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Enhancing grasshopper (Orthoptera: Acrididae) communities in sown margin strips: the role of plant diversity and identity

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Abstract Grasshoppers are important components of grassland invertebrate communities, particularly as nutrient recyclers and as prey for many bird species. Sown margin strips are key features of agri-environmental schemes in European agricultural landscapes and have been shown to benefit grasshoppers depending on the initial sown seed mixture. Understanding the mechanisms by which the sown mixture impacts grasshoppers in sown margin strips is the aim of our study. Here, we investigated plant–grasshopper interactions in sown margin strips and the respective effects of plant identity and diversity on grasshoppers. We surveyed plants and grasshoppers in 44 sown margin strips located in Western France which were initially established with three sowing mixtures dominated, respectively, by alfalfa, *Festuca rubra* and *Lolium perenne* and *Festuca arundinacea*. Grasshopper species contrasted in their response to plant diversity and to the abundance of sown and non-sown plant species. Some grasshopper species were positively correlated with the abundance of grass and especially of a single sown plant species, *F. rubra*. In contrast, other grasshopper species benefited from high plant diversity likely due to their high degree of polyphagy. At the community level, these contrasted responses were translated into a positive linear relationship between grass cover and grasshopper abundance and into a quadratic relationship between plant diversity and grasshopper diversity or abundance. Since plant identity and diversity are driven by the initial sown mixture, our study suggests that by optimizing the seed mixture, it is possible to manage grasshopper diversity or abundance in sown margin strips.

Keywords Agri-environmental schemes · Field margin · Grasshopper · Grassland · Biodiversity · Farmland · Plant–herbivore interaction

Introduction

Agricultural intensification is currently considered as a major driver of large-scale declines in plants, vertebrates and invertebrates in Europe (Robinson and Sutherland 2002). Declines in the diversity and abundance of grassland invertebrates have been attributed to the substitution of natural habitats for arable fields or improved grasslands to insure maximum yield of forage (Barker 2004). Intensified grassland management has resulted in the simplification and homogenization of grassland swards which are generally floristically species poor and structurally uniform (Vickery et al. 2001) and explain their low conservation value for invertebrates (Di Giulio et al. 2001). Adding grasslands with high ecological values in agricultural landscape may help to support invertebrate communities

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and their predators in farmlands (Woodcock et al. 2013). In this context, field margins represent an interesting opportunity as these habitats do not compete for space with agricultural production.

In Europe, sown margin strips have been a key feature of agri-environmental measures (Frampton and Dorne 2007). Positive impacts of sown margin strips on invertebrate biodiversity were reported on butterflies (Delattre et al. 2010), bees, Orthoptera and lycosid spiders (Marshall et al. 2006) due to the direct effects of their extensive management (Meek et al. 2002; Cole et al. 2012; Woodcock et al. 2009). Furthermore, some studies (e.g., Asteraki et al. 2004; Woodcock et al. 2009; Ernoult et al. 2013) have suggested that beneficial impact of sown margin strips was mediated by the identity of the sown plant species and the diversity of weed species settled through time.

Plant community structure is widely recognized as a driving factor of arthropod communities in grassland habitats (Schaffers et al. 2008; Woodcock et al. 2009; Ernoult et al. 2013). Highly diverse plant communities are structurally complex and offer spatially and temporally more feeding and habitat niches for arthropods (Schaffers et al. 2008; Dinnage et al. 2012), resulting in higher arthropod diversity and abundance (Otway et al. 2005). However, the effect of plant species diversity on arthropods is difficult to separate from the effect of one particular plant species or functional group of plants (Rzanny and Voigt 2012). Higher plant diversity may increase the probability of having a plant species that favors a particular arthropod species (i.e., similar to the sampling effect in Huston 1997). Also, higher plant diversity may have direct benefits for arthropod herbivore species which need to achieve a diverse diet for nutrient regulation (Unsicker et al. 2008; Scherber et al. 2010).

Grasshoppers are important components of temperate grasslands (Baldi and Kisbenedek 1997). They have a considerable functional importance as primary consumers, nutrient recyclers (Belovsky and Slade 2000) and prey for a wide range of taxa such as birds (Barker 2004). Consequently, conservation strategies of farmland bird species include specific agri-environmental schemes to enhance grasshopper abundances in grasslands (Bretagnolle et al. 2011). Although precise data are lacking, grasshoppers are currently thought to decline in farmlands, as a consequence of agricultural intensification and decrease in grassland cover at the landscape scale (Barker 2004). In this context, sown margin strips have been demonstrated to enhance grasshopper abundances (Marshall et al. 2006; Badenhausser and Cordeau 2012) depending on the sowing mixture used to establish the margin strips (Badenhausser and Cordeau 2012). Badenhausser and Cordeau (2012) showed that seed mixture dominated by alfalfa had low value for grasshoppers compared with grass mixtures. Grass constitutes a prime source of food for many European grasshopper species in grassland habitats (Bernays and Chapman 1970), but beneficial effects of multiple foods including legumes and forbs have been shown even for grass specialists (Unsicker et al. 2008). As a consequence, plant diversity in sown margin strips may be a driver of grasshopper abundance and diversity. However, the relative importance of plant diversity versus plant identity in explaining the relationships between plant and grasshopper diversity remains unknown. This question is particularly relevant in the context of highly disturbed landscapes where other factors, such as dispersal, may be prime determinants of arthropod community dynamics (Tscharntke and Brandl 2004).

In this paper, we investigated how plant communities in sown grass margin strips may impact grasshopper communities. To do so, we tested (1) how contrasted sown seed mixtures used to establish margin strips impacted the composition and diversity of the plant community, and (2) how the identity of the sown species as well as plant diversity impacted the abundance and species richness of grasshoppers. We tested the following predictions: (1) Species-rich plant communities have a positive impact on grasshopper species richness and abundance; (2) plant species identity affects grasshopper abundance. Specifically, grass species may have a major impact on grasshopper abundance through their effect on the dominant grass-feeding guild; (3) effects of plant diversity and identity may be related to grasshopper species identity, according to their degree of polyphagy.

