

Rabbit grazing as the major source of intercanopy heterogeneity in a juniper shrubland

Gábor Markó

Department of Ethology, Eötvös Loránd University

Gábor Ónodi

Institute of Ecology and Botany, Hungarian Academy of Sciences

Miklós Kertész

Institute of Ecology and Botany, Hungarian Academy of Sciences

Vilmos Altbäcker

Department of Ethology, Eötvös Loránd University

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Address correspondence to Gábor Markó, Department of Ethology, Eötvös Loránd University, Pázmány P. stny. 1/C, Budapest H-1117, Hungary. E-mail: magvacska@hotmail.com

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Abstract

Semi-arid shrubland is prone to wildfires especially if there are no firebreaks separating shrubs to alleviate the spread of fire. The accumulated grass vegetation is a potential combustion source which also contributes to the spread of wildfires. We present a field study conducted in a semi-arid community, where the fire risk is high and the grass density surrounding the *Juniperus communis* shrubs is highly varied. We tested simultaneously the relative significance of the main factors contributing plant cover around shrubs: allelopathy, shading, herbivory. Grass cover was compared around junipers which were either currently occupied by rabbits or were unoccupied. We visually estimated plant cover and measured the Normalized Difference Vegetation Index. Both sides of the shrubs were sampled at various distances to see if allelopathy and/or shading reduced grass density. The allelopathy effect was also tested by lettuce bioassay. We found that the vegetation was open only around occupied junipers and that the effect of occupation decreased by distance from the shrub. The spatial distribution of plant cover showed that, while we could detect significant allelopathic effect of juniper by bioassay, neither shading nor allelopathy were as important as herbivory. We also compared the rabbit diet composition with plant availability for each occupied patch and found that the consumed species were under represented due to selective grazing. Our findings indicate that local herbivore activity could affect the spatial heterogeneity of combustible material, therefore moderate rabbit grazing can be considered as a management tool to reduce the spread of fire.

Keywords

allelopathy, fire, grassland, herbivore, *Juniperus communis*, NDVI, semi-arid environment, shading.

Introduction

Shrublands are comprised of highly combustible fuels in Mediterranean countries (Fernandes, 2001; Xanthopoulos et al., 2006), Southern US states (Baisan & Swetnam, 1990; Floyd et al., 2004), and most of Australia (Luke & McArthur, 1978). Main purposes in the shrubland management are to reduce both the accumulated biomass and their areal permanence (Valdecantos et al., 2009) to reduce and prevent the severity and spread of wildfires, respectively. It is becoming even more essential for resource managers to predict which habitat types are likely to suffer from hazards due to climate change (Dale et al., 2000), and how land management practices influence the process (Fernandes & Botelho, 2003).

Spatial and temporal heterogeneity of shrubland could influence the development and spread of fire (Minnich, 1995). Shrubs isolated from each other by natural firebreaks (e.g. open sand, extensive soil disturbance, cryptogams, incombustible materials, etc.) are less susceptible to fire. The intercanopy grassland vegetation plays a fundamental role in fire transmission among the juniper-poplar woody patches in the forest-steppe vegetation (van Langevelde et al., 2003). Fire spread limitation depends on the vegetation density, patch size and quality (Keane et al., 2002). Habitat patchiness is common in extreme environments where different plant populations using the same resources (e.g. water, soil nutrition etc.) congregate and compose a special patchy structure (Adler et al., 2001).

The canopy of the woody plants is especially important in low production communities for creating a patchy mosaic structure (Aguilar & Sala, 1999). In the neighborhood of high shrubs or trees, the patterns of light and heat exposure may also alter the plant production and thus the accumulation of combustible material. Shading can modify plant growth, morphology, biomass allocation and competitive abilities of grass species. Seedling survival and growth of light demanding and shade tolerant species were affected differentially by shading (Bloor & Grubb, 2003). The understory grass species presence, abundance and diversity were negatively correlated with the size and distribution of *Pinus ponderosa* (Dougl.) trees in a forest vegetation (Naumburg & DeWald, 1999). Another study presented a positive relationship in spatial distribution between eastern red cedar (*Juniperus virginiana* L.) and tree seedlings (Meiners & Gorchov, 1998). Red fescue (*Festuca rubra*, L.) clones showed canopy structure modification and reduced survival rates due to high interspecific competition among monocots for the light (Skalova & Krahulec, 1992). The biomass allocation and the morphology changed in *Festuca pallescens* (St. Yves) leading to increased light interception in open pasture compared with that in forested plots (Fernandez et al., 2004). These direct and indirect factors were also observed in juniper communities (Schott & Pieper, 1985).

Canopy removal experiments showed the importance of allelopathy to the grass vegetation surrounding juniper shrubs (Bates et al., 1998). Plants' secondary metabolic product emission from the accumulated canopy litter reduces the cover of other plants. This effect was demonstrated in the vicinity of aromatic shrubs, such as whiteleaf sage (*Salvia leucophylla*, Greene) or California sagebrush (*Artemisia californica*, Less.), where no annual plants were found within a diameter of 90 cm (Muller et al., 1964; Muller, 1965). *Juniperus virginiana* (L.) contains essential oils (Meiners & Gorchov, 1998) which inhibit seed germination and plant growth in understory vegetation (Dudai et al., 1999). All species of the *Juniperus* genus are rich in monoterpene-dominated essential oils (Adams, 1998; Owens et al., 1998; Koukos et al., 2002; Cavaleiro et al., 2003). Monoterpenes are allelochemicals which often cause phytotoxic effects (Muller et al., 1964) and they may play a major role in allelopathy to the grasslands around juniper patches (Mahmoud & Croteau, 2002).

