Short-term effects of horse grazing on spider assemblages of a dry meadow (Western France)

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Abstract

In this study, the biodiversity impacts of a little studied herbivore, horse, were assessed in a high conservation value habitat of Brittany (Western France), dry meadows. Spiders, a diversified and abundant group of predators, were used as bioindicators. Three complementary sampling techniques were used to assess changes in spider assemblages in both soil and vegetation strata, over time (diachronic comparison of managed unit before vs. after management) and space (synchronic comparison of managed vs. control units). Few effects of grazing, i.e. only one significantly indicative species, were found on assemblage composition (Anosim), and none on abundances, α- and β- diversities (GLM on pitfall trap data). On the contrary, important differences were found between units before management took place. The main effects of grazing management were revealed over time (after one year), and not between managed and control units (CCA on pitfall trap data and χ^2 tests on guilds from each sampling method), showing the relevance of diachronic approach more than synchronic approach in such a management monitoring. Grazing by horses could be relevant to manage meadows because it creates a high spatial heterogeneity, but that would require more (long-term) studies, also including other model groups.

Key-words: Indicators, Management, Synchronic and diachronic approaches, Araneae, Brittany.

Introduction

Management is frequently carried out in grasslands to simulate disturbances naturally occurring in the past, like grazing by large herbivores (Bakker, 1989), or fire (Valkó et al., 2014). The impact of management practises is usually monitored using plant diversity (e.g. Kahmen et al., 2002). However, plant species diversity seems to be a poor predictor for the diversity of other groups, such as arthropods (Kirby, 1992; Morris, 2000; Van Klink et al., 2015). It is therefore necessary to use various groups of organisms to evaluate the potential of a management to conserve overall biodiversity. Grazing affects arthropods both directly and indirectly. Direct effects of grazing concern trampling and accidental predation of insects (as well as scavengers and dung feeders: Lumaret et al., 1992), whereas indirect effects are more complex and mainly encompass vegetation and soil-mediated changes (Van Klink et al., 2015).

In general grazing by large herbivores has mostly a negative impact on species richness and abundances of arthropods as it reduces plant cover and biomass. Many large herbivores roughly produce similar effects on the diversity of phytophagous (including flower-visiting) arthropods (Van Klink et al., 2015). Some studies linked changes in arthropod diversity with changes in plant diversity (e.g. Foote & Hornung, 2005), height (Ausden et al., 2005; Ryder et al., 2005) or biomass (Kruess & Tscharntke, 2002), but shifts in functional plant groups are believed to have a higher explanative power (Van Klink et al., 2015).

On the contrary, measured indirect effects are likely more dependent on the target taxa or metrics considered, and not consistently reported for all herbivores (Read & Andersen, 2000). As an example, arthropods have been shown to be more diverse and more abundant under ungulate grazing, but with a reduced arthropod biomass overall (González-Megías et al., 2004). The effects on predatory arthropods depends on the intensity of grazing (e.g. Dennis et al., 1998; Dennis et al., 2002; Pétillon et al., 2007; Rosa García et al., 2009; Van Klink et al., 2013). Yet several studies did not find any effect on arthropod diversity, some found some on their species composition (Gardner et al., 1997; Woodcock et al., 2005; Fadda et al. 2008).

Reported effects of management on arthropod diversity are overall negative, but differ depending on the types of herbivores and grazing intensity, and are likely context-dependent. Conclusions are also dependent on the taxa and metrics used, and thus on the manager's objectives (e.g. Leroy et al., 2014; Török et al., 2016). In this study, the impact of horse grazing on spiders was assessed in a high conservation value habitat in Brittany, dry meadows. Despite its high potential for conservation management (mainly because of an increased plant consummation, higher than e.g. cow at similar stocks: Ménard et al., 2002), the effects of horse on arthropod diversity remains poorly documented (Bell et al., 2001; Joern & Laws 2013). Spiders were used because of their bioindicative values (Maelfait & Baert, 1988; Marc et al., 1999), e.g. to monitor the effects of biological invasions (Pétillon et al., 2005; Mgobozi et al., 2008), success in habitat restoration (Cristofoli et al., 2010; Pétillon et al., 2014) or changes in land use (Schmidt et al., 2005; Prieto-Benítez & Méndez, 2011). A pre-management inventory was performed, so both synchronic and diachronic approaches could be used. Changes in assemblages of both epigeic and vegetation-dwelling spider assemblages were assessed by using (three) complementary sampling methods.

Taxonomic and functional changes in community structure were finally evaluated in the short-term to test the following hypotheses: i) Grazing alters the functional composition of spider community as it will select aeronautic and disturbance-resistant species (Bell et al., 2001) as well as hunting spider species, that are less dependent on the plant physiognomy (e.g. Churchill & Ludwig, 2004). ii) Abundance and alpha diversity are both expected to be lower in the grazed unit compared to the non-grazed unit because of reduced plant biomass and cascading effects (e.g. Kruess & Tscharntke, 2002) whereas β-diversity is expected to be higher in the grazed unit compared to the non-grazed unit due to an increased heterogeneity of vegetation (Loucougaray et al., 2004).

Material and Methods

Study site

The study site is located in Brittany (Western France), 20km south-West of Rennes, near the city of Guichen (47°97’16N, -1°89’20W). The natural reserve (‘Vallée du Canut’) is a public land of 147 ha, part of a larger Natura 2000 site (total of 427 ha) that encompasses meadows, heathlands, forests and a dense network of hedgerows. The dry meadows are located on Cambrian red shales outcropping on the slopes of a small valley (‘le Canut’ river). The meadows have a N-S slope, with the lower part dominated by braken (*Pteridium aquilinum*). The upper part, where the sampling took place, had (before the introduction of horses) a mean vegetation height of 1.3m (visual estimation), and the following dominant plants: *Dactylus glomerata*, *Rumex* spp., *Stellaria holostea*, *Plantago lanceolata*, *Holcus mollis*, and different species of Apiaceae, *Geranium*, *Ranunculus*, *Centaurea* and *Trifolium*. The sampled area was 4 ha in total, subdivided into two experimental units (further called ‘units’), grazed and non-grazed (during the second year of the study). Two horses were then introduced in October 2003 after the first year sampling. Although the impact of grazers on vegetation cover and diversity was obvious (see Fig. S1 in Appendix), data on habitat changes were not used here because our hypotheses relate to changes in spider assemblages using both diachronic and synchronic approaches (effects of time vs. management).

