This is the final accepted version of Rácz et al. (2013) Biodiversity and Conservation 22: 2321-2335. DOI: 10.1007/s10531-013-0466-8. The final published version is available at http://link.springer.com/article/10.1007/s10531-013-0466-8

Title:

EARLY CHANGES OF ORTHOPTERAN ASSEMBLAGES AFTER GRASSLAND RESTORATION: A COMPARISON OF SPACE-FOR-TIME SUBSTITUTION VERSUS REPEATED MEASURES MONITORING

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ABSTRACT

Grasslands harbour significant biodiversity and their restoration is a common intervention in biodiversity conservation. However, we know very little on how grassland restoration influences arthropod groups. Here we compared orthopteran assemblages in croplands, natural grasslands and one to four-year-old grasslands restored in a large-scale restoration on former croplands in Hortobágy National Park (E-Hungary). Sampling was done by standardized sweep-netting both in a repeated measures design and space-for-time substitution (chronosequence) design. General linear models with repeated measures from five years showed that species richness, abundance and Shannon diversity of orthopterans decreased in the year following restoration but increased afterwards. By the fourth year, species richness almost doubled and abundance increased almost ten-fold in restored grasslands compared to croplands. Multivariate analyses showed that species composition in the first two years did not progress much but by the third and fourth year there was partial overlap with natural grasslands. Local restoration conditions (last crop, seed mixture) and landscape configuration (proportion of natural grasslands < 1 km away) did not influence the above patterns in either the repeated measures or the chronosequence design, whereas time since restoration affected almost all community variables. Our results suggest that generalist ubiquitous species appeared in restored grasslands first and the more sensitive species colonized the restored fields gradually in later years. The qualitative and quantitative properties of the orthopteran assemblages in restored fields did not yet reach those of natural grasslands, therefore, our study suggests that the full regeneration of the orthopteran assemblages takes more than four years.

KEY-WORDS

arthropods; chronosequence; grasshoppers katydids and crickets; grassland diversity; habitat restoration; space-for-time substitution

INTRODUCTION

Lowland natural and seminatural grasslands play an important role in the maintenance of biological diversity. In most of Europe, the majority of such grasslands have been ploughed for crop production or used as pastures, and thus natural grasslands have remained only in very small fragments (Bakker and Berendse 1999). The preservation and enhancement of these fragments by habitat restoration have become a priority. It is not surprising that grassland restoration is one of the most frequent habitat restoration intervention (Hedberg and Kotowski 2010; Kiehl et al. 2010; Török et al. 2011).

Habitat restoration has traditionally aimed to enhance or re-create vegetation patterns and less attention has been paid to the restoration of animal assemblages. As a result, studies of habitat restoration based on trophic levels other than plants have remained rare (Woodcock et al. 2008; Mortimer et al. 1998). However, invertebrates such as ground-dwelling collembolans, lumbricids and carabids as well as herbivores such as orthopterans and butterflies also play highly important roles in grassland ecosystems (Walker et al. 2004). Arthropods can also be important as tools or subjects for biological control and in providing ecosystem services, therefore, they need to be involved into studies of habitat restoration (Woodcock et al. 2008; Young 2000; Longcore 2003).

Orthopterans (including the superfamilies of grasshoppers Acridoidea, katydids/bush crickets Tettigonioidea and crickets Grylloidea) are highly suitable to monitor grassland ecosystems for several reasons. Orthopterans are a diverse taxa and most species can be reliably sampled and easily identified in their imago stage (Gardiner et al. 2005). Most orthopterans are herbivorous and thus orthoptera assemblages are expected to correlate particularly well with plant community composition (Báldi and Kisbenedek 1997). Their habitat and food specialization vary greatly from generalist to specialist (mono- or oligophagous on forbs) and they can have substantial impact on plants (Whiles and Charlton 2006).

The aim of this study was to quantify changes in the richness, diversity and composition of orthopteran assemblages following grassland restoration. A previous study of ours using habitat affinity indices showed that combined arthropod species richness did not vary significantly between croplands and restored grasslands but that the naturalness of arthropod assemblages increased between the first and the second year following restoration (Déri et al. 2011). Based on these results, our first hypothesis was that orthopterans will also respond to grassland restoration with a change in species composition but not with changes in species richness, abundance or diversity. Our alternative hypothesis was that orthopteran assemblages will show large numerical responses to restoration because our restoration method involved deep ploughing which likely corresponded with the destruction of many orthopteran eggs laid in the soil of the croplands. We tested these two hypotheses by measuring the species richness, abundance, diversity, and species composition of orthopteran assemblages in croplands (restoration start), natural grasslands (restoration target) and one to four-year-old fields restored in a large-scale grassland restoration programme on former croplands in Hortobágy National Park (E-Hungary). Furthermore, we also quantified the four most important aspects of restoration (last crop, seed mixture, restoration year, proportion of target vegetation in the landscape) and used general linear models to test relationships between restoration conditions and orthopteran responses to restoration.

