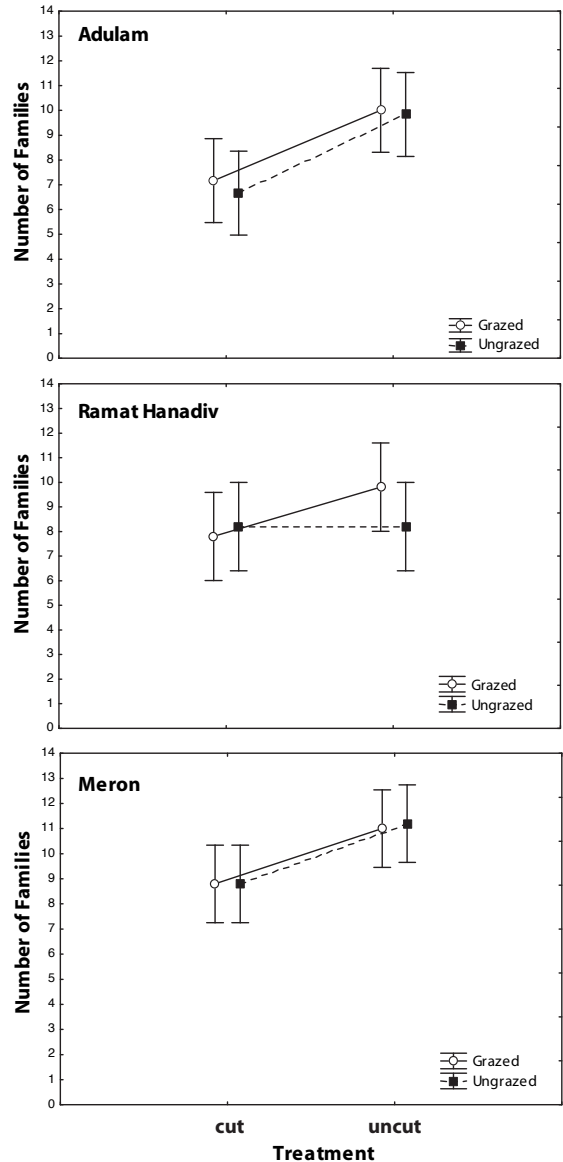
| Treatment -patch type      | R            | Significance |
|----------------------------|--------------|--------------|
| <i>open vs. woody</i>      | <i>0.382</i> | <i>0.001</i> |
| <i>cut-open vs. woody</i>  | <i>0.31</i>  | <i>0.001</i> |
| <i>cut-woody vs. woody</i> | <i>0.293</i> | <i>0.001</i> |
| cut-woody vs. open         | 0.006        | 0.4          |
| cut-open vs. open          | -0.04        | 0.7          |
| cut-open vs. cut-woody     | -0.06        | 0.85         |

**C. Meron**

| Treatment -patch type      | R            | Significance |
|----------------------------|--------------|--------------|
| <i>open vs. woody</i>      | <i>0.7</i>   | <i>0.001</i> |
| <i>cut-open vs. woody</i>  | <i>0.564</i> | <i>0.001</i> |
| <i>cut-woody vs. woody</i> | <i>0.386</i> | <i>0.001</i> |
| <i>cut-woody vs. open</i>  | <i>0.141</i> | <i>0.01</i>  |
| cut-open vs. cut-woody     | 0.005        | 0.4          |
| cut-open vs. open          | -0.014       | 0.5          |

treatment and patch type was low in all three sites (Adulam: 22 %, Ramat Hanadiv: 13 %, Meron: 29 %). Grazing was not a significant variable in any of the sites ( $p > 0.5$ ). Both patch type and cutting were significant in Adulam (patch type:  $F = 6.71$ ,  $p = 0.002$ ; cutting:  $F = 3.84$ ,  $p = 0.002$ ) and in Meron (patch type:  $F = 11.21$ ,  $p = 0.002$ ; cutting:  $F = 3.77$ ,  $p = 0.004$ ). In Ramat Hanadiv patch type was the only significant explanatory variable ( $F = 2.62$ ,  $p = 0.036$ ); cutting was not significant ( $F = 1.94$ ,  $p = 0.096$ ), but was included in the analysis as it appears to influence the distribution of some families.