Materials and methods

The study area (46.11°N, 0.28°W) was an area of about 450 km^2 in Western France and contained over 18,000 fields of intensive agriculture, mostly dedicated to cereal crop production. Grasslands represented about 10 % of the total surface. A total of 44 5-m wide sown margin strips were selected over the study area. The same sown margin strips were sampled over a 2-year period (2008 and 2009).

Three types of seed mixtures were sown by farmers in the margin strips: GL ($n = 4$), grass-legume mixtures dominated by *Medicago sativa* L. (>75 % of the total seed weight), associated with *Lolium perenne* L. or *Festuca pratense* Huds. in lower rates (<25 %); GFrLp ($n = 20$), grass mixtures dominated by *L. perenne* (>58 %) and *Festuca rubra* L. (40 %), sometimes associated with *Trifolium repens* L. (<2 %); and GFa ($n = 20$), grass mixtures dominated by *Festuca arundinacea* Scherb. (either >72 % if associated with others grasses or 100 % in pure-stand). Other species were sown in lower proportion, *i.e., T. repens* (2 %), *Dactylis glomerata* L. (10 %) and *F. pratense*

(15 %). Most of the margin strips were established in 2005 or 2006 (34 among 44), and their mean age was 4.40 ± 0.32 year in 2008. The average size of the margin was 0.17 ha (±0.02).

Vegetation data

Plant surveys were carried out in July 2008 and 2009 in ten quadrats (0.36 m^2) within each sown margin strip using the methodology described by Cordeau et al. (2010). The cover of each plant species in each quadrat was recorded using a linear index from 1 to 5. The mean cover of each plant species was calculated over the ten quadrats per sown margin strip. Plant cover indexes of grasses, legumes and forbs were calculated by adding species cover indexes according to the group they belong to, including both sown and weed (spontaneous) species. Plant species richness (total, grasses, legumes, forbs) was quantified based on plant species surveys. The Shannon index was used as a measure of plant diversity.

Grasshopper sampling technique

Grasshoppers were sampled by removal trapping with a one square meter cage sampler (Badenhausser et al. 2009). It was thrown randomly ten times within each sown margin strip (Badenhausser et al. 2009). All grasshoppers caught were preserved in alcohol and subsequently identified. The same sown margin strips were sampled in 2008 and 2009 at the beginning of August (over a 10-day period) which matched the maximum adult abundance in the study area (Badenhausser et al. 2009). The mean number of individuals per square meter was calculated over the ten replicates per sown margin strip and was taken as a measure of the abundance of grasshoppers. We described grasshopper species richness using the number of species per sown margin strip.

Statistical analyses

All statistical analyses were performed using the R environment (R Development Core team 2013) version 3.02.

Effect of sown mixture on plant community

To test the effect of the sown mixture on plant cover indexes (grasses, legumes), plant diversity (Shannon index) and plant species richness (total, grasses, legumes, forbs), we used linear mixed-effect models fitted using the R package nlme (Pinheiro and Bates 2000). Models were fitted with sown mixture as explanatory variable. We included in the model year as a fixed effect to account for the 2 years of our sampling design and sown margin strips as random effects to account for the repeated measures for the 2 years. An interaction term between year and sown mixture was added to each model. The residuals were inspected to meet parametric test assumption. Each model was simplified using maximum likelihood tests, and parameters were estimated using restricted maximum likelihood method. Random effects were tested using a likelihood ratio test.

Co-occurrences between sown and weed plant species

We tested for non-random associations between sown and weed (spontaneous) plant species using a restricted data set composed of 18 plant species (90 % of the total plant cover). Seven species among them were recommended (Journal Officiel de la République Française 2005) to be sown in margin strips: *L. perenne*, *D. glomerata*, *F. rubra*, *F. arundinacea*, *F. pratense*, *T. repens*, *M. sativa* and the 11 other species were spontaneous (Appendix 1). For each of the seven sown plant species, we performed a randomization of its cover indexes across sown margin strips in a given year (1000 times). Then, for each of the 1000 runs, single weed species cover indexes were independently modeled using linear mixed-effect models with single sown plant species cover index as explanatory variable and year as fixed effect. We included in the model sown margin strips as random effects to account for the repeated measures for the 2 years. The rank of the observed P associated with the effect of each sown species cover index was calculated among the 1000 values and was used as a statistics to test the null hypothesis of non-random co-occurrences between sown and weed species (significance = 1, 5 and 10 % when, respectively, $\mathrm{rank}(P) \leq 10$, $11 \leq \mathrm{rank}(P) \leq 50$, $51 \leq \mathrm{rank}(P) \leq 100$) (Gotelli 2000).

Effect of plant communities on grasshopper communities

The effect of plant diversity and functional identity on grasshopper species richness and abundance was modeled using linear mixed-effect models. Models were fitted with plant cover indexes (grasses, legumes), plant diversity (Shannon index) and plant species richness (total, grasses, legumes, forbs) as explanatory variables. We included in the model year as a fixed effect and sown margin strips as random effects to account for the repeated measures for the 2 years. Two groups of models were fitted: (1) the grass models, based on the hypothesis that grasshopper species richness and total abundance vary depending on grass abundance and on plant species richness or diversity, (2) the legume models, based on the hypothesis that legume abundance had an adverse effect on grasshopper species richness and abundances (Badenhausser and Cordeau 2012). Since plant community variables may be correlated, different competing models were fitted within the two groups of models:

