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Sown grass strip—A stable habitat for grasshoppers (Orthoptera: Acrididae) in dynamic agricultural landscapes

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ABSTRACT

This study assessed the benefits of sown grass strips on grasshopper communities in intensive farmland, and the effects of farming practices and landscape context. Results showed that sown grass strips were high quality habitats for grasshoppers compared to grasslands. Farming practices influenced grasshopper densities in sown grass strips while landscape context affected more the species richness of grasshoppers. Sown mixture and cutting export option were the main factors driving grasshopper density. Mixtures composed of grasses without legumes were the best, as well as hay export compared to no export. Increased grasshopper species richness occurred in sown grass strips located in landscapes with low grassland field availability and high connectivity. Enhanced use of sown grass strips by grasshoppers can be seen as a direct effect of establishment and management options, but also as an effect of the rarity and instability of other grassland habitats in agricultural landscapes.

1. Introduction

Agri-environment schemes (AES) were introduced in Europe in the early 1990s to reduce biodiversity loss in agricultural landscapes by providing financial incentives to farmers for adopting friendly practices mostly at the field scale. Establishment of semi-natural habitats on arable land has been seen as a useful way to promote biodiversity (Benton et al., 2003). Herbicide free field edge strips were initiated in Germany in 1978 to protect native arable flora in crop edges (Frampton and Dorne, 2007) and have been later incorporated as management options within AES (Kleijn and Sutherland, 2003). Since this period, unsprayed crop edges have been implemented in at least 13 European countries (Frampton and Dorne, 2007). In France, 5 m wide strips sown with grasses have been widely established in fields located along watercourses for environmental purposes, primarily to act as buffer strips reducing pesticide drifts and soil erosion (Legifrance.gouv, 2012). Establishment and management requirements on these sown grass strips specified that the vegetation (a grass and/or legume mixture) had to be implemented at least during five years without any ploughing, and had to be cut at least once every year. Fertilizer and pesticide applications were prohibited. Indeed, positive impacts of agri-environment field margin prescriptions on farmland biodiversity were demonstrated using different taxa and species among flora (Marshall et al., 2006) and fauna (Delattre et al., 2010; Fuentes-Montemayor et al., 2011; Marshall et al., 2006).

Grasshoppers are important components of grassland invertebrate assemblages in European agricultural ecosystems (Baldi and Kisbenedek, 1999), particularly as prey for bird species (Barker, 2004). Although precise data are lacking grasshoppers are currently thought to decline in farmland as a consequence of agricultural intensification (Barker, 2004; Vickery et al., 2001). The effects of agricultural practices on grasshoppers have been widely described in grassland ecosystems (Gardiner and Hassall, 2009; Kruess and Tscharntke, 2002; Wingerden et al., 1992) but not in sown grass strips. Indeed, some studies have evaluated the impact of sown grass strip management on the whole herbivore functional group (Noordijk et al., 2010) or on the whole Orthoptera assemblages including both grasshoppers and crickets (Marshall et al., 2006). Sown grass strips may be beneficial to grasshoppers because setting-up and management practices are quite similar to those performed in extensive grasslands, which have been shown to benefit grasshoppers (Wingerden et al., 1992; Marini et al., 2008). Sown grass strip configuration (high perimeter/area ratio) may enhance colonisation. Finally, their location along ditches, streams or rivers could favour species richness by providing wetland habitats favourable to some grasshopper species.

Here, the benefits of sown grass strips and the influence of farming practices and landscape context were assessed at two spatial scales on farmland grasshopper communities in Western France. Grasshopper assemblages in Western France are typical of

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Table 1
Explanatory variables of grasshopper species richness and density grouped according to main factors (same SGS (sown grass strips) surveyed both in 2008 and 2009).

Groups of variables	Explanatory variables	Meaning	Levels or range of values	Number of SGS
Establishment	Sown mixture	Type of sown mixture	GL: quasi-equal mixture of grasses and legumes	4
			GFrLp: grass mixtures with *Festuca rubra* L. and *Lolium perenne* L.	20
			GFa: grass mixtures dominated by *Festuca arundinacea* Schreb.	20
	Age	Number of years since the establishment of the SGS	1–17 year	44
Management practices	Management type	Type of mowing practices	Mown without export of the cuttings	6
			Mown with export of the cuttings	38
Local environment	Watercourse	Type of watercourses along SGS	River or stream	25
			Ditch	14
			No watercourse	5
Landscape context	Grassy paths	Length (m) of grassy paths (<4 m wide) in a 400 m radius of the SGS	58–2549 m	44
	Grassland amount	Proportion of grasslands in a 400 m radius of the SGS	0–40%	44

