

How do sheep affect plant communities and arthropod populations in temperate grasslands?

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Grasslands being used in sheep farming systems are managed under a variety of agricultural production, recreational and conservational objectives. Although sheep grazing is rarely considered the best method for delivering conservation objectives in seminatural temperate grasslands, the literature does not provide unequivocal evidence on the impact of sheep grazing on pasture biodiversity. Our aim was therefore to review evidence of the impacts of stocking rate, grazing period and soil fertility on plant communities and arthropod populations in both mesotrophic grasslands typical of agriculturally improved areas and in native plant communities. We therefore conducted a literature search of articles published up to the end of the year 2010 using 'sheep' and 'grazing' as keywords, together with variables describing grassland management, plant community structure or arthropod taxa. The filtering process led to the selection of 48 articles, with 42 included in the stocking rate dataset, 9 in the grazing period dataset and 10 in the soil fertility dataset. The meta-analysis did not reveal any significant trends for plant species richness or plant community evenness along a wide stocking rate gradient. However, we found frequent shifts in functional groups or plant species abundance that could be explained by the functional properties of the plants in the community. The meta-analysis confirmed that increasing soil fertility decreased plant species richness. Despite the very limited dataset, plant species richness was significantly greater in autumn-grazed pastures than in ungrazed areas, which suggests that choosing an appropriate grazing period would be a promising option for preserving biodiversity in sheep farming systems. Qualitative review indicated that low grazing intensity had positive effects on Orthoptera, Hemiptera (especially phytophagous Auchenorrhyncha) and, despite a diverse range of feeding strategies, for the species richness of Coleoptera. Lepidoptera, which were favoured by more abundant flowering plants, also benefited from low grazing intensities. Spider abundance and species richness were higher in ungrazed than in grazed pastures. In contrast, there are insufficient published studies to draw any firm conclusions on the benefits of late grazing or stopping fertilization on insect diversity, and no grounds for including any of this information in decision support tools at this stage.

Keywords: biodiversity, grazing period, insect, stocking rate, soil fertility

Implications

There is a general trend toward a gradual intensification of ruminant production to meet the increasing demand for livestock products (Bouwman *et al.*, 2005), which logically raises major concerns over the environmental consequences involved. Grassland intensification entails higher livestock densities and fertilizer application rates to increase soil productivity, which negatively affects the diversity of resident plant communities. Grasslands are being managed under a variety of agricultural production and conservation objectives; the question of how their biodiversity could be improved by adapting grazing management is a crucial issue,

and there is demand from managers interested in interventions and policies for a synthesis of published data.

Introduction

Grassland-based sheep farming is the most common sheep production system worldwide; typical cases include lamb production systems in France and the United Kingdom, New Zealand's dairy and sheep enterprises or Mongolia's steppe system. Native grassland communities are species-rich because of low or inexistent fertilizer input and continuous long-term use as grasslands; however, a major environmental concern is grassland degradation through inappropriate management practices. Over the second half of the 20th century, there has been a substantial decline in the extent of

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these seminatural grasslands in countries such as the United Kingdom, Germany or France where lowland seminatural grasslands can be converted for arable use, with the remaining resource consisting of fragmented small stands (Stewart and Pullin, 2008). At the same time, grazing pressure has decreased radically in Central and Eastern Europe because of competition from the West and uncertainties over land ownership, with the result that large areas have been left unmanaged (Emanuelsson, 2008). Overall, Ostermann (1998) estimated that among the European habitats considered important for biodiversity, 65 pasture types are under threat from grazing intensification, whereas 26 are under threat from abandonment.

Plant communities and arthropod populations are highly sensitive to local field management practices and to the impact of grazing herbivores on small-scale vegetation structure (Collinge *et al.*, 2003; Klimek *et al.*, 2007; Marini *et al.*, 2008). The use of fertilizers to boost grassland productivity combined with more frequent disturbances favors a relatively small number of competitive plant species at the expense of stress-tolerant species (*sensu* Grime, 1979), with a consequent loss of overall floristic diversity (Tallowin *et al.*, 2005; Parfitt *et al.*, 2010). Diversity is also assumed to follow a unimodal response along disturbance gradients such as stocking rate or grazing intensity (Grime, 1979; Huston, 1994). Moderate grazing intensity is assumed to benefit plant diversity by creating a mosaic of short and tall patches with contrasting growth forms and competitive interactions (Milchunas *et al.*, 1988). Spring rest from grazing is another recommendation to preserve plant species richness in grasslands, as it allows flowering, seed production and replenishment of root reserves (Eddy, 2002; Lunt, 2005). Among the mechanisms that explain higher insect diversity in lightly grazed swards, one is that the trophic interactions between plants and herbivorous insects are not disrupted, that is, tall vegetation provides important food resources in the form of nectar for butterflies and live plant biomass for caterpillars and herbivorous insects (Öckinger *et al.*, 2006; Dumont *et al.*, 2009). A second explanation draws on the observation that tall grassland vegetation maintains a higher number of ecological niches, decreases predation risk and increases habitat quality for species that require buffered microclimates (Dennis *et al.*, 1998; Morris, 2000; WallisDeVries *et al.*, 2007). Exploiting plots during short grazing periods decreases the time grassland arthropods are exposed to disturbance compared with continuous grazing, with late grazing favoring phytophagous species that can benefit from higher food resources throughout most of the grazing season. Late grazing and fertilizer cessation can also favor pollinator abundance and species richness via positive trophic interactions with flowering plants (Carvell, 2002; Sjödin, 2007).

