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7   **Title:**

8   LOCAL HABITAT MANAGEMENT AND LANDSCAPE-SCALE RESTORATION

9   INFLUENCE SMALL MAMMAL COMMUNITIES IN GRASSLANDS

10

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26 **Short title:**

27 Effect of grassland restoration on small mammals

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29 **Word count** (excl. title page, references, tables and figures): 4302

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31 ABSTRACT

32 Ecosystem/habitat restoration has become a major goal of international biodiversity policy.

33 However, restorations are often limited in space or time, and we know little on whether and how

34 restoration and management affect vertebrates. Here we assessed the local and landscape-scale

35 effects of habitat restoration and management on small mammal communities in the Egyek-

36 Pusztakócs marsh system (Hortobágy National Park, Hungary), site of the largest active restoration

37 of grasslands on former croplands in Europe. We live-trapped mice, voles and shrews in spring and

38 autumn in 2 years (four sampling periods) at two sites in six habitat types: croplands, grasslands

39 restored three to six years earlier, and natural grasslands. Data on 421 individuals of 12 species

40 showed that restored grasslands were similar to croplands and natural grasslands in species richness,

41 abundance and composition. At the local scale, management influenced abundance because there

42 were more small mammals in unmanaged and early-mown grasslands with taller vegetation than in

43 late-mown or grazed grasslands with lower vegetation, or in ploughed croplands. Elevation was also

44 important because sites at higher elevation provided refuges during spring floods or summer

45 droughts. At the landscape scale, the proportion of restored and natural grasslands positively

46 affected the abundance of small mammals, whereas the proportion of linear habitats (roads, canals)

47 had a negative effect on abundance. Our results show that management is more important than

48 restoration per se at the local scale, which is expected for habitat generalists such as small mammals

49 in contrast to specialists such as plant-feeding invertebrates. However, restoration provides

50 landscape-scale benefits by increasing the area of grasslands which can serve as refuges for small

51 mammals in unfavourable periods. We thus conclude that a mosaic of restored and appropriately

52 managed grasslands with tall vegetation will provide the best chances for the persistence of small

53 mammal communities in dynamic landscapes.

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55 *Key-words*: community assembly, ecosystem services, grassland restoration, local extinction,

56 population dynamics, recolonisation, rodent, shrew

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INTRODUCTION

59

60 Agriculture and other human land uses have transformed the surface of Earth, resulting in the

61 decline, degradation and fragmentation of natural habitats (Lubchenco *et al.*, 1991). The restoration

62 of ecosystems/habitats can theoretically counter these processes (Young, 2000) but is rarely

63 implemented at spatial and temporal scales that are adequate to make a difference (Lengyel *et al.*,

64 2014; Woodcock *et al.*, 2010). Restoration has recently been incorporated as explicit targets into

65 relevant policy instruments (e.g. Aichi Biodiversity Targets, EU Biodiversity Strategy for 2020), yet

66 our knowledge on the design, implementation and impact of restoration remains limited in several

67 aspects. Habitat restoration is typically followed up by monitoring vegetation development, and

68 studies of trophic groups other than plants are scarce (Brudvig, 2011; Mortimer *et al.*, 1998;

69 Woodcock *et al.*, 2008). This is surprising because many invertebrate and vertebrate animals are

70 important for ecosystem functioning and a full evaluation of restoration success needs to integrate

71 higher trophic levels (animals) (Longcore, 2003; Young, 2000). Despite these calls, the number of

72 studies of restoration effects on vertebrates is still low and most of them focus on birds in forests

73 and shrubs (e.g. Brawn, 1998; Germaine and Germaine, 2002; Hoover, 2008; Machmer, 2002).

74

75 Small mammals (voles, mice and shrews) play important roles in ecosystems. Most voles and mice

76 are herbivores or granivores and several species hoard plant seeds for storage. Small mammals may

77 thus alter plant species composition (Howe and Brown, 2000; Torre *et al.*, 2007) and provide

78 ecosystem services such as seed dispersal (Mohammadi, 2010; Schnurr *et al.*, 2004; Williams *et al.*,

79 2001) and pollination (Vieira *et al.*, 2009). Subterranean small mammals play a role in maintaining

80 soil structure (Medin and Clary, 1989). Finally, small mammals are important in grassland food

81 webs, both as consumers or top-down regulators of vegetation and arthropods (e.g. most shrews are

82 insectivores), and as a food resource for reptiles, birds and mammals (Castién and Gonsálbez, 1999;

83 Mohammadi, 2010; Torre *et al.*, 2007; Vieira *et al.*, 2009).

84

85   The proportion of grasslands decreased considerably due to agriculture, and grasslands have

86   become the focus of many conservation actions in Europe (Hedberg and Kotowski, 2010; Kiehl *et*

87   *al.*, 2010) and North America (Gerla *et al.*, 2012). The impact of grassland restoration on small

88   mammals has been addressed in a handful of studies in North America. Stone (2007) found that

89   restoration led to a short-term decline in the number of captures, total biomass and species richness

90   of small mammals, followed by a partial recovery 3-5 years after restoration. A comparison of a

91   successional gradient from prairie to forest (Moro and Gadal, 2007) showed that time since

92   restoration (abandonment) did not directly affect small mammals and that their abundance was

93   highest in middle, rather than early or late, successional stages, where the structural diversity of

94   vegetation was highest. Finally, in the most comprehensive study of grassland restoration and small

95   mammals to date, Mulligan (2012) found that the colonization of restored fields occurred rapidly

96   and was positively related to the connectivity of habitats, and that restored grasslands served as

97   refuges during regional declines. Only the latter study involved a landscape context, which should

98   be addressed and considered in practice (Brudvig, 2011; Lengyel *et al.*, 2014) because local studies

99   may overlook larger-scale factors such as refuges and dispersal corridors that may influence

100   restoration outcome.

101

102   The aim of this study was to evaluate the local and landscape-scale effects of habitat restoration and

103   management on small mammal communities after a large-scale restoration of grasslands on former

104   croplands. We used a chronosequence design (space-for-time substitution) to sample small

105   mammals on natural grasslands (restoration target), restored grasslands (restoration process) and

106   croplands (restoration start). We then analysed the data to evaluate the effects of local factors

107   (management, elevation) and landscape configuration (proportion of natural grasslands, restored

108   grasslands, croplands, woodlands, and linear habitats such as roads and canals) on the species

109   richness, abundance, and composition of small mammal communities. We further tested whether

110 small mammal communities change with time since restoration, and also evaluated the links

111 between the dynamics of small mammal communities and the spatial and temporal changes in

112 habitats due to weather, restoration and management.

