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Ground-dwelling invertebrate communities in mountain grasslands in South Tyrol (Italy): Surveying changes in abundances, diversity, and sex ratio

Abstract

There are few studies of ground-dwelling invertebrates from alpine grasslands, often with only one or a few samplings per growing season. However, to get a comprehensive picture of the faunal community present, sampling over a full season is required. Here we present data on ground-dwelling macro-invertebrate communities from two differently managed mountain grasslands (i.e. an intensively managed hay meadow and an extensively grazed dry pasture). Both sites were monitored continuously over a full growing season (April to early December) using pitfall traps.
We found considerable differences in abundances of the entire ground-dwelling invertebrate communities and in Araneae species diversity between the two grassland types, with the pasture having the lower abundances (i.e. activity densities as individuals per sampling day) but higher spider species diversity. We still found clear effects of management, most likely due to differences in habitat structure and presumably also in prey availability. Sex ratios of spiders did not differ much between the grasslands, however, a negative effect of mowing on the abundances of Araneae and adult Coleoptera was found. Management intensity negatively affected invertebrate abundances and species diversity, but not population dynamics.

Keywords: pitfall traps, dry pastures, Araneae, spiders, LTER

Introducation

Grasslands globally account for 40 % of the terrestrial area (FAO 2005), and are therefore important ecosystems. In the European Alps, 18 % of the area is grasslands (Flury et al. 2013; Tappeiner et al. 2020) and they show a high diversity of flora and fauna (Spehn et al. 2010; Dengler et al. 2014). Most grasslands have been formed and shaped by extensive human or human-associated activities over centuries and even millennia, mainly through agricultural practices such as fodder production (hay) and/or grazing by domestic animals (Schirpke et al. 2017). In mountainous areas such as the European Alps natural grasslands occur predominantly above the natural treeline and on exposed locations where trees cannot grow (e.g. in very steep slopes or along riverbanks), while managed grasslands in the subalpine and montane zones were created by clearing forests close to farms in order to reduce the distance between fodder and farm. These mountain meadows and pastures were extensively managed until the end of the 20th century, resulting in semi-natural biodiversity hotspots (Kampmann et al. 2008) that can provide a wide range of ecosystem services beneficial to human well-being (Schirpke et al. 2013; Villoslada Peciña et al. 2019).
In South Tyrol, the northernmost province of Italy, extensively managed grasslands have become rare (i.e. only 2.23 % of the total agricultural area, see Tappeiner et al. 2020), as intensification accelerated in the post-war period – like in most areas of Europe (MacDonald et al. 2000). However, even when intensification leads to higher

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yields, a decline in biodiversity is increasingly observed (Gossner et al. 2016; Hilpold et al. 2018), including negative effects on soil and ground-dwelling invertebrates (Tsiafouli et al. 2015; Lessard-Therrien et al. 2018; Guariento et al. 2020). But these animals play an important role in ecosystem functioning by contributing to litter decomposition, nutrient cycling, and many other essential ecosystem processes (Seeber et al. 2022).

So far, only few studies exist which surveyed the dynamics of ground-dwelling invertebrate communities in mountain grasslands over a full growing season (but see Damisch et al. 2020; Steinwandter et al. 2022a). Surveys in mountainous areas are often limited due to the difficult access and harsh environmental conditions, especially as snow can persist for a long period in spring and reoccur in late summer and autumn (Seeber et al. 2021; Steinwandter & Seeber 2023).

Here we investigated the abundances of ground-dwelling macro-invertebrates and their community compositions in two major types of mountain grassland, an intensively managed hay meadow and an traditionally managed dry pasture over a full vegetation period. We identified Araneae to species level and assessed changes in developmental status and sex ratio (i. e. males, females, and juveniles) to gain insights into the population dynamics of this important predator group. The results of this study will contribute to a better understanding of how management intensity supports or suppresses the invertebrate diversity in mountain grasslands.

Material and Methods

Study area

The study was conducted in two grasslands at the research site 'Muntatschinig/Montescino' which is part of the Long-Term (Socio-)Ecological Research ('LT(S)ER') area 'Val Mazia/Matschertal' in the municipality of Mals/Malles Venosta in South Tyrol, the northernmost province of Italy (LTER_EU_IT_097, N 46.6840° – E 10.5860°, https://deims.org/11696de6–0ab9–4c94-a06b-7ce40f56c964). The area is located in the upper Vinschgau Valley, a dry inner-alpine valley with a low mean annual precipitation of 525 mm and a mean air temperature of 5.6 °C (years 1925–2005, at 1580 m a.s.l., Weather and Avalanche Service of the Autonomous Province of Bozen/Bolzano – South Tyrol). The area is further part of the southern Oetztal Alps in the Central European Alps.

The two sampled plots were fenced areas within (1) an intensively managed hay meadow (i. e. regularly irrigated and fertilised) that was mown twice a year (mid-July and end of September) and (2) a traditionally and extensively managed dry pasture that was grazed by small stocks of cattle, horses, and donkeys in the summer and autumn (Fig. 1); some scattered stones and dwarf shrubs were present in the pasture. The fence protected the meteorological stations from mowing activities (on the meadow) and grazing animals (on the pasture), but respective management was also emulated within the fences (see below). The meadow was located at 1465 m and the pasture at 1570 m; they had the same exposition and inclination of 225° (SW) and 10°, respectively. The soil properties of the meadow and the pasture were: soil pH 5.57 ±0.25 and 5.36 ±0.28, soil organic matter (SOM) 15.58 % ±1.19 and 8.86 % ±1.61, total C content (C_{tot}) 8.08 % ±0.90 and 4.44 % ±0.84, total N content (N_{tot}) 0.79 % ±0.11 and 0.36 % ±0.06, and C:N ratio 10.18 ±0.48 and 12.50 ±0.84, respectively.

Sampling design

On each of the grassland plots, we installed nine pitfall traps in a 3 × 3 pattern (Fig. 1). The traps consisted of plastic yoghurt cups (500 ml) with an opening of 8 cm and a depth of 9 cm and were filled with 200 ml of 75 % ethylene glycol solution as collection fluid, mixed with a few drops of detergent to reduce surface tension. A transparent polycarbonate roof (20 × 20 cm, 5 mm thick, 10 cm above the traps) on two metal poles protected the traps from rain. A second yoghurt cup with drainage holes as a base facilitated the replacement of the pitfall traps.

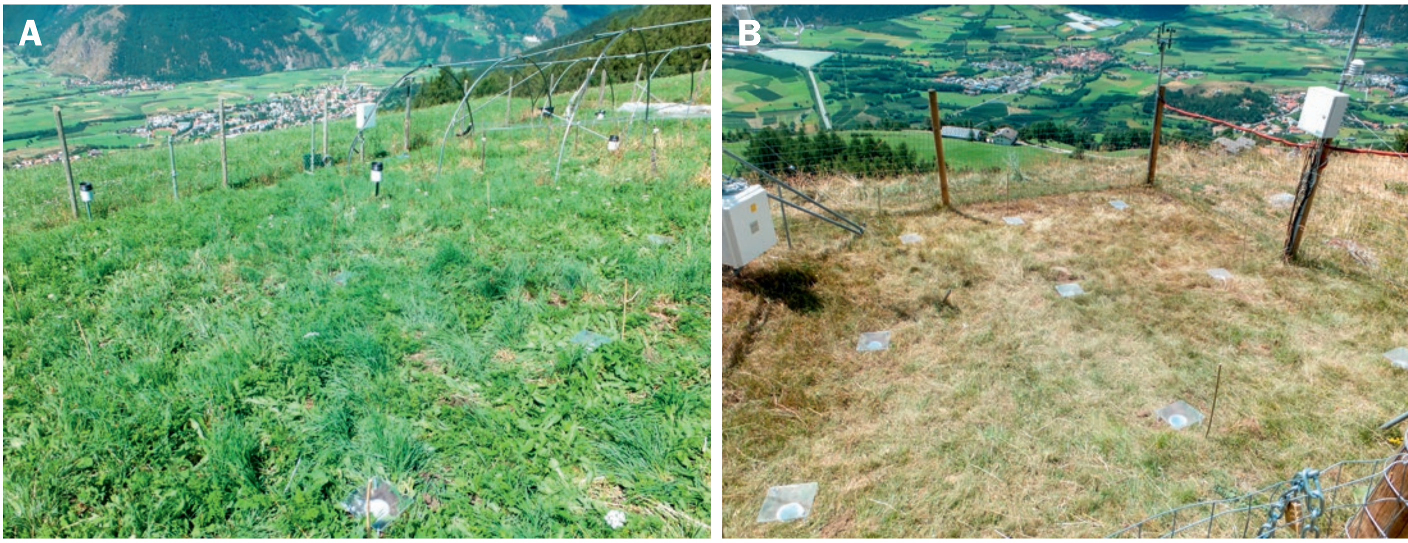

Fig. 1: Overview of the studied grasslands in the LT(S)ER area 'Val Mazia/Matschertal', at the 'Muntatschinig' site (South Tyrol, Italy). The grasslands were fenced to protect the installed meteorological stations. The plots were part of (A) an intensively managed hay meadow that was irrigated and fertilised, and (B) an extensively grazed dry pasture (Photo: Michael Steinwandter).

The sampling period consisted of two half-years (i. e. summer and autumn 2015, and spring and summer 2016) and therefore spanned over a full growing season; in total we had 10 sampling dates resulting in 90 pitfall trap samples. All pitfall traps in 2015 were activated on 30 July 2015 and emptied on 21 August (active for 22 days), 11 September (21d), 8 October (27d), 2 November (25d), and 1 December (29d), representing the second half of the growing season. In 2016, the pitfall traps were activated on 18 April and emptied on 4 May (16d), 30 May (26d), 17 June (18d), 5 July (18d), and finally on 25 July (20d), representing the first half of the growing season. The collected animals were rinsed with tap water and transferred to 75 % ethanol until identification in the laboratory of the Institute for Alpine Environment of Eurac Research.
To emulate the mowing and grazing activities within the fenced plots, the two plots were mowed twice with a string trimmer timely when the farmers mowed the adjacent hay meadows (i. e. mid-July 2016 and end of September 2015).

