

1 Long-term weather sensitivity of open sand grasslands of the Kiskunság Sand Ridge forest-
2 steppe mosaic after wildfires

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4 Running title: Long-term weather sensitivity after wildfires

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27

28 **Abstract**

29

30 We studied the long-term impact of wildfire on the vegetation dynamics of sand grasslands in
31 a forest-steppe vegetation mosaic in Central Hungary (Kiskunság). Long-term permanent
32 quadrat monitoring was carried out from 1997 to 2008. We sampled the forest-steppe mosaic
33 both in burnt and unburnt areas in 100 patches altogether using one by one meter quadrats.
34 The effect of fire and precipitation on vegetation dynamics was characterized by patch type
35 transitions between years. Patch types were defined by means of Cocktail method. Nine patch
36 types of sand grasslands were altogether identified. The least productive patch types, bare soil
37 and cryptogam dominance, did not occur in the burnt patches, while annual dominated patch
38 type appeared only in burnt patches. The frequencies of patch type changes were significantly
39 higher in burnt patches than in unburnt ones, independently on the time since fire. All the
40 eight patch types found in the unburnt patches proved permanent, while in the burnt patches
41 only four of seven were so. The relative frequency of patch type changes did not correlate to
42 the precipitation in the vegetation period in the unburnt patches, while positively correlated in
43 the burnt patches. It was concluded that the long-term difference in grassland dynamics
44 between the unburnt and burnt patches, i.e. the excess of the patch type transitions in the burnt
45 grasslands, are due to increased drought sensitivity of the grassland, which is the consequence
46 of the elimination of the woody component of the forest-steppe vegetation.

47

48 Nomenclature: Simon 2000

49 **Introduction**

50

51 The impact of fire is one of the focal areas in the long-term ecological research on arid and
52 semi-arid ecosystems (Bowman and Murphy 2010, Keeley 1986, Whelan 1995). The majority
53 of the studies in Mediterranean shrublands (Capitaniao and Carcaillet 2008, Esposito et al.
54 1999, Montenegro et al. 2004, Uys et al. 2004), tall-grass prairies (Collins 1992, Feldman and
55 Lewis 2005), and tropical savannahs (Greenville et al. 2009, Langevelde et al. 2003, Lewis et
56 al. 2010) focus on ecological processes of fire-adapted ecosystems (Keeley 1986, Lewis et al.
57 2010). However, the impact of the fire is the most severe in ecosystems which are not adapted
58 to fire (Engel and Abella 2011). Studying these ecosystems are particularly important if they
59 have been recently exposed to more fire due to human activity and increasing aridity caused
60 by climate change (Bowman and Murphy 2010). Fire is a primary disturbance factor of the
61 grassland vegetation, which most often reduces the abundance of the woody elements (Belsky
62 1992, Montenegro et al. 2004), but can also lead to invasion of bushes or trees (Franzese et al.
63 2009).

64

65 We studied poplar-juniper-grassland vegetation complex belonging to the transitional forest-
66 steppe biome in the Kiskunság Sand Ridge of Central Hungary (Kovács-Láng et al. 2000),
67 which is particularly rich in endemic plant species (Molnár 2003). This is a two-phase system
68 consisting poplar-juniper woods and sand grassland patches, forming a dynamic mosaic
69 pattern. This pattern is sensitive to drought, wildfire, and changes in herbivory (Katona et al.
70 2004, Kertész et al. 1993, Ónodi et al. 2006, Ónodi et al. 2008), thus particularly suitable for
71 studying the impacts of these disturbances and stress factors.