113

114 METHODS

115

116 **The Egyek-Pusztakócs marsh system and the sampling design**

117 Our study site was the Egyek-Pusztakócs marsh and grassland complex (4073 ha; N 47.54-47.62°,

118 E 20.86-20.99°) in Hortobágy National Park (eastern Hungary). Grassland restoration was carried

119 out in 2005-2008 on a total of 760 ha of former cropland by sowing of two seed mixtures after

120 ploughing, followed by mowing or grazing as post-restoration management. To our knowledge, this

121 is currently the largest non-spontaneous grassland restoration in Europe. More details on restoration

122 and vegetation development are given in Lengyel et al. (2012) and on changes in arthropod

123 communities in Déri *et al.* (2011) and Rácz *et al.* (2013).

124

125 We sampled small mammals (mice, voles and shrews) at 12 sites in three habitat types (**Table 1**):

126 two on croplands (wheat fields, starting point of restoration), eight on restored grasslands (process

127 of restoration) and two on natural grasslands (restoration targets). Within restored grasslands, four

128 levels of restoration age (3- to 6-year-old restorations) were replicated at two sites each (n = 8

129 sites). Sampling was conducted in the spring and autumn of 2011 and 2012 (four sampling periods

130 total). Spring 2011 was characterized by floods after snowmelt, whereas the spring and summer

131 were relatively dry (total precipitation: 350 mm). Significant precipitation in winter led to intense

132 floods in spring 2012 followed by a long drought (270 mm) between May and September (**Fig. S1**).

133 Sampling sites were at least 800 m away from each other to minimise spatial non-independence.

134 The sampled habitat patches ranged from 16 to 300 hectares in area [mean 66.6 ha ± standard

135 deviation (SD) 81.68]. None of the response variables (see below) showed significant correlations

5

136 with patch area (Spearman rank correlations, n.s.), therefore, we did not control for it in statistical

137 analyses. Sites were chosen to represent the management practices characteristic to the general area.

138 Restored grasslands chosen were managed either by mowing early in the season (June, n = 4 sites),

139 by mowing late in the season (August, n = 2) or by grazing by sheep (from April to November, n =

140 2) (Lengyel *et al.*, 2012). The two natural grasslands sampled were not managed, whereas the two

141 croplands were regularly ploughed. We also recorded elevation and vegetation height at each site.

142 Although the differences in elevation were small (89-91 m a.s.l.), lower-lying areas were more often

143 flooded and less suitable for small mammals than were higher plateaus. Elevation of the sites was

144 determined from a detailed topographic map (accuracy: 0.5 m). We also measured the height of

145 vegetation (accuracy 5 cm) 0.5 m from each trap in a random direction.

146

147 To characterise landscape configuration, we calculated the proportion of five habitat types

148 (croplands, restored grasslands, natural grasslands, woodlands, and linear habitats such as roads and

149 canals) at each sampling site. We used a habitat map prepared in 2010 of the entire Egyek-

150 Pusztakócs system as part of other studies and used ESRI ArcMap GIS 10.0 to calculate the

151 proportion of each habitat type in non-overlapping buffers of 400-m radius around each sampling

152 site.

153

154 **Small mammal sampling**

155 We live-trapped small mammals using Sherman live traps (H. B. Sherman Traps, Tallahassee,

156 Florida, U.S.). Sherman traps have been repeatedly found to perform as well or, more frequently,

157 better than other live traps in multi-species studies of small mammals (e.g. Anthony *et al.*, 2005;

158 Belant and Windels, 2007; Hayes *et al.*, 1996; Kaufman and Kaufman, 2007; Morris, 1968; Santos-

159 Filho *et al.*, 2006; Torre *et al.*, 2010), and were found to cause less mortality than other live traps

160 (Dizney *et al.*, 2008). Because Sherman traps may be less effective at capturing small shrews than

161 other live traps (Sibbald *et al.*, 2006), we performed all analyses with or without data on shrews

162 (i.e., mice and voles only). However, as the inclusion or exclusion of shrews led to qualitatively

163 similar results, we presented results based on the full dataset. Although Sherman traps are

164 particularly effective in combination with other types of traps (e.g. pitfall traps, Longworth traps) to

165 attain a full complement of small mammals found in a habitat (Sibbald *et al.*, 2006), our study did

166 not aim to find all species, rather, it aimed to characterise differences among habitat and

167 management types by an adequately high, appropriately replicated constant sampling effort

168 designed to achieve a reasonable compromise between the requirements of spatiotemporal

169 replication and on-site effort intensity.

170

171 At each site, we installed 36 traps in a 6×6 grid covering 1 hectare (distance between traps: 20 m).

172 We baited the traps with seed mixture (grains, sunflower) and bacon following the

173 recommendations of the trap manufacturer and our previous experience. Traps were operated for

174 five nights to ensure compatibility with the National Biodiversity Monitoring System of Hungary.

175 Five nights appeared appropriate because captures peaked on day 2-4 and decreased by day 5 (**Fig.**

176 **S2**). Total sampling effort amounted to 8640 trap-nights (36 traps×5 nights×12 sites×4 sampling

177 periods). The traps were checked twice a day (7:00-9:00, 18:00-20:00 hours). Before each check,

178 we counted potential avian predators in and 200 m around the sampling grids for 5 minutes from a

179 distance. Small mammals captured in the traps were identified to species and weighed. We marked

180 individuals by a permanent felt pen at the base of the tail to enable the detection of recaptures. Our

181 previous experience showed that this marking could be detected for at least a week.