Herbivory not only reduces the combustible material accumulation on the surface of the ground, but changes the vegetation structure as well. The relative density and species composition of herbivores are able to modify the browsing impact (Mysterud, 2006). Herbivore density correlates with the browsing pressure that is reflected by the plant damage (Tsujino & Yumoto, 2004). Herbivory can be judged from plant epidermis remnants identified in the fecal pellets of local grazers (Chapuis, 1990; Mátrai et al., 1998). Herbivores living in defined patch types may be the source of the extended disturbance in nearby plant associations as the warren digging European rabbit (*Oryctolagus cuniculus*, L.) affects grasslands surrounding junipers (Villafuerte & Moreno, 1997). Such impacts alter the grassland composition for a few meters, where only plants that are suboptimal for consumption can survive.

In the present paper we show a field study conducted in a mosaic of common juniper (*Juniperus communis*, L.) shrubs and open perennial sand grassland (*Festucetum vaginatae*, Rapaics) in Hungary. The sparse vegetation of sand dunes has been grazed by livestock and wild rabbits for centuries, but grazing as a management was discontinued after the establishment of the Kiskunság National Park in 1976. The community became particularly sensitive to wildfires; two large stands of the park were severely burned in 1994 and 2000. According to our recent field experiments, intercanopy grass cover increased after the disappearance of rabbits (Katona et al., 2004), and rabbit grazing substantially reduced the spread of induced fire (Ónodi et al., 2008). In this study we therefore focused on the grasslands surrounding the juniper shrubs, supposing that the sparse grasslands may serve as natural firebreaks. However, reduced grass cover could arise for different reasons.

We considered the following three non-exclusive alternative hypotheses as possible causes of reduced intercanopy vegetation density surrounding junipers. (i) We intended to test the impact of herbivory by comparing intercanopy grassland vegetation surrounding pairs of junipers occupied or unoccupied by rabbits. If

reduced plant cover around junipers is caused by grazing, then we expect reduced plant density only around occupied shrubs. Moreover, we expect differential change of consumed plants due to selective grazing, which can be judged by the plant fragments present in the rabbit fecal pellets. (ii) Variation in grass cover might reflect directional impact of light / temperature exposure. The grass cover can be low from mortality due to heat exposure on the southern side of junipers. In contrast, shading on the northern edge of tall shrubs might increase plant production and reproduction in semi-arid vegetation. Such effects should lead to directional changes in grass cover and should extend to a few meters. (iii) Vascular plant cover can be low due to allelopathy of junipers. We intended to test the allelopathic effect of the common juniper in two steps. On the one part, a bioassay is performed to show the ability of *Juniperus communis* (L.) to reduce plant development. On the other part, spatial distribution of reduced plant cover should reveal such an impact. Reduced plant cover in this case should be restricted to the edge of all junipers, regardless of the rabbit presence and without differences between the shaded and exposed side of the junipers.

Materials and methods

Study location

The study was performed in Tatárszentgyörgy, central Hungary (47°05'56"N; 19°23'47"E) in July, 2006. The study area is covered by juniper-poplar forest-steppe vegetation, which is a natural wooded community on Pleistocene calcareous, nutrient deficient (humus content <1%) sand soil deposited from the Danube River (ISSS Working Group RB, 1998). The natural vegetation of the formerly wind driven sand dune systems is the juniper-poplar forest-steppe composed a special mosaic of xeric grasslands, wood and shrub patches. This habitat provides special climatic and edifice properties for specialized vegetation and herbivores (Kertész et al., 1993). The plant species have semi-desert features because of the extreme soil moisture regime conditions (Molnár, 2003). The range of the monthly temperature means is between -1.8°C (January) and 21 °C (July). In the summer period, the midday soil surface temperature may reach 60°C at the southern edge of the junipers and 43°C on the shaded northern side. The annual mean precipitation is around 550 mm (Kovács-Láng et al., 2000). Drought occurs frequently in spring and at the end of the summer season.

In order to separate the possible causes of intercanopy heterogeneity in our study site, seven pairs of juniper patches were chosen. The occupied pair contained an inhabited rabbit warren, while the unoccupied pair had no evidence of rabbit presence such as dunghills, browsed shrubs, scratches, etc. For distinguishing allelopathy and shading, a series of 1 × 1 m quadrants were made in a two compass orientation (south and north)

at each shrub. As all three impacts manifest a distance-dependent change in plant cover, quadrants were established at three distances (0-1 m, 2-3 m, 4-5 m), starting from the drip line of the junipers (Figure 1). Thus, we described 84 quadrants (2 groups x 7 patches x 2 orientations x 3 distances) for the vegetation analysis.

For reducing variation due to confounding variables, we have chosen pairs of juniper patches being similar in their size (area and shrub height) and exposure. Pairs must have been at least 50 m apart from other sample units corresponding to rabbit home range size (Moreno & Villafuerte, 1995). Pairing was effective, as the patch area was similar between occupied and unoccupied patches (paired t-test: $t(6) = -1.45$, $P = 0.19$; occupied mean = 281.8 m², SD=97.3; unoccupied mean = 318.6 m², SD=143.2). The height of juniper shrubs (paired t-test: $t(6) = 1.54$, $P = 0.17$) was not different in the occupied and unoccupied shrubs. Patch exposure was also similar (Southern orientation $t(6) = -0.42$, $P = 0.68$; Northern orientation $t(6) = -0.71$, $P = 0.49$). Moreover, the exposure variation had no impact on vegetation in the given range as there was no significant correlation between the angle of slope and the total vascular plant cover ($R = 0.013$, $P = 0.699$). Distance between patch pairs was 477 meters (SD = 518, min = 108, max = 1596); distance to the closest patch was on average 142 meters (SD = 96). During the study we did not observe any other abiotic or biotic patch characteristics that could influence the results.

Vascular plant cover estimation

Within each 1 x 1 m quadrant, the cover percentage of each plant species, litter and bare sand surface were estimated visually as a percentage of the total area of the quadrant, then Total plant cover was calculated. Visual cover estimation has low expected errors when performed on a quadrant larger than 0.06 m², specially in nutrient deficient habitats (Klimes, 2003). One experienced observer (G. Markó) made all such cover estimations.