Grass Model 1: $Y = \text{year} + \text{GCI} + \text{GCI}^2 + \text{PSR} + \text{PSR}^2 + \text{interaction terms}$
Grass Model 2: $Y = \text{year} + \text{GCI} + \text{GCI}^2 + \text{ShI} + \text{ShI}^2 + \text{interaction terms}$
Grass Model 3: $Y = \text{year} + \text{GCI} + \text{GCI}^2 + \text{GSR} + \text{FSR} + \text{interaction terms}$
Grass Model 4: $Y = \text{year} + \text{GCI} + \text{GCI}^2 + \text{LSR} + \text{interaction terms}$
Legume Model 1: $Y = \text{year} + \text{LCI} + \text{LCI}^2 + \text{PSR} + \text{PSR}^2 + \text{interaction terms}$
Legume Model 2: $Y = \text{year} + \text{LCI} + \text{LCI}^2 + \text{ShI} + \text{ShI}^2 + \text{interaction terms}$
Legume Model 3: $\text{Y} = \text{year} + \text{LCI} + \text{LCI}^2 + \text{GSR} + \text{interaction terms}$

where Y is grasshopper species richness or abundance, year is the sampling year, GCI is grass cover index, LCI is legume cover index, PSR is plant species richness, GSR is grass species richness, FSR is forb species richness, LSR is legume species richness, ShI is plant diversity (Shannon index). Quantitative explanatory variables were standardized (mean $= 0$ and SD $= 1$). All one-way interaction terms with the year effect were added to the models. In order to match the distributional assumption of linear models, the response variables were transformed using power transformations, following Turchin (2003) ($\theta = 0.5$ for species richness and $\theta = 0.25$ for total abundance). For all models, the residuals were inspected to meet parametric test assumption. After fitting each full model, we simplified it step-by-step using maximum likelihood tests. The second-order Akaike information criterion corrected for small sample size (AICc, Burnham and Anderson 2002) was calculated for each simplified model (Table 1). Then, we compared the two simplified models using Akaike weights (Burnham and Anderson 2002). Parameters were estimated using restricted maximum likelihood method. Random effects were tested using a likelihood ratio test.

Co-occurrences between plant and grasshopper species

We tested for non-random associations between single grasshopper species and single plant species. Rare grasshopper species were not included in the analysis, and six grasshopper species were selected: *Chorthippus albomarginatus* De Geer, *Chorthippus biguttulus* L., *Chorthippus dorsatus* Zetterstedt, *Euchorthippus elegantulus* Zeuner, *Pezotettix giornae* Rossi and *Pseudochorthippus parallelus* Zetterstedt. For each of the 18 plant species corresponding to 90 % of the total plant cover, we performed a randomization of its cover indexes across sown margin strips in a given year (1000 times). Then, for each of the 1000 runs, single grasshopper species abundances were independently modeled using linear mixed-effect models with single plant species cover index as explanatory variable and year as fixed effect. We included in the model sown margin strips as random effects to account for the repeated measures for the 2 years. The rank of the observed P associated with the effect of each plant species cover index was calculated among the 1000 values and was used as a statistics to test the null hypothesis (Gotelli 2000).

Grasshopper species response to plant identity and diversity

In order to explain the pattern of the relationships between grasshoppers and plants at the community level, we studied single grasshopper species responses to both plant diversity and identity. Explanatory variables were selected from the previous analyses, i.e., plant diversity (Shannon index) and the cover indexes of sown plant species which had a positive effect on at least two dominant grasshopper species (namely *F. rubra* and *T. repens*). Year was included as fixed effect and sown margin strips as random effects to account for the repeated measures for the 2 years. The models had the following form:

$$Y = \text{year} + \text{FESRU} + \text{FESRU}^2 + \text{TRFRE} + \text{TRFRE}^2 + \text{ShI} + \text{ShI}^2 + \text{interaction terms}$$

where Y is single grasshopper species abundance, year is the sampling year, FESRU is *F. rubra* cover index, TRFRE is *T. repens* cover index, and ShI is plant diversity (Shannon index). Quantitative explanatory variables were standardized (mean $= 0$ and SD $= 1$). One-way interaction terms with the year effect were added to these models. In order to match the distributional assumption of linear models, the response variables were transformed using log transformation. For all models, the residuals were inspected to meet parametric test assumption. Each full model was simplified it step-by-step using maximum likelihood tests. Parameters were estimated using restricted maximum likelihood method. Random effects were tested using a likelihood ratio test.

Results

Fourteen grasshopper species were recorded in sown margin strips. Among them, *E. elegantulus* and *P. giornae* were the most abundant. Two other species were abundant, i.e., *P. parallelus* and *C. dorsatus*. Other Gomphocerinae species were often observed at low abundances: *C. albomarginatus, C. biguttulus, Euchorthippus declivus* Brisout and *Omocestus rufipes* Zetterstedt, while some species were observed only once (e.g., *Gomphocerippus rufus* L., *Chorthippus brunneus*

Table 1 Effects of plant diversity and plant functional group cover on grasshopper species richness and abundance

Response variable	Model name	Model structure	AICc	AICc weight
Species richness	GM1	Y = year + GCI + PSR + PSR^2	118.0	0.001
	GM2	Y = year + GCI + GCI^2 + ShI + ShI^2	104.6	0.937
	GM3	Y = year + GCI + GCI^2 + GSR	110.1	0.060
	GM4	Y = year + GCI + GCI^2	116.7	0.002
	LM1	Y = year + LCI + LCI^2 + PSR + PSR^2 + year:PSR + year:LCI + year:LCI^2	117.3	0.029
	LM2	Y = year + LCI + ShI + ShI^2	115.6	0.069
	LM3	Y = year + LCI + LCI^2 + GSR + LCI:GSR + LCI^2:GSR	110.4	0.902
Total abundance	GM1	Y = year + GCI	27.2	0.060
	GM2	Y = year + GCI + ShI + ShI^2 + year:ShI + year:ShI^2	21.9	0.821
	GM3	Y = year + GCI + GSR	27.2	0.060
	GM4	Y = year + GCI	27.2	0.060
	LM1	Y = year + PSR + PSR^2	33.2	0.038
	LM2	Y = year + LCI + ShI + ShI^2 + year:ShI + year:ShI^2	27.4	0.710
	LM3	Y = year + LCI + GSR	29.4	0.257

Selected models (grass models: GM, legume models: LM) and model selection results

Grasshopper species richness: square root transformation of the number of species

Grasshopper abundance: double square root transformation of the number of grasshoppers m^{-2}

GCI grass cover index (standardized), *LCI* legume cover index (standardized), *PSR* plant species richness (standardized), *GSR* grass species richness (standardized), *FSR* forb species richness (standardized), *LSR* legume species richness (standardized), *ShI* Shannon index of plant community (standardized)

Thunberg, *Chorthippus mollis* Charpentier). Grasshopper species richness per sown margin strip (mean ± SE) was 3.16 ± 0.23 in 2008 and 4.50 ± 0.29 in 2009. Grasshopper abundances (mean ± SE) were 1.68 ± 0.26 m^{-2} in 2008 and 2.58 ± 0.39 m^{-2} in 2009. Grasshopper abundances in sown margin strips increased with grasshopper species richness (2008: $r^2 = 0.38$; $P < 0.001$; 2009: $r^2 = 0.58$; $P < 0.001$).