Identification of invertebrates

All sampled specimens were identified using dissection stereo microscopes (SMG-TLED 171, MoticEurope S. L.U., Barcelona, Spain). The ground-dwelling macro-invertebrates (i. e. visible to the naked eye) were counted and – where possible – identified to family level (e.g. Myriapoda, adult Coleoptera and larvae) following the identification keys of Hauser & Voigtländer (2019) and Klausnitzer (2011, 2019). Araneae were identified to species level using the identification keys available online by Nentwig et al. (2023); in addition, their sex and developmental status were documented as female, male, and juvenile. Pterygote insects such as adult Diptera, Hymenoptera, and Lepidoptera (i. e. moths) were documented but declared as by-catch and therefore excluded from all analyses.

Statistical analysis

As nine pitfall traps were considered too many for the relatively small sampling areas, abundances were averaged over three traps (i. e. sum of all 9 traps and divided by 3). Abundance data (i. e. activity densities) were standardised by dividing the number of individuals caught per taxon by the number of active days (i. e. individuals per sampling day). For a better comparability between species and sex ratios, the numbers of Araneae were also used as whole numbers. For biodiversity measures, annual means

were calculated from the standardised data to depict a most complete community present throughout the full growing season.
The ordination was calculated in the multivariate data exploration software CANOCO 5 (version 5.15; Šmilauer & Lepš 2014) using the highest taxonomic resolution available (i.e. family level where possible and Araneae at species level).

Results

Community composition

When comparing the faunal data of the meadow and the pasture, we found considerable differences (Fig. 2 and Table 1) and two well separated communities (Fig. A1, in the appendix). In the meadow, we collected twice as many invertebrates as in the pasture (25.196 vs. 12.567 ind./day). The meadow was dominated by adults and larvae of Coleoptera (12.956 and 2.268 ind./day, respectively), while adult Coleoptera were the second most abundant taxon in the pasture (i.e. 4.396 ind./day). The activity densities of Araneae were similar in both grasslands, but they represented almost 60 % of the pasture community compared to 30 % in the meadow community (Fig. 2). Isopoda and Dermaptera were among the five most abundant taxa in the meadow, while this was the case for Orthoptera in the pasture.
At the family and order level, we were able to identify a total of 54 taxa, 48 of which were present in both grasslands (Table 1). In both habitats, the six unique taxa were: in the meadow Isopoda, the Araneae families Pisauridae and Miturgidae, the Coleoptera families Hydrophilidae, Cantharidae, and Silphidae larvae; in the pasture, the Araneae families Eresidae, Agelenidae, Zodariidae, and Salticidae, and the Coleoptera families Mordellidae and Trogidae.

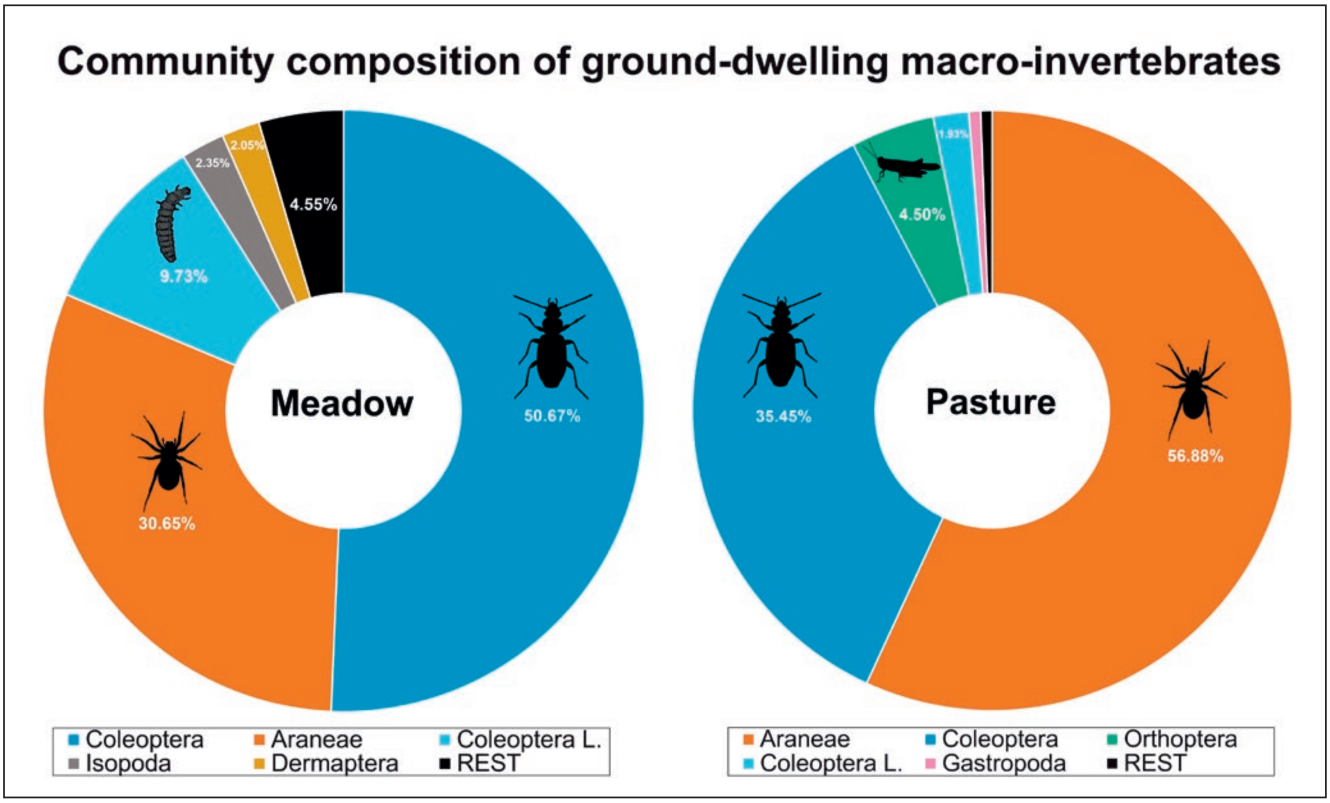

Fig. 2: Community composition (in percent) of ground-dwelling macro-invertebrates from an intensively managed hay meadow and an extensively managed dry pasture at the LT(S)ER area 'Val Mazia/Matschertal', South Tyrol, Italy. The figures show the mean (i.e. annual) abundances of the five most common taxa, along with the rest of the communities in black. Icons for animals were found in the silhouette image repository PhyloPic 2.0 (https://www.phylopic.org/, Araneae (copyright Denis Lafage CC BY 3.0) and Coleoptera, (copyright Michael Day CC0 1.0); the icon for Coleoptera larvae on http://www.zeno.org/nid/20008000492 (Edmund Reitter, 1911, 'Fauna Germanica. Die Käfer des deutschen Reiches', CC0 1.0).

Table 1: Mean activity densities (individuals per sampling day, ind./d) of ground-dwelling macro-invertebrates from an intensively managed hay meadow and an extensively managed dry pasture in the LT(S)ER area 'Val Mazia/Matschertal', South Tyrol, Italy. The data cover a full growing season and were obtained by sampling in two half-years in 2015 (summer to autumn) and in 2016 (spring to summer); all values were standardised to individuals per sampling day.

