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1 **The implications of seed rain and seed bank patterns for plant succession at the edges of**
2 **abandoned fields in Mediterranean landscapes**

3
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24 **Abstract**

25 Some environmental variables and above-ground vegetation, seed rain, ant-borne seeds and
26 seed banks were studied on three abandoned fields, at the margins between these fields and a
27 remnant patch of a native steppe vegetation of a high value for nature and species
28 conservation. While the fields were the same size, were adjacent to the same patch of
29 remnant steppe and were cultivated with the same crop, site-specific environmental variables
30 contributed to 23% of the vegetation patterns; each site was characterised by its unique
31 historical trajectory and thus, by a particular set of species. Distance from boundaries
32 contributed to 10% of the vegetation patterns. Species characterising the surrounding steppe
33 were found close to boundaries; species characterising abandoned fields were found further
34 away. Winter seed banks and summer deep seed bank did not contribute much to either effect
35 and were characterised by species dating back from past cultivation. Conversely, summer
36 surface seed bank greatly contributed to (83%) the differences in species composition
37 between the three fields. Seed rain contributed to differences in species composition between
38 fields (91%) and distance (76%). Ant-borne seeds largely contributed to the differences
39 between fields (87%). The colonisation of steppe species on field margins occurs mainly
40 through seed rain and is very slow and incomplete. In a semi-arid fragmented open-
41 landscape, patches of native vegetation do not play a great role in colonisation processes, and
42 itinerant sheep grazing is insufficient to initiate recovery.

43

44 *Keywords:* ants; dry grassland; mosaic of herbaceous communities; seed bank; seed rain;
45 steppe

1. Introduction

While many studies on grazing, mowing and burning regimes have been carried out to plan conservation management for individual grasslands (Hillier et al., 1990; Poschlod and WallisDeVries, 2002), only few studies plan for long-term management within fragmented open-landscapes and studies on secondary succession and edges have yet to be relevant to long-term management. Studies focusing on edges assessed either the influence of agriculture-related factors on field-margin vegetation (Kleijn et al., 1997) or the influence of field-margin vegetation on crops (Dutoit et al., 1999; Von Arx et al., 2002).

Investigating colonisation processes at edges of abandoned fields is important (Wilson and Aebischer, 1995) because the field potential to recover via long-term seed bank or long-distance seed rain has often been found to be relatively low in Northern Europe (Graham and Hutchings, 1988; Hutchings and Booth, 1996a; Kalamees and Zobel, 2002). Studying edges is even more important in dry climates, where drought induces conditions that dramatically slow down successional processes (Blondel and Aronson, 1999). Results may have important conservation implications, particularly in the Mediterranean basin where grasslands harbour a high proportion of endangered taxa (Médail and Quézel, 1999).

The hypothesis of this research was that remnant patches of vegetation are a source of seeds for the colonisation of abandoned fields either by seed rain or ant dispersal. The aims of the present study were (1) to describe the colonisation processes on abandoned field margins over a complete growing season in order to determine how steppe vegetation re-establishes at the margins between abandoned fields and a remnant patch of steppe in order (2) to provide information for the long-term management of abandoned fields.

2. Methods

2.1. Study area

The study was carried out in the plain of La Crau, located ~50 km north-west of Marseille in south-eastern France. The steppe vegetation of the plain evolved with: 1) a dry Mediterranean climate; 2) a shallow soil (<400 mm) and an impermeable bedrock; 3) itinerant sheep grazing since 3000 BP (Buisson and Dutoit, 2004). The steppe vegetation is dominated by the stress-tolerant species *Brachypodium retusum* and *Thymus vulgaris*, which represent ~50% of the biomass, and is composed of a great diversity of annual species (Buisson and Dutoit, in press). The remnant central patch of steppe was fragmented by row crop and melon cultivations between 1965 and 1985, after which all patches of steppe and fields were grazed by itinerant sheep from February to June.

Three abandoned fields (A, B, C) were selected on the sheepfold of Peau de Meau (43°33'E 4°50'N, elevation 10m), in the centre of the plain. All fields were adjacent to one same remnant patch of undisturbed steppe (D) in order to avoid confounding changes in the floristic composition on the margins of abandoned fields with differences due to species composition of steppe patches (Römermann et al., 2005). However, fields had varied cultivation periods, dates of abandonment and locations given in Table 1.

2.2. Sampling

On each studied field (A, B, C), three transects (1, 2, 3) were set out perpendicular to the field boundary. Each transect started at the boundary and stretched towards the centre of abandoned fields and measured 10 m because the visible gradient of the typical steppe perennial species *T. vulgaris* % cover never exceeded 10 m. The three transects per field were laid 10 m apart because most herbaceous species do not disperse by wind over more

94 than a few meters (Verkaar et al., 1983), especially in the plain were vegetation grow very
95 low. Collection points were set 1 m apart along the transects starting at the field edge (point
96 0) between steppe and fields (0 to 10 m; 11 samples). All data were collected in 2001, a year
97 with an average climate.

98 Above-ground vegetation was recorded in 10 sub-quadrats of 40 × 40 cm at each
99 sampling point totalling 990 sub-quadrats, in May 2001. *T. vulgaris* and *B. retusum* % cover,
100 as well as stones, vegetation and bare ground % cover were visually estimated by one
101 observer in each quadrat. All other species were sampled in each quadrat using the
102 presence/absence method. To avoid disturbing the vegetation, other sampling was taken on
103 the other side of the transects.

104 200g of soil was taken at sampling points 0, 5 and 10 m along each transect in
105 February 2001 (27 samples total). Samples were dried and sieved through a 200 µm mesh
106 sieve. Total nitrogen was measured using the Kjeldahl method, phosphorus using the Olsen
107 method and total carbon using the Anne method (Baize, 2000). The concentrations of
108 calcium, potassium and magnesium available to plants were measured using the
109 Shollenberger and Dreibelbis method (Baize, 2000). The soil pH was also measured in H₂O
110 (Baize, 2000).