Sampling design and methods

In order to sample spiders both at ground level and in the different strata of vegetation, three complementary sampling methods were carried out during the two years of the study: pitfall trapping, hand-collecting and sweep-netting.

Traps to catch ground-active spiders consisted of polypropylene cups (diameter: 12 cm, height: 15 cm) filled with ethanol 70° and covered with a wooden roof to prevent overflow by rainfall. Four traps arranged in a square grid were set up in each unit, and spaced 10 m apart (Topping & Sunderland, 1992; Churchill & Arthur, 1999; Ward et al., 2001), each trap representing one sample (for a total of 4 replicates per treatment, 16 samples in total). Traps were active 2 times 30 days, 15 days in June and September 2003 and 2004 (i.e. the most favorable periods for spiders in this region: e.g. Varet et al., 2013). Numbers of individuals in traps were finally divided by the number of days traps were actually active (Luff, 1975; Curtis, 1980). Hand collections were carried out to sample all visible ground-living spiders, including some less mobile species that would have been few or not sampled by traps (Churchill, 1993). Hand collections were time-standardized (2 collectors during 10 min in each unit represent one sample, for a total of 8 samples) and carried out during afternoons 4 times in June and September 2003 and 2004. Vegetation-dwelling spiders were collected using sweep-netting (40 cm diameter) along 2 parallel transects (20m+10m and 45 sweeps, which represents one sample altogether), 2 times in each unit (June and September 2003 and 2004, for a total of 8 samples).

Identification and conservation of specimens

Spiders were sorted and stored in tubes with 70% ethanol (University of Rennes 1, France). Adults were identified to species using Roberts (1987), Heimer & Nentwig (1991) and Roberts (1995).

Data analysis

Differences in species composition between years and management were visualized by a Venn diagram of shared vs. exclusive species of grazed and un-grazed units before and after the management took place, and tested using an Analysis of Similarity (ANOSIM) completed by IndVal calculations (Dufrêne & Legendre, 1997) on species abundances using individuals sampled using pitfall traps. A Detrended Correspondence Analysis (DCA) was done on individual counts as response variables and year / management as predictors. A Redundancy (RDA) or a Constrained Correspondence (CCA) analysis was then chosen according to the axis length of the DCA, < 3 or > 4 respectively (Legendre & Gallagher 2001). Here a CCA (first axis of the DCA = 1.40) was performed using vegan R package (Oksanen et al. 2013). Monte Carlo tests with 999 permutations were carried out to test the significance of the two factors and constrained analyses axes. Hunting guilds were defined according to Uetz et al. (1999), and assigned to species according to the families they belong to. Guild composition differences between years and management were studied using χ^2 tests for each sampling method.

As the same pitfall trap was operative in 2003 and 2004, abundances and species richness were pair-matched over time and consequently compared using repeated analysis of variance (Pétillon et al., 2010 and Lafage & Pétillon). Tests were performed using spider activity-density and species richness as dependent variables, management (grazed or non-grazed) as a fixed factor and date (pre- vs. post-grazing) as a within subject effect. If the interaction between fixed factors was not significant (in model 1), a second GLM with logit link and negative binomial distribution (model 2, see O'Hara & Kotze, 2010) was used to test significant effects of separated fixed factors, without their interaction. If the interaction was not significant, t-tests were used to detect significant differences between sampling periods. If grazing had an effect on the variable responses, a significant interaction between management and date was expected (i.e. the within subject factor being expressed differentially for the two units due to grazing effects in one of them). For each analysis, the level of statistical significance used was α=0.05.

β-diversity was estimated through a dissimilarity matrix (corresponding to Sørensen pair-wise dissimilarity), then partitioned into its two components—species turnover (βt) and nestedness (βn)—following Baselga (2010) and using the betapart R package (Baselga and Orme 2012). Only data from pitfall traps were used for the β-diversity.

All statistical analyses were performed using R 3.2.3 (R Core Team, 2015).

Results

Totals of 1990 spiders belonging to 55 species and 1040 spiders belonging to 66 species were collected in 2003 and 2004 respectively (see Table S1 in Appendix). Most spiders were sampled using pitfall traps (1801 individuals), followed by sweep-net and hand-collection (702 and 537 individuals, respectively).

There was a slight increase in the number of species shared between the two units from 2003 to 2004 (22 to 24 species: Figure 1). Overall, no difference in species composition was found between experimental units in 2003 (R=-0.02, P=0.537) and 2004 (R=0.31, P=0.056). Only *Pachygnatha degeeri* had a significant IndVal, with a preference for the grazed vs. non-grazed unit (IndVal=4.24 vs. 2.49 respectively, P=0.028). Furthermore, no significant difference was found in species composition of the non-grazed unit between 2003 and 2004 (R=0.47, P=0.057). Conversely a significant difference in species composition of the grazed unit was found between 2003 and 2004 (R=0.84, P=0.026), which was confirmed by the CCA (significant effect of year along the axis 1, $F_{1,13}$=2.17, P<0.001; Figure 2). CCA was significant ($F_{2,13}$=1.76, P< 0.001) explaining 34,5% of the observed variance with the first axis being significant ($F_{1,13}$=2.29, P=0.003).
No significant difference was found in guild frequencies (Table 1) for individuals sampled by pitfall trap (Figure 3), sweep net (Figure 4) or hand collecting (Figure 5).

A significant interaction between “management” and “date” effects was found for total activity-density ($F_{1,6}$=7.33, P=0.035). Total activity-density decreased in the two units (non-grazed: t=5.56, df=3, P=0.011; grazed: t=8.85, df=3, P=0.003) but the decrease was more important in the grazed unit (Figure 6). No significant interaction between “management” and “date” effects was found for total species richness ($F_{1,6}$<0.001, P>0.999). No significant effect of year ($F_{1,13}$=2.049, P=0.387) or management was found on species richness ($F_{1,13}$=2.049, P=0.176).