Meadow	2016					2015					Annual mean [ind./day (±sd)]	
	4. May	*30. May*	*17. Jun*	*5. Jul*	*25. Jul*	*21. Aug*	*11. Sep*	*8. Oct*	*2. Nov*	*1. Dec*		
GASTROPODA	**0.042**	**0.115**	**0.519**	**0.204**	**0.200**	**0.258**	**0.159**	**0.654**	**0.427**	**0.115**	**0.269**	**(0.189)**
Gastropoda (shell)	–	0.026	0.259	0.148	0.150	0.106	0.127	0.012	0.013	0.011	0.085	(0.082)
Gastropoda (no shell)	0.042	0.090	0.259	0.056	0.050	0.152	0.032	0.642	0.413	0.103	0.184	(0.190)
LUMBRICIDAE	**0.104**	**0.090**	**0.870**	**0.167**	**0.133**	**0.258**	**0.206**	**0.086**	**0.280**	**0.092**	**0.229**	**(0.224)**
ISOPODA	**0.188**	**0.231**	**1.278**	**2.704**	**0.583**	**0.303**	**0.635**	**0.123**	**0.173**	**0.069**	**0.629**	**(0.772)**
DIPLOPODA	**–**	**0.026**	**0.185**	**0.630**	**0.050**	**0.061**	**0.032**	**0.037**	**0.040**	**–**	**0.106**	**(0.181)**
Glomeridae	–	0.013	–	–	0.017	0.045	–	0.025	0.040	–	0.014	(0.017)
Julidae	–	0.013	0.185	0.630	0.033	0.015	0.032	0.012	–	–	0.092	(0.187)
ARANEAE	**5.375**	**9.179**	**8.370**	**26.556**	**8.267**	**7.803**	**4.603**	**1.444**	**3.653**	**2.494**	**7.775**	**(6.753)**
Eresidae	–	–	–	–	–	–	–	–	–	–	–	
Theridiidae	–	0.026	–	–	0.017	–	–	–	–	–	0.004	(0.009)
Linyphiidae	0.021	0.179	0.407	1.259	0.850	4.424	1.937	0.247	2.840	2.253	1.442	(1.351)
Tetragnathidae	0.667	1.038	1.056	1.926	0.500	0.136	0.048	0.012	0.013	0.034	0.543	(0.606)
Araneidae	–	–	–	–	–	–	–	0.012	–	–	0.001	(0.004)
Lycosidae	4.313	7.692	6.870	23.278	6.617	3.121	2.524	1.099	0.773	0.195	5.648	(6.400)
Pisauridae	–	0.064	–	–	0.050	–	0.032	–	–	0.011	0.016	(0.023)
Miturgidae	–	–	–	0.019	–	–	–	–	–	–	0.002	(0.006)
Agelenidae	–	–	–	–	–	–	–	–	–	–	–	
Cheiracanthiidae	–	–	–	0.019	0.117	–	–	–	–	–	0.014	(0.035)
Liocranidae	–	–	–	0.019	–	–	–	–	–	–	0.002	(0.006)
Phrurolithidae	–	–	–	–	–	0.015	–	–	–	–	0.002	(0.005)
Zodariidae	–	–	–	–	–	–	–	–	–	–	–	
Gnaphosidae	–	0.013	–	–	–	0.015	–	–	–	–	0.003	(0.006)
Philodromidae	0.021	0.013	–	–	0.017	–	–	–	–	–	0.005	(0.008)
Thomisidae	0.354	0.154	0.037	0.037	0.100	0.091	0.063	0.074	0.027	–	0.094	(0.096)
Salticidae	–	–	–	–	–	–	–	–	–	–	–	
OPILIONES	**–**	**–**	**–**	**0.037**	**0.550**	**0.182**	**0.730**	**1.506**	**0.227**	**0.034**	**0.327**	**(0.461)**
DERMAPTERA	**0.063**	**0.026**	**0.167**	**1.944**	**1.550**	**0.242**	**0.175**	**0.346**	**0.440**	**0.218**	**0.517**	**(0.632)**
ORTHOPTERA	**–**	**0.038**	**–**	**0.037**	**0.050**	**0.318**	**0.206**	**0.296**	**0.267**	**–**	**0.121**	**(0.127)**
Ensifera	–	0.038	–	–	0.017	0.197	0.016	–	0.013	–	0.028	(0.058)
Caelifera	–	–	–	0.037	0.033	0.121	0.190	0.296	0.253	–	0.093	(0.109)
COLEOPTERA	**3.958**	**13.026**	**20.000**	**41.852**	**16.350**	**16.591**	**9.032**	**5.185**	**3.187**	**0.379**	**12.956**	**(11.48)**
Carabidae	1.958	6.013	9.722	29.630	11.267	10.121	5.937	1.420	0.627	0.103	7.680	(8.305)
Hydrophilidae	–	–	–	–	–	0.348	–	0.037	–	–	0.039	(0.104)
Histeridae	–	0.013	0.111	0.056	–	0.015	–	0.012	–	–	0.021	(0.034)
Silphidae	0.042	0.551	0.333	5.407	2.900	1.864	2.365	1.864	1.400	–	1.673	(1.568)
Leiodidae (Cholevinae)	0.042	0.167	0.074	0.815	0.067	1.530	0.016	–	–	–	0.271	(0.481)
Staphylinidae	1.479	3.128	8.870	4.889	1.617	2.606	0.397	1.049	0.773	0.149	2.496	(2.521)
Cantharidae	–	0.026	0.019	–	–	–	–	–	–	–	0.004	(0.009)
Elateridae	–	0.103	0.222	0.315	0.017	–	–	–	–	–	0.066	(0.108)
Byrrhidae	–	–	–	–	–	–	–	0.012	–	–	0.001	(0.004)
Coccinellidae	–	–	0.019	–	–	–	–	–	–	–	0.002	(0.006)
Nitidulidae	–	0.526	0.111	0.241	–	–	–	–	–	–	0.088	(0.164)

Meadow	2016					2015					Annual mean [ind./day (±sd)]	
	4. May	*30. May*	*17. Jun*	*5. Jul*	*25. Jul*	*21. Aug*	*11. Sep*	*8. Oct*	*2. Nov*	*1. Dec*		
Cryptophagiidae	–	0.218	0.037	–	–	0.015	–	0.012	–	0.023	0.031	(0.064)
Mordellidae	–	–	–	–	–	–	–	–	–	–	–	
Trogidae	–	–	–	–	–	–	–	–	–	–	–	
Geotrupidae	–	–	–	0.056	0.050	–	–	–	–	–	0.011	(0.021)
Scarabaeidae	0.167	0.013	0.093	0.019	0.083	–	0.032	0.037	0.067	0.011	0.052	(0.049)
Chrysomelidae	1.104	0.115	–	–	–	0.061	0.286	0.580	0.040	0.069	0.226	(0.339)
Brentidae	–	0.064	0.019	0.019	–	–	–	0.062	–	0.023	0.019	(0.024)
Curculionidae	0.104	0.756	0.370	0.407	0.350	0.030	–	0.099	0.280	0.046	0.244	(0.224)
COLEOPTERA Larvae	**0.188**	**0.141**	**0.667**	**3.296**	**0.350**	**6.970**	**4.698**	**2.222**	**3.147**	**1.000**	**2.268**	**(2.157)**
Carabidae Larvae	0.063	–	–	0.167	0.017	1.303	0.857	1.086	0.253	0.161	0.391	(0.470)
Silphidae Larvae	–	–	–	0.407	0.067	2.318	1.810	0.111	–	0.011	0.472	(0.812)
Staphylinidae Larvae	–	0.026	0.259	1.222	0.100	1.045	1.397	0.086	0.120	0.034	0.429	(0.529)
Cantharidae Larvae	0.063	–	0.019	0.074	0.100	2.197	0.603	0.914	2.773	0.782	0.752	(0.932)
Melyridae Larvae	0.042	–	–	–	–	–	0.032	–	–	0.011	0.008	(0.015)
Coccinellidae Larvae	–	0.051	0.204	0.037	0.050	–	–	–	–	–	0.034	(0.060)
Chrysomelidae Larvae	0.021	0.064	0.185	1.389	0.017	0.106	–	0.012	–	–	0.179	(0.407)
Scarabaeidae Larvae	–	–	–	–	–	–	–	0.012	–	–	0.001	(0.004)

Pasture	2016					2015					Annual mean [ind./day (±sd)]	
	4. May	*30. May*	*17. Jun*	*5. Jul*	*25. Jul*	*21. Aug*	*11. Sep*	*8. Oct*	*2. Nov*	*1. Dec*		
GASTROPODA	**–**	**–**	**0.037**	**0.278**	**0.033**	**0.015**	**0.048**	**0.160**	**0.120**	**0.034**	**0.073**	**(0.084)**
Gastropoda (shell)	–	–	–	0.037	–	0.015	0.048	0.160	0.107	0.034	0.040	(0.051)
Gastropoda (no shell)	–	–	0.037	0.241	0.033	–	–	–	0.013	–	0.032	(0.071)
LUMBRICIDAE	**0.042**	**0.013**	**0.204**	**0.019**	**–**	**–**	**–**	**0.062**	**0.080**	**0.011**	**0.043**	**(0.060)**
ISOPODA	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	
DIPLOPODA	**–**	**–**	**–**	**–**	**–**	**0.015**	**–**	**–**	**0.067**	**–**	**0.008**	**(0.020)**
Glomeridae	–	–	–	–	–	–	–	–	0.013	–	0.001	(0.004)
Julidae	–	–	–	–	–	0.015	–	–	0.053	–	0.007	(0.016)
ARANEAE	**4.208**	**5.885**	**14.278**	**27.630**	**5.267**	**5.000**	**4.556**	**3.198**	**2.027**	**1.046**	**7.309**	**(7.578)**
Eresidae	–	0.013	–	–	0.017	–	–	–	–	–	0.003	(0.006)
Theridiidae	–	0.026	–	0.056	–	–	–	–	–	–	0.008	(0.018)
Linyphiidae	0.063	0.115	0.111	0.204	0.267	0.530	0.254	0.198	0.387	0.506	0.263	(0.154)
Tetragnathidae	–	–	–	–	–	–	0.016	–	–	–	0.002	(0.005)
Araneidae	–	–	–	–	–	–	0.016	–	–	–	0.002	(0.005)
Lycosidae	3.417	5.141	13.611	24.926	3.950	2.061	2.397	2.111	1.387	0.437	5.944	(7.236)
Pisauridae	–	–	–	–	–	–	–	–	–	–	–	
Miturgidae	–	–	–	–	–	–	–	–	–	–	–	
Agelenidae	–	–	–	–	0.050	–	–	–	–	–	0.005	(0.015)
Cheiracanthiidae	0.250	0.218	0.056	–	0.017	0.955	1.016	0.198	0.027	0.011	0.275	(0.366)
Liocranidae	–	–	–	–	0.017	–	–	–	–	–	0.002	(0.005)
Phrurolithidae	–	–	0.093	0.019	–	–	–	–	–	–	0.011	(0.028)
Zodariidae	–	–	–	1.444	0.200	0.015	–	–	–	–	0.166	(0.430)
Gnaphosidae	0.250	0.244	0.241	0.796	0.483	1.364	0.762	0.667	0.160	0.069	0.504	(0.378)
Philodromidae	–	0.013	0.111	0.074	0.083	0.015	0.048	–	–	–	0.034	(0.039)
Thomisidae	0.208	0.115	0.056	0.111	0.183	0.045	0.032	0.025	0.067	0.011	0.085	(0.064)
Salticidae	0.021	–	–	–	–	0.015	0.016	–	–	0.011	0.006	(0.008)
OPILIONES	**–**	**–**	**–**	**–**	**–**	**–**	**0.032**	**0.025**	**0.040**	**0.057**	**0.015**	**(0.020)**

