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Enhancing beetle and spider communities in agricultural grasslands: the roles of seed addition and habitat management

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Abstract

Over three years, a replicated block design was used to investigate the effects of seed mixtures (grasses only; grasses and legumes; grasses, legumes and non-legume forbs), establishment techniques and long term management on beetle and spider communities of grassland swards. We quantified trophic links between phytophagous beetles and their host plants to assess the effect of these seed mixtures and management practices on food web structure. When managed under low intensity cutting regimes the most diverse seed mixture supported the highest biomass of beetles and spiders ($c.$ 3.6 kg ha^{-1}). Species richness of predatory beetles, phytophagous beetles and spiders were all increased by the sowing of legumes, although the addition of other forbs tended to result in at most modest further increases in invertebrate species richness. Analysis of food web structure suggests that the number of host plants utilised by beetles was greatest within the most diverse seed mixtures, but that this declined rapidly after the establishment year. We demonstrate that by sowing cheap and simple seed mixtures agriculturally improved grasslands can be managed to support increased diversity of spiders and beetles. While seed mixtures do not necessarily need to be of the highest diversity to achieve these benefits, the inclusion of legumes does appear to be crucial. The lower costs of intermediate diversity seed mixtures increase appeal to farmers, increasing the likely uptake of these methodologies in voluntary agri-environment schemes.

1. Introduction

Across lowland Europe management systems that emphasise the use of inorganic fertilisers, selective herbicides, reseeding and improved drainage have dramatically increased grassland agricultural production (Frame, 2000). This has come at a high cost to native biodiversity, with farmland plants, vertebrates and invertebrates suffering large scale declines (e.g. Blackstock et al., 1999; Vickery et al., 2001; Stoate et al., 2009; Littlewood et al., 2012). For invertebrates, reductions in both abundance and species richness have been attributed to the simplification and homogenisation of grassland swards, both in terms of their flora and physical architecture (Morris, 2000; Vickery et al., 2001; Woodcock et al., 2009). Reductions in the size of invertebrate populations have also acted to limit crucial resources for other grassland taxa, for example farmland birds (Vickery et al., 2001; Stoate et al., 2009). By enhancing floristic diversity in areas of agriculturally improved grasslands abundant and complex invertebrate communities may be supported (Siemann et al., 1998; Morris, 2000; Woodcock and Pywell, 2010; Littlewood et al., 2012). This may be achieved by the use simple and cost effective seed mixtures which contain species that have agronomic value, are able to establish effectively in fertile soils and are known to support a wide spectrum of associated invertebrates (Pywell et al., 2002; Mortimer et al., 2006).

In addition to the diversity of the floral community, the type and intensity of management used on grasslands can have huge effects on invertebrate community structure. For example, cutting can directly kill many sward active invertebrates (Humbert et al., 2009), as well as also having longer term impacts by removing key plant structures on which species feed or hunt (Gibson et al., 1992; Morris, 2000). Conversely, the selective nature of cattle grazing can promote structural heterogeneity in both sward structure and floral composition (Morris, 2000). Of particular importance for invertebrates is the intensity with which

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management is applied, as the more frequent defoliation events are so the less likely invertebrate populations and the plants they feed on are to recover (Morris, 2000; Humbert et al., 2009; Woodcock et al., 2009). Changes in management intensity are also likely to impact on trophic links between phytophagous species and their host plants (Dobson, 2009; Gagic et al., 2011). For example, phytophagous beetles with endophagous seed-feeding larvae would be lost from grasslands where the frequency of management operations prevents the development of seed heads (Morris, 2000; Woodcock et al., 2006). Importantly, this means that the occurrence of a host plant alone may be insufficient for phytophagous species where management intensity results in the loss of a plant structures on which they feed (Morris, 2000; Woodcock and Pywell, 2010).

