

Effects of grazing and habitat structure on the epigeic spider fauna in an open xerothermic area in southern Germany

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Summary

Due to land use changes, sandy open xerothermic areas in southern Germany have become rare, small, and isolated. Consequently, many xero-, thermo- or psammophile spider species have become restricted in their distribution, and endangered. The remaining open landscapes are priority sites for nature conservation. This also applies to the large (70 ha) former military site “Alter Flugplatz” within the urban area of Karlsruhe. There we studied the effects of management measures and habitat structure on the spider assemblages in three biotope types using one year of pitfall trapping. Ruderalized sites showed distinct assemblages from sandy turf and mat grass sites. The mowed mat grass sites differed from the grazed sites, which were more similar to the sandy turf. Apparently, habitat structure was more important for spider assemblages than plant species composition. Spider diversity correlated positively with vertical structural diversity, and negatively with bare ground in the trap surroundings. Grazing strongly increased the spider species richness in the ruderalized sites, but only slightly in grassland biotopes. Target species were more frequently caught under grazing. The spider guild composition was altered by grazing in sandy turfs and *Nardus* grassland, but not in the ruderalized sites, while guild diversity was always lower under grazing.

Introduction

In southern Germany, sandy and oligotrophic grassland biotopes are rare and endangered. The sand deposits mostly originate from wind-blown dispersals out of river beds, which had been dry and without vegetation cover towards the end of the last glacial. Hence, their origin is strongly linked to the existence of big river courses like the river Rhine. In contrast, fluvio-glacial sand deposits of Pleistocene glaciations cover large areas in the northern German lowlands (Burkart *et al.* 2004).

While in Central Europe nearly the whole terrestrial surface may once have been covered by forest, the first human agricultural activities during the Neolithic (as well as large herbivores) created and conserved open landscapes and deprived them of nutrients. The enrichment of the flora and fauna by open landscape species, which often depend on oligotrophic conditions, was the direct consequence of these changes (Burkart *et al.* 2004). During the last decades, intensification of agriculture, abandonment of use, afforestation, and building have reduced the open landscapes to small patches, and led to a dramatic loss of open landscape species. This also applies to the open sand biotopes in the Upper Rhine valley, which once had been more frequent (Zimmermann 2011). The remaining areas today often accommodate a specialized fauna and flora with xero-thermophilous species, of which a considerable portion is restricted to such sites (e.g. Leist 1994; Quinger 2000). Being anthropogenic, these open sandy biotopes are

characterized by, and dependent upon, disturbances (Burkart *et al.* 2004). To keep the areas open, and to preserve their species inventories, special management is essential, which often mimics the former usage, like grazing, mowing, burning, or mechanical barring of soil by agricultural or military machines.

Our study area is a 70 ha open area on windblown sand within the city of Karlsruhe (Upper Rhine valley, southern Germany), which recently got the status of nature reserve (Naturschutzgebiet “Alter Flugplatz Karlsruhe”). The area was already known to accommodate several endangered plant and animal species as well as rare biotope types, and is also a protected site according to the Habitats Directive of the European Union. The open character of the area originated from the historic use as military drill ground and airfield (until 1945) and is maintained by mowing and grazing (Zimmermann 2011).

While the effects of grazing and mowing on vegetation are rather apparent and well studied, the effects on arthropods are more obscure and complex. Mowing is a rare and short, but instantaneous and punctual strong impact on the ecosystem; extensive grazing, in contrast, influences it in the longer term by (particularly) trampling, selective browsing, and dung deposition, and thereby produces a small scale co-existence of different successional stages and a spatial relocation of nutrients. Therefore, extensively grazed areas are often more diversely structured than mowed meadows. In this respect, the degree of management is an important factor: while extensive grazing in general provokes a higher structural diversity, intensive land use, in contrast, reduces it (e.g. Kratochwil & Schwabe 2001; Morris 2000). Although many studies found a positive correlation between the heterogeneity of habitat structure and the species diversity, contradictory results have been reported as well (the decrease of animal species diversity with the increase of habitat heterogeneity; see Tews *et al.* 2004). For a successful habitat management, controls of the applied management measures are essential; they have to be an integrated component of every protection measure (Hänggi 1989). Because plant and animal species generally do not show the same ecological needs, it is advisable to survey the development of some selected groups of animals. According to Hänggi (1989), spiders are well suited for ecological target control: they exist in high abundances and with high taxa numbers in almost every terrestrial biotope, and show a large amount of stenoeccious species. Moreover, being unspecialized predators, they are independent of special plant species or prey animals.

In our study we wanted to contribute to the knowledge of the diversity of spiders in the nature reserve “Alter Flugplatz Karlsruhe” and to survey the effects of the management measures and of small scale aspects of habitat structure on the spider fauna. Therefore, we designed a one-year pitfall trap study. Results are crucial for a successful control of the protection and management of the area and a base for ecological monitoring.