111 The persistent seed bank, seeds that persist in the seed bank >1year, (Thompson et al.,
112 1997) was sampled in February 2001 before the input of fresh seeds and after the
113 germination of most seeds in the fall and winter. To deduce the transient seed bank, the
114 summer seed bank, seeds that persist in the seed bank <1year, (Thompson et al., 1997), was
115 sampled at the beginning of July 2001 after seeds were shed. Cores could not be taken
116 because the soil was extremely rocky. For each sampling point, two 500 cm³ containers were
117 filled, one for the 0-10 cm depth and one for the >10 cm depth (198 samples for summer and
118 198 for winter seed bank). The volume of soil sampled was 1500 cm³/soil layer/field/distance
119 from the boundary; the volume recommended by Bakker et al. (1996) was 1200 cm³. The 396
120 samples of soil seed bank were set to germinate using the standard procedure recommended
121 by Ter Heerdt et al. (1997). Soil samples were washed with water on sieves of 4 mm and 200
122 µm mesh sizes to reduce bulk and clay. The concentrated soil was spread in a thin layer in
123 trays filled with 20mm of vermiculite and topped with medical compresses of 100 µm mesh
124 size. Trays were watered every day from below. Emerged seedlings were identified, counted
125 and removed weekly.

126 Seed rain was sampled from April 15th to October 15th 2001. Sticky traps, made of
127 paper filters coated with grease and placed in 140 mm diameter Petri dishes (Hutchings and
128 Booth, 1996a), were fixed with pegs at all sampling points along the transects. Sticky papers
129 were changed every two weeks (1287 traps total). Seeds were identified to the species or
130 genus level under a dissecting microscope using a reference collection.

131 To assess ant seed dispersal from the steppe to the abandoned fields, ant pitfall traps
132 were set out at all sampling points along the transects. These traps, consisting of 50 mm
133 diameter × 100 mm high containers, were filled with a non-attractive liquid of 50% glycol to
134 conserve seeds and reduce evaporation, 49% water, 1% acetic acid to act as an anti-fungic
135 and a few drops of tensioactive detergent to make the ants sink. Traps were changed every
136 two weeks from April 15th to October 15th 2001 (1287 traps total). Seeds were identified to
137 the species or genus level and harvesting ants (*Messor barbarus* and *Messor sanctus*) were
138 identified and counted.

139

140 2.3. Data analyses

141 Multivariate analyses were used to study simultaneously the complex relationships among
142 species, and between the species and their environment. A partial canonical correspondence
143 analysis pCCA (Ter Braak, 1987) was used to determine 1) the relationship between the
144 above-ground vegetation and a set of environmental variables once the impact of distance
145 variables was statistically removed; and 2) the relationship above-ground vegetation and the
146 distance from boundaries once the impact of the environmental variables was statistically
147 removed (McIntyre and Lavorel, 1994). The above-ground vegetation data and some
148 environmental variables (pH, P₂O₅, C:N, K₂O and % cover of vegetation) were used at points
149 0, 5 and 10 m from boundary.

150 To identify which of the six data-sets best contributed to the composition of the
151 above-ground vegetation, a K-sets principal component analysis was used (K-sets PCA,
152 Pagès and Escofier, 1994). Classical multivariate approaches consider alternatively: i) as
153 many separate PCAs as there are data-sets, but the interpretation is doubtful as it is based on
154 empirical comparisons of separate analyses; ii) a unique overall PCA of all six data-sets,
155 although some may weigh more than others in the analysis. A K-sets PCA allowed us to
156 analyse all six data-sets by weighting differently each variable so that they played a balanced
157 role in the analysis. Separate PCAs were first conducted for each data-set and then the
158 inverse of the first eigenvalue was used as a weighting coefficient for the global K-PCA
159 analysis (Pagès and Escofier, 1994). Computations for the pCCA and the K-sets PCA were
160 performed using ADE4 software (Thioulouse et al., 1997)

161 To explain plant distribution at field margins, the means per distance (n=9 transects)
162 were calculated for (1) soil variables (2) total and steppe-only species richness and density of
163 above-ground vegetation, seed rain, seeds in ant-traps, summer and winter surface and deep
164 seed banks. Data were directly compared or log₁₀ transformed (Sokal and Rohlf, 1998)
165 before being compared with one-way ANOVAs (Statistica software, version 6.0), followed
166 by post-hoc tests (Least Significant Difference). Non-parametric multiple comparisons by
167 STP tests (Simultaneous Test Procedure, based on Mann-Whitney U test, Sokal and Rohlf,
168 1998) were performed on non-normal data.

169

170 3. Results

171 The total number of species found in the vegetation, seed bank, seed rain and ant-traps are
172 given for each field in Table 2. All the species found during this study are listed in the
173 Appendix and their frequency of occurrence in each of the various types of data are recorded.

174 The partial CCA showed that the environmental variables alone explained 23% of the
175 variance of the above-ground vegetation matrix (no figure). The partial CCA also showed
176 that distances from sampling points to boundary contributed to 10% of the above-ground
177 vegetation matrix (Fig. 1). This distance effect showed that points close to the boundary were
178 associated with species such as *Asphodelus ayardii*, *B. retusum*, *Filago pyramidata*, *Linaria*
179 *arvensis* and *T. vulgaris*, whereas points far from the boundary were associated with species
180 such as *Calamintha nepeta*, *Lepidium graminifolium*, *Rumex pulcher* and *Cynoglossum*
181 *officinale* (Fig. 1). Non-parametric multiple comparisons by STP tests confirmed that *T.*
182 *vulgaris* % cover was significantly higher at 0, 1 and 2 m from boundaries than at 10 m
183 (U=34.7 $p<0.001$); and phosphorus contents significantly increased with the distance from
184 boundaries (U=11.7 $p<0.001$).

185 Axis 1 of the K-sets PCA was correlated with the first principal components of all
186 seven matrices and particularly with above-ground vegetation (89%), seed rain (91%), ant-
187 borne seed (87%) and summer surface seed bank (83%) matrices (Fig. 2), showing

188 correlation between these variables. This axis (6%) separated abandoned field A, associated
189 with species, such as *Bromus* sp., *Diplotaxis tenuifolia*, *Polycarpon tetraphyllum* and *Vulpia*
190 sp., from abandoned field C points associated with species, such as *Aegilops* sp., *Bellis*
191 *sylvestris*, *Carthamus lanatus* and *Senecio vulgaris*. Abandoned field B points were grouped
192 between A and C. A site effect was thus observable not only on above-ground vegetation but
193 also on most of the types of data studied except on winter seed bank. Axis 2 of the K-sets
194 PCA was particularly correlated with the second components of above-ground vegetation
195 (80%) and seed rain (76%) matrices (Fig. 2). This axis (4%) separated the points close to the
196 boundary from the points far from the boundary. Points close to the boundary were
197 associated with species, such as *Erodium cicutarium*, *Euphorbia exigua*, *Galium* sp. and *P.*
198 *tetraphyllum* for both matrices as well as *Linum trigynum*, *Sideritis romana* and *T vulgaris* in
199 the vegetation and *Brachyposium distachyon* and *Plantago bellardii* in the seed rain (Fig. 3).
200 Points far from the boundary were associated with species, such as *Conyza* sp. in the
201 vegetation and *Lobularia maritima* in the seed rain (Fig. 3).