Beetles and spiders are a potentially abundant and speciose component of grasslands that have strong responses to plant community structure and management (Gibson et al., 1992; Woodcock et al., 2009; Batáry et al., 2012). Both taxa contribute to the delivery of ecosystem services (Losey and Vaughn, 2006), although their contribution to these is typically realised in systems other than the grasslands that support them, e.g. pest control in arable agriculture (Tscharntke et al., 2005) . Here we examine whether invertebrate biomass, species richness and trophic complexity can be promoted by sowing seed mixtures that incorporate the key plant functional types of grasses, legumes and non-legume flowering plants (referred to as forbs hereafter). We also identify how different management types (cattle grazing vs. cutting), management intensities (intensive vs. extensive) and cultivation techniques (shallow vs. deep cultivation) impact on these same characteristics. We predict that: 1) the species richness and biomass of beetles and spiders will increase in response to a gradient of increasing plant diversity (Siemann et al., 1998; Woodcock and Pywell, 2010); 2) catastrophic management events that are implemented over a single day, such as cutting, will

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have a greater negative impact on beetle and spider species richness than more gradual grazing management (Morris, 2000; Humbert et al., 2009); 3) Extensive management that allows plants to flower and set seed will promote phytophagous beetle species richness (Morris, 2000; Woodcock et al., 2009).

2. Methods

In April 2008, a field-scale experiment was established on agriculturally-improved and floristically species-poor (3.0 ± 0.1 species m^{-2}) lowland grassland in Warfield, Berkshire (Long. 51°26′30″N Lat. 000°43′43″W). The sward was on heavy clay soils of moderately high fertility (total soil phosphorous 911 mg kg^{-1}) and was dominated by the grass *Lolium perenne* and legume *Triofolium repens*. We used a randomised split-split-split-plot design, replicated across four blocks. Our whole-plot factor was the establishment of one of three seed mixes: 1) a 'grass only' mix (Grass), comprising five species selected for good agronomic performance under low inputs of fertiliser. These were sown at 30 kg ha^{-1} at a cost of equivalent to *c.* €83 ha^{-1}; 2) 'grass & legume' mix (GL), comprising five grasses and seven agricultural legumes sown at 34 kg ha^{-1} (*c.* €120 ha^{-1}); 3) 'grass, legume & non-legume forb' mix (GLF), comprising five grasses, seven legumes and six non-leguminous forbs at 33.5 kg ha^{-1} (*c.* €190 ha^{-1}). Species composition of individual seed mixes is given in Supplementary Material Appendix A. Management was imposed as a split-plot factor over the seed mixtures, with two treatment levels of grazing by cattle (*c.* three livestock unit ha^{-1}), or cutting for silage to a height of ten cm. Superimposed over management type was the split-split-plot treatment of management intensity, defined as either intensive (cattle grazing from May to October, or silage cuts in May and August) or extensive (grazing as before, but suspended from June-August, or a single silage cut in May). For both cutting and grazing

the extensive management was intended to provide a summer window allowing the plants to flower and seed (Morris, 2000; Woodcock et al., 2009). Finally, superimposed over management intensity was the split-split-split plot factor of cultivation technique used to establish the original seed bed. Cultivation had two levels: minimum cultivation with soil disturbance to a depth of *c.* five cm created using tractor drawn disc ploughs; and sward destruction with herbicide application (Glyphosate at five l ha^{-1} a.i) followed by deep cultivation using conventional reversible plough (25-30 cm deep). The overall experimental design had 24 treatment levels, split across 96 experimental plots in four blocks. Average plot size was *c.* 875 m^2. Over the three year sampling period none of these plots received any inorganic fertiliser. Percentage cover of plant species in each experimental plot was recorded using vertical projection in five randomly positioned 1 m^2 quadrats. Plant community composition was recorded in July of 2009, 2010 and 2011.

2.1. Invertebrate sampling

Adult beetles and spiders were sampled using Vortis suction samplers (Burkhard Ltd, UK) in 2009, 2010 and 2011. Suction sampling is a standard technique for the quantitative collection of grassland invertebrates (Brook et al., 2008). In each year two samples were taken respectively on dry days in June and September, between 10.00 and 16.00 h.. Each plot sample represented 55 × ten sec. suctions (Brook et al., 2008). All beetles and spiders were identified to species. All spiders are predatory, but beetles were classified as being either predominantly predatory or predominantly phytophagous (BRC, 2009). As invertebrates provide food for higher trophic levels their biomass within grasslands has important implications for other taxa, in particular farmland birds that have seen wide scale declines across the UK (Vickery et al., 2001). To identify the importance of the treatments in

providing food resources for higher trophic levels the combined biomass of beetles and spiders was determined for each experimental plot based on the length *vs*. mass relationship described by Rogers et al. (1976).