NDVI measurement

Field spectroscopy (Goodin & Henebry, 1998; Kertész et al., 2001; Ónodi et al., 2006) provided a non-destructive estimation of the ground-surface green biomass. We used a Cropscan MSR87 multispectral radiometer (Cropscan Inc.®). We calculated NDVI (Normalized Difference Vegetation Index) to estimate the amount of the ground-surface green biomass, based on the data of red- and near-infrared channels of the instrument. The main driver of NDVI is the leaf area index (Roujean & Breon, 1995). We determined NDVI for each quadrant except those quadrants situated in the shade where the apparatus was not useable.

Diet composition analysis

In order to understand the differential impact of grazing, we quantified which plants were eaten by the rabbits. Five fresh fecal pellets were collected from each rabbit colony at the same time when the plant cover estimation was done. Pellets were taken from different dunghills, but not farther than 10 m from the warren to exclude overlap with the neighboring colonies. Thus, we collected samples from 7 occupied patches x 5 pellets, altogether 35 droppings for diet analysis. Fecal pellets were labeled and stored in a freezer at -20°C until further investigations. Diet composition was described by micro-histological feces analysis (Mátrai & Kabai, 1989; Katona & Altbäcker, 2002). We identified the diet composition of each rabbit's fecal pellets following the technical process described by Katona and Altbäcker (2002). We used a same amount (about 0.01 g) from each pellet. After boiling these samples in 1 ml of 20% nitric acid solution in a 10 ml test tube for 1 minute, the epidermis fragments were dispersed on microscopic slides into a mixture of 0.1 ml of 87% glycerin and 0.05 ml of 0.1% Toluidine-Blue. Microscopic slides were covered, labeled and systematically scanned under 160× magnification. We identified 100-100 epidermis fragments from each pellet using our reference collection containing all plant species of the study area (Mátrai et al., 1986). Diet composition was separately determined by the relative frequency of the epidermis fragments from 5-5 pellets for each patch.

Grazing impact

We compared the rabbit diet composition to the actual plant availability for each occupied juniper patch. Diet was calculated as an average of the composition of five pellets, with the average plant cover of the six quadrants of the occupied juniper patch used as a measure of plant availability. Overlap of both the main diet categories (Monocots, Dicots, Angiosperms) and the plant species were compared to their availability, these were described using Renkonen similarity index (Hurlbert, 1978). In an other comparison, we calculated the cumulative percent of vascular plant cover divided into plants either consumed or not consumed by the local rabbits, for each pair of juniper patches. These calculated cover values were analyzed by the presence of herbivore and distance effect.

Lettuce seed bioassay

We used lettuce (*Lactuca sativa*, L.) seed bioassay for testing the allelopathic effect of *Juniperus communis* (L.) on lettuce seed germination. There were three groups, Litter, Twig and Control, each replicated five times. For all groups, twenty lettuce seeds were placed in a Petri dish (9 cm diam.) on Whatman 2 mm paper soaked in 4 ml distilled water. For the Litter treatment, we added 1 g of juniper litter (mainly needles) to

the Petri dishes, for the Twig group, we added 1 g of fresh juniper twigs, while the dishes of the Control group did not contain any additional material. The dishes were then placed in a thermostatically controlled light box (total darkness at 19°C) to germinate. The radical length of germinated seeds was measured (accuracy to the nearest mm) after three days. Treatments were replicated five times.

Statistical analysis

The Total vascular plant cover were analyzed with General Linear Mixed Model (GLMM), using herbivore presence, compass orientation, and the quadrant distance from the juniper patch as fixed factors, and the patch as a random factor. Separate GLMMs were run for comparing specific coverage types, as Monocots, Dicots, Sand, Dead Leaf and Cryptogams, estimated at the distance of 1 m. The herbivore presence and the compass orientation were included as fixed factors in this analysis, while the patch was a random factor.

We used Nested Design ANOVA in the case of NDVI analysis. It was not possible to determine the NDVI-value in the shaded quadrants, thus data for 1 m in the north and for another two quadrants were not included. Therefore, seven pairs of data for distance 3 m and 5 m in the north and also seven pairs for distance 1 m, 3 m, and 5 m in the south were compared.

We compared the plant availability by diet composition using GLMM. The herbivore presence and the quadrant distance were fixed factors and patch as random factor. The compass orientation had insignificant effect in the total vascular plant cover, so it was not included in the present analysis. For comparing the number of plant species at three distances, GLMM was used and the herbivore presence and the distance were included as fixed factors and patch as random factor. The compass orientation was also not included in that analysis.

We analyzed the lettuce seed bioassay using GLMM, where the treatment was a fixed factor, while replicates were included as a random factor.

We compared the groups according to Day and Quinn (1989) only when the GLMM or Nested design ANOVA resulted in a significant difference. Only planned comparisons testing *a priori* assumptions originating from the design were performed. Statistica® program (version 7.0) was used for all statistical data analyses.

Results

The hypotheses of herbivore presence, allelopathic effect and shading were tested in the same design for the different variables.

Total vascular plant covers (Figure 2.)

The data set was analyzed with GLMM, which indicated a significant effect of herbivore presence ($F_{1,74} = 26.57$, $P < 0.001$) and distance ($F_{1,74} = 7.36$, $P < 0.001$). There was no impact of the compass orientation ($F_{1,74} = 2.09$, $P = 0.09$). The patch effect was also significant ($F_{6,74} = 5.69$, $P < 0.001$).

NDVI measured with CropScan (Figure 3.)

