

# Spatial Autocorrelation in Farmland Grasshopper Assemblages (Orthoptera: Acrididae) in Western France

I. BADENHAUSSER,<sup>1,2,3\*</sup> M. GOUAT,<sup>1,2\*</sup> A. GOARANT,<sup>1</sup> T. CORNULIER,<sup>1</sup> AND V. BRETAGNOLLE<sup>1</sup>

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**ABSTRACT** Agricultural intensification in western Europe has caused a dramatic loss of grassland surfaces in farmlands, which have resulted in strong declines in grassland invertebrates, leading to cascade effects at higher trophic levels among consumers of invertebrates. Grasshoppers are important components of grassland invertebrate assemblages in European agricultural ecosystems, particularly as prey for bird species. Understanding how grasshopper populations are distributed in fragmented landscapes with low grassland availability is critical for both studies in biodiversity conservation and insect management. We assessed the range and strength of spatial autocorrelation for two grasshopper taxa (Gomphocerinae subfamily and *Calliptamus italicus* L.) across an intensive farmland in western France. Data from surveys carried out over 8 yr in 1,715 grassland fields were analyzed using geostatistics. Weak spatial patterns were observed at small spatial scales, suggesting important local effects of management practices on grasshopper densities. Spatial autocorrelation patterns for both grasshopper taxa were only detected at intermediate scales. For Gomphocerinae, the range of spatial autocorrelation varied from 802 to 2,613 m according to the year, depending both on grasshopper density and on grassland surfaces in the study site, whereas spatial patterns for the Italian locust were more variable and not related to grasshopper density or grassland surfaces. Spatial patterns in the distribution of Gomphocerinae supported our hypothesis that habitat availability was a major driver of grasshopper distribution in the landscape, and suggested it was related to density-dependent processes such as dispersal.

**KEY WORDS** geostatistics, dispersal, spatial pattern, Italian locust, Gomphocerinae

Agricultural intensification currently is considered a major driver of European biodiversity loss (Benton et al. 2003). Intensification of farming practices at the field scale involves high usage of pesticides and fertilizers, short crop-rotations and frequent mechanical disturbances reducing the suitability of agricultural fields for a wide range of organisms. At the landscape scale, intensification has caused the substitution of most natural or seminatural habitats for arable fields or improved grasslands generally managed to ensure maximal yields of forage. As a result, swards tend to be dominated by one or two cultivated species with high plant densities, frequently cut or grazed and replaced a few years after establishment (Chamberlain et al. 2000). These swards are often of little wildlife interest (Wilson et al. 1999) especially for invertebrates (Di Giulio et al. 2001, Gardiner 2009). Loss of grassland habitats associated with the deterioration of habitat quality have resulted in strong declines in European

grassland invertebrates (Barker 2004) leading to cascade effects at higher trophic levels among consumers of invertebrates (Vickery et al. 2001). Grasshoppers are important components of grassland invertebrate assemblages in European agricultural ecosystems, particularly as prey for bird species (Barker 2004). Although precise data are lacking, grasshoppers are currently thought to be in decline in farmlands as a consequence of agricultural intensification (Vickery et al. 2001, Barker 2004).

Grasshopper assemblages in western France are typical of temperate grasshopper species in that they have only a single generation each year (Richards et al. 1954) with an obligate egg diapause stage in the soil during winter. Therefore, plowing for crop establishment leads to local extinctions that may be counteracted by recolonization from surrounding grassland habitats (Kruess and Tscharnkte 2002). By providing new habitats to colonize and source habitats from where to emigrate, as well as paths to connect them, landscape quality and connectivity could have important consequences for grasshopper spatial distribution and may ultimately affect, along with species dispersal behavior and ability, species persistence (Tscharnkte and Brandl 2004, Gardiner 2009). Grasshopper assemblages in farmlands in western France mainly are composed of species of Gomphocerinae (Acrididae): *Pe-*

<sup>1</sup> Centre d'Etudes Biologiques de Chizé, CNRS, UPR 1934, F-79360 Beauvoir sur Niort, France.

<sup>2</sup> INRA, USC 1339, Centre d'Etudes Biologiques de Chizé, F-79360 Beauvoir sur Niort, France.

<sup>3</sup> Corresponding author: Badenhauer, INRA, USC CEBC, Villiers en Bois, F-79360 Beauvoir sur Niort, France (e-mail: badenh@cebc.cnrs.fr).

\* Badenhauer and Gouat contributed equally to this work.

*zotettix giornae* Rossi (Acrididae: Catantopinae), a wingless grasshopper; and *Calliptamus italicus* L. (Acrididae: Calliptaminae), a locust hopper (Voisin 2003, Badenhauer et al. 2009). Dispersal in these species comprises essentially localized flights and walking activities (Uvarov 1977) leading to overall limited movement compared with other insects (Reinhardt et al. 2005), and must be separated from migration (i.e., long-distance movement that occurs during the gregarious phases in the locust species *C. italicus*). This is seldom observed in western France where populations of this locust are maintained at low densities in solitary phase (Uvarov 1977, Louveaux et al. 1988).

Understanding how grasshopper populations persist in fragmented landscapes with low grassland availability is critical for both studies in biodiversity conservation and insect management, and requires large-scale and long-term monitoring programs. Landscape-scale distribution data are difficult to analyze because of the spatial structure of the data. Indeed, sampling points are distributed over space, which possibly induces spatial dependency (i.e., spatial autocorrelation between pairs of points). Spatial autocorrelation can be defined as the property of random variables taking values at pairs of locations a certain distance apart; values could be more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected for randomly associated pairs of observations (Legendre 1993). One part of spatial dependency in ecological data is because of the effects of measured or unmeasured environmental variables, such as temperature, rainfall, or altitude, that are themselves spatially structured and related with species abundance. Another part comes from biological processes (Begueria and Pueyo 2009) such as extinction, competition, dispersion, or species interactions (Dormann et al. 2007, Bahn et al. 2008). Among ecological processes, dispersal limitation is thought to be the major cause of spatial autocorrelation in animal distributions (Dormann et al. 2007, Bahn et al. 2008). Spatial autocorrelation represents an opportunity to obtain relevant information about the spatial structure of populations and to infer ecological process from pattern (Palma et al. 1999). Quantitative statements about spatial patterns and methods for incorporating spatial autocorrelation in data analysis may be achieved by using the semivariogram, a standard tool in geostatistics (Dormann et al. 2007) that measures the semivariance between pairs of points as a function of distance between them (Wackernagel 1995).