METHODS

Grassland restoration

In the Egyek-Pusztakócs landscape-scale rehabilitation program, grassland restoration was started on 760 hectares of former cropland south of the village of Egyek (47°33'N, 20°54'E) in Hortobágy National Park (E-Hungary) between 2005 and 2008. The area has continental climate, the mean annual temperature is 9.5 °C and mean annual precipitation is 550 mm. Large fluctuations in both rainfall and temperature are typical. The region was an active floodplain until 1856, when the regulation of river Tisza ended the floods. The area underwent several steps of drainage and marshes have retreated to the deepest parts by 1969. A long-term landscape rehabilitation programme between 1976 and 1997 restored the water supply to the marshes. Most areas between the marshes, however, continued to be cultivated as croplands. The second phase of the restoration programme aimed to decrease the areal proportion of croplands and restore grasslands in ecological corridors, buffer zones and other critical areas.

Areas selected for restoration were cultivated as alfalfa, cereal (wheat, barley) and sunflower fields. Restoration was started after harvest (late August) by soil preparation that included one round of deep ploughing and two rounds of smoothing. This was followed by sowing of two low-diversity seed mixtures (in September-October) at 20-25 kg/ha. The alkali mixture, sown on lower-lying fields (< 90 m a.s.l.), consisted of seeds of two grass species (67% *Festuca pseudovina*, 33% *Poa angustifolia*), and the loess mixture, sown on higher-lying loessy plateaus, consisted of seeds of three grass species (40% *Festuca rupicola*, 30% *Poa angustifolia*, 30% *Bromus inermis*). Restoration was started in early September and completed in early October in each year between 2005 and 2008. Restored fields in Year 1 after restoration were covered by weedy forbs, which facilitated the growth of grass cover of the sown species. Perennial grass cover dominated most fields by Year 3 and the diversity of common species and the cover of species typical to target natural grasslands increased continuously from Year 1 to 4 after restoration. A more detailed overview of the restoration programme and its early results on vegetation development is given in Lengyel et al. (2012) and references therein.

Sampling of orthopterans

We established one sampling site per c. 25 ha restored grassland. In this study, we used data from 33 sampling sites on 22 fields scattered in a landscape of 4000 ha. The distance between sampling sites was at least 250 m but usually much more. At each sampling site, two pitfall traps were installed 50 m apart from each other for other studies. For the present study, we conducted standardized sweep-netting around the pitfall traps in each year between 2005 and 2009. Sweep-netting was carried out once every three weeks or a total of six times in the vegetation period (May to September) to allow the recording of phenological changes in Orthoptera assemblages. On any one occasion, we collected Orthoptera and other vegetation-dwelling arthropods by taking 200 strokes with a sweep-net (diameter: 0.45 m) along transects (50 strokes/transect) in two different directions from any pitfall trap (total of four transects per sampling site), which resulted in 1200 strokes/site/year. Because the identity of the sampler and variation in sampling technique are known to influence orthopteran diversity and abundance estimates, we standardized collection height, distance and speed to reduce sampling noise as much as possible (O'Neill et al. 2002). The collected individuals were frozen and stored in the laboratory at -20 °C until processing and identification. Imago individuals were identified to the species level. Larval individuals, for which species-level identification was not possible, are included in our abundance calculations but not in species richness or diversity estimates. Besides monitoring restored fields, we also collected data from natural (alkali and loess) grasslands and croplands following the above sampling protocol.

Variables and data analysis

We defined species richness as the number of species identified and abundance as the number of individuals. We calculated both the Shannon index ($H = - \Sigma p_i \ln(p_i)$), where p_i is the relative abundance of species *i*) and the Simpson index ($D = \Sigma p_i^2$) of species diversity because the former is more sensitive to rare species and the latter is more sensitive to common species (Magurran 2004). Finally, we calculated evenness as $E = H / \ln(S)$, where S is the number of species. Response variables in statistical analyses were species richness, abundance, species diversity and evenness (‘assemblage variables’ hereafter). We used four predictor variables (three local, one landscape-scale) to describe restoration conditions. The previous history of the field was characterized by the last crop type that was present in the fields in the vegetation period just before restoration (spring/summer of Year 0; alfalfa, cereal or sunflower). The restoration method was the sowing either the alkali or the loess seed mixture. The years passed since restoration was the time since restoration. Finally, we used ArcGIS 10.0 for Windows to calculate the proportion of natural grasslands in 1000-m circular buffers around the sampling sites to quantify the landscape context of potential sources of the colonization of orthopterans.

In data analysis, we first compared assemblage variables among habitat types (croplands, restored fields, natural grasslands). Second, we used paired tests (t-test and Wilcoxon signed ranks test) to directly compare assemblage variables on fields that were croplands during 2005 and restored grasslands in 2009. Third, we analyzed the effects of restoration conditions (four predictor variables) on assemblage variables in two ways. We first analyzed data collected in 2009 as a space-for-time substitution design (chronosequence), where we compared data from croplands, from fields restored four, three, two and one year before data collection and from natural grasslands using General Linear Models (GLM). Because some fields had two and some had one sampling site, which can introduce non-independence at the field level, we performed this analysis also as a Generalized Linear Mixed-effects Model (GLMM) in which "Field" was a random factor. The random factor did not have a substantial contribution to explaining total variance (residual SD > intercept SD) (Pinheiro and Bates 2000), thus, we present results from the original GLM. In the second approach, we used GLM with repeated measures from those fields that were restored in 2005 and had data from all five years (Year 0 as cropland and Years 1 to 4 as restored fields). Finally, we used non-metric multidimensional scaling (NMDS) based on presence-absence data and Euclidean distances to evaluate changes in the species composition of restored fields based on data collected in 2009. We used by the 'metaMDS' function of R package 'vegan' (Oksanen et al. 2011). All statistical analyses were performed in SPSS 17.0 for Windows or R 2.13.0. (R Development Core Team 2011).