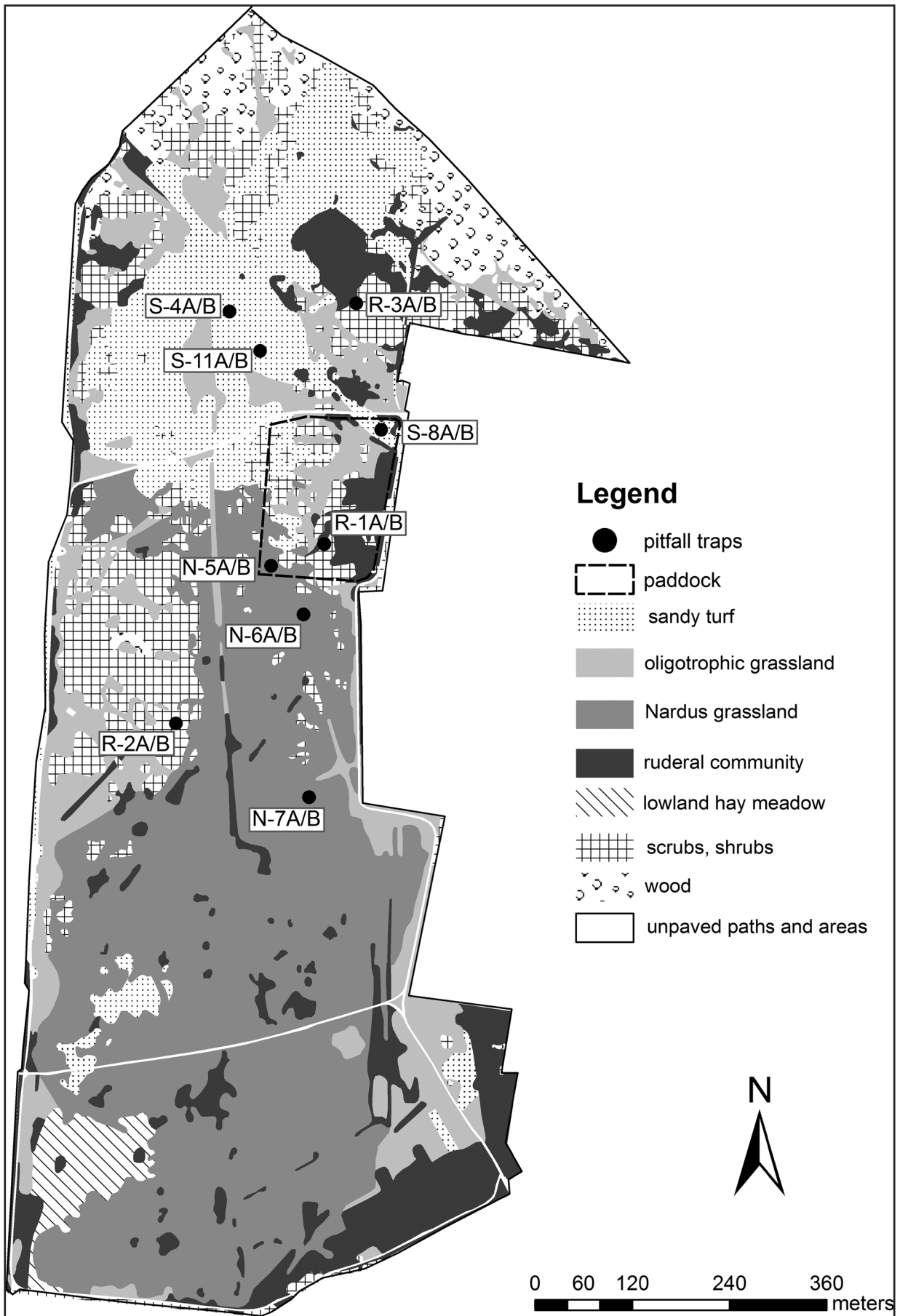


Fig. 1: Biotope types of the study area “Alter Flugplatz Karlsruhe” and location of paddock and pitfall traps. Vegetation mapping by Institut für Botanik und Landschaftskunde Karlsruhe on behalf of the Regional Council of Karlsruhe, based on the spatial information and planning system (RIPS) of the Landesanstalt für Umwelt, Messungen und Naturschutz Baden-Württemberg (LUBW) and on the topographic/cartographic information system (ATKIS) of the Landesamt für Geoinformation und Landentwicklung Baden-Württemberg (LGL). Modified and published on the authority of the Regional Council of Karlsruhe (Regierungspräsidium).

Material and methods

Study area

The nature reserve “Alter Flugplatz Karlsruhe” is situated in the north-western urban area of Karlsruhe in the Upper Rhine valley (Baden-Württemberg, Germany: 49.028017°N, 8.379787°E; WGS 84; 113–116 m a.s.l.). The geology is characterized by sand and gravel of the Rhine lower terrace, which is partly covered by windblown sand and the remains of an inland dune. Accordingly, the soil (predominantly a Luvic Arenosol) is nutrient poor, acidic, and extremely dry. During the period of use as drill ground and airfield, sporadic cutting and grazing by sheep were applied in order to keep the field – which once had been forested – open and prevent scrubs from taking hold. This low-intensity grassland use, in combination with the above-mentioned soil conditions, has resulted in the development of special habitat types of dry grasslands: tall grass cover dominated by the mat grass *Nardus stricta*, short dry acid turfs on inland sand with many open sand patches, and further acidic and oligotrophic grassland assemblages which are interspersed with *Rubus* scrubs, shrubs, and single trees (Fig. 1). Being very special and rare habitat types within the moist and forest-dominated Rhine valley, these biotopes are inhabited by a specialized, heat-preferring, open-landscape fauna (Rietschel & Strauss 2010; Vogel & Breunig 2000; Zimmermann 2011).

The habitat management during the last few years was aimed at maintaining the area's open character, and preserving the grassland communities with their associated species inventories. For this purpose, the southern part of the field with the taller grass (*Nardetalia*) stands was mowed in late summer every second year, whereas the northern part, especially the short dry acid turf, was managed since 2004 by year-round grazing. For this purpose, about ten donkeys and several goats were fenced in variable paddocks of 5–7 ha size. The modalities and areas of grazing changed

from time to time in order to adapt to current vegetation developments; particularly the expansion of woody plants and of rhizome-generating plant species like *Calamagrostis epigejos*. Mowing and grazing was supplemented by sporadic cutting of woody plants. A rabbit population also generates small-scale dynamics by creating patches of open sand.