202 ANOVA showed that steppe species richness of above-ground vegetation and steppe
203 species richness of seed rain were significantly higher at 0, 1, 2, and 3 m as well as 4 m for
204 vegetation than at 7 to 10 m from boundaries (respectively $F=9.5$ and $F=6.1$, $P<0.001$ and
205 LSD test $P<0.05$).

206

207 **4. Discussion**

208 Independently from the site effect and from the differences in species number found on each
209 field (Table 2) which are well-known phenomena (Buisson and Dutoit, 2004), original
210 patterns were observed which were comparable on the three field margins. The composition
211 of above-ground vegetation changed with distance from boundary: there were more steppe
212 species close to boundaries and more arable weed species and mesophilous species further
213 away. Soil pH and soil concentrations in phosphorus increased with distance from boundary
214 because more fertiliser was applied on the fields than on the field margins that were less
215 deeply ploughed. Grime et al. (1987) and Gough and Marrs (1990) have shown that ruderal
216 species out-compete dry grassland species when phosphorus is in excess. Although a
217 phosphorus gradient existed on the field margins in this study, Buisson and Dutoit (2004)
218 have shown that concentrations observed in La Crau were not high enough on field margins
219 (mean phosphorus = 0.019g/kg) to explain the degree of vegetation change (Janssens et al.,
220 1998).

221 On field margins, the deep seed bank mainly consisted of arable weed species
222 (*Kickxia elatine* and *Portulaca oleracea*), ruderal and nitrophilous species (*Calamintha*
223 *nepeta*, *L. maritima*, *Polygonum aviculare*, *S. vulgaris*, *Solanum nigrum*) dating back to
224 melon cultivation. The surface seed bank consisted not only of recently established steppe
225 species (seed bank <1 year), but also of the species cited above, some of which (e.g. *P.*
226 *oleracea* and *S. nigrum*) have not been found in above ground vegetation since the
227 abandonment of melon cultivation because favourable conditions no longer exist (ploughing,
228 fertiliser, irrigation etc.). Re-establishment of steppe species from seed bank appeared to be
229 minimal, as most steppe species were shown to have a transient seed bank (see also
230 Römermann et al., 2005), although margins offered better environmental conditions for
231 stress-tolerant steppe species than the middle of the fields.

232 The stress-tolerant steppe species now growing on field margins, but absent in the
233 seed bank, came from seed rain or ant-borne seeds. Seed dispersal by ants on the margins,
234 while worth noting (about 10000 seeds and 10000 ants trapped throughout the study), was
235 probably limited to small distances, as observed by Harrington and Driver (1995). Seed rain

236 thus contributed to most steppe species colonisation. Even sampled over a complete
237 fructification and dispersal season, seed rain and seed dispersal by ants did not suffice for the
238 re-establishment of steppe species on the fields since only a few steppe species were found
239 on margins while typical steppe species such as *Stipa capillata*, *A. ayardii*, *Plantago*
240 *holosteum*, *Hyssopus canescens*, and *Fumana procumbens* were not. These results contrast
241 strongly with Etienne et al.'s (1998) assessment of potential steppe vegetation re-
242 establishment in La Crau and with results found in north-western Europe (Gibson and
243 Brown, 1992).

244
245 The results of this study under Mediterranean climate show that the role of the seed
246 bank in the re-establishment of former steppe on abandoned fields is minimal and thus
247 corroborate those found elsewhere (Graham and Hutchings, 1988; Hutchings and Booth,
248 1996a). While in many landscapes, remnant patches of native vegetation have a positive role
249 on the secondary succession of abandoned fields, in a Mediterranean fragmented open-
250 landscape, remnant patches of steppe adjacent to abandoned fields do not seem to have much
251 of a role in the colonisation processes of steppe species as seed dispersal by wind or ants is
252 limited.

253 Plant and insect dispersal in fragmented landscape has been studied in open
254 landscapes and it has been concluded that livestock (Poschlod et al., 1998) are an excellent
255 vector to disperse seeds between plots by epizoochory and endozoochory (Fischer et al.,
256 1996) in Northern Europe. The steppe of La Crau and abandoned fields are grazed by
257 itinerant sheep and their daily ranging patterns could easily be planned so that they graze on
258 the steppe first, then on fields, in order to disperse steppe-species seeds and insects onto
259 fields. However, grasshoppers thrive and most plants set seeds in summer (Bourrelly et al.,
260 1983) when all flocks are in transhumance in the Alps. Also, Fischer et al. (1996) have
261 shown that most of the seeds dispersed came from plants bigger than 80 cm high and Dutoit
262 et al. (2003) have shown that, in a Mediterranean area where sheep graze year around, sheep
263 were not a good vector of rare arable weeds. In La Crau, most dicotyledons grow rather small
264 and have small and smooth seeds resembling those of rare arable weeds. Therefore, although
265 sheep grazing is required to maintain steppe vegetation (Fabre and Pluinage, 1998), it is not
266 sufficient for the long-term management of abandoned fields.

267 The long-term conservation of the steppe has to include a plan to re-connect the larger
268 patches of steppe. Future experiments should focus on sowing seeds or transplanting nurse
269 species. This management tool has been used to enhance species richness of grasslands in
270 northern Europe. Its success depends on the seeds sown (Hutchings and Booth, 1996b), on
271 facilitation processes between transplanted nurse species and others native species (Pywell et
272 al., 2002) or on concurrent vegetation management (Warren et al., 2001).

