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Enhancing floral diversity to increase the robustness of grassland beetle assemblages to environmental change.

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Abstract

Intensive grassland management has produced floristically species poor swards supporting a limited invertebrate fauna. Low cost seed mixtures can be used to increase floristic diversity and so diversify the food resource of phytophagous invertebrate. We quantify trophic links between plants and phytophagous beetles in grasslands established using three seed mixtures. Using food webs, we model secondary extinctions from the beetle communities caused by the loss of host-plants. Plant species were eliminated according to three scenarios: 1) drought intolerant first; 2) low nutrient status first; 3) stress tolerant first. Diverse seed mixtures containing grasses, legumes and non-legume forbs, were more robust to secondary beetle extinctions. The highest diversity seed mixture increased robustness under scenarios of extreme drought in three out of four tested management regimes. Simple and low cost seed mixtures have the potential to promote landscape scale robustness to future environmental change for native invertebrates.

Introduction

Grasslands are one of the most important biomes in Europe, covering 230 million hectares (Carlier et al. 2009). Inorganic fertilisers, reseeding and improved drainage have increased productivity across large areas by supporting intensive cutting and grazing regimes (Stoate et al. 2009). This has come at a cost to native biodiversity, with declines in plants, vertebrates and invertebrates (e.g. Vickery et al. 2001; Stoate et al. 2009; Bullock et al. 2011; Littlewood et al. 2012). Decreases in invertebrate diversity have been attributed to the simplification of grassland swards, both floristically and architecturally (Lawton 1983; Morris 2000). Enhancement of floristic diversity could support complex invertebrate communities by providing additional host plants, while providing more prey for predatory invertebrates (Siemann et al. 1998; Woodcock and Pywell 2010; Littlewood et al. 2012). This would support improved ecosystem service delivery (e.g. pollination) and provide food for higher trophic levels, e.g. farmland birds (Vickery et al. 2001; Losey and Vaughn 2006).

Restoration that attempts to replicate specific grassland communities (e.g. lowland hay meadows) could be used to achieve this (Bakker and Berendse 1999; Pywell et al. 2007; Littlewood et al. 2012). The cost and technical complexity of restoring such habitats, however, means that wide-scale implementation is likely to be limited (Littlewood et al. 2012). A cheaper alternative is to promote modest increases in floristic diversity by introducing functionally important plant species, that are cheap, widely available and establish well under fertile conditions (Pywell et al. 2007; Pywell et al. 2010). Development of these seed mixtures and the management to establishment them could inform new agri-environment schemes options (Pywell et al. 2010). It is unclear, however, what biodiversity benefits might arise from such modest floristic enhancements.

Studies on the effects of environmental change rarely consider how complex trophic interactions can mitigate cascading effects of species loss within communities (Araujo et al. 2011). Increased robustness to secondary extinctions is a potential benefit that may be derived by enhancing floristic diversity in improved grasslands (Dunne et al. 2002). Robustness is considered here to be the capacity of species within a community to persist in response to the extinction of other species within the community on which they feed (Dunne et al. 2002). Food webs, representing quantitative trophic relationships between species, can vary considerably in the distribution and density of links between species (Dunne et al. 2002; Memmott et al. 2004). The density of these links can affect the robustness of these communities to cascading secondary extinctions (Dunne et al. 2002; Memmott et al. 2004). In this paper we quantify food webs between phytophagous beetles and plants within floristically enhanced grassland and make predictions about community robustness resulting from the non-random loss of plant species. Beetles represent one of the most diverse taxa of grasslands insects (Woodcock et al. 2012). The order of plant species loss follows three realistic scenarios: 1) drought intolerant species first, reflecting the A2 scenario for climate change predicting reduced summer rainfall (IPCC 2007); 2) low nutrient status species first, reflecting the effects of increased atmospheric nitrogen deposition (Smart et al. 2005; Stevens et al. 2010); 3) Linked to prediction 2, and reflecting national trends in UK plants, stress tolerant plants species will be deleted first (Smart et al. 2005). We predict that by using seed mixtures to increase the diversity of plant species, beetle assemblages will establish that are more robust to secondary extinctions. We will determine whether changes in community robustness are consistent under different management regimes (cutting vs. grazing) and intensities (extensive vs. intensive). This has direct relevance for conservation practitioners and policy makers where local approaches to management can vary considerably between farmers. We will not, however, make generalisations as to the effects of specific grassland management practices on community robustness as these represent our effective replicates in this study.

