

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

J. Pétillon, A. François, D. Lafage

▶ **To cite this version:**

J. Pétillon, A. François, D. Lafage. Short-term effects of horse grazing on spider assemblages of a dry meadow (Western France). Animal Biodiversity and Conservation, 2018, 41 (1), pp.19-32. 10.32800/abc.2018.41.0019 . hal-01681216

HAL Id: hal-01681216

https://univ-rennes.hal.science/hal-01681216

Submitted on 25 May 2018

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

J. Pétillon, A. François, D. Lafage

Pétillon. J., François, A., Lafage, D., 2018. Short–term effects of horse grazing on spider assemblages of a dry meadow (Western France). *Animal Biodiversity and Conservation*, 41.1: 19–32.

Abstract

Short–term effects of horse grazing on spider assemblages of a dry meadow (Western France). In this study, the biodiversity impacts of a little studied herbivore, the horse, were assessed in a high conservation value habitat of dry meadows in Brittany (Western France). 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 a diachronic approach more than a synchronic approach in such management monitoring. Grazing by horses could be relevant to manage meadows because it creates a high spatial heterogeneity, but further (long–term) studies including other model groups are required.

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

Resumen

Efectos a corto plazo del pastoreo de equinos en las comunidades de arañas de una pradera seca (Francia occidental). En este estudio se evaluaron los efectos de un herbívoro poco estudiado, el caballo, en la biodiversidad de un hábitat de alto valor de conservación en las praderas secas de la Bretaña (Francia occidental). Se utilizaron como bioindicadores las arañas, que constituyen un grupo de depredadores diversificado y abundante. Se emplearon tres técnicas complementarias de toma de muestras para evaluar los cambios en las comunidades de arañas en el estrato edáfico y en la vegetación a lo largo del tiempo (comparación diacrónica de la unidad gestionada antes y después de la gestión) y del espacio (comparación sincrónica de las unidades gestionadas y las de control). En la composición de las comunidades se encontraron pocos efectos del pastoreo, esto es, una única especie significativamente indicativa (ANOSIM) y ninguno en la abundancia ni en la diversidad α y β (modelo linear general en los datos obtenidos mediante trampas de caída). Por el contrario, se encontraron diferencias importantes entre las unidades antes de que se llevara a cabo la gestión. Los principales efectos de la ordenación del pastoreo se revelaron con el tiempo (un año después) y no entre las unidades gestionadas y las de control (análisis de correspondencias restringido de los datos obtenidos en la trampa de caída y pruebas de la χ^2 de los gremios obtenidos con cada método de muestreo), lo que pone de manifiesto la importancia de utilizar un planteamiento diacrónico más que uno sincrónico en este tipo de seguimiento de la ordenación. El pastoreo de equinos podría revestir interés para gestionar las praderas porque crea una elevada heterogeneidad espacial; no obstante, es necesario realizar más estudios (a largo plazo) que comprendan otros grupos de modelos.

Palabras clave: Indicadores, Ordenación, Planteamientos sincrónico y diacrónico, Araneae, Bretaña

Received: 10 VIII 16; Conditional acceptance: 4 XI 16; Final acceptance: 9 VI 17

Julien Pétillon, Denis Lafage, Univ. de Rennes 1, EA 7316, 263 Av. du Général Leclerc, CS 74205, 35042 Rennes Cedex, France.– Denis Lafage, Dept. of Environmental and Life Sciences/Biology, Karlstad Univ., Sweden.– Alexandre François, Emirates Center for Wildlife Propagation, PB 47, 33250 Missour, Maroc.

Corresponding author: Julien Pétillon. E–mail: julien.petillon@univ–rennes1.fr

ISSN: 1578–665 X
eISSN: 2014–928 X

© 2018 Museu de Ciències Naturals de Barcelona

Introduction

Management is frequently carried out in grasslands to simulate past, naturally occurring disturbances such as grazing by large herbivores (Bakker, 1989) or fire (Valkó et al., 2014). The impact of management practices 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 practice 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 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 and Hornung, 2005), height (Ausden et al., 2005; Ryder et al., 2005) or biomass (Kruess and 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 and Andersen, 2000). As an example, arthropods have been shown to be more diverse and more abundant under ungulate grazing, but arthropod biomass overall is reduced (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). Although several studies did not find any effect on arthropod diversity, some found effects 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 they 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 objectives of management (e.g. Leroy et al., 2014; Török et al., 2016). In this study, we assessed the impact of horse grazing on spiders in a high conservation value habitat in Brittany, dry meadows. Despite its high potential for conservation management (mainly because of an increased plant consummation, for example, higher than similar numbers of cows grazing (Ménard et al., 2002), the effects of horses on arthropod diversity remains poorly documented (Bell et al., 2001; Joern and Laws 2013). Spiders were used because of their bioindicative values (Maelfait and Baert, 1988; Marc et al., 1999), such as 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), and changes in land use (Schmidt et al., 2005; Prieto–Benítez and Méndez, 2011). We conducted a pre–management inventory so both synchronic and diachronic approaches could be used. Changes in assemblages of both epigeic and vegetation–dwelling spider assemblages were assessed using (three) complementary sampling methods.