72

73 The biodiversity of natural and semi-natural communities increasingly depends on human
74 management (Chapin et al. 2010). Thus, the proper management, i.e. selection of wood
75 species for plantation, forestry technology practices, regulation of grazing, alteration of the
76 landscape pattern, and control of the water regime should mitigate the chance of ignition, fire
77 propagation and fire severity in communities exposed to increasing fire risk. Despite this
78 demand, a sort of management changes in the Kiskunság region has increased the fire risk for
79 the Sand Ridge forest-steppe vegetation. Thus, as a combined effect of drainage, forest and
80 orchard plantations, and increased water exploitation, the ground water level has decreased
81 since the late 1970s (Pálfai 1994), and the subsequent decrease of soil moisture (Kertész and
82 Mika 1999) may have also contributed to the larger extent of the fires. The grazing pressure
83 has declined since the 1960s (Bíró 2003, Katona et al. 2004), increasing the hazard of wildfire
84 (Ónodi et al. 2008). Similarly, after the sharp decrease of the animal stock in Southern Russia
85 wildfires began to appear from the end of 1990s, and in 2006-07, wildfires spread over large
86 areas (Dubinin et al. 2010). Since 1990, three out of the four large protected juniper-poplar
87 forest grassland mosaics have been almost completely burnt in the Kiskunság Sand Ridge
88 area. The extensive alien *Pinus nigra* plantations have invariably played major role in
89 conducting the fire across the landscape (Kiskunság National Park, personal communication).
90 So far, all the known wildfire events are man made in this region, thus the fire is not part of
91 natural disturbance regime. According to climate change studies, the summer temperature and
92 the inter-annual variation of the precipitation will keep increasing (Bartholy et al. 2007,
93 Bartholy et al. 2009), thus we predict an increase of frequency and extension of wildfires,
94 similarly to the Mediterranean areas (Bowman and Murphy 2010, Veblen 2003). In spite of
95 these facts, there are very few well documented studies in Central-Europe concerning
96 grassland burning (but see Ónodi et al. 2007, 2008; Deák et al. 2012, Valkó et al. 2012).
97

98 Hereinafter, we call “patch type” the clusters of the vegetation compositions of grassland
99 patches, and “vegetation dynamics” the year to year changes of the patch types, and we
100 consider “burnt” and “unburnt” states of the patches as natural treatments.

101

102 We aimed at studying the impact of wildfires on the vegetation dynamics in the grassland
103 component of this transitional biome. Grasslands burnt by wildfires were compared with
104 unburnt grasslands. The following questions were raised. 1. Does the wildfire modify the
105 sensitivity of vegetation dynamics of the grasslands to drought? 2. How long does wildfire
106 affect the vegetation dynamics?

107 Our null-hypotheses were as follows: a) the frequency distributions of the patch types on the
108 burnt and unburnt patches are not different; b) the distribution of year to year transitions of
109 the patch types on the burnt and unburnt patches are not different; c) if there were differences
110 in the distributions of transitions, these differences do not depend on the time since fire; d) the
111 frequencies of transitions do not depend on the precipitation.

112

113

114 **Materials and methods**

115

116 The study sites are in the Kiskunság National Park in Central Hungary, in vegetation mosaics
117 consisting juniper-poplar woods and open sand grasslands. This two-component vegetation
118 type can be found in the western edge of the Eurasian forest-steppe zone (Kovács-Láng et al.
119 2000). The two-phase character is enhanced by the extreme moisture regime of the soil caused
120 by the high hydraulic conductivity of the calcareous sand soil of low (<1%) humus content
121 (Calcaric Arenosol) (Várallyay 2005). The precipitation quickly infiltrates through the root
122 zone of the grassland, while remains available for woody vegetation (Molnár 2003). The

123 climate is moderately continental with sub-Mediterranean effects (Zólyomi et al. 1997).
124 Annual mean precipitation is around 500–550 mm and mean monthly temperatures range
125 from -1,8 °C in January to 21 °C in July (Kovács-Láng et al. 2000). The main growing season
126 in the open sand grassland is the late spring.