temperate grasshopper species in that they have only a single generation each year with an obligate egg diapause stage in the soil during winter. Species persistence when local extinctions occur depends thus on re-colonisation from surrounding perennial habitats which serve as overwintering habitats and contain resources for grasshoppers (Kruess and Tscharntke, 2002). By providing new habitats to colonise and source habitats from where to emigrate, as well as paths to connect them, landscape context may be a key in species persistence (Tscharntke and Brandl, 2004). Consequently, three questions were addressed: (1) do grasshoppers benefit from sown grass strips compared to grasslands? (2) which establishment and management practices in sown grass strips have the greatest effect on grasshopper density and species richness? (3) does the landscape context impact grasshopper populations in terms of density and species richness?

2. Material and methods

The study area (46.11°N, 0.28°W) covered 450 km^2 in western France and contained over 18,000 fields of intensive agriculture, mostly dedicated to cereal crop production. Grassland surfaces represented about 10% of the total surface and included legumes (e.g., alfalfa and clover) and grass fields managed by grazing, mowing or set-aside. Since 1995, land use has been annually recorded and mapped onto a Geographical Information System (ArcGis 9.2, ESRI, Redlands, CA, USA) using 42 classes (including 38 crops) to accurately describe land use.

A total of 44 sown grass strips were registered over the study area, representing a quasi-exhaustive design. The same sown grass strips were sampled over a two year period (2008 and 2009). During the same period, an additional design was used to compare grasshopper densities in sown grass strips to those in grassland fields. It consisted in 146 grassland fields in 2008 and 102 grassland fields in 2009 randomly selected each year over the study site among grassland fields. Pure legume grassland fields (alfalfa, clover) were not sampled because no sown grass strip was covered with pure legume.

2.1. Grasshopper surveys

Grasshoppers were sampled by removal–trapping with a one square metre cage sampler (Badenhausser et al., 2009). It was thrown at random ten times within each sown grass strip and grassland field. Badenhausser et al. (2007) showed that this sample size leads to a good precision on mean grasshopper density. All grasshopper adults caught in the sown grass strips were put in alcohol to identify some *Chorthippus*, *Euchorthippus* and *Omocestus* species. Immature individuals were classified into four groups: *Calliptamus* sp., Gomphocerinae sub-family, *Pezotettix giornae* Rossi or “other spp”. In grassland fields, grasshoppers were identified in the field and were classified into the same four groups as for immatures, distinguishing also immature individuals and adults.

The sown grass strips and grassland fields were sampled each year at the beginning of August (over a ten day period) which matched the maximum adult density in the study area (Badenhausser et al., 2009). Vegetation height was measured during the grasshopper surveys.

The mean density of individuals per m^2 was calculated over the ten replicates per sown grass strip or grassland field and was taken as a measure for the abundance of grasshoppers. Grasshopper species richness was described by the number of species per sown grass strip. Species richness did not take into account immature individuals of the Gomphocerinae sub-family. The few sown grass strips in which there were only immature individuals of this group were omitted when calculating species richness.

2.2. Grassland and sown grass strip descriptors

Four groups of qualitative and quantitative variables (establishment and management practices, local environment and landscape context) were chosen in order to account for the grasshopper species richness and density (Table 1). Sown grass strips were described with all variables. Farmers were interviewed about the practices used to establish (age, sown mixture) and manage (type of management) sown grass strips. The local environment was described by the type of watercourse (streams and rivers, ditches, none) directly adjacent to the sown grass strip. Using the GIS database, the landscape context was quantified by the length of grassy paths less than four metre width (range: 58–2549 m) and by the proportion of grassland surfaces (pure or mixed grasses, legume and grass mixtures, alfalfa and clover fields; range: 0–40%) in a radius of 400 m around the sown grass strip. Arable fields were considered non-habitat patches for grasshoppers (Gardiner and Hill, 2004; Marshall et al., 2006). The scale of 400 m was mentioned to approximate dispersal distance of the farmland grasshopper species (Wiesner et al., 2011). Independence between sown grass strip descriptors was checked. Grassland fields were classified only by their age deducted from the GIS database.

2.3. Statistical analyses

Grasshopper species richness and density were analysed with linear-fixed effect models and linear-mixed effect models. Grasshopper frequencies of occurrence were analysed with generalised linear models when densities were too low. In order to match the distributional assumption of linear models, the grasshopper species richness and density were transformed using power transformations following Turchin (2003). Specifically we used theta = 0.5 (species richness, density of *P. giornae*, *Chorthippus parallelus* Zetterstedt, *Chorthippus dorsatus* Zetterstedt) and theta = 0.25 (density of other taxa). All analyses were computed using the R software (R Development Core Team, 2011) (respectively the lm function, nlme library and glm function).