182

183 **Statistical analysis**

184 Response variables were the number of species (species richness), and the number of individuals

185 (abundance) of small mammals (rodents, i.e., mice and voles, and shrews). For both response

186 variables, data from traps at one site (n = 36 traps) during one sampling period (n = 5 nights) were

187 pooled to obtain one datapoint per site and per period (total n = 48). Exploratory analyses revealed a

highly significant interactive effect of year and season on both species richness and abundance

(richness, $F_{1,33} = 43.918$, $p < 0.0001$; abundance, $F_{1,33} = 36.242$, $p < 0.0001$) because richness and

abundance increased substantially from spring to autumn in 2011 but not in 2012, while the effect

of location was not significant ($p > 0.32$). To evaluate the effects of local and landscape-scale

variables on the species richness and abundance of small mammals while also considering this

temporal fluctuation, we constructed generalized linear mixed-effects models (GLMMs) with

season (spring/autumn) nested within year as a random effect. GLMMs allow the incorporation of

nested random effects even when variances are unequal and within-group errors are correlated, and

are robust to unbalanced designs (Crawley, 2007). We fitted GLMMs using the 'glmer' function of

R with Poisson error distribution and log link function, as recommended for count data (R Core

Team, 2014). Local predictor variables were elevation (in m) and management (early mowing, late

mowing, grazing on restored grasslands, no management on natural grasslands, ploughing on

croplands). Landscape-scale predictor variables were the proportion of five habitat types in 400-m

buffers around the sampling sites. The five landscape-scale variables were not correlated (Pearson

correlation, n.s.). To allow for testing whether predictor variables had similar or different effects in

the four sampling periods, we also used sampling period as a fixed effect with four levels.

To test the effect of restoration age on small mammals, we repeated the GLMMs using data only

from restored grasslands. In these models, both the local and landscape-scale predictors described

above were included, and we also included the time since restoration (in years) to test whether and

how small mammal communities change after restoration. In all GLMMs, we started with the full

model including all main effects and their interactions with sampling period and removed non-

significant terms in a backward stepwise algorithm (removal if $p \geq 0.1$) to obtain minimum

adequate models. We then used the reduced model to estimate coefficients for predictors. For post-

hoc comparison of management, a categorical variable, we specified contrasts to compare each

management type to regularly ploughed croplands (restoration start) in the analysis of all sites, and

214   to grazing in the analyses restricted to restored sites. In additional statistical tests, data were log-

215   transformed (log x + 1) for parametric tests (one-way ANOVA), if necessary, to meet the

216   assumption of homogeneous variances. All statistical tests were implemented in R (version 3.1.1.).

217

218   RESULTS

219

220   In total, we captured 421 individuals of 12 species (full list of species and number of individuals

221   captured are given in **Table S1**). We detected 20 individuals of three species in the spring and 359

222   individuals of 12 species in the autumn of 2011. In 2012, we caught 24 individuals of five species

223   in the spring and 18 individuals of eight species in the autumn. Recapture rate was on average 9%

224   (n = 465 captures total) and ranged between 0 and 30% per site (n = 12). Recaptured individuals

225   were counted only once in all statistical analyses.

226

227   **Effects on species richness of small mammals**

228   GLMMs showed that species richness was little influenced by the local and landscape factors

229   studied. There was a weak interaction between sampling period and management (GLMM, $z =$

230   2.178, $p = 0.029$), likely because the number of species decreased less from autumn 2011 to spring

231   2012 in late-mown restorations than in other habitat types (**Fig. 1A**). Furthermore, there were

232   marginally non-significant effects of sampling period ($z = -1.907$, $p = 0.057$) and the interaction

233   between sampling period and elevation ($z = 1.915$, $p = 0.056$). The latter was mostly because small

234   mammals disappeared from autumn 2011 to spring 2012 in three of four sites under 90 m a.s.l. and

235   only one individual was found in the fourth site. In areas at or above 90 m, at least one individual

236   was caught in five of eight sites (total n = 23 individuals), suggesting higher chances for survival

237   during the harsh late winter and spring flooding in early 2012. Neither the remaining local and

238   landscape variables nor their interactions with sampling period influenced species richness

239   significantly.

Factors influencing small mammal abundance

At the local scale, the abundance of small mammals was significantly influenced by management, elevation, and interactions between sampling period and management and between sampling period and elevation (**Table 2**). Significant coefficient estimates showed that early-mown restorations had more individuals, whereas late-mown and grazed restorations had fewer individuals than ploughed croplands (**Table 2**), particularly when abundance was generally high (autumn 2011, **Fig. 1B**). The interaction between sampling period and management was because abundance decreased more from 2011 to 2012 in early-mown restorations than in late-mown restorations (**Fig. 1**). The interaction between sampling period and elevation was because the relationship between elevation and abundance was negative in autumn 2011 and slightly positive or constant in the three periods of lower abundance (**Fig. 2**).

In autumn 2011, when abundance was generally high, non-managed natural grasslands had taller vegetation (mean 5.8 ± S.D. 2.98 cm, n = 72 traps) than either early-mown (3.6 ± 2.18, n = 144), late-mown (3.5 ± 1.96, n = 72) or grazed restored grasslands (3.2 ± 1.99, n = 72) (one-way ANOVA on log-transformed data, $F_{3,356}$ = 12.060, p < 0.0001; Tukey HSD-test, p < 0.001 for each of the three comparisons), and thus probably provided better chances to avoid predators than did restored grasslands. This was supported by a negative correlation between average vegetation height and the number of predators in autumn 2011 (Pearson r = -0.695, n = 10 grasslands, p = 0.026). Predators most often recorded at the sites included Marsh Harrier *Circus aeruginosus*, Common Buzzard *Buteo buteo*, Kestrel *Falco tinnunculus* and Great Egret *Egretta alba*, and other potential predators observed in the vicinity were Red Fox *Vulpes vulpes*, Least Weasel *Mustela nivalis*, European polecat *Mustela putorius* and Steppe Polecat *M. eversmanii*.

265   At the landscape scale, the proportion of natural and restored grasslands influenced abundance

266   positively, whereas the proportion of linear habitats had a negative effect on abundance (**Table 2**).

267   None of the interaction terms between landscape variables and either sampling period or

268   management influenced abundance significantly.

269

270   **Differences by restoration age**

271   In the smaller sample of restored fields (n = 8), restoration age strongly influenced species richness

272   (GLMM, z = 29.020, p < 0.0001) because sites restored in 2005 had fewer species (1.3 ± SE 0.74)

273   than sites restored in later years (2006: 2.3 ± 0.67, 2007: 2.3 ± 0.80, 2008: 1.9 ± 0.99). Restoration

274   age also influenced the abundance of small mammals (**Table 2**), however, no consistent temporal

275   trend could be observed (2005: 5.4 ± 4.54 individuals, 2006: 13.3 ± 5.54, 2007: 6.3 ± 2.82, 2008:

276   8.4 ± 6.18).

277

278   Although the spatial distribution of captures was rather consistent across periods for common

279   species, species composition varied greatly in the four sampling periods due to rare species and

280   there was no sign of a clear separation in species composition either by habitat type, management or

281   restoration age (**Fig. S3**).