127

128 Long-term monitoring on three partially burnt sand dune areas have been carried out since
129 1997, combining space-for-time substitution (Pickett 1989) with long-term permanent plot
130 observations (Bakker et al. 1996). The study is part of the KISKUN LTER project (Kovács-
131 Láng et al. 2008). The Bugac site was burnt in 1976, the Bócsa site in 1993. On these sites the
132 vegetation changes have been recorded since 1997. The Orgovány site was burnt in 2000, and
133 we started the monitoring in 2002. In all three sites, the burnt area ranged several square-
134 kilometers, affecting planted forests as well as forest-steppe stands. We consider the unburnt
135 areas reference vegetation for the burnt areas before the fire. Both unburnt and burnt areas are
136 covered by a mosaic of woods and grassland patches. On the unburnt areas, the woods are
137 dominated by either juniper (*Juniperus communis*), or poplar species (*Populus alba*, *P.*
138 *canescens*, and *P. nigra*) and juniper. On the burnt areas junipers can not regenerate, but
139 poplar species resprout after the wildfire.

140

141 Our sampling unit were 1 by 1 m quadrats. Five quadrats were placed in each selected
142 grassland patches of the open sand grassland component of the mosaic, both in burnt and
143 unburnt areas (Fig. 1). Samples were taken from 100 patches, 46 burnt and 54 unburnt, from
144 ten groups of patches in three sites. Groups of patches were fenced in order to control the
145 previously very high grazing pressure; this resulted in spatially aggregated patch distribution
146 (Fig. 2). In the Bugac site (Fig. 2c) patches were grouped in two partially burnt (N 46° 39,30',
147 E 19° 36,49'; N 46° 39,20', E 19° 36,48') and two unburnt (N 46° 38,91', E 19° 36,43'; N 46°

148 38,88', E 19° 36,21') areas. From 1997 to 2001 we took samples in ten burnt and 26 unburnt
149 patches, and in 2002 we enlarged the sample to 12 burnt and 28 unburnt patches (Table 1). In
150 the two partially burnt areas (N 46° 38,68', E 19° 28,08'; N 46° 38,60', E 19° 28,03') of the
151 Bócsa site (Fig. 2b) ten burnt and six unburnt patches were sampled from 1997 to 2001. In
152 2002 we enlarged the sample to 14 burnt and six unburnt patches. In the Orgovány site (Fig.
153 2a) 20 burnt from two burnt areas and 20 unburnt patches from two unburnt ones were
154 sampled.

155

156 In the quadrats, we visually estimated the cover of the vascular plants as well as the cover of
157 the mosses, lichens, litter, and exposed soil surface twice a year. Visual estimation has low
158 expected errors at the scale of our sampling, especially in nutrient deficient habitats (Klimeš
159 2003), like in open sand grasslands. The first sampling was carried out each year in late May
160 or early June, at the time of the biomass peak before the summer drought, and the second in
161 late September or early October, at the secondary biomass peak.

162

163 Vegetation dynamics was studied at the spatial scale of the patches, represented by five
164 quadrats. We associated a patch type to each patch in each year, applying the Cocktail method
165 (Bruehlheide 2000). First, the spring and autumn data were pooled within years and within
166 quadrats choosing the higher score, then cover in the five quadrats were averaged, and these
167 patch level cover values were used in the subsequent analysis. Species groups were formed
168 based on the positive associations among species (Bruehlheide and Chytrý 2000). The
169 interspecific associations were measured by hypergeometric u-value (Chytrý et al. 2002)
170 calculated from binary data. Group forming started with the pair of ungrouped species that
171 had the highest interspecific association. It stopped when the u-value of the new candidate
172 species to the group was below 5. We modified the original Cocktail algorithm, and instead of

173 presence of species groups we used their total cover to define the patch types. If the cover of
174 vascular plants exceeded 5%, the patch was classified according to the vascular species group
175 which has the highest cover. Otherwise, it was classified either into cryptogam patch type, if
176 cover of cryptogams was at least 50%, or bare soil patch type. We choose the above method
177 in order to get of patch types which provide us opportunity (1) to compare the patch type
178 distributions of burnt and unburnt patches, (2) to calculate the frequency of year to year
179 transitions between patch types.