For the plant community, 179 plant species were recorded in sown margin strips. Plant species richness per margin strip (mean ± SE) was 29.3 ± 1.2 in 2008 and 23.8 ± 1.3 in 2009. Mean (±SE) of Shannon index was 2.03 ± 0.11 in 2008 and 2.19 ± 0.13 in 2009. Grasses were dominant (70 % of the sum of all plant cover indexes, 2008: 69.5 ± 3.9 %; 2009: 72.6 ± 2.8 %), while leguminous plants were not abundant (2008: 7.5 % ± 2.9 %; 2009: 6.2 ± 2.1 %). The initial sown mixture had a strong effect on grass and legume cover indexes as well as plant diversity and plant species richness (Appendix 2). When testing the hypothesis of non-random association between sown and weed species, we found clear plant–plant co-occurrences or avoidances (Fig. 1; see Appendix 1 for more details).

Effects of plant community on grasshopper community

Grasshopper species richness was best explained by the grass models than by the legume models (Table 1; AICc weight = 0.977 for the best grass model (Grass Model 2); AICc weight = 0.023 for the best legume model (Legume Model 3). In the Grass Model 2 (Table 2), plant diversity was the most significant explanatory variable and had a quadratic effect on grasshopper species richness (Fig. 2a). The selected model also revealed that grass cover had a quadratic effect on grasshopper species richness (Table 2). Grass cover index and Shannon index were not correlated (2008: $r = -0.17$, $P = 0.27$; 2009: $r = 0.10$, $P = 0.51$).

Grasshopper abundance was best explained by the Grass Model 2 than by any other competing model (Table 1), and grass cover was the most significant explanatory variable compared with plant diversity (Table 2). Grasshopper abundance increased linearly with grass cover in the sown margin strips (Table 2; Fig. 2b). Plant species diversity had a significant positive effect on grasshopper abundance only in 2009 (Table 2).

Co-occurrences between plant and grasshopper species

When testing the hypothesis of non-random association between single plant species and single grasshopper species, we found contrasting results between grasshopper species (Fig. 1; Appendix 3) in terms of responses to sown plant species versus weed species and single versus large number of plant species. Sown grasses positively correlated with the abundances of *E. elegantulus* (Fig. 1a), *C. albomarginatus*