β-diversity was nearly constant over time in each unit, yet the nestedness increased in the non-grazed unit (Table 2), whereas its species turnover decreased. Differences among the units were similar in the two years of sampling, i.e. before and after management by grazing took place.

Discussion

Species composition

Among the species that were not shared between the two units in 2004, but were in 2003, most of species were Linyphiids (e.g. *Bathyphantes gracilis* or *Lepthyphantes ericaeus*), a family well known for its long-distance dispersal abilities, at both young and adult stages (e.g. Blandenier, 2009; Simonneau et al., 2016). This change is therefore probably due to inter-annual variations in ballooning and/or under-sampling due to their small size. Almost all new shared species in 2004 were also Linyphiids (e.g. *Erigone atra*, *Meioneta mollis*, *M. beata* and *Pelecopsis radicicola*), so hardly attributable to any management effect. Among the species that disappeared after the management took place, some are strongly dependent on vegetation structure (a key factor in shaping spider assemblages: e.g. Hatley & Macmahon, 1980), and were thus likely disfavored by the grazing. This could be the case of several ambush hunters (*Xysticus cristatus*, *X. erraticus* and *X. tortuosus*) and web-builders (e.g. *Enoplognatha ovata*). It is harder to link the disappearance of the other species from the grazed unit to the grazing, because they were not initially in high numbers and/or they are not directly linked to the vegetation. Yet, the appearance of several thermophilous species (either at ground or at vegetation levels: *Myrmarachne formicaria* and *Tegenaria agrestis*, *Cyclosa oculata*, *Dictyna latens* and *Hypsosinga albovittata* respectively; Harvey et al., 2002) can be explained by a more open micro-habitat under grazing (e.g. Gibson et al., 1992). This tendency should yet be verified by a longer-term monitoring.

Overall, few, if any (see e.g. the preference of *Pachynatha degeeri*, an ubiquist species, for the grazed meadow), significant change in species composition was observed after the introduction of horse on the dry meadow, which conforms to few other studies on the impact of grazing on spider composition (Pozzi et al., 1998; Dennis et al., 2001; Pétillon et al. 2007). No significant change after the grazing took place was found in spider hunting guilds, although web-builders tend to be reduced in the grazed unit (visible for sweep-net sampling only). Hunting guilds are usually affected by grazing, with several studies showing a decrease in web-builders (Gibson et al., 1992; Kirby, 1992; Bell et al., 2001; Hemm & Höffer, 2012; Ford et al., 2013), mainly explained by a reduced vegetation complexity (Churchill & Ludwig, 2004; Kovac & Mackay, 2009).

Structural diversity

A decrease in total activity-density was observed in both units over time, but at a higher rate in the grazed unit. This is likely the result of both deleterious effects of grazing on ground-dwelling spiders (see above) and of inter-specific competition-mediated changes (Wise, 2006; Van Klink et al., 2015). Competition among spider species is indeed higher in simple habitats (Hurd & Fagan, 1992; Marshall & Rypstra, 1999). A closer attention to change in abtioic and biotic conditions would be necessary to disentangle direct and indirect effects of habitat change on spider abundance (the local factors are likely more important here, in an extensively managed land: Horváth et al., 2015).

Contrary to several previous studies on other large herbivores (e.g., Pozzi & Borcard, 2001; Pétillon et al., 2007), no significant effect of grazing was found on spider species richness. Indeed, as for many other taxa, and as with many other disturbances, grazing by large herbivores is usually reported to be negative on spiders (Bell et al., 2001; see also the meta-analysis of Prieto-Benítez & Méndez, 2011). Mechanisms usually involved in such a richness decrease encompass local habitat simplification (litter and vegetation strata: Dennis et al., 2001) and related food reduction (Kruess & Tscharntke, 2002; for soil functioning: Koppel et al., 1997). Yet, Lafage et al. (2014) recently demonstrated that spiders were not influenced by the plant biomass (both in terms of abundance and species richness). Finally, it is also possible that the effects are too short in time to be visible (but see below).

Our hypothesis on an increased β-diversity was not verified. Two main explanations can be advanced for this lack of result: the effects of grazing are too short to be visible (but arthropods, and especially spiders, are known to quickly react to changes in habitat structure: Pétillon et al., 2014) and/or the effects of grazing are counterbalanced by inter-annual variations. Our second explanation is the most likely, also because it would explain the increased nestedness in the ungrazed unit. Plant heterogeneity is usually higher under grazing treatment (e.g. Gallet & Rozé, 2001; Van Klink et al., 2015), which reinforces the idea that plants and arthropods, here spiders, do react in a different way to management practices (probably due to differences in mobility: Lafage et al., 2015; Lafage & Pétillon, 2016). It has to be stressed that our sampling design did not necessarily encompass the spatial heterogeneity resulting from grazing in general (e.g. for spiders: Bonte et al., 2000), and especially by horses (Loucougaray et al., 2004), and would deserve a higher replication for all the sampling methods to properly assess spider diversity (including beta-diversity, see e.g. Klimek et al., 2008; Báldi et al., 2013).

Concluding remarks

In this study, despite the existence of true replicates within each unit, units were confounded with the management treatment, which can be considered as a case of pseudoreplication in the sense of Hurlbert (1984). Comparing stations between different sites are likely to increase the inter-class variance, by the existence of other co-varying factors (Oksanen, 2001). Here, even at a small scale, we showed a high variance between stations, with differences between units before the grazing took place. This underlines the importance of carrying out diachronic approaches, also because the effects of management were sometimes only visible over time, and not when comparing grazed vs. non-grazed units. Spiders, although presenting high dispersal abilities and high mobility (Lafage & Pétillon, 2014) that may hide or lower management effects (Pech et al., 2015), can be considered as a relevant group for monitoring biodiversity consequences of management, bringing complementary information to changes in vegetation structure.

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Table 1. Chi² tests on hunting guilds (2df).