RESULTS

We collected a total of 5883 individuals of 37 species on the restored fields, 562 individuals of 19 species on croplands and 3535 individuals of 36 species on natural grasslands. When assemblages from the three different habitat types were compared, the abundance of orthopterans was highest, whereas evenness was lowest in restored fields (**Fig. 1**). While there was no significant difference in overall species richness among habitat types, the contrasting patterns in Shannon and Simpson diversity suggested that croplands and restored fields were richer in common species and that natural grasslands were richer in rare species (**Fig. 1**).

Croplands were dominated by *Calliptamus italicus*, the abundance of which, however, decreased considerably in Year 1 and later (Online Resource, **Table S1**). Fields in Year 1 to 3 after restoration were dominated by the widespread generalist *Chorthippus parallelus* and the ubiquitous *Ch. brunneus*. Acridoidea species more characteristic to alkali grasslands appeared from Year 2 (*Chorthippus oschei*, *Omocestus rufipes*) and Year 3 (*Euchorthippus declivus*, *E. pulvinatus*). The species richness and abundance of Tettigonioids, likely related to the development of perennial grass cover fields, also increased with time, and species typical in natural loess/alkali grasslands appeared in higher numbers (e.g. *Metrioptera roeselii*) or sporadically (e.g. *Gampsocleis glabra*) in Year 3 and 4 after restoration (**Table S1**).

Paired tests using data from fields that were croplands in 2005 and restored by 2009 (n = 8 sites) showed a significant increase in species richness (5.3 ± S.D. 2.82 to 9.5 ± 2.73, paired t_7 = -3.991, p = 0.005), a ten-fold increase in abundance (25.3 ± 23.86 to 254.3 ± 243.14, Wilcoxon signed rank test, Z = -2.521, p = 0.012) and a decrease in evenness (0.8 ± 0.07 to 0.5 ± 0.08, t_7 =

9.785, $p < 0.001$). There were also non-significant decreases in Shannon and increases in Simpson diversity.

The space-for-time-substitution analysis based on data from 2009 showed that the development of Orthoptera assemblages was not sensitive to either local (last crop, seed mix) or landscape-scale (proportion of natural grasslands in 1000-m buffers around sampling sites) restoration conditions (**Table 1**). Abundance, Shannon diversity and evenness, however, were affected by time since restoration (**Table 1**). Abundance was higher in older than in younger restorations, and Shannon diversity as well as evenness were higher in one-year-old restored fields than in older ones (**Fig. 2**).

General linear models using repeated measures from fields sampled in all five years ($n = 7$) confirmed the above patterns in that neither the previous history (last crop type) nor the seed mixture used (alkali/loess) played a role in shaping Orthoptera assemblages, whereas time since restoration affected all but one community variable (**Table 2**). After a sharp decline in Year 1, species richness increased nearly two-fold, whereas abundance increased almost ten-fold by Year 4 after restoration (**Fig. 3**). Shannon and Simpson diversity changed in opposite directions with time, whereas evenness decreased from a peak in Year 1 to Year 4 (**Fig. 3**). General linear models on a larger sample (fields sampled in at least three years, $n = 17$) also showed that neither the previous history nor the seed mixture influenced Orthoptera assemblages, whereas time since restoration affected all but one community variable (Online Resource, **Table S2**).

The species composition of restored fields did not change much in Year 1 and 2 after restoration (except for one site) but became more variable and progressed slowly towards that of target alkali and loess grasslands in older restorations (**Fig. 4**).

DISCUSSION

Our study provided three key results. First, restored fields had higher orthopteran species richness than did croplands and the abundance of orthopterans increased considerably on restored fields compared to both croplands and natural grasslands (**Fig. 1**). Second, the methods of restoration (last crop, seed mixture) did not influence orthopteran assemblages which nevertheless showed substantial changes with time after restoration. The most important of these changes were the doubling of species richness, the ten-fold increase in abundance and the decreasing evenness from Year 1 to 4 after restoration (**Fig. 3**). Finally, species composition diversified and progressed slowly towards target-state natural grasslands, although declining evenness showed that assemblages on restored fields were increasingly dominated by a few common species.