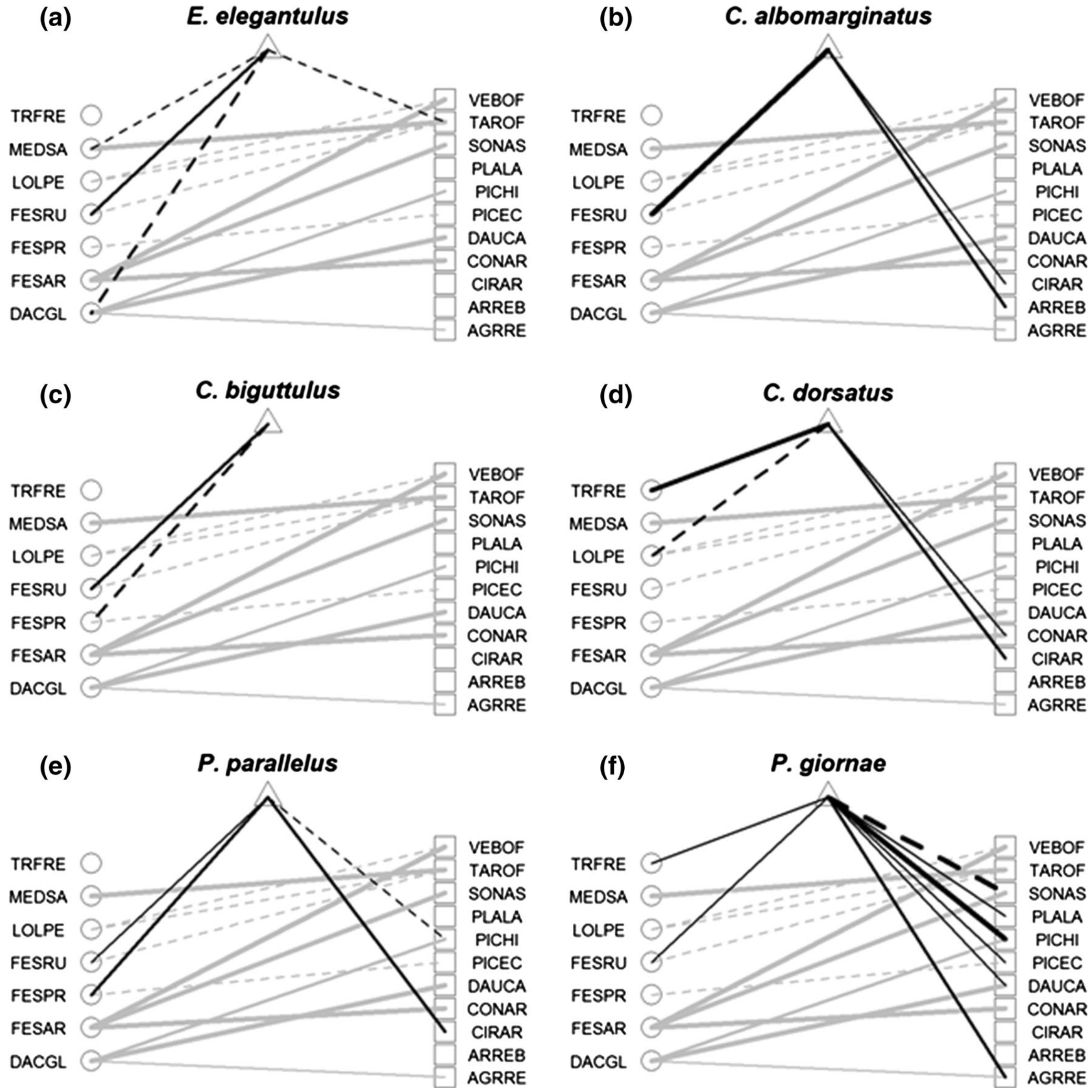

Fig. 1 Co-occurrences between sown (*left panel* of *each figure*) and non-sown (*right panel*) plant species (*gray lines*) and between plant species and six grasshopper species (**a**–**f**) (*black lines*). *Lines* represent the intensity of plant species cover effect (rank of the observed *P* among 1000 simulated runs in linear mixed-effect models). *Solid lines* positive effects, *dashed lines* negative effects; large thickness: rank ≤ 10 (1 % significant), intermediate: 11 ≤ rank ≤ 50 (5 % significant), thin: 51 ≤ rank ≤ 100 (10 % significant). Plant species are named with their EPPO code (http://eppt.eppo.org/; Appendix 1)

(Fig. 1b), *C. biguttulus* (Fig. 1c), *P. parallelus* (Fig. 1e) and *P. giornae* (Fig. 1f), while it was legumes for *C. dorsatus* (Fig. 1d) and mainly forbs for *P. giornae* (Fig. 1f). Only one species, *C. dorsatus*, did not respond positively to the abundance of any sown grass species. Among grasses, *F. rubra* was beneficial for all species except *C. dorsatus* which responded strongly to the cover of clover. Conversely, high covers in *D. glomerata*, *L. perenne* and *M. sativa* had negative effects on most grasshopper species. Opposite effects of some plant species on grasshoppers were also observed. This was the case of *F. pratense* whose cover was negatively correlated with *C. biguttulus* abundance and positively with *P. parallelus* abundance. While *C. biguttulus* and *E. elegantulus* depended only on one resource, *P.*

Table 2 Effect of plant community structure on grasshopper species richness and total abundance in sown strips

Term	Grasshopper species richness		Grasshopper abundance	
	Est. ± SE	*P*	Est. ± SE	*P*
Grass Model 2				
Intercept	1.93[a] ± 0.08	<0.001	1.04[a] ± 0.04	<0.001
Year = 2009	0.33 ± 0.09	0.001	0.21 ± 0.05	<0.001
GCI	0.16 ± 0.11	0.13	0.20 ± 0.06	0.004
GCI^2	−0.33 ± 0.12	0.009	–	–
ShI	0.13 ± 0.09	0.15	0.09 ± 0.08	0.30
ShI^2	−0.53 ± 0.13	<0.001	0.001 ± 0.12	0.99
I(2009:ShI)	–	–	−0.09 ± 0.09	0.33
I(2009:ShI^2)	–	–	−0.39 ± 0.14	0.01

Grasshopper species richness: square root transformation of the number of species

Grasshopper abundance: double square root transformation of the number of grasshoppers m^{-2}

Parameter estimates (Est.), standard errors (SE) and *P* of the fixed-effect terms in mixed-effect models

Each parameter is tested marginally, i.e., in the presence of all other terms in the simplified model

GCI grass cover index (standardized), *ShI* Shannon index of plant community (standardized)

–: Terms excluded during model simplification

[a] The intercept term is the mean of the response variable for sown strips surveyed in 2008

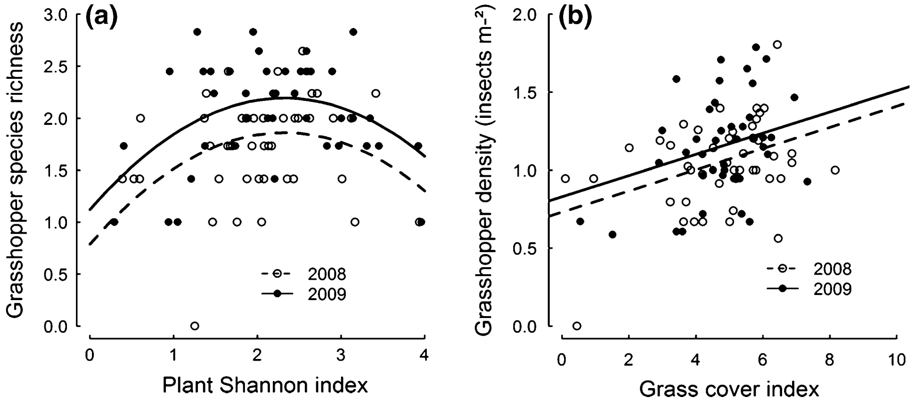

Fig. 2 Observed and predicted effects of plant community structure on grasshoppers (**a**) species richness (transformed data $-\sqrt{x}$) and (**b**) abundance (transformed data $-\sqrt{\sqrt{x}}$) in sown strips

giornae depended on multiple resources (seven plant species), the stronger positive effect being related to the weed *P. hieracioides*. An intermediate number of plant species had a positive effect on the abundance of *C. albomarginatus*, *C. dorsatus* and *P. parallelus.* The weed *C. arvense* had a positive effect on the three species.

Grasshopper species responses to plant identity and diversity

When evaluating the relative importance of plant diversity and plant identity on the abundances of single grasshopper species (Table 3), we also found contrasted results. The most abundant grasshopper species *E. elegantulus* benefited from the sown plant species *F. rubra,* while an increase in plant diversity had an adverse effect on this species. *P. parallelus C. albomarginatus* and *C. biguttulus* abundances were not impacted by plant diversity but benefited from *F. rubra*. Plant diversity was the main driver of *P. giornae* abundances which increased with plant diversity and *T. repens* cover index and marginally with *F. rubra* cover index. The positive effect of plant diversity was also observed for *C. dorsatus,* while *F. rubra* cover had no effect on this species which benefited from *T. repens*.