Comparison		Pitfall trap	Sweep net	Hand collection
2003/2004	Non grazed	χ^2=7.52, P=0.023	χ^2=14.97, P<0.001	χ^2=14.79, P<0.001
	Grazed	χ^2=37.35, P<0.001	χ^2=39.04, P<0.001	χ^2=8.77, P=0.012
Non grazed/grazed	2003	χ^2=5.94, P=0.051	χ^2=1.02, P=0.600	χ^2=0.89, P=0.639
	2004	χ^2=4.76, P=0.092	χ^2=3.94, P=0.139	χ^2=0.16, P=0.921

Table 2. Partition of Beta-diversity into species turnover and nestedness in both grazed and non-grazed units, before (2003) and after (2004) the management took place (data from pitfall traps, βt: β turnover, βn: β nestedness).

Year	Unit	β (Sørensen)	βt	βn
2003	Grazed	0.561	0.449	0.112
	Non-grazed	0.461	0.429	0.033
2004	Grazed	0.539	0.458	0.082
	Non-grazed	0.431	0.282	0.148

Figure captions

Figure 1. Venn diagram of exclusive vs. shared species of the grazed and non-grazed units, before (2003) and after (2004) the management took place.

Figure 2. Projection of significant variables from the CCA on spider species. Pitfall traps are represented by circles and species by crosses.

Figure 3. Percentage activity density of each hunting guild sampled by pitfall trapping in 2003 and 2004. (AH: Ambush hunters; GR: Ground runners; WB: Web-builders).

Figure 4. Percentage abundance of each hunting guild sampled by sweep netting in 2003 and 2004. (AH: Ambush hunters; GR: Ground runners; WB: Web-builders).

Figure 5. Percentage abundance of each hunting guild sampled by hand collecting in 2003 and 2004. (AH: Ambush hunters; GR: Ground runners; WB: Web-builders).

Figure 6. Activity-density of spiders in the grazed and non-grazed units in 2003 and 2004 (data from pitfall traps).

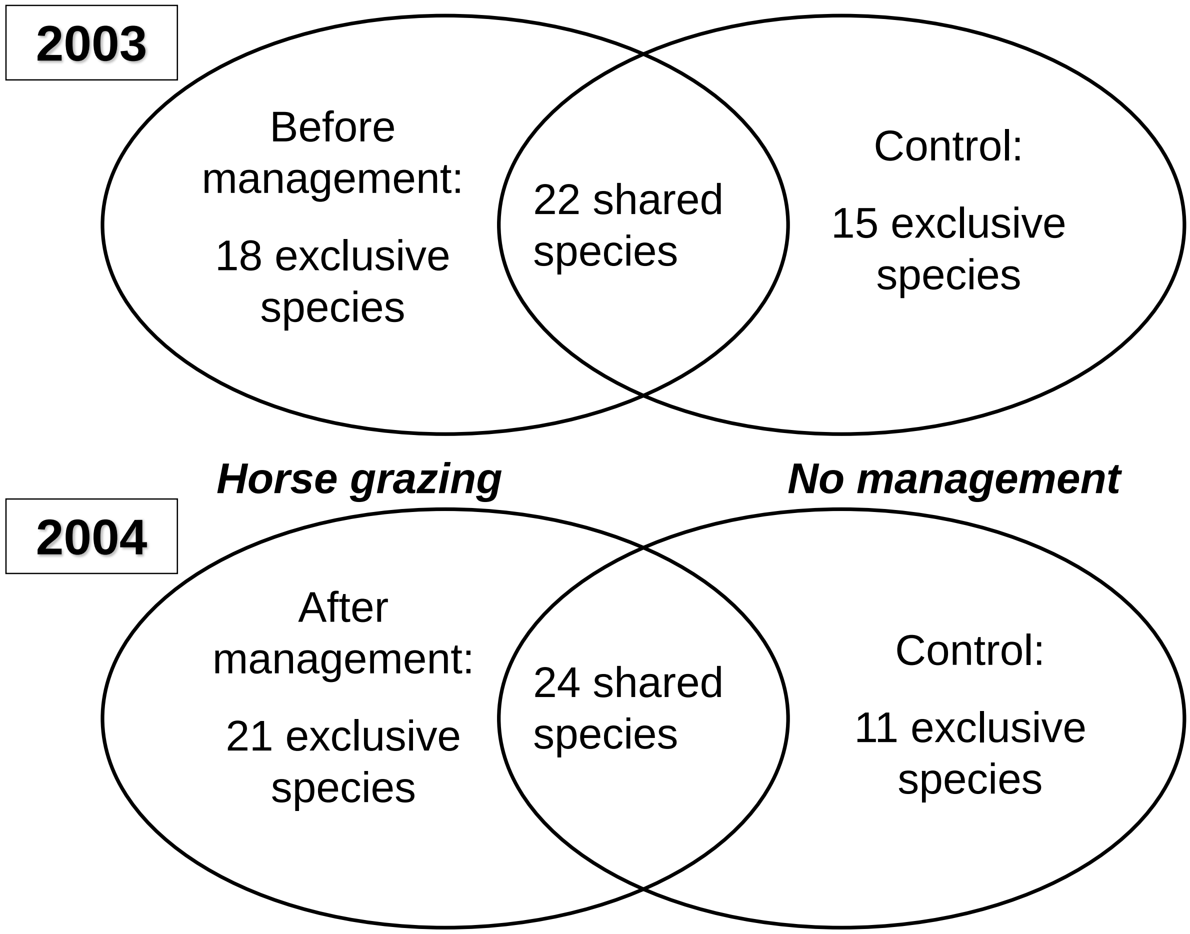

Figure 1: Pétillon et al.