Taxonomic and functional changes in community structure were evaluated in the short–term to test the following hypotheses: i) grazing alters the functional composition of a 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 and Ludwig, 2004); ii) abundance and alpha diversity are both expected to be lower in the grazed unit than in the non–grazed unit because of reduced plant biomass and cascading effects (e.g. Kruess and Tscharntke, 2002) whereas β–diversity is expected to be higher in the grazed unit than in 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), 20 km south–west of Rennes, near the city of Guichen (47° 97' 16 N–1° 89' 20 W). The natural reserve, Vallée du Canut, is a public land of 147 ha, part of a larger Natura 2000 site (total 427 ha) that encompasses meadows, heathlands, forests and a dense network of hedgerows. The dry meadows are located on Cambrian outcrops of red shale on the slopes of a small valley, Le Canut River. The meadows have a N–S slope, with the lower part dominated by bracken (*Pteridium aquilinum*). Before horses were introduced, the upper part, where the sampling took place, had a mean vegetation height of 1.3 m (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 (hence referred to as 'units'), grazed and non–grazed (during the second year of the study). Two horses were then introduced in October 2003 after the first year of sampling. Although the impact of grazers on vegetation cover and diversity was obvious (see fig. 1s in supplementary material), 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, we conducted three complementary sampling methods over 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 and Sunderland, 1992; Churchill and Arthur, 1999; Ward et al., 2001), each trap representing one sample (for a total of four replicates per treatment, 16 samples in total). Traps were active on 15 days in June and 15 days in September (i.e. the most favorable periods for spiders in this region: Varet et al., 2013) in 2003 and in 2004. The numbers of individuals caught in traps were divided by the number of days traps were 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 (two collectors for 10 min in each unit represent one sample, for a total of eight samples). Vegetation–dwelling spiders were collected using sweep–netting (40 cm diameter) along two parallel transects (20 m + 10 m and 45 sweeps, which represents one sample altogether), two times in each unit (June and September 2003 and 2004, for a total of eight 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 and 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 and 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 analysis (CCA) was then chosen according to the axis length of the DCA, < 3 or > 4, respectively (Legendre and 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 traps were 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; Lafage and Pétillon, 2014). 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 and Kotze, 2010) was used to test significant effects of separated fixed factors, without their interaction. If the interaction was significant, t–tests were used to detect significant differences between sampling periods. In the case of grazing effects, 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 $\alpha = 0.05$.

β–diversity was estimated through a dissimilarity matrix (corresponding to Sørensen pair–wise dissimilarity), then partitioned into its two components —pecies 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

A total of 1990 spiders belonging to 55 species were collected in 2003 and 1,040 spiders belonging to 66 species were collected in 2004, respectively (see table 1s in supplementary material). Most spiders were sampled using pitfall traps (1,801 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: fig. 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, $P = 0.026$); this was confirmed by the CCA (significant effect of year along the axis 1, $F_{1,13} = 2.17$, $P < 0.001$; fig. 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 (fig. 3), sweep net (fig. 4) or hand collecting (fig. 5).

A significant interaction between 'management' and 'date' effects was found for total activity–den-

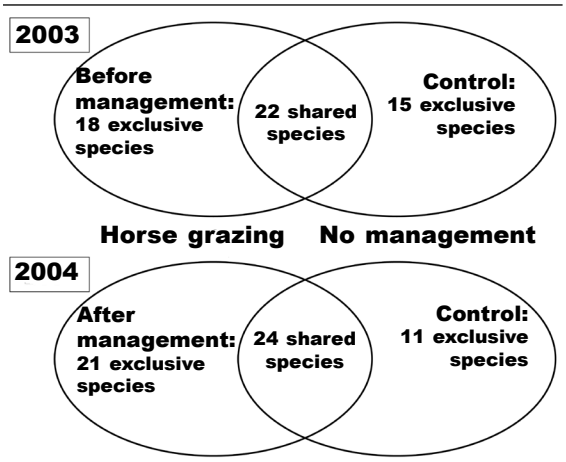


Fig. 1. Venn diagram of exclusive *vs.* shared species of grazed and non–grazed units, before (2003) and after (2004) management took place.

Fig. 1. Diagrama de Venn de las especies exclusivas y las compartidas de las unidades con y sin pastoreo, antes (2003) y después (2004) de que se realizara la ordenación.

sity ($F_{1,6}$ = 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 (fig. 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 between the units were similar in the two years of sampling, i.e. before and after management by grazing took place.

Discussion

Species composition

Considering the species that were not shared between the two units in 2004 but that were shared in 2003, the most numerous species was 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*), and therefore unlikely 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 and 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. However, the appearance of several thermophilous species (either at ground level or at vegetation level: *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 be verified by 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 were observed after horses were introduced on the dry meadow, a finding in agreement with a 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 changes were found after the grazing took place in spider hunting guilds, although web–builders tended to be reduced in

Table 1. χ^2–tests on hunting guilds (2df).

Tabla 1. Pruebas de la χ^2 en los gremios de especies cazadoras (2gl).

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^{22} = 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) management took place (data from pitfall traps: βt, β turnover; βn, β nestedness).

Tabla 2. Partición de la diversidad beta en el anidamiento y la renovación de especies en unidades con y sin pastoreo, antes (2003) y después (2004) de que se realizara la ordenación (datos de trampas de caída: βt, β renovación; βn, β anidamiento).

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

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 and Höffer, 2012; Ford et al., 2013), mainly explained by a reduced vegetation complexity (Churchill and Ludwig, 2004; Kovac and Mackay, 2009).