Sheep differ from large ruminants in terms of their nutrient requirements relative to gut capacity, their ability to feed selectively and their slightly lower ability to digest low-quality forages (Demment and Greenwood, 1988). Their behavioral adjustments in response to reduced food availability are

therefore chiefly geared to maintaining the nutrient value of the diet (Hodgson *et al.*, 1991; Dumont *et al.*, 1995; Garcia *et al.*, 2003). Grazing with sheep can thus lead to a dominance of grasses in temperate plant communities because of their high selectivity for legumes and forbs (Krahulec *et al.*, 2001; Warren *et al.*, 2002). In the Pyrenees, highly selective sheep grazing also produced a strong homogenization effect but helped maintain specific plant species and communities of high conservation value (Sebastià *et al.*, 2008). Stewart and Pullin (2008) recommended maintaining taller sward heights in sheep-grazed pastures than in pastures grazed by cattle and horses in order to maximize forb abundance and plant species richness in the *Cynosurus cristatus*–*Centaurea nigra* community. The authors pinpointed sheep selectivity and the lack of sheep-created bare ground niches compared with cattle as detrimental to biodiversity. Consistently, sheep were less likely than cattle to maintain short patches over successive years in lightly grazed mesotrophic grasslands, and could not therefore buffer the negative effects of competition for light on small-sized plants (Dumont *et al.*, 2011). Sheep have also been assumed to negatively impact nectar-dependent insect groups as a result of their preferential use of flowering plants; the species richness of bumblebees (Carvell, 2002) and butterflies (Öckinger *et al.*, 2006) is lower in sheep-grazed pastures than in similar grasslands used by cattle.

Although sheep grazing is thus rarely considered the best method for delivering conservation objectives on seminatural grasslands, the literature does not provide unequivocal evidence on the impact of sheep grazing on pasture biodiversity (Stewart and Pullin, 2008). Our aim was therefore to review evidence of the impact of stocking rate, grazing period and soil fertility on plant communities and arthropod populations in sheep-grazed temperate grasslands. This review is split into two sections because of the quality and number of papers available for each section. A systematic review including a meta-analysis is presented for the effects of stocking rates of sheep on vegetation height, species composition and diversity and for the effects of grazing period and soil fertility on plant species richness. A qualitative review is presented for the effects of management practices on plant functional groups and arthropod populations and diversity.

Material and methods

Literature search and study inclusion criteria

We ran a literature search on articles published up to the end of the year 2010, using the two online databases ISI Web of Knowledge and Science Direct and the Google Scholar search engine. Search queries used the keywords 'sheep' and 'grazing' together with variables describing grassland management (either 'stocking rate', 'period', 'season', 'rotational', 'soil fertility' or 'fertilization'), plant community structure ('vegetation', 'sward heterogeneity', 'plant', 'plant species' or 'plant diversity') or arthropod populations ('insect', 'insect species', 'insect diversity', 'arthropods', 'Aranae', 'Orthoptera', 'Coleoptera', 'Lepidoptera', 'Hymenoptera', 'Hemiptera', 'Collembola' or 'pollinators').

Articles were then split into three datasets in order to analyze the impact of sheep grazing on plant and arthropod diversity according to stocking rate (52 articles), grazing period (12 articles) and soil fertility (11 articles). Only studies that were easily available were included in this dataset. To reduce the risk of availability bias, we also reviewed the technical reports and PhD theses cited in the collected papers. This led us to add seven more references to the first dataset, two more to the second dataset and four more to the third dataset. Given the different reactions of plant communities to grazing intensity depending on habitat productivity (Bakker *et al.*, 2006; de Bello *et al.*, 2006) and salinity levels (Olf and Ritchie, 1998), the few data available on semiarid grasslands (Osem *et al.*, 2002; Li *et al.*, 2008; Campbell *et al.*, 2010) and marshland plant communities (Bouchard *et al.*, 2003; Hofmann and Mason, 2006; Milotić *et al.*, 2010) were excluded from this analysis. Assessment of study quality also led us to exclude surveys dealing with mixed grazing, as well as those where stocking rate could not be calculated from plot size and number of grazing days. Some redundant data were further excluded to avoid duplication bias, along with data from surveys in which only 1 year of recordings were reported. This filtering process led to the selection of 48 articles, with 42 included in the stocking rate dataset, 9 in the grazing period dataset and 10 in the soil fertility dataset.

Data extraction

The following information was registered for each reference: country and grassland type (Australia sown-fertilized grassland, United Kingdom *Agrostis-Festuca* grassland, etc.), grazing management, number of replicates, years since treatment application, and where available, plant species richness, plant evenness, abundance of plant functional groups (grasses, forbs, legumes, stress-tolerant species, etc.) and species richness and abundance of the different arthropod taxa. Stocking rate was estimated by multiplying 'instantaneous' stocking density by number of grazing days, and translated into livestock unit days per hectare, while specifying grazing management (continuous, spring grazing, target sward height, etc.). Grazing period was analyzed by factoring in the four following groups: 'ungrazed', 'early grazing' when there was spring grazing, 'late grazing' when the first period of grazing occurred during summer or autumn and 'continuous grazing' when pastures were grazed for at least three seasons. Soil fertility was analyzed by selecting articles in which either the same plant community received different levels of mineral fertilization or pastures with plant communities that indicate different levels of fertility (*Agrostis-Festuca* v. *Nardus-Festuca*) were directly compared. Each treatment was given a global score and then aggregated into three groups along a soil fertility gradient: poor or moderate soil fertility without any mineral fertilization (poor fertility), rich soil fertility without mineral fertilization or moderately fertilized seminatural grasslands (moderate fertility) and rich soil fertility with high added mineral fertilization (high fertility).