Sampling methods and design

We aimed to establish a sample design by delimiting/defining replicates for grazed and ungrazed sites in different biotope types. However, we had to adapt to the current management system, as well as to local conditions like the spatial distribution of the investigated biotope types. Hence, ungrazed reference sites include sites which were not managed or only by mowing during our study period, but could well have been grazed in the past (Table 1). The grazing intensity in the grazed reference sites was relatively high because a smaller area (3.4 ha, paddock in Fig. 1) was fenced and grazed by 10 donkeys (but no goats; stocking rate: 1.5 livestock units ha⁻¹), but lasted only for three months (Table 1). Thus, we still consider the grazing regime as extensive in the longer term.

For the sampling of epigeic spiders, pitfall traps were used in three different biotope types: in mat grass (acidophilous psammophytic *Nardetalia*; dense cover of *Nardus stricta* with occurrences of *Festuca filiformis*, *Hieracium pilosella* and *Luzula campestris*), in short sandy turf (Thero-Airion) dominated by annual plant species (e.g. *Aira praecox*, *Ornithopus perpusillus*) and succulents (e.g. *Sedum acre*) and in ruderal communities (e.g. occurrence of *Calamagrostis epigeios*, *Poa angustifolia*) with *Rubus* scrubs (Table 1, Fig. 1). Classification of vegetation was done by Vogel & Breunig (2000). Each biotope type was represented by three groups of different historic and actual use. Each group

Biotope type	Site	Characteristics	General management	Management during study period
sandy turf	S-11A S-11B	<i>Sedum acre</i> dominated, on lime-free gravelly sand	sporadic grazing by donkeys and goats	ungrazed
sandy turf	S-4A S-4B	<i>Cynodon dactylon</i> dominated, slightly calcareous sand, less gravel	sporadic grazing by donkeys and goats	ungrazed
sandy turf	S-8A S-8B	<i>Sedum acre</i> dominated turf on lime-free gravelly sand	sporadic grazing by donkeys and goats	grazed by donkeys from 24 April–15 July 2010
mat grass	N-5A N-5B	<i>Nardus stricta</i> grassland on lime-free gravelly sand	sporadic grazing by donkeys and goats	grazed by donkeys from 24 April–15 July 2010
mat grass	N-6A N-6B	<i>Nardus stricta</i> grassland on lime-free gravelly sand	biennial mowing (last summer 2009)	untreated
mat grass	N-7A N-7B	<i>Nardus stricta</i> grassland on lime-free gravelly sand	biennial mowing (last summer 2009)	untreated
ruderal	R-1A R-1B	Ruderals with <i>Rubus</i> scrubs on lime-free gravelly sand	sporadic grazing by donkeys and goats	grazed by donkeys from 24 April–15 July 2010
ruderal	R-2A R-2B	Ruderals with <i>Rubus</i> scrubs on lime-free gravelly sand	no treatment	untreated
ruderal	R-3A R-3B	Ruderals with <i>Rubus</i> scrubs on lime-free gravelly sand	sporadic grazing by donkeys and goats	ungrazed

Table 1: Characteristics of the 18 study sites.

consisted of two sites (A and B), where three pitfall traps were installed in a triangle, spaced 5 m from each other.

The cups used for trapping were 65 mm wide by 100 mm deep, filled with 5% acetic acid with a drop of detergent, and covered by transparent roofs. The collected material was transferred to ethanol, and adult spiders were identified to species using Heimer & Nentwig (1991), Metzner (2011), Nentwig *et al.* (2011), Roberts (1993), and Tongiorgi (1966). Spiders, as well as bycatches, are deposited at the Staatliches Museum für Naturkunde Karlsruhe (SMNK). Catches of pitfall traps depend on both species abundance and activity (Thomas, Parkinson & Marshall 1998) and are therefore often called activity densities.

The small-scale habitat structure of the area surrounding the pitfall trap (1 m²) was determined in spring, summer and autumn. The squares were divided in four 50 × 50 cm² parts in which the cover percentages of the following seven functional classes were estimated: moss/lichens, graminaceous/herbaceous plants, shrubs, bare ground, stones, dung (of rabbits, goats and donkeys), and litter. In addition, the vertical vegetation structure was determined by estimating the percentages of vegetation cover in six layers of different heights: 0–5 cm, 5–10 cm, 10–25 cm, 25–50 cm, 50–80 cm and >80 cm.

Data analysis

The similarity of the sampling sites and biotope types with regard to their spider assemblages was analysed by multivariate methods using the software Canoco 4.53 and WinKyst 1.0. A non-metric multidimensional scaling (NMDS) was performed as unconstrained ordination. Furthermore, a detrended correspondence analysis (DCA) was done in order to find out whether a unimodal or linear model would better be used to ordinate the sites by estimating the length of gradient on the first axis. Because a gradient length of 3.7 did not unequivocally indicate unimodal or linear conditions, both a canonical correlation

analysis (CCA) and a redundancy analysis (RDA) with habitat structure parameters as environmental variables were carried out subsequently as constrained method.