Structural diversity

A decrease in total activity–density was observed in both units over time, but the rate was higher in the grazed unit. This is likely the result of the deleterious effects of grazing on ground–dwelling spiders (see above) and inter–specific competition–mediated changes (Wise, 2006; Van Klink et al., 2015). Competition among spider species is indeed higher in simple habitats (Hurd and Fagan, 1992; Marshall and Rypstra, 1999). Closer attention to change in abiotic and biotic conditions would be necessary to disentangle direct and indirect effects of habitat change on spider abundance (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 and 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 and Méndez, 2011). Mechanisms usually involved in such a rich-

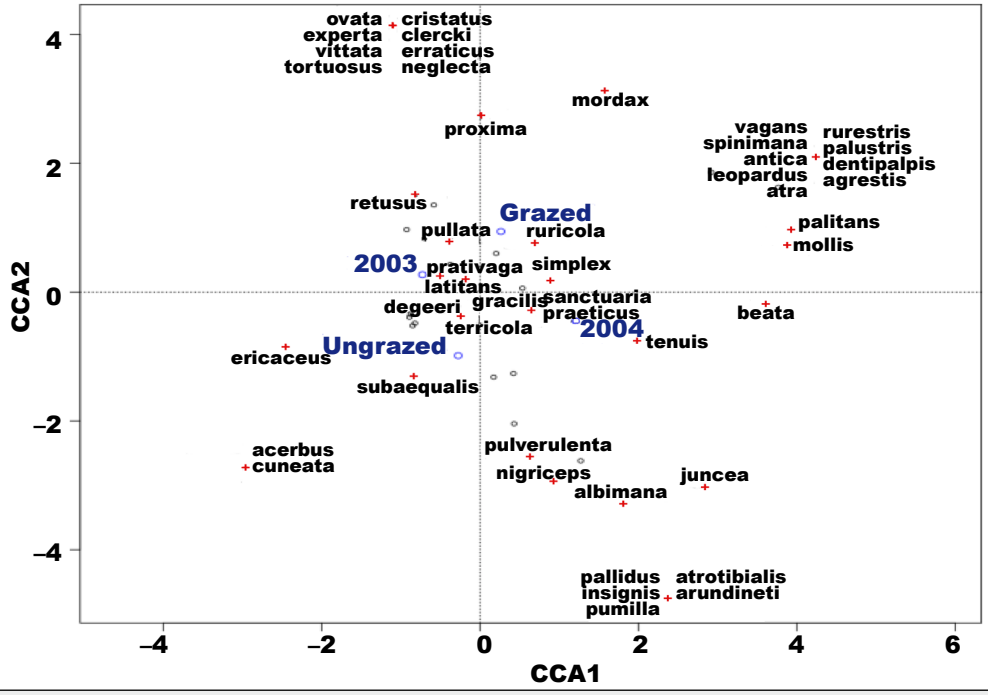


Fig. 2. Projection of significant variables from the CCA on spider species. Pitfall traps are represented by circles and species by crosses.

Fig. 2. Previsión de las variables significativas a partir del análisis de correspondencias restringido en especies de arañas. Las trampas de caída se representan con círculos y las especies, con cruces.

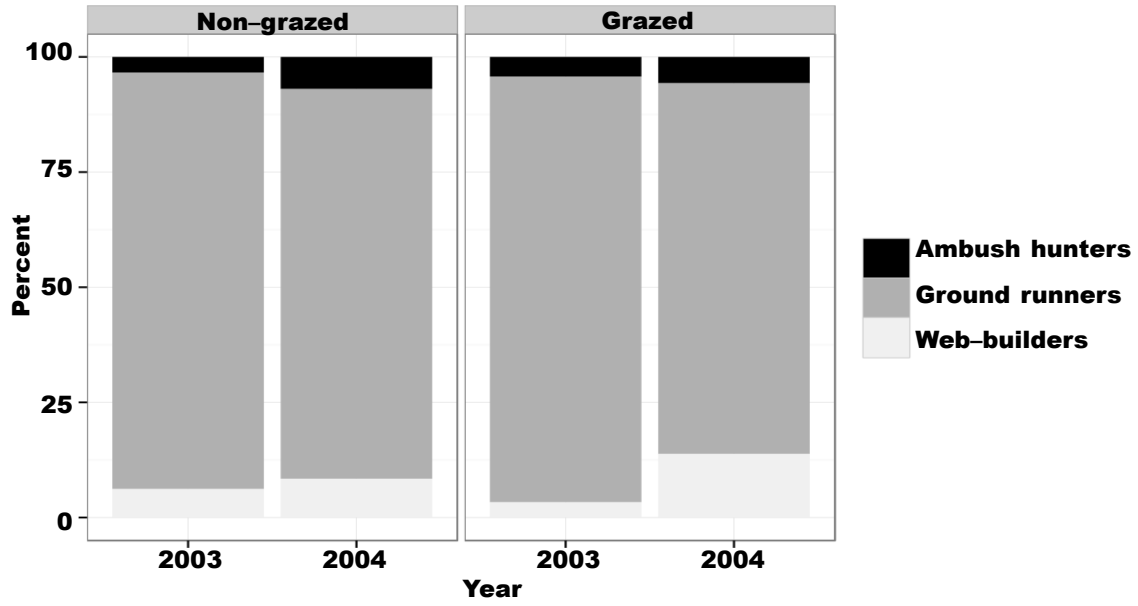


Fig. 3. Percentage activity density of each hunting guild sampled by pitfall trapping in 2003 and 2004.

Fig. 3. Porcentaje de la densidad de actividad de cada gremio de especies cazadoras recogidas en trampas de caída en 2003 y 2004.