We applied a geostatistical approach to analyze a large data set to provide quantitative statements about the range and strength of spatial autocorrelation in grasshopper distribution across a 450-km<sup>2</sup> intensive agricultural landscape in western France. Our main postulate was that spatial autocorrelation in grasshopper distribution in the landscape and its temporal variations resulted mainly from dispersal processes. Because of their relatively limited dispersal abilities and to low grassland habitat availability in the study site, we expected grasshopper species to be con-

strained by habitat distribution and hence to have clustered distributions in the landscape resulting in strong and short range spatial autocorrelation. We also expected spatial autocorrelation to decrease in strength and increase in range as grasshopper density increased because of the importance of density-dependent processes in grasshoppers (Uvarov 1977, Applebaum and Heifetz 1999) and distance of movement (Narisu et al. 1999, Gardiner and Hill 2004). Consequently, we addressed the following questions: 1) Does spatial autocorrelation exist in grasshopper populations, and what is its strength and at what scale does it occur? 2) Does spatial autocorrelation vary between years and between grasshopper taxa? and 3) Is spatial autocorrelation correlated with population density and with habitat availability? We used data from a collection of surveys carried out over 8 yr in 1,715 grassland fields. To pool data from different sampling schemes, we used a generalized additive model (GAM) and a geostatistical approach called "the two-point declustering" method (Richmond 2002) to correct for the spatial heterogeneity in sampling intensity.

## Materials and Methods

**Study Area and Habitat Availability.** The study area "Zone Atelier Plaine et Val de Sèvre" (46.11° N, 0.28° W, Fig. 1) covers ≈450 km<sup>2</sup> in western France and contains >18,000 fields of intensive agriculture, mostly dedicated to cereal crop production. Since 1995, land use in all fields has been recorded annually and mapped using ArcGis 9.2 (ESRI 2006) by using 42 classes to accurately describe land use. Grassland surfaces represent ≈10% of the total surface and include artificial grasslands (95% of alfalfa and 5% of clover), and other grasslands (temporary or permanent, sown with grasses, or resulting from spontaneous flora) (Huyghe 2005) managed by grazing, mowing, or abandoned. For simplicity, we refer to artificial grassland fields as alfalfa fields and other grasslands as meadows. Across the 8 yr of our study, the mean ± SD field size was 1.52 ± 1.61 ha for meadows, 2.21 ± 2.01 ha for alfalfa fields, and 3.48 ± 3.41 ha for all other fields (sunflower, maize, wheat, rapeseed).

Grasshoppers are exclusively herbivorous and tend to feed on grasses in preference to herbs (Richard et al. 1954), but the opposite also is observed in some species. Therefore, we described annual habitat availability by distinguishing between alfalfa fields and meadows irrespective of their prior management practices (such a grazing or mowing), which we could not ascertain. We calculated the proportion of land covered with alfalfa fields and with meadows, and the average distance between habitats by using the 10 closest fields of the same type of habitat for each targeted habitat (alfalfa fields, meadows).

**Sampling Schemes.** We used data from four different sampling schemes conducted between 2003 and 2010 that shared the same sampling method but differed in the type of grasslands targeted, the procedure used to select the fields within the study site, the

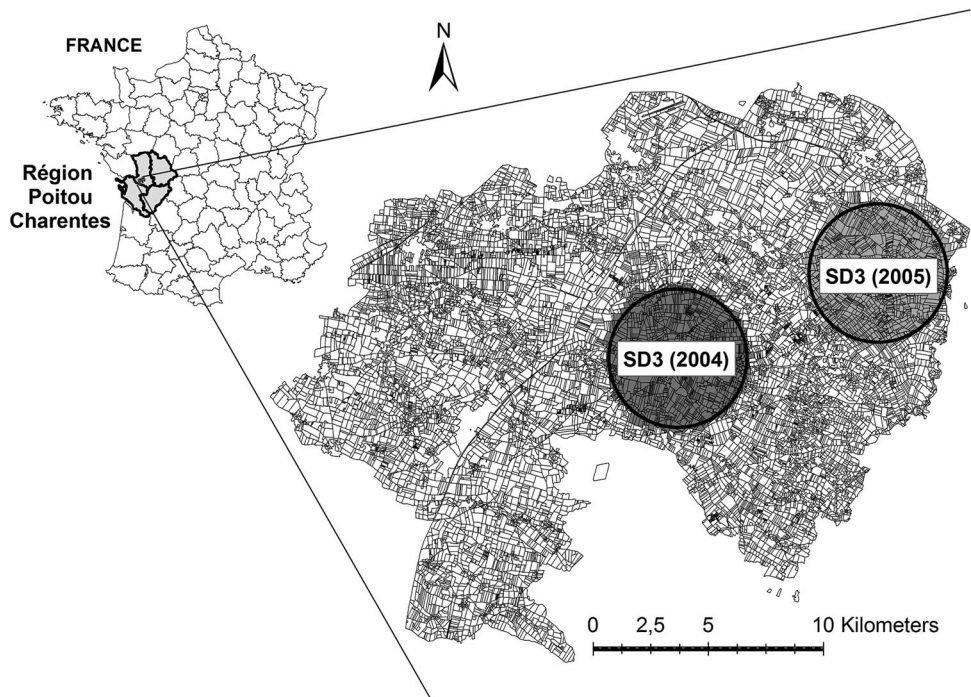


Fig. 1. Study site “Zone Atelier Plaine et Val de Sèvre” and location of the areas delineated for the SD3 sampling scheme in 2004 and 2005.

sample size, and the sampling date (Table 1). The sampling schemes had four different goals. Sampling design 1 (SD1) was established to estimate the average annual grasshopper density in grasslands (all types) throughout the study site at peak adult density; each year, grasslands were randomly selected in the study site. Sampling design 2 (SD2) was used to investigate the seasonal dynamics of grasshopper species in grass-