Methods

Study site and experimental design

In April 2008 a multi-factorial experiment was established on an agriculturally improved and floristically species-poor (3.0±0.1 species m^{-2}) lowland grassland in Berkshire, England (Long. 51°26′30″N Lat. 000°43′43″W). The heavy clay soils had moderately high fertility (total soil phosphorous of 911 mg kg^{-1}) and were dominated by *Lolium perenne* and *Trifolium repens*. We used a randomised split-split-plot design, replicated across four blocks, to establish three seed mixtures (our whole plot factor). These seed mixes were: 1) a 'grass only' mix (G), comprising five species that perform well under low inputs of fertiliser and sown at 30 kg ha^{-1} (*c.* € 83 ha^{-1} in 2010); 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 & forb' mix (GLF), comprising five grasses, seven legumes and six non-leguminous forbs (referred hereafter to as 'forbs') at 33.5 kg ha^{-1} (*c.* € 190 ha^{-1}). See Appendix 1 for full species lists. To facilitate future implementation by farmer's species within these seed mixtures were both widely commercially available and were known to establish well into agriculturally improved soils. Original vegetation was destroyed by the application of glyphosate (2.16 kg ha^{-1} a.i. in 100 l water ha^{-1}) followed by ploughing to create a seed bed. The split-plot management treatment was of grazing by cattle, or cutting for silage. The split-split-plot varied 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 provided a summer window allowing the phenological development of flowering plants (Morris 2000). This design represented 12 treatment levels, split across 48 experimental plots in four replicate blocks (see Appendix 2 for an overview of the experimental design). Average plot size was *c.* 1750 m^2. None of these plots received inorganic fertiliser.

In addition to these main experimental treatments, two plots were added to each block. These represented the original improved grassland, dominated by *L. perenne* and *T. repens*. One plot was managed by intensive grazing and the other by intensive cutting, with both receiving nitrogen fertiliser (50 kg ha^{-1}) each spring (Natural England 2010). Percentage cover of all plants was recorded in July of 2009, 2010 and 2011 for each plot using vertical projection of 5 randomly positioned 1 m^2 quadrats.

Phytophagous beetle sampling

Adult phytophagous beetles were sampled using a Vortis suction sampler (Burkland Ltd, UK) in 2009, 2010 and 2011. Samples were taken on dry days in June and September, each representing 55 × ten second suctions per plot (Brook et al. 2008). All phytophagous beetles (Chrysomelidae, Curculionoidea, Apionidae, Bruchidae, Elateridae and Oedomeridae) were identified to species. Total biomass of each species was used in place of abundance in subsequent analyses as this represents the flow of energy from plants to beetles (Saint-Germain et al. 2007). Individual species biomass was determined from body length vs. mass relationships (Rogers et al. 1976). Length was determined from direct measurement of 10 individual of each species.

Larval feeding associations were ascertained from the ‘Database of Insects and their Food Plants’ (Smith and Roy 2008). Monophagous species and species with one host plant at the site were assumed to feed on that plant species only. For species with multiple potential host plants, their summed biomass was split proportionally according to the relative percentage covers of host plants within experimental plots. Quantified trophic interactions were described using bipartite interaction networks of feeding associations between plants and beetle (Dormann et al. 2008). To produce the highest resolution data the biomass of beetles for a particular treatment level were summed across the four blocks and for the three sampling years. This produced 14 bipartite webs, representing one each for the 12 treatment levels as well as the two original grassland control plots managed either by cutting or grazing.