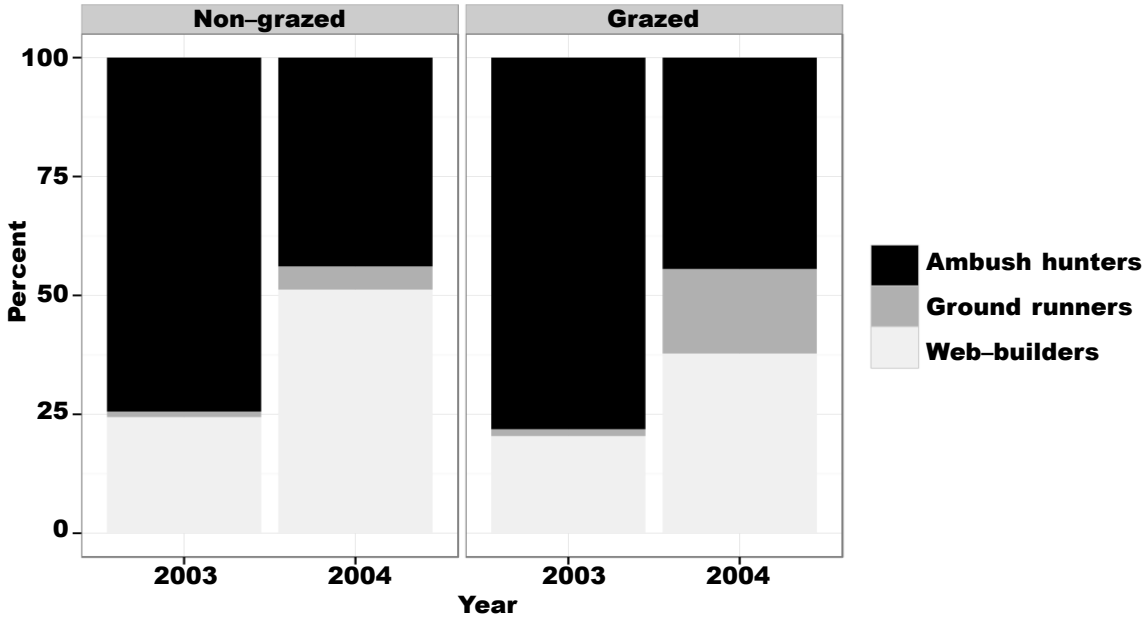


Fig. 4. Percentage abundance of each hunting guild sampled by sweep netting in 2003 and 2004.

Fig. 4. Porcentaje de la abundancia de cada gremio de especies cazadoras recogidas en red de barrido en 2003 y 2004.

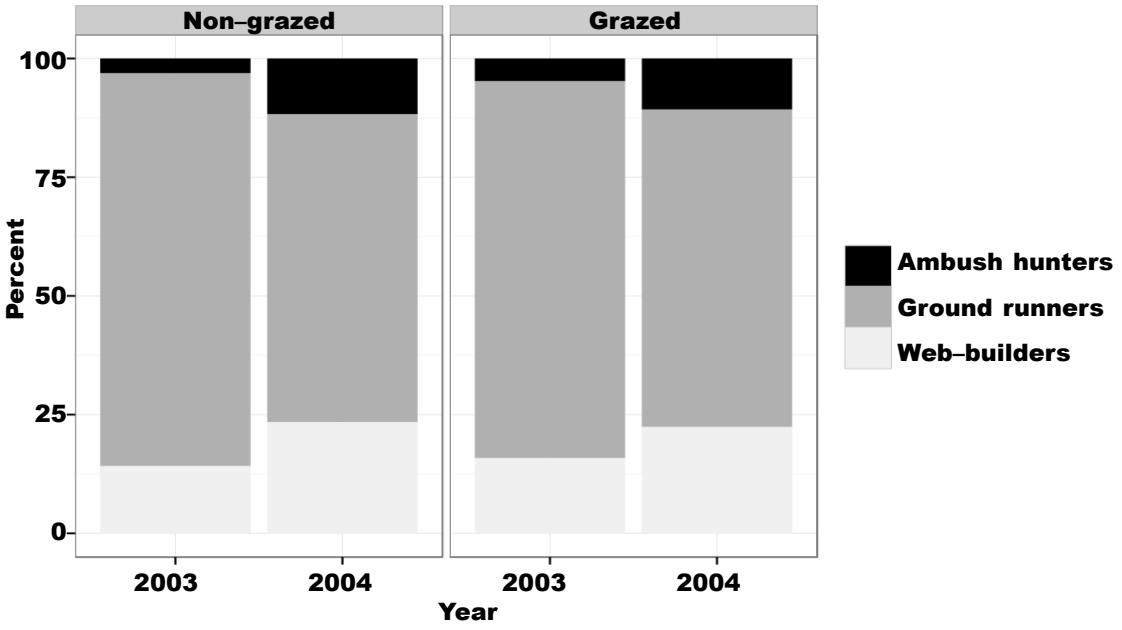


Fig. 5. Percentage abundance of each hunting guild sampled by hand collecting in 2003 and 2004.

Fig. 5. Porcentaje de la abundancia de cada gremio de especies cazadoras recogidas manualmente en 2003 y 2004.

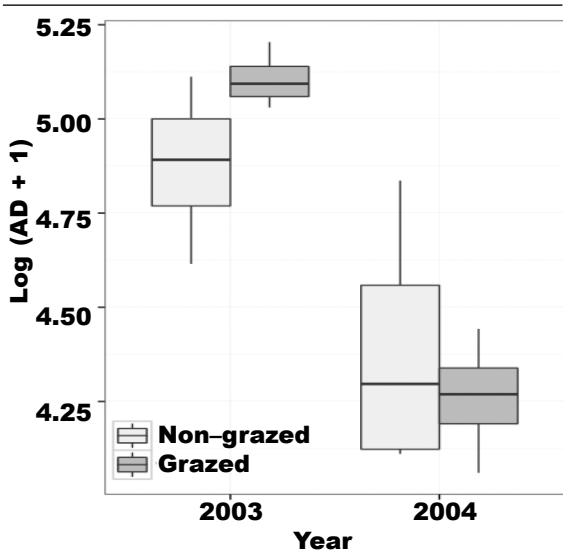


Fig. 6. Activity–density of spiders in the grazed and non–grazed units in 2003 and 2004 (data from pitfall traps).