Table 1. Number of grassland fields sampled (alfalfa fields in parenthesis), sampling schemes, and sampling period							
Year	Sampling scheme	Number of fields	Sampling period	Gomphocerinae		<i>Calliptamus italicus</i>	
				d/m <sup>2</sup> (SE)	P	d/m <sup>2</sup> (SE)	P
2003	SD1	96 (12)	10–24 July	2.55 (0.35)	0.95	0.34 (0.06)	0.58
	SD2	6 (2)	26–29 July	3.60 (1.87)	1	0.45 (0.24)	0.83
	Total	102 (14)	10–24 July	2.59 (0.35)	0.95	0.35 (0.05)	0.60
2004	SD1	101 (24)	12–26 July	7.65 (1.11)	0.93	0.44 (0.08)	0.58
	SD2	11 (3)	24–26 July	9.79 (4.78)	1	3.10 (1.79)	0.82
	SD3	171 (52)	19 July–5 Aug.	4.66 (0.60)	0.92	0.27 (0.06)	0.53
2005	Total	283 (79)	12 July–5 Aug.	5.95 (0.59)	0.93	0.43 (0.08)	0.57
	SD1	100 (24)	24–31 July	3.39 (0.46)	0.98	0.26 (0.09)	0.58
	SD2	8 (1)	31 July–3 Aug.	4.81 (2.45)	1	0.51 (0.14)	0.88
2006	SD3	139 (61)	26 July–8 Aug.	1.23 (0.17)	0.92	0.24 (0.04)	0.55
	Total	247 (86)	24 July–8 Aug.	2.25 (0.23)	0.94	0.25 (0.04)	0.57
	SD1	98 (26)	22–30 July	3.76 (0.72)	0.92	0.53 (0.09)	0.67
2007	SD2	11 (3)	24–26 July	5.27 (1.71)	1	1.31 (0.55)	0.91
	SD4	28 (28)	4–8 Aug.	0.77 (0.16)	0.85	0.62 (0.16)	0.92
	Total	137 (57)	22 July–8 Aug.	3.28 (0.54)	0.93	0.62 (0.09)	0.75
2008	SD1	179 (43)	23 July–1 Aug.	1.33 (0.17)	0.78	0.11 (0.04)	0.25
	SD2	9 (2)	29 July	2.84 (0.87)	0.55	0.05 (0.02)	0.22
	SD4	44 (44)	31 July–2 Aug.	0.03 (0.01)	0.27	0.01 (0.01)	0.07
2009	Total	232 (89)	23 July–2 Aug.	1.14 (0.14)	0.69	0.09 (0.03)	0.23
	SD1	221 (48)	27 July–5 Aug.	0.64 (0.07)	0.68	0.02 (0.01)	0.07
	SD2	11 (3)	3 Aug.	0.81 (0.36)	0.82	0.08 (0.04)	0.27
2010	Total	232 (51)	27 July–6 Aug.	0.65 (0.07)	0.69	0.02 (0.00)	0.08
	SD1	234 (68)	17 July–5 Aug.	1.27 (0.20)	0.80	0.06 (0.01)	0.21
	SD1	248 (97)	26 July–12 Aug.	2.22 (0.27)	0.89	0.13 (0.03)	0.36

The mean and standard error (SE) of grasshopper density (“d” equals number of grasshoppers/m<sup>2</sup>) are reported. The frequency of occurrence (P) is the percentage of fields where the grasshopper taxa was recorded.

lands. From 2003 to 2007, grasslands were randomly chosen among those located <10 km away from the laboratory for logistical efficiency; grasshopper populations were monitored every 2 wk from mid-May (egg hatching) to the end of October (adult death). Sampling design 3 (SD3) was designed to investigate the effect of the local neighborhood on grasshopper density in grasslands; in 2004 and 2005, we defined for each year a different circular area (3-km radius) for which center was randomly chosen (Fig. 1). Grasshopper populations were monitored in all grasslands contained in the area. Sampling design 4 (SD4) was established to investigate the effect of farming practices on grasshopper density by sampling over a gradient of forage yields in alfalfa fields in 2006 and 2007. On average, 214 grassland fields ( $\pm 62$ ) were sampled every year from 2003 to 2010, resulting in an overall total of 1,715 grasslands, including 548 alfalfa fields and 1,167 meadows.

**Grasshopper Surveys.** For a given year, all surveys were performed within 3 wk. In sampling scheme SD1, grasshopper sampling period matched peak adult density at the beginning of August (Badenhausser et al. 2009). In SD2, data were extracted at the sampling date closest to that of the scheme SD1. SD3 and SD4 were conducted as soon as SD1 was completed. Grasshoppers were sampled by means of trapping with a 1-m<sup>2</sup> square cage sampler (Badenhausser et al. 2009). It was thrown haphazardly within each grassland 10 times (15 times in SD2 and SD4) (Badenhausser et al. 2007). All grasshoppers caught in the cage sampler were counted in the field and classified into four groups: Gomphocerinae subfamily, among which the two species *Euchorthippus elegantulus* Zeuner and *Chorthippus biguttulus* L. dominated over the 8 yr (Badenhausser et al. 2009); *C. italicus*; and *P. giornae* and all other species, distinguishing also nymphs and adults. This classification was chosen because a more precise identification is impossible for grasshopper nymphs, and is difficult in the field for adults belonging to Gomphocerinae assemblages composed of morphologically similar species. This is especially the case of species such as *Chorthippus albomarginatus* De Geer; *E. elegantulus*; *Euchorthippus declivus* Brisout; and *C. biguttulus*; *Chorthippus brunneus* Thunberg, all of which are widespread in the study area (Badenhausser et al. 2009).

Grasshopper density was calculated for each taxon over the 10-m<sup>2</sup> replicates per grassland and was taken as a measure for the abundance of grasshoppers. We measured the spatial autocorrelation for the Gomphocerinae subfamily and for *C. italicus*, whereas *P. giornae* and other species were not analyzed because of their very low densities in the surveys.

**Statistical Analyses.** A geostatistical approach was used to analyze the spatial structure of the two grasshopper taxa for each year. The semivariogram describes the spatial contiguity of a variable. It is calculated by averaging the empirical variogram values  $\gamma(h)$  for a range of distance interval  $h$  (Wackernagel 1995):

$$\gamma(h) = \frac{1}{2N(h)} \sum_{\alpha=1}^{N(h)} [z(x_{\alpha}) - z(x_{\alpha} + h)]^2, \quad [1]$$

where  $z(x_{\alpha})$  is the value of the variable located at point  $x_{\alpha}$ .

The variogram is central to spatial statistics theory for continuous variables (Cressie 1993) and is now widely used in modern spatial ecology (Monestiez et al. 2006, Dormann et al. 2007). Additional statistical methods are available to relate the distance between a variable's values at pairs of points and the spatial distance between them, such as the Mantel's test. Because of its assumption of a linear relationship between these two sets of distances, the Mantel's test is less general than the variogram as a tool to investigate spatial dependence, whereas empirical variograms can be fitted with a number of parametric or nonparametric functions.