Larval feeding associations were ascertained from the Phytophagous Insect Data Bank (BRC, 2009). Monophagous species and species with only one known host plant within a plot were assumed to feed on that plant species only. For species with multiple potential host plants, their biomass was split proportionally among the host plants within an experimental plot according to the relative percentage cover of each species. Bipartite interaction networks showing feeding associations between the trophic levels of plants and phytophagous beetle were then constructed (Dormann et al., 2008). These represent quantified feeding relationships between host plant and phytophagous beetle. Following Bersier et al. (2002) quantitative measures of food web structure were determined for each of the 288 bipartite webs (96 experimental plots recorded over three y.). These were generality (mean number of host plant species per beetle), vulnerability (mean number of beetle species per host plant) and food web connectance (realised proportion of possible trophic links in food web). These measures were determined using the Bipartite package (Dormann et al., 2008) of the R statistical environment (R Core Development Team, 2008).

2.2. Analysis

Following Schabenberger and Pierce (2002), general linear mixed models in SAS 9.1 were used to assess the response of total biomass, species richness (spider, phytophagous beetle and predatory beetle) and food web statistics to the effects of year and the four treatments. Fixed effects were seed mix, management, management intensity, cultivation and

year, with the saturated model containing all possible interaction terms. To account for the split-split-split plot design, the random effects of block nested in seed mix, management $\times$ block (seed) and intensity $\times$ management $\times$ block (seed) were included. Random effects were only estimated where variance components differed. Year was also treated as a repeated measure, with cultivation $\times$ intensity $\times$ management $\times$ block (seed) identifying the subject on which the repeated measure was based. Degrees of freedom were calculated using the iterative Kenward-Rogers approach and a first order autoregressive covariance structure was used for the repeated measure of year (Schabenberger and Pierce, 2002). Model simplification was by sequential deletion of the least significant terms from a saturated model containing all possible interaction terms. Deletion of terms continued until a significant drop in the explained variance of the model was observed. Species richness was $\log_e$ N+1 transformed for all analyses, although mean values presented in the paper represent raw values.

3. Results

Overall 30,185 beetles from 116 species and 5,312 spiders from 36 species were recorded during the three year period. Establishment of seed mixtures sown into the experimental plots was generally high, with the legumes dominating the GL and GLF plots in the first year of establishment (cf. Supplementary Material Appendix B for summary information on legume and forb establishment and Pywell et al. (2010) for additional detail). Although the floristic composition was dominated by the sown component, many unsown plant species established over the three year period, including some weed species such as *Cirsium arvense* (Asteraceae) which are key food plants for phytophagous invertebrates.

3.1. Beetle and spider biomass

The highest combined biomass of beetles and spiders occurred during the establishment year for the GLF seed mix, where it was sown into shallow cultivated soils that were managed subsequently by low intensity cutting (357.2 ± 32.8 mg m^{-2}). This was considerably higher than in the next best treatment, which while being managed through the same combinations of treatments was sown with the GL seed mix (247.5 ± 37.3 mg m^{-2}). These patterns were supported by an overall interaction term between seed mix, management, management intensity, cultivation and year ($F_{64,162}=7.29$, $p<0.001$). Across all treatment levels there was a common trend of declining biomass from the 2009 establishment year (111.5 ± 8.79 mg m^{-2}) into the following two sampling years (2010: 69.6 ± 5.35 mg m^{-2}; 2011: 77.8 ± 6.62). Overall total biomass was greatest in the more diverse seed mixtures, with the greatest values seen in the most diverse GLF seed mixtures (grass: 33.3 ± 2.43 mg m^{-2}; GL=104.2 ± 6.42; GLF=121.3 ± 8.33). Cutting management (100.0 ± 6.43 mg m^{-2}) supported greater beetle and spider biomass than grazing (72.6 ± 5.18 mg m^{-2}), with extensive management (109.9 ± 6.48 mg m^{-2}) being superior to continuous high intensity management (62.7 ± 4.59 mg m^{-2}). Shallow seed bed cultivation (95.9 ± 6.86 mg m^{-2}) supported a greater biomass than deep cultivation (76.7 ± 7.74 mg m^{-2}).