The decline of species richness, Shannon diversity and abundance in Year 1 after restoration (**Fig. 3**) could be explained by our restoration method, in which deep ploughing was applied, which probably led to the destruction of orthopteran eggs laid in the ground. In Year 1, we found a mere 328 individuals belonging to an average of 3.9 species per site, which resulted in high evenness in Year 1 (**Fig. 2, 3**). In Year 2, species richness increased greatly, whereas abundance and Shannon diversity have reached values obtained on the originating croplands (**Fig. 3**). We conclude that most orthopterans appearing in Year 2 must have resulted from a quick colonization of the restored fields from neighboring semi-natural and natural grasslands. For example, fields restored in 2005, most of them alfalfa fields, had several specialist species (*Metrioptera roeselii*, *Gampsocleis glabra*, *Euchorthippus declivus*), which disappeared in Year 1 but re-appeared in later years (**Table S1**). The increase in species richness, Shannon diversity and abundance continued in Year 3. In Year 4, orthopteran assemblages could be characterized by increasing abundance and Simpson diversity and by decreasing Shannon diversity and evenness (**Fig. 2**). The abundance of common species (*Chorthippus brunneus*, *Ch. oschei*, *Omocestus rufipes*) increased gradually in Year 2 to 4, whereas new species also appeared in Year 3 (e.g. *Ruspolia nitidula*) and Year 4 (e.g. *Omocestus petraeus*) (**Table S1**). These results suggest that assemblages became more homogeneous in Year 4, and were dominated by fewer common species rather than by many rare species. The lack of rare species in Year 4 may be explained either that no further establishment occurred from the neighboring grasslands or that nearby natural grasslands were also deficient in rare species. Alternatively, it is also possible that the colonization and establishment of rare species take more time than the four years studied. For example, rare plant species, especially forbs, are also slow to colonize the newly restored fields (Lengyel et al. 2012). Because Orthopteran species show strong associations with plant communities (Mortimer et al. 1998; Craig et al. 1999), it appears plausible that specialist species may lack the resources they need even in four-year-old restored fields.

Our results differ from previous findings on the effect of grassland restoration on Orthopteran assemblages in several aspects. Bomar (2001) compared remnant and restored tallgrass prairie patches in western Wisconsin and found higher overall diversity on natural than on restored patches, with the exception of the largest (48-ha) prairie fragment, where species richness (10 species) was comparable to that of remnant prairies. Nemec & Bragg (2008) studied Hemiptera and Orthoptera communities at three restored and three native tallgrass prairie sites in central Nebraska. Although Orthoptera species richness was higher in restored than in native sites, mostly due to the higher species richness of Acrididae, both the species richness and Shannon diversity of Tettigoniidae showed an opposite relationship (native > restored). The abundance of either group did not differ between native and restored sites (Nemec and Bragg 2008). In contrast to these studies, our results suggested no difference in species richness but higher Shannon and lower Simpson diversity on natural grasslands than on restored fields as well as higher total abundance on restored fields than on natural grasslands (**Fig. 1**). These differences may be explained by the facts that in both of the above studies (i) the time scales (time since restoration) were longer than in our study and (ii) the restored areas were small and rather isolated. In a shorter, nine-year study of primary succession of natural revegetation of abandoned mine tailings, Picaud & Petit (2007) found that Orthoptera species richness peaked around 3-4 years after restoration and decreased afterwards. Although we followed secondary succession after an active grassland restoration, our results using repeated measurements corroborated this pattern, although continued monitoring is required to test whether species richness will decrease beyond four years.

Our study, which, to our knowledge, is the first to apply both a space-for-time substitution and repeated measurements of Orthopteran assemblages following habitat restoration, provides important insights into the effectiveness of these two approaches in detecting post-restoration changes in Orthoptera assemblages. Space-for-time substitution is frequently the method of choice in restoration studies (Michener 1997; Pickett 1989) due to its feasibility and convenience. Chronosequences record the combined end results of (i) the effect of restoration, (ii) variation in environmental conditions (weather, e.g. rainfall, groundwater level, or other factors, e.g. salinity) and (iii) population fluctuations in previous years, which can be substantial in insects (Whiles and Charlton 2006). Older restorations will be subject to more environmental fluctuations, and the detection of post-restoration processes may be more difficult by the masking effect of such fluctuations. On the other hand, younger restorations may not be effective at detecting post-restoration processes operating on longer time scales. For these and other reasons, recent reviews warn against the widespread use of space-for-time substitution (Johnson and Miyanishi 2008). Instead, repeated, long-term measurements on the same sites provide a trajectory of changes occurring at a place and are less subject to the masking effect of environmental fluctuations (Foster and Tilman 2000). Our study suggests that some trends, e.g. increasing orthopteran abundance after restoration, are found similarly by both methods, e.g. increasing abundance on older restorations, cf. **Fig. 2B** vs. **3B**). However, the space-for time approach did not detect any increase in species richness (**Fig. 2A** vs. **3A**) and found a one-time decline rather than a gradual decrease of evenness (**Fig. 2E** vs. **3E**). Our results support the view that repeated measurements provide more information and slightly more precise information on post-restoration processes. Our study thus provides an example for recent calls to supplement chronosequences with repeated measurements (Johnson and Miyanishi 2008).