Stationarity (i.e., lack of spatial trends in the mean and variance of the data) is a critical assumption when using a variographic approach in ecological studies (Rossi et al. 1992). Moreover, grasshopper density can vary with the type of grassland and according to the time of sampling along the season (Badenhausser et al. 2009). Several procedures can be used to correct non-stationarity (Rossi et al. 1992, Wackernagel 1995, Dormann et al. 2007), and to remove any trend in the data because of different sampling procedures and effects of exogenous variables (grassland type and sampling date). We chose to use a generalized additive model (GAM) approach that models spatial trends in log-grasshopper densities by constructing flexible smooth terms of the spatial coordinates (Dormann et al. 2007). In addition to the large scale spatial trends, the models included the type of grassland (classified as alfalfa or meadow) and the sampling date:

$$\text{Grasshopper density} \approx s(\text{latitude, longitude}) \\ + \text{Grassland type} + s(\text{sampling date})$$

The maximum number of degrees of freedom for the spatial trend was set to five, which we found to represent a good trade-off for allowing sufficient flexibility in capturing broad trends in our study area although ensuring that only large scale trends were modeled.

All geostatistical analyses were thus carried out on the GAM residuals. A spherical model was chosen to model the variogram because this function fitted the data satisfactorily and its parameters are straightforward to interpret. Following Maestre et al. (2005), the parameters were estimated by minimizing the mean squared error between the variogram model and the sample variogram data weighted by the number of pairs per distance lag. The parameters of interest for the spherical model are the range (distance beyond which the semivariance reaches a plateau and samples become spatially independent); nugget ( $C_0$ , the variogram intercept, usually interpreted as local random effects and measurement error); and sill ( $C$ , the value of the plateau). The ratio  $C_0/C$  can be calculated to indicate the strength of spatial autocorrelation in the



data (Rong et al. 2007). The smaller this ratio is, the more autocorrelated the data tend to be at short range. In the case of a constant model (pure nugget effect) this ratio is 1. Both  $C_0$  and  $C$  were taken from the variogram model parameters.

More intensive surveys (SD3) were conducted on selected areas in 2004 and 2005 (Fig. 1). Clustered data without preferential sampling is not a problem for the variogram calculation. However, biased sampling with respect to location, value, or both (when the cluster area shows significant differences in density compared with the rest) has to be taken into account during the variogram computation by using, for instance, a de-clustering method (Richmond 2002, Olea 2007). Richmond (2002) suggested two different procedures based on computing weighted variograms and demonstrated a resulting improvement of the accuracy of the variogram in the case of spatially clustered sampling. Here we used this two-point declustering method that allowed us to cumulate several sampling schemes without excluding any data (Richmond 2002). Two samples are considered to belong to the same cluster if they are separated by a distance  $\leq t$ . Each pair of points (corresponding to two sampled fields) is weighted by the number of possible pairs of points between the clusters they belong to. For example, a pair of points belonging to clusters of four and three samples, respectively is weighted by 12 ( $w_{\alpha\alpha'}$ ). We chose  $t$  so that the density of clusters was similar between the preferential sampling area and elsewhere, thereby giving equivalent weight to all areas. In this study,  $t = 400$  m met this condition, leading to the creation of 119 and 126 clusters in 2004 and 2005, respectively.

The weighted sample variogram was computed as follows:

$$\gamma(d) = \frac{1}{2W_d} \sum_{\alpha=1}^{N_d} [z(x_\alpha) - z(x_{\alpha'})]^2 w_{\alpha\alpha'}, \quad [2]$$

where  $z(x_\alpha)$  is the GAM residual located at point  $x_\alpha$  and  $W_d = \sum_{\alpha=1}^{N_d} w_{\alpha\alpha'}$  is the sum of the weights between the pairs of points for the distance lag  $d$ .

Distance lags started at 0 with 500-m increments in years with standard sampling effort (2003, 2006, 2007, 2008, 2009, 2010) and 200-m increments when sampling was more intensive (2004 and 2005). We extended the first lag to 750 m in 2003 to include at least 30 pairs of samples to ensure more robust results.

All statistical and spatial analyses were conducted in R (R Development Core Team 2011). Variograms were computed and fitted using functions from the geoR 1.6–22 package and we wrote our own functions for the declustering method.

## Results

**Spatial Autocorrelation in Grasshopper Density.** Weak large scale trends over the study site only were detected in 2004 for both taxa (GAM analysis:  $P$  (smooth term) = 0.003 for *C. italicus* and 0.05 for

Gomphocerinae), although they were not significant in any other year (all  $P > 0.05$ ).

Empirical and modeled variograms were computed for each year for the two grasshopper taxa and are shown in Fig. 2 for *C. italicus* and in Fig. 3 for Gomphocerinae. For *C. italicus*, the spatial autocorrelation of grasshopper densities was best described using a spherical variogram model in all years except in 2003 (Fig. 2A), 2008 (Fig. 2F), and 2009 (Fig. 2G) in which cases a constant model was more adequate that revealed spatial independence regardless of scale (Table 2). In 2003, sample size was the smallest (102 fields), whereas in 2008 and 2009, *C. italicus* densities were very low (0.02 and 0.06/m<sup>2</sup>, respectively). In the other years, *C. italicus* densities were spatially correlated up to distances that varied, according to the year, between 672 m (in 2007, Table 2, Fig. 2E) and 6,800 m (in 2005, Table 2, Fig. 2C). The normalized expression  $C_0/C$  provided a relative measure of structural versus nugget variance. Values of 0.27 observed in 2005 indicated that a large fraction of spatial dependence was because of spatial autocorrelation over a short range, whereas other values (0.57, 0.94, 1) indicated nugget variance. The declustering of the data extended the estimated range of autocorrelation in 2005 (Fig. 2C) but did not affect the results in 2004 (Fig. 2B).

For Gomphocerinae, the autocorrelation range and  $C_0/C$  also varied according to the year (Fig. 3; Table 2). Densities were spatially correlated up to distances varying between 802 m (in 2007, Table 2, Fig. 3E) and 2,613 m (in 2004, Table 2, Fig. 3B). Over a short range, the spatial autocorrelation was still a major source of structural variance in Gomphocerinae densities compared with nugget variance in 2003, 2005, 2007, and 2008 as shown by the small values of  $C_0/C$  in these years (Table 2). The declustering of the data did not affect the results in 2005 (Fig. 3C), although it extended the estimated range of autocorrelation in 2004 (Fig. 3B). *C. italicus* and the Gomphocerinae did not differ in their average variogram range (mean  $\pm$  SD), 1,410  $\pm$  2,271 m against 1,589  $\pm$  685 m, but between-year variability was much higher for *C. italicus*.