3.2. Beetle and spider species richness

The species richness of phytophagous beetles differed little between the GL and GLF seed mixtures (ten species), although both were approximately three times greater than that in the grass only seed mix (three species). In addition, grazing management tended to support

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fewer phytophagous beetle species than silage cutting, although this difference was small. These two effects were supported by a significant response of species richness to seed mix ($F_{2,43.5}$=165.3, p<0.0001; Fig. 1a) and management ($F_{1,43.5}$=7.38, p<0.0001; Fig. 1b). No other response to year, intensity, cultivation or other interaction terms were found (p>0.05).

For the predatory beetles a similar pattern was found, with the more diverse GL and GLF seed mixtures supported approximately double the species (*c.* eight species) of the grass only mix (3.95, SE ± 0.25). This was supported by a significant response of predatory beetle species richness to seed mix ($F_{2,44.6}$, 30.1<0.0001; Fig. 2c). In contrast to the patterns seen for the phytophagous beetles, predatory beetle species richness declined after the 2009 establishment year (Year: $F_{2,180}$, 38.4<0.0001; Fig. 2d). No other interaction terms or responses to management, intensity or cultivation were identified (p>0.05).

Spider species richness showed a similar pattern to that seen of the phytophagous and predatory beetles, being lowest in the grass only seed mix (4.02, SE ± 0.15), while differing little between the more floristically diverse GL (5.63, SE ± 0.20) and GLF (5.37, SE ± 0.20). Within the more diverse seed mixtures, the highest species richness was found for extensive cutting applied to GL (6.95, SE ± 0.25) or GLF (6.37, SE ± 0.34) seed mixes. These patterns were supported by significant interactions between seed mix, management and management intensity ($F_{7, 76.4}$=2.51, p=0.02; Fig. 2e). No other interaction terms or responses to cultivation or year were found (p>0.05).

3.3. Food web structure of phytophagous beetles

Quantitative vulnerability (the mean number of beetle species per host plant) was typically lowest within the grass only seed mix. For GL and GLF seed mixes vulnerability

was greatest where extensive management was applied, and typically peaked in the second year of establishment. Overall this pattern was explained by interactions between seed mix, the intensity of management and year ($F_{6,180}$=2.41, p=0.03; Fig. 2a). No other significant terms were identified. Quantitative generality (the mean number of host plant species per beetle species) also responded to management intensity ($F_{1,22.9}$=12.1, p=0.002), with extensive management regimes supporting food webs with significantly higher mean numbers of host plants per beetle. For the GL and GLF seed mixes, generality was also much higher than that observed in the grass only seed mix, although only in the establishment year (seed mix × year: $F_{4,181}$=21.4, p<0.001; Fig. 2b). No other significant individual or interaction terms were identified for generality. In contrast to the pattern seen above, food web connectance was highest within the grass only seed mixture, with this high value declining over subsequent years. Although connectance was lower within the GL and GLF seed mixtures, their values still peaked in the second year of establishment. This pattern was supported by a significant interaction between seed mix and year ($F_{4,189}$=2.61, p=0.04; Fig 2c), and no other significant terms were identified.