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- 282 **References**
- 283 Baize, D., 2000. Guide des analyses en pédologie. INRA, Paris.
- 284 Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M., Thompson, K., 1996. Seed banks
285 and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica*
286 45, 461-490.
- 287 Blondel, J., Aronson, J., 1999. *Biology and Wildlife of the Mediterranean Region*. Oxford
288 University Press, Oxford.
- 289 Bourrelly, M., Borel, L., Devaux, J.P., Louis-Palluel, J., Archiloque, A., 1983. Dynamique
290 annuelle et production primaire nette de l'écosystème steppique de Crau. *Biologie-*
291 *Ecologie méditerranéenne* 10, 55-82.
- 292 Buisson, E., Dutoit, T., 2004. Colonisation by native species of abandoned farmland adjacent
293 to a remnant patch of Mediterranean steppe. *Plant Ecology* 174, 371-384.
- 294 Buisson, E., Dutoit, T., in press. Creation of the Natural Reserve of La Crau: implications for
295 the creation and management of protected areas. *Journal of Environmental*
296 *Management*.
- 297 Dutoit, T., Gerbaud, E., Ourcival, J.M., 1999. Field boundary effects on soil seed banks and
298 weed vegetation distribution in an arable field without weed control (Vaucluse,
299 France). *Agronomie, Agriculture and Environnement* 19, 579-590.
- 300 Dutoit, T., Jäger, M., Gerbaud, E., Poschlod, P., 2003. Rôles des ovins dans le transport de
301 graines d'espèces messicoles: le cas d'une exploitation agricole du Parc Naturel
302 Régional du Luberon. *Courrier scientifique du Parc régional du Luberon* 7, 68-75.
- 303 Etienne, M., Aronson, J., Le Floc'h, E., 1998. Abandoned lands and land use conflicts in
304 southern France. Piloting ecosystem trajectories and redesigning outmoded landscapes in
305 the 21st century. In: Rundel, P.W., Montenegro, G., Jaksic, F. (Eds), *Landscape*
306 *degradation and biodiversity in Mediterranean-type ecosystems*. Ecological Studies Series
307 n°136. Springer, Berlin, pp. 127-140.
- 308 Fabre, P., Pluvinage, J., 1998. Intégration des mesures agri-environnementales aux systèmes
309 d'élevage ovin de la Crau. In: CEEP Ecomusée de Crau (Eds), *Patrimoine nature et*
310 *pratiques pastorales en Crau*. Saint-Martin de Crau, France, pp. 100-113.
- 311 Fischer, S.F., Poschlod, P., Beinlich, B., 1996. Experimental studies on the dispersal of
312 plants and animals on sheep in calcareous grasslands. *Journal of Applied Ecology* 33,
313 1206-1222.
- 314 Gibson, C.W.D., Brown, V.K., 1992. Grazing and vegetation change: deflected or modified
315 succession? *Journal of Applied Ecology* 29, 120-131.
- 316 Gough, M.W., Marrs, R.H., 1990. A comparison of soil fertility between semi-natural and
317 agricultural plant communities: implications for the creation of species-rich grasslands
318 on abandoned agricultural land. *Biological Conservation* 51, 83- 96.
- 319 Graham, D. J., Hutchings, M.J., 1988. A field investigation of germination from the seed
320 bank of a chalk grassland ley established on former arable land. *Journal of Applied*
321 *Ecology* 25, 253-263.
- 322 Grime, J.P., MacKey, J.M.L, Hillier, S.H., Read, D.J., 1987. Floristic diversity in a model
323 system using experimental microcosms. *Nature* 328, 420-422.
- 324 Harrington, G.N., Driver, M.A., 1995. The effect of fire and ants on the seed-bank of a shrub
325 in a semi-arid grassland. *Australian Journal of Ecology* 20, 238-247.
- 326 Hillier, S.H., Walton, D.W.H., Wells, D.A., 1990. *Calcareous grassland: ecology and*
327 *management*. Bluntisham Books, Bluntisham.

328 Hutchings, M.J., Booth, K.D., 1996a. Studies on the feasibility of re-creating chalk grassland
329 vegetation on ex-arable land. I. The potential roles of the seed bank and the seed rain.
330 *Journal of Applied Ecology* 33, 1171-1181.

331 Hutchings, M.J., Booth, K.D., 1996b. Studies on the feasibility of re-creating chalk grassland
332 vegetation on ex-arable land. II. Germination and early survivorship of seedlings under
333 different management regimes. *Journal of Applied Ecology* 33, 1182-1190.

334 Janssens, F., Peeters, A., Tallowin, J.R.B., Bakker, J.P., Bekker, R.M., Fillat, F., Oomes,
335 M.J.M., 1998. Relationship between soil chemical factors and grassland diversity. *Plant*
336 *and Soil* 202, 69-78.

337 Kalamees, R., Zobel, M., 2002. The role of the seed bank in gap regeneration in a calcareous
338 grassland community. *Ecology* 83, 1017-1025.

339 Kerguélen, M., 1999. Index synonymique de la flore de France. [pages html]. INRA Dijon.
340 <http://www.dijon.inra.fr/flore-france/> [October 1999 ; last checked in September 2005].

341 Kleijn, D., Joenje, W., Kropff, M.J., 1997. Patterns in species composition of arable field
342 boundary vegetation. *Acta Bot. Neerl.* 46, 175-192.

343 McIntyre, S., Lavorel, S., 1994. How environmental and disturbance factors influence
344 species composition in temperate Australian grasslands. *Journal of Vegetation Science*
345 8, 521-531.

346 Médail, F., Quézel, P., 1999. Biodiversity hotspots in the Mediterranean Basin: setting global
347 conservation priorities. *Conservation Biology*, 13, 1510-1513.

348 Pagès, J., Escofier, B., 1994. Multiple factor analysis (AFMULT package). *Computational*
349 *Statistics and Data Analysis* 18, 121-140.

350 Poschlod, P., Kiefer, S., Tränkle, U., Fisher, S., Bonn, S., 1998. Plant species richness in
351 calcareous grasslands as affected by dispersability in space and time. *Applied*
352 *Vegetation Science* 1, 75-90.

353 Poschlod, P., WallisDeVries, M.F., 2002. The historical and socio-economic perspective of
354 calcareous grasslands-lessons from the distant and recent past. *Biological Conservation*
355 104, 361- 376.

356 Pywell, R. F., Bullock, J.M., Hopkins, A., Walker, K.J., Sparks, T.H., Burke, M.J.W., Peel,
357 S., 2002. Restoration of species-rich grassland on arable land: assessing the limiting
358 processes using a multi-site experiment. *Journal of Applied of Ecology* 39, 294-309.

359 Römermann, C., Dutoit, T., Poschlod, P., Buisson, E., 2005. Influence of former cultivation
360 on the unique Mediterranean steppe of France and consequences for conservation
361 management. *Biological Conservation* 121, 21-33

362 Sokal, R. R., Rohlf, F.J., 1998. *Biometry: the principles and practice of statistics in biological*
363 *research*. 3rd edition, W. H. Freeman Company, New York.

364 Ter Braak, C.J.F., 1987. The analysis of vegetation-environment relationships by canonical
365 correspondence analysis. *Vegetatio* 69, 69-77.

366 Ter Heerdt, G.N.J., Verweij, G.L., Bekker, R.M., Bakker, J.P., 1997. An improved method
367 for seed-bank analysis: seedling emergence after removing the soil by sieving.
368 *Functional Ecology* 10, 144-151.