Analysis

Following the approach of Memmott *et al*. (2004), food web robustness was determined by the sequential deletion of plant species in order to determine if this resulted in secondary beetle extinctions. This allowed inferences to be made about the rates at which secondary extinctions accrue in response to the ordered plant species loss. It was assumed that the loss of a beetle's host plants resulted in its extinction. For each host plant deletion the cumulative proportion of the original number of beetle species that had become extinct was recorded. Two approaches were used to simulate the sequential loss of plant species from food webs. The first was a control, whereby the order of plant species extinction was at random, representing a base line from which to assess changes in community robustness. For each food web plant species were deleted at random until all had been lost. This was repeated 500 times and a mean value for the cumulative proportion of secondary beetle extinctions for each plant species loss was recorded. Secondly, we deleted plant species in an ordered fashion reflecting their sensitivity to environmental change: 1) Species were ranked in terms of mean precipitation preference based on UK distribution and climatic data (Hill et al. 2004), and were deleted in order of those preferring the wettest conditions first; 2) Plant species preferring low nutrient status, as determined by Ellenberg's N, were deleted first (Ellenberg 1988; Hill et al. 2004); 3) Using Grime's et al's (1988) classification of plants based on life history strategy (C-S-R), stress tolerant (high Grime's S) species were deleted first. In many cases different plant species had the same score for a particular index (e.g. Ellenberg's N). A randomisation approach similar to that described above was repeated, with the choice of species to be deleted for a particular index score being chosen at random. This approach was repeated 500 times and the mean value for the cumulative proportion of secondary beetle extinctions was recorded.

The difference in the proportion of cumulative secondary beetle extinctions that occurred for each plant species lost was determined between the random and the ordered models of plant species deletion. One sample t-tests were then used to determine if this difference was greater than or less than zero for each of the sequential plant species extinctions performed on a particular web. Overall negative deviations in the proportion of secondary beetle extinctions (relative to the random model of species deletion) indicated that community robustness has been increased by using sown seed mixtures. This was undertaken using the Bipartite package (Dormann et al. 2008) of the R statistical environment (R Core Development Team, 2008). Following Bersier, et al. (2002), summary quantitative measures of food web structure were also determined. These were generality (mean number of host plants per beetle), vulnerability (mean number of beetles per host plant), linkage density (mean number of links per species) and food web connectance (realised proportion of possible trophic links in food web).

Results

In total the 14 bipartite food webs were constructed from 24,717 beetles from 37 species. Establishment of sown plant species was good, resulting in distinctive plant communities corresponding to the seed mixtures (see Pywell et al. 2010). Beetle species richness was higher in the diverse seed mixtures, i.e. those containing legume and other forb species (Table 1). Food web statistics suggest generality, vulnerability and linkage densities increased where more diverse seed mixes were sown (Table 1; Fig 1).

Food web robustness

The robustness of phytophagous beetles' community was lower than predicted only for the intensively grazed improved grassland, and only where plant species loss was in order of stress tolerant species (t_3=4.95, $p<0.05$; Fig. 2a). The remaining original grassland, managed by intensive cutting, contained too few species (n=3) for meaningful analysis. For all other seed mixtures and management regimes robustness either increased relative to the random model of plant species deletion (Fig. 2b-d) or showed no significant difference ($p>0.05$).

For seed mixes containing only grasses, beetle assemblage robustness increased where low nutrient status plant species went extinct first, under both the intensive cutting (t_4=-5.94, p=0.01; Fig. 2b) and extensive grazing (t_5=-2.93, $p<0.05$; Fig. 2b) regimes. No other scenario of plant species extinction or management regime resulted in a significant change in robustness ($p>0.05$). In the case of the grass & legume seed mix robustness in response to ordered plant species extinctions was found for three of the management treatments (Fig. 2c). These were the intensive cutting regime following deletions of low nutrient plant species first (t_5=-2.71, $p<0.05$), the extensive cutting regime for drought intolerant species first (t_9=-3.02, p=0.01) and the intensive grazing regime for stress tolerant species first (t_{11}=-5.78, $p<0.01$). No other scenario of plant species extinction or management regime resulted in a significant change in robustness for the grass & legume seed mix ($p>0.05$).