In conclusion, grassland restoration resulted in significant increases in species richness and abundance of Orthoptera. Restoration methods did not directly affect any of the major variables describing Orthoptera assemblages. Several results suggested that the increase in species richness and abundance in time co-occurs with assemblages becoming more homogeneous and dominated by a few common species rather than by rare species of conservation importance. Although changes in species composition generally point to target natural grasslands, the species composition of older restorations only partially overlaps with those of target natural grasslands. These results support the hypothesis that generalist species appear first (in Year 1 to 4, e.g. *Chorthippus biguttulus*, *Ch. brunneus*, *Ch. parallelus*) and more sensitive, rare species (e.g. *Gampsocleis glabra*, *Chorthippus albomarginatus/oschei*, *Dirshius haemorrhoidalis*, *D. petraeus*, *Stenobothrus stigmaticus*, *Aiolopus thalassinus*, *Dociostaurus brevicollis*, *Euchorthippus declivus*) are colonizing later. The quantitative and qualitative properties of species composition did not yet reach those of natural grasslands in four years. We thus believe that reaching the state of seminatural grasslands takes more time and that continued monitoring is warranted.

ACKNOWLEDGMENTS

We thank colleagues in Hortobágy National Park Directorate for their help in the design and implementation of the restoration. The restoration project was co-financed by the LIFE-Nature programme of the European Commission (LIFE04NAT/HU/000119, http://life2004.hnp.hu). This study was funded by two joint grants from the Norway Financing Mechanism and the Hungarian Scientific Research Fund (OTKA NNF 78887, 85562) and a Bolyai Research Fellowship of the Hungarian Academy of Sciences to SL.

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FIGURE LEGENDS

Fig. 1 Mean ± S.E. values of Orthoptera assemblage variables on croplands (n = 12), restored fields (n = 33) and natural grasslands (n = 24) in the Egyek-Pusztakócs marsh-grassland complex (E-Hungary). (A) ANOVA, $F_{2,66} = 2.354$, n.s.; (B) Kruskal-Wallis $H_2 = 15.899$, $p < 0.001$; (C) $H_2 = 22.008$, $p < 0.001$; (D) $H_2 = 22.795$, $p < 0.001$; (E) ANOVA, $F_{2,66} = 20.218$, $p < 0.001$

Fig. 2 Mean ± S.E. values of Orthoptera assemblage variables by year of restoration on restored fields sampled in 2009 (n = 33 or 11, 11, 6, 5 sites in 2005 to 2008, respectively). Statistics are given in **Table 1**

Fig. 3 Mean ± S.E. values of Orthoptera assemblage variables on croplands sampled in all five years (n = 7), i.e., before restoration (Year 0) and after restoration (Year 1 to 4). Statistics are given in **Table 2**

Fig. 4 Changes in Orthoptera species composition with restoration age based on data collected in 2009 (one-year-old: restored in 2008, four-year-old: restored in 2005). Non-metric multidimensional scaling based on Euclidean distances of species presence-absence data (stress value: 0.177)

Figure 1.