282

283   DISCUSSION

284

285   At the local scale, management had the largest influence on small mammals. The management

286   effect was mediated by vegetation height because sites with taller vegetation had more species and

287   individuals than sites with lower vegetation. Elevation was also important because higher areas

288   provided better chances for survival during unfavourable periods such as floods. At the landscape

289   scale, small mammals were influenced positively by the proportion of natural and restored

290   grasslands and negatively by the proportion of linear habitats. These results suggest that restored

11

291 grasslands can be important landscape-level refuges, although when conditions are favourable, e.g.

292 in autumn 2011, local management and not restoration or time since restoration *per se* appears

293 primarily important in shaping small mammal communities in grasslands. Our study is the first to

294 provide evidence of both local and landscape-scale factors influencing small mammal assemblages

295 after grassland restoration. The patterns found support the view that the effects of population

296 fluctuations and restoration are difficult to disentangle and that restorations play an unexpected but

297 important role as refuges during regional declines of small mammals (Mulligan, 2012).

298

299 Several results showed that restoration provided habitats that were comparable or better than

300 croplands for small mammals. Only three restorations and one cropland had small mammals after

301 the spring 2011 bottleneck, and only restorations and natural grasslands had small mammals after

302 the extreme summer drought of 2012. Moreover, the proportion of restored grasslands positively

303 affected small mammal abundance after the spring flood in 2011 and the summer drought of 2012.

304 These results show that in only three to six years, restoration can lead to grasslands that serve as

305 refuges for small mammals during unfavourable periods.

306

307 Our results also suggest that the effect of management was mediated by vegetation height.

308 Vegetation cover was highest in unmanaged areas, and was low in mown or grazed sites in autumn

309 2011, and predators were more numerous in sites with lower vegetation. These patterns may explain

310 the differences in small mammal abundance because vegetation provides safe microsites for the

311 movement, hiding, feeding or food gathering activities of small mammals (Moro and Gadal, 2007).

312 The risks of predation on small mammals both by birds and mammals are probably higher when

313 vegetation cover is low because small mammals can be more easily spotted and captured by

314 predators at sites with poor vegetation cover (Sutherland and Dickman, 1999). In extremely dry

315 years such as 2012, areas with higher vegetation cover probably also provided more abundant food

316 than areas which are mowed or grazed. A study in Switzerland found the highest density of small

mammals in non-mown grasslands (Aschwanden *et al.*, 2007), whereas an African study found that intensive grazing negatively affects the abundance and diversity of small mammals (Yarnell *et al.*, 2007). Consequently, the differences in abundance in relation to management found here are likely to exist due to the mediating effect of vegetation cover.

Our results showed that the large temporal, weather-driven fluctuations typical in small mammal communities (Butet *et al.*, 2006; Merritt *et al.*, 2001) may be modified by both local effects (elevation, management) and landscape-scale effects (proportion of restored/natural grasslands). Almost all species disappeared from lower-lying areas (< 90 m a.s.l.) during the winter, whereas populations of some species survived in higher areas. Higher areas may thus be particularly important refuges for several small mammal species during harsh winters and springs with extensive floods (Wijnhoven *et al.*, 2005). During the winter, small mammal populations typically decrease to a minimum due to the combined effects of predation, cold weather, food shortage or competition for resources (Aars and Ims, 2002; Hansen *et al.*, 1999). The chances of successful survival during the winter are highest in refuge patches where vegetation cover is high enough and food supply is adequate (van Deventer and Nel, 2006). Our observations followed these patterns because species richness and abundance increased with the proportion of restored or natural grasslands around the sites in each spring period, but they also provided further insight. For example, the connectivity of patches, as estimated by the proportion of linear habitats, negatively affected small mammal richness in spring 2012, likely due to the higher exposure of individuals to predators. These patterns suggest that homogeneous patches that are rich in natural and restored grasslands with no management or early mowing and that are poor in croplands, roads or canals thus can serve as refuges and can mitigate the fluctuations of small mammals.

The lack of a direct, local effect of restoration on small mammals is likely to be related to their broad food spectrum and life history traits (fast reproduction, good dispersal ability, quick

13

343 colonisation after local extinction etc.). The studied restoration led to the acceleration of secondary

344 succession in vegetation development towards the target natural grasslands, with grassland-

345 dominated vegetation forming as early as Year 2 after restoration (Lengyel *et al.*, 2012). The

346 species composition of arthropods (orthopterans, true bugs, spiders, carabid beetles) also changed

347 considerably from Year 1 to Year 2 because species characteristic to target grasslands appeared in

348 greater numbers in Year 2 and after (Déri *et al.*, 2011). In only four years, the species richness of

349 orthopterans (crickets and grasshoppers) has doubled and their abundance increased nearly ten-fold

350 on restored grasslands compared to croplands (Rácz *et al.*, 2013). The restoration of phytophagous

351 insects, most of which specialize on certain plants, positively correlated with the restoration success

352 of the vegetation in restored calcareous and mesotrophic grasslands (Woodcock *et al.*, 2010),

353 indicating that more specialized animal groups may more closely follow the vegetation restoration

354 process. The generally broad food spectrum and the life history characteristics of small mammals,

355 in combination with their weather-driven population dynamics, make it likely that the restoration of

356 small mammal communities does not correlate well with the restoration process of vegetation or

357 other animal taxa.

358

359 In conclusion, habitat management was primarily important in shaping small mammal communities

360 at the local scale and restoration had little effect locally. Management by mowing and grazing

361 decreased vegetation height, which increased predation risks on small mammals. However,

362 grassland restoration provided benefits to small mammals at the landscape scale by increasing the

363 total area of grasslands, which provide better conditions for the persistence of small mammals

364 during unfavourable periods. Grassland restoration and management should thus re-create a mosaic

365 of habitat types that combines restored and natural vegetation and no management in at least a

366 portion of the landscape to maximise the chances of persistence for small mammals. The policy

367 implications of our study are that both the local effects and landscape configuration should be

368 considered in the design of restoration and management, and in the monitoring of biodiversity and

369 ecosystem services. The restoration of small mammals as important providers of ecosystem services

370 should also consider the inherent spatiotemporal dynamics of populations that operates at the

371 landscape scale and that can be managed locally.

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496

498   **Table 1.** General characteristics, local and landscape factors of sampling sites. Grassland: natural grasslands, restoration: restored grasslands, linear
499   habitats: roads, canals.