Statistical analysis

A meta-analysis was conducted to analyze the effect of stocking rate on sward surface height, plant species richness, and the Shannon index as an indicator of plant community evenness. Only the mean values were used in the meta-analysis. We chose not to weight the data in terms of a measure of their 'importance', as (i) there is no unique criterion for the importance of a study (dispersion of data, number of replicates, duration of the survey, etc.), (ii) data dispersion, when available, was reported in different ways and estimated either from raw data or from statistical models (s.d., s.e.m., s.e.d., etc.) and (iii) using any weighting criterion would have led to the exclusion of further data, thus generating a higher risk of selection bias in this relatively small dataset.

The impact of stocking rate on mean SSH (in cm) was analyzed using the nonlinear mixed model of the SAS software package (1999) with an equation

$$SSH_{i,j} = a + (b + S_i) \exp(-c \cdot stock_i),$$

where a is the asymptote of the curve, b is the mean SSH of ungrazed plots, S_i is the effect of experiment i (random effect) and c is the slope coefficient, with $stock_i$ expressed in livestock unit days per hectare in experiment i . Integral approximation was performed with the adaptive Gauss-Hermite quadrature method. In a preliminary adjustment step, parameter ' a ' systematically converged to zero (its lower limit), and was thus removed from subsequent adjustments.

Data on plant species richness and the Shannon index were analyzed using Minitab (v.14) with a GLM, with stocking rate and its quadratic component as classes and experimental treatments in the different articles as factors. Finally, the effects of grazing period and soil fertility on plant species richness were tested using the nonparametric Friedman test. The effect of management practices on the abundance of plant functional groups and on arthropod populations was studied via qualitative analysis, as there was insufficient data for a meta-analysis.

Results

Impact of stocking rate

Decreasing stocking rate in our set of seminatural or fertilized temperate pastures led to an increase in the mean SSH (Figure 1):

$$\begin{aligned} SSH_{i,j} &= (19.6 + S_i) \exp(-0.0046 \cdot stock_i); \\ RMSE &= 3.04 \text{ cm}; F_{1,32} = 13.29; P < 0.01; \\ \text{variance of } S_i &= 42.99 \text{ cm}^2. \end{aligned}$$

Conversely, we did not find a global effect of stocking rate on plant species richness ($F_{1,47} = 0.31$; $P = 0.58$; Figure 2), despite significant effects in some experiments showing evidence of a detrimental effect of intensive grazing (Bullock *et al.*, 2001; Dorrough *et al.*, 2004; Louault *et al.*, 2005) or of grassland abandonment (Fothergill *et al.*, 2002; Sebastià *et al.*, 2008),

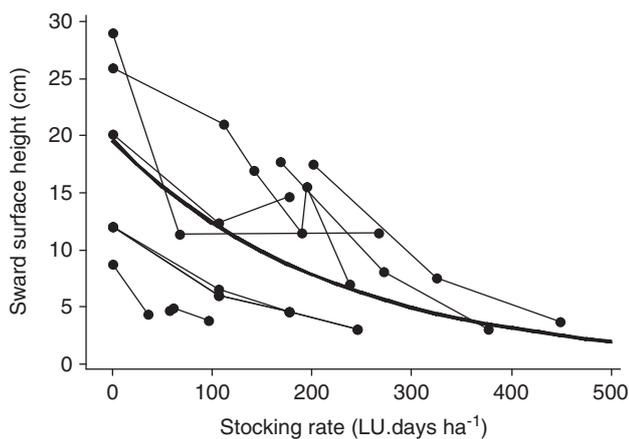


Figure 1 Effect of stocking rate ($stock_i$), expressed in livestock days per hectare (LU days per ha), on mean sward surface height ($SSH_{i,j}$) in temperate grasslands. $SSH_{i,j}$ was expressed in cm, based on a nonlinear regression of the equation: $SSH_{i,j} = (19.6 + S_j) \exp(-0.0046 \cdot stock_i)$; RMSE = 3.04; $F_{1,32} = 13.29$; $P < 0.01$. Data are from Keiller *et al.* (1995), Treweek *et al.* (1997), Dennis *et al.* (1998), Zhou *et al.* (2006), Scimone *et al.* (2007) and Mayer *et al.* (2009).

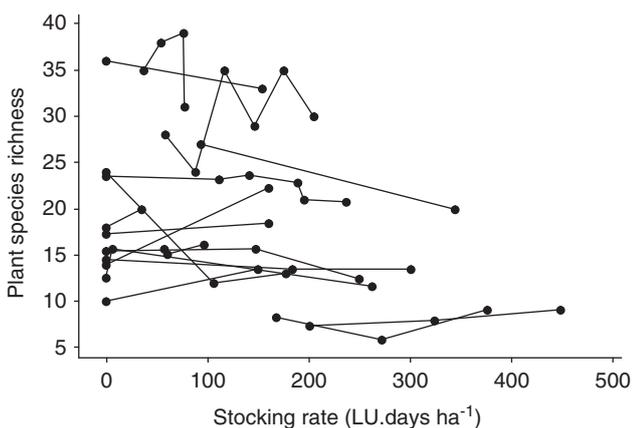


Figure 2 Effect of a stocking rate gradient, expressed in livestock days per hectare (LU days per ha), on plant species richness in temperate grasslands. Data are from Dutoit *et al.* (1995); Dennis *et al.* (1997), Treweek *et al.* (1997), Carvell (2002), Dorrrough *et al.* (2004), Louault *et al.* (2005), Del Pozo *et al.* (2006), Zhou *et al.* (2006), Scimone *et al.* (2007), Gross *et al.* (2009), Marriott *et al.* (2009), Mayer *et al.* (2009), Meisser and Chatelain (2010) and Dumont *et al.* (2011).