Pasture	2016					2015					Annual mean [ind./day (±sd)]	
	4. May	*30. May*	*17. Jun*	*5. Jul*	*25. Jul*	*21. Aug*	*11. Sep*	*8. Oct*	*2. Nov*	*1. Dec*		
DERMAPTERA	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**0.023**	**0.002**	**(0.007)**
ORTHOPTERA	**0.042**	**0.013**	**0.056**	**0.259**	**0.583**	**0.485**	**1.905**	**0.877**	**0.267**	**0.540**	**0.503**	**(0.537)**
Ensifera	0.042	–	0.056	0.019	0.017	0.106	0.079	0.012	0.013	–	0.034	(0.034)
Caelifera	–	0.013	–	0.241	0.567	0.379	1.825	0.864	0.253	0.540	0.468	(0.526)
COLEOPTERA	**1.396**	**2.782**	**7.704**	**13.556**	**2.267**	**4.788**	**5.460**	**1.556**	**2.000**	**2.448**	**4.396**	**(3.604)**
Carabidae	0.229	0.397	0.963	0.648	0.350	1.879	3.810	0.309	0.147	0.034	0.877	(1.103)
Hydrophilidae	–	–	–	–	–	–	–	–	–	–	–	
Histeridae	–	–	–	–	–	0.136	0.063	–	–	–	0.020	(0.043)
Silphidae	–	–	–	–	–	0.803	0.683	–	–	–	0.149	(0.298)
Leiodidae (Cholevinae)	–	–	–	0.037	–	0.015	0.016	–	0.027	–	0.009	(0.013)
Staphylinidae	0.396	0.538	5.074	10.889	1.467	1.212	0.413	0.543	0.947	2.011	2.349	(3.140)
Cantharidae	–	–	–	–	–	–	–	–	–	–	–	
Elateridae	–	0.026	–	–	–	–	–	–	–	–	0.003	(0.008)
Byrrhidae	–	0.038	0.037	0.056	0.067	0.015	–	–	–	–	0.021	(0.025)
Coccinellidae	0.167	–	–	0.019	–	0.015	–	–	–	–	0.020	(0.049)
Nitidulidae	–	0.090	0.204	0.463	0.017	–	0.048	–	–	0.011	0.083	(0.140)
Cryptophagiidae	–	0.038	–	–	–	0.121	–	–	–	0.023	0.018	(0.037)
Mordellidae	–	–	–	–	0.017	0.030	0.016	–	–	–	0.006	(0.010)
Trogidae	–	–	–	–	–	0.015	–	–	–	–	0.002	(0.005)
Geotrupidae	–	–	–	0.222	–	–	–	–	–	–	0.022	(0.067)
Scarabaeidae	0.021	0.013	0.148	0.093	0.067	0.182	0.095	0.074	0.107	0.023	0.082	(0.052)
Chrysomelidae	–	–	–	0.019	0.017	0.197	0.159	0.420	0.707	0.345	0.186	(0.226)
Brentidae	–	0.013	–	–	–	0.015	–	0.012	–	–	0.004	(0.006)
Curculionidae	0.583	0.756	1.278	1.111	0.267	0.152	0.159	0.198	0.067	0.034	0.460	(0.427)
COLEOPTERA Larvae	**0.229**	**0.192**	**0.130**	**0.167**	**0.400**	**0.242**	**0.079**	**0.383**	**0.120**	**0.241**	**0.218**	**(0.101)**
Carabidae Larvae	–	–	–	–	–	0.136	–	0.062	0.040	0.046	0.028	(0.042)
Silphidae Larvae	–	–	–	–	–	–	–	–	–	–	–	
Staphylinidae Larvae	0.042	0.090	0.130	0.074	0.033	0.091	0.032	0.049	–	0.046	0.059	(0.036)
Cantharidae Larvae	–	0.064	–	–	0.050	–	–	–	0.040	0.011	0.017	(0.024)
Melyridae Larvae	–	–	–	–	0.017	0.015	0.048	0.272	0.027	0.103	0.048	(0.081)
Coccinellidae Larvae	–	0.013	–	–	0.300	–	–	–	–	–	0.031	(0.090)
Chrysomelidae Larvae	0.188	0.026	–	0.056	–	–	–	–	0.013	0.023	0.031	(0.055)
Scarabaeidae Larvae	–	–	–	0.037	–	–	–	–	–	0.011	0.005	(0.011)

Seasonal dynamics

We observed different seasonal activity patterns for the main taxa Coleoptera, Araneae, Isopoda, and Orthoptera, with the highest activities during the summer months (Table 1). In the meadow, Coleoptera, Araneae, and Isopoda showed the highest activity in early July (i.e. 41.852, 26.556, and 2.704 ind./day, respectively), while Coleoptera larvae peaked in mid-August (i.e. 6.970 ind./day). In the pasture, the activity densities of Araneae and Coleoptera showed a clear peak in early July (i.e. 27.630 and 13.556 ind./day, respectively) and decreased considerably for the rest of the growing season. In contrast, Orthoptera showed their activity peak in early September (i.e. 1.905 ind./day); no pattern was found for Coleoptera larvae as they showed a constant activity throughout the season.

Araneae diversity and sex ratio

In total, we found 68 Araneae species in 17 families in both grassland types (Tables A1 and A2, in the appendix). The most diverse families were Linyphiidae with 22 species, followed by Lycosidae with 13 and Gnaphosidae with 10 species. The meadow harboured 39 species, 12 of which were unique to this grassland type. On the other hand, the pasture was much richer in species with 56 species (i. e. an increase of 69.64 %), of which 29 were unique. We also found differences in the activity densities for individual Araneae families between meadow and pasture. Linyphiidae were much more abundant in the meadow (1.442 vs. 0.263 ind./day in the pasture, Table 1), while Gnaphosidae were more abundant in the pasture (0.504 vs. 0.003 in the meadow). Overall, Lycosidae had the highest annual activity density in both the meadow and the pasture (5.648 and 5.944 ind./day, respectively), which remained similar throughout the season.

The seasonal changes in the Araneae sex ratios were comparable for both grassland types (Fig. 3). In early summer, juveniles dominated (i. e. ~ 60 %) and decreased towards the end of July (i. e. < 5 %). We found a considerable increase in males until the end of July which then decreased again towards autumn (mid-October); the most active were male Lycosidae representing almost 90 % of all males on the fourth sampling date (5 July). We found a smooth transition between the two halves of the season in the meadow, while there was a gap in the values for the pasture. In the second half of the growing season (i. e. summer to autumn 2015) we can see a clear increase in juveniles and a clear decrease in males. Overall, females were found in lower percentages, except for the pasture where they reached > 40 % in the second half of the growing season.

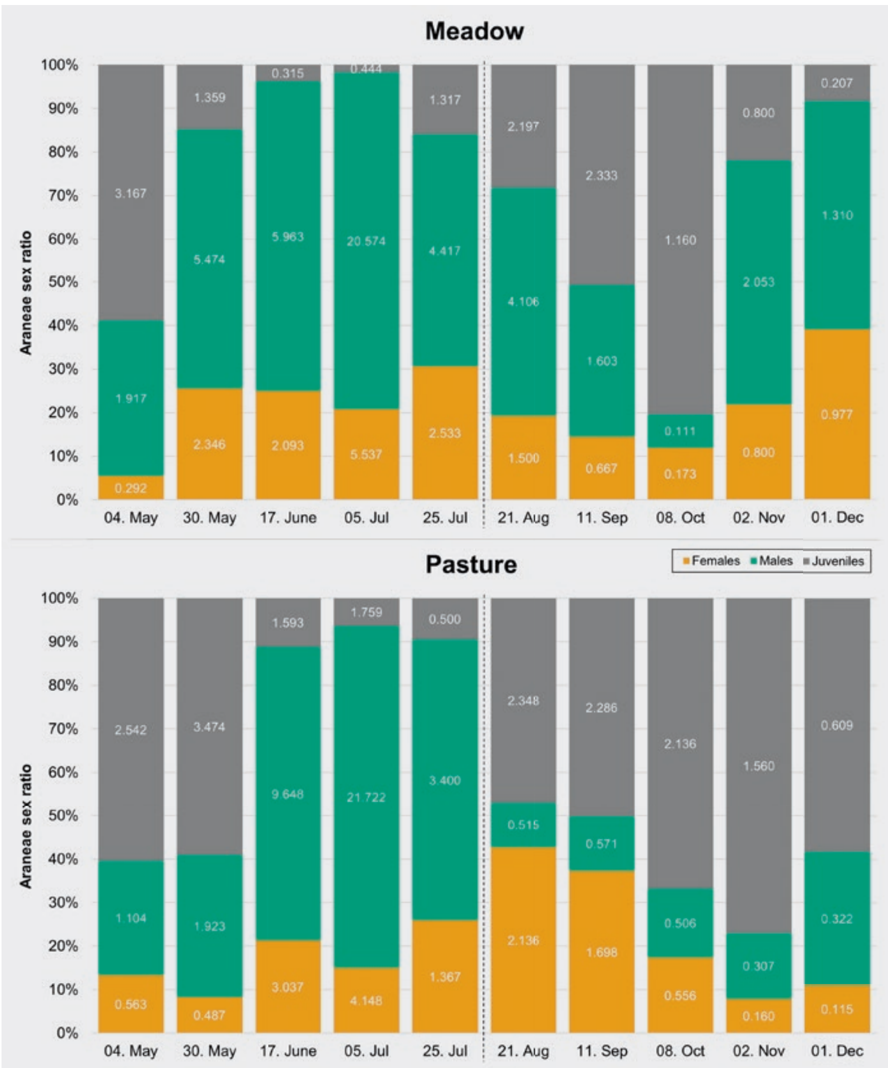

Fig. 3: Seasonal dynamics (i. e. activity densities) of sex ratios of ground-dwelling Araneae from an intensively managed hay meadow and an extensively managed dry pasture in the LT(S)ER area 'Val Mazia/Matschertal', South Tyrol, Italy. The data cover an entire growing season and were obtained by sampling in two half-years (summer to autumn 2016, left side of the dashed line, and spring to summer 2015, right side); all values were standardised to individuals per sampling day.