4. Discussion

In agreement with prediction one there was strong evidence that beetle and spider species richness could be increased by diversifying swards using sown seed mixtures. Given the implicit link between phytophagous insects and their host plants, the establishment of new plant species should provide opportunities for colonisation by specialist and oligophagous species (Woodcock and Pywell, 2010). The positive relationship between plant and phytophagous invertebrate diversity has been demonstrated in several other grassland studies (e.g. Siemann et al., 1998; Haddad et al., 2001; Woodcock and Pywell, 2010). For predatory

invertebrates, including beetles and spiders, increased plant species richness would diversify sward structural complexity as the availability of novel physical structures linked with individual plant species would be increased (Morris, 2000; Haddad et al., 2001). For predatory invertebrates, an increased diversity of phytophagous species would increase the spectrum of available prey types increasing the potential for the partitioning of resources between different species (Schmitz, 2007). There is also evidence from other studies that by promoting species richness of grassland plants can increase the temporal stability of invertebrate populations (Haddad et al., 2011). Although not demonstrated in the current study, this has implications for the use of diverse seed mixes to promote the delivery of ecosystem services, such as natural pest control (Losey and Vaughn, 2006; Haddad et al., 2011), as well as the reliability of these swards to provide food resources for higher trophic levels (Vickery et al., 2001).

The catastrophic loss of vegetation as a result of cutting management was predicted to result in a reduction in species richness across all invertebrate groups, particularly where multiple cuts were taken during a single season (Morris, 2000; Humbert et al., 2009). This was not found to be the case, with species richness of both phytophagous beetles and spiders being highest under cutting regimes. While this may seem counterintuitive, the continuous nature of grazing within the investigated system meant that its impacts were maintained over several months. While cutting resulted in an instantaneous loss of vegetation, the periods between cutting events were sufficiently long to allow this assemblage of competitive and rapidly recovering plant species to regrow and flower. In part this rapid recovery of the plant community may have been aided by high residual soil fertility, combined with sown species able to rapidly utilise such nutrients. For grasslands where soil fertility is lower, such rapid recovery of the plant community following cutting may be far more subdued. Another factor

potentially reducing the benefits seen from grazing may be linked to the selective nature of what cattle fed upon. Plant species preferentially eaten by livestock would have been reduced in terms of cover and physical structure, reducing their importance for invertebrates utilising them (Gibson et al., 1992; Crofts and Jefferson, 1999; Morris, 2000). Although this study points to cutting being the preferential management practice it is suggested that its implementation should be applied with some level of asynchrony at the scale of individual farms and even within different sections of a single field (Humbert et al., 2009). This would allow immigration from surrounding uncut grasslands to occur as the plant communities recover from a particular cutting event (Morris, 2000; Humbert et al., 2009).

Extensive management, whereby grazing or cutting was suspended over the summer period, was predicted to have a positive effect on both beetles and spiders species richness as it would allow the development of key plant structures on which they either fed, used as refuges or hunted upon (Morris, 2000). Only in the case of spiders did a suspension of management over the summer period promote increased species richness, with no response seen by either trophic level of the beetles. Why this was important for the spiders alone may reflect their dependence on emergent plant structures likely to be lost under intensive management regimes, in particular tall flowering stems utilised by web building spiders (Gibson et al., 1992). In the context of this system, many of the phytophagous beetles fed on legumes (BRC, 2009). As legume seeds planted in this study represented agricultural varieties selected for their ability to regrow under intensive management (Halling et al., 2004), beetles feeding on these plants would be less affected by frequent cutting or grazing as the plants were always able to rapidly recover.

4.1. Links between plants and phytophagous beetles

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While phytophagous beetle species richness showed no response to the intensity of management, the underlying structure of their feeding relationships with plants was influenced by the intensity of management operations. This is in agreement with previous research that has shown that species richness may not differ in response to management intensity, but the underlying structure of food web interactions will be influenced by such anthropogenic disturbance (Tylianakis et al., 2007; Gagic et al., 2011). The mean number of beetle species feeding on individual host plants (food web vulnerability) was found to be highest within the more diverse GL and GLF seed mixes, particularly where either cutting or grazing management was suspended over the summer. Grasslands with high vulnerability are likely to be at greater risk to cascading secondary extinctions as the loss of a single plant species would be more likely to remove a food source from multiple beetle species (Schoener, 1989). Such local plant extinctions may become more likely as a result of future environmental change, for example increased drought frequency (IPCC, 2007). Where food webs have high levels of generality, so that individual beetles are more likely to feed on multiple host plants, this could act to buffer these communities against such secondary extinctions. Specifically, high generality means that the loss of a single plant species would be less likely to result in the loss of all the potential host plants from a sward for individual beetle species. Food webs within the GL and GLF seed mixes did have higher levels of generality than those of the grass only seed mix; however, this was high only in the establishment year. The buffering effect to secondary beetle extinctions of high generality may therefore not be expected to persist throughout the lifetime of these swards, particularly for swards in place for more than five years as is typical under UK agri-environmental schemes (DEFRA, 2005). For the diverse seed mixes the decline in generality is likely the result of colonisation by beetles with increased levels of host plant specialisation as the succession proceeds (Woodcock et al., 2012).