The following univariate diversity indices were calculated for the summed species abundances of each site: the number of species *S*, the total number of individuals *N*, the Shannon diversity index *H'*, and Pielou's Evenness index *J'* (Magurran 2004). *H'* was calculated with the free software package Past 2.09. In addition, diversity (*H'*) and Evenness (*J'*) were calculated for the guild abundances of the sampling sites. For this purpose, the spider species were assigned to one of eight guilds (Table 2). Spider guilds represent life forms, meaning "a group of species utilizing the same resource in similar ways" (Uetz, Halaj & Cady 1999, p. 270). For spiders, it is mainly based on foraging strategies: hunting (running spiders, stalkers, ambushers) or web-building, diurnal or nocturnal activity, and the main stratum, e.g. preference for vegetation or ground. Spider guild classification was done on the basis of Uetz, Halaj & Cady (1999), further differentiated by nocturnal or diurnal activity.

For quantifying the microspatial heterogeneity of the pitfall trap surroundings, Shannon indices for the horizontal and vertical structure, as well as the mean vegetation height, were calculated (Tews *et al.* 2004). These indices were correlated with species diversity *H'* (performing regression analyses in SigmaPlot 8.0) in order to detect the relationship between habitat structural diversity and species diversity (Greenstone 1984). Furthermore, different structural measures were correlated with species diversity, in order to identify those which are most influential.

The effect of grazing was analysed by performing analyses of variance (using GLM in Statistica 9.0 – Statsoft Inc. 2009). To meet the requirement of a balanced data set, we reduced the number of sampling sites to 12 (see Table 3). In order to test if significant effects of biotope type and/or grazing and the number of taxa *S* exist, a two-factorial ANOVA was carried out based on a Poisson distribution. The same reduced set of sampling sites was analysed with a two-factorial ANOVA in order to detect influences of the biotope type and/or grazing on the guild diversity (*H'*, test based on a gamma probability distribution) and on the abundances of Red List species of Baden-Württemberg (percentages of the total abundances of species; test based on a gamma probability distribution).

Results

Overview

A total of 9009 adult spiders representing 21 families, 79 genera, and 123 species were collected and identified. The largest portion of the individuals belonged to the family Lycosidae (39%), whereas Linyphiidae was the most species-rich family (44 species). Half of all species are known to be xerophilous (*n* = 61). A status of endangerment for Baden-Württemberg and/or Germany applies to 29 species (Nährig & Harms 2003; Platen *et al.* 1998). Detailed faunistic aspects as well as guild and habitat classifications are described in Hemm, Meyer & Höfer (in press). The

spider guild	spider taxa
ground runners (diurnal)	Lycosidae (except <i>Aulonia</i>), <i>Micaria</i> , <i>Phrurolithus</i> , <i>Zodarion</i> , <i>Pachygnatha</i>
ground runners (nocturnal)	Gnaphosidae (except <i>Micaria</i>), Dysderidae, Liocranidae (except <i>Phrurolithus</i>), <i>Clubiona neglecta</i>
foliage runners (diurnal)	<i>Zora</i>
foliage runners (nocturnal)	<i>Clubiona</i> (except <i>Clubiona neglecta</i>), <i>Cheiracanthium</i>
ambushers (diurnal)	<i>Xysticus</i> , Philodromidae, <i>Pisaura</i>
ambushers (nocturnal)	<i>Ozyptila</i>
stalkers	Mimetidae, Salticidae
web builders	Linyphiidae, Hahniidae, Araneidae, <i>Aulonia</i> , Dictynidae, Theridiidae, Agelenidae

Table 2: Spider guild classification on the basis of Uetz *et al.* (1999), further differentiated by nocturnal or diurnal activity.