The NDVI values of quadrants were analyzed with Nested Design ANOVA. Only the herbivore presence as a fixed factor had a significant effect ($F_{1,55} = 23.95$, $P < 0.0001$), while the other fixed factors, compass orientation nested in herbivore presence ($F_{1,55} = 1.54$, $P = 0.21$) and the distance nested in compass orientation ($F_{3,55} = 0.57$, $P = 0.63$), were not significantly affecting plant cover. The impact of juniper patches as a random factor ($F_{6,55} = 1.68$, $P = 0.14$) was also insignificant suggesting that each grassland has a unique composition. The NDVI-value and the cover estimation were highly correlated ($R = 0.49$, $P < 0.0001$) with each other.

Detailed analysis of plant cover and composition at 1 m distance (Figure 4.)

We performed a detailed analysis of vegetation characteristics for the 1 m quadrants, established at the edge of junipers, where grazing impact was highest. Figure 4 shows the relative cover of Monocots, Dicots, Sand, Dead Leaves, and Cryptogams. We analyzed these vegetation categories separately with GLMM, using herbivore presence and compass orientation as fixed factors, and the patch effect as a random factor. The analysis indicated significant effects of herbivore presence in relative cover of Monocots ($F_{1,19} = 17.32$, $P < 0.001$), Dicots ($F_{1,19} = 6.40$, $P = 0.02$), and Dead Leaves ($F_{1,19} = 5.46$, $P = 0.03$), while the rabbit presence did not affect the cover of Sand ($F_{1,19} = 2.00$, $P = 0.17$) and Cryptogams ($F_{1,19} = 2.65$, $P = 0.11$). We also did not find significant effect of compass orientation in the major plant groups (Monocots: $F_{1,19} = 0.36$, $P = 0.55$; Dicots: $F_{1,19} = 0.06$, $P = 0.8$; Sand: $F_{1,19} = 1.12$, $P = 0.30$; Dead Leaves: $F_{1,19} = 0.003$, $P = 0.95$; Cryptogam: $F_{1,19} = 0.16$, $P = 0.68$). The patch effect was not significant either (Monocots: $F_{6,19} = 1.54$, $P = 0.21$; Dicots: $F_{6,19} = 0.99$, $P = 0.45$; Sand: $F_{6,19} = 0.58$, $P = 0.73$; Dead Leaves: $F_{6,19} = 0.66$, $P = 0.67$; Cryptogam: $F_{6,19} = 1.68$, $P = 0.17$).

Plant availability and rabbit diet composition (Table 1.)

We determined which plants were actually consumed by the rabbits from the plant remnants in their fecal pellets. Any mismatch between availability and consumption would indicate selective feeding by the rabbits. On the major plant group level, high values of Renkonen similarity indices calculated for the seven pairs

of data indicated that the diet composition reflected well the plant availability. This was not the case on the species level, which reflects that the seven grasslands surrounding the junipers have rather unique plant compositions and that the same was also true for the rabbit diets.

The impacts of rabbits judged from the differential change in eaten plants around occupied junipers (Figure 5.)

We determined the impact of the rabbits by separating the cover of plant species, which were either consumed by the rabbits or were absent in the diet. There was a significantly reduced plant cover of the consumed plants in the areas around junipers containing rabbits compared to paired unoccupied areas (Figure 5. A). We analyzed the cumulative cover of the species present and absent in the rabbit diet separately with GLMM. Decreased cover of consumed plant species indicated a significant effect of the herbivore presence ($F_{1,75} = 14.29$, $P < 0.001$) and the distance ($F_{1,75} = 7.39$, $P = 0.008$) as fixed factors and the patch effect ($F_{6,75} = 4.02$, $P = 0.001$) as random factor was also significant. Moreover, the same kind of difference existed in the covers of unconsumed plants, which were also affected by the rabbit presence (Figure 5. B), suggesting that the effects of herbivory should not be restricted to grazing (herbivore presence: $F_{1,75} = 30.79$, $P < 0.001$; distance: $F_{1,75} = 2.18$, $P = 0.14$; patch: $F_{6,75} = 4.39$, $P < 0.001$).

Plant species diversity (Figure 6)

The number of plant species were different between the occupied and unoccupied pairs only on the southern side of the junipers (GLMM; herbivore presence: $F_{1,33} = 12.38$, $P = 0.001$). This variable was marginally significant distance-dependent ($F_{1,33} = 3.45$, $P = 0.07$) without a significant patch effect ($F_{1,33} = 1.91$, $P = 0.10$). However, we did not find significant differences in the same fixed factors on the northern side (Herbivore presence: $F_{1,33} = 1.99$, $P = 0.16$; Distance: $F_{1,33} = 0.82$, $P = 0.36$), while the effect of patch as a random factor was significant there (Patch: $F_{1,33} = 2.48$, $P = 0.04$).

Common juniper allelopathic effect bioassay on lettuce seeds

We found no difference in the germination rate of lettuce seeds among the treatments ($F_{2,8} = 2.69$, $P = 0.127$). The germination of seeds was similar in the Control seeds (93 %), compared to what we obtained in the presence of *Juniperus communis* (L.) dry Litter (97 %) or fresh Twigs (97 %). The effect of repetitions (Petri dishes) was insignificant ($F_{4,8} = 1.46$, $P = 0.297$). However, the development of the germinated seeds did differ ($F_{2,8} = 41.79$, $P < 0.001$), as the radicals of the germinated seeds were much longer in the Control (13.6 ± 1.9 mm) than in the juniper Litter treated (10.2 ± 0.5 mm) or fresh Twig treated (6.5 ± 0.7 mm) groups,

respectively. The effect of repetitions (Petri dishes) was insignificant ($F_{4,8} = 0.90$, $P = 0.56$) on the development of the radicals.

Discussion

By analyzing the probable factors behind the variation in plant cover in sand grasslands surrounding junipers, we were able to separate the effects of herbivory, shading, and allelopathy in creating bare sand rings around certain shrubs. The most remarkable difference in the sand grass vegetation surrounding junipers could be attributed to the presence of rabbits, as the grassland was consistently more open around the junipers hiding a rabbit warren than around the neighboring shrubs of matching size and exposure. We found a marginally significant distance-effect in vascular plant coverage and the strongest effect of herbivory was revealed at a distance of 1m from the junipers.