as predicted by the unimodal response of diversity along disturbance gradients (Grime, 1979). After a change in grazing intensity, species abundance changes more rapidly than plant species richness (Marriott *et al.*, 2002; Louault *et al.*, 2005; Scimone *et al.*, 2007). However, we could not find any global effect of stocking rate on the Shannon index ($F_{1,30} = 0.06$; $P = 0.81$; Figure 3) or other indicators of plant community evenness (log normal diversity index: Bullock *et al.*, 2001; Simpson dominance index: Scimone *et al.*, 2007).

Qualitative review indicated that grazing abandonment rapidly changed plant species composition over a wide range of plant communities, such as ryegrass/white clover sown swards (Marriott *et al.*, 2002) or *Lolium perenne*–*Agrostis capillaris*-dominated pasture (Fothergill *et al.*, 2002). Legumes

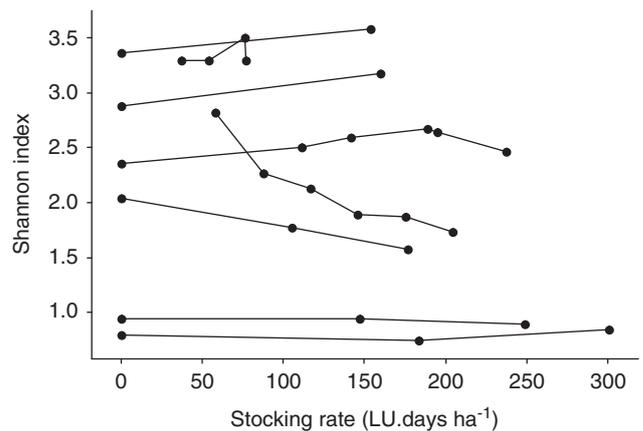


Figure 3 Effect of a stocking rate gradient, expressed in livestock days per hectare (LU days per ha), on plant Shannon index in temperate grasslands. Data are from Dutoit *et al.* (1995), Dennis *et al.* (1997), Louault *et al.* (2005), Del Pozo *et al.* (2006), Zhou *et al.* (2006), Gross *et al.* (2009), Marriott *et al.* (2009) and Meisser and Chatelain (2010).

dropped in abandoned grasslands (Dutoit *et al.*, 1995; Gross *et al.*, 2009). A reduction in plant community evenness was also reported in the *Arrhenatherum elatius*–*Bromus erectus* community (Moog *et al.*, 2002) and in calcareous grasslands (Dutoit *et al.*, 1995). In upper alpine grasslands, stress-tolerant species, plants with low nutritive value and mosses declined after sheep exclusion (Mayer *et al.*, 2009). In contrast to abandonment, reported changes in species composition were much slower when stocking rate was manipulated (Hulme *et al.*, 1999; Marriott *et al.*, 2004; Scimone *et al.*, 2007). This was, for example, the case over the first 5 years of measurements in extensively used ryegrass/white clover sown swards (Marriott *et al.*, 2002), although this last survey did find long-term patterns with *A. capillaris*, *Poa trivialis*, *Festuca rubra* and *Holcus lanatus* being favored by a reduction in stocking rate, whereas more competitive or ruderal species such as *T. repens* and *Poa annua* increased with increasing stocking rate (Marriott *et al.*, 2009). In other mesotrophic grasslands typical of agriculturally improved sites, competitive and ruderal species such as *L. perenne*, *Taraxacum officinale* and *Cerastium fontanum* also performed better in heavily grazed plots, whereas *Agrostis stolonifera*, *Dactylis glomerata*, *F. rubra* and *Trifolium pratense* all benefited from a reduction of grazing intensity (Bullock *et al.*, 2001). Many native species declined with grazing in an Australian temperate grassland, even when grazing was restricted to less than 20 days/year. Only a few native species persisted in year-round set-stocked plots (Dorrrough *et al.*, 2004).

The effect of decreasing stocking rate on arthropod populations was usually consistent across sites, despite broad between-site variation in insect community structure and composition. Phytophagous and epigeal species negatively reacted to the decrease in herbage biomass in heavily grazed plots. Grasshoppers benefited from a decrease in grazing intensity in various types of sheep-grazed pastures (Table 1). Hemiptera, comprising phytophagous Auchenorrhyncha and