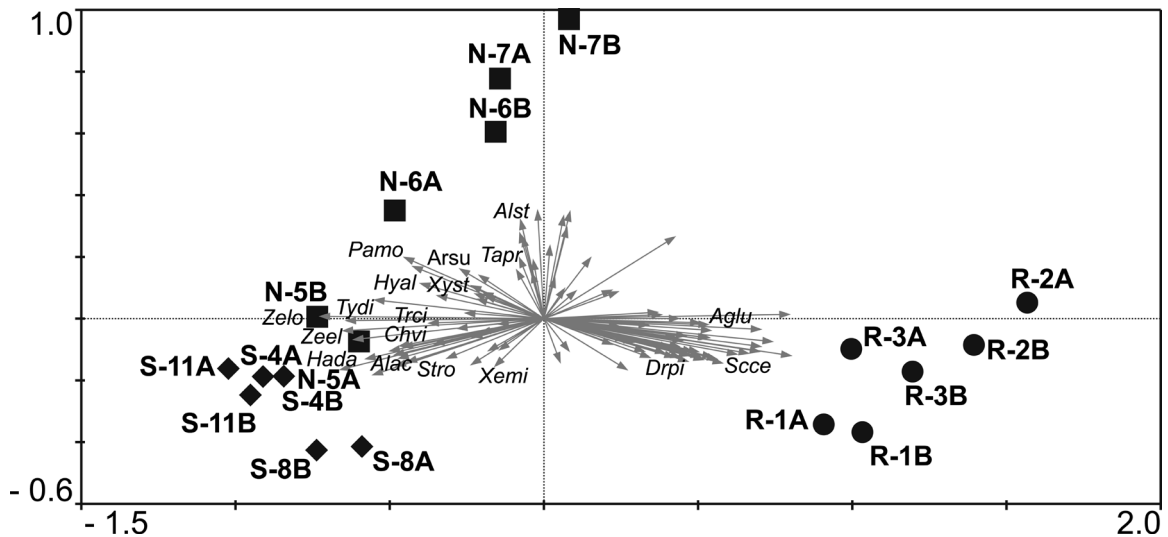


Fig. 2: Biplot resulting from a non-metric multidimensional scaling (NMDS) (stress value = 0.029) with the 18 sample sites and species vectors. ● = ruderalized sites; ■ = mat grass sites; ◆ = sandy turf sites. Labelled species vectors represent Red List species of Germany or Baden-Württemberg (excluding singletons and doubletons): Aglu = *Agroeca lusatica*, Alac = *Alopecosa accentuata*, Alst = *Alopecosa striatipes*, Arsu = *Argenna subnigra*, Chvi = *Cheiracanthium virescens*, Drpr = *Drassyllus praeficus*, Hada = *Haplodrassus dalmatensis*, Hyal = *Hypsosinga albovittata*, Pamo = *Pardosa monticola*, Scce = *Scotina celans*, Stro = *Styloctetor romanus*, Tapr = *Tapinocyba praecox*, Trci = *Trichopterna cito*, Tydi = *Typhochrestus digitatus*, Xemi = *Xerolycosa miniata*, Xyst = *Xysticus striatipes*, Zeel = *Zelotes electus*, Zelo = *Zelotes longipes*.

number of individuals which were included in statistical analyses amounted to 7474 adults (derived from the period, when pitfall traps were captive in all sites).

Effects of biotope type and habitat structure

The NMDS ordination shows a very clear separation of the ruderal from both grassland spider assemblages (Fig. 2, stress value: 0.029). The ruderal as well as the sand sites are clustered very well. The spider assemblages in *Nardus* grassland show the highest variability and cannot be separated from the sand sites assemblages clearly: the grazed *Nardus* sites N-5A and N-5B are close to the sandy turfs, while the mowed *Nardus* sites N-6A, N-6B, N-7A and N-7B show great distances to both sandy turfs and ruderalized sites. Accordingly, one part of the species vectors (see biplot in Fig. 2) shows a strong bundling to the direction of the ruderal sites, whereas in the direction of the two grassland sites the species vectors diverge strongly. The two open grassland biotope types play a considerably higher role as habitat for endangered species (see labelled species vectors) than the ruderals. The second axis might represent grazing effects: grazed sites are always positioned on one side of the second axis. Moreover, within the cluster of the ruderalized sites, a clear progression along the second axis can be perceived: from the two recently grazed sites (R-1A, R-1B), over the generally grazed but recently ungrazed sites (R-3A, R-3B), to the sites which were not grazed during the last few years (R-2A, R-2B).

For the constrained ordination analyses (CCA, RDA), all ten environmental variables shown in Table 4 were introduced. But, because several of these showed collinearity (e.g. vegetation height and cover percentages of shrubs), they were reduced by an automatic forward selection in the programme Canoco to the five most influential (significant) variables shown in the ordination. The canonical

correspondence analysis (CCA) and the redundancy analysis (RDA) showed accordant results. The RDA (Fig. 3) shows a similar sample distribution as the NMDS ordination in Fig. 2, whereas the sample distances are slightly higher because of the inclusion of further variables. Here, the habitat structure appears highly responsible for the ordination of the sampling sites (67.1%). The first axis may reflect a vegetation cover gradient: sites with higher vegetation, which are characterised by higher percentages of gramineous/herbaceous plants, shrubs and litter on the

Site	S (species)	N	H' (species)	H' (guilds)
S-11A	26	329	2.23	1.15
S-11B	31	384	2.49	1.25
S-4A	33	359	2.73	1.34
S-4B	33	347	2.83	1.45
S-8A	37	462	2.14	1.13
S-8B	34	287	2.68	1.31
N-5A	37	417	2.87	1.28
N-5B	41	403	2.77	1.31
N-6A	42	422	2.85	1.51
N-6B	47	536	3.07	1.60
N-7A	37	341	2.71	1.32
N-7B	32	341	2.66	1.39
R-1A	53	767	3.14	1.12
R-1B	52	760	3.02	1.13
R-2A	36	219	2.93	1.23
R-2B	40	281	2.84	1.25
R-3A	42	224	3.10	0.98
R-3B	41	395	3.08	0.93

Table 3: Diversity indices of spider species and guild composition of the 18 sample sites. Sites included in the two-factorial ANOVAs are shown in bold.