Firstly, the effect of the habitat on grasshopper density and frequency of occurrence was analysed independently in 2008 and in 2009 with linear-fixed effect models and generalised linear models. Explanatory variables were the age of habitat (age in year) and the type of habitat (grassland or sown grass strip) as a fixed effect. First, the most complicated models with the following sequence of fixed effects were fitted: Age + Age^2 + Habitat, plus the interactions between the type of habitat and the age of habitat. Then, models were simplified by removing one-by-one the least significant terms. Parameter estimates (Est.) were compared using successive difference contrasts. Adjusted means of grasshopper densities were calculated. *P* was 0.05 for model selection and parameter significance.

Finally, the effect of landscape context and farming practices were assessed on grasshopper species richness and density. Data were analysed using linear mixed-effect models fit by maximum likelihood. All explanatory variables were independent except the length of grassy paths and the sown mixture (R^2 = 0.13; P = 0.02). For this reason, two competing models with the following sequence of fixed effects were fitted with year included as a fixed effect and sown grass strips nested within year included as random effects: (Model 1) Year + age + age^2 + type of management + type of watercourse + Grassy Paths(400 m) + Grasslands(400 m) + Grasslands(400 m)^2; (Model 2) Year + sown mixture + age + age^2 + type of management + type of watercourse + Grasslands(400 m) + Grasslands(400 m)^2. One-way interaction terms that had a biological meaning and sufficient data in the cells were added to these models. Grassy Paths(400 m) was the cumulated length of small roads and paths less than four metre wide used as a proxy of grassy paths in a radius of 400 m, and Grasslands(400 m) was the proportion of the surfaces of all types of grassland habitats in a radius of 400 m (Table 1). Each of these most complicated models was simplified step-by-step by removing the least significant interaction terms and explanatory variables, using Maximum Likelihood test. Then, the simplified Model 1 was compared to the simplified Model 2 using AIC criteria. Parameters of the best model were estimated using Restricted Maximum Likelihood method. Random effects were tested using a Likelihood ratio test. All quantitative explanatory variables were standardised. For all models, the residuals were inspected for normality, constant mean and variance. *P* was set to 0.10 for model selection due to the low number of replicates in some cells.

3. Results

Comparisons of grasshopper density in grasslands and sown grass strips revealed that grasshopper assemblages in both habitats consisted mostly of Gomphocerinae species and *P. giornae*. In both habitats Gomphocerinae were numerically dominant (grassland fields: 82.2% of the individuals in 2008 and 83.5% in 2009 – sown grass strips: 83.3% of the individuals in 2008 and 74.8% in 2009) while the proportion of *P. giornae* ranged between 12.8% and 23.3% of the individuals (grassland fields: 14.8% in 2008 and 12.8% in 2009 - sown grass strips: 15.5% in 2008 and 23.3% in 2009). Other grasshopper taxa were not abundant in sown grass strips and in grassland fields. The species *Calliptamus italicus* L. was quasi absent in 2008 in both habitats and was observed at very low densities (mean ± SE) in 2009 (0.03 ± 0.01 grasshoppers/m^2 in sown grass strips and in grasslands).

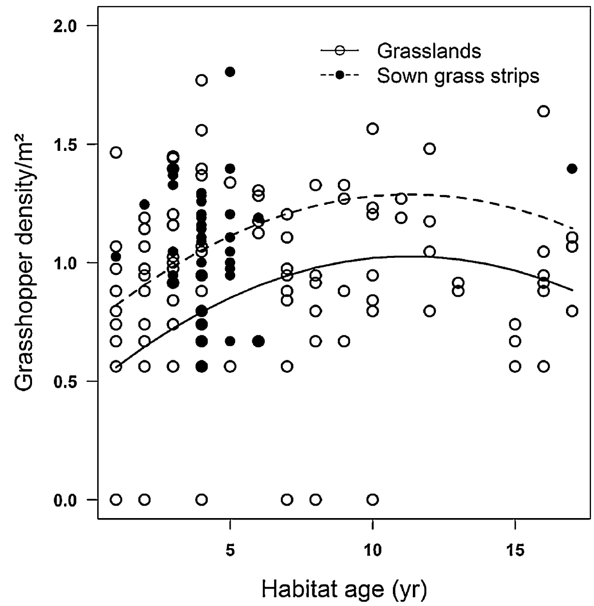

Fig. 1. Observed and predicted effect of habitat age on grasshopper density (transformed data $-\sqrt{\sqrt{x}}$) in sown grass strips and in grassland fields in 2008.