Table 1 Effect of decreasing SR on the species richness and abundance of Coleoptera, Orthoptera, Lepidoptera, Hemiptera and Aranea

| Country, grassland type | Treatments | Management | Replic. | Year | Species richness | Abundance | Reference |
|---------------------------------|-----------------|---------------------------|---------|-----------|------------------|-----------|------------------------------------|
| Coleoptera | | | | | | | |
| France, sown-fertilized | Grazed v. ungr. | Spring grazing | 12 | 4 | + | + | Blight <i>et al.</i> (2011) |
| UK, semi-natural | Grazed v. ungr. | Continuous | 6 | 4 | 0 | + | Gibson <i>et al.</i> (1992a) |
| | Grazed v. ungr. | Spring grazing | 6 | 4 | 0 | 0 | |
| | Grazed v. ungr. | Autumn grazing | 6 | 4 | + | 0 | |
| UK, <i>Agrostis-Festuca</i> | Grazed v. ungr. | Continuous | 4 | 16 | 0 | – | Keiller <i>et al.</i> (1995) |
| UK, <i>Nardus-Festuca</i> | Grazed v. ungr. | Continuous | 4 | 16 | 0 | – | |
| UK, <i>Calluna vulgaris</i> | Grazed v. ungr. | | 1 | 4 | – | – | |
| UK, <i>Nardus stricta</i> | Grazed v. ungr. | Target sward height | 2 | 6 | | – | Dennis <i>et al.</i> (1997) |
| UK, <i>Alopecurus pratensis</i> | Grazed v. ungr. | Autumn grazing | 3 | 14 | + | + | Woodcock <i>et al.</i> (2006) |
| UK, semi-natural | Grazed v. ungr. | Continuous | 6 | 3 | | 0 | Dennis <i>et al.</i> (2008) |
| Australia, sown-fertilized | SR gradient | Continuous | 2 | 10 | | 0 | Hutchinson and King (1980) |
| UK, sown-fertilized | SR gradient | Target sward height | 2 | 3 | + | 0 | Dennis <i>et al.</i> (2004) |
| Australia, fertilized | SR gradient | Spring and autumn grazing | 2 | 3 | | 0 | Oliver <i>et al.</i> (2005) |
| New-Zealand, fertilized | SR gradient | Continuous | 6 | 30 | | – | Schon <i>et al.</i> (2008) |
| New-Zealand, fertilized | SR gradient | Continuous | 5 | 3 | | – | Parfitt <i>et al.</i> (2010) |
| UK, <i>Calluna vulgaris</i> | SR gradient | | 1 | 4 | + | + | Keiller <i>et al.</i> (1995) |
| UK, <i>Nardus stricta</i> | SR gradient | Target sward height | 2 | 6 | | 0 | Dennis <i>et al.</i> (1997) |
| Italy, semi-natural | SR gradient | Rotation | 3 | 3 | | 0 | WallisDeVries <i>et al.</i> (2007) |
| UK, semi-natural | SR gradient | Continuous | 6 | 3 | | 0 | Dennis <i>et al.</i> (2008) |
| Orthoptera | | | | | | | |
| Australia, sown-fertilized | SR gradient | Continuous | 2 | 10 | | + | Hutchinson and King (1980) |
| France, semi-natural | SR gradient | Summer grazing | 1 | 10 | + | + | Barataud (2005) |
| Italy, semi-natural | SR gradient | Rotation | 3 | 3 | + | + | WallisDeVries <i>et al.</i> (2007) |
| Lepidoptera | | | | | | | |
| Sweden, semi-natural | Grazed v. ungr. | | 8 | 5 | + | | Öckinger <i>et al.</i> (2006) |
| UK, semi-natural | Grazed v. ungr. | Continuous | 6 | 4 | 0 | 0 | Littlewood (2008) |
| Australia, sown-fertilized | SR gradient | Continuous | 2 | 10 | | + | Hutchinson and King (1980) |
| Italy, semi-natural | SR gradient | Rotation | 3 | 3 | + | + | WallisDeVries <i>et al.</i> (2007) |
| UK, semi-natural | SR gradient | Continuous | 6 | 4 | + | + | Littlewood (2008) |
| Hemiptera | | | | | | | |
| UK, fertilized | Grazed v. ungr. | Target sward height | 54 | Long term | 0 | 0 | Maczey (2004) |
| UK, semi-natural | Grazed v. ungr. | Continuous | 6 | 4 | + | 0 | Gibson <i>et al.</i> (1992a) |
| | Grazed v. ungr. | Spring grazing | 6 | 4 | + | + | |
| | Grazed v. ungr. | Autumn grazing | 6 | 4 | + | + | |
| UK, semi-natural | Grazed v. ungr. | Target sward height | 46 | Long term | 0 | + | Maczey (2004) |
| UK, semi-natural | Grazed v. ungr. | Spring or summer grazing | 4 | 9 | + | + | Morris <i>et al.</i> (2005) |
| UK, semi-natural | Grazed v. ungr. | Continuous | 6 | 3 | | + | Dennis <i>et al.</i> (2008) |
| Australia, sown-fertilized | SR gradient | Continuous | 2 | 10 | | 0 | Hutchinson and King (1980) |
| New-Zealand, fertilized | SR gradient | Continuous | 6 | 30 | | + | Schon <i>et al.</i> (2008) |
| Italy, semi-natural | SR gradient | Rotation | 3 | 3 | | 0 | WallisDeVries <i>et al.</i> (2007) |
| UK, semi-natural | SR gradient | Continuous | 6 | 3 | | 0 | Dennis <i>et al.</i> (2008) |
| Aranea | | | | | | | |
| UK, semi-natural | Grazed v. ungr. | Continuous | 6 | 4 | + | + | Gibson <i>et al.</i> (1992b) |
| | Grazed v. ungr. | Spring grazing | 6 | 4 | + | + | |
| | Grazed v. ungr. | Autumn grazing | 6 | 4 | + | + | |
| UK, <i>Agrostis-Festuca</i> | Grazed v. ungr. | Continuous | 4 | 16 | + | + | Keiller <i>et al.</i> (1995) |
| UK, <i>Nardus-Festuca</i> | Grazed v. ungr. | Continuous | 4 | 16 | + | + | |
| UK, <i>Nardus stricta</i> | Grazed v. ungr. | Target sward height | 2 | 2 | + | + | Dennis <i>et al.</i> (2001) |
| UK, semi-natural | Grazed v. ungr. | Continuous | 6 | 3 | | + | Dennis <i>et al.</i> (2008) |
| Australia, sown-fertilized | SR gradient | Continuous | 2 | 10 | | + | Hutchinson and King (1980) |
| UK, <i>Nardus stricta</i> | SR gradient | Target sward height | 2 | 2 | 0 | 0 | Dennis <i>et al.</i> (2001) |
| Italy, semi-natural | SR gradient | Rotation | 3 | 3 | | 0 | WallisDeVries <i>et al.</i> (2007) |
| UK, semi-natural | SR gradient | Continuous | 6 | 3 | | 0 | Dennis <i>et al.</i> (2008) |