Fig. 6. Actividad–densidad de arañas en las unidades con y sin pastoreo en 2003 y 2004 (datos obtenidos en las trampas de caída).

ness decrease encompass local habitat simplification (litter and vegetation strata: Dennis et al., 2001) and related food reduction (Kruess and Tscharntke, 2002; for soil functioning: Koppel et al., 1997). However, Lafage et al. (2014) recently demonstrated that spiders were not influenced by the plant biomass (either in terms of abundance or species richness). Finally, it is possible that the study period was too short to show effects.

Our hypothesis about increased β–diversity was not verified. This negative result has two main explanations: the study period on the effects of grazing was too short to be visible (although arthropods, and especially spiders, are known to quickly react to changes in habitat structure: Pétillon et al., 2014), and/or the effects of grazing were counterbalanced by inter–annual variations. We consider our second explanation is the most likely because it would explain the increased nestedness in the ungrazed unit. Plant heterogeneity is usually higher under grazing treatment (e.g. Gallet and Rozé, 2001; Van Klink et al., 2015), which reinforces the idea that plants and arthropods, here spiders, react in a different way to management practices (probably due to differences in mobility: Lafage et al., 2015; Lafage and Pétillon, 2016). We should stress 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 is likely to increase inter–class variance through 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. Although spiders present high dispersal ability and high mobility (Lafage and Pétillon, 2014) that may hide or decrease the effects of management (Pech et al., 2015), they can be considered a relevant group for monitoring biodiversity consequences of management, bringing complementary information to changes in vegetation structure.

Acknowledgements

We are grateful to the land manager Jean–François Lebas (Conseil Général d'Ille–et–Vilaine) for funding and providing access to the site, Dr. Jesse Eiben and two anonymous referees for useful comments, and GRETIA (Armorican Entomological Society) for technical support.

References

Ausden, M., Hall, M., Pearson, P., Strudwick, T., 2005. The effects of grazing on tall–herb fen vegetation and molluscs. *Biological Conservation*, 122: 317–326.

Bakker, J. P., 1989. *Nature Management by Grazing and Cutting*. Kluwer Academic Publishers, Dordrecht.

Báldi, A., Batáry, P., Kleijn, D., 2013. Effects of grazing and biogeographic regions on grassland biodiversity in Hungary –analysing assemblages of 1200 species. *Agriculture, Ecosystems and Environment*, 166: 28–34.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19: 134–143.

Baselga. A., Orme, C. D. L., 2012. betapart : an R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3: 808–812.

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

Blandenier, G., 2009. Ballooning of spiders (Araneae) in Switzerland: general results from an eleven–year survey. *Bulletin of the British Arachnological Society*, 14: 308–316.

Bonte, D., Maelfait, J.–P., Hoffmann, M., 2000. The impact of grazing on spider communities in a mesophytic calcareous dune grassland. *Journal of Coastal Conservation*, 6: 135–144.

Churchill, T. B., 1993. Effects of sampling methodology on the composition of a Tasmanian coastal heathland spider community. *Memoirs of the Queensland Museum*, 33: 475–481.

Churchill, T. B., Arthur, J. M., 1999. Measuring spider richness: effects of different sampling methods and spatial and temporal scales. *Journal of Insect Conservation*, 3: 287–295.

Churchill, T. B., Ludwig, J. A., 2004. Changes in spider assemblages along grassland and savanna grazing gradients in Northern Australia. *Rangeland Journal*, 26: 3–16.

Cristofoli, S., Mahy, G., Kekenbosch, R., Lambeets, K., 2010. Spider communities as evaluation tools for wet heathland restoration. *Ecological Indicators*, 10: 773–780.

Curtis, D. J., 1980. Pitfalls in spider community studies (Arachnida, Araneae). *Journal of Arachnology*, 8: 271–280.

Dennis, P., Aspinall, R. J., Gordon, I. J., 2002. Spatial distribution of upland beetles in relation to landform, vegetation and grazing management. *Basic and Applied Ecology*, 3: 183–193.

Dennis, P., Young, M. R., Bentley, C., 2001. The effects of varied grazing management on epigeal spiders, harvestmen and pseudoscorpions of *Nardus stricta* grassland in upland Scotland. *Agriculture, Ecosystems and Environment*, 86: 39–57.

Dennis, P., Young, M. R., Gordon, I. J., 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecological Entomology*, 23: 253–264.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67: 345–366.

Fadda, S., Henry, F., Orgeas, J., Ponel, P., Buisson, E., Dutoit, T., 2008. Consequences of the cessation of 3000 years of grazing on dry Mediterranean grasslands ground–active beetle assemblages. *Comptes Rendus Biologies*, 331: 532–546.

Foote, A. L., Hornung, C. L. R., 2005. Odonates as biological indicators of grazing effects on Canadian prairie wetlands. *Ecological Entomology*, 30: 273–283.

Ford, H., Garbutt, A., Jones, L., Jones, D. L., 2013. Grazing management in saltmarsh ecosystems drives invertebrate diversity, abundance and functional group structure. *Insect Conservation and Diversity*, 6: 189–200.