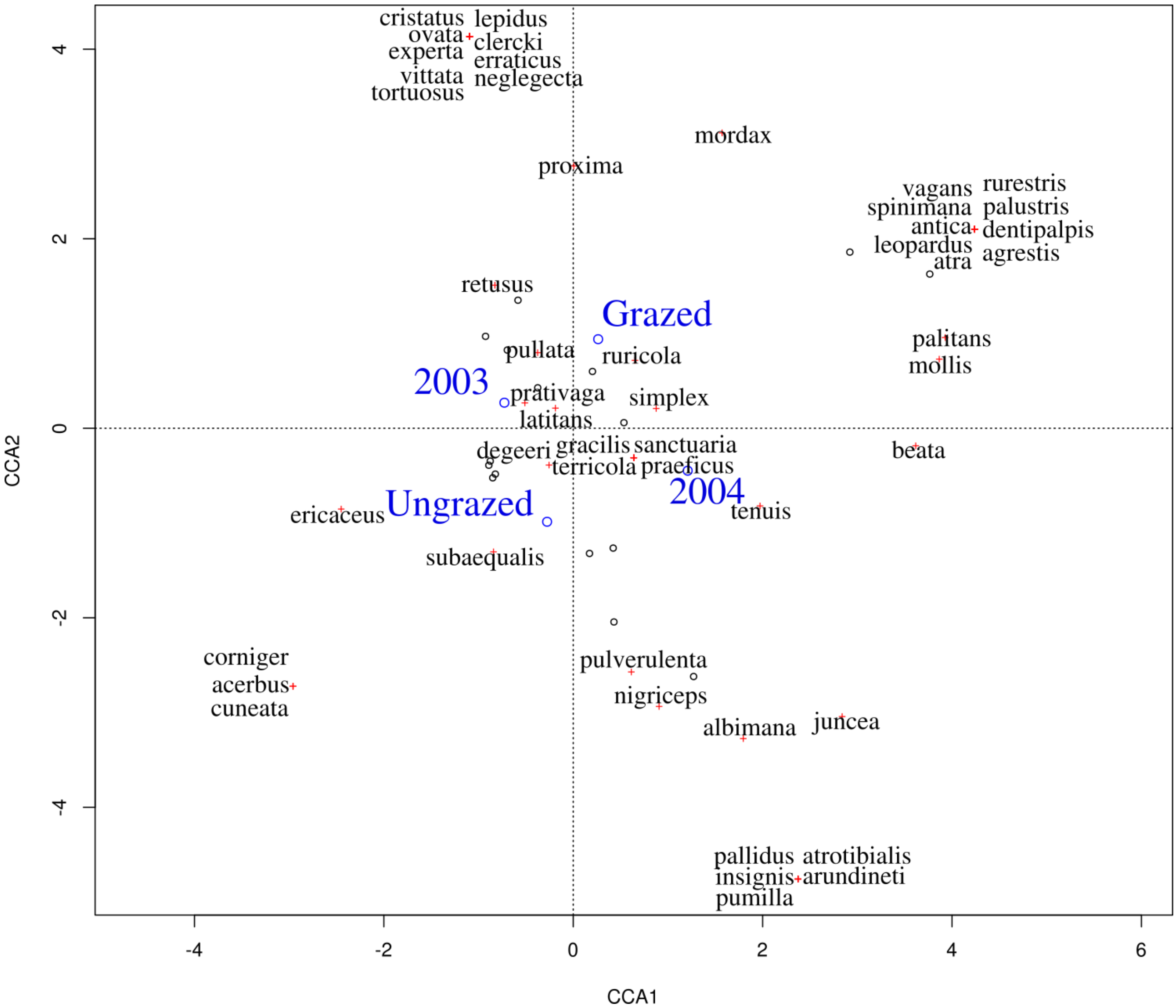

Figure 2: Pétillon et al.

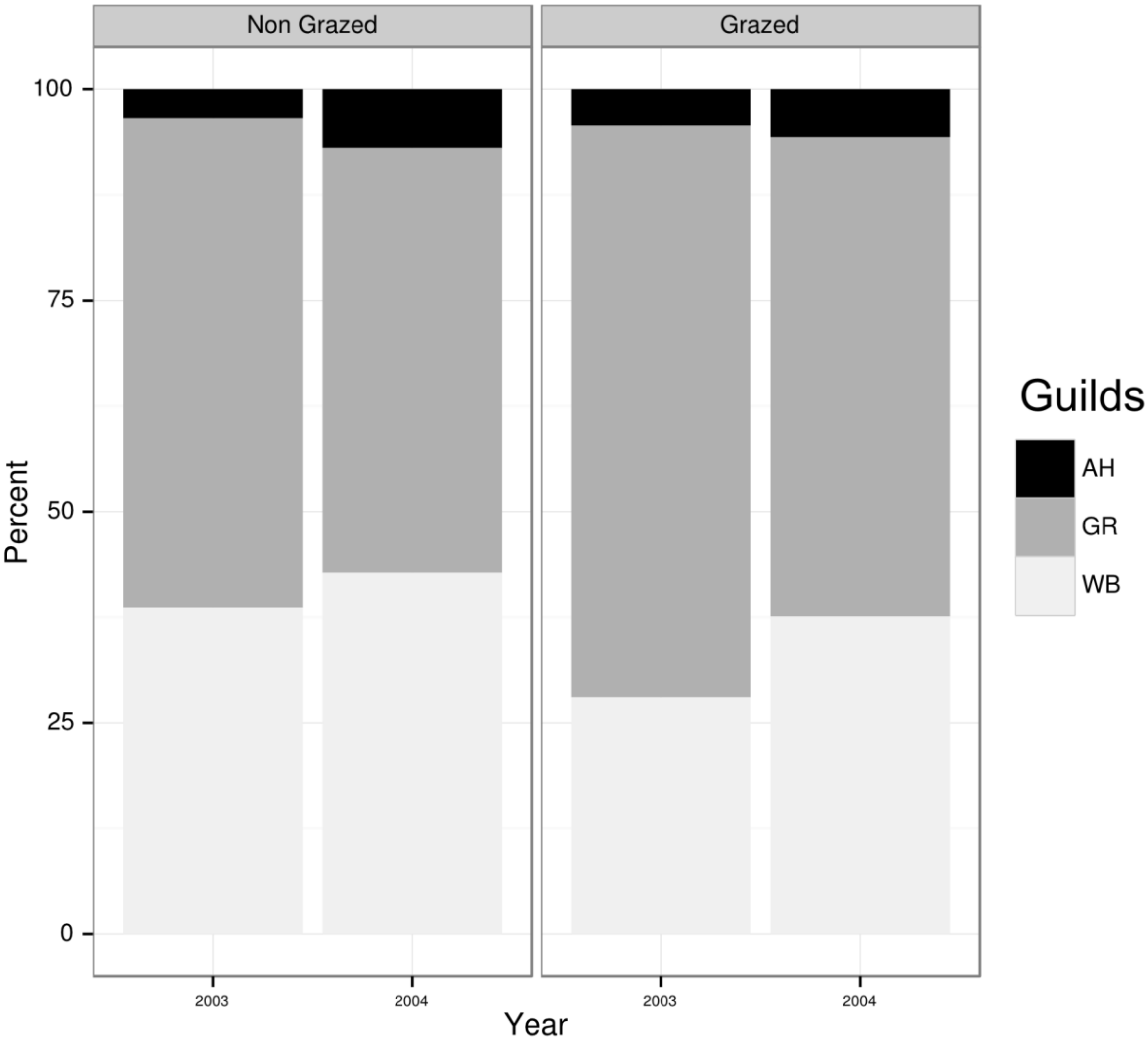

Figure 3: Pétillon et al.