**Relationship Between Grasshopper Spatial Autocorrelation and Grasshopper Density.** Gomphocerinae and *C. italicus* were present in every year in 85  $\pm$  10% and 42  $\pm$  24% of sampled fields, respectively. There were highly significant differences in the probability of presence among years as well as between species (logistic GLM; year effect:  $\chi^2 = 349.4$ ; df = 7;  $P < 0.001$ ; species effect:  $\chi^2 = 778.32$ ; df = 1;  $P < 0.001$ ). Grasshopper density also varied significantly across years between 2003 and 2010 and between species (negative binomial GLM; year:  $\chi^2 = 616.3$ ; df = 7;  $P < 0.001$ , species:  $\chi^2 = 1606.4$ ; df = 1;  $P < 0.001$ , year\*species:  $\chi^2 = 61.4$ ; df = 7;  $P < 0.001$ ). Based on sampling scheme SD1, which was an unbiased design to estimate grasshopper density throughout the study site, *C. italicus* densities were low in all years and ranged between 0.02 and 0.53/m<sup>2</sup> (Table 1). Year 2008 showed the lowest grasshopper densities for all taxa (Gomphocerinae: 0.64/m<sup>2</sup>, *C. italicus*: 0.02/m<sup>2</sup>), whereas Gomphocerinae were the most abundant in

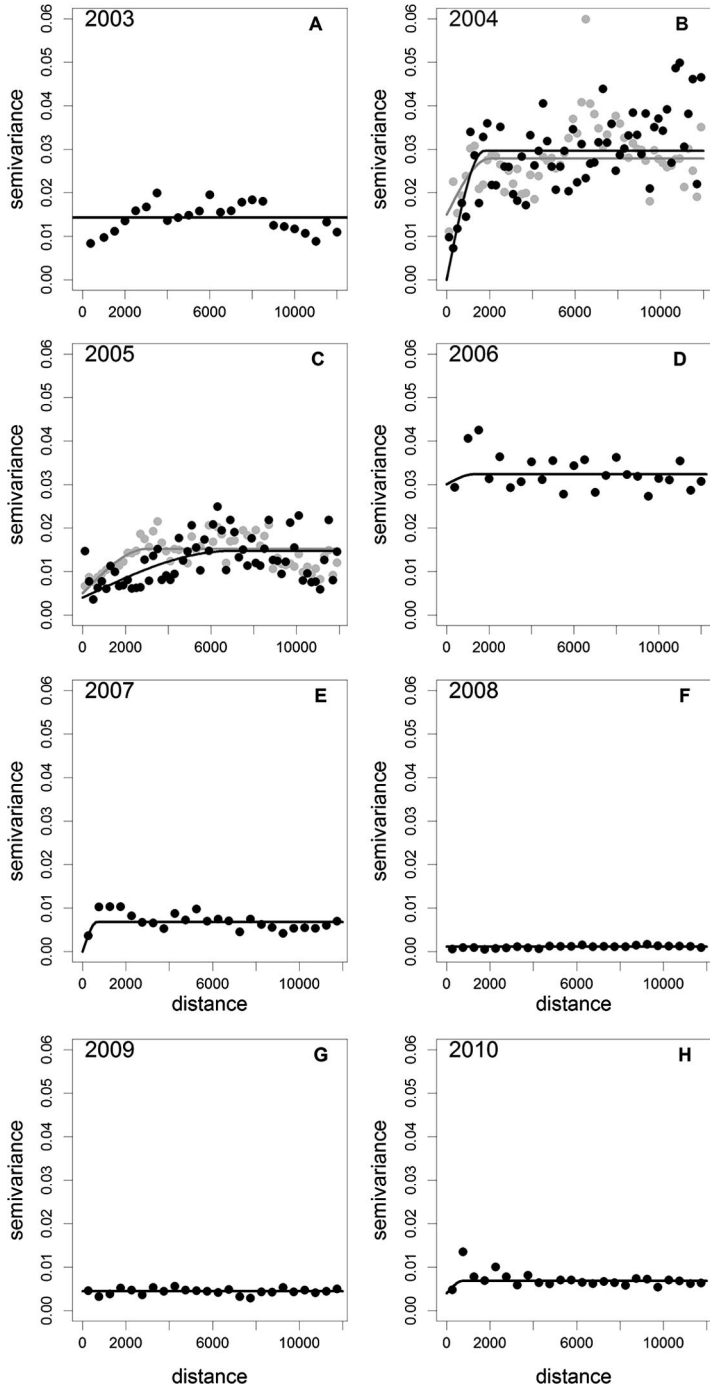


Fig. 2. Standard empirical and fitted variogram computed on GAM residuals for *C. italicus* from (A) 2003 to (H) 2010. In 2004 and 2005, black and gray symbols represent variograms computed using the standard method and the two-point declustering method, respectively.

2004 ( $7.65/\text{m}^2$ ) and *C. italicus* in 2006 ( $0.53/\text{m}^2$ ). Depending on the year, between 1.2 and 6.6% of the deviance was explained by the GAM analysis for *C. italicus* (Table 3). The type of grasslands (alfalfa fields or meadows) had no significant effect on *C. italicus*

density in all years, excepted in 2010 where higher densities were observed in alfalfa fields than in meadows (Table 3). *C. italicus* densities significantly decreased with sampling date in only 3 yr (Table 3). The GAM analysis for Gomphocerinae showed higher ex-