180

181 Originally, the Cocktail method (Bruehlheide 2000) was developed for finding groups of
182 species, which then define plant associations in databases of preferentially selected relevés.
183 We looked for all species groups which define an exhaustive classification of the sample. The
184 application of this method, to define patch types, allows describing the vegetation dynamics
185 by means of analysis of transitions between a few discrete states, which provides a general
186 picture of the changes in the composition. The species abundance data themselves are loaded
187 with high noise because of the effect of the weather immediately previous to the sampling,
188 while patch types are less affected by this noise.

189

190 The type associated to a patch could change from year to year. The changes between
191 consecutive years were summarized in transition matrices for burnt and unburnt patches,
192 separately. The transition matrices calculated from the pooled data were compared with a
193 null-model in which transition probabilities depended on the proportion of vegetation types
194 before and after the transition only. First, the global difference was tested by chi-square test,
195 and if it proved to be significant, Freeman-Tukey deviates were used to find the significantly
196 over- and under-represented transitions. For each site, we calculated the proportion of values
197 in the diagonal of transition matrices (i.e. no-change between consecutive years) and

198 compared it between burnt and unburnt areas applying u-test for proportions (Zar 1999). The
199 complement of this proportion (i.e. the proportion of changes) was calculated from the pooled
200 data set and it was correlated with precipitation in the vegetation period from April to
201 September when the new vegetation type appeared. Separate correlations were calculated for
202 burnt and unburnt patches. We interpret the significantly over-represented year to year
203 transitions from a patch type to the same one, as resistance, and from one patch type to
204 another, as sensitivity.

205

206

207 **Results**

208

209 Nine patch types were identified: bare soil, cryptogam dominance, annual dominance,
210 *Festuca vaginata* group dominance, *Stipa borysthenica* group dominance, *Carex liparicarpos*
211 group dominance, *Poa bulbosa* group dominance, *Calamagrostis epigeios* group dominance,
212 and *Poa angustifolia* group dominance. (Henceforth, we refer the patch types without the
213 notion 'group dominance'). Fig. 3a and 3b show the relative frequency of the patch types in
214 each year, for burnt and unburnt patches separately.

215

216 The patch types 'bare soil' and 'cryptogam' occurred only in the unburnt patches, while the
217 patch type 'annual' only in burnt patches. Of the characteristic patch types of the open
218 perennial sand grasslands, the patch type '*Festuca vaginata*' was frequent in both burnt and
219 unburnt patches, while patch type '*Stipa borysthenica*' gradually spread in burnt patches,
220 together with the disappearance of the more closed '*Calamagrostis epigeios*' and '*Poa*
221 *angustifolia*' patch types.

222

223 All the patch types found in the unburnt patches were permanent, i.e. the frequencies of the
224 transitions into themselves proved significantly higher than expected, based on the
225 frequencies of their occurrences (Freeman-Tuckey deviates; $p < 5\%$). On the contrary, in the
226 burnt patches only the patch types '*Festuca vaginata*', '*Stipa borysthena*', '*Carex*
227 *liparicarpos*', and '*Calamagrostis epigeios*' were permanent, and we got transitions of
228 significantly higher frequency than expected, namely, between '*Calamagrostis epigeios*' and
229 'annual' and between '*Calamagrostis epigeios*' and '*Poa bulbosa*' (Fig. 4a and 4b).

230

231 By means of two-sample u-test we found that the frequency of patch type changes were
232 significantly higher in burnt than in unburnt patches in Bugac ($Z = 2.52$, $p = 0.012$) and Bócsa
233 ($Z = 2.06$, $p = 0.039$) sites (Fig. 5). The most recently burnt Orgovány site the same tendency
234 was found close to be significant ($Z = 1.89$, $p = 0.059$).