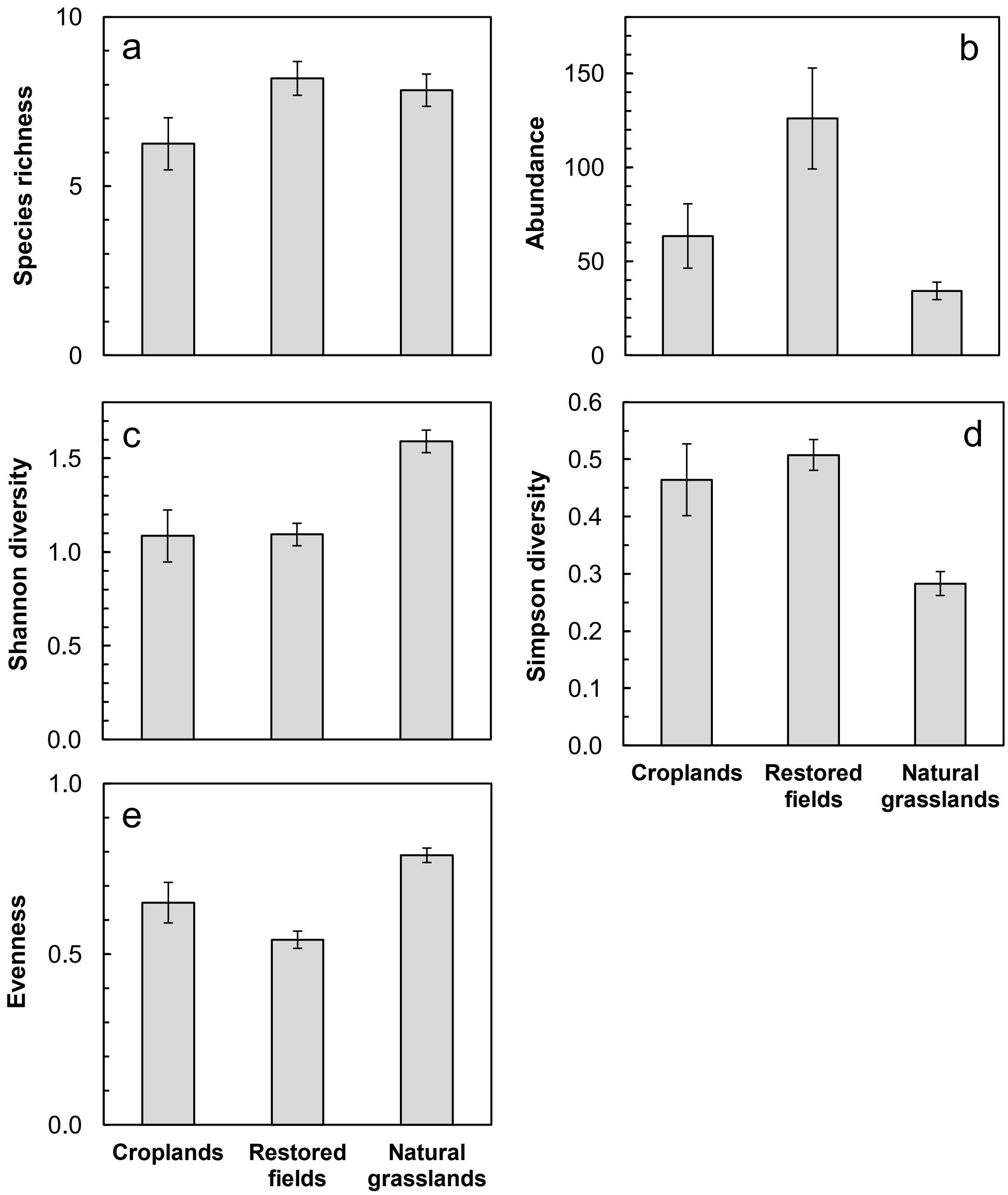
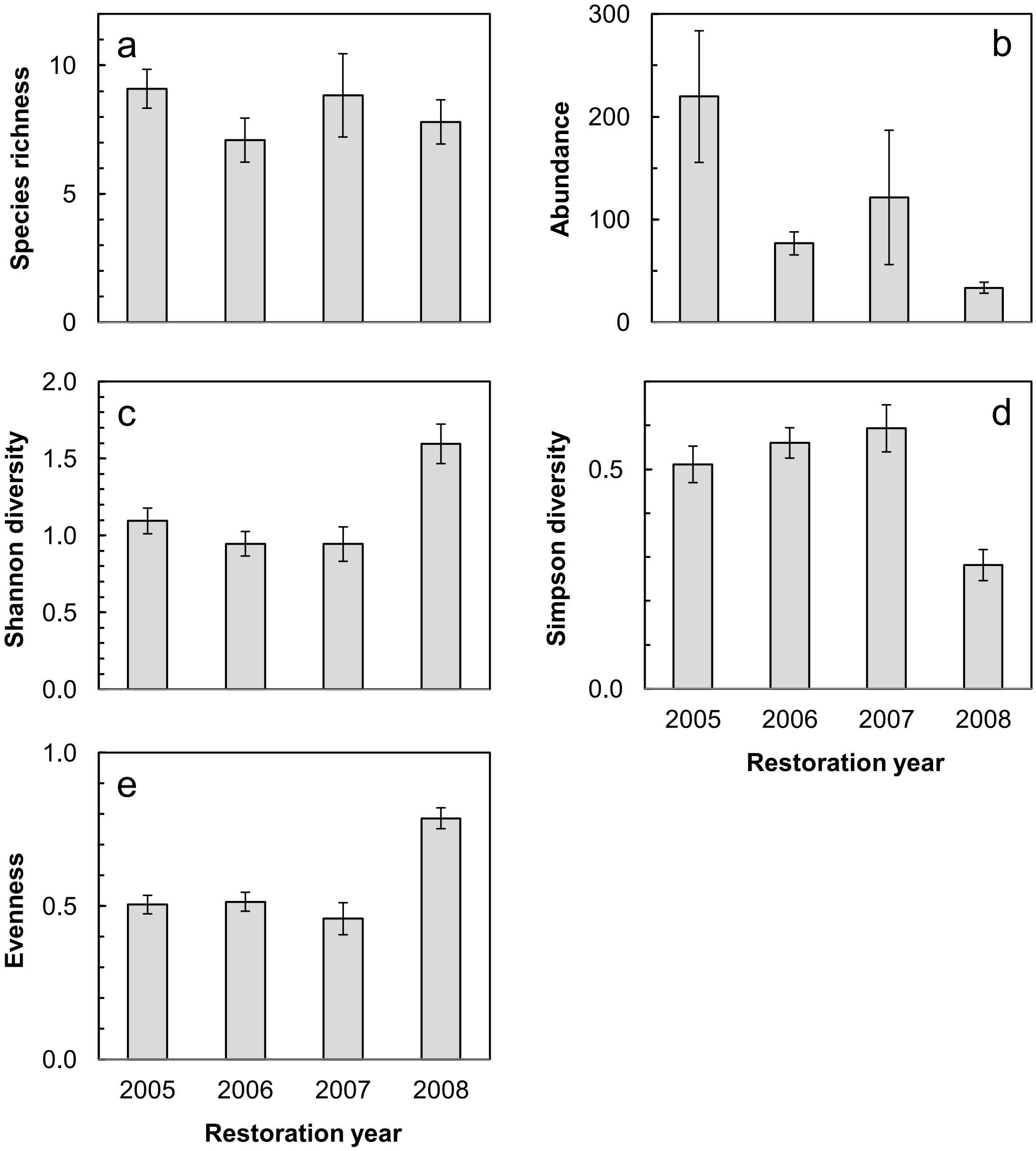

a
Species richness
0
5
10
b
Abundance
0
50
100
150
c
Shannon diversity
0.0
0.5
1.0
1.5
d
Simpson diversity
0.0
0.1
0.2
0.3
0.4
0.5
0.6
e
Evenness
0.0
0.5
1.0
Croplands
Restored fields
Natural grasslands