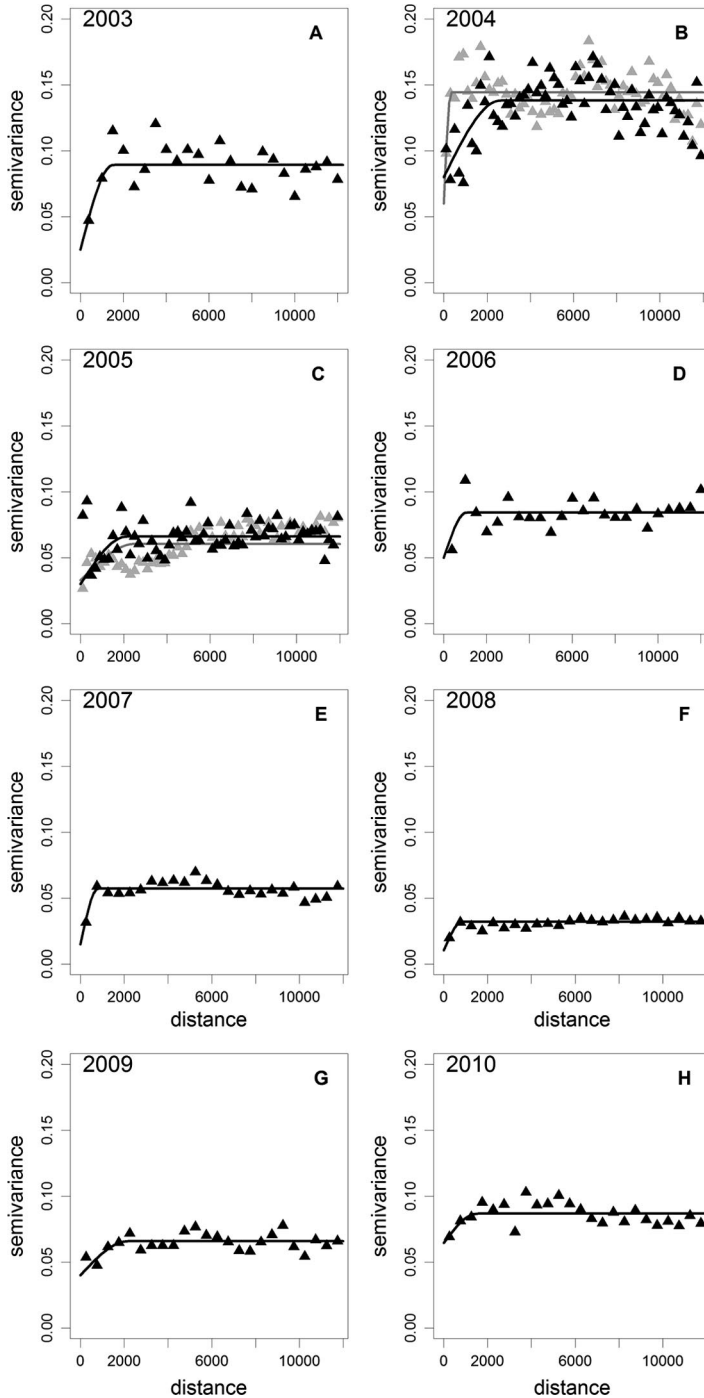


Fig. 3. Standard empirical and fitted variogram computed on GAM residuals for Gomphocerinae from (A) 2003 to (H) 2010. In 2004 and 2005, black and gray symbols represent variograms computed using the standard method and the two-point declustering method, respectively.

plained deviance, ranging from 11.1 to 37.4% between years (Table 3). In all years, Gomphocerinae densities were significantly higher in meadows than in alfalfa fields (Table 3). Gomphocerinae densities significantly decreased with sampling date in 4 yr.

We investigated the relationships between spatial autocorrelation parameters (range, and  $C_0/C$ , all sampling schemes combined) and grasshopper density of the year (calculated from sampling scheme SD1). For *C. italicus*, there was no relationship between  $C_0/C$

**Table 2.** Best fitted variogram models of grasshopper densities (ind/m<sup>2</sup>) by year and species when pooling data from all sampling schemes

Year	Taxon	Model	Nugget (C <sub>0</sub> )	Sill (C)	Range (in m)	C <sub>0</sub> /C
2003	<i>C. italicus</i>	Constant	0.019	0.019	0	1
2004	<i>C. italicus</i>	Spherical	0	0.032	1,760	0
2005	<i>C. italicus</i>	Spherical	0.004	0.015	6,800	0.27
2006	<i>C. italicus</i>	Spherical	0.028	0.032	1,300	0.94
2007	<i>C. italicus</i>	Spherical	0	0.007	672	0
2008	<i>C. italicus</i>	Constant	0.001	0.001	0	1
2009	<i>C. italicus</i>	Constant	0.004	0.004	0	1
2010	<i>C. italicus</i>	Spherical	0.004	0.007	754	0.57
2003	Gomphocerinae	Spherical	0.025	0.089	1,509	0.28
2004	Gomphocerinae	Spherical	0.080	0.138	2,613	0.58
2005	Gomphocerinae	Spherical	0.030	0.066	2,131	0.45
2006	Gomphocerinae	Spherical	0.050	0.084	1,052	0.59
2007	Gomphocerinae	Spherical	0.015	0.057	802	0.26
2008	Gomphocerinae	Spherical	0.010	0.032	839	0.31
2009	Gomphocerinae	Spherical	0.043	0.066	2,270	0.65
2010	Gomphocerinae	Spherical	0.065	0.087	1,500	0.75

Variograms were computed on GAM residuals, and in 2004 and 2005 by using the two-point declustering method.

and density ( $F = 0.089$ ;  $df = 1,6$ ;  $P = 0.77$ ) or between spatial autocorrelation range and density ( $F = 0.39$ ;  $df = 1,6$ ;  $P = 0.55$ ; Fig. 4A). For Gomphocerinae, there was no relationship between C<sub>0</sub>/C and Gomphocerinae density ( $F = 0.69$ ;  $df = 1,6$ ;  $P = 0.44$ ). However, range of autocorrelation increased with grasshopper density ( $F = 3.32$ ;  $df = 1,6$ ;  $P = 0.10$ ) (Fig. 4B).

**Relationship Between Habitat Availability and Grasshopper Spatial Autocorrelation.** The proportion of land covered with grasslands in the study site over the 8-yr study period was 13.2% (ranged between 11.3% in 2004 and 15.6% in 2007; Fig. 5). Meadows covered on average  $10.2 \pm 1.5\%$  (mean  $\pm$  SD) of the study site area, whereas alfalfa fields covered  $3.1 \pm 0.2\%$ . Interannual variations in the proportion of grassland surfaces were attributable to meadows, which increased from 2003 to 2007 and then decreased, whereas the proportion of alfalfa surfaces slightly increased from 2003 to 2010 (Fig. 5). Annual mean

distance ( $\pm$  SD) between alfalfa fields significantly decreased (Welch's  $t = 3.89$ ;  $df = 1031$ ;  $P < 0.001$ ) from 2003 ( $954 \pm 452$  m) to 2010 ( $848 \pm 440$  m) (Fig. 5). The same trend was observed for meadows (Welch's  $t = 13.62$ ;  $df = 4,020$ ;  $P < 0.001$ ) (2003:  $454 \pm 223$  m – 2010:  $363 \pm 220$  m). Average distances between meadows decreased with increasing proportion of surfaces in meadows ( $F = 7.83$ ;  $df = 1,6$ ;  $P = 0.03$ ). This trend was also observed for alfalfa fields ( $F = 2.83$ ;  $df = 1,6$ ;  $P = 0.14$ ).