The overall grasshopper abundances in grassland fields at peak density were the same (Appendix A, Table A) in 2008 and 2009 (Year effect in fixed-effect model tested in presence of the age of grassland fields: t = 1.60; P = 0.11) while overall grasshopper abundances in sown grass strips were higher (Appendix A, Table A) in 2009 than in 2008 (Year effect in mixed-effect model: P = 0.01).

Type of habitat impacted grasshopper densities whatever the taxa (Appendix A, Table A; Table 2). Higher overall grasshopper densities and higher Gomphocerinae densities were observed in sown grass strips (Adjusted means (transformed data) ± SE: – all taxa: 1.04 ± 0.06 in 2008 and 1.10 ± 0.07 in 2009 – Gomphocerinae: 1.02 ± 0.07 in 2008 and 0.99 ± 0.06 in 2009) than in grassland fields (all taxa: 0.78 ± 0.03 in 2008 and 0.85 ± 0.04 in 2009 – Gomphocerinae: 0.72 ± 0.03 in 2008 and 0.80 ± 0.04 in 2009). Interestingly, increased grasshopper densities in sown grass strips were attributable to increased adult densities while the densities of immature individuals were the same in sown grass strips and in grassland fields (Appendix A, Table A; Table 2). In both years, the effect of the age of habitat on overall grasshopper density was quadratic (Table 2) increasing during the ten first years and then declining (Fig. 1). Mean age of habitats was quite similar in grassland fields (mean ± SE) (5.18 ± 0.38 year in 2008 and 5.45 ± 0.53 year in 2009) and in the sown grass strips (4.40 ± 0.32 year in 2008 and 5.40 ± 0.32 year in 2009). However, frequency distributions of habitat ages were quite different in sown grass strips and in grassland fields. Most of grassland fields were

Table 2
Effects of the age and type of habitat (sown grass strip (SGS) or grassland field) on grasshopper density (total and Gomphocerinae), and on the frequency of occurrence of *P. giornae*.

Year	Term	Total grasshopper abundance		Gomphocerinae abundance						*P. giornae* frequency of occurrence	
				Immature individuals		Adults		Total			
		Est. ± SE	*P*	Est. ± SE	*P*	Est. ± SE	*P*	Est. ± SE	*P*	Est. ± SE	*P*
2008	Intercept	0.46 ± 0.07	<0.001	0.30 ± 0.07	<0.001	0.18 ± 0.07	0.013	0.39 ± 0.07	<0.001	−1.42 ± 0.29	<0.001
	Age	0.10 ± 0.02	<0.001	0.09 ± 0.02	<0.001	0.11 ± 0.02	<0.001	0.11 ± 0.02	<0.001	0.16 ± 0.04	<0.001
	Age^2	−0.01 ± 0.01	0.002	−0.01 ± 0.01	0.003	−0.01 ± 0.01	<0.001	−0.01 ± 0.01	<0.001	–	–
	SGS	0.26 ± 0.07	<0.001	–	–	1.13 ± 0.32	0.001	0.91 ± 0.33	0.006	1.62 ± 0.38	<0.001
	I(SGS:Age)	–	–	–	–	−0.26 ± 0.10	0.010	−0.22 ± 0.10	0.027	–	–
	I(SGS:Age^2)	–	–	–	–	0.01 ± 0.01	0.007	0.01 ± 0.01	0.025	–	–
2009	Intercept	0.65 ± 0.08	<0.001	0.33 ± 0.08	<0.001	0.62 ± 0.04	<0.001	0.60 ± 0.08	<0.001	−0.44 ± 0.20	0.031
	Age	0.07 ± 0.03	0.017	0.07 ± 0.03	0.012	–	–	0.07 ± 0.03	0.017	–	–
	Age^2	−0.01 ± 0.01	0.033	−0.01 ± 0.01	0.029	–	–	−0.01 ± 0.01	0.034	–	–
	SGS	0.24 ± 0.09	0.004	–	–	0.34 ± 0.08	<0.001	0.19 ± 0.08	0.023	2.23 ± 0.48	<0.001
	I(SGS:Age)	–	–	–	–	–	–	–	–	–	–
	I(SGS:Age^2)	–	–	–	–	–	–	–	–	–	–

Parameter estimates (Est.), standard errors (SE) and *P* of the fixed-effects terms in fixed-effects models with total grasshopper density and Gomphocerinae density (immature individuals, adults and total) (double square transformation of the number of grasshoppers/m^2); Each parameter is tested marginally, i.e. in presence of all other terms in the simplified model; The intercept term is the mean of the response variable for grassland habitat. –, Term excluded during model simplification.

one or two year old in 2008 (38%) and 2009 (37%) while this age category represented only 5% of sown grass strips in 2008 and 2% in 2009. Frequency of *P. giornae* occurrence (Table 2) was higher in sown grass strips (2008: 70%; 2009: 86%) than in grasslands (2008: 36%; 2009: 39%) in the two years and increased with habitat age. Vegetation height at sampling date did not differ between both habitats (mean ± SE) (sown grass strips, 2008: 26.1 ± 2.5 cm; 2009: 18.5 ± 2.6 cm–grassland fields, 2008: 31.5 ± 1.7 cm; 2009: 23.3 ± 2.3 cm).