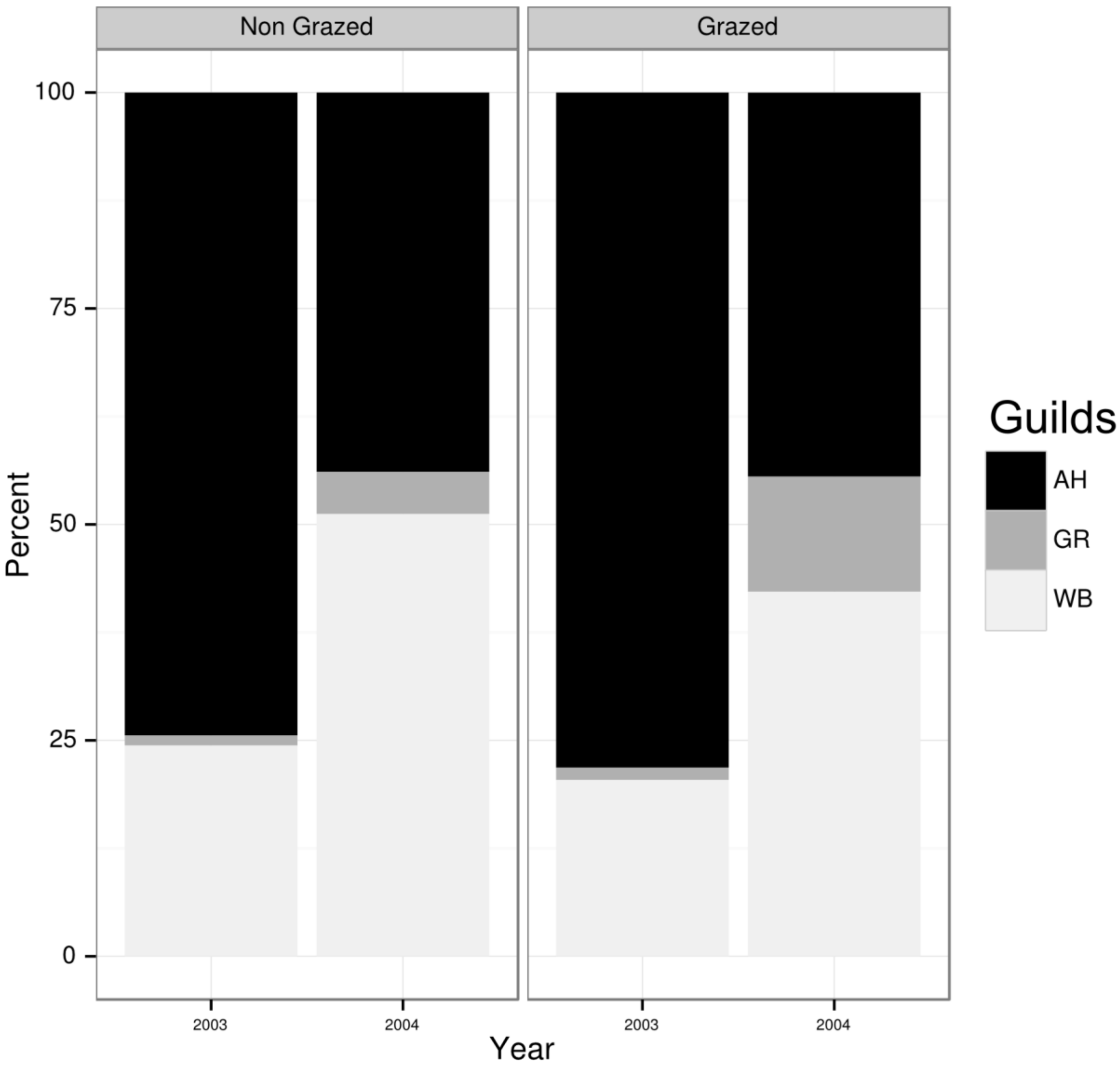

Figure 4: Pétillon et al.