235

236 In the unburnt patches, the relative frequency of patch type changes proved to be independent
237 from the precipitation in the vegetation period ($R^2_{\text{adj}} = 6.4 \cdot 10^{-7}$, $p = 0.998$, Fig. 6a), while
238 positively correlated in the burnt patches ($R^2_{\text{adj}} = 0.406$, $p = 0.035$, Fig. 6b). The driest year
239 was 2003, and we found the less patch type changes in that year, while we found the most
240 changes in the next, wet year. In case of the burnt patches, the 2008 data (in the lower right
241 part of Fig. 6b) proved to be a leverage point as Cook's $D > 1$ (Cook 1979, Reiczigel et al.
242 2007). Without this point $R^2_{\text{adj}} = 0.72$, $p = 0.0019$.

243

244

245 **Discussion**

246

247 *General pattern of post-fire regeneration*

248 Both patch type data (Fig. 3b) and our field experience show that the patch types dominated
249 by perennials are the starting stages of the post-fire succession. Those patch types were the
250 most frequent on the non-burnt areas too, and they were also present before the fire. We
251 observed that the perennial plant species of the sand grassland were persistent; i.e. they re-
252 sprouted after the fire from their buds, in accordance with 'regeneration' type post-fire
253 succession of Ghermandi et al. (2004). This ability of fast regeneration is indicative to fire
254 adaptation of the vegetation (Lewis et al. 2010). The same fast regeneration was found in fire-
255 adapted grasslands in South Africa (Uys et al. 2004), where the grass species tolerated the
256 four-year burning cycle, while most of the dicots tolerated even the yearly burning.

257

258 However, the post-fire regeneration of plant species in our grasslands highly varied by life
259 forms. Most of the drought tolerant perennial vascular plants have high below-ground/above-
260 ground biomass ratio, and the below-ground parts easily survive the fast spreading fire. On
261 contrary, we did not find 'cryptogam' patch type on the burnt areas (Fig. 3b). This result is in
262 contradiction with our first null-hypothesis and shows that fire has long-term effect on
263 grassland composition. The fire reduces the cover of cryptogams, especially the abundance of
264 lichens (Johansson and Reich 2005). Esposito et al. (1999) found quick establishment of
265 pioneer moss species in burnt macchia vegetation. In our case, the regeneration process of
266 *Tortella* and *Tortula* species was very slow, while lichens could not re-establish in the
267 timescale of our study.

268

269 Another characteristic difference between unburnt and burnt areas was that the 'annual' patch
270 type appeared only in the latter ones (Fig. 3a and 3b). Similar increase in the abundance of
271 annuals can be observed in wet years after dry years. All of those annuals live in the studied

272 grasslands, and they are generally prolific after disturbance. Thus we consider the ‘annual’
273 patch type an expected ordinary response of the annual species of the open grasslands.

274

275 The woody perennial species were variously affected by the fire. The fire induced intensive
276 re-sprouting of poplar species, together with spreading of other clonal species like
277 *Calamagrostis epigeios*, in accordance with the findings of Marozas et al. (2007). We
278 observed the spreading of poplar species (*Populus alba* and *P. nigra*) which have resprouter
279 and clonal spreading strategy (Menges and Kohfeldt 1995). Szujkó-Lacza and Komáromy
280 (1986) also detected the fast spreading of the poplar two years after the Bugac wildfire. On
281 contrary, the common juniper (*Juniperus communis*) does not regenerate after fire (Marozas et
282 al. 2007, Wink and Wright 1973). According to our observations, even the partially burnt
283 specimens died in a year. The lack of junipers (the darkest element of the vegetation) is
284 noticeable around the burnt patches in Fig. 2. The sensitivity of the juniper to the fire causes
285 major change in the structure of the vegetation, where it was dominant before. Consequently,
286 the whole vegetation mosaic cannot be considered fire-adapted, as both the dominant juniper
287 and the widespread cryptogams do not recover after the fire.

288

289 *The long-term effect of wildfire*

290 According to the observed patch type transitions (Fig. 4) the vegetation is more dynamic after
291 fire than in unburnt areas: contrary to our second null-hypothesis, less patch types are
292 significantly permanent and statistically significant transitions from one patch type into
293 another appear in burnt areas. The long-term effect of fire, which we found in all of our sites
294 in the Kiskunság Sand Ridge, shows the lack of fire adaptation based on Engel and Abella
295 (2011). According to our third null-hypothesis, application of space-for-time-substitution
296 (Pickett 1989) for the patch type transitions (Fig. 5) shows that the excess of dynamics in the

297 burnt areas does not disappear even in longer time. Engel and Abella (2011) also found
298 dynamics independent from time since fire and high long-term post-fire variability in
299 *Coleogyne ramosissima* dominated community of Mojave.