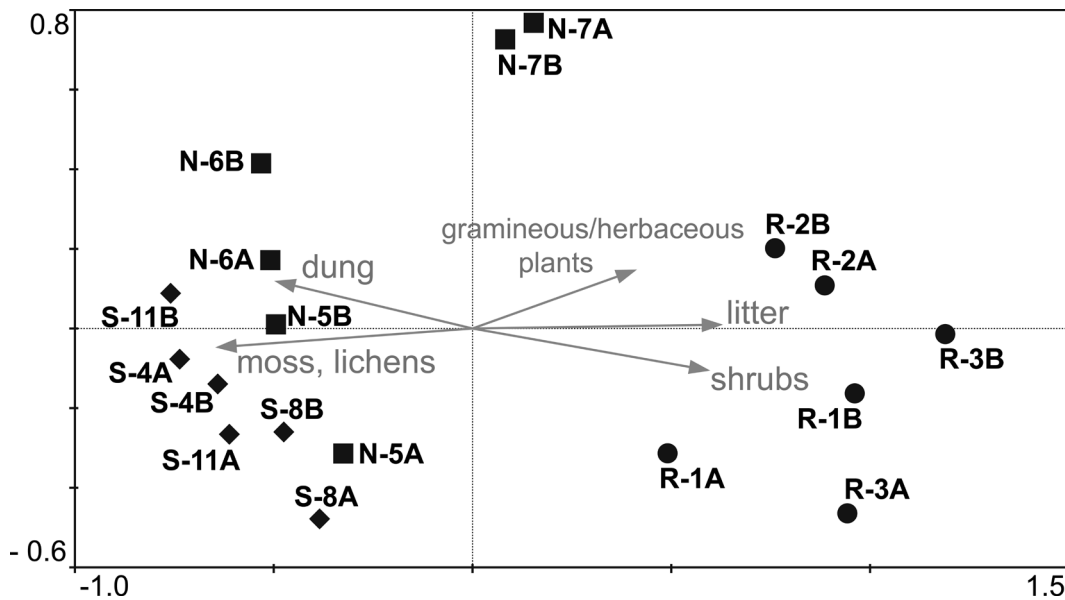


Fig. 3: Biplot resulting from a redundancy analysis (RDA) with the 18 sample sites (first and second axes displayed). ● = ruderalized sites; ■ = mat grass sites; ◆ = sandy turf sites. Five structural variables were included as environmental variables. Portion of variance explained by the environmental variables is 66%, of which the first axis accounts for 67.0%, the second axis for 18.4%.

right and the sandy sites with lower vegetation and parts of the *Nardetalia*, which are rich in moss and lichens on the left. The two sites N-7A and N-7B are separated from the other four *Nardus* sites. They show a higher amount of gramineous and herbaceous plants and seem to be strongly influenced by the second axis, which also seems to represent grazing effects.

Two Red List species were collected exclusively in *Nardus* grassland: *Alopecosa striatipes* (C. L. Koch, 1837) and *Tapinocyba praecox* (O. P.-Cambridge, 1873). The dictynid spider *Argenna subnigra* (O. P.-Cambridge, 1861) appeared predominantly in *Nardus* grassland, but was also common in sandy and ruderalized sites. One Red List species was captured exclusively in sandy turf: the lycosid *Alopecosa accentuata* (Latreille, 1817). Ten of the species which are relevant in terms of nature conservation seemed to avoid the ruderalized sites: *Styloctetor romanus* (O. P.-Cambridge, 1872), *Cheiracanthium virescens* (Sundevall, 1833), *Haplodrassus dalmatensis* (L. Koch, 1866), *Hypsosinga albovitata* (Westring, 1851), *Pardosa monticola* (Clerck, 1757), *Trichopterna cito* (O. P.-Cambridge, 1872), *Typhochrestus digitatus* (O. P.-Cambridge, 1872), *Xysticus striatipes* L. Koch, 1870, *Zelotes electus* (C. L. Koch, 1839) and *Zelotes longipes* (L. Koch, 1866). But the ruderalized sites also accommodated several Red List species, three of them even seem to prefer these sites, although they were also captured in the grassland: *Agroeca lusatica* (L. Koch, 1875), *Scotina celans* (Blackwall, 1841) and *Drassyllus praeficus* (L. Koch, 1866). Interestingly, the lycosid *Xerolycosa miniata* (C. L. Koch, 1834) appeared particularly abundant in sandy turf sites, but was also very often collected in ruderalized sites. It is remarkable that in both biotope types *X. miniata* was clearly more frequent in the sites which had been grazed during the sampling period. Four more species also showed a considerable higher activity density in grazed sites: *Styloctetor romanus* in *Nardus* grassland and sand sites; *Haplodrassus dalmatensis*, *Trichopterna cito* and *Zelotes electus* were also found in both grassland communities, but

showed higher activity density under grazing only within the *Nardus* grass, but not in the sandy turf.

Species and guild diversity indices (H') of spiders are shown in Table 3. The results suggest that, in general, the sandy turfs accommodate the lowest species diversity, whereas the ruderalized areas offer the highest. In contrast, most ruderalized sites show lower guild diversity than *Nardus* grassland and sandy turf. The regression analyses (Table 4) allow the identification of five variables which significantly influence the species diversity H' . The vertical structural diversity, the mean vegetation height and the percentages of shrubs and litter are positively correlated with species diversity, whereas the portion of bare-ground shows a highly significant negative correlation.

Effects of grazing

Grazing clearly increased the spider species richness in the ruderalized area, but only slightly in sandy turf and *Nardus* grassland (Fig. 4, raw data shown in Table 3). Hence, this effect was not significant (at the level of $p < 0.05$) in total (Wald $\chi^2(1) = 3.4$, $p = 0.065$). Biotope type however showed a significant influence on the species number (Wald $\chi^2(1) = 6.1$, $p = 0.047$). There is no significant interaction between grazing and biotope type (Wald $\chi^2(2) = 1.4$, $p = 0.49$).

In regard to the relative activity densities of Red List species (of Baden-Württemberg), grazing significantly increased the activity densities within mat grass and sandy turfs, but not in ruderal sites (Wald $\chi^2(1) = 36.9$, $p = 0.0000$); the interaction between grazing and biotope type is highly significant (Wald $\chi^2(2) = 9.4$, $p = 0.009$). Biotope type also had a significant effect (Wald $\chi^2(1) = 278.0$, $p = 0.0000$): In ruderalized sites very few individuals of Red List species were caught (Fig. 5).