SR = stocking rate.

+: beneficial; 0: neutral; -: detrimental.

Replic.: number of replicates; Year: number of years since the start of treatment application; ungr.: ungrazed.

mixed feeders plus carnivorous true bugs, differ in ecological requirements and may thus have shown inconsistent responses to changes in grazing intensity (Gibson *et al.*, 1992a). However, we found a general positive trend with abundance and species richness increasing along decreasing stocking rate gradients (Table 1). Spider abundance and species richness were also higher in ungrazed than in grazed pastures (Table 1). This could be related to increased prey availability and to tall and more complex vegetation structures benefiting web-building species. Different grazing intensities did not further affect spider abundance in three seminatural grasslands (Dennis *et al.*, 2001; WallisDeVries *et al.*, 2007; Dennis *et al.*, 2008), whereas spider abundance progressively declined with each increase in stocking rate in an intensively grazed sown pasture (Hutchinson and King, 1980), where the reduction of habitat as stocking rate increased up to 30 sheep per ha was an obvious factor.

Lepidoptera benefited from low or zero grazing intensities (Table 1). In southern Sweden, there were fewer butterfly species in sheep-grazed than in abandoned seminatural grasslands, which was seen as the indirect effect of sheep selectivity for flowering plants (Öckinger *et al.*, 2006). High-intensity sheep grazing with 2.7 sheep per ha also produced the lowest moth abundance and species richness in an upland acid grassland; moths peaked in abandoned plots and at a low grazing intensity of 0.9 sheep per ha (Littlewood, 2008). Conversely, bumblebee species richness and abundance were higher in sheep-grazed than in unmanaged grasslands (Carvell, 2002). This was the consequence of a greater diversity and abundance of flowering plants such as *T. pratense*, which is considered an important food resource for bumblebees.

The Coleoptera assemblage showed different trends across sites, and Coleoptera abundances were consequently not systematically higher in lightly grazed plots (Table 1). This could be explained by the diverse range of feeding strategies found in the Coleoptera order, ranging from herbivorous to coprophagous and predatory species among the carabid and staphylinid beetles. Coleoptera species richness was, however, favored by a reduction of stocking rate in half of the ten surveys (Table 1) and unaffected by grazing intensity in four more sites. The only detrimental effect was reported in a *Calluna vulgaris* moorland 4 years after grazing cessation (Keiller *et al.*, 1995).

Collembola belongs to the hypogeal fauna but can be indirectly affected by biomass accumulation via its effects on litter decomposition. The abundance of Collembola was positively correlated to herbage biomass in a fertilized grassland (Oliver *et al.*, 2005) and consistently shot up in response to a decrease in stocking rate in another sown pasture (King and Hutchinson, 1976). Collembola abundance was unaffected by stocking rate in the only published survey conducted in a temperate seminatural grassland; however, this may mainly be due to pitfall traps being inadequate for sampling soil mesofauna (WallisDeVries *et al.*, 2007).

Impact of grazing period

Plant species richness was greater in autumn-grazed pastures compared with ungrazed controls in the meta-analysis

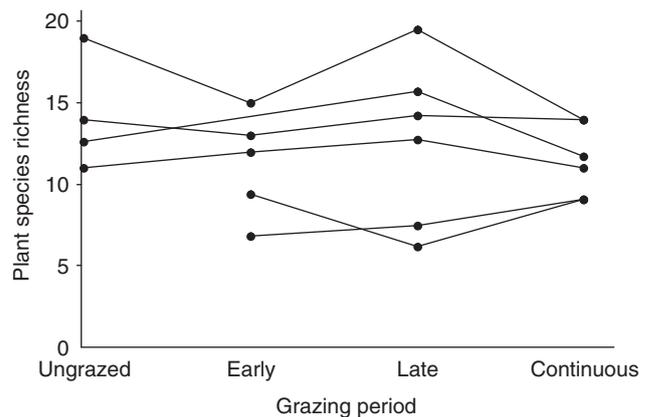


Figure 4 Effect of grazing period on plant species richness in temperate grasslands. Grazing period was 'early' when there was spring grazing and 'late' when the first grazing period occurred during summer or autumn. Data were compared with ungrazed controls and continuously grazed (i.e. grazed for at least three seasons) pastures. Data are from Bullock *et al.* (2001), Dorrrough *et al.* (2004) and Turner and Zimmer (2007).