Sampling site	Habitat type	Year restored	Area (ha)	Local factors		Landscape factors: Proportion of				
				Elevation (m)	Management	Cropland	Grassland	Restoration	Linear	Woodland
Sóút É szántó	cropland	–	60	90.5	ploughing	0.99	0.00	0.00	0.00	0.00
Kilátó szántó	cropland	–	50	90.0	ploughing	0.56	0.29	0.00	0.02	0.00
27 ha-os gyep	restoration	2005	27	89.5	mowing early	0.22	0.21	0.32	0.01	0.01
Hagymás-hát	restoration	2005	26	91.0	sheep-grazing	0.00	0.08	0.36	0.00	0.00
Górés észak	restoration	2006	48	90.0	mowing early	0.00	0.03	0.86	0.02	0.04
Nyírházi halom	restoration	2006	28	91.0	mowing early	0.00	0.24	0.67	0.02	0.04
Csepregi szántó	restoration	2007	46	89.0	mowing late	0.00	0.06	0.60	0.00	0.00
K Csepregi	restoration	2007	21	90.0	mowing late	0.00	0.36	0.41	0.01	0.01
Csattag ÉK	restoration	2008	28	89.5	mowing early	0.00	0.00	0.59	0.00	0.00
Görbeszék-halom	restoration	2008	16	90.0	sheep-grazing	0.06	0.47	0.35	0.00	0.02
Csattag-hát	grassland	–	300	89.0	none	0.00	0.77	0.00	0.00	0.00
Fekete-rét DK	grassland	–	150	90.0	none	0.00	0.99	0.00	0.01	0.00

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Table 2. Results of generalized linear mixed-effects models testing the effects of management, elevation and landscape variables on abundance of small mammals (random effect: season within year) in all sites and in restored grasslands only. Significant effects are highlighted in Bold.

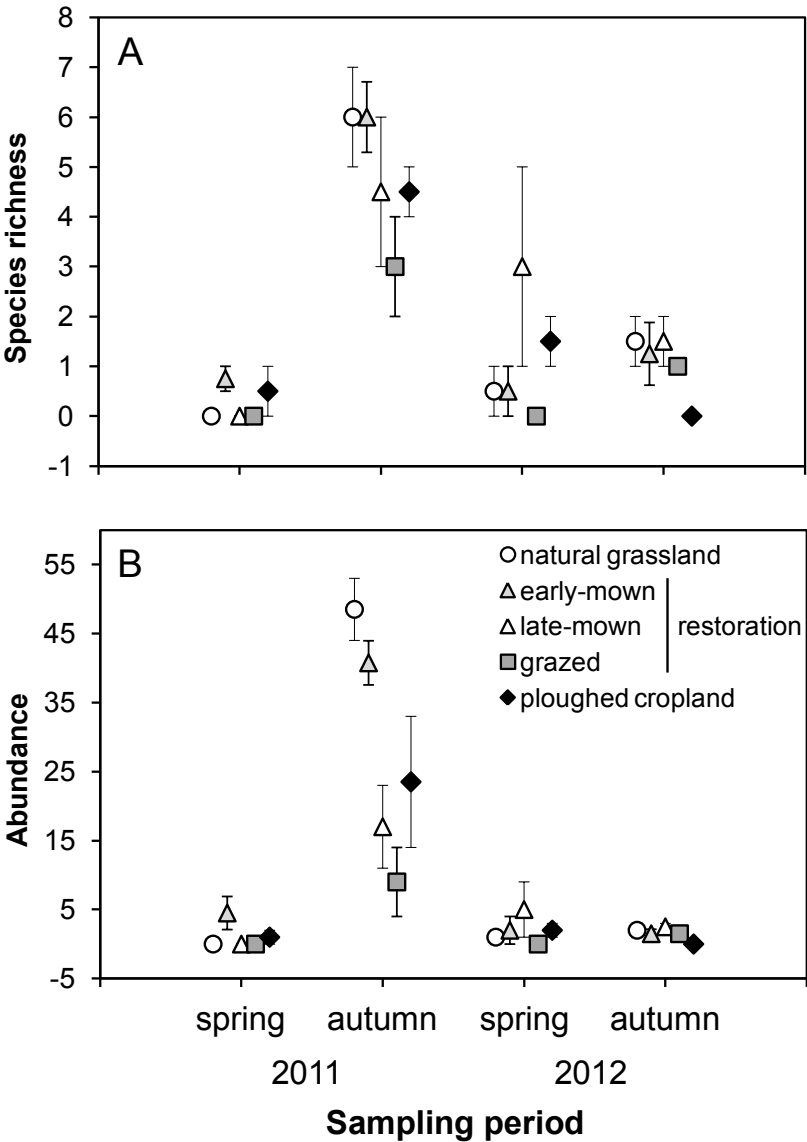| Response	Species richness	Estimate ± S.E.	z value	Pr(>|z|)
Abundance (all sites)	(Intercept)	79.52 ± 37.444	2.124	0.034
	Sampling period	**-44.31 ± 16.942**	**-2.616**	**0.009**
	Management$_{None}$	-0.08 ± 0.560	-0.140	0.888
	Management$_{Early-mown}$	**1.99 ± 0.417**	**4.762**	**< 0.0001**
	Management$_{Late-mown}$	**-2.20 ± 0.514**	**-4.275**	**< 0.0001**
	Management$_{Grazed}$	**-1.80 ± 0.677**	**-2.659**	**0.008**
	Elevation	**-0.89 ± 0.417**	**-2.106**	**0.035**
	Proportion of grassland	**1.85 ± 0.817**	**2.269**	**0.023**
	Proportion of restoration	**1.59 ± 0.703**	**2.262**	**0.023**
	Proportion of linear habitats	**-35.78 ± 11.824**	**-3.026**	**0.002**
	Period × Mgmt$_{None}$	0.07 ± 0.204	0.344	0.731
	Period × Mgmt$_{Early-mown}$	**-0.64 ± 0.186**	**-3.452**	**0.001**
	Period × Mgmt$_{Late-mown}$	**0.88 ± 0.208**	**4.238**	**< 0.0001**
	Period × Mgmt$_{Grazed}$	0.24 ± 0.285	0.830	0.407
	Period × Elevation	**0.49 ± 0.188**	**2.609**	**0.009**
Abundance (restored sites)	**Sampling period**	**-34.76 ± 17.135**	**-2.028**	**0.043**
	Management$_{Early-mown}$	**2.11 ± 0.395**	**5.343**	**< 0.0001**
	Management$_{Late-mown}$	**-0.97 ± 0.460**	**-2.100**	**0.036**
	Elevation	-0.36 ± 0.430	-0.831	0.406
	Restoration age	**-0.47 ± 0.146**	**-3.204**	**0.001**
	Proportion of cropland	**3.56 ± 1.670**	**2.132**	**0.033**
	Proportion of linear habitat	**29.24 ± 14.529**	**2.012**	**0.044**
	Period × Mgmt$_{Early-mown}$	**-0.68 ± 0.173**	**-3.914**	**< 0.0001**
	Period × Mgmt$_{Late-mown}$	**0.57 ± 0.188**	**3.006**	**0.003**
	Period × Elevation	**0.39 ± 0.190**	**2.027**	**0.043**