369 Thioulouse, J., Chessel, D., Dolédec, S., Olivier, J.M., 1997. ADE-4: a multivariate analysis
370 and graphical display software. *Statistics and Computing* 7, 75-83.

371 Thompson, K., J. Bakker, and R. Bekker. 1997. *The soil seed bank of North West Europe:*
372 *methodology, density and longevity*. Cambridge University Press, Cambridge.

373 Verkaar, H.J., Schenkeveld, A.J., Van De Klashorst, M.P., 1983. On the ecology of short
374 lived forbs in chalk grasslands: dispersal of seeds. *New Phytologist* 95, 335-344.

375 Von Arx, G., Bosshard, A., Dietz, H., 2002. Land-use intensity and border structures as
376 determinants of vegetation diversity in an agricultural area. Bulletin of the
377 Geobotanical Institute ETH 68, 3-15.

378 Warren, J., Christal, A., Wilson, F., 2001. Effects of sowing and management on vegetation
379 succession during grassland habitat restoration. Agriculture, Ecosystems and
380 Environment 1909, 1-10.

381 Wilson, P.J., Aebischer, N.J., 1995. The distribution of dicotyledonous arable weeds in
382 relation to distance from the field edge. Journal of Applied Ecology 32, 295-310.
383

384 **Appendix**

385 Total frequency of occurrence (%) of species in all three fields in the vegetation (990
 386 quadrats of 40 × 40 cm), in the 1287 seed rain traps, in the 1287 ant traps and in the various
 387 seed banks Nomenclature according to Kerguélen (1999).

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Species	Typical steppe vegetation (Römhann et al. 2005)	Above-ground vegetation	Seed rain	Ant-borne- seeds	Summer surface seed bank	Summer deep seed bank	Winter surface seed bank	Winter deep seed bank
<i>Aegilops ovata</i> L.	X	98.4	0.9	0.3	0.4			
<i>Aira cupaniana</i> Guss.	X	98.2	0.1	0.4	1.3			
<i>Anagallis arvensis</i> L.		32.1			5.2	30.6	12.0	20.1
<i>Anagallis foemina</i> Miller		50			3.8		36.2	10.0
<i>Anagallis</i> sp.				100.0				
<i>Asperula cynanchica</i> L.	X	100.0						
<i>Asphodelus ayardii</i> L.	X	100.0						
<i>Asterolinon linum-stellatum</i> (L.) Duby in DC.	X	96.6	3.0	0.4				
<i>Avena barbata</i> Link	X	98.8	0.7	0.4	0.1	<0.05		
<i>Bellis sylvestris</i> Cirillo	X	99.3	0.5	0.2				
<i>Brachypodium distachyon</i> (L.) P. Beauv.	X	37.7	9.4	2.5	50.0	0.4		
<i>Brachypodium retusum</i> (Pers.) P. Beauv.	X	100.0						
<i>Bromus hordeaceus</i> L. subsp. hordeaceus		87.8	2.0	0.5	9.5	0.2		
<i>Bromus intermedius</i> Guss.		85.1	8.8	1.4	4.3	0.4		
<i>Bromus madritensis</i> L.		84.6	1.4	8.1	5.9			
<i>Bromus rubens</i> L.		78.7	6.6	0.6	14.0	0.1		
<i>Bromus</i> sp.							50.00	50.00
<i>Calamintha nepeta</i> (L.) Savi		91.4		<0.05	5.2	0.7	2.1	0.4
<i>Carduus nigrescens</i> Vill.		58.6	9.9	25.7	5.8			
<i>Carduus tenuiflorus</i> Curtis		99.7	0.18	0.02	0.1			
<i>Carex</i> sp.								100.0
<i>Carlina corymbosa</i> L.	X	100.0						
<i>Carlina lanata</i> L.	X	99.8	0.1	0.1				
<i>Carthamus lanatus</i> L.	X	99.99	0.01					
<i>Catapodium rigidum</i> (L.) C.E. Hubbard in Dony	X	90.1	0.9	0.2	8.8	<0.05		
<i>Cerastium glomeratum</i> Thuill.	X	98.6			1.4			
<i>Cerastium</i> sp.				13.6			86.40	0.00
<i>Chenopodium album</i> L.					11.4	22.7	20.45	45.45
<i>Convolvulus cantabrica</i> L.		100.0						
<i>Conyza</i> sp.		54.4	0.2	0.6	26.5	5.5	10.53	2.27
<i>Crepis foetida</i> L.	X	100.0						
<i>Crepis sancta</i> (L.) Bornm.	X	100.0						
<i>Crepis</i> sp.			29.3	31.3	26.3	13.1		
<i>Cynoglossum officinale</i> L.		92.6	7.4					
<i>Dactylis glomerata</i> L.	X	90.4	5.06	0.3	3.8	0.4	<0.05	0.01
<i>Daucus carota</i> L.	X	100.0						
<i>Diplotaxis tenuifolia</i> (L.) DC.		98.4	0.1		0.4	0.2	0.7	0.2
<i>Erodium cicutarium</i> (L.) L'Hérit. in Aiton		99.0	0.4	0.3	0.3			
<i>Eryngium campestre</i> L.	X	99.8	0.1	0.1	<0.05			
<i>Euphorbia cyparissias</i> L.	X	99.8	0.1	0.1				
<i>Euphorbia exigua</i> L.	X	98.8	0.8	0.3	0.1	<0.05		
<i>Euphorbia seguieriana</i> Necker		100.0						
<i>Evax pygmaea</i> (L.) Brot.	X	99.8		0.2				
<i>Filago pyramidata</i> L.	X	99.7					0.15	0.15
<i>Filago</i> sp.			98.9	1.1				
<i>Galactites elegans</i> (All.) Soldano		98.3	0.1	1.3	0.3			
<i>Galium murale</i> (L.) All.	X	99.3	0.2		0.5			
<i>Galium parisiense</i> L. / <i>G. pumilum</i> Murray	X	97.3	1.7	0.4	0.4	0.1	0.1	<0.05
<i>Gastridium ventricosum</i> (Gouan) Schinz & Thell.	X	93.8	3.5	0.4	2.3			
<i>Geranium molle</i> L.	X	95.1	1.3	0.5	3.0	0.1		
<i>Hedypnois cretica</i> (L.) Dum.-Cours.		98.23	0.01	0.23	1.4	<0.05		<0.05
<i>Hordeum murinum</i> L.		96.1	1.9	0.3	1.7	<0.05		
<i>Hypochaeris glabra</i> L.	X	97.1	1.9	0.6	0.4			
<i>Juncus bufonius</i> L.							50.0	50.0