($P < 0.05$; Figure 4). However, none of the other pair-wise comparisons were significant. This first confirms the lack of a clear effect of stocking rate on plant species richness in sheep-grazed temperate pastures (Figure 2). Second, the fact that the meta-analysis could not reveal any global benefit of late v. early grazing on plant species richness ($P = 0.18$; Figure 4) suggests complex responses of plant communities to sheep grazing in different seasons. Although a benefit of late grazing was measured in an Australian native pasture, in which native forbs performed better in plots that were not grazed during spring (Turner and Zimmer, 2007), spring grazing increased dicot species number in a mesotrophic grassland dominated by fast-growing grasses, probably through the beneficial effects of grazing on interspecific competition (Bullock *et al.*, 2001).

Late grazing was assumed to favor phytophagous species such as Orthoptera, Auchenorrhyncha and herbivorous Coleoptera that can benefit from an increase in sward height or herbage biomass throughout most of the grazing season. Autumn grazing slightly increased grasshopper abundance on sown-fertilized grasslands (Branson and Haferkamp, 2003) and cricket abundance on dry grasslands (Morón-Ríos *et al.*, 2010). Hemiptera abundance and species richness were slightly higher in plots grazed by sheep during autumn than in spring (Gibson *et al.*, 1992a; Morris *et al.*, 2005), with Auchenorrhyncha logically benefiting from greater food resources (Morris *et al.*, 2005). Carnivorous true bugs were also more abundant in autumn-grazed than in spring-grazed plots in seminatural chalk grasslands (Gibson *et al.*, 1992a). Spider abundance was higher in autumn-grazed plots, although species richness was unaffected by grazing season (Gibson *et al.*, 1992b). Continuous grazing was the most damaging treatment for spider abundance, giving a different species assemblage. In the same experiment, spring grazing increased the abundance and species richness of Coleoptera compared with autumn grazing or spring and autumn grazing (Gibson *et al.*, 1992a). The majority of beetles recorded

were legume feeders, which explains the success of spring grazing that favored small-sized legume species such as *T. repens*, *Medicago lupulina* and *Lotus* spp., which need light to grow (Bullock *et al.*, 2001).

Impact of soil fertility

Increasing soil fertility decreased plant species richness in the meta-analysis (Figure 5), although the effect was only significant between the two most extreme treatments (high *v.* poor: $P < 0.05$; high *v.* moderate: $P = 0.32$; moderate *v.* poor: $P = 0.32$). Consistently with this pattern, mineral fertilization led to a significant 12% to 21% reduction in number of plant species in mesotrophic grasslands of northern England (Smith *et al.*, 1996a). Mineral fertilization reduced the cover of relatively stress-tolerant grasses (*Anthoxanthum odoratum*, *C. cristatus*) and small-stature *Bellis perennis* and *Plantago lanceolata*, whereas benefiting competitive *H. lanatus* and *P. trivialis*. Tall competitive species such as *Alopecurus pratensis*, *D. glomerata* and *Rumex acetosa* also benefited from mineral fertilization (Smith *et al.*, 1996b), whereas *A. capillaris*, *H. lanatus* and *T. repens* decreased in fertilized swards (Marriott *et al.*, 2009). Fertilizer input to enhance production, although decreasing *Hieracium pilosella* dominance, led to a decline in overall native species richness in New Zealand's short tussock grassland (Norton *et al.*, 2006); in this particular case, it is hard to distinguish whether fertilizer inputs or increase in stocking densities is the greater cause of decline. Increasing fertility and grazing intensity in a low-productive plant community of southern France consistently reduced the cover of native stress-tolerant species that were gradually replaced by ruderal species (Fayolle, 2008).

Mineral fertilization increases herbage biomass but usually decreases plant species diversity and sward heterogeneity, which might in turn affect grassland arthropods. Only six surveys published have tackled the effects of soil fertility on arthropod diversity in sheep-grazed temperate pastures. Collembola density was higher in fertilized than in unfertilized grasslands (Oliver *et al.*, 2005; Schon *et al.*, 2008). This increase was positively correlated with the level of superphosphate input, resulting in an increase in vegetation ground cover and soil organic carbon and a lower soil pH in plots where the highest superphosphate levels were applied (Oliver *et al.*, 2005). Amongst epigeal insects, Formicidae decreased in abundance in superphosphate-fertilized swards, but no further effect of the level of mineral fertilization could be detected (Oliver *et al.*, 2005). Mineral fertilization had no effect on Auchenorrhyncha abundance but was detrimental to their species richness (Maczey, 2004). In an Australian native grassland, superphosphate application ranging from 5.5 to 22 kg P/ha per year slightly decreased Coleoptera abundance relative to unfertilized plots (Oliver *et al.*, 2005), whereas an application of 34 kg P/ha per year increased their abundance in another fertilized farmland (Parfitt *et al.*, 2010). This apparently inconsistent conclusion could result from differences in Coleoptera assemblages and in sampling methods between the two experiments. At a high stocking density of 10 sheep per ha, Dennis *et al.* (2004) found

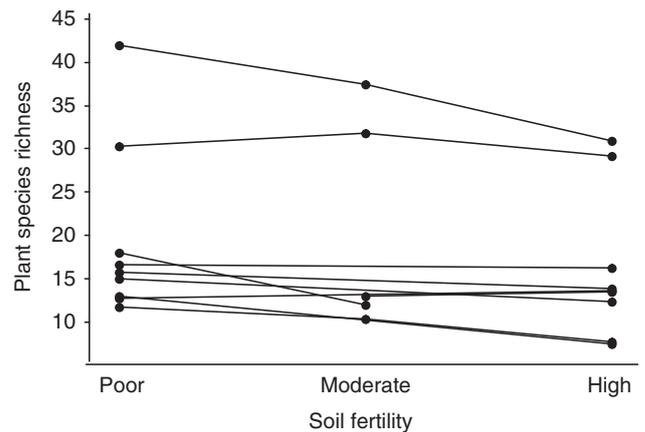


Figure 5 Effect of soil fertility on plant species richness in temperate grasslands. 'Poor': poor or moderate soil fertility without any mineral fertilization; 'Moderate': rich soil fertility without mineral fertilization or moderately fertilized seminatural grasslands; 'High': rich soil fertility with high additional mineral fertilization. Data are from Fothergill *et al.* (2002), Maczey (2004), Norton *et al.* (2006), Fayolle (2008) and Marriott *et al.* (2009).