Discussion

Here, we present one of the few studies in which ground-dwelling macro-invertebrates were surveyed in two types of mountain grassland over a full growing season. This allowed us to gain insight into population dynamics, how management intensity affects the invertebrate communities, and to better understand which taxa are predominantly active in which month.

Although we were unable to carry out extensive statistical analysis due to the limited data available (for example, we did not conduct a vegetation survey), we were still able to observe effects of management intensity. The hay meadow plot, which was managed intensively with regular irrigation and fertilisation, harboured twice as many individuals as the extensively grazed dry pasture (Table 1). This confirms the results of previous studies on the same and neighbouring plots, where the hay meadows had the highest abundance of soil- and ground-dwelling invertebrates (Hilpold et al. 2018; Damisch et al. 2020). In particular, carabid beetles prefer the hay meadows and are not negatively affected by intensive management, which has also been shown in other studies (e.g. Lessard-Therrien et al. 2018; Schirmel & Gerlach 2022). However, species diversity (i. e. Araneae diversity) was much higher for our dry pasture (i. e. 70 % more), which again confirmed our previous studies. This is also in line with general patterns showing that intensification, such as irrigation, can increase abundances but reduces (soil) biodiversity due to habitat homogenisation and a reduction of available ecological niches for the communities (Tsiafouli et al. 2015; Gossner et al. 2016). Even without a vegetation survey, it was clear that the habitat structures differed greatly between the irrigated and fertilised hay meadows and the semi-natural dry pastures, and it is known that, for example, vegetation height, vegetation density, and proportion of bare ground influence the abundance and diversity of Araneae (Bell et al. 2001). Prey availability (e.g. Collembola) may also differ between the two grassland types due to differences in vegetation structure, soil properties, and soil depth. Grassland management may thus indirectly affect Araneae (Bell et al. 2001), but also other predators such as ground and rove beetles.

We found that the Araneae were a dominant group, especially in the dry pasture (Fig. 2), where some species were found exclusively (Tables A1 and A2). For example, the Eresidae *Eresus kollari* Rossi, 1846 is a known spider of dry grasslands and was frequently found together with *E. sandaliatus* (Martini & Goeze, 1778) in the Upper Vinschgau (Steinwandter et al. 2022b). Lycosidae were the most abundant Araneae, with eight common species and some species being documented only in the meadow or pasture. For example, *Pardosa palustris* (Linnaeus, 1758) was the most abundant spider species overall and predominantly present in the meadow (Table A1), while *P. bifasciata* (C. L. Koch, 1834) was its counterpart in the pasture and is known to live in dry and sandy areas (Nentwig et al. 2023). We found some interesting spiders in the pasture, where Gnaphosidae were almost exclusively present (Tables 1 and A1) and species such as the Zodariidae *Zodarion rubidum* Simon, 1914 (mainly males) and the Cheiracanthiidae *Cheiracanthium virescens* (Sundevall, 1833) were present in relatively high numbers, both inhabiting dry areas (Nentwig et al. 2023; Růžička & Řezáč 2023), the former preying on Formicidae which were abundant in the pasture but almost absent in the meadow (Wagner & Glaser 2017).

Looking at the population dynamics of the two main taxa Araneae and Coleoptera, we found an influence of the mowing activities with a decrease in numbers (i. e. especially between dates 4 and 5, but also between dates 6 and 7 in the Tables 1, A1, and A2). Among the Araneae, we mainly found ground-dwelling hunters and only a few stationary web-weavers (e.g. Araneidae, some Linyphiidae), which are known to be able to evade such disturbances and spill over into the surrounding areas (Tölgyesi et al. 2018). However, from our data it seems that mowing strongly declined the numbers of some ground-dwelling families of Araneae and Coleoptera, both directly (i. e. by killing and/or dispersal) and indirectly (i. e. by reducing habitat heterogeneity, see Guariento et al. 2020; Nardi & Marini 2021), even if evasion shelters were present, especially in the dry pasture (e.g. scattered dwarf shrubs and stones).

Nevertheless, the intensity of management did not affect the sex ratios of spiders in our grasslands. The mowing seems to have affected all Araneae in the same way, as the sex ratios before and after the events do not show any inconsistencies. The patterns are similar for both grassland types, with a peak in adults in late June to late July and a second, smaller peak in autumn. The second peak may be due to species with two generations per year, as some species may use the period after mowing to produce a second generation (Samu & Szinetár 2002).
In conclusion, our small case study of two differently managed mountain grasslands shows that management intensity affects the abundance of ground-dwelling invertebrates and also species diversity (in our case spider diversity) but does not affect population dynamics. It seems that species adapted to a certain type of grassland management can cope well with any disturbances caused by agricultural practices.

Zusammenfassung

Es gibt nur wenige Studien über Bodenoberflächen-bewohnende Wirbellose in alpinen Graslandschaften, oft mit nur einer oder wenigen Probenahmen pro Vegetationsperiode. Um jedoch ein umfassendes Bild der vorhandenen Faunengemeinschaft zu erhalten, sind Probenahmen über eine ganze Saison erforderlich. In diesem Beitrag werden Daten über Makroinvertebraten-Gemeinschaften von zwei unterschiedlich bewirtschafteten Bergwiesen (d. h. einer intensiv bewirtschafteten Heuwiese und einer extensiv beweideten Trockenweide) vorgestellt. Beide Standorte wurden über den Zeitraum einer vollen Vegetationsperiode (April bis Anfang Dezember) kontinuierlich mit Barberfallen überwacht.
Wir fanden beträchtliche Unterschiede zwischen den beiden Graslandschaften bezüglich der Abundanz der gesamten Makrofauna-Gemeinschaft und auch der Artenvielfalt von Araneae; die Weide wies die geringere Abundanz auf (d. h. Aktivitätsdichte als Individuen pro Beprobungstag), aber eine höhere Zahl von Spinnenarten. Wir fanden dennoch deutliche Auswirkungen der Bewirtschaftung, die sehr wahrscheinlich auf Unterschiede in der Lebensraumstruktur und vermutlich auch in der Beuteverfügbarkeit zurückzuführen sind. Das Geschlechterverhältnis im Falle der Araneae unterschied sich nicht wesentlich zwischen den zwei Grünlandflächen, allerdings wurde ein negativer Effekt der Mahd auf die Häufigkeit von Araneae und adulter Coleoptera festgestellt. Zudem wirkte sich die Bewirtschaftungsintensität negativ auf die Häufigkeit und die Artenvielfalt der Oberflächen-aktiven Wirbellosen aus, nicht aber auf deren Populationsdynamik.

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References

Bell J. R., Wheater C. P. & Cullen W. R., 2001: The implications of grassland and heathland management for the conservation of spider communities: a review. Journal of Zoology, 255: 377–387.

Damisch K., Steinwandter M., Tappeiner U. & Seeber J., 2020: Soil macroinvertebrate distribution along a subalpine land use transect. Mountain Research and Development, 40: R1–R10.

Dengler J., Janišová M., Török P. & Wellstein C., 2014: Biodiversity of Palaearctic grasslands: a synthesis. Agriculture, Ecosystems & Environment, 182: 1–14.

Flury C., Huber R. & Tasser E., 2013: Future of mountain agriculture in the Alps. In: Mann S. (ed), The future of mountain agriculture. Springer Berlin Heidelberg, Berlin, Heidelberg, Germany.

Food and Agriculture Organization of the United Nations (FAO), 2005: Grasslands of the World (FAO Plant Production and Protection Series). FAO, Rome, Italy.

Gossner M. M., Lewinsohn T. M., Kahl T., Grassein F., Boch S., Prati D., Birkhofer K., Renner S. C., Sikorski J., Wubet T., Arndt H., Baumgartner V., Blaser S., Blüthgen N., Börschig C., Buscot F., Diekötter T., Jorge L. R., Jung K., Keyel A. C., Klein A-M., Klemmer S., Krauss J., Lange M., Müller J., Overmann J., Pašalić E., Penone C., Perović D. J., Purschke O., Schall P., Socher S. A., Sonnemann I., Tschapka M., Tscharntke T., Türke M., Venter P. C., Weiner C. N., Werner M., Wolters V., Wurst S., Westphal C., Fischer M., Weisser W. W. & Allan E., 2016: Land-use intensification causes multitrophic homogenization of grassland communities. Nature, 540: 266–269.

Guariento E., Colla F., Steinwandter M., Plunger J., Tappeiner U. & Seeber J., 2020: Management intensification of hay meadows and fruit orchards alters soil macro-invertebrate communities differently. Agronomy, 10: 767.

Hauser H. & Voigtländer K., 2019: Doppelfüßer (Diplopoda) Deutschlands: Verhalten, Ökologie, Verbreitung, Lebendbestimmung. DJN Deutscher Jugendbund für Naturbeobachtung, Göttingen, Germany.

Hilpold A., Seeber J., Fontana V., Niedrist G., Rief A., Steinwandter M., Tasser E. & Tappeiner U., 2018: Decline of rare and specialist species across multiple taxonomic groups after grassland intensification and abandonment. Biodiversity and Conservation, 27: 3729–3744.

Kampmann D., Herzog F., Jeanneret P., Konold W., Peter M., Walter T., Wildi O. & Lüscher A., 2008: Mountain grassland biodiversity: Impact of site conditions versus management type. Journal for Nature Conservation, 16: 12–25.

Klausnitzer B., 2011: Stresemann – Exkursionsfauna von Deutschland, Band 2: Wirbellose: Insekten, 11. Aufl. Spektrum Akademischer Verlag, Heidelberg, Germany.

Klausnitzer B., 2019: Stresemann – Exkursionsfauna von Deutschland. Band 1: Wirbellose (ohne Insekten), 9. Aufl. Springer Berlin Heidelberg, Berlin Heidelberg, Germany.