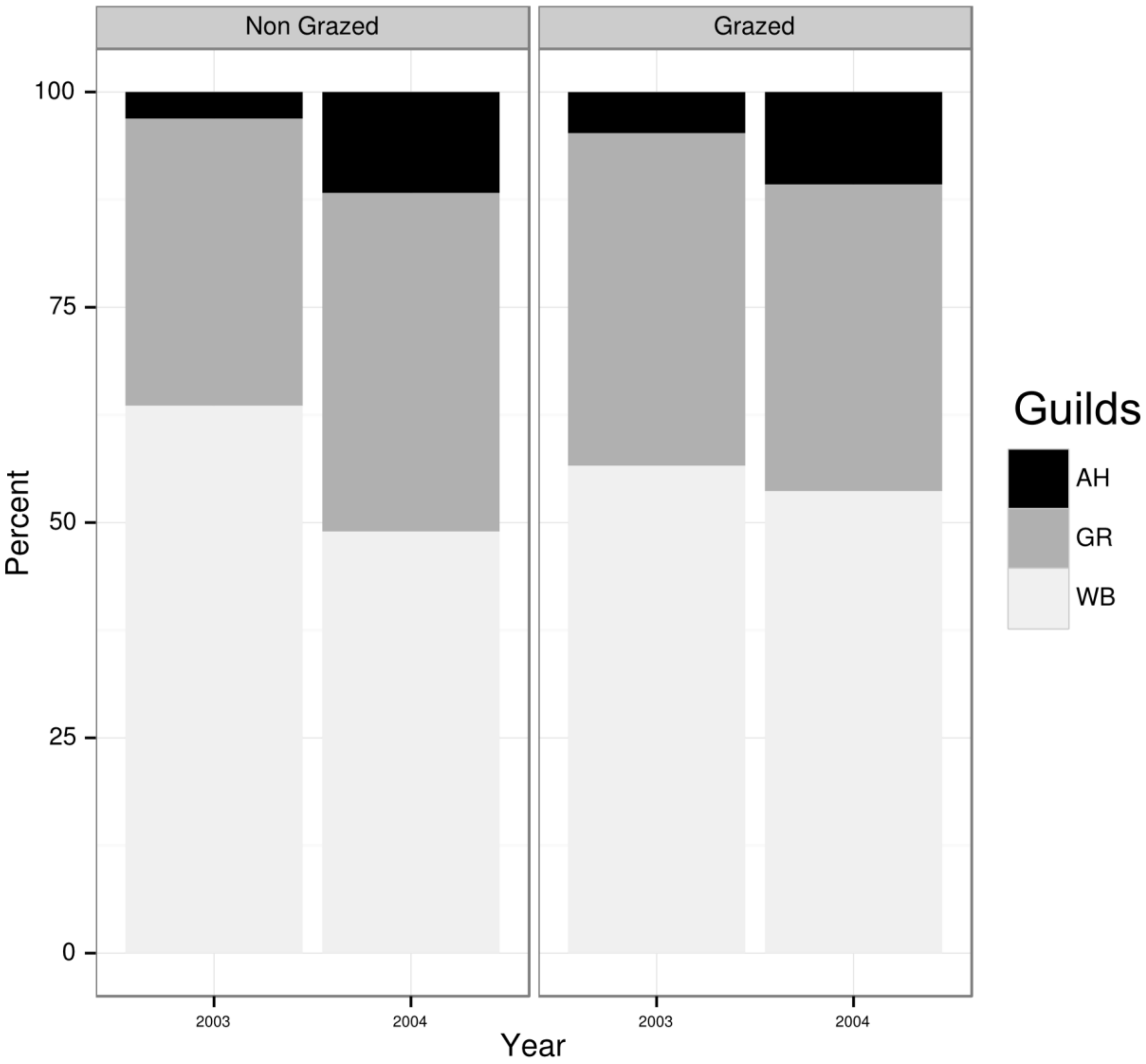

Figure 5: Pétillon et al.

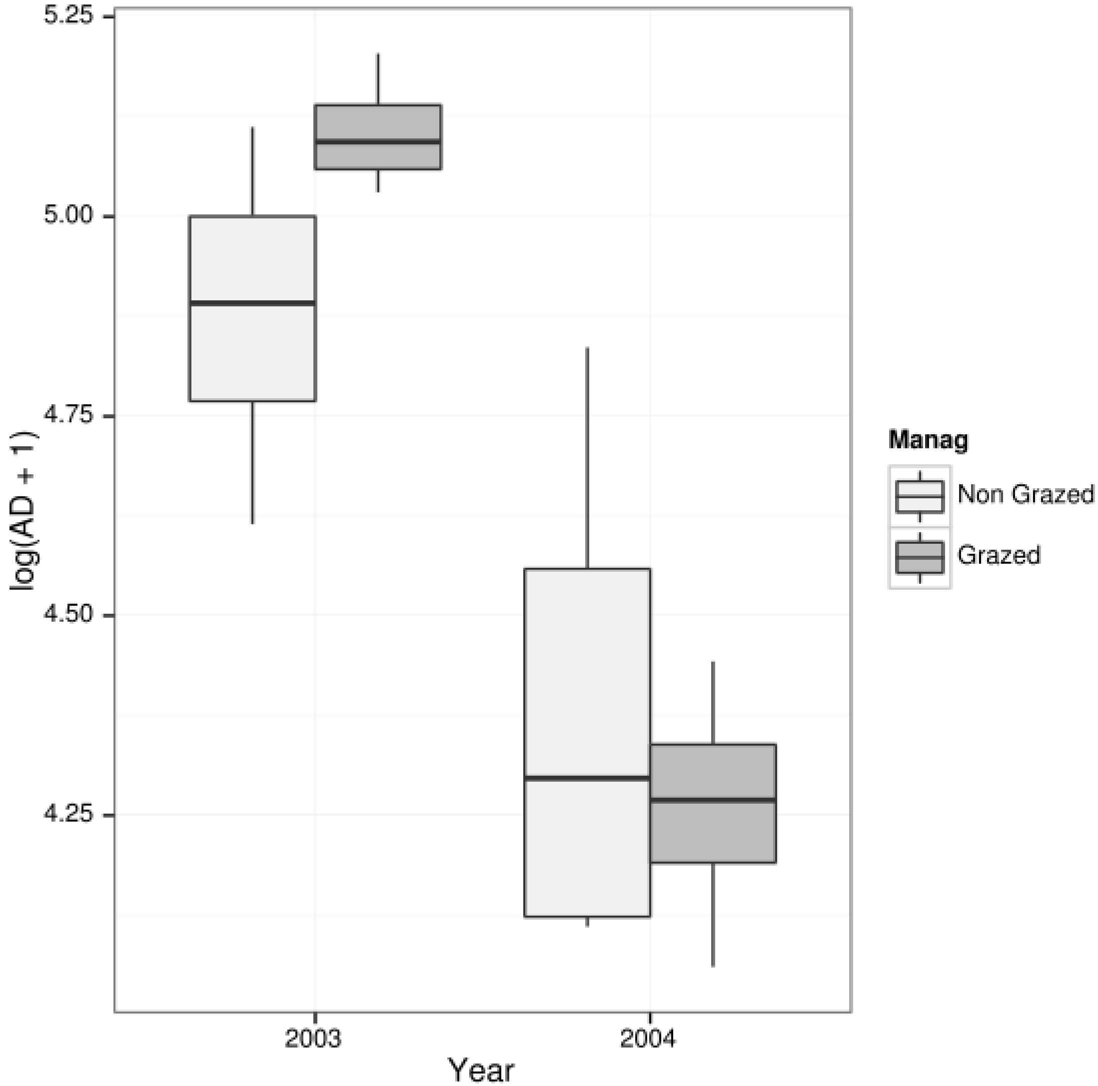

Figure 6: Pétillon et al.