In contrast, grazing decreased the guild diversity of spiders with low effect size but high significance (Fig. 6,

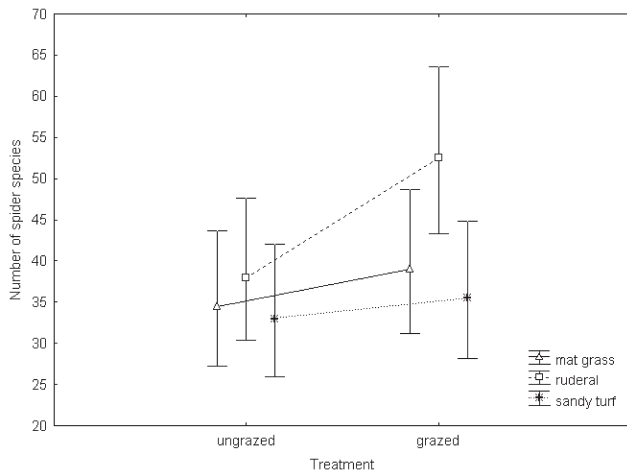


Fig. 4: Results of the two-way ANOVA with means and 95% confidence intervals of the number of spider species (S) in grazed and ungrazed sites (based on a Poisson probability distribution).

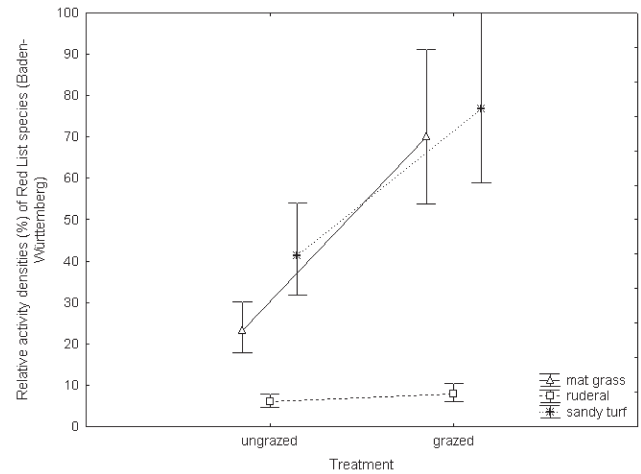


Fig. 5: Results of the two way ANOVA with means and 95% confidence intervals of the relative activity densities of Red List species in Baden-Württemberg (in % of the total activity; based on a gamma probability distribution).

Wald $\chi^2(1) = 19.3$, $p < 0.001$), most strongly in sandy turf and the ruderalized area. The influence of the biotope type on the guild diversity was also highly significant (Wald $\chi^2(1) = 24.3$, $p < 0.001$). There was no significant interaction between grazing and biotope type (Wald $\chi^2(2) = 2.9$, $p = 0.23$). When looking behind the index at the proportion of the guilds, the following emerges: within ungrazed *Nardus* grassland diurnal ground runners were dominant, while under grazing higher numbers of web-building and nocturnal ground runners and lower numbers of diurnal ambushers were captured. In sandy turf biotopes, ungrazed sites showed spider assemblages with high portions of web-building and nocturnal ground runners; in grazed sites, in contrast, diurnal ground runners were caught to a greater extent, web-building species more rarely, and stalkers were almost absent in grazed sandy turfs. In ruderalized sites, the spider guild composition was not strongly altered by grazing.

Discussion

Our data clearly show different spider assemblages in (shrubby) ruderalized sites in comparison with grassland sites. The ruderalized sites and the sandy turfs seem to

accommodate a characteristic spider fauna, whereas the *Nardus* grassland shows the highest variability. The extent of the spider assemblages of the *Nardus* grassland from the centrally situated, mowed sites (N-7) over the more marginal, mowed sites (N-6) to the more patchy, grazed sites (N-5) seems to be correlated with different structural properties, e.g. the density of the mat grass cover. Considering that the structural characteristics of habitats are directly influenced by habitat management (Downie, Butterfield & Coulson 1995), it seems that the grazing of the mat grass sites (N-5) did result in a lower plant cover and higher amounts of moss and lichens in comparison to the sporadically mowed sites. As a consequence, the spider assemblage of the grazed mat grass was more similar to the assemblage of the short-grass covered sandy turfs. In this sense, the group of spiders which shows a positive reaction to the grazing of the mat grass but no reaction to the grazing of the sandy turf (*Haplodrassus dalmatensis*, *Trichopterna cito*, *Zelotes electus*) may benefit from the changed light situation. This indicates that habitat structure seems to be more important for the formation of spider assemblages than plant sociology. Being unspecialized predators, spiders rather depend on the spatial characteristics of their environment which influence, on the one hand, climatic conditions (e.g. humidity, exposure) and, on the other hand, several behavioural aspects (e.g. foraging,

variable	type of correlation	R ²	p
horizontal structural diversity (H')	positive (linear)	0.21	0.054
vertical structural diversity (H')	positive (linear)	0.40	0.005
mean vegetation height	positive (exponential rise to maximum)	0.38	0.007
moss/lichen cover	negative (linear)	0.19	0.07
grass/herb cover	positive (linear)	0.19	0.07
shrub cover	positive (linear)	0.39	0.005
litter cover	positive (linear)	0.38	0.006
bare ground	negative (linear)	0.52	0.0007
stones	negative (linear)	0.005	0.78
dung	negative (linear)	0.03	0.50

Table 4: Correlations between spider species diversity (Shannon H') and structural variables. Strong and significant correlations are shown in bold.

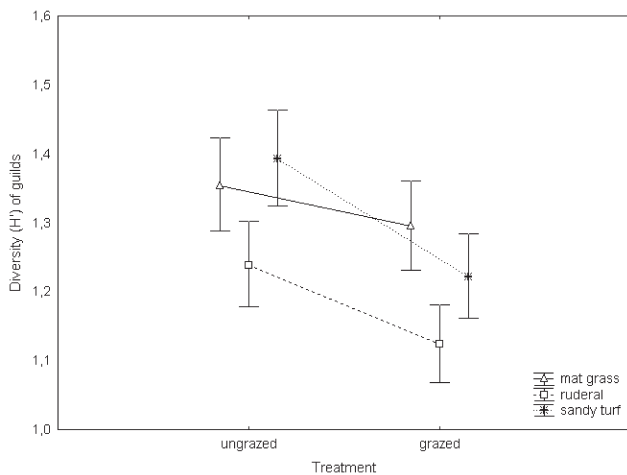


Fig. 6: Results of the two way ANOVA with means and 95% confidence intervals of the guild diversity (Shannon H') in grazed and ungrazed sites (based on gamma probability distribution).

inter-species communication); this applies to web-building species as well as to hunting spiders (Greenstone 1984; Uetz 1991).