The relationships between spatial autocorrelation parameters (range, and C<sub>0</sub>/C) and the annual proportion of grassland surfaces were not significant for *C. italicus*, whatever the type of grasslands (alfalfa fields, meadows, all grasslands) (All grasslands: C<sub>0</sub>/C:  $F = 0.01$ ;  $df = 1,6$ ;  $P = 0.92$ ; Range:  $F = 0.25$ ;  $df = 1,6$ ;  $P = 0.63$ ) (Fig. 4C). For Gomphocerinae, C<sub>0</sub>/C was not related to the annual proportion of grassland surfaces in the study site, whatever the type of grasslands

**Table 3.** Statistical results of GAM analysis of grasshopper densities (number of grasshoppers/m<sup>2</sup> log-transformed)

Year	Taxon	Grassland type		Sampling date		% deviance explained (edf)
		Est. alfalfa field (SE)	P value	Est. (SE)	P value	
2003	<i>C. italicus</i>	-0.06 <sup>a</sup> (0.04)	0.11	0.003 (0.003)	0.46	6.0 (2.71)
2004	<i>C. italicus</i>	0.00 (0.02)	0.88	-0.006 (0.002)	0.003	6.6 (2.00)
2005	<i>C. italicus</i>	-0.02 (0.01)	0.30	-0.001 (0.001)	0.53	2.2 (2.00)
2006	<i>C. italicus</i>	0.07 (0.04)	0.08	-0.005 (0.004)	0.17	5.8 (2.00)
2007	<i>C. italicus</i>	0.02 (0.01)	0.16	-0.006 (0.002)	0.001	5.7 (2.80)
2008	<i>C. italicus</i>	-0.01 (0.01)	0.25	-0.000 (0.000)	0.44	3.9 (3.34)
2009	<i>C. italicus</i>	0.01 (0.01)	0.45	-0.000 (0.000)	0.90	1.2 (2.00)
2010	<i>C. italicus</i>	0.03 (0.01)	0.01	-0.002 (0.001)	0.04	5.3 (2.00)
2003	Gomphocerinae	-0.29 (0.08)	0.001	0.017 (0.008)	0.04	16.1 (2.35)
2004	Gomphocerinae	-0.48 (0.05)	<0.001	-0.015 (0.005)	0.004	28.1 (3.76)
2005	Gomphocerinae	-0.34 (0.03)	<0.001	-0.010 (0.004)	0.02	37.4 (2.00)
2006	Gomphocerinae	-0.41 (0.06)	<0.001	-0.000 (0.006)	0.97	31.2 (2.00)
2007	Gomphocerinae	-0.27 (0.03)	<0.001	-0.003 (0.005)	0.57	25.4 (2.00)
2008	Gomphocerinae	-0.20 (0.03)	<0.001	-0.006 (0.003)	0.06	20.0 (3.39)
2009	Gomphocerinae	-0.21 (0.04)	<0.001	-0.007 (0.003)	0.03	11.1 (2.00)
2010	Gomphocerinae	-0.21 (0.04)	<0.001	-0.006 (0.003)	0.08	16.0 (2.52)

Parameter estimates and P values of the effects of grassland type (alfalfa field or meadow) and sampling date are provided. The percentage of deviance explained by the GAM is given by the estimated degrees of freedom (edf) of the trend surface.

<sup>a</sup> The reference (intercept term) is the mean of the response variable for meadows.



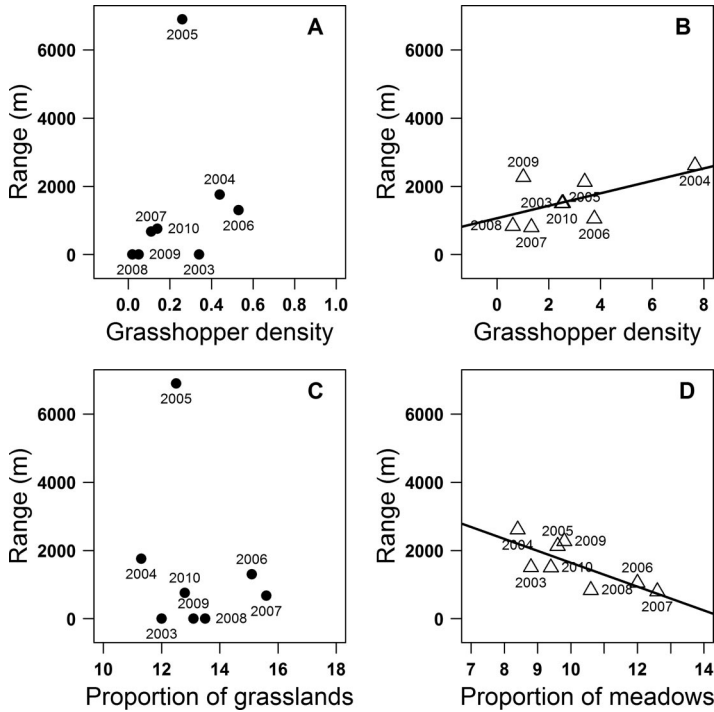


Fig. 4. Range (m) of the modeled variograms in relation to annual grasshopper density (number of grasshoppers per m<sup>2</sup>) for (A) *C. italicus* and (B) Gomphocerinae, and to the annual proportion of grassland surfaces in the study site for (C) *C. italicus* (all types of grasslands) and (D) Gomphocerinae (meadows). The line indicates the linear relationship.

(All grassland surfaces:  $F = 0.29$ ;  $df = 1,6$ ;  $P = 0.61$ ). However, the range of the spatial autocorrelation significantly decreased with the proportion of meadow cover ( $F = 8.09$ ;  $df = 1,6$ ;  $P = 0.03$ ) (Fig. 4D), although it was not significant with the proportion of alfalfa fields ( $F = 0.003$ ;  $df = 1,6$ ;  $P = 0.96$ ). Lower habitat availability did not result in lower Gomphocerinae densities ( $F = 0.52$ ;  $df = 1,6$ ;  $P = 0.50$ ).