<i>Juncus subnodulosus</i> Schrank							50.0	50.0
<i>Kickxia elatine</i> (L.) Dumort.				14.3	48.2		23.2	14.3
<i>Lepidium graminifolium</i> L.		97.9	0.2	0.1			1.6	0.2
<i>Linaria arvensis</i> (L.) Desf.	X	99.9	0.1					
<i>Linum strictum</i> L.	X	98.5	1.3	0.2				
<i>Linum trigynum</i> L.		100.0						
<i>Lobularia maritima</i> (L.) Desv.		91.1	0.3	0.2	5.5	0.5	1.6	0.8
<i>Logfia gallica</i> (L.) Cosson & Germain	X	97.0	1.7	0.1	0.9		0.2	0.1
<i>Lolium perenne</i> L.		100.0						
<i>Lolium rigidum</i> Gaudin		100.0						
<i>Lolium</i> sp.			22.5	2.3	75.0	0.2		
<i>Marrubium vulgare</i> L.		100.0						
<i>Medicago minima</i> (L.) L.	X	99.7	0.3					
<i>Medicago praecox</i> DC.		100.0						
<i>Medicago rigidula</i> (L.) All.		99.8	0.2					
<i>Melica ciliata</i> L.		37.1	36.0	24.1	1.9	0.9		
<i>Neatostema apulum</i> (L.) I.M. Johnston		100.0						
<i>Onopordum illyricum</i> L.		98.1		1.9				
<i>Panicum capillare</i> L.	X						100.0	
<i>Petrorhagia prolifera</i> (L.) P.W. Ball & Heywood		99.6	0.3	0.1				
<i>Phleum pratense</i> L.		87.3	1.1	3.7	7.9			
<i>Plantago bellardii</i> All.	X	72.5	27.2	0.3				
<i>Plantago lagopus</i> L.		92.8	0.2		5.8	1.2		
<i>Poa annua</i> L.				34.8	40.6	4.9	14.8	4.9
<i>Polycarpon tetraphyllum</i> (L.) L.		95.0	2.8	0.4	0.2	<0.05	1.3	0.3
<i>Polygonum aviculare</i> L.					69.2	23.1	7.7	
<i>Portulaca oleracea</i> L.					6.8	44.1	19.6	29.5
<i>Potentilla</i> sp.					100.0			
<i>Psilurus incurvus</i> (Gouan) Schinz & Thell.			54.9	25.5		18.7	0.9	
<i>Ranunculus paludosus</i> Poiret					100.0			
<i>Reichardia picroides</i> (L.) Roth	X	100.0						
<i>Reseda</i> sp.		100.0						
<i>Rostraria cristata</i> (L.) Tzvelev	X	92.8	2.8	1.1	3.0	0.3		
<i>Rumex pulcher</i> L.		99.9	0.1					
<i>Sagina apetala</i> Ard.	X	83.3			16.7			
<i>Salvia verbenaca</i> L.	X	99.8		<0.05	0.2		<0.05	
<i>Samolus valerandi</i> L.							100.0	
<i>Sanguisorba minor</i> Scop.	X	99.8			0.2			
<i>Scirpus</i> sp.							39.9	60.1
<i>Senecio vulgaris</i> L.		13.1			75.0	2.2	8.4	1.3
<i>Sherardia arvensis</i> L.	X	99.98		0.02				
<i>Sideritis romana</i> L.	X	98.0	<0.05	0.2	1.6	0.2		
<i>Silene gallica</i> L.	X	95.4	4.6					
<i>Solanum nigrum</i> L.				0.6	8.1	14.2	24.4	52.7
<i>Sonchus asper</i> (L.) Hill		95.4	1.4	0.2	3.0			
<i>Stipa capillata</i> L.	X				100.0			
<i>Taeniatherum caput-medusae</i> (L.) Nevski	X	99.0	0.3	0.5	0.2			
<i>Thymus vulgaris</i> L.	X	93.0	1.1	0.5	4.6	0.3	0.4	0.1
<i>Torilis nodosa</i> (L.) Gaertner		100.0						
<i>Trifolium campestre</i> Schreber in Sturm	X	95.5		0.2	4.3			
<i>Trifolium glomeratum</i> L.	X	95.8	0.02	0.2	2.5	0.48	0.3	0.7
<i>Trifolium scabrum</i> L.		99.48	<0.05	0.08	0.2	0.1		0.1
<i>Trifolium</i> sp.		97.8	0.2		1.6	0.40		
<i>Trifolium stellatum</i> L.	X	98.6	0.1	0.6	0.7			
<i>Trifolium subterraneum</i> L.		100.0						
<i>Trifolium suffocatum</i> L.		93.3	0.2	1.5	4.6	0.3		0.1
<i>Trigonella monspeliaca</i> L.	X	97.1	0.1	0.4	2.2	0.2		
<i>Typha latifolia</i> L.							72.2	27.8
<i>Verbascum sinuatum</i> L.		100.0						
<i>Verbena officinalis</i> L.					12.8	18.0	43.6	25.6
<i>Veronica arvensis</i> L.		96.1	0.2	<0.05	3.3	<0.05	0.3	<0.05
<i>Vulpia</i> sp.		61.4	6.3	1.3	30.3	0.7	<0.05	

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392 Table 1. Cultivation history of the three abandoned fields A, B, C and the steppe on the
 393 sheepfold of Peau de Meau. After abandonment, grazing occurred on all fields, as on the
 394 steppe, by itinerant sheep from February to June.

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Sites	Type of cultivation	Duration of cultivation & year of abandonment	Field location
Field A 5 ha	Melons (small tunnels) Cereals and alfalfa	1 year in 1971 1 year in 1972	N-NW of the steppe patch (D)
Field B 5 ha	Cereals and alfalfa Melons (small tunnels) Cereals and alfalfa	from 1960 to 1966 1 year in 1971 1 year in 1972	W of the steppe patch (D)
Field C 5 ha	Melons (small tunnels) Cereals and alfalfa Melons, courgettes, aubergines, peppers (large tunnels)	1 year in 1968 1 year in 1969 from 1979 to 1984	W-SW of the steppe patch (D)
Steppe D 6500 ha	Not cultivated	na	na

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399 Table 2. Species and germination or seed number of abandoned field A, B and C in the
 400 vegetation, soil seed bank, seed rain and ant-borne seeds.