Food web connectance was lowest between the plant and phytophagous beetles of the diverse GL and GLF seed mixtures. This high connectivity is a result of the grass only seed mix containing relatively few plant and beetle species. As a result the realised proportion of possible trophic links was comparatively high in these food webs. For more diverse GL and GLF seed mixes, the potential number of trophic links was far greater, although only a small fraction of these were realised. Although this suggests that there was a greater degree of unfilled niche space in these diverse plant communities, many of these potential trophic links between beetles and plants would be biologically unrealistic and so would not per se indicate unfilled niches. High levels of connectance have been shown to result in increased robustness to secondary species extinctions (Dunne et al., 2002). And this is perhaps in agreement with a more general suggestion that invertebrates present within floristically simple swards, such as those typical of intensively managed grasslands, are generalists in habitat requirements that are able to persist under relatively harsh environmental conditions (Woodcock et al., 2009). However, as the grass only species mix contains only a sub-set of those beetle species found in the more diverse GL and GLF seed mixes, the importance of increased robustness to secondary extinctions is arguably of minor importance.

4.2. Food for higher trophic levels

The GLF seed mix under extensive cutting supported the highest biomass of beetles and spiders at *c.* 3.5 kg ha^{-1}. This was much higher than currently achieved under the widely implemented EK2 English agri-environment scheme option of low input nitrogen fertiliser grasslands (DEFRA, 2005) (0.663, SE $\pm$ 0.008 kg ha^{-1} n=24, unpublished data). High diversity seed mixes support increased invertebrate biomass through greater primary productivity in the plant community combined with stabilisation of plant species richness

over time (Haddad et al., 2011). The inclusion of legumes has also been shown to result in increased invertebrate abundance in other grasslands, which could be linked to increases in overall biomass (Koricheva et al., 2000).

This increase in available biomass could potentially translate into population changes for higher trophic levels, such as farmland birds, though increased resource provisioning within grasslands (Vickery et al., 2001; Peach et al., 2007; Eschen et al., 2012). With an average calorific value for invertebrates of 5.2 kcal g^{-1} (Driver, 1981) a hectare of GLF grassland managed as above would provide *c.* 18,500 kcal worth of spider and beetle food resource. For a moderately sized passerine (30 g) requiring 27 kcal day^{-1} (Nagy, 1987), this would support *c.* 1.9 birds ha^{-1} over a year. This is six times greater than the 0.34 birds ha^{-1} likely to be supported by the typical low input agri-environment scheme grassland management as described above. However, high levels of biomass were seen in the establishment year only, and subsequently dropped rapidly to levels that were only slightly greater than that seen in low input grassland options. In part, this may be the result of two relatively dry years at the study site in 2010 and 2011, that negatively impacted on the net primary productivity of the grasslands. For agri-environment agreements lasting upwards of five years, it is questionable if the expense of the diverse GLF seed mixes (€190 ha^{-1} relative to the next most expensive GL seed mix at €120 ha^{-1}) could justify such short term return where the sole intention was to feed higher trophic levels. However, the wider benefits in terms of invertebrate diversity achieved by more diverse seed mixtures need to be taken into account.