The horizontal structural diversity seems to play only a minor role for spider species diversity. However, in terms of vertical structural diversity, our results follow the “habitat heterogeneity hypothesis” (Lack 1969): species diversity increases with higher habitat structure diversity. The more complex habitats are, in terms of spatial structure, the more niches can be occupied by species with different environmental needs (Tews 2004). Having higher vegetation (e.g. shrubs), vertical structural diversity, and more litter, the ruderalized sites in our study area offer a more shaded habitat which is important for several species (forest dwellers, e.g. *Pardosa lugubris* and hygrophilous species, e.g. *Pirata uliginosus*) without losing most of the open landscape species, and therefore show a higher species diversity and richness than the other habitat types (edge effect in ecotones). In contrast, the sandy turfs, being poorly structured habitats with low and sparse plant cover and a higher amount of bare ground, offer very special conditions to a small number of species, and therefore show a lower diversity. However, those are the rare and endangered photo- and xero-/thermophilous species (target species).

Other investigations about spiders in dune habitats emphasised the important role of spatial patterns as well. Merckens (2000) assumed the degree of vegetation cover and its structural composition to be one of the most influential factors on spider assemblages in sandy and dry habitats of northern Germany. Gallé, Torma & Körmöczy (2010) inferred from their studies in sandy grasslands in the Hungarian Great Plain that the main variables that influence the spider species composition are soil moisture, elevation, and the total coverage of the herbaceous vegetation. Moreover they could not find a significant correlation between plant taxonomic diversity and spider diversity. Also, investigations of submontane spiders in *Nardus* grasslands of northern England suggested that vegetation density is the major factor influencing the spider distribution (Downie, Butterfield & Coulson 1995).

In general, grazing effects are rather weak. In our opinion, this is due to the extensive grazing resulting in a low effect size, and the fact that actually ungrazed sites may have been grazed in the past, which introduces further variability. Certainly, grazing effects have to be regarded for each biotope type separately. Within the sandy turfs, only marginal changes in species composition by grazing are apparent (NMDS, Fig. 2). Only slightly higher species richness was observed, while the percentages of Red List species increased significantly. However, the diversity of guilds (life forms) decreased strongly. Being already inherently a poorly structured two-dimensional biotope, this fact is quite remarkable. The species composition of the mat grass biotope seems to be influenced by the habitat architecture, and thus by grazing, which leads to the appearance of species which predominantly inhabit the sandy grasslands of the area. This might be the reason for the increase of the Red List species percentages. An increase of spider species and a decrease of guild diversity were observed to a minor degree only. The ruderalized sites showed a different species composition under grazing. Grazed ruderals may be additionally inhabited by (e.g. photophilous) species of the mat grass and sandy turf areas because of, for instance, changed light situations. Therefore, grazing (by the donkeys) seems to reduce gramineous/herbaceous plants in ratio to scrubs in the ruderals, so that the spread of *Rubus* scrubs is actually not hindered (see Fig. 3). Further, with respect to the number of spider taxa, especially the ruderalized sites benefit from grazing. But in this biotope type the percentages of Red List species cannot be increased by grazing. Moreover, a distinct decrease of guild diversity has been observed as well.

Herbivory of grazing animals and the resulting decrease of structural plant architecture (vertical structural aspects in particular) might be the reason for this reduction of guild diversity. It remains unclear why this trend goes along with higher species numbers. This combination might lead to a higher competitive pressure: A higher number of species are using the habitat resources in the same way, while the numbers of individuals remain more or less at the same level. Consequences of grazing on the spider guild composition are varying for the different biotope types. As it is correlated to species composition, guild composition of grazed *Nardus* grassland gets closer to the sandy turfs. Grazing of sandy turfs seems to make web building more difficult (which applies in this case especially to ground-level living Linyphiidae), which might be caused directly by the action of the grazing animals or indirectly through altered plant architecture.

When comparing grazing effects of this study with others, unexplained variabilities by different grazing duration, intensity and different grazer species have to be kept in mind. Gibson, Hambler, & Brown (1992), who performed a controlled grazing experiment with sheep on calcareous grasslands, reported an accumulation of spider species along a successional gradient. But, according to them, managed grasslands often contain fewer invertebrate species than unmanaged, which is not in accordance with our results. They explained this by assuming that management like grazing or cutting is decreasing the structural diversity.

In conclusion, the current habitat management of the nature reserve “Alter Flugplatz Karlsruhe” is well qualified

and essential for conserving the open landscape spider species of the area. Quantitatively, the ruderalized sites as ecotones offer, at present, the highest species richness, but without maintaining the grassland biotopes of the area this richness would probably decrease. In contrast, qualitatively (regarding target species from a species conservation perspective) the *Nardus* grassland and sandy turfs are more valuable, although they accommodate lower species richness. Grazing, therefore, supports spider species richness and particularly living space for Red List species in the area. However, grazing of *Nardus* grassland is not advisable because it would probably lead to an assimilation of the typical mat grass spider fauna by spider assemblages of sandy turfs.

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