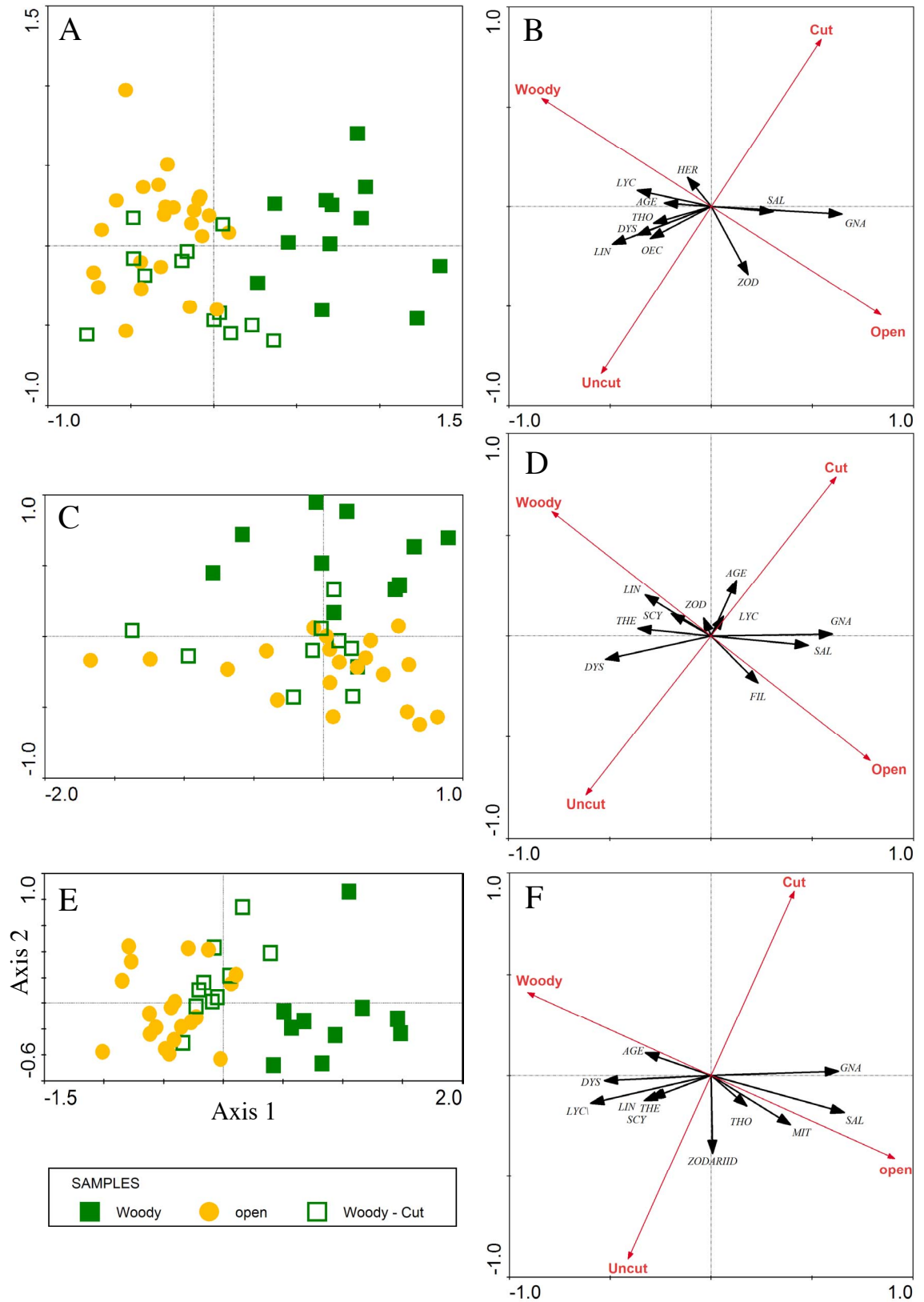
Most of the spider families at the three sites were segregated along the axis of patch type, showing an