4.3. Conclusions

Given the dependence of many invertebrates on grasslands (Mortimer et al., 2006; Woodcock et al., 2009; Littlewood et al., 2012), their contribution to ecosystem services (Losey and Vaughn, 2006) and declining population status (Vickery et al., 2001; Mortimer et al., 2006), methods to raise the invertebrate diversity of improved grasslands are urgently needed (Pywell et al., 2010; Littlewood et al., 2012). Other benefits of increasing the area of diverse grassland include promoting landscape scale functional connectivity, which will help mitigate against climate change by increasing linkages in fragmented landscapes (Lawton et al., 2010). Ambitious grassland restoration that attempts to replicate specific high quality habitats, such as species-rich hay meadows, could be used to achieve these goals (Lawton et al., 2010). However, the high expense and practical difficulties of grassland restoration makes its wide scale implementation unrealistic (Littlewood et al., 2012). We have presented here a more economically viable and reliable approach that would be to achieve moderate increases in biodiversity over large areas of productive grassland using cheap and easy to establish seed mixtures compatible with conventional farming systems (Pywell et al., 2010). In this study, the inclusion of legumes in seed mixtures achieved these goals, and supported comparable beetle and spider diversity to more expensive seed mixes that included non-legume forbs. However, long term persistence of agricultural varieties of legumes is likely to be limited without reseeding (Pywell et al., 2010). As such the more diverse seed mixes containing other non-legume flowering plants may increase stability in invertebrate species richness if implemented through longer-term agri-environment schemes (Haddad et al., 2001).

Acknowledgements

Appendix A. Supplementary data detailing species composition of sown seed mixtures

Appendix B. Supplementary data detailing mean percentage cover of legumes and forbs in first year of establishment.

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Figure captions

Fig. 1. Response of grassland beetle and spider species richness to year, establishing seed mix, sward management (cutting vs. grazing) and management intensity (extensive vs. intensive). Where seed mixes are: G = grass; GL = grass and legume; GLF =grass, legume and non-legume forb.
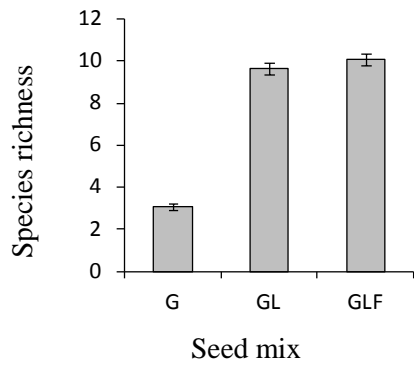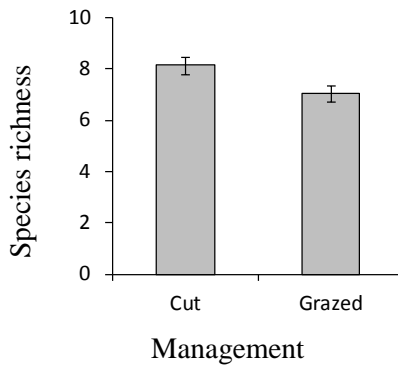
Fig. 2. Changes in the vulnerability, generality and connectance of plant – phytophagous beetle food webs in response to year, establishing seed mix and management intensity (extensive vs. intensive). Where seed mixes are: G = grass; GL = grass and legume; GLF =grass, legume and non-legume forb.

Fig. 1.