Table S1. Taxonomic list of the species collected in grazed and non-grazed units (2003-2004), all sampling methods confounded.

Species	2003 Non Grazed	Grazed	2004 Non Grazed	Grazed
Agalenatea redii (Scopoli, 1763)	1		3	1
Agroeca proxima (O. Pickard-Cambridge, 1871)	1			
Agroeca sp.			1	
Agyneta affinis (Kulczyński, 1898)			1	2
Agyneta mollis (O. Pickard-Cambridge, 1871)			3	9
Agyneta rurestris (C. L. Koch, 1836)	1			4
Alopecosa cuneata (Clerck, 1757)	3			
Alopecosa pulverulenta (Clerck, 1757)	2		2	1
Alopecosa sp.	22	9	2	1
Anelosimus vittatus (C. L. Koch, 1836)	9	1		1
Araneus diadematus Clerck, 1757		4		
Araneus quadratus Clerck, 1757				1
Arctosa leopardus (Sundevall, 1833)				1
Argiope bruennichi (Scopoli, 1772)			1	3
Aulonia albimana (Walckenaer, 1805)	2	3	11	1
Bathyphantes approximatus (O. Pickard-Cambridge, 1871)				1
Bathyphantes gracilis (Blackwall, 1841)	2	3		2
Brigittea latens (Fabricius, 1775)				1
Cercidia prominens (Westring, 1851)	2			
Clubiona neglecta O. Pickard-Cambridge, 1862		1		
Clubiona sp.	11		2	7
Cyclosa oculata (Walckenaer, 1802)				1
Drassodes sp.				6
Drassyllus praeficus (L. Koch, 1866)	1			1
Drassyllus praeficus (L. Koch, 1866)		1		
Enoplognatha mordax (Thorell, 1875)		1		2
Enoplognatha ovata (Clerck, 1757)		2		
Enoplognatha sp.		1	3	1
Eratigena agrestis (Walckenaer, 1802)				1
Erigone atra Blackwall, 1833		2	2	1
Erigone dentipalpis (Wider, 1834)				6
Ero cambridgei Kulczyński, 1911		1		
Genus sp.	35	397	119	172
Heliophanus sp.	1	1		2
Hypsosinga albovittata (Westring, 1851)				1
Larinioides cornutus (Clerck, 1757)	2		2	
Lepthyphantes sp.	2	19		
Mangora acalypha (Walckenaer, 1802)	28	26		

Micrargus subaequalis (Westring, 1851)	7	5	5	1
Myrmarachne formicaria (De Geer, 1778)				1
Neoscona adianta (Walckenaer, 1802)		1	15	1
Neottiura bimaculata (Linnaeus, 1767)			3	
Neriene clathrata (Sundevall, 1830)	1			
Oedothorax fuscus (Blackwall, 1834)		1		
Oedothorax retusus (Westring, 1851)	3	3		1
Ozyptila sanctuaria (O. Pickard-Cambridge, 1871)		1	1	
Ozyptila simplex (O. Pickard-Cambridge, 1862)	7	24	19	14
Ozyptila sp.	11		1	5
Pachygnatha clercki Sundevall, 1823		4		
Pachygnatha degeeri Sundevall, 1830	252	239	151	133
Palliduphantes ericaeus (Blackwall, 1853)	8	4		
Palliduphantes insignis (O. Pickard-Cambridge, 1913)			1	
Palliduphantes pallidus (O. Pickard-Cambridge, 1871)	1		1	
Pardosa nigriceps (Thorell, 1856)	5	1	7	4
Pardosa palustris (Linnaeus, 1758)				8
Pardosa prativaga (L. Koch, 1870)	19	20	7	8
Pardosa proxima (C. L. Koch, 1847)	2	6		2
Pardosa pullata (Clerck, 1757)	74	117	32	41
Pardosa sp.	131	69	1	1
Pardosa vittata (Keyserling, 1863)		1	2	10
Pelecopsis radicicola (L. Koch, 1872)			2	1
Pirata sp.	8	6		
Piratula latitans (Blackwall, 1841)	54	69	37	31
Pisaura mirabilis (Clerck, 1757)	3	3	2	1
Pocadicnemis juncea Locket & Millidge, 1953	1	1	6	2
Pocadicnemis pumila (Blackwall, 1841)			1	
Prinerigone vagans (Audouin, 1826)				1
Robertus arundineti (O. Pickard-Cambridge, 1871)			1	
Scotina celans (Blackwall, 1841)			1	
Sintula corniger (Blackwall, 1856)	1			
Stemonyphantes lineatus (Linnaeus, 1758)	1		1	
Tallusia experta (O. Pickard-Cambridge, 1871)		1		
Tapinopa longidens (Wider, 1834)				1
Tenuiphantes tenuis (Blackwall, 1852)	3	3	9	8
Tibellus oblongus (Walckenaer, 1802)			3	
Tibellus sp.	14	17	13	12
Trochosa ruricola (De Geer, 1778)	3	3	1	4
Trochosa sp.	5	2	7	
Trochosa terricola Thorell, 1856	4	6	6	4
Walckenaeria acuminata Blackwall, 1833	1			
Walckenaeria antica (Wider, 1834)		1	1	1
Walckenaeria atrotibialis (O. Pickard-Cambridge, 1878)			2	
Xysticus acerbus Thorell, 1872	2			
Xysticus cristatus (Clerck, 1757)		2		

Xysticus erraticus (Blackwall, 1834)		2		
Xysticus ferrugineus Menge, 1876	1			
Xysticus sp.	115	25		
Xysticus tortuosus Simon, 1932		1		
Zelotes sp.			3	1
Zora armillata Simon, 1878		3		1
Zora sp.	3	11	18	3
Zora spinimana (Sundevall, 1833)		1	6	1

Fig. S1. Change in grazed vs. ungrazed vegetation over time.