Table 3 Effect of plant diversity, *F. rubra* cover and *T. repens* cover on the abundances of six grasshopper species in sown margin strips

Term	*C. albomarginatus*		*C. biguttulus*		*C. dorsatus*		*E. elegantulus*		*P. giornae*		*P. parallelus*	
	Est. ± SE	*P*	Est. ± SE	*P*	Est. ± SE	*P*	Est. ± SE	*P*	Est. ± SE	*P*	Est. ± SE	*P*
Intercept	−2.10 ± 0.05	0.001	−2.04 ± 0.06	0.001	−2.07 ± 0.09	0.001	−0.59 ± 0.16	0.001	−1.34 ± 0.15	0.001	−2.23 ± 0.14	0.001
Year = 2009	–	–	0.17 ± 0.09	0.06	0.55 ± 0.13	0.003	0.08 ± 0.15	0.60	0.74 ± 0.21	0.001	0.38 ± 0.09	0.001
FESRU	0.45 ± 0.09	0.001	0.29 ± 0.10	0.009	–	–	0.25 ± 0.28	0.37	0.32 ± 0.17	0.07	−0.84 ± 0.40	0.04
FESRU^2	–	–	–	–	–	–	–	–	–	–	1.05 ± 0.38	0.009
TRFRE	–	–	–	–	0.33 ± 0.13	0.01	–	–	0.37 ± 0.17	0.04	–	–
ShI	–	–	–	–	0.16 ± 0.17	0.34	−0.10 ± 0.23	0.65	0.87 ± 0.18	0.002	–	–
ShI^2	–	–	–	–	0.10 ± 0.26	0.68	−0.82 ± 0.33	0.01	0.22 ± 0.39	0.57	–	–
I(2009:FESRU)	–	–	–	–	–	–	0.75 ± 0.30	0.01	–	–	0.74 ± 0.20	0.001
I(2009:TRFRE)	–	–	–	–	0.83 ± 0.31	0.01	–	–	–	–	–	–
I(2009:ShI)	–	–	–	–	−0.02 ± 0.23	0.92	–	–	−0.49 ± 0.35	0.17	–	–
I(2009:ShI^2)	–	–	–	–	−0.70 ± 0.34	0.04	–	–	−1.05 ± 0.53	0.06	–	–

Grasshopper abundance: log transformation of the number of grasshoppers m^{-2}

Parameter estimates (Est.), standard errors (SE) and *P* of the fixed-effect terms in mixed-effect models

Each parameter is tested marginally, i.e., in the presence of all other terms in the simplified model

The intercept term is the mean of the response variable for sown strips surveyed in 2008

FESRU: *F. rubra* cover index (standardized); TRFRE: *T. repens* cover index (standardized); ShI: Shannon index of plant community (standardized)

–: Terms excluded during model simplification

Discussion

In this study, we investigated plant–grasshopper interactions in sown margin strips. Our results suggest that both plant identity and diversity are important drivers of grasshopper community structure in sown margin strips. Grasshopper abundance and diversity were partly explained by the abundance in the sown margin strips of grass species. In particular, the grass species *F. rubra* had highly beneficial impact on most of the dominant grasshopper species. Grasshopper responses to plant diversity were more contrasted among species.

We identified two groups of grasshopper species based on their response to plant identity or diversity. A first group of species increased in abundance as grass cover increased (*C. albomarginatus, C. biguttulus, E. elegantulus* and *P. parallelus*). These Gomphocerinae species are known to be grass feeders and to perform better in grass-dominant vegetation (Unsicker et al. 2008). They especially took advantage from the presence of one species, namely *F. rubra* (Gardiner et al. 2002). *F. rubra* is typically a slow-growing species characterized by low N and high dry matter content in leaves compared to other grass species in our study (Maire et al. 2009). The strong positive effect of *F. rubra* may indicate that the four Gomphocerinae species targeted tough leaves with low N content and high carbohydrate content (Deraison et al. 2015). This group of grasshopper species did not benefit from high plant diversity and contrasted with the second group of grasshoppers strongly dependent on it (*C. dorsatus* and *P. giornae).* These two species increased in abundance with increasing plant diversity and benefited from different functional groups of plants such as legumes and forbs. This is consistent with Deraison et al. (2015) who found that *P. giornae* and *C. dorsatus* eat mostly subordinate plant species in grasslands such as forb and legume species. They may thus benefit from a higher plant diversity than strictly grass feeders (e.g., *E. elegantulus*).

At the community level, a positive relationship between grasshopper species richness and plant diversity has been reported in many grassland ecosystems, such as tall rangelands in southern Idaho (Fielding and Brusven 1993) and flooded grasslands in Greece (Kati et al. 2012). Some other studies did not yield any links between plant richness and grasshopper richness (Torrusio et al. 2002; Hudewenz et al. 2012) indicating that the positive plant–grasshopper richness relationship was not necessarily general. Consistently with our predictions, plant species diversity determined grasshopper species richness. However, while increasing plant diversity enhanced grasshopper species richness up to an optimal value, beyond this optimum it had an adverse effect resulting in a quadratic relationship between plant diversity and grasshopper species richness and abundance. Our approach integrating the effect of both plant diversity and identity, and the species-specific response of grasshoppers helps us to understand the nonlinear response of grasshopper communities to plant diversity and the conflicting results observed in previous studies on the relationship between plant and grasshopper diversity (e.g., Scherber et al. 2006; Hudewenz et al. 2012). While some grasshoppers seemed to increase in abundance with high plant diversity, a majority of species benefited mainly from a single resource (*F. rubra*) and were independent or even negatively impacted by high plant diversity (e.g., *E. elegantulus*). At the community level, these differences can explain the quadratic relationship we observed between plant and grasshopper diversity. At first, an increase in grasshopper species richness was possible because of high *F. rubra* cover and the maintenance of plant species-rich communities. However, in sown margin strips characterized by high plant species richness, *F. rubra* cover index was generally low and may explain the decrease in grasshopper species richness.

In our study, we did not explicitly quantify the trophic interactions between grasshopper species and plant species but inferred their relationship using observational data. We acknowledge that mechanisms other than direct trophic interactions may impact the plant–grasshopper relationships. For instance, diverse vegetation provides habitats with contrasted microclimatic conditions which affect grasshoppers differently (Gardiner and Hassall 2009). In addition, plant diversity may impact predator communities, which have been reported to strongly impact grasshopper communities (Schmitz 1998). Further studies are needed to explicitly test the functional link between plant and grasshopper species in order to understand the relative importance of trophic linkage between plants and grasshoppers compared to other drivers (microclimate, dispersal abilities).