We found no indication of allelopathy at the edge of junipers, even though the high aromatic content of *Juniperus communis* (L.) (Adams, 1998), and our bioassay suggested the possibility for such interaction. The dense vegetation in the drip line of unoccupied shrubs (see Figure 2) indicated that plant-to-plant interaction had a negligible impact compared to grazing. It is still possible that the allelochemical effect was underestimated in our study using rather low sample size, or it only affects certain plant species underrepresented in our cover estimates or NDVI measures. Castro and colleagues (2005) found that germination of *Pinus silvestris* (L.) seeds was lowered close to *Juniperus communis* (L.), although allelopathy had a weak effect compared to climatic factors. Another study also found that allelopathy is less effective than other factors such as the physical barrier of the pine litter and the moisture condition (Williams et al., 1990). We suggest further investigations to clarify the importance of the allelochemical effects in the common juniper dominated communities.

There was no significant difference in the total plant cover between the shaded and the sunlit sides of the junipers. Due to shading, the exposure to light and heat certainly differed on the two sides of the junipers (Altbäcker, 1998), thus we expected a denser plant cover on the northern side. The shade of tall plants reduces topsoil temperature and decrease the evaporation of soil-moisture (Domingo et al., 1999), which may be an additional support in seed germination and seedling growth. Plants have reduced thermal stress and transpiration and are more protected from photo-inhibition in the shade (Moro et al., 1997). Although the plant cover around rabbit-free shrubs was more or less even, the impact of shading did not result in significant differences in the plant species composition between the shaded and the sunlit sides of the junipers. This suggests that the light and heat exposure are less important determinants of grass cover variation than grazing, in our system.

We applied both conventional plant cover estimates and measured NDVI to estimate ground-surface green biomass. The two estimates were highly correlated even though it was impossible to measure NDVI for the shaded quadrants (Kertész et al., 2001) at 1m distance on the northern side. Comparing the plant density sampled at different distances from the shrub, the NDVI was not sensitive enough to detect the distance effect, partly because NDVI also reflects cryptogam cover. However, rabbits did not consume cryptogams even though they could reduce the cryptogam cover by trampling and digging. The close match of NDVI pattern and conventional plant cover estimates supports that grazing is a highly important determinant of grassland heterogeneity in our study site. NDVI values were sensitive tools to demonstrate differences in plant production in similar systems (Csillag et al., 2001; Ónodi et al., 2006), but density estimates are still valuable tools where obtaining NDVI data is less feasible.

Rabbits were quite effective in shaping the vegetation within a few meters surrounding the shrubs. The localized impact was expected because rabbits in other shrublands were found foraging close to their warren (Villafuerte & Moreno, 1997; Bakker et al., 2005) where cover by tall shrubs could reduce predation risk. Such restricted foraging could have been a contributor to the low covers of both the monocots and the dicots in our case. We determined the actual diet composition of rabbits and found that the cover of those plant species consumed by the local herbivores decreased. Earlier nutritional studies demonstrated that grass species were composed a major and important part of the rabbit diet (Chapuis, 1990; Katona et al., 2004) and our present data also showed that the rabbit diet contained some, but not all, of the dominant grass species. Although comparing plant cover with diet compositions around seven localities offered limited power, we found remnants of some species in the diet composition that were not present in the quadrants. This indicates that rabbits may forage in a larger area than we sampled, similar to what Hudson and colleagues (2005) found by studying grazing of the cottontail rabbit (*Sylvilagus floridanus*, Allen) in a Mexican shrubland.

Rabbit presence reduced the cover of not only the consumed plants, but to a certain extent the unconsumed species around the junipers. There are some alternative explanations for this unexpected pattern. Although we only sampled the vegetation in the summer period, both the plant composition and the diet indicated seasonality (Mátrai et al., 1998). Some plant species could have been consumed by the rabbit earlier in the season but were not present in their current diet. Additionally, the reduced cover of unconsumed species could result from other activities like nest material collection and physical disturbances (trampling, digging, scraping). Such impacts can be accelerated by physical interactions if unprotected soil surface is exposed to wind or water erosion which keeps it bare (Wink & Wright, 1973). In our case, a higher percentage of bare sand was correlated with the rabbit presence and heat exposure on the southern slopes, which might have also

contributed to the lack of plant cover around certain shrubs. Wild rabbits prefer shrublands, not only for using canopy cover as a shelter, but they prefer vegetation that shows a high level of patchiness (Monzon et al., 2004). Their territorial system and localized grazing habits create sharp edges around shrubs sheltering their burrows.

Decreased abundance of herbs caused by heavy grazing can decrease the role of fire (Miller & Rose, 1999) and lead to increased woody vegetation on the savannah (van Langevelde et al., 2003), while on fire-prone habitats can be ruled to a herb dominant vegetation by decreased herbivory, because mainly the woody vegetation sensitive to fire damages (Belsky, 1992). According to Barney and Frischknecht (1974), in semi-arid habitats, woody species have a long recovery period. Moreover, they affect the survival of the seedlings and thus the age distribution of juniper shrubs (Markó et al., 2008). The spatial heterogeneity of combustible material is important in the prevention of the ignition of shrubs. Our former field study (Ónodi et al., 2008) showed that moderate grazing could successfully reduce the spread of fire on open sand grasslands. In this study we found that rabbits make the vegetation sparse around the occupied junipers, thus implying that rabbit-grazed bare sand rings can act as natural firebreaks by increasing large scale patchiness, thus altering the spread of fire. Moderate sheep grazing could also keep the fire away from the larger continuous areas of the juniper-poplar forest-steppe (Ónodi et al., 2008) because their activity is limited to the center of the open areas, isolating intercanopy zones, thus creating patchiness on a different scale.