Discussion

The GAM and geostatistical analyses we conducted provided a description of the spatial patterns of grass-

hopper densities, and can be used in other systems. 1) The small percentage of deviance explained by the spatial term in GAM models, except in 2004, indicated weak large scale trends over the study site in both grasshopper taxa, despite the fact that the study site was 450 km<sup>2</sup>. Similar results were found for grasshopper assemblages in different landscape types (Bazelet and Samways 2011a) and in the same study area for different taxa, such as the common vole *Microtus arvalis* Pallas (Gauffre et al. 2009). With (1994) suggested similarities in landscape interactions among species occupying the same habitat, which could reflect that a general set of rules may determine how

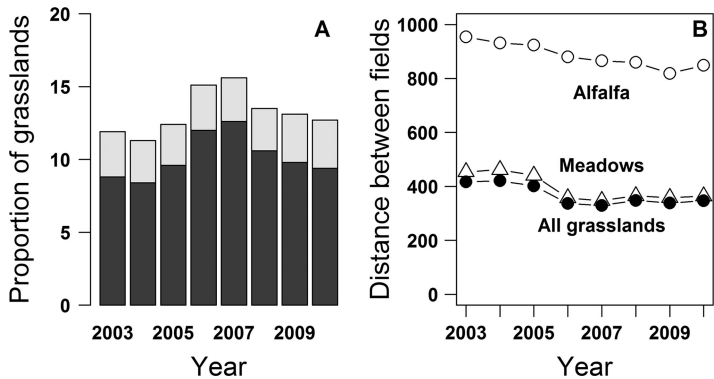


Fig. 5. Description of habitat availability in the study site. (A) Proportion of grassland surfaces (alfalfa fields in gray, meadows in black). (B) Mean distance (in m) between alfalfa fields, meadows and all grasslands from 2003 to 2010.

different organisms respond to landscape structure across a range of scales. 2) Fitted variograms revealed spatial autocorrelation in grasshopper densities, depending on the year and on grasshopper taxa. The strength of autocorrelation at small scales, estimated by the expression  $C_0/C$  derived from fitted variogram models, was unexpectedly weak in most of the cases. An explanation could be that there were not enough close pairs of samples in the study area to detect autocorrelation at short distances. This was partly suggested by the results obtained in 2004 and 2005 when comparing the range of autocorrelation with and without the declustering method. Because the standard method gave more weight to more intensively sampled areas, the smaller range of autocorrelation observed in two out of four cases with the standard method suggested that grasshopper densities in the intensively sampled areas were autocorrelated at a shorter range than elsewhere in the study area, or as an alternative explanation, that there were not enough close pairs of samples in the rest of the study area to detect autocorrelation at short distances. The last hypothesis is supported by Tobin (2004) who established that in field data, the estimate of the local spatial autocorrelation was greatly affected by sample size, and preconized to increase the number of pairs of points that are close in space to capture the local spatial structure. Another explanation could be that fragmented and disturbed landscapes induced investment in dispersal-related traits (Tscharntke and Brandl 2004) and selected for species with relatively high dispersal abilities and/or behavior (Ronce 2007). Lastly, grasshoppers may be more sensitive to farming practices occurring within grasslands than to variables which affect the landscape at small scales (Bazelet and Samways 2011b), leading to independent grasshopper densities in nearby grasslands.

The range of spatial autocorrelation and  $C_0/C$  varied among years for both grasshopper taxa. Sample variograms indicated that Gomphocerinae densities were spatially correlated over ranges from 802 to 2613 m depending on the year. Autocorrelation ranges were different from those established by Ni et al. (2003) for an assemblage of 10 grasshopper species among which Gomphocerinae species were dominant. Their results revealed spatial clustering at different scales, such as 120–150 m for the dominant species *Myrmeleotettix palpalis* Zub., and 300–1,300 m and 13–16 km for the whole assemblage. They hypothesized that spatial autocorrelation at local scales reflected unevenness in host plant and habitat patterns, while clustering at a larger scale reflected the variation in the spatial distribution of the vegetation. Because we were primarily interested in between-field variation, our spatial sampling schemes were not well suited to quantify aggregation at the smallest spatial scale found by Ni et al. (2003), which essentially corresponded to variation within grasslands in our system. Second, the size of our study area ( $\approx 25$  km in length and width) resulted in estimated ranges of spatial autocorrelation that were not reliable over  $\approx 8$  km because of the low number of pairs at larger scales. In

accordance with Ni et al. (2003), we found that the range of autocorrelation varied in the intermediate spatial scales, as our values tended to be larger (802–2613 m as opposed to 300–1,300 m). For *C. italicus*, autocorrelation ranges and  $C_0/C$  were highly variable among years (spatial autocorrelation range reached 6,800 m in 2005, whereas it was only 672 m in 2007, and in some other years there was no spatial autocorrelation), and this was the main difference to note with Gomphocerinae. *C. italicus* is considered a semidesert species that is presumably highly mobile in connection to the extreme and unstable microclimatic conditions of the habitats in these areas (Uvarov 1977), which could explain the weak spatial pattern and variation in the range of spatial autocorrelation that we observed. High variability in the range of spatial autocorrelation for this species suggested that *C. italicus* was more impacted by biotic or abiotic effects varying among years than Gomphocerinae, which was an assemblage of several species, each of which varied in abundance and relative frequency from year to year (Badenhausser et al. 2009).

The causes of spatial autocorrelation in species distribution are manifold (Dormann et al. 2007). Among them, we hypothesized that dispersal and habitat availability were key factors in intensive agricultural landscapes. For *C. italicus*, we did not observe any trend in the effect of population density and habitat availability on spatial autocorrelation. We suggested that the low densities we observed ( $<0.5/\text{m}^2$  regardless of year) may explain the lack of spatial relationships. For Gomphocerinae, which was the dominant grasshopper taxon in the study site, we established that as grasshopper populations became more dense, distant sites had more similar grasshopper abundance at a larger scale. This result supported our hypothesis that spatial patterns in grasshoppers were density-dependent and might be related to dispersal processes. Gomphocerinae densities varied among years mainly because of abiotic environmental variables (Köhler et al. 1999, Gardiner 2009) and could have affected dispersal, increasing densities of insects leading to greater probability of dispersal (Narisu et al. 1999). This was shown for British Gomphocerinae species that moved more when the densities of adult populations were high (Richards et al. 1954). We also established that habitat availability (expressed in the proportion of meadow surfaces in the study site or in distances between meadow habitats) had a major effect on the range of spatial autocorrelation. Lower habitat availability increased the distance at which densities in distant fields became independent, suggesting increased grasshopper movement across the landscape. This could be achieved through a higher use of alternative habitats, such as road margins by Gomphocerinae, in landscapes experiencing low grassland availability.

Our study provided a quantitative assessment of grasshopper spatial patterns in responses to habitat scarcity in farmlands. Grasshopper taxa differed in their response to population density and to habitat availability. However, similar weak spatial autocorre-

lation at small scales, and similar average range of spatial autocorrelation, as well as similar weak large scale spatial trends, suggested that species persistence in these landscapes implied some general characterization in species distribution.

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