For the most speciose seed mix (grass, legume & non-legume forbs) each of the four management regimes resulted in increased robustness (Fig. 2c). For the intensive cutting (t_9=-2.23, p=0.05), extensive cutting (t_{11}=-3.88, $p<0.01$) and intensive grazing (t_8=-2.28, p=0.05) robustness was greater where drought intolerant plants were deleted first. Robustness was also greater for the intensive (t_8=-2.40, $p<0.05$) and extensive (t_7=-3.92, $p<0.01$) grazing regimes where plant species loss was in order of low nutrient status species. No other ordered deletions affected robustness for this seed mix ($p>0.05$).

Discussion

Previous investigations into food web robustness have focused primarily on species loss following a sequence that reflects characteristics of food web topography, for example deleting species with the greatest number of trophic links first (e.g. Dunne et al. 2002; Memmott et al. 2004; Estrada 2007). This has indicated that the robustness to cascading secondary extinctions is lowest where highly connected species are lost last (Dunne et al. 2002; Curtsdotter et al. 2011). Under natural situations species loss is likely to be ordered by traits that dictate sensitivity to environmental change, such as drought tolerance (Curtsdotter et al. 2011; Layer et al. 2011). Such sensitivity to environmental factors is not necessarily determined by the degree of connectedness that a species has within a food web. Realistic patterns of species loss in response to future environmental change may therefore have unpredictable effects on robustness. By testing these scenarios predictions can be made as to the value of seed mixtures in promoting stability of native biodiversity to future environmental change (Memmott et al. 2004).

Only in the case of the single improved grassland food web was robustness found to be diminished relative to the random extinction model, in this case where stress tolerant plant species went extinct first. While it is not possible to make unequivocal inferences from this single food web, this suggests that current agriculturally improved grassland are less robust to future patterns of environmental change (e.g. Smart et al. 2005; IPCC 2007; Stevens et al. 2010). This highlights the benefits that could be accrued by the wide scale enhancement of floral diversity using simple and low cost seed mixtures, as tested in the current study. It is important to note that the original grassland plots were fertilised at a relatively low rate (50 kg N ha^{-1} yr^{-1}), replicating a widespread UK agri-environment scheme (Natural England 2010). The failure of this option to increase robustness to future scenarios of environmental change is therefore of particular concern (Pywell et al. 2010).

As seed mixture diversity increased, communities were more likely to be robust to the ordered loss of plant species. This ranged from the grass only seed mix, where only two of the four food webs showed increased robustness in response to plant species loss, to the grass, legume and forb seed mix where greater robustness was seen for all four management regimes. While there is a general pattern of grasslands being more robust to environmental change as seed mix diversity increases, the form of environmental change to which they are robust varies within a seed mix according to management regime and intensity. This is most apparent for the intermediate diversity seed mix (grasses and legumes), where increased robustness occurred to the loss of drought intolerant, stress intolerant and low nutrient status plant species under different management regimes and intensities. In the case of the most diverse seed mix (grass, legume & forb), however, three out of four of the management / intensity regimes were robust to the loss of drought tolerant species, and two out of four to the loss of low nutrient status species. Seed mixtures with over ten species of flowering plant are therefore suggested to help support increased robustness to cascading species loss, with the most diverse seed mixes showing the greatest tendency to be robust to drought even when managed under a variety of regimes and intensities. Prioritisation of these more expensive diverse seed mixes could therefore be justified where future climate change in the form of reduced summer rainfall (IPCC 2007).