3.1. Drivers of grasshopper species richness

A total of 12 and 13 grasshopper species were recorded in sown grass strips in 2008 and 2009 respectively (14 species in total). Among them, two species dominated grasshopper assemblages (Appendix A, Fig. A): *Euchorthippus elegantulus* Zeuner, a Gomphocerinae species, and *P. giornae*. Two other Gomphocerinae species were well represented, i.e., *C. parallelus* and *C. dorsatus*, especially in 2009. Some other Gomphocerinae species were observed frequently but not in high densities like *Chorthippus albomarginatus* De Geer, *Chorthippus biguttulus* L., *Euchorthippus declivus* Brisout and *Omocestus rufipes* Zetterstedt, while some species were observed only once with few individuals (e.g., *Gomphocerippus rufus* L., *Chorthippus brunneus* Thunberg, *Chorthippus mollis* Charpentier). Rare individuals of the Tetrigidae family and *Aiolopus thalassinus* F. were recorded.

Species richness was significantly higher in 2009 than in 2008 (mean ± SE), 4.47 ± 0.29 against 3.16 ± 0.23 (year effect in linear-mixed effect model: $P < 0.001$; Table 3). Grasshopper species richness was significantly influenced by the landscape context 400 m around the sown grass strip (Table 3). Indeed, Model 1 which was the best model showed that the length of grassy paths had a significant positive and linear effect whereas the grassland proportion around sown grass strips had a significant negative effect. The length of grassy paths and grassland proportion were not correlated ($R^2 = 0.05$; $P = 0.12$). Sown grass strip establishment nearby a river and in a lesser extent nearby a ditch, had an adverse effect on grasshopper species richness when sown grass strips were managed without export of the cuttings, while it had no effect when managed with export of the cuttings (Table 3; Fig. 2). Establishment variables did not affect the species richness of grasshoppers (Table 3).

3.2. Drivers of grasshopper density

The overall grasshopper densities in sown grass strips increased with grasshopper species richness (2008: $R^2 = 0.38$; $P < 0.001$–2009: $R^2 = 0.58$; $P < 0.001$). Higher overall grasshopper abundance in 2009 than in 2008 was mainly due to Gomphocerinae and *P. giornae* (Table 4). This was not the case for the dominant species *E. elegantulus* (year effect in linear-mixed effect model: $P = 0.59$).

Overall grasshopper densities were only explained by sown mixture (Fig. 3A; Table 4) and by management type (Fig. 3B; Table 4). Landscape explanatory variables were not significant in both Models 1 and 2. Grasshopper density decreased with the presence of legumes in the sown mixture and when cuttings were not exported. These results reflected the responses of Gomphocerinae (Fig. 3B; Table 4). Among them, the dominant species *E. elegantulus* had a similar response to sown mixture (Sown mixture effect in linear-mixed effect model: $P = 0.02$), and management type (Management effect in linear-mixed effect model: $P = 0.04$). Less frequent

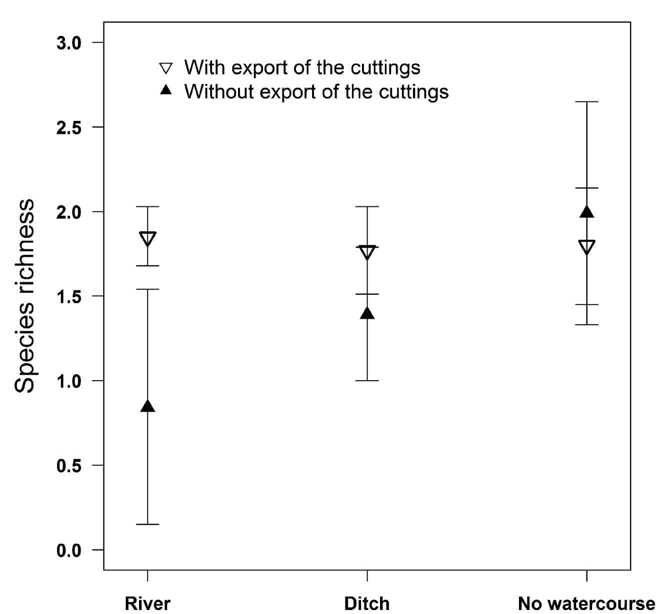

Fig. 2. Grasshopper species richness (transformed data $-\sqrt{x}$) in sown grass strips according to cutting export options and nearby watercourse.