Gallet, S., Rozé, F., 2001. Conservation of heathland by sheep grazing in Brittany (France): Importance of grazing period on dry and mesophilous heathlands. *Ecological Engineering*, 17: 333–344.

Gardner, S. M., Hartley, S. E., Davies, A., Palmer, S. C. F., 1997. Carabid communities on heather moorlands in northeast Scotland: the consequences of grazing pressure for community diversity. *Biological Conservation*, 81: 275–286.

Gibson, C. W. D., Hambler, C., Brown V. K., 1992. Changes in spider (Araneae) assemblages in relation to succession and grazing management. *Journal of Applied Ecology*, 29: 132–142.

Gonzàlez–Megías, A., Gómez, J. M., Sànchez–Piñero, F., 2004. Effects of ungulates on epigeal arthropods in Sierra Nevada Park (southeast Spain). *Biodiversity and Conservation*, 13: 733–752.

Hatley, C. L., Macmahon, J. A., 1980. Spider community organization: seasonal variation and the role of vegetation architecture. *Environmental Entomology*, 9: 632–639.

Harvey, P. R., Nellist, D. R., Telfer, M. G., 2002. *Provisional atlas of British spiders (Arachnida, Araneae)*. Biological Records Centre, Huntingdon.

Heimer, S., Nentwig, W., 1991. *Spinnen mitteleuropas*. Verlag Paul Parey, Berlin.

Hemm, V., Höffer, H., 2012. Effects of grazing and habitat structure on the epigeic spider fauna in an open xerothermic area in southern Germany. *Bulletin of the British Arachnological Society*, 15: 260–268.

Horváth, R., Magura, T., Szinetár, C., Eichardt, J., Kovács, E., Tóthmérész, B., 2015. In stable, unmanaged grasslands local factors are more important than landscape–level factors in shaping spider assemblages. *Agriculture, Ecosystems and Environment*, 208: 106–113.

Hurd, L. E., Fagan, W. F. 1992. Cursorial spiders and succession: age or habitat structure? *Oecologia* 92: 215–221.

Joern, A., Laws, A. N., 2013. Ecological mechanism underlying arthropod species diversity in grasslands. *Annual Review of Entomology,* 58: 19–36.

Kahmen, S., Poschlod, P., Schreiber, K.–F., 2002. Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. *Biological Conservation*, 104: 319–324.

Klimek, S., Marini, L., Hofmann, M., Isselstein, J., 2008. Additive partitioning of plant diversity with respect to grassland management regime, fertilisation and abiotic factors. *Basic and Applied Ecology*, 9: 626–634.

Kirby, P., 1992. *Habitat management for invertebrates: a practical handbook*. English Nature Research Report n°89, Peterborough.

Koppel, J. van de, Rietkerk, M., Weissing, F. J., 1997. Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends in Ecology and Evolution*, 12: 352–356.

Kovac, K.–J., Mackay, D. A., 2009. An experimental study of the impacts of cattle on spider communities of artesian springs in South Australia. *Journal of Insect Conservation*, 13: 57–65.

Kruess, A., Tscharntke, T., 2002. Grazing intensity and the diversity of grasshoppers, butterflies, and trap–nesting bees and wasps. *Conservation Biology*, 16: 1570–1580.

Lafage, D., Maugenest, S., Bouzillé, J.–B., Pétillon, J., 2015. Disentangling the influence of local and landscape factors on alpha and beta diversities: opposite response of plants and ground–dwelling arthropods in wet meadows. *Ecological Research*, 30: 1025–1035.

Lafage, D., Pétillon, J., 2014. Impact of cutting date on carabids and spiders in a wet meadow. *Agriculture, Ecosystems and Environment*, 185: 1–8.

– 2016. Relative importance of management and natural flooding on spider, carabid and plant assemblages in extensively used grasslands along the Loire. *Basic and Applied Ecology*, 17: 535–545.

Lafage, D., Secondi, J., Georges, A., Bouzillé, J.–B., Pétillon, J., 2014. Satellite–derived vegetation indices as surrogate of species richness and abundance of ground beetles in temperate floodplains. *Insect Conservation and Diversity*, 7: 327–333.

Legendre, P., Gallagher, E. D., 2001. Ecologically meaningful transformation for ordination of species data. *Oecologia*, 129: 271–280.

Leroy, B., Le Viol, I., Pétillon, J., 2014. Complementarity of rarity, specialisation and functional diversity metrics to assess responses to environmental changes, using an example of spider communities in salt marshes. *Ecological Indicators*, 46: 351–357.

Loucougaray, G., Bonis, A., Bouzillé, J.–B., 2004. Effects of grazing by horses and/or cattle on the diversity of coastal grasslands in western France. *Biological Conservation*, 116: 59–71.

Luff, M. L., 1975. Some features affecting the efficiency of pitfall traps. Oecologia, 19: 345–357.

Lumaret, J.–P., Kadiri, N., Bertrand, M., 1992. Changes in resources: consequences for the dynamics of dung beetle communities. *Journal of Applied Ecology*, 29: 349–356.

Maelfait, J.–P., Baert, L., 1988. Les araignées sont–elles de bons indicateurs écologiques? *Bulletin de la Société scientifique de Bretagne*, 59: 155–160.

Marc, P., Canard, A., Ysnel, F., 1999. Spiders (Araneae) useful for pest limitation and bioindication. *Agriculture, Ecosystems and Environment*, 74: 1–46.

Marshall, S. D., Rypstra, A. L. 1999. Spider competition in structurally simple ecosystems. *Journal of Arachnology*, 27: 343–350.