Lessard-Therrien M., Humbert J-Y., Hajdamowicz I., Stańska M., van Klink R., Lischer L. & Arlettaz R., 2018: Impacts of management intensification on ground-dwelling beetles and spiders in semi-natural mountain grasslands. Agriculture, Ecosystems & Environment, 251: 59–66.

MacDonald D., Crabtree J. R., Wiesinger G., Dax T., Stamou N., Fleury P., Gutierrez Lazpita J. & Gibon A., 2000: Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. Journal of Environmental Management, 59: 47–69.

Nardi D. & Marini L., 2021: Role of abandoned grasslands in the conservation of spider communities across heterogeneous mountain landscapes. Agriculture, Ecosystems & Environment, 319: 107526.

Nentwig W., Blick T., Bosmans R., Gloor D., Hänggi A. & Kropf C., 2023: Spiders of Europe. Version 09.2023. https://araneae.nmbe.ch [accessed 01.09.2023].

Růžička V. & Řezáč M., 2023: Seznam pavouků České republiky. List of spiders of the Czech Republic. https://www.arachnology.cz/seznam-pavouku-cr-26.html [accessed 01.09.2023].

Samu F. & Szinetár C., 2002: On the nature of agrobiont spiders. Journal of Arachnology, 30: 389–402.

Schirmel J. & Gerlach R., 2022: Conservation value of traditional meadow irrigation for carabid beetles. Ecological Indicators, 144 :109553.

Schirpke U., Kohler M., Leitinger G., Fontana V., Tasser E. & Tappeiner U., 2017: Future impacts of changing land-use and climate on ecosystem services of mountain grassland and their resilience. Ecosystem Services, 26: 79–94.

Schirpke U., Leitinger G., Tasser E., Schermer M., Steinbacher M. & Tappeiner U., 2013: Multiple ecosystem services of a changing Alpine landscape: past, present and future. International Journal of Biodiversity Science, Ecosystem Services & Management, 9: 123–135.

Seeber J., Newesely C., Steinwandter M., Rief A., Körner C., Tappeiner U. & Meyer E., 2021: Soil invertebrate abundance, diversity, and community composition across steep high elevation snowmelt gradients in the European Alps. Arctic, Antarctic, and Alpine Research, 53: 288–299.

Seeber J., Steinwandter M., Tasser E., Guariento E., Peham T., Rüdisser J., Schlick-Steiner B. C., Steiner F. M., Tappeiner U. & Meyer E., 2022: Distribution of soil macrofauna across different habitats in the Eastern European Alps. Scientific Data, 9: 632.

Šmilauer P. & Lepš J., 2014: Multivariate Analysis of Ecological Data using CANOCO 5. 2nd ed. Cambridge University Press, Cambridge, United Kingdom.

Spehn E. M., Rudmann-Maurer K., Körner C. & Maselli D., 2010: Mountain biodiversity and global change. GMBA-DIVERSITAS, Bern, Switzerland.

Steinwandter M., Blasbichler H. & Seeber J., 2022a: Vegetation shapes alpine ground-dwelling macro-invertebrate communities: A case study from the Stilfserjoch/Stelvio National Park (Martell/Martello, South Tyrol, Italy). Gredleriana, 22: 128–140.

Steinwandter M., Von Spinn J., Thaler-Knoflach B. & Seeber J., 2022b: Neufunde von Spinnen (Arachnida: Araneae) für Südtirol und Italien aus dem Obervinschgau. Gredleriana, 22: 141–148.

Steinwandter M. & Seeber J., 2023: Ground-dwelling invertebrates of the high alpine: Changes in diversity and community composition along elevation (1500–3000 m). Applied Soil Ecology, 190: 104988.

Tappeiner U., Marsoner T. & Niedrist G., 2020: Landwirtschaftsreport zur Nachhaltigkeit – Südtirol. Eurac Research, Bozen/Bolzano, Italy.

Tölgyesi C., Császár P., Torma A., Török P., Bátori Z. & Gallé R., 2018: Think twice before using narrow buffers: Attenuating mowing-induced arthropod spillover at forest – grassland edges. Agriculture, Ecosystems & Environment, 255: 37–44.

Tsiafouli M. A., Thébault E., Sgardelis S. P., de Ruiter P. C., van der Putten W. H., Birkhofer K., Hemerik L., de Vries F. T., Bardgett R. D., Brady M. V., Bjornlund L., Jørgensen H. B., Christensen S., Hertefeldt T. D., Hotes S., Gera Hol W. H., Frouz J., Liiri M., Mortimer S. R., Setälä H., Tzanopoulos J., Uteseny K., Pižl V., Stary J., Wolters V. & Hedlund K., 2015: Intensive agriculture reduces soil biodiversity across Europe. Global Change Biology, 21: 973–985.

Villoslada Peciña M., Ward R. D., Bunce R. G.H., Sepp K., Kuusemets V. & Luuk O., 2019: Country-scale mapping of ecosystem services provided by semi-natural grasslands. The Science of the Total Environment, 661: 212–225.

Wagner H. C. & Glaser F., 2017: Faunistik und Nestdichten von Ameisen (Hymenoptera: Formicidae) in Matsch (Südtirol, Italien). Gredleriana, 17: 217–226.

Appendix

Note: The Tables 1 as well as A1 and A2 can also be found online as Microsoft Excel file along the digital OpenAccess version of this article: https://doi.org/10.5281/zenodo.10116123

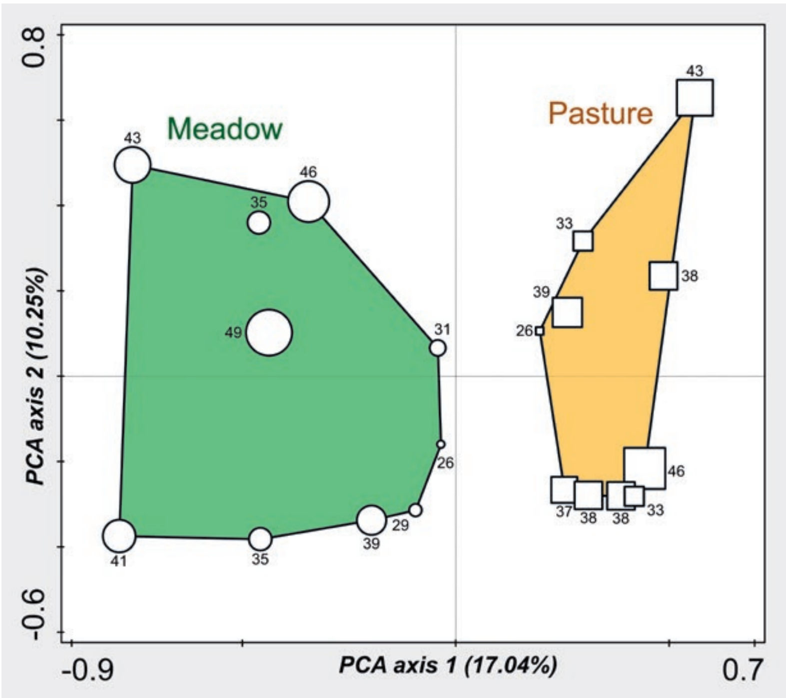

Fig. A1: Constraint Principal Component Analysis (PCA) plot of ground-dwelling macro-invertebrates from an intensively managed hay meadow and an extensively managed dry pasture in the LT(S)ER area 'Val Mazia/Matschertal', South Tyrol, Italy. Each data point represents the invertebrate community form one of the ten sampling dates (April to December, n = 9). The small numbers and the point sizes show the taxa diversity (from 26 to 49).

Table A1: Araneae abundances (♂/♀/juv.) from the intensively managed hay meadow.