This apparent importance of diverse seed mixtures for promoting robustness contrasts with some previous findings, where the number of interacting species was not seen to influence this food web property (Dunne et al. 2002). To a certain extent this disparity may be attributed to sampling effects (Banasek-Richter et al. 2004), whereby plant species sown in this study were not chosen at random, but were derived from cultivated varieties. Common traits are likely to exist that make plants suitable for seed harvesting on economically viable scales (Glemin and Bataillon 2009), and these traits may impact on characteristics of food web structure that affect robustness (Dunne et al. 2002). For example, nationally widespread plants tend to be those for which commercially available seed stocks exist, and such widespread species tend to be those that have the largest numbers of associated phytophagous invertebrates (Leather 1986). Indeed many of the sown legumes in this study had a high diversity of associated UK invertebrates (Smith and Roy 2008). If the seed mixtures were dominated by plants with high levels of connectance (i.e. those fed on by many beetle species) then this may have made these grasslands more likely to be robust to plant species loss (Dunne et al. 2002; Curtsdotter et al. 2011). From an applied management perspective, however, the causes of increased robustness are unimportant as it does not detract from the value of seed mixtures in promoting stability to future environmental change.

Conclusions

The long-term effects of future environmental change on trophic interactions has theoretical and applied implications for the way agricultural land is managed (Layer et al. 2011). The increased awareness of the role played by invertebrates in the delivery of ecosystem services (Losey and Vaughn 2006) means that ensuring stability of their populations can contribute to food security (Carvalheiro et al. 2011; Garibaldi et al. 2011). The value of ecosystem services, such as pollination and pest control, are often derived in habitats other than grasslands (Benayas et al. 2009; Littlewood et al. 2012). In many cases, however, the availability of diverse grasslands at a landscape scale can be crucial in supporting such ecosystem service delivery. For example, insect pollination of arable crops has been shown to be dependent upon that availability of diverse grassland in the wider landscape (Morandin et al. 2007; Benayas et al. 2009). While the beetles considered in this study do not directly deliver ecosystems services, the implications of increased robustness resulting from diverse seed mixtures are a good indicator that this management may have wider benefits. Importantly, this points to the value of increasing the area of floristically diverse grasslands using low cost seed mixtures as a means of promoting community robustness to catastrophic environmental change within agricultural landscapes.

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Appendix 1. Establishing seed mixtures and individual species environmental sensitivity.

Appendix 2. Overview of experimental design.

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Tables

Management	**Management intensity**	**Species richness**		G_q	V_q	LD_q	C_q
		Plants	***Beetles***				
Original low input grassland (50 kg N ha^{-1} yr^{-1})							
Cutting	Intensive	3	13	1.00	3.88	2.44	0.15
Grazing	Intensive	5	13	1.01	3.84	2.43	0.13
Grass only seed mixture							
Cutting	Extensive	6	15	1.78	3.44	2.61	0.12
Cutting	Intensive	5	11	1.93	4.82	3.37	0.21
Grazing	Extensive	7	17	1.62	6.02	3.82	0.15
Grazing	Intensive	5	12	1.22	3.96	2.59	0.15
Grass and legume seed mixture							
Cutting	Extensive	11	21	2.54	5.37	3.96	0.12
Cutting	Intensive	7	18	2.68	5.86	4.27	0.17
Grazing	Extensive	11	26	2.67	6.71	4.69	0.12
Grazing	Intensive	6	18	2.73	5.74	4.23	0.17
Grass, legume and non-legume forb seed mixture							
Cutting	Extensive	13	23	2.79	5.51	4.15	0.11
Cutting	Intensive	11	22	2.59	6.36	4.47	0.13
Grazing	Extensive	9	25	2.78	6.50	4.64	0.13
Grazing	Intensive	10	21	2.76	5.74	4.25	0.13

Table 1. Summary food web statistics for the trophic links between phytophagous beetles and their host plants in response to seed mixture, management and the intensity of management. Where: G_q = quantitative generality (mean number of host plants per beetle); V_q = quantitative vulnerability (mean number of beetles per host plant); LD_q = quantitative linkage density; C_q = quantitative connectance.