Ménard, C., Duncan, P., Fleurance, G., Georges, J.–Y., Lila, M., 2002. Comparative foraging and nutrition of horses and cattle in European wetlands. *Journal of Applied Ecology*, 39: 120–133.

Mgobozi, M. P., Somers, M. G., Dippenaar–Schoeman, A. S., 2008. Spider responses to alien plant invasion: the effect of short– and long–term *Chromolaena odorata* invasion and management. *Journal of Applied Ecology*, 45: 1189–1197.

Morris, M. G., 2000. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. *Biological Conservation*, 95: 129–142.

O'Hara, R. B., Kotze, D. J., 2010. Do not log–transform count data. *Methods in Ecology and Evolution*, 1: 118–122.

Oksanen, L., 2001. Logic of experiments in ecology: is pseudoreplication a pseudoissue? *Oikos*, 94:

27–38.
Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Henry, M. H., Wagner, S., Wagner, H., 2013. *Vegan: Community Ecology Package*. Available online at http://cran.r–project.org/package=vegan.
Pech, P., Dolanský, J., Hrdlička, R., Lepš, J., 2015. Differential response of communities of plants, snails, ants and spiders to long–term mowing in a small–scale experiment. *Community Ecology*, 16: 115–125.
Pétillon, J., Georges, A., Canard, A., Ysnel, F., 2007. Impact of cutting and sheep–grazing on ground–active spiders and ground beetles in some intertidal salt marshes (Western France). *Animal Biodiversity and Conservation*, 30: 201–209.
Pétillon, J., Lambeets, K., Montaigne, W., Maelfait, J.–P., Bonte, D., 2010. Habitat structure modified by an invasive grass enhances inundation withstanding in a salt–marsh wolf spider. *Biological Invasions*, 12: 3212–3226.
Pétillon, J., Potier, S., Carpentier, A., Garbutt, A., 2014. Evaluating the success of managed realignment for the restoration of salt marshes: lessons from invertebrate communities. *Ecological Engineering*, 69: 70–75.
Pétillon, J., Ysnel, F., Canard, A., Lefeuvre, J.–C., 2005. Impact of an invasive plant (*Elymus athericus*) on the conservation value of tidal salt marshes in western France and implications for management: responses of spider populations. *Biological Conservation*, 126: 103–117.
Pozzi, S., Borcard, D., 2001. Effects of dry grassland management on spider (Arachnida: Araneae) communities on the Swiss occidental plateau. *Ecoscience,* 8: 32–44.
Pozzi, S., Gonseth, Y., Hänggi, A., 1998. Evaluation de l'entretien de prairies sèches du plateau occidental suisse par le biais de leurs peuplements arachnologiques (Arachnida: Araneae). *Revue suisse de Zoologie*, 105: 465–485.
Prieto–Benítez, S., Méndez, M., 2011. Effects of land management on the abundance and richness of spiders (Araneae): A meta–analysis. *Biological Conservation*, 144: 683–691.
R Core Team, 2015. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.r–project.org.
Read, J. L., Andersen, A. N., 2000. The value of ants as early warning bioindicators: responses to pulsed cattle grazing at an Australian arid zone locality. *Journal of Arid Environments*, 45: 231–251.
Roberts, M. J., 1987. *The Spiders of Great Britain and Ireland*. Harley Books, Colchester.
– 1995. *Spiders of Britain and Northern Europe*. HarperCollins Publishers, London.
Rosa García, R., Jáuregiu, B. M., Garciá, U., Osoro, K., Celaya, R., 2009. Effects of livestock breed and grazing pressure on ground–dwelling arthropods in Cantabrian heathlands. *Ecological Entomology*, 34: 466–475.
Ryder, C., Moran, J., Mc Donnell, R., Gormally, M., 2005. Conservation implications of grazing practices on the plant and dipteran communities of a turlough in Co. Mayo, Ireland. *Biodiversity and Conservation*, 14: 187–204.
Schmidt, M. H, Roschewitz, I., Thies, C., Tscharntke, T., 2005. Differential effects of landscape and management on diversity and density of ground–dwelling farmland spiders. *Journal of Applied Ecology*, 42: 281–287.
Simonneau, M., Courtial, C., Pétillon, J., 2016. Phenological and meteorological determinants of spider ballooning in an agricultural landscape. *Comptes Rendus Biologies*, 339: 408–416.
Topping, C. J., Sunderland, K. D., 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *Journal of Applied Ecology*, 29: 485–491.
Török, P., Valkó, O., Deák, B., Kelemen, A., Tóth, E., Tóthmérész, B., 2016. Managing for species composition or diversity? Pastoral and free grazing systems in alkali steppes. *Agriculture, Ecosystems and Environment*, 234: 23–30.
Uetz, G. W., Halaj, J., Cady, A. B., 1999. Guild structure of spiders in major crops. *Journal of Arachnology*, 27: 270–280.
Valkó, O., Török, P., Deák, B., Tóthmérész, B., 2014. Prospects and limitations of prescribed burning as a management tool in European grasslands. *Basic and Applied Ecology*, 15: 26–33.
Van Klink, R., Rickert, C., Vermeulen, R., Vorst, O., WallisDeVries, M. F., Bakker, J. P., 2013. Grazed vegetation mosaics do not maximize arthropod diversity: evidence from salt marshes. *Biological Conservation*, 164: 150–157.
Van Klink, R., van der Plas, F., van Noordwijk, C. G. E., WallisDeVries, M. F., Olff, H., 2015. Effects of large herbivores on grassland arthropod diversity. *Biological Reviews*, 90: 347–366.
Varet, M., Burel, F., Lafage, D., Pétillon, J., 2013. Age–dependent colonization of urban habitats: a diachronic approach using carabid beetles and spiders. *Animal Biology*, 63: 257–269.
Ward, D. F., New, T. R., Yen, A. L., 2001. Effects of pitfall trap spacing on the abundance, richness and composition of invertebrate catches. *Journal of Insect Conservation*, 5: 47–53.
Wise, D. H., 2006. Cannibalism, food limitation, intraspecific competition, and the regulation of spider populations. *Annual Review of Entomology*, 51: 441–465.
Woodcock, B. A., Pywell, R. F., Roy, D. B., Rose, R. J., Bell, D., 2005. Grazing management of calcareous grasslands and its implications for the conservation of beetle communities. *Biological Conservation*, 125: 193–202.