Given the contribution of many grassland invertebrates to ecosystem services (Losey and Vaughan 2006) and their declining population status (Vickery et al. 2001; Barker 2004), methods to increase the invertebrate diversity and abundance in agricultural landscapes are needed. Adding grassland habitats with high ecological values in agricultural landscapes may help to support invertebrate communities and their predators in farmlands. Field margins are good candidates to achieve this goal because they do not compete for space with crops and they increase landscape connectivity and the area of extensively managed habitats in agricultural landscape (Cole et al. 2012). We have shown here that the sown seed mixture used to establish the margin strips determined not only weed diversity but also weed identity in the sown margin strips, which in turn produced a feedback in the grasshopper community structure. For instance, *F. arundinacea* seed mix was characterized by the lowest level of weed diversity. *F. arundinacea* is a tall fast-growing species which can achieve high yield compared to other sown species (Maire et al. 2009). It is characterized by a strong competitive effect (Maire et al. 2012), and its ability to prevent high level of weed diversity in sown experimental mixture has been already reported (Tracy et al. 2004). Our study suggests that sowing contrasted species may be used as an efficient way to either increase weed diversity or decrease weed abundance depending on management purpose (Meiss et al. 2010). More importantly, our study showed that this result equally applied to grasshoppers as sown species identity and weed diversity directly affected grasshopper communities. Therefore, our study suggests that it is possible to design optimal sown seed mixtures in order to both manage plant diversity, grasshopper diversity or abundance. Considering the role of grasshoppers as prey for other taxa, one objective could be to maximize their abundance (Barker 2004). Another objective could be to maximize the grasshopper diversity and equitability in order to maintain a wide range of species or to diversify the food for predators. More generally, our findings could help to design seed mixtures to support an extended range of invertebrate taxa since the effects of seed mixtures have been established on other taxa (e.g., carabid beetles, spiders) (Woodcock et al. 2013).

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Appendix 1: Co-occurrences analysis between sown and weed plant species

See Fig. 3.

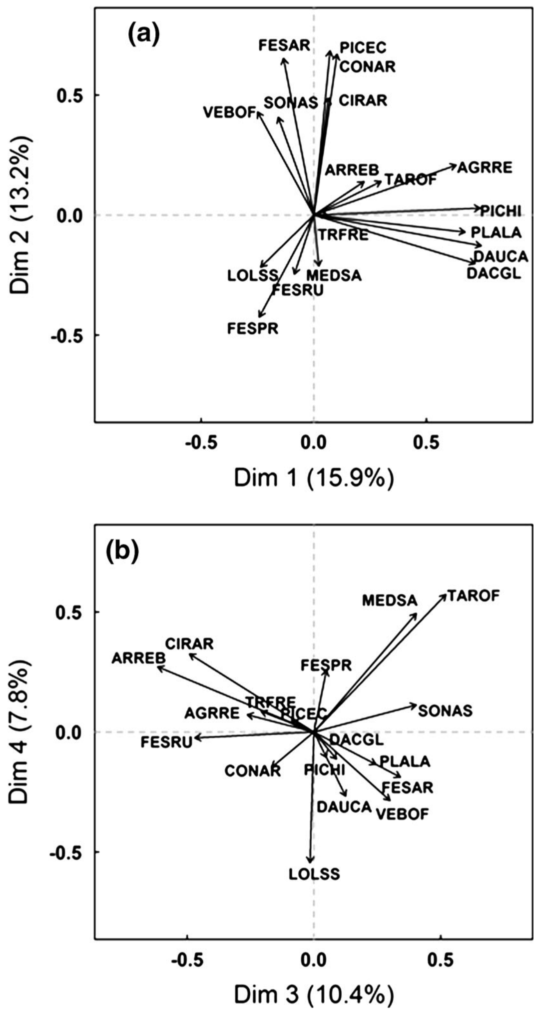

Fig. 3 Principal component analysis (PCA) on the sown strip/plant species cover index matrix

Eleven weed species dominated weed communities: *Elytrigia repens* L. (ELREP), *Arrhenatherum elatius* L. (ARREL), *Cirsium arvense* L. (CIRAR), *Concolvulus arvensis* L. (CONAR), *Daucus carota* L. (DAUCA), *Picris echioides* L. (PICEC), *Picris hieracioides* L. (PICHI), *Plantago lanceolata* L. (PLALA), *Sonchus asper* L. (SONAS), *Taraxacum officinale* Weber (TAROF), *Verbena officinalis* L. (VEROF). Co-occurrence between sown and weed species was observed for *D. glomerata* with *E. repens, D. carota, P. hieracioides,* for *F. arundinacea* with *C. arvense* and *S. asper* and for *M. sativa* with *T. officinale* (Figs. 1, 3). At the opposite end, *P. echioides* was not present in sown margin strips where *F. pratense* was abundant (Figs. 1, 3). The same trend was observed for *T. officinale* which was not observed when *F. rubra* or *L. perenne* dominated in sown margin strips and for *V. officinale* when *L. perenne* was abundant (Figs. 1, 3).

Appendix 2: Effect of sown seed mixture on plant community

See Fig. 4.

Total grass cover index was higher when margin strips were sown with mixtures containing *F. rubra* and *L. perenne* (GFrLp) or dominated by *F. arundinacea* (GFa) than with grass–legume mixture (GL) (Fig. 4a) (sown mixture effect: $P < 0.001$). Legume almost had no cover in sown margin strips sown with GFa, compared to those sown with GFrLp and to GL mixture (Fig. 4b) (sown mixture effect: $P < 0.001$). Forb cover index did not differ between margin strips sown with the three types of mixtures (sown mixture effect: $P = 0.11$). GL mixture resulted in higher plant diversity compared to the other mixtures (Fig. 4c) (sown mixture effect: $P = 0.04$). Plant species richness in 2009 was the highest in sown margin strips established with the GL mixture (Fig. 4d) (year effect: $P < 0.001$; sown mixture effect: $P = 0.13$; interaction term: $P = 0.004$).