Phytophagous beetles

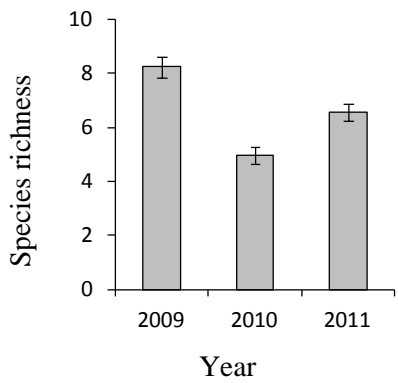*a) Establishing seed mix*

b) Sward management

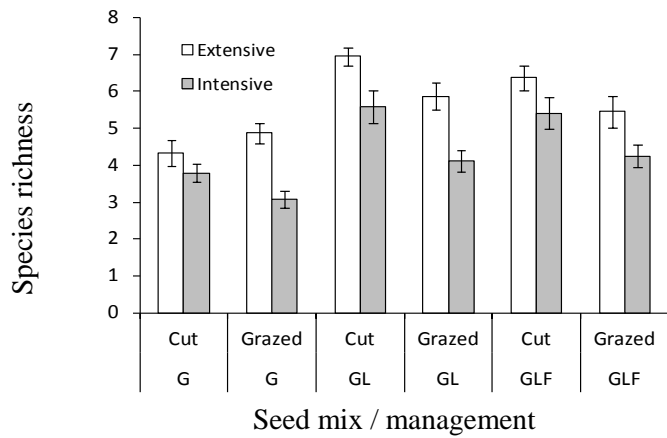**Predatory beetles**

c) Establishing seed mix
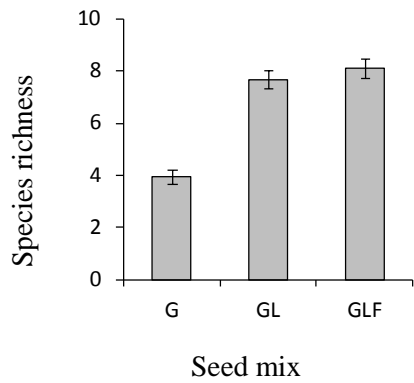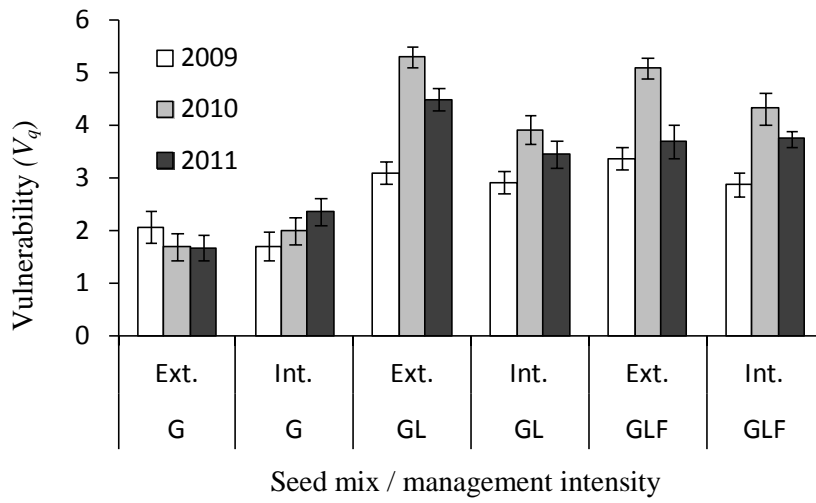
d) Year

Spiders

e) Seed mix, management and management intensity
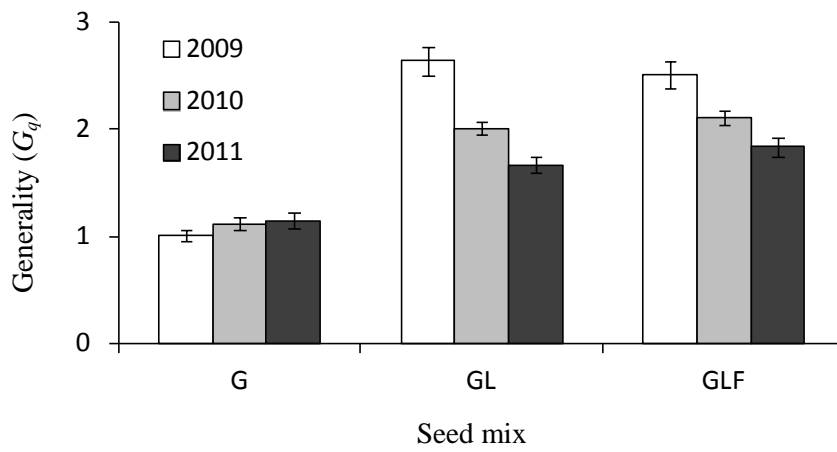

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Fig. 2.

a) Vulnerability: mean number of beetles per host plant

b) Generality: mean number of host plants per beetle

c) Connectance: realised proportion of all possible trophic links