Supplementary material

Table 1s. Taxonomic list of the species collected in grazed and non–grazed units (2003–2004), all sampling methods confounded.

Tabla 1s. Lista taxonómica de las especies recogidas en las unidades con y sin pastoreo (2003 y 2004) con todos los métodos de muestreo.

	2003		2004	
Species	Non–grazed	Grazed	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

Table 1s. (Cont.)

	2003		2004	
Species	Non–grazed	Grazed	Non–grazed	Grazed
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

Table 1s. (Cont.)

	2003		2004	
Species	Non–grazed	Grazed	Non–grazed	Grazed
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

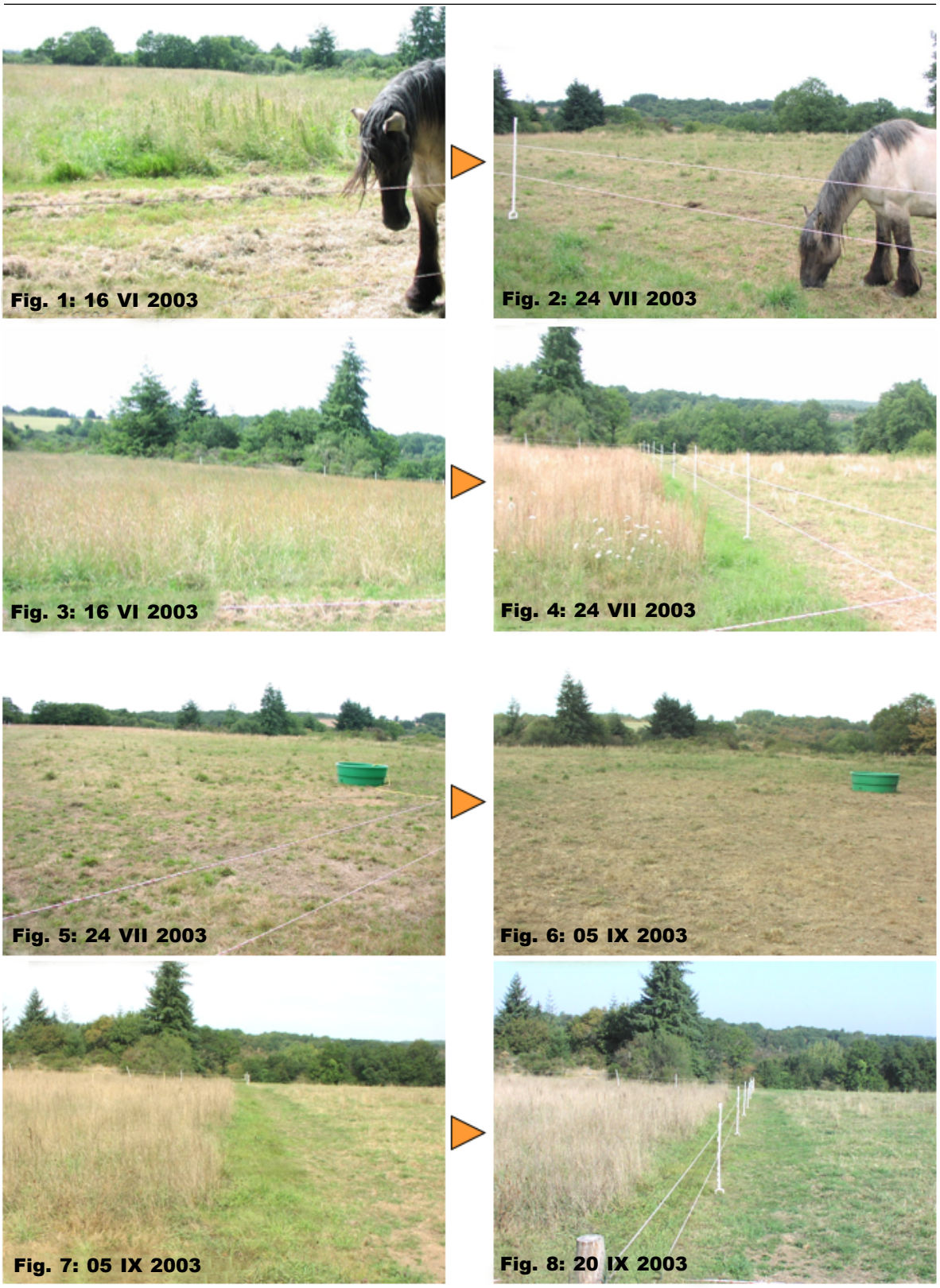


Fig. 1s. Change in grazed vs. non–grazed vegetation over time.

Fig. 1s. Cambio de la vegetación en las unidades con y sin pastoreo con el tiempo.