Figure 2.


a
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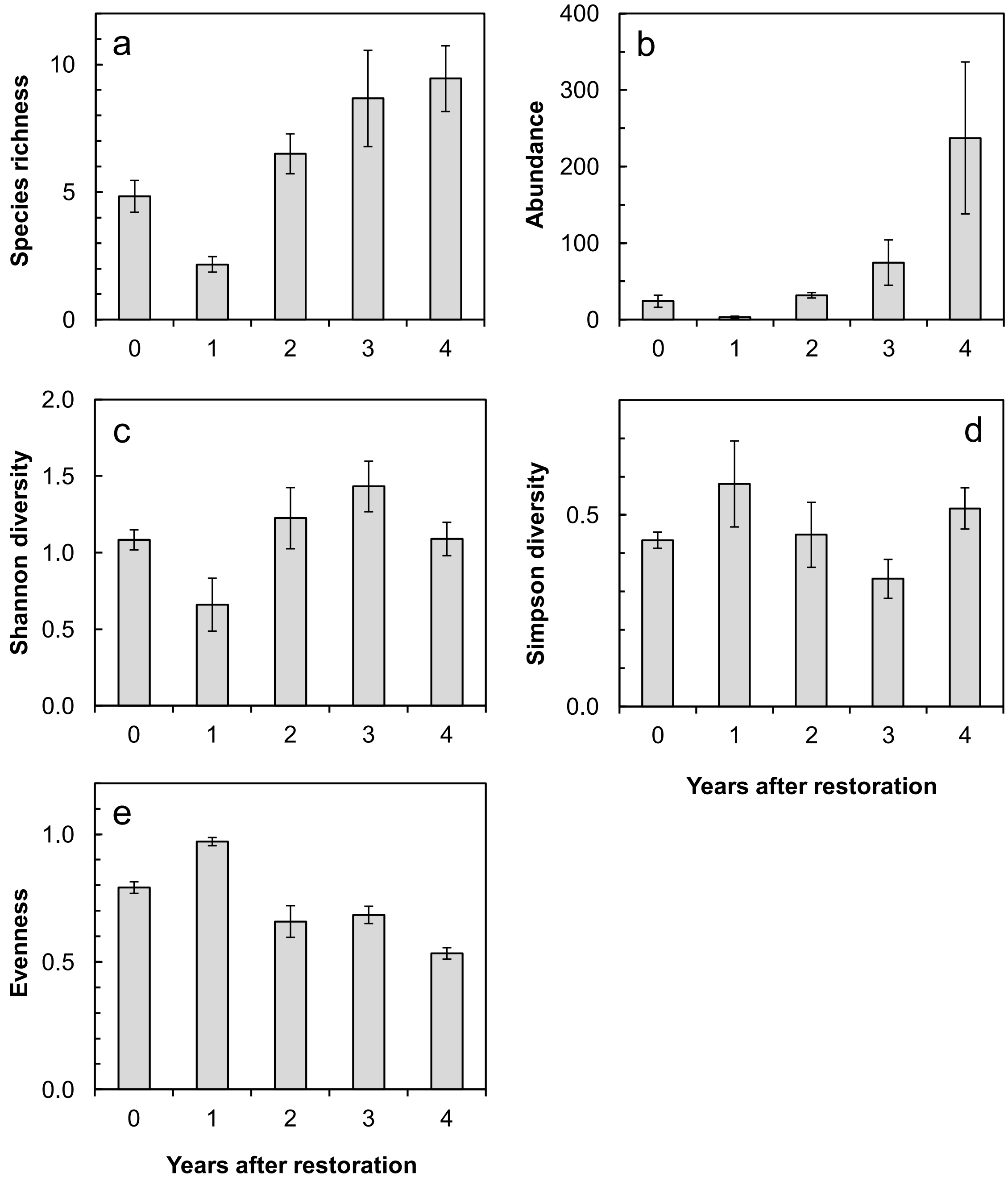
d
e
Species richness
Abundance
Shannon diversity
Simpson diversity
Evenness
0
5
10
100
200
300
0.0
0.5
1.0
1.5
2.0
2005
2006
2007
2008
Restoration year

Figure 3.