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	A	B	C	Total
Vegetation (33 sampling points / field)				
Species number in the vegetation	63	66	83	94
Soil seed bank (198 soil samples / season)				
Species number in summer seed bank	58	54	58	73
Seedling number in summer seed bank	7562	7292	4684	19538
Species number in winter seed bank	27	28	21	39
Seedling number in winter seed bank	691	375	497	1563
Seed rain (1287 traps)				
Number of taxa	52	62	65	76
Seed number	20880	13802	8019	42701
Ant-borne seeds (1287 traps)				
Number of taxa	46	49	61	69
Seed number	4402	3140	2414	10588

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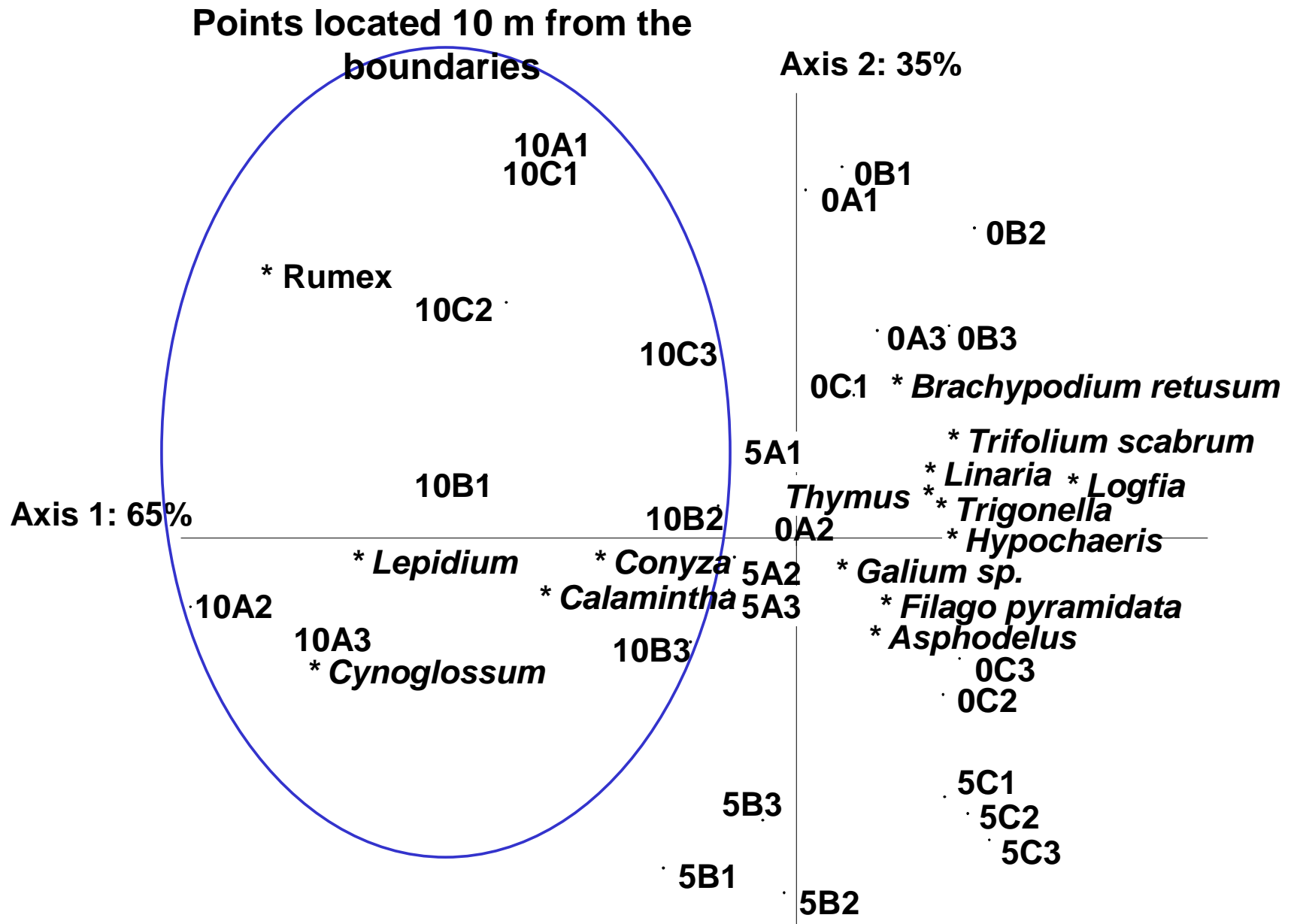


Fig. 1. Partial CCA performed on distance and vegetation variables once the impact of environmental variables was statistically removed. All sampling points are shown. Point abbreviations: first number = distance to boundary (0 to 10 m); letter = field A, B or C; second number = transect number (1, 2 or 3). Only the species with high contributions are shown. The nine sampling points far from the boundaries are circled.