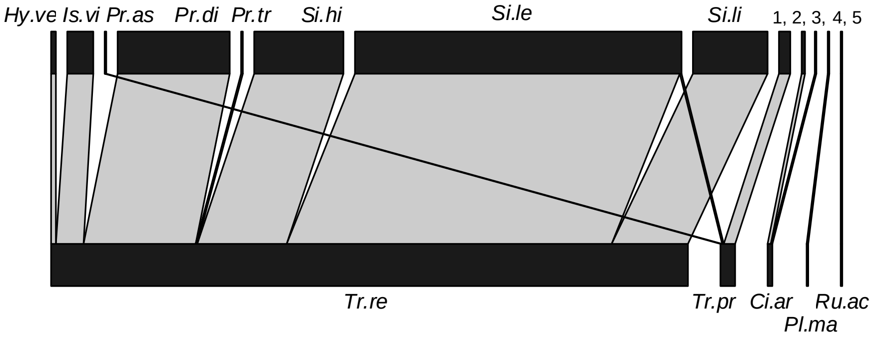
Figure captions

Fig. 1. Example bipartite food webs showing trophic links between the phytophagous beetles and host plants for i) original grassland, ii) grass only seed mix, iii) grass & legume seed mix, and iv)grass, legume and forb seed mix. Only food webs under intensive grazing management are shown. Individual beetle species are represented by bars on the upper tier, the length of which is proportional to the summed biomass of that beetle species feeding on that plant. Individual plants are represented by bars on the lower tier, the length of these bars is proportional to the total biomass of beetles with feeding associations with those plants. Species abbreviations refer to the first and second letters of the generic and specific names, or numbers where space is limited (see caption below figure).

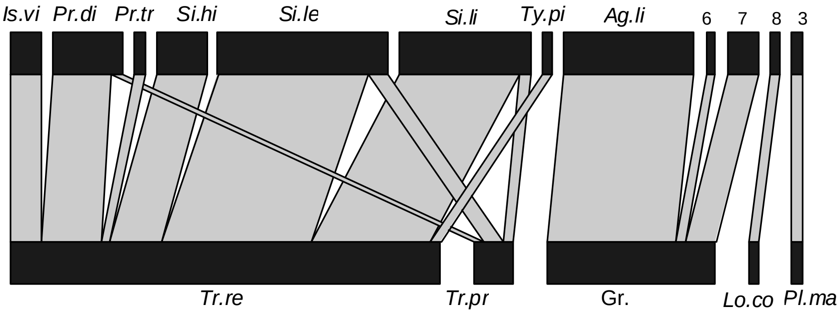
Fig. 2. The robustness of phytophagous beetle assemblages to cascading secondary extinctions that result from the local loss of host plants. Each graph shows deviation in the proportion of secondary beetle extinctions seen between models of random plant species loss and ordered plant species loss from food webs. The order of plant species extinctions reflects drought tolerance, nutrient preference, stress toleration and competitive ability. Negative values show increased robustness to secondary extinctions in the beetle communities relative to the random deletion model.

Fig 1

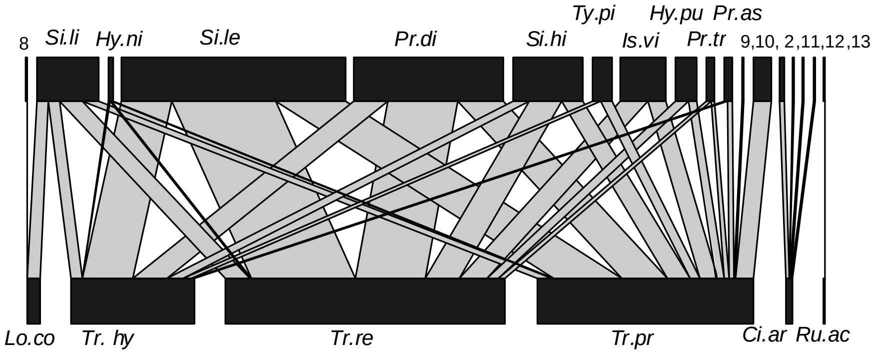
a) Original low input grassland (50 kg ha^{-1} yr^{-1} Nitrogen)