a
b
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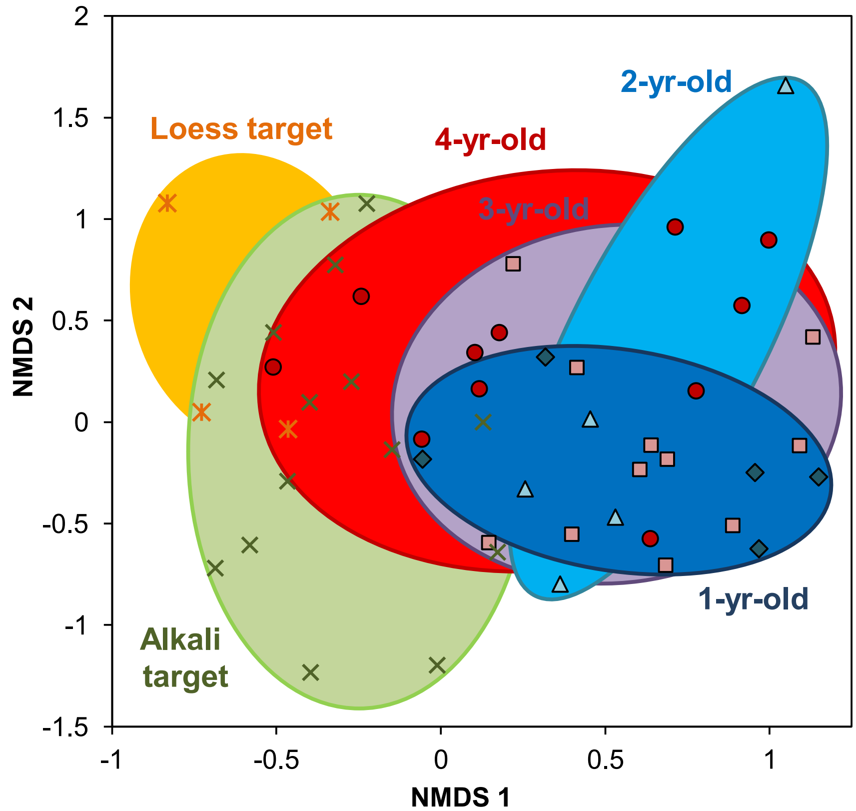
Species richness
Abundance
Shannon diversity
Simpson diversity
Evenness
Years after restoration
0
1
2
3
4
5
10
100
200
300
400
0.0
0.5
1.0
1.5
2.0

Figure 4.



2-yr-old
Loess target
4-yr-old
3-yr-old
1-yr-old
Alkali target
NMDS 2
NMDS 1
2
1.5
1
0.5
0
-0.5
-1
-1.5
-1
-0.5
0
0.5
1

TABLES

Table 1. Results of General Linear Models testing the effects of restoration conditions on Orthoptera assemblages using data collected in 2009 on fields restored in 2005-2008. Restoration conditions were (i) previous field history - Last crop with three levels (alfalfa, cereal, sunflower), (ii) restoration method - Seed mixture with two levels (alkali, loess), (iii) Time since restoration (Year 0 to 4) and (iv) Proportion of natural grasslands in a 1-km circular buffer zone around the sampling site. Results shown are from backward stepwise elimination of non-significant ($p > 0.05$) factors and covariates from the full model (Last crop + Seed mixture + Last crop * Seed mixture + Time since restoration + Proportion of natural grasslands). Significant effects are in Bold.

Response variable	**Predictor variable**	**df_{num}**	**df_{denom}**	**F**	**p**
Species richness	Last crop	2	26	0.541	0.589
	Seed mixture	1	26	0.030	0.864
	Last crop * Seed mixture	2	26	2.049	0.149
	Proportion of natural grasslands	1	26	2.684	0.113
Abundance	**Time since restoration**	**1**	**31**	**5.150**	**0.030**
Shannon diversity	**Time since restoration**	**1**	**30**	**4.560**	**0.041**
	Proportion of natural grasslands	1	30	2.600	0.118
Simpson diversity	Time since restoration	1	31	4.035	0.053
Evenness	**Time since restoration**	**1**	**31**	**9.075**	**0.005**

Table 2. Results of General Linear Models using repeated measures of seven sampling sites for five years, testing the effects of restoration conditions on Orthoptera assemblages. Restoration conditions were (i) previous field history - Last crop with two levels (alfalfa, cereal) and (ii) restoration method - Seed mixture with two levels (alkali, loess) as between-subject effects and time since restoration (Time as within-subject effect with five levels, with df adjusted by Huynh-Feldt's correction against deviations from sphericity when necessary). Significant effects are in Bold.

Response variable	**Predictor variable**	**df_{denom}**	**F**	**p**
Species richness	Last crop	4	0.322	0.601
	Seed mixture	4	0.269	0.631
	Time	**3.550**	**11.859**	**< 0.001**
Abundance *	Last crop	4	1.000	0.374
	Seed mixture	4	2.288	0.205
	Time	**4**	**45.048**	**< 0.001**
Shannon diversity	Last crop	4	0.380	0.571
	Seed mixture	4	0.095	0.773
	Time	**4**	**5.668**	**0.005**
Simpson diversity	Last crop	4	0.229	0.657
	Seed mixture	4	0.093	0.776
	Time	3.495	2.115	0.138
Evenness	Last crop	4	0.728	0.483
	Seed mixture	4	0.112	0.769
	Time	**3.668**	**38.355**	**< 0.001**

* log-transformed before analysis to correct for heteroscedasticity in the original data