**Figure 1:** Mean and 95 % CI of the number of families in plots under two landscape manipulations, cutting and grazing, at three Mediterranean woodland sites (from south to north): Adulam (31°40' N, 34°50' E, 200 m elevation, c. 400 mm annual rainfall), Ramat Hanadiv (32°30' N, 34°55' E, 120 m elevation, c. 600 mm annual rainfall) and Mt. Meron (32°00' N, 35° 20' E, 900 m elevation, c. 800 mm annual rainfall).

affinity either to woody patches or to open patches. At Adulam and Ramat Hanadiv, the two southern sites, there were more families associated with woody patches than with open patches (Figs. 2B and 2D, respectively). Families with strong woody-patch affinity (indicated by the length of the arrows) included





one of the four dominant families, namely the wolf spiders (Lycosidae), as well as sheetweb spiders (Linyphiidae), cobweb spiders (Theridiidae, mainly juveniles of *Crustulina*, *Enoplognatha* and *Euryopis*), and woodlouse hunters (Dysderidae, mainly unidentified species of *Harpactea*). The families associated with the open, herbaceous patches were the remaining three numerically dominant families: the ground spiders (Gnaphosidae, mainly *Pterotricha levantina* Levy, 1995 and *Zelotes scrutatus* (O. P.-Cambridge, 1872) at Meron and Adulam and *Pterotricha cambridgei* (L. Koch, 1872) and *Z. scrutatus* at Ramat Hanadiv), jumping spiders (Salticidae, unidentified species of *Aelurillus* at all sites) and ant-eating spiders (Zodariidae, e.g., *Ranops exers* (O. P.-Cambridge, 1876) and *Zodarion lutipes* (O. P.-Cambridge, 1872) at Meron, *Palaestina expolita* O. P.-Cambridge, 1872 and *Z. lutipes* at Ramat Hanadiv and *Zodarion judaeorum* Levy, 1992 at Adulam). Cutting had a positive influence on funnel-web spiders (Agelenidae, mainly juveniles of *Agelena* and *Maimuna*) and wolf spiders (Lycosidae) at Ramat Hanadiv (Fig. 1D).

Analysis of similarity (ANOSIM) results (Table 2) showed that there were significant differences in family composition between cut-woody patches and woody patches (uncut) at all sites. We conducted a percentage similarity analysis (SIMPER) of family dissimilarity between these two patch types in order to determine which families contributed most to this difference. The results support the segregation of families along the axis of cut-woody versus woody patches as suggested in the RDA. Among the families that contributed the most to the community dissimilarity between these two habitats at Adulam and Meron were Gnaphosidae and Salticidae (together, 36 % and 21 % contribution to dissimilarity at Adulam and Meron, respectively), with higher average abundance of both families in cut-woody patches and Linyphiidae

(12.5 % and 11 % contribution, respectively) found only in woody patches. At Ramat Hanadiv, Lycosidae and Gnaphosidae together contributed 49 % of the dissimilarity between cut and uncut woody patches and both had higher average abundance in cut-woody patches.

## Discussion

At two of the three sites, plots where trees had been cut and removed (with or without grazing) had fewer spider families on average than did control plots. The ground spider community of cut woody patches differed significantly from that of uncut woody patches and was more similar to that of open patches. Grazing had no significant effect on family richness, nor did it influence the family composition at any of the sites. Intensive grazing and browsing by goats at Ramat Hanadiv reduced the cover of woody vegetation (BAR MASSADA et al. 2008), and yet we found no effect on spider family composition in our analysis. Grazing alone also had little effect on the species richness of herbaceous plants at all three sites (AGRA & NE'EMAN 2009; Y. Lubin, G. Ne'eman & A. Per-evolotsky unpubl.). There may be several reasons for the lack of a strong grazing effect. First, the Mediterranean flora and fauna has a long history of grazing and organisms are well-adapted to it (NOY-MEIR et al. 1989, WARD 2005); second, grazing may have been insufficient in duration and intensity to produce a change; and third, the sampling of herbaceous vegetation and of spiders took place several months after the livestock were removed from the plots and there may have been sufficient time for the new annual vegetation to emerge following winter rains and for spiders to re-colonise following the disturbance.

At all sites, cutting and removal of the woody vegetation had a marked effect on the spider family composition at the patch level. Analysis of similarity (ANOSIM) gave low, but significant values of R for the difference between cut and uncut plots. The reason for the low global R values is that the open patches in both cut and uncut plots were similar in family composition, reducing the overall strength of the difference between the two treatments.