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19

507   FIGURE LEGENDS

508

509   **Figure 1.** Mean ± S.E. species richness (A) and abundance (B) in unmanaged natural grasslands,

510   early-mown, late-mown and grazed grassland restorations and ploughed croplands in four sampling

511   periods. Datapoints were jittered along the X axis for clarity.

512

513   **Figure 2.** Relationships between abundance of small mammals and elevation. Spring datapoints

514   were jittered along the X axis for clarity and lines are for visual guidance only (please see statistics
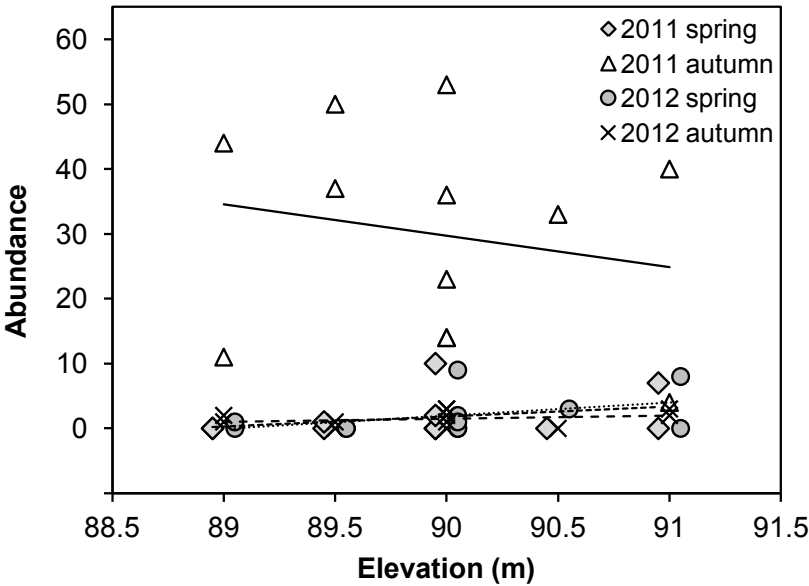
515   in Table 2).

516

517   Figure 1

518

519

Figure 2

523 SUPPORTING INFORMATION

524 Additional Supporting Information may be found in the online version of this article at the

525 publisher's web-site.

526 (see below)

527

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529
530 SUPPORTING INFORMATION
531
532 to accompany "Local habitat management and landscape-scale restoration influence small mammal
533 communities in grasslands" by Mérő et al.
534
535 **Contents:**
536 WEATHER INFORMATION: Fig. S1
537 SUPPORTING INFORMATION RESULTS
538 Number of daily captures: Fig. S2
539 Species and individuals captured: Table S1
540 Changes in species composition: Fig. S3
541
542
543 WEATHER INFORMATION
544
545 The study site is characterised by a continental climate with large annual fluctuations in weather.
546 The mean annual temperature is 9.5 °C and the mean total annual precipitation is 550 mm. We
547 sampled small mammals in the spring (March-April) and autumn (September-October) of both 2011
548 and 2012 (four periods total). Spring 2011 was characterised by high water and large flooded areas
549 due to extremely high precipitation in 2010 (**Fig. S1**; total 2010 precipitation in Hortobágy region:
550 950 mm, source: Hungarian Meteorological Service, http://www.met.hu). Summer 2011 was dry
551 (total precipitation: 350 mm) and water receded gradually from all grasslands. Winter 2011/2012
552 again brought significant precipitation (**Fig. S1**) and intense flooding at snowmelt. Summer 2012
553 had a long drought (total precipitation 270 mm), with hardly any rain in August and September
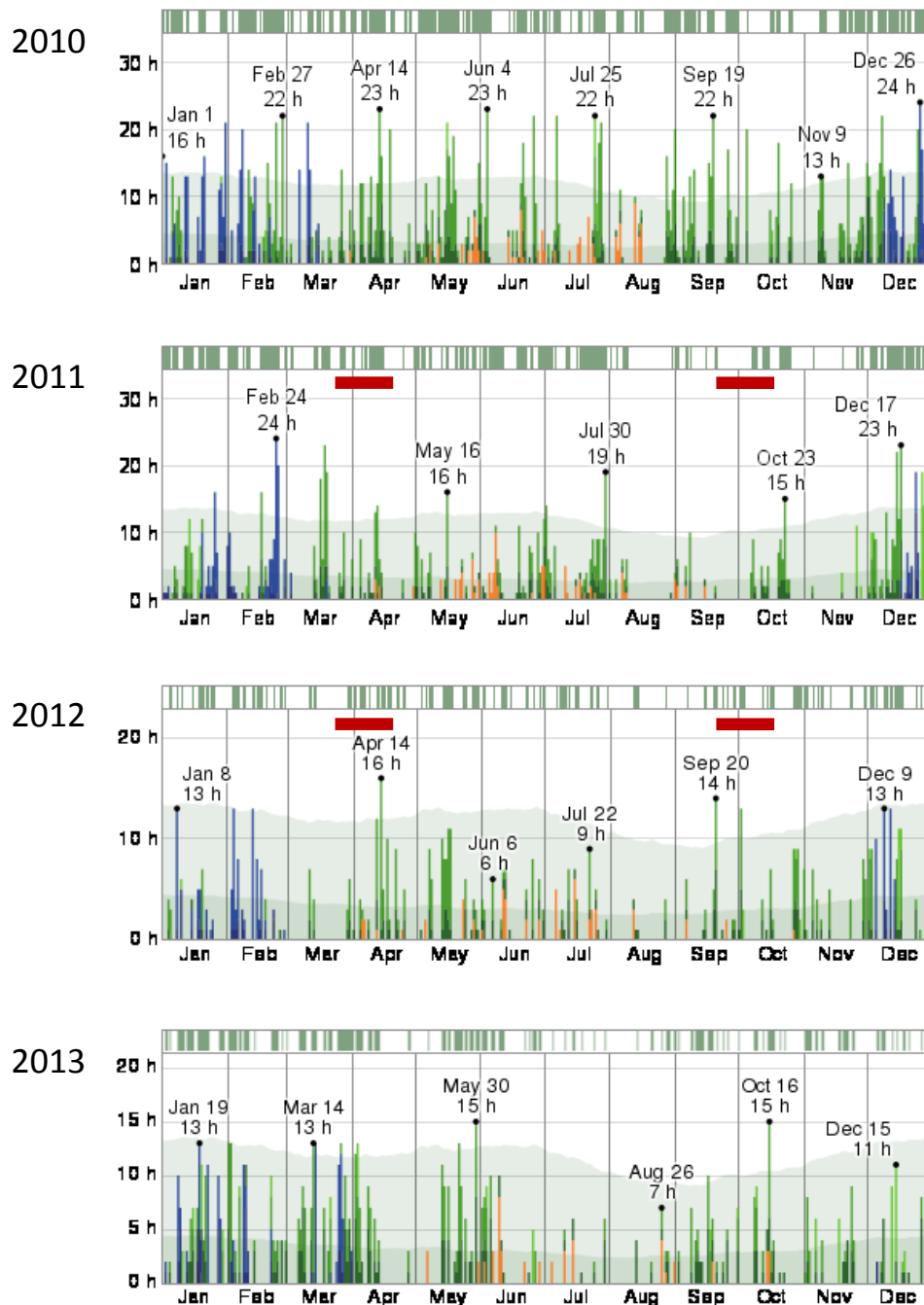554 (**Fig. S1**).
555