Meadow	2016					2015				
	4 May	*30 May*	*17 Jun*	*5 Jul*	*25 Jul*	*21 Aug*	*11 Sep*	*8 Oct*	*2 Nov*	*1 Dec*
ARANEAE	**258**	**716**	**452**	**1434**	**496**	**515**	**290**	**117**	**274**	**217**
FEMALE ♀	*14*	*183*	*113*	*299*	*153*	*99*	*42*	*14*	*60*	*85*
MALE ♂	*92*	*427*	*322*	*1111*	*270*	*271*	*101*	*9*	*154*	*114*
JUVENILE	*152*	*106*	*17*	*24*	*73*	*145*	*147*	*94*	*60*	*18*
Eresidae	**–**	**1**	**–**	**–**	**1**	**–**	**–**	**–**	**–**	**–**
Eresus kollari	–	–	–	–	1/–/–	–	–	–	–	–
Eresus sp.	–	–/–/1	–	–	–	–	–	–	–	–
Theridiidae	**–**	**2**	**–**	**3**	**–**	**–**	**–**	**–**	**–**	**–**
Asagena phalerata	–	–	–	–/1/–	–	–	–	–	–	–
Enoploghata thoracica	–	–/2/–	–	–/2/–	–	–	–	–	–	–
Enoplognatha sp.	–	–	–	–	–	–	–	–	–	–
Linyphiidae	**3**	**9**	**6**	**11**	**16**	**35**	**16**	**16**	**29**	**44**
Agyneta affinis	–	–	–	–	–	–	–	–	–	–
Agyneta conigera	–	–	–	1/–/–	–	–	–	–	–	–
Agyneta rurestris	–	–	–	–	–	–/3/–	1/–/–	–	–	–
Araeoncus humilis	–	–	–	–	–	1/–/–	–	–	–	–/3/–
Centromerita bicolor	–	–	–	–	–	–	–	–	2/–	–
Centromerus sylvaticus	–	–	–	–	–	–	–	1/–/–	1/3/–	1/3/–
Erigone atra	–	–	–	–	–	–/2/–	–	–	–	–
Erigone dentipalpis	–	–	–	–	–	–/1/–	–/2/–	–	–	1/–/–
Macrargus carpenteri	–	–	–	–	–	–	–	–	–	–/3/–
Mermessus trilobatus	–/1/–	1/–/–	1/–/–	–/3/–	2/1/–	14/5/–	–/5/–	–/2/–	2/3/–	4/10/–
Micrargus subaequalis	–	–	–	–	–	–	–	–	–	–
Oedothorax apicatus	–	–	–	–	–	–	–	–	–	–
Scotargus pilosus	–	–	–	–	–	–	–	–	–/1/–	–/1/–
Scotinotylus alpigenus	–	–	–	–	–	–	–	–	–	–/3/–
Stemonyphantes lineatus	2/–/–	–	–	–	–	–	–	–	–	–/2/–
Syedra gracilis	–	–	–/1/–	–	1/–/–	–	–	1/–/–	–/1/–	–
Tenuiphantes mengei	–	–	–	–	–	–	–	–	–/2/–	–
Tenuiphantes tenuis	–	–	–	–	–	–	–	–	–	–
Tiso vagans	–	–	–/1/–	–	–	1/1/–	–	–	–	–
Trichoncus affinis	–	–/1/–	–/2/–	–/6/–	1/10/–	2/1/–	4/–/–	–	–	0.33
Trichopterna cito	–	–	–/1/–	1/–/–	–	1/–/–	–	–/2/–	2/1/–	–
Typhochrestus inflatus	–	–	–	–	–	–	–	–	–	–/2/–
indet. / juvenile	–	–/–/7	–	–	–/–/2	–/–/3	–/–/4	–/–/10	–/–/10	–/–/11
Tetragnathidae	**–**	**–**	**–**	**–**	**–**	**–**	**1**	**–**	**–**	**–**
Pachygnatha degeeri	–	–	–	–	–	–	–/1/–	–	–	–
Pachygnatha sp.	–	–	–	–	–	–	–	–	–	–
Araneidae	**–**	**–**	**–**	**–**	**–**	**–**	**1**	**–**	**–**	**–**
Araneus diadematus	–	–	–	–	–	–	–	–	–	–
Hypsosinga albovittata	–	–	–	–	–	–	1/–/–	–	–	–
Pisauridae	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**
Pisaura mirabilis	–	–	–	–	–	–	–	–	–	–
Pisaura sp.	–	–	–	–	–	–	–	–	–	–
Miturgidae	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**
Zora spinimana	–	–	–	–	–	–	–	–	–	–

Meadow	2016					2015				
	4 May	*30 May*	*17 Jun*	*5 Jul*	*25 Jul*	*21 Aug*	*11 Sep*	*8 Oct*	*2 Nov*	*1 Dec*
Agelenidae	**–**	**–**	**–**	**–**	**3**	**–**	**–**	**–**	**–**	**–**
Agelena labyrinthica	–	–	–	–	1/2/–	–	–	–	–	–
Cheiracanthiidae	**12**	**17**	**3**	**–**	**1**	**63**	**64**	**16**	**2**	**1**
Cheiracanthium virescens	9/2/–	14/1/–	1/2/–	–	–/1/–	–	–	–	–	1/–/–
Cheiracanthium sp.	–/–/1	–/–/2	–	–	–	–/–/63	–/–/64	–/–/16	–/–/2	–
Lycosidae	**207**	**600**	**371**	**1257**	**397**	**206**	**397**	**89**	**58**	**17**
Alopecosa cuneata	–/15/–	–/5/–	–	3/–/–	–	–	–/1/–	–	–	–
Alopecosa cursor	–	–	–	–	–	–	–	–	–	–
Alopecosa fabrilis	–	–	–	–	–	–	–	–	–	–
Alopecosa inquilina	–	–	–	–	–	–	–	–	–	–
Alopecosa pulverulenta	–/1/–	–/1/–	–	–	–	–	–	–	–	–
Alopecosa trabalis	2/10/–	1/13/–	3/25/–	1/29/–	–/3/–	–	1/–/–	–/1/–	–	–
Alopecosa sp.	–/–/1	–	–/–/4	–	–/–/5	–/–/1	–/–/8	–	–/–/19	–/–/1
Pardosa amentata	1/–/–	–	–	–	–	–	–	–	–	–
Pardosa bifasciata	–/1/–	–	–/1/–	–	–/2/–	–	–	–	–	–
Pardosa blanda	–	–	–	–	–/2/–	–	–	–	–	–
Pardosa lugubris	–	–	–	–/2/–	–/1/–	–	–	–	–	–
Pardosa palustris	3/31/–	129/343/–	77/247/–	161/1033/	126/230/–	50/15/–	15/–/–	–	1/–/–	–
Pardosa prativaga	–	–	–	–/7/–	–	–	–	–	–	–
Pardosa sp.	–/–/137	–/–/106	–/–/14	–/–/21	–/–/28	–/–/99	–/–/128	–/–/80	–/–/39	–/–/16
Trochosa terricola	–/5/–	–/2/–	–	–	–	1/–/–	5/–/–	–/2/–	–	–
Trochosa sp.	–	–	–	–	–/–/1	–/–/1	–/–/1	–	–	–
Liocranidae	**–**	**–**	**–**	**1**	**–**	**–**	**–**	**–**	**–**	**–**
Agroeca cuprea	–	–	–	1/–/–	–	–	–	–	–	–
Phrurolithidae	**–**	**–**	**–**	**–**	**–**	**1**	**–**	**–**	**–**	**–**
Phrurolithus minimus	–	–	–	–	–	1/–/–	–	–	–	–
Phrurolithus festivus	–	–	–	–	–	–	–	–	–	–
Zodariidae	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**
Zodarion rubidum	–	–	–	–	–	–	–	–	–	–
Gnaphosidae	**–**	**1**	**–**	**–**	**–**	**1**	**–**	**–**	**–**	**–**
Drassodes lapidosus	–	–	–	–	–	–	–	–	–	–
Drassodes pubescens	–	–	–	–	–	–	–	–	–	–
Drassodes sp.	–	–	–	–	–	–	–	–	–	–
Drassyllus praeficus	–	–	–	–	–	–	–	–	–	–
Drassyllus pusillus	–	–	–	–	–	1/–/–	–	–	–	–
Drassyllus sp.	–	–	–	–	–	–	–	–	–	–
Haplodrassus signifer	–	–/1/–	–	–	–	–	–	–	–	–
Haplodrassus sp.	–	–	–	–	–	–	–	–	–	–
Micaria formicaria	–	–	–	–	–	–	–	–	–	–
Micaria fulgens	–	–	–	–	–	–	–	–	–	–
Zelotes electus	–	–	–	–	–	–	–	–	–	–
Zelotes longipes	–	–	–	–	–	–	–	–	–	–
Zelotes petrensis	–	–	–	–	–	–	–	–	–	–
Zelotes sp.	–	–	–	–	–	–	–	–	–	–
Philodromidae	**1**	**1**	**–**	**–**	**1**	**–**	**–**	**–**	**–**	**–**
Thanatus arenarius	–/1/–	–/1/–	–	–	–/1/–	–	–	–	–	–
Thanatus sp.	–	–	–	–	–	–	–	–	–	–

Meadow	2016					2015				
	4 May	30 May	17 Jun	5 Jul	25 Jul	21 Aug	11 Sep	8 Oct	2 Nov	1 Dec
Thomisidae	**17**	**12**	**2**	**2**	**6**	**6**	**4**	**6**	**2**	**–**
Ozyptila atomaria	–	–	–	–	–	–	–	–	–	–
Ozyptila scabricula	–	–	–	–	–	–	–	–	–	–
Ozyptila sp.	–	–	–	–	–	–	–	–	–	–
Xysticus audax	–	–	–	–	–	2/–/–	–	–	–	–
Xysticus cristatus	–/8/–	–/8/–	–	–	3/–/–	–	–	–	–	–
Xysticus erraticus	–	–	–/1/–	–/1/–	–	–	–	–	–	–
Xysticus kochi	–/8/–	1/9/–	–/1/–	–/1/–	–	–	–	–	–	–
Xysticus ninnii	–	–	–	–	–	–	–	–	–	–
Xysticus sp.	–/–/1	–	–	–	–/–/3	–/–/4	–/–/4	–/–/6	–/–/2	–
Salticidae	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**
Heliophanus lineiventris	–	–	–	–	–	–	–	–	–	–
Heliophanus sp.	–	–	–	–	–	–	–	–	–	–

Table A2: Araneae abundances (♂/♀/juv.) from the extensively grazed dry pasture.