no benefit of discontinuing nitrogen fertilizer application on the abundance and species richness of Carabidae and Staphylinidae in an upland sheep pasture. The species richness of different Coleoptera groups was also similar in *Agrostis-Festuca v. Nardus-Festuca* grasslands, but their assemblage was modified: Carabidae evenness and Elateridae abundance were higher in the less-fertile *Nardus-Festuca* grasslands, whereas Staphylinidae were unaffected by the plant community (Keiller *et al.*, 1995).

Discussion

Our literature survey highlights that research on the impact of sheep grazing on biodiversity in temperate grasslands has so far focused much more on the impacts of grazing abandonment or reduced stocking rates than on the impacts of fertilizer cessation or late grazing. The meta-analysis revealed an interesting resistance by different plant community parameters to variations in stocking rate (see Figures 2–4), despite the fact that significant results are more likely to get published than nonsignificant results (i.e. the so-called 'publication bias'). This absence of any consistent response of plant species richness and plant community evenness along a wide stocking rate gradient suggests that agri-environmental schemes based solely on reducing stocking rate are probably too crude to effectively increase plant diversity. In contrast, we found frequent shifts in functional groups or plant species abundance that could be explained by the functional properties of the plants in the community. Future decision support tools for farmers or end users should therefore take account of dominant functional types in the community in order to propose appropriate management strategies for temperate pastures (Duru *et al.*, 2008; Farruggia *et al.*, 2008; Cadotte *et al.*, 2011). Given that reducing stocking rate decreases the amount of milk or meat produced per hectare, other options will need to be tested in order to achieve biodiversity outcomes while meeting

production objectives in sheep farming systems. Among the options available, choosing an appropriate grazing period appears a promising candidate, as, although the dataset was very limited, it showed that plant species richness was significantly higher in autumn-grazed pastures than in ungrazed controls. However, this overview was founded on a small number of published studies, meaning that the meta-analysis could not reveal any global benefit of late *v.* early grazing on plant species richness (Figure 4).

The meta-analysis confirmed that increasing soil fertility led to an overall decrease in plant species richness (Figure 5). This contrasts with the conclusions from surveys analyzing the effect of fertilizer cessation as an opportunity for restoring plant community diversity in fertile grasslands. Marriott *et al.* (2004) and Tallowin *et al.* (2005) found no great difference in the structure and composition between intensive grasslands and extensive grasslands that had been managed intensively in the past. High nutrient availability is indeed a major factor limiting the restoral of greater plant diversity in temperate grasslands (Janssens *et al.*, 1998; Bakker and Berendse, 1999; Suding *et al.*, 2005). Reducing nitrogen inputs to below the critical load in order to support natural and seminatural grassland communities will prove slow and costly for most intensively farmed landscapes (Bakker and Berendse, 1999). A poor seed bank in intensively managed landscapes also hampers the reestablishment of ecological diversity (Poschold and Bonn, 1998).

Recommendations for protecting grassland arthropod communities usually favor management systems designed to enable the simultaneous presence of tall and short swards that meet the ecological requirements of different functional groups (Morris, 2000). As for plants, arthropod diversity is assumed to follow a unimodal response along grazing intensity gradients (Huston, 1994), but the species richness of grassland insects is expected to peak in taller vegetation compared with vascular plants (Pöyry *et al.*, 2006). In line with this weaker disturbance tolerance of insects compared with plants, we highlighted positive effects of decreasing grazing intensity for Orthoptera, Hemiptera (especially phytophagous Auchenorrhyncha) and, despite a diverse range of feeding strategies, for Coleoptera species richness (Table 1). Lepidoptera, which need nectar from flowering plants, and web-building spiders, which face fewer disturbances in tall swards, also benefited from low grazing intensities or grassland abandonment (Table 1). These taxa could act as relevant indicators, as they fulfill the objectives of agri-environmental indicators (Bockstaller *et al.*, 2008): the environmental impact is directly linkable to agricultural practices (stocking rate in the present case), they simplify a more complex system and are measurable, although the drawback of these direct indicators will be their high measurement costs. Finally, development of agri-environmental schemes for protecting grassland arthropods would benefit from a qualification of the relative position of species populations within their geographic distribution range, as some species have been shown to need different stocking rate regimes to maintain species' niches in different parts of their range (Bourn and Thomas, 2002).

Adding mineral fertilizer inputs has been assumed to decrease the abundance and species richness of epigeal insects, and might not be ecologically sustainable from a grassland fauna conservation standpoint (Fenner and Palmer, 1998; Vickery *et al.*, 2001). However, we were unable to draw any firm conclusions on the benefits of fertilizer cessation or late grazing on arthropod diversity in temperate sheep-grazed pastures, especially given that much of the overview was founded on a very small number of published studies. The literature features a series of specific instances of complex grazing interactions with plant groups and arthropods, but it remains difficult to identify any robust generalizations to inform the development of agri-environment schemes liable to conserve biodiversity.

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