Appendix 3

See Table 4.

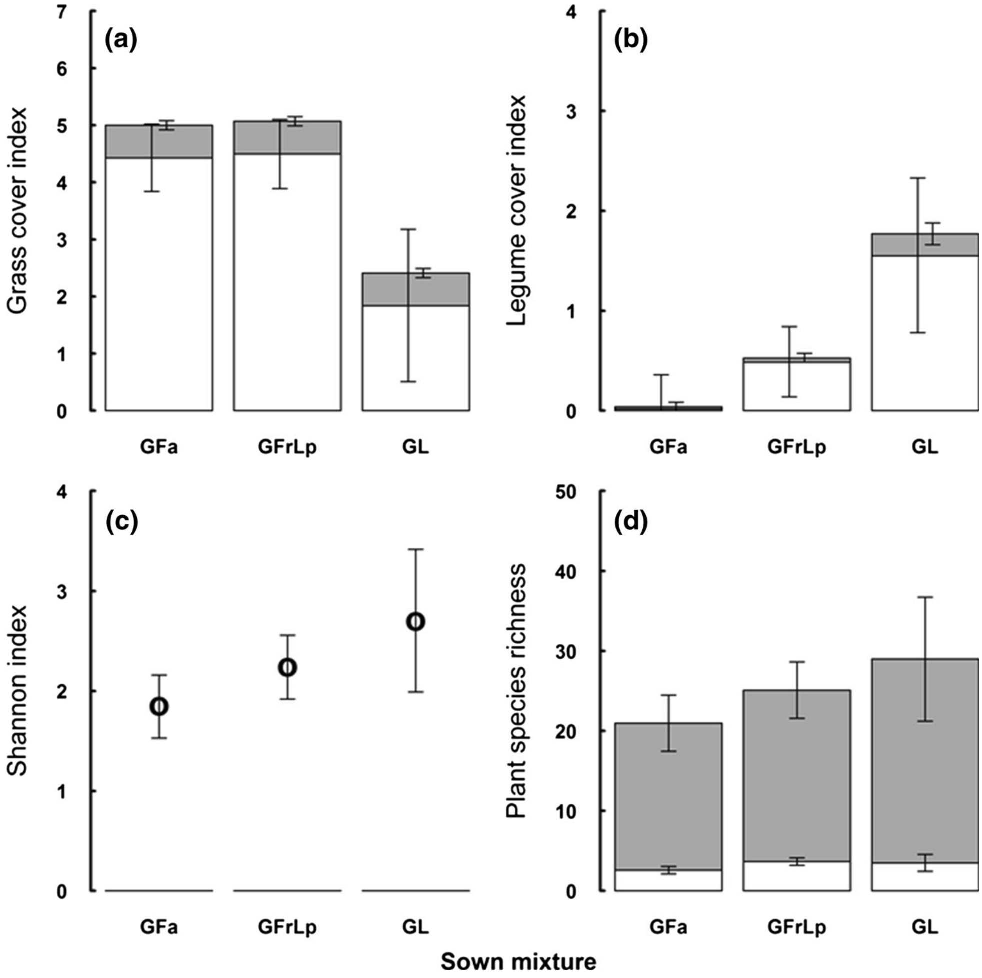

Fig. 4 Predicted mean (±SE) of grass cover index (**a**) and legume cover index (**b**), plant Shannon index (**c**), plant species richness in 2009 (**d**), in sown strips established using three types of sown mixture [GFa: mixture dominated by *F. arundinacea* ($n = 40$), GFrLp: mixture dominated by *F. rubra* and *L. perenne* ($n = 40$), GL: mixture with equal proportion of legumes and grasses ($n = 8$)]. *Bars in white* are sown plant species, and *bars in gray* are weed species

Table 4 Effect of plant communities on grasshopper species-specific abundances in sown margin strips in 2008 and 2009

Term	*C. albomarginatus*		*C. dorsatus*		*E. elegantulus*		*P. giornae*		*P. parallelus*	
	Est. ± SE	*P*	Est. ± SE	*P*	Est. ± SE	*P*	Est. ± SE	*P*	Est. ± SE	*P*
Intercept	–		–		−0.76 ± 0.15	<0.001	−1.30 ± 0.13	<0.001	–	–
Year = 2009	–		–		0.009 ± 0.06	0.95	0.43 ± 0.17	0.01	–	–
PCA_1	–		–		0.008 ± 0.05	0.92	0.16 ± 0.06	0.01	–	–
$I(2009:PCA_1)$	–		–		−0.28 ± 0.02	0.02	–	–	–	–
Intercept	−2.10 ± 0.06	<0.001	−2.03 ± 0.09	<0.001	–	–	–	–	−1.95 ± 0.11	<0.001
Year	–		0.30 ± 0.10	0.009	–	–	–	–	0.32 ± 0.10	0.003
PCA_3	−0.11 ± 0.03	<0.001	−0.13 ± 0.05	0.01	–	–	–	–	−0.005 ± 0.06	0.83
$I(2009:PCA_3)$	–		–		–	–	–	–	−0.29 ± 0.080	0.001
Intercept	–		–		−0.75 ± 0.13	<0.001	−1.33 ± 0.13	<0.001	–	–
Year	–		–		–	–	0.48 ± 0.16	0.005	–	–
PCA_4	–		–		−0.21 ± 0.09	0.03	−0.21 ± 0.08	0.01	–	–
$I(2009:PCA_4)$	–		–		–	–	–	–	–	–

Linear mixed-effect models had the form: $Y = \text{year} + PCA_i + I(\text{year}:PCA_i)$ where PCA_i were the four components (PCA_1, PCA_2, PCA_3 and PCA_4) of PCA conducted on the plant species matrix (Fig. 3)

Grasshopper abundance: logarithm transformation of the number of grasshoppers m^{-2}

Parameter estimates (Est.), standard errors (SE) and *P* of the fixed-effect terms in mixed-effect models

Each parameter is tested marginally, i.e., in the presence of the other terms in the simplified model

The intercept term is the mean of the response variable for sown strips surveyed in 2008

–: Terms excluded during model simplification

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