Table 3
Effects of farming practices and landscape context (Table 1) on the species richness of grasshoppers in sown grass strips (Model 1 was selected).

Term	Grasshopper species richness	
	Est. ± SE	*P*
Intercept	0.85[a] ± 0.34	0.01
Year = 2009	0.36 ± 0.09	<0.001
Age	–	–
Age^2	–	–
Management Type = with export	1.01 ± 0.34	0.005
Watercourse = ditch	0.55 ± 0.36	0.14
Watercourse = no watercourse	1.14 ± 0.48	0.02
Grassy paths	0.29 ± 0.12	0.02
Grassland amount	−0.10 ± 0.12	0.43
(Grassland amount)^2	−0.28 ± 0.16	0.09
I(Management Type = with export: Watercourse = ditch)	−0.64 ± 0.38	0.10
I(Management Type = with export: no watercourse)	−1.20 ± 0.50	0.02

Grasshopper species richness: square transformation of the number of species; Parameter estimates (Est.), standard errors (SE) and *P* of the fixed-effects terms in mixed-effects models; Each parameter is tested marginally, i.e. in presence of all other terms in the simplified model. –, Terms excluded during model simplification; only significant interaction terms are shown.

[a] The intercept term is the mean of the response variable for sown grass strips surveyed in 2008, managed without export of the cuttings and adjacent to a river.

species in Gomphocerinae sub-family such as *C. parallelus* and *C. dorsatus* showed different responses to landscape and establishment variables. *C. dorsatus* density was only significantly explained by the sown mixture (sown mixture effect in linear-mixed effect model: $P = 0.01$), mixture containing *F. rubra* and *L. perenne* (GFrLp) being preferred to mixture dominated by *F. arundinacea* (GFa) or grass–legume mixture (GL). At the opposite, none of farming practices influenced the *C. parallelus* density which was only and slightly influenced by the length of grassy paths (Est. = 0.17 ± 0.09; $P = 0.06$).

P. giornae density was higher in sown grass strips established with sown mixture containing *F. rubra* and *L. perenne* than legumes or *F. arundinacea* (Fig. 3C; Table 4). The density of *P. giornae* increased with the age of sown grass strips. Management type did not affect *P. giornae* density (Table 4). Landscape context at the two spatial scales influenced *P. giornae* density which was higher when sown grass strips were adjacent to a river (Fig. 3D; Table 4) and decreased as grassland proportion in the landscape increased (Table 4).

4. Discussion

Grasshopper densities were about twice higher in sown grass strips than in grassland fields due to higher densities of the dominant taxa in both habitats (Gomphocerinae and in a lesser extend *P. giornae*). Higher Gomphocerinae densities resulted from higher adult densities and not from immature individuals, and could be explained by several processes. Firstly, grasshopper fitness and developmental rates could be higher in sown grass strips due to higher habitat quality and heterogeneity (Wingerden et al., 1992; Guido and Gianelle, 2001) which were mainly determined by farming practices. Secondly, balance between immigration and emigration could vary between both habitats due to differences in habitat geometry (area and perimeter) which has been shown to be involved in dispersal processes (Tscharntke and Brandl, 2004). Sown grass strips could act as corridors during dispersal processes as shown for *Maniola jurtina* L. (Delattre et al., 2010). Indeed, greater rates of movement in adults than in immature individuals were demonstrated in Gomphocerinae (Gardiner, 2009). Lastly, avian predation of grasshoppers could be smaller in sown grass strips than in grassland fields due to higher vegetation height in sown grass strips which reduced the accessibility for birds to eat insects (Douglas et al., 2009). However, this hypothesis did not hold in our study because mowing occurred at the same time in both habitats and vegetation height did not differ.

4.1. Effect of farming practices

Grasshopper density varied according to farming practices while grasshopper species richness was poorly explained by these practices.

Table 4
Effect of farming practices and landscape context (Table 1) on grasshopper densities (total, Gomphocerinae and *P. giornae*) in sown grass strips (Model 2 was selected for each taxa).