Wildfire is one of the most important factors in shaping the arid and semi-arid communities and is affected by the increasing influence of climate change and land use alteration (Fernandes, 2001). Outbreak and spreading of fire are positively correlated with arid weather conditions (Briggs & Knapp, 1995) and with an increase in accumulation of combustible plant material (Whelan, 1995; Neary et al., 1999; Fernandes, 2001), which depends on the productivity of the community (Miller & Rose, 1999; Ónodi et al., 2008) and the intensity of herbivory (Ónodi et al., 2008). We suggest facilitating patchy grazing by introducing rabbits or increasing their density as a natural conservation tool to aid fire prevention, as it enhances habitat diversity and can be part of the management of shrublands in semi-arid regions.

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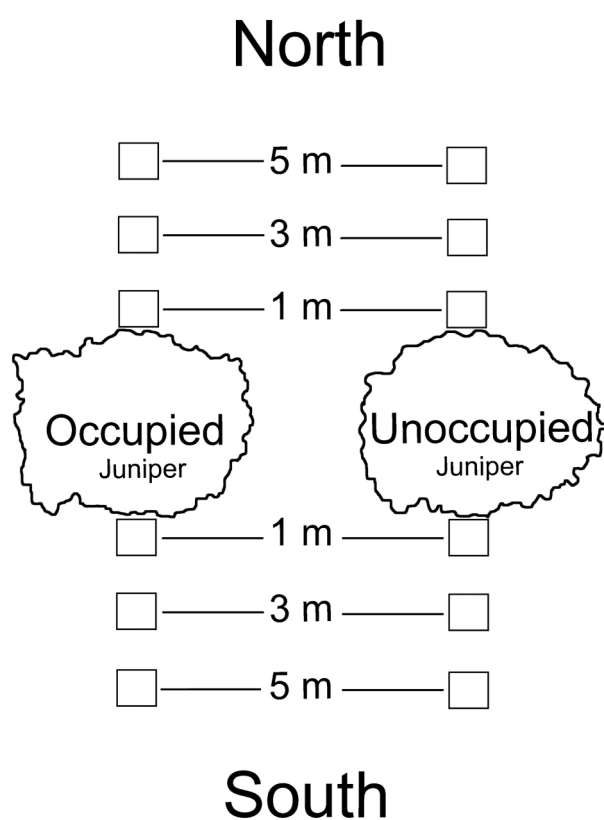


Figure 1. The sampling protocol. We chose similarly sized and positioned juniper patches (n=7). One patch was occupied by a rabbit warren (occupied), the other had no indication of rabbit occupation (unoccupied). At each shrub pair we established a series of 1 x 1 m quadrants in N/S compass orientation (southern and northern) in three-three distances (0-1 m, 2-3 m, 4-5 m), starting from the drip line of the juniper patch. Patches were at least 50 m apart to avoid colony overlapping.

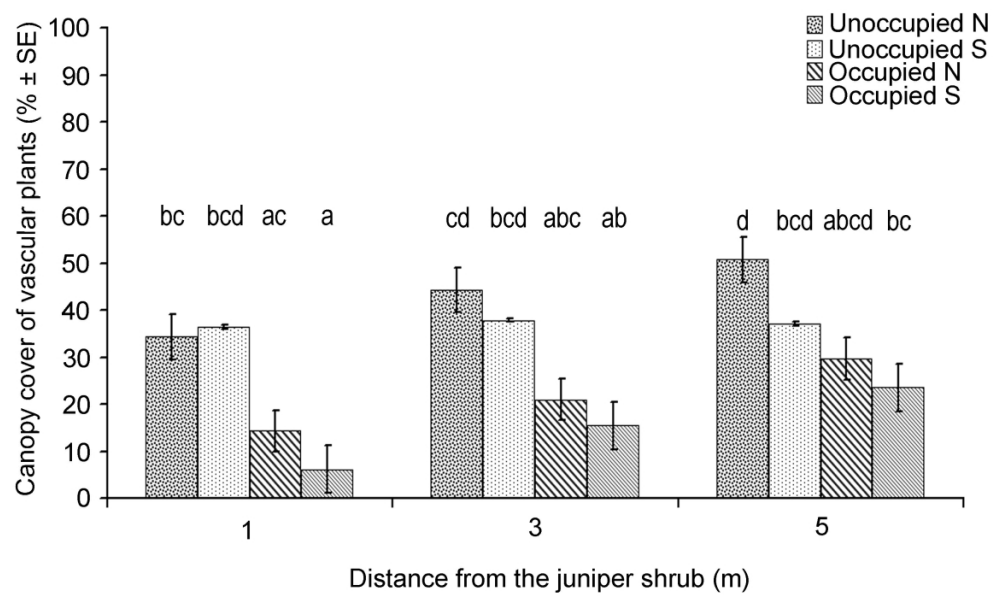


Figure 2. Total canopy vascular plant coverage in relation to the factor effects. The plant coverage is significantly lower near rabbit colonies and there is a minimum meter distance-dependent effect. Mean values and standard errors are shown.