Figure S1. The number of hours per day with precipitation assembled from hourly present weather reports (days/months on the horizontal and hours of the day on the vertical axis) from the closest weather station with detailed measurement (Debrecen airport, c. 50 km E from the study site). Colour coding: green - rain; blue - snow, orange - thunderstorms, light blue shaded area - climate normals (average probability of precipitation per day). Bars at the top of the graphs indicate days with any precipitation (green) or no precipitation (white). Dark red horizontal bars in 2011 and 2012 indicate the sampling periods, data for 2010 and 2013 are shown for comparison only. Source: WeatherSpark (http://www.weatherspark.com).

SUPPORTING INFORMATION RESULTS

Number of daily captures

The number of individuals captured per day was highest on day 4 (croplands and restored grasslands) or on day 3 (natural grasslands) and decreased by day 5 in each of the three habitat types (**Fig. S2**).
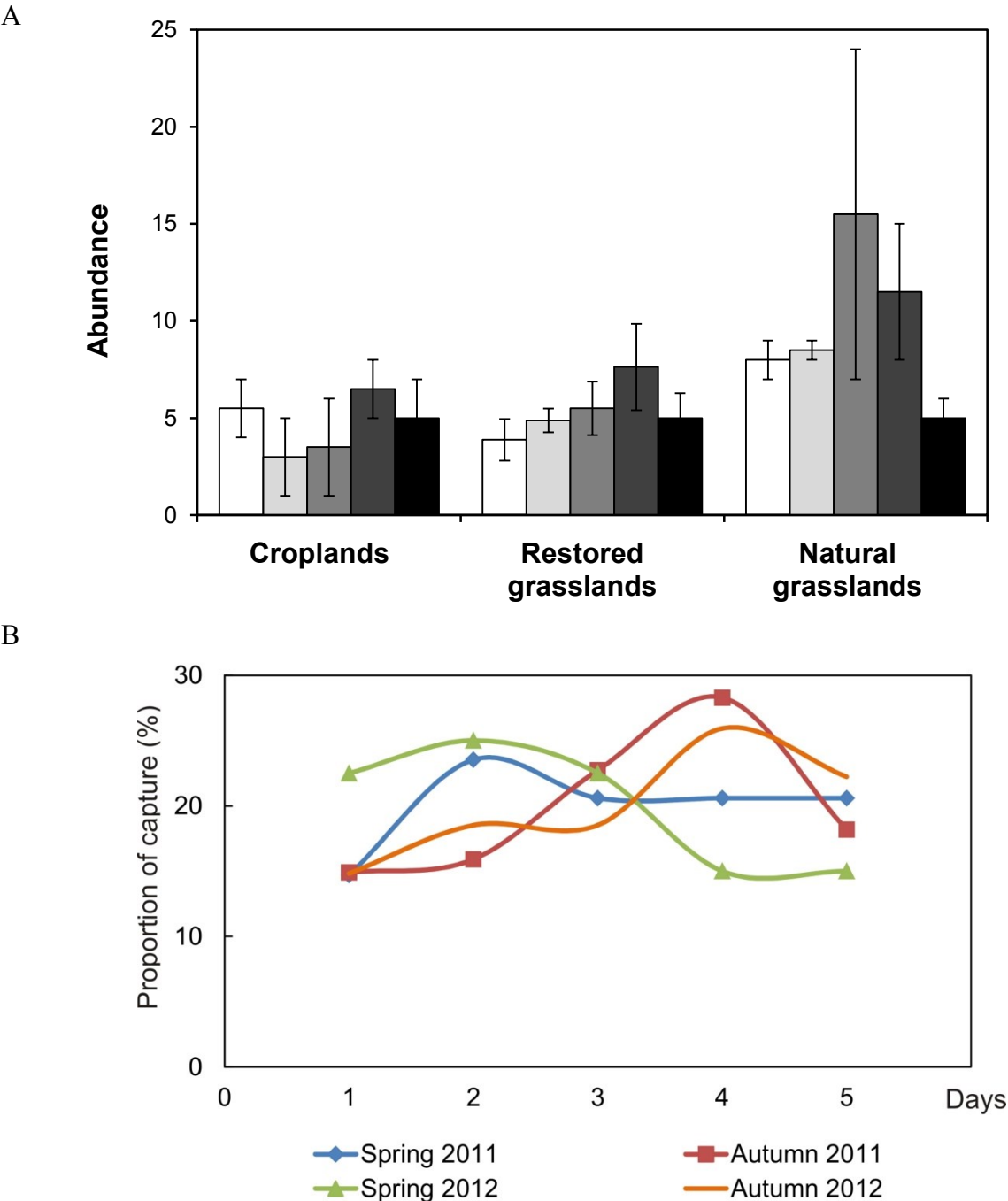
A

B

Figure S2. Mean ± S.E. number of individuals captured on day 1 (white columns) through day 5 (black column) in three habitat types based on n = 421 individuals, with recaptures (n = 44) excluded (A), and proportion of all captures falling on day 1 through 5 in the four sampling periods (B).