Term	Total grasshopper density		Gomphocerinae density		*P. giornae* density	
	Est. ± SE	*P*	Est. ± SE	*P*	Est. ± SE	*P*
Intercept	0.82[a] ± 0.10	<0.001	0.98[b] ± 0.05	<0.001	0.42[c] ± 0.10	<0.001
Year = 2009	0.11 ± 0.04	0.01	0.09 ± 0.04	0.04	0.19 ± 0.07	0.02
Sown mixture = GFrLp	0.04 ± 0.07	0.54	0.04 ± 0.07	0.58	0.20 ± 0.08	0.02
Sown mixture = GL	−0.33 ± 0.13	0.01	−0.61 ± 0.13	<0.001	0.01 ± 0.15	0.92
Age	–	–	–	–	0.19 ± 0.08	0.04
Age^2	–	–	–	–	–	–
Management type= with export	0.25 ± 0.10	0.02	–	–	–	–
Watercourse = ditch	–	–	–	–	−0.24 ± 0.08	0.009
Watercourse = no watercourse	–	–	–	–	−0.20 ± 0.12	0.11
Grassland amount	–	–	–	–	−0.23 ± 0.08	0.007
(Grassland amount)^2	–	–	–	–	–	–

All grasshopper taxa and Gomphocerinae: double square root transformation of the number of grasshoppers/m^2; *P. giornae*: square root transformation of the number of individuals/m^2; Parameter estimates (Est.), standard errors (SE) and *P* of the fixed-effects terms in mixed-effects models; Each parameter is tested marginally, i.e. in presence of all other terms in the simplified model. –, Terms excluded during model simplification; Interaction terms were not significant.

[a] The intercept term is the mean of the response variable for sown grass strips surveyed in 2008, managed without export of the cuttings and sown with GFa mixture.

[b] The intercept term is the mean of the response variable for sown grass strips surveyed in 2008, sown with GFa mixture.

[c] The intercept term is the mean of the response variable for sown grass strips surveyed in 2008, sown with GFa mixture and adjacent to a river.

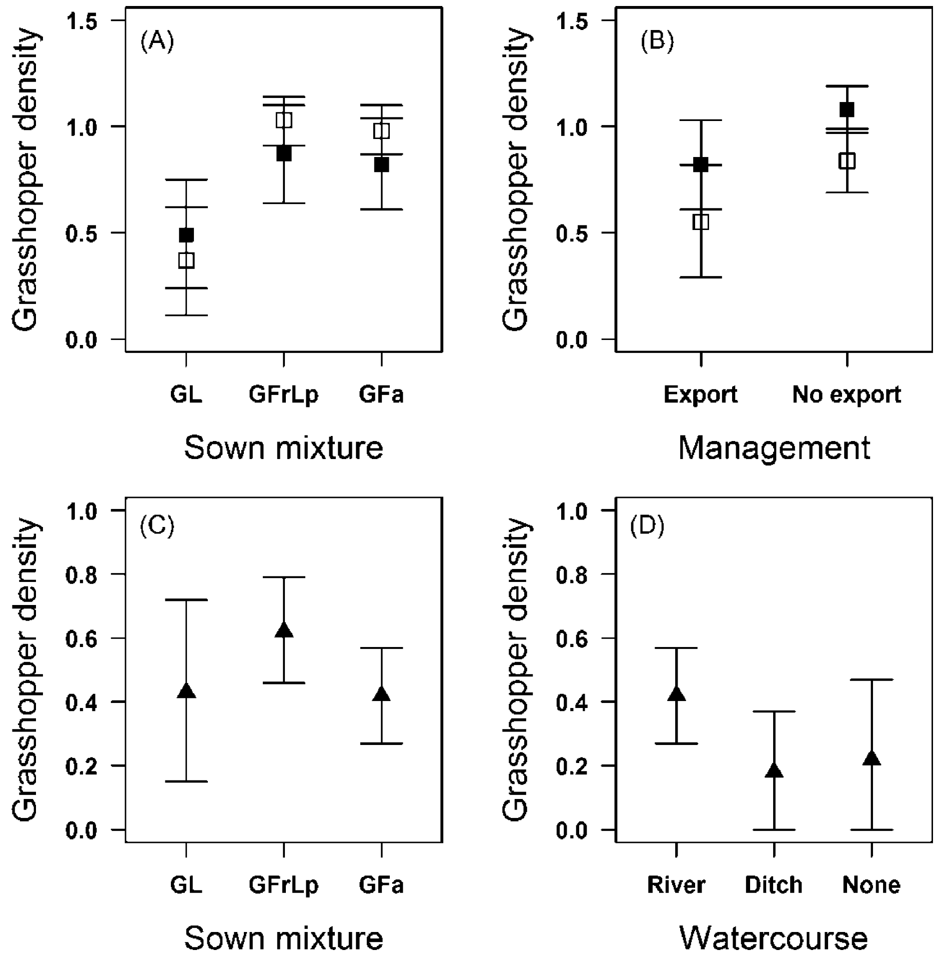

Fig. 3. Effects of (A) sown mixture and (B) cutting export options on grasshopper density (transformed data $-\sqrt{\sqrt{x}}$) in sown grass strips: all species (black square) and Gomphocerinae (empty square). Effects of (C) sown mixture and (D) type of watercourse on *P. giornae* (black triangle) density (transformed data $-\sqrt{x}$).