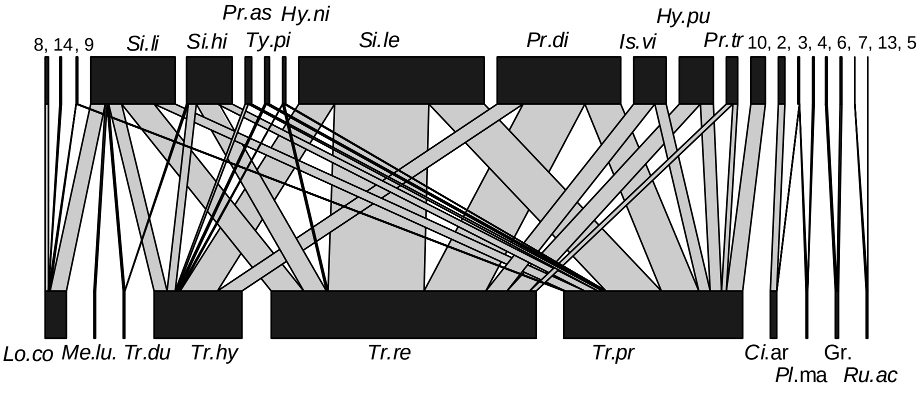
b) Grass only seed mix



c) Grass and legume seed mix

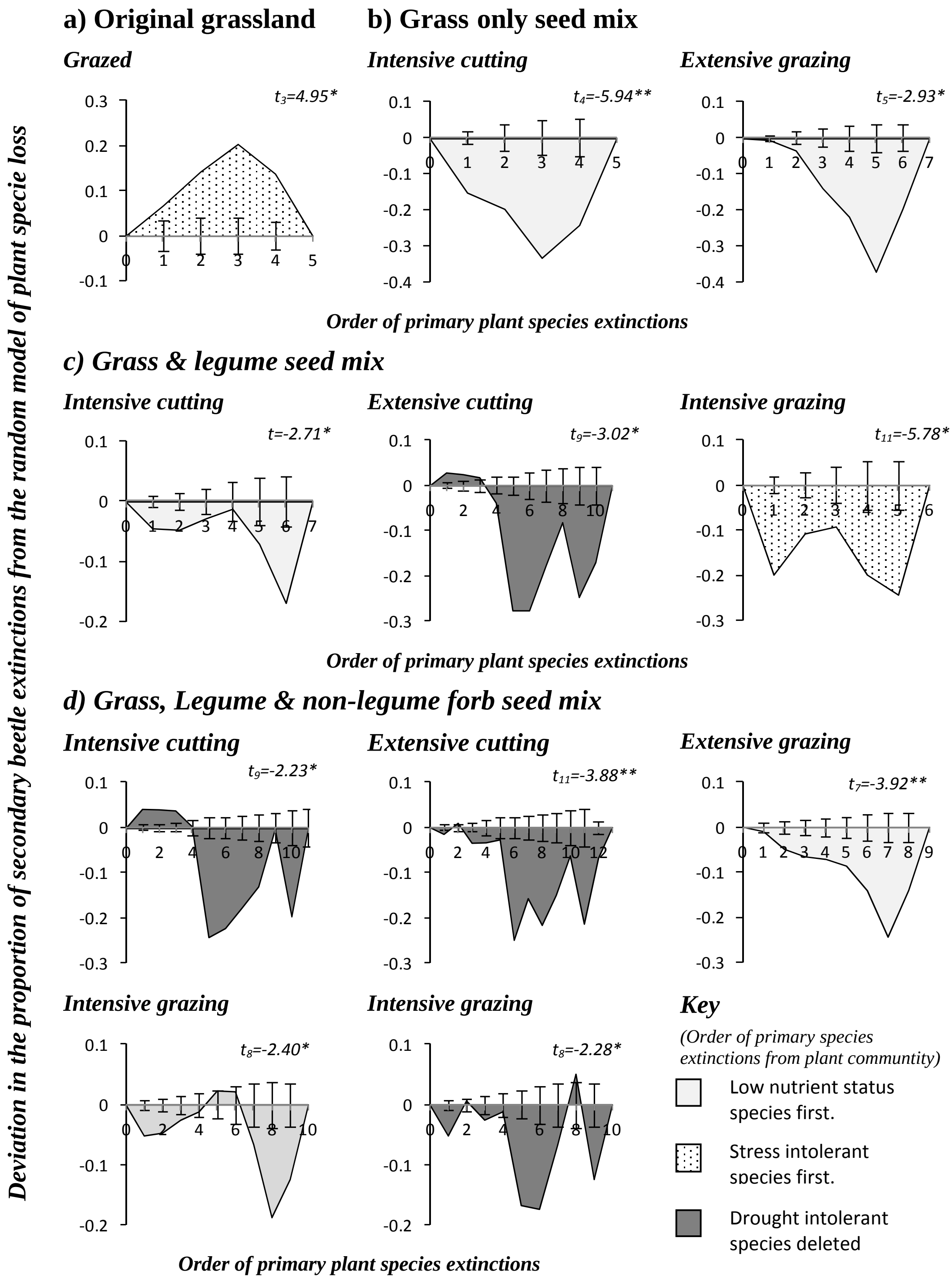


D) Grass, legume and non-legume forb seed mix



BEETLES: Si.li.=*Sitona lineatus; Si.hi.=S. hispidulus; Si.le.=Sitona lepidius; Ty.pi.=Tychius picirostirs; Is.vi=Ischnopterapion virens; Pr.di=Protapion dichroum; Pr.as=P. assimilie; Pr.tr.=P. trifolii; Hy.ve.=Hypera venusta; Hy.ni.=H. nigrirostris; Hy.pu.=H. punctata; Ag.li.=Agriotes lineatus;* 1=*Tychius picirostris*; 2=*Asiorestia ferruginea*; 3=*Longitarsus luridus*; 4=*Longitarsus pratensis*; 5=*Perapion marchicum*; 6=*Chaetocnema hortensis*; 7=Oulema melanopa; 8=*Ischnopterapion loti*; 9=*Sitona sulcifrons*; 10=*Protapion apricans*; 11=*Ceratapion cardorum*; 12=*Sphaeroderma rubidum*; 13=*Chaetocnema concina*; 14=*Tychius stephensi*. PLANTS: Lo.co.=Lotus corniculatus; Tr.=*Trifolium* (du.= *dubium*, hy = hybridum; re=repens, pr=pratense); Me.lu = *Medicago lupulina*; Ci.ar=*Cirsium* arvense; Pl.ma=*Plantago major*; Ru.ac=*Rumex acetosa*.; Gr.=all grass species.

Fig 2


a) Original grassland
Grazed
t₃=4.95*
b) Grass only seed mix
Intensive cutting
t₄=-5.94**
Extensive grazing
t₅=-2.93*
Order of primary plant species extinctions
c) Grass & legume seed mix
Intensive cutting
t=-2.71*
Extensive cutting
t₉=-3.02*
Intensive grazing
t₁₁=-5.78*
Order of primary plant species extinctions
d) Grass, Legume & non-legume forb seed mix
Intensive cutting
t₉=-2.23*
Extensive cutting
t₁₁=-3.88**
Extensive grazing
t₇=-3.92**
Intensive grazing
t₈=-2.40*
Intensive grazing
t₈=-2.28*
Order of primary plant species extinctions
Deviation in the proportion of secondary beetle extinctions from the random model of plant specie loss
Key
(Order of primary species extinctions from plant communtity)
Low nutrient status species first.
Stress intolerant species first.
Drought intolerant species deleted
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
0 1 2 3 4 5 6 7 8 9 10 11 12