Pasture	2016					2015				
	4 May	30 May	17 Jun	5 Jul	25 Jul	21 Aug	11 Sep	8 Oct	2 Nov	1 Dec
ARANEAE	**258**	**716**	**452**	**1434**	**496**	**515**	**290**	**117**	**274**	**217**
FEMALE ♀	14	183	113	299	153	99	42	14	60	85
MALE ♂	92	427	322	1111	270	271	101	9	154	114
JUVENILE	152	106	17	24	73	145	147	94	60	18
Eresidae	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**
Eresus kollari	–	–	–	–	–	–	–	–	–	–
Eresus sp.	–	–	–	–	–	–	–	–	–	–
Theridiidae	**–**	**2**	**–**	**–**	**1**	**–**	**–**	**–**	**–**	**–**
Asagena phalerata	–	–/1/–	–	–	–	–	–	–	–	–
Enoploghata thoracica	–	–/1/–	–	–	–	–	–	–	–	–
Enoplognatha sp.	–	–	–	–	–/–/1	–	–	–	–	–
Linyphiidae	**0.33**	**4.67**	**7.33**	**22.67**	**17.00**	**97.33**	**40.67**	**6.67**	**71.00**	**65.33**
Agyneta affinis	–	–/1/–	–/1/–	–/1/–	2/–/–	–/2/–	–	–	–	–
Agyneta conigera	–	–	–	–	–	–	–	–	–	–
Agyneta rurestris	–	–	–	–	–	–/1/–	–	–	–/1/–	–
Araeoncus humilis	–	–	–	–	–	–	–	–/1/–	–	–
Centromerita bicolor	–	–	–	–	–	–	–	9/–/–	57/146/–	83/108/–
Centromerus sylvaticus	–	–	–	–	–	–	–	–/1/–	–/7/–	–/3/–
Erigone atra	–/1/–	–/4/–	–/8/–	1/25/–	2/7/–	2/124/–	6/34/–	–/1/–	–	–
Erigone dentipalpis	–	–/3/–	–/7/–	–/27/–	2/7/–	10/133/–	6/65/–	1/3/–	–	–/1/–
Macrargus carpenteri	–	–	–	–	–	–	–	–	–	–
Mermessus trilobatus	–	1/–/–	–	–	1/–/–	–/1/–	–	–	–	–
Micrargus subaequalis	–	–	–	–	1/4/–	–	–	–	–	–
Oedothorax apicatus	–	–/1/–	–	–	–	2/–/–	1/2/–	–	–	–
Scotargus pilosus	–	–	–	–	–	–	–	–	–	–
Scotinotylus alpigenus	–	–	–	–	–	–	–	–	–	–
Stemonyphantes lineatus	–	1/–/–	–	–	1/2/–	–	–	–	–/1/–	–
Syedra gracilis	–	–	–	–	–	–	–	–	–	–
Tenuiphantes mengei	–	–	–	–	–	–	–	–	–	–
Tenuiphantes tenuis	–	–	–	–	–	–	–	–	1/–/–	–
Tiso vagans	–	1/2/–	–/6/–	5/7/–	7/–/–	13/2/–	6/–/–	1/–/–	–	–/1/–

Pasture	2016					2015				
	4 May	*30 May*	*17 Jun*	*5 Jul*	*25 Jul*	*21 Aug*	*11 Sep*	*8 Oct*	*2 Nov*	*1 Dec*
Trichoncus affinis	–	–	–	–	–	–	–	–	–	–
Trichopterna cito	–	–	–	–	–	–	–	–	–	–
Typhochrestus inflatus	–	–	–	–	–	–	–	–	–	–
indet. / juvenile	–	–	–	–/–/2	–/–/15	–	–	–/–/3	–/–/1	–
Tetragnathidae	**32**	**81**	**57**	**104**	**30**	**9**	**3**	**1**	**1**	**3**
Pachygnatha degeeri	7/12/–	48/33/–	34/23/–	42/61/–	5/6/–	7/2/–	1/–/–	–	1/–/–	2/1/–
Pachygnatha sp.	–/–/13	–	–	–/–/1	–/–/19	–	–/–/2	–/–/1	–	–
Araneidae	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**1**	**–**	**–**
Araneus diadematus	–	–	–	–	–	–	–	1/–/–	–	–
Hypsosinga albovittata	–	–	–	–	–	–	–	–	–	–
Pisauridae	**–**	**5**	**–**	**–**	**3**	**–**	**2**	**–**	**–**	**1**
Pisaura mirabilis	–	2/2/–	–	–	2/1/–	–	–	–	–	–
Pisaura sp.	–	–/–/1	–	–	–	–	–/–/2	–	–	–/–/1
Miturgidae	**–**	**–**	**–**	**1**	**–**	**–**	**–**	**–**	**–**	**–**
Zora spinimana	–	–	–	–/1/–	–	–	–	–	–	–
Agelenidae	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**
Agelena labyrinthica	–	–	–	–	–	–	–	–	–	–
Cheiracanthiidae	**–**	**–**	**–**	**1**	**7**	**–**	**–**	**–**	**–**	**–**
Cheiracanthium virescens	–	–	–	1/–/–	2/4/–	–	–	–	–	–
Cheiracanthium sp.	–	–	–	–	–/–/1	–	–	–	–	–
Lycosidae	**164**	**401**	**735**	**1346**	**237**	**136**	**151**	**171**	**104**	**38**
Alopecosa cuneata	1/7/–	–/2/–	–	–	–	–	–	–	–	–
Alopecosa cursor	–/1/–	–/1/–	–/1/–	–	–	–	–	–	–	–
Alopecosa fabrilis	–	–	–	–	–	–	–	–/4/–	–	–
Alopecosa inquilina	–	–	–	–	–	–	–/3/–	–/3/–	–	–
Alopecosa pulverulenta	–	–	–	–	–	–	–	–	–	–
Alopecosa trabalis	–/6/–	–/1/–	2/1/–	4/2/–	–	–	–	–	–	–
Alopecosa sp.	–/–/6	–/–/1	–	–/–/2	–	–/–/14	–/–/9	–	–/–/5	–/–/3
Pardosa amentata	–	–	–	–	–	–	–	–	–	–
Pardosa bifasciata	–	7/31/–	139/496/–	258/987/–	59/156/–	93/–/–	67/–/–	37/–/–	5/–/–	3/–/–
Pardosa blanda	–	–	–	2/3/–	–	–	–	–	–	–
Pardosa lugubris	–	–	–/1/–	1/–/–	–	–	–	–	–	–
Pardosa palustris	–	3/5/–	2/2/–	–	3/5/–	16/–/–	11/–/–	–	1/–/–	–
Pardosa prativaga	–	–	–	–/4/–	–/1/–	–	–	–	–	–
Pardosa sp.	–/–/143	–/–/346	–/–/91	–/–/83	–/–/11	–/–/13	–/–/61	–/–/115	–/–/94	–/–/32
Trochosa terricola	–	–	–	–	–	–	–	–	–	–
Trochosa sp.	–	–	–	–	–/–/2	–	–	–	–	–
Liocranidae	**–**	**–**	**–**	**–**	**1**	**–**	**–**	**–**	**–**	**–**
Agroeca cuprea	–	–	–	–	1/–/–	–	–	–	–	–
Phrurolithidae	**–**	**–**	**5**	**1**	**–**	**–**	**–**	**–**	**–**	**–**
Phrurolithus minimus	–	–	–	–	–	–	–	–	–	–
Phrurolithus festivus	–	–	–/5/–	–/1/–	–	–	–	–	–	–
Zodariidae	**–**	**–**	**–**	**78**	**12**	**1**	**–**	**–**	**–**	**–**
Zodarion rubidum	–	–	–	3/75/–	3/9/–	–/1/–	–	–	–	–
Gnaphosidae	**12**	**19**	**13**	**43**	**29**	**90**	**48**	**54**	**12**	**6**
Drassodes lapidosus	–	–	–	–/2/–	–	1/–/–	–	–	–	–
Drassodes pubescens	–	–	1/–/–	–/6/–	2/2/–	1/–/–	–	–	–	–
Drassodes sp.	–/–/1	–/–/4	–	–	–	–/–/4	–/–/1	–/–/1	–/–/1	–

Pasture	2016					2015				
	4 May	*30 May*	*17 Jun*	*5 Jul*	*25 Jul*	*21 Aug*	*11 Sep*	*8 Oct*	*2 Nov*	*1 Dec*
Drassyllus praeficus	–	–	–	1/2/–	–	–	–	–	–	–
Drassyllus pusillus	–	–/1/–	–/1/–	–	–	–	–	–	–	–
Drassyllus sp.	–	–	–	–	–	–	–	–	–	–/–/1
Haplodrassus signifer	3/–/–	1/4/–	–/3/–	5/9/–	–/1/–	–	–	–	–	–
Haplodrassus sp.	–	–/–/2	–/–/1	–	–	–	–/–/3	–/–/8	–/–/4	–/–/4
Micaria formicaria	–	–	–	–	–	–	1/–/–	–	–	–
Micaria fulgens	–	–	–	1/–/–	–/2/–	–	–	1/–/–	–	–
Zelotes electus	–	–	1/2/–	1/1/–	–	1/–/–	–	–/1/–	–	–
Zelotes longipes	7/–/–	2/–/–	2/–/–	5/–/–	6/–/–	10/19/–	6/24/–	6/27/–	–/7/–	–/1/–
Zelotes petrensis	–	–	–	–	–	–	–	–/1/–	–	–
Zelotes sp.	–/–/1	–/–/5	–/–/2	–/–/10	–/–/15	–/–/54	–/–/13	–/–/9	–	–
Philodromidae	**–**	**1**	**6**	**4**	**5**	**1**	**3**	**–**	**–**	**–**
Thanatus arenarius	–	–/1/–	–/6/–	–/4/–	–/5/–	–	–	–	–	–
Thanatus sp.	–	–	–	–	–	–/–/1	–/–/1	–	–	–
Thomisidae	**10**	**9**	**3**	**6**	**11**	**3**	**2**	**2**	**5**	**1**
Ozyptila atomaria	–	–	–	–	–	–	1/–/–	–	–	–
Ozyptila scabricula	–/4/–	–/2/–	–	–	–	–	–	–/1/–	–/3/–	–
Ozyptila sp.	–	–	–	–	–/–/2	–/–/2	–	–/–/1	–/–/1	–/–/1
Psammitis ninnii	–	–	–/1/–	–/6/–	2/6/–	1/–/–	–	–	–	–
Xysticus audax	–	–	–	–	–	–	–	–	–	–
Xysticus cristatus	1/–/–	–	–	–	–	–	–	–	–	–
Xysticus erraticus	–	–	–	–	–/1/–	–	–	–	–	–
Xysticus kochi	–/5/–	1/1/–	2/–/–	–	–	–	–	–	–	–
Xysticus sp.	–	–/–/5	–	–	–	–	–/–/1	–	–/–/1	–
Salticidae	**1**	**–**	**–**	**–**	**–**	**1**	**1**	**–**	**–**	**1**
Heliophanus lineiventris	–/1/–	–	–	–	–	–	–	–	–	–
Heliophanus sp.	–	–	–	–	–	–/–/1	–/–/1	–	–	–/–/1