Species and individuals captured

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604

605 **Table S1.** Number of males, females and juveniles by species caught in the four sampling periods.

Species	Year	Season	Males	Females (gravid/lactating)	Juveniles (males/females)
Sorex araneus	2011	spring			
		autumn	3	4	
	2012	spring			
		autumn	1	1	
S. minutus	2011	spring			
		autumn	1	3 (1)	
	2012	spring			
		autumn		2	
Crocidura leucodon	2011	spring		1 (1)	
		autumn	12	47 (7)	1 (0/1)
	2012	spring			
		autumn			1 (0/1)
C. suaveolens	2011	spring			
		autumn	2	5 (2)	
	2012	spring			
		autumn		1	
Apodemus agrarius	2011	spring			
		autumn	15	16	3 (1/2)
	2012	spring			
		autumn	3		
A. flavicollis	2011	spring			
		autumn	1		
	2012	spring			
		autumn		1	
A. sylvaticus	2011	spring			
		autumn	7	6 (1)	5 (3/2)
	2012	spring		1	
		autumn			
A. uraliensis	2011	spring			
		autumn	2		
	2012	spring		2	
		autumn		1	
Mus spicilegus	2011	spring	2		
		autumn	6	6	
	2012	spring	2	1	
		autumn			
Micromys minutus	2011	spring			
		autumn		3	
	2012	spring			
		autumn			
Microtus arvalis	2011	spring	8	9 (3)	
		autumn	35	100 (47)	58 (12/46)
	2012	spring	7	8 (1)	
		autumn		3 (1)	6 (2/4)
M. subterraneus	2011	spring			
		autumn		3	1 (1/0)
	2012	spring			
		autumn			
Total	2011	spring	10	10 (4)	0
		autumn	84	193 (58)	68 (17/51)
	2012	spring	12	12 (1)	0
		autumn	2	9 (1)	7 (2/5)

Changes in species composition

We compared the small mammal species composition of restored and natural grasslands and
croplands by non-metric multidimensional scaling (NMDS) using Sørensen similarity as
implemented in the 'metaMDS' function of the R package 'vegan' (Oksanen et al. 2011).

Ordination based on NMDS showed that species composition varied greatly through the four
sampling periods (**Fig. S3**). There was no sign of a clear separation of species composition of the
sites either by habitat type or management. The extent of the scatter of centroids confirmed that
species composition was most diverse in autumn 2011, in the period of highest abundance, followed
by 2012 autumn and the two spring periods (**Fig. S3**).
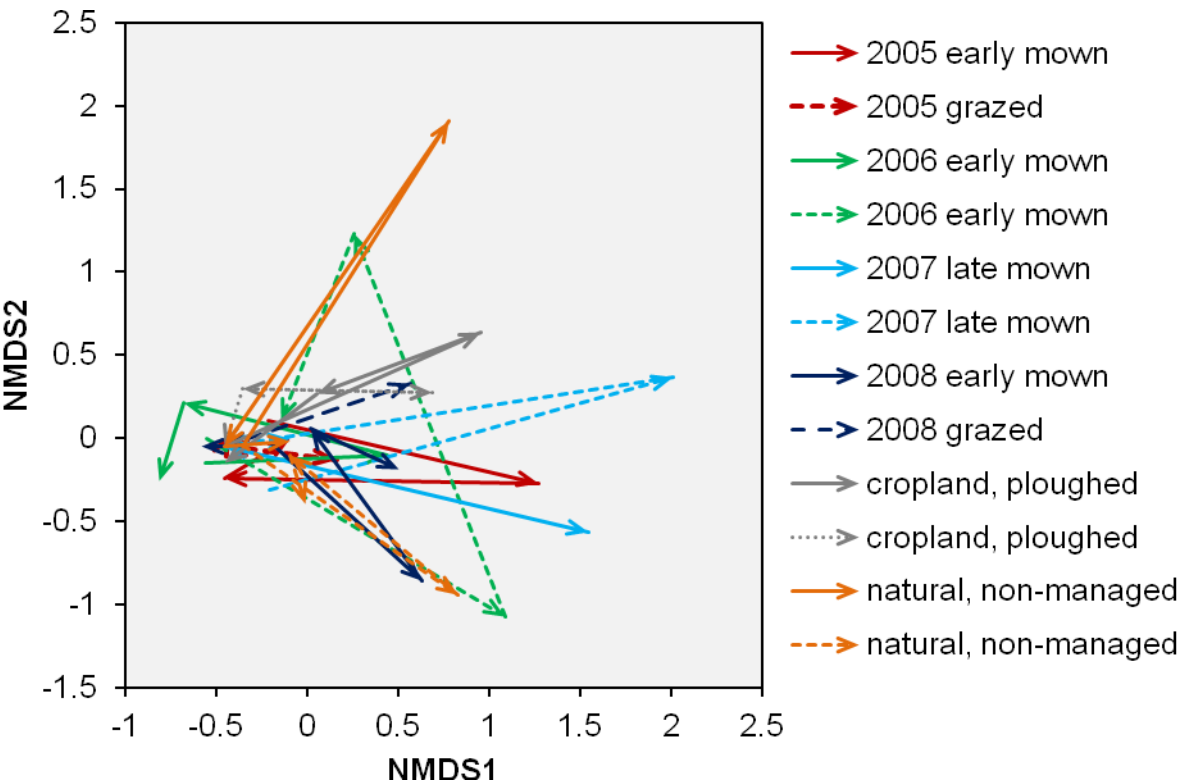

Figure A3. Changes in species composition of small mammals on restored grasslands (indicated by
year of restoration and management), croplands and natural grasslands in four sampling periods
from spring 2011 to autumn 2012. Symbols are omitted for clarity and arrows indicate temporal
trends (trajectories) at the 12 sampling sites. Ordination was conducted by non-metric
multidimensional scaling using Sørensen similarity based on the presence/absence of species
(stress: 0.130).