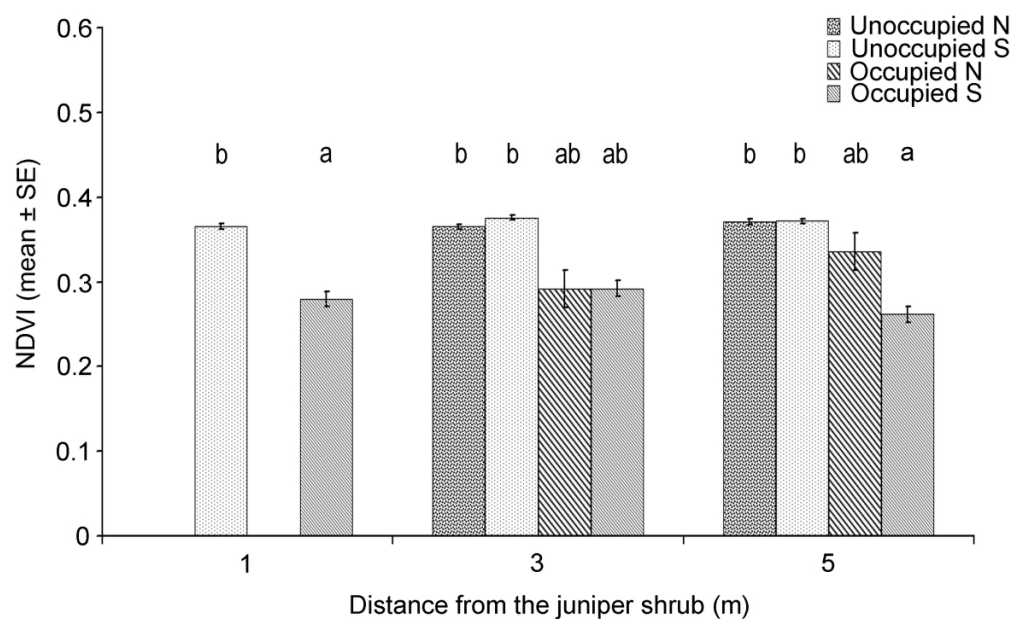


Figure 3. Normalized Differential Vegetation Index (NDVI) measured by Cropscan. NDVI-values were determined for each quadrant, except for those situated in the shade where the apparatus was not useable. The plant coverage is significantly lower near the rabbit colonies. Mean values of NDVI and standard errors are shown.

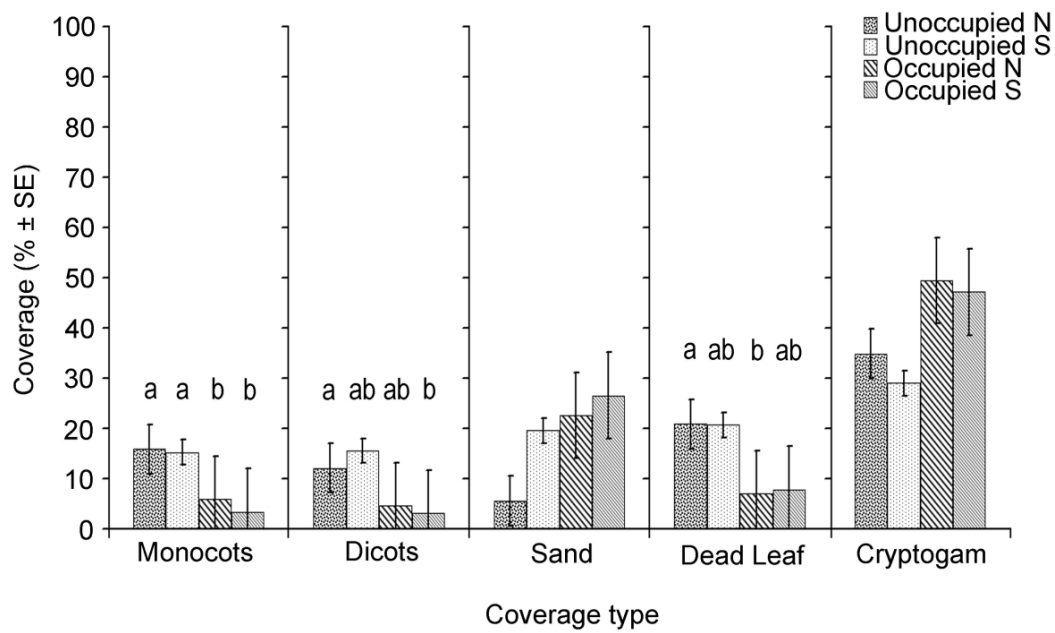


Figure 4. Means of the coverages and standard errors are shown at 1m distance, where the herbivore effect was relatively high. There is a significantly lower relative cover of Monocots, Dicots and Dead Leaf near occupied juniper patches. The groups of cover types are not compared with each other.