The PCA diagrams show that the spiders from former woody patches (cut-woody) were more similar in family composition to those from open patches than to those from uncut woody patches. Thus, community composition shifted from families typically found beneath trees and shrubs toward families typical of open patches with herbaceous vegetation. The

**Figure 2:** Multivariate analyses of ground spider families at three sites Adulam (A, B), Ramat Hanadiv (C, D) and Meron (E, F). Figures A, C, and E show the spider family composition per plot along the first (x) and second (y) principal component axes, coded by patch type (woody, open and cut-woody). Figures B, D, and F show plots of the spider families along the first two RDA axes representing the environmental variables of habitat type (axis 1, woody vs. open) and cutting (axis 2, cut vs. uncut). The spider family codes are: AGE=Agelenidae, DYS=Dysderidae, GNA=Gnaphosidae, HER=Hersiliidae, LIN=Linyphiidae, LYC=Lycosidae, MIT=Miturgidae, OEC=Oecobiidae, SAL=Salticidae, SCY=Scytodidae, THE=Theridiidae, THO=Thomisidae, ZOD=Zodariidae

shift was not complete, however, as some cut-woody samples overlapped with the woody samples at all three sites, and there were significant differences in family composition between cut-woody and open habitats at two of the three sites. One reason for the incomplete shift may be that the cut trees re-sprout rapidly following cutting and at the time of sampling most cut trees had new growth to a height of 0.3–1 m, thus providing conditions that may allow shade-loving species to persist or to recolonise. Another option is that, owing to modification of soil characteristics around woody plants (SEGOLI et al. 2008), the litter and soil moisture conditions surrounding the cut tree change only slowly and thus spiders still perceive this habitat as a woody patch.

The distinct family preferences for either woody or open patches are seen in the RDA, as this was the main axis of separation at all three sites. Most families were associated with the tree habitat, an association possibly related to a more favorable microclimate and higher prey abundance. Gnaphosids and salticids were notable exceptions being clearly associated with open patches. Most of the gnaphosid species at these sites are nocturnal (personal observation), while the jumping spiders are all diurnal, which suggests that these two taxa temporally partition the terrestrial niche of open, herbaceous vegetation patches.

Differences in family composition between cut and uncut plots (ANOSIM) largely reflect differences between cut-woody patches and woody (uncut) patches. In the percentage similarity analysis (SIMPER), families that showed strong associations with either open or woody patches in the RDA also contributed the most to the dissimilarity between the cut-woody and woody patches. This again supports the view that open habitat species benefitted from tree cutting. Two families in particular, Agelenidae and Lycosidae, showed an association with cutting at Ramat Hanadiv (RDA) and also contributed the most to the dissimilarity between cut-woody and woody patches at this site (SIMPER). The funnelweb spiders (Agelenidae) at Ramat Hanadiv mostly belonged to a single species, *Agelescape livida* (Simon, 1875). These spiders construct their webs on shrubs and were able to take advantage of an abundance of websites on the regenerating trees (personal observation). A large proportion of agelenids and lycosids trapped at Ramat Hanadiv were juveniles (90 % and 77 %, respectively). Juvenile lycosids and agelenids are highly mobile (e.g., WALKER et al. 1999) and young individuals searching

for suitable sites may have moved preferentially into the newly accessible cut-woody patches. At the other two sites, both of these families were associated with the woody habitat. However, overall there were lower proportions of juveniles at Adulam (20 %) and Meron (16 %) than at Ramat Hanadiv (42 %), and in particular, the proportion of juvenile lycosids was lower at these two sites (39 % and 19 %, respectively) than at Ramat Hanadiv. Thus the shift from woody patches into the cut woody patches at Ramat Hanadiv may have been a consequence of the preponderance of mobile juveniles in these two families.

In conclusion, opening the woodland by tree-cutting had a small, but significant effect on family richness, and a pronounced effect on spider family composition. In general, there was a shift of family composition from predominately woody habitat taxa to more open-habitat taxa. The patterns observed here at a family level should be verified at the species level once species identifications are available. The extent to which such changes will increase or decrease overall diversity at the landscape scale will depend greatly on the spatial scale of removal of the woody vegetation.

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