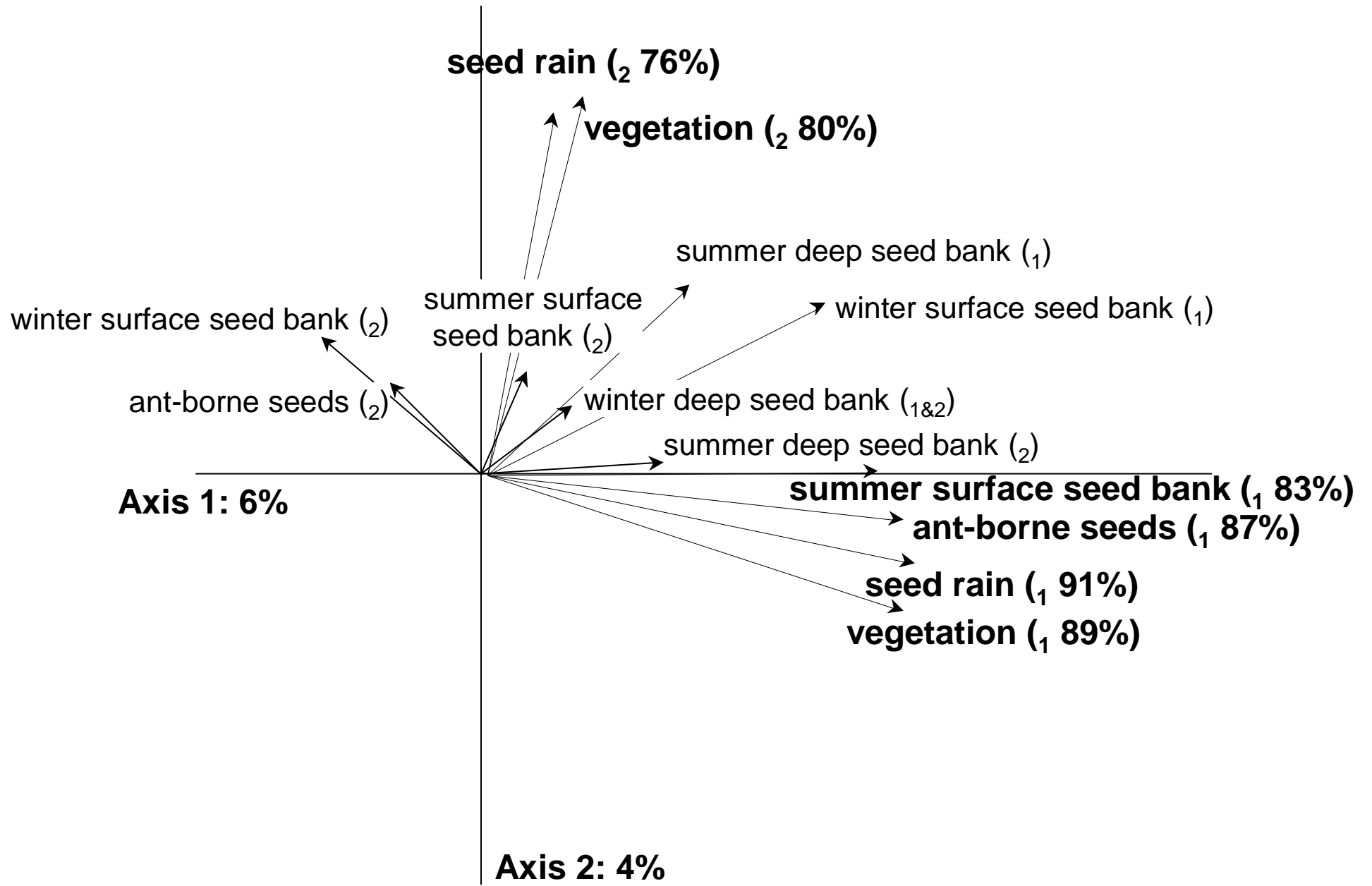


Fig. 2. Projection of the first two principal components of the separate analysis of each of the seven matrices onto the K-set PCA best plane. Sets with the highest contributions to axes 1 or 2 are written in bold and their contribution written in brackets.

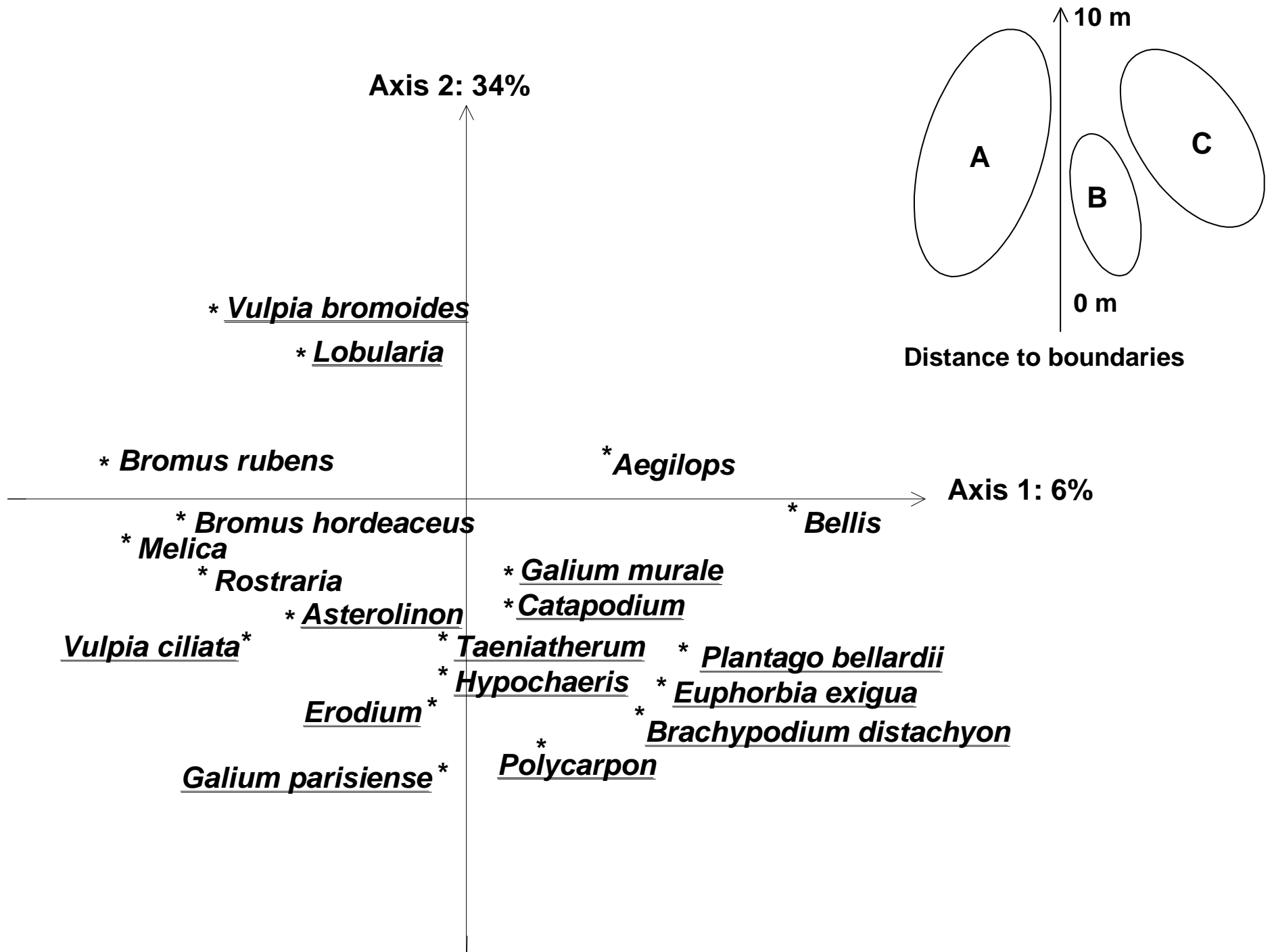


Fig. 3. Factor map of species in the seed rain only, resulting from the K-set PCA. Only species with the highest contributions to axes 1 or 2 are written. Underlined species contribute to axis 2. The K-set PCA map of sampling points is schematized on the top right corner.