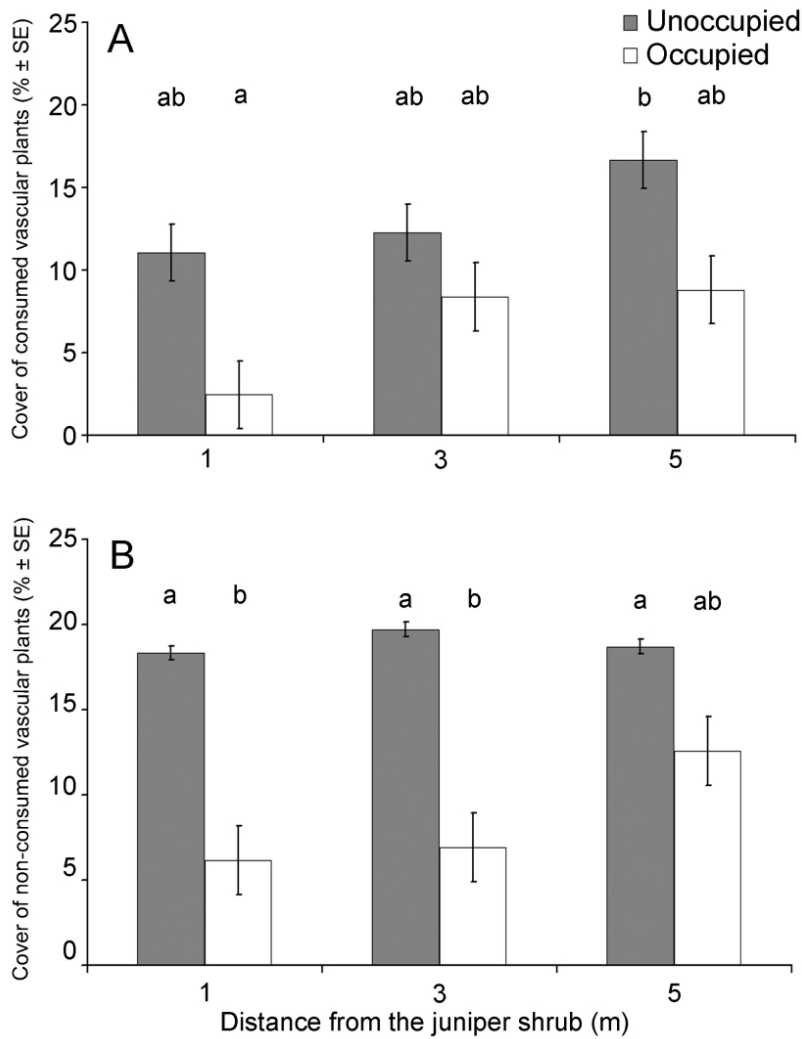


Figure 5. Canopy coverage of vascular plants consumed (part A) and non-consumed (part B) by rabbits.

At each occupied patch we summarized the coverage of the plant species found in rabbit pellets on that particular patch. Then we summarized the coverage of the same species for the pair of that patch. Mean and standard errors are shown.

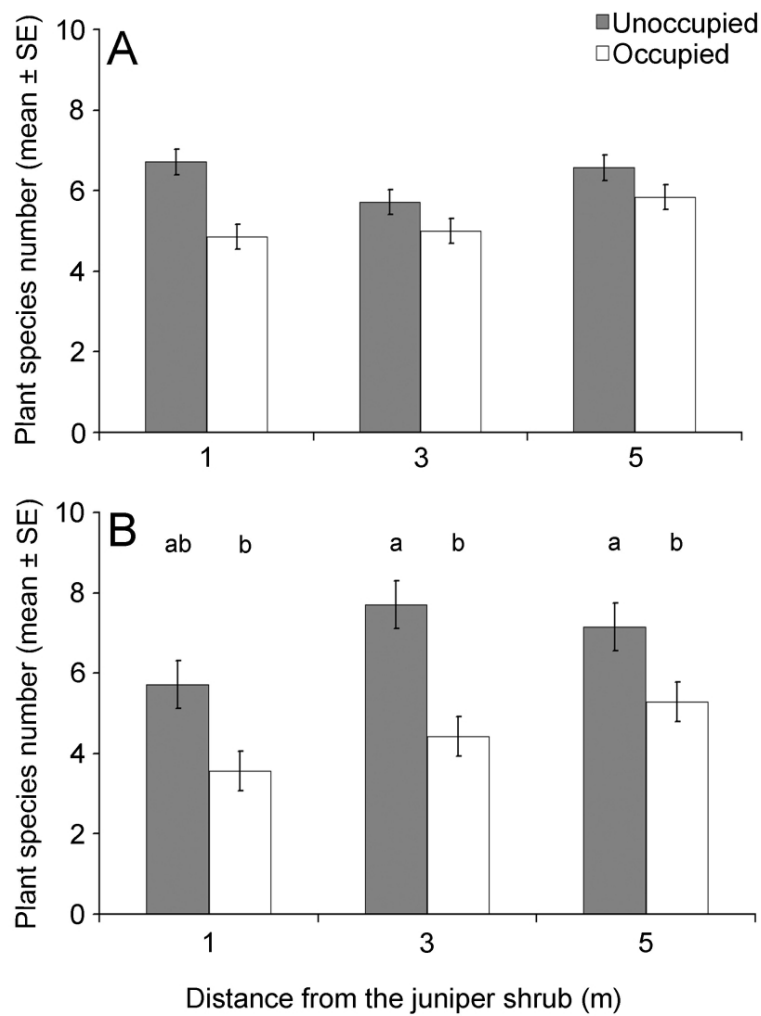


Figure 6. Plant species richness is shown for grasslands around occupied and unoccupied juniper patches. Species numbers around the unoccupied shrubs are significantly higher and there is a distance-effect, although this applies only to the rabbit occupied juniper patches. Mean and standard errors are shown. Significant differences among groups are represented by different letters above the bar graphs. (A: Northern side of the juniper patch; B: Southern side of the juniper patch)

39 **Table 1. This table shows comparative data between rabbit diet and plant availability.**

Plant groups	Total		Juniper patch with rabbit warren						
	Fecal composition	Plant cover	Fecal composition / Plant cover						
			1	2	3	4	5	6	7
Monocots	61 (3.1)	67.1 (8.3)	61.8 / 85.2	64.2 / 83.4	70.9 / 75.9	52.6 / 35.7	70.7 / 74.5	56 / 79.7	50.7 / 35
Dicots	33.8 (2.7)	29.8 (6.8)	36.1 / 14.8	34.3 / 16.6	28 / 24.1	37.2 / 42.1	23.1 / 25.5	32.2 / 20.3	45.8 / 65
Angiosperms	3.5 (1.5)	3.2 (3.2)	1.5 / 0	1.1 / 0	0.6 / 0	5.2 / 22.2	0.7 / 0	11.7 / 0	3.5 / 0
Seeds	1.7 (0.9)	0 (0)	0.6 / 0	0.4 / 0	0.6 / 0	5 / 0	5.5 / 0	0.2 / 0	0 / 0
Renkonen index by									
Plant species	19.4 (4.6)		11.2	34.9	9.4	42.2	23.2	10.5	25.6
Plant groups	82.3 (3.2)		76.6	80.8	94.9	78.1	93.8	76.3	80.8

40 Epidermis remnant fragments and plant cover mean values are in the columns, while the rows contain the mean values of plant group categories. The epidermis remnant
41 fragments mean values are calculated from the average of five rabbit pellets from each rabbit juniper patch, and the cover mean values are from the average of six quadrants
42 of occupied juniper patches. The total fecal column contains the mean and standard errors of all juniper patches of rabbit fecal averages. The total cover column contains the
43 mean and standard errors of all juniper patches of cover averages.
44