The sown mixture was the main factor explaining grasshopper densities. The sown mixture could significantly affect the spontaneous flora (Cordeau et al., 2010) or not (Critchley et al., 2006), considering that age tended to overwhelm the effect of the sown mixture (De Cauwer et al., 2005) especially where there was little management (Haaland et al., 2011). Gomphocerinae (e.g. *E. elegantulus*) performed better in grass-dominant mixtures than in mixtures containing legumes. Gomphocerinae taxa (e.g., genus *Chorthippus* and *Euchorthippus)* were known to be grass-feeders (Bernays and Chapman, 1970). However, some other Gomphocerinae species such as *C. parallelus* and *C. dorsatus* were not affected by the presence of legumes as also observed by Unsicker et al. (2008) for these species.

Habitat age did not affect grasshopper species richness. This result did not contradict previous studies (Gardiner and Hill, 2004; Denys and Tscharntke, 2002) showing a decrease in species richness five years after margin establishment because most of our sown grass strips were younger than six year old. Habitat age influenced grasshopper density in both habitats, depending on grasshopper taxa. The relationship was quadratic when considering all taxa and linear for the wingless species *P. giornae*. A quadratic relationship has also been observed by Noordijk et al. (2010) who showed that herbivore densities increased during the first three years of margin establishment, then stabilised and declined after eight years. Habitat age effects can be direct or mediated through their effect on vegetation composition (Cordeau et al., 2010) and structure, and through their effect on the whole invertebrate community, as shown by Denys and Tscharntke (2002) who demonstrated higher predator–prey ratios in old grassy margins.

Hay export increased species richness and overall grasshopper density compared to no export of the cuttings. Reductions in grasshopper density due to the direct impact of mowing has been demonstrated to vary a lot depending on grasshopper species (Gardiner and Hassall, 2009; Humbert et al., 2010) and on many factors such as the number of mowing operations per year (Gardiner, 2009), the mowing techniques and the speed at which the tractor move across the field (Humbert et al., 2010), and the grasshopper developmental stage during mowing (Gardiner and Hassall, 2009). No removal of the cutting could have led to cooler environments with possible negative effects on the most thermophilous species such as *E. elegantulus* (Wingerden et al., 1992) while removal of the cuttings created high sward temperatures (Gardiner and Hassall, 2009) which benefited to this species and had negative effects on less thermophilous species such as *C. parallelus* (Gardiner and Hill, 2004).

4.2. Effect of landscape context

Conversely to what was expected from higher habitat diversity (Marini et al., 2010), privileged location of sown grass strips along watercourses did not enhance the species richness of grasshoppers, as shown by the adverse effect of a nearby river on grasshopper species richness especially when sown grass strips were cut without export of the cuttings.

Landscape context within 400 m of the sown grass strips explained grasshopper species richness, while it did not impact significantly overall grasshopper densities whose response lagged behind the changes in species richness, as shown by the positive correlation between these two variables. Haaland et al. (2011) also highlighted the impact of landscape context on insect species diversity in sown wildflower strips. In our study, the most significant results involved positive effects of landscape connectivity described by a proxy of the length of boundaries with grassy vegetation and secondarily, negative effects of landscape composition in grassland habitats. Concepcion et al. (2008) also observed that grasshopper species richness was influenced by landscape connectivity, but negatively. However, landscape connectivity in Concepcion et al. (2008) was described by different metrics than ours and influenced the species richness of grasshoppers depending on the regional landscape complexity, i.e., only in landscapes with intermediate complexity. Positive effect of landscape connectivity on grasshopper species diversity suggested that grassy paths and sown grass strips were efficient to connect a variety of habitats (Guido and Gianelle, 2001). The negative effects of the proportion of grassland in the surrounding landscape on grasshopper species richness was also established by Marini et al. (2008, 2010) who suggested an enhanced mortality due to mowing of large areas. High habitat availability could also result in a less investment in dispersal-related traits in grasshoppers (Tscharntke and Brandl, 2004), and thus in less dispersal from surrounding grasslands. Lastly, higher habitat availability might have increased the probability for grasshoppers during dispersal to reach a grassland habitat before a sown grass strip which had smaller area (Tscharntke and Brandl, 2004; Marini et al., 2010) and was scarce in the landscape.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2012.06.017.

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