300

301 The changes of patch types show a network-like pattern of transitions. Thus, most of the patch
302 types, except the rare ones, have more than one connection, and most of the connections are
303 bidirectional (Fig. 4). This pattern of transitions differs from the Clementian directional
304 succession (Clements 1916), and rather corresponds to Egler's (1954) concept of initial
305 floristic composition which he applied to secondary succession. In accordance to our results,
306 Capitanio and Carcaillet (2008) also found Egler's concept applicable to post-fire succession
307 of Mediterranean vegetation mosaic of Aleppo pine forest and sclerophyll shrubs (*garrigue*).
308 The regeneration was quick, and in both studies, the species of the post-fire vegetation had
309 been present in the pre-fire vegetation. These findings put the question, if the post-fire
310 vegetation dynamics could be considered secondary succession, or rather a quick
311 development towards a patchwork of metastable stages which could also be built up without
312 fire (Trabaud 1987).

313

314 *Factors influencing the dynamics*

315 The vegetation dynamics in our study sites is regulated at two levels: locally in short term,
316 and at landscape scale in longer terms. Locally, the resistance of the patch types is different.
317 By 2007 and 2008, the *Festuca vaginata* and *Stipa borysthenica* patch types reached a
318 combined frequency of more than 90 % in the burnt patches (Fig. 3b). Fewer transitions can
319 be found between these years, which we interpret as the impact of the high resistance of those
320 patch types (Fig. 4). The contradiction between the impact of precipitation and spreading of

321 permanent patch types might result in the leverage point of 2008 in the precipitation-transition
322 relation (Fig. 6b).

323

324 Despite our fourth null-hypothesis, the burnt state of the landscape resulted in precipitation
325 dependent vegetation dynamics, however, the dynamics of control patches were independent
326 from precipitation. Fire increased the dynamics of the grassland vegetation of the wood-
327 grassland mosaic on the long run as less patch types were found permanent in the burnt areas
328 (Fig. 4). We found this in the sites which had burnt two to eight, four to fourteen, and twenty
329 to thirty years before the study. The independence of the increased dynamics from the time
330 passed from the fire implies to long-term indirect effect of the fire. The most conspicuous
331 impact of the fire is the disappearance of the juniper, which is a long-term change of habitat
332 structure (Bond and Keeley 2005). This disappearance leads to less shade in the grasslands.
333 The different reaction (Fig. 6) to the precipitation of the partially shaded unburnt patches and
334 the open burnt patches is a result of higher resistance due to the presence of woody vegetation
335 or the shades (Bartha et al. 2008). In our opinion, this buffering effect of the shades is the
336 major factor reducing the impact of droughts in the more woody areas. We observed the
337 dynamics by means of year to year transitions of patch types. Thus, the impact of drought can
338 be observed in the subsequent wet years when the damaged vegetation regenerates.

339

340 We propose a conceptual scheme on the changing dynamics after fire (Fig. 7). The same wet
341 years, in which there are higher biomass production and more opportunity to change in
342 composition, lead to transitions of patch types only after the fire which made the vegetation
343 more open.

344

345 Our main finding is that the grassland patches of the juniper-poplar-grassland mosaic is more
346 dynamic after wildfire, and remain more dynamic even for decades. We observed that the
347 changes mostly occurred in wet years; however, we suppose that the cause of the changes is
348 the increased vulnerability of the grassland species for the drought in the bunt sites, where the
349 shadows of the junipers does not reduce the effect of drought. As the wildfire is not part of the
350 natural disturbance regime of the juniper-poplar stands, we think that they should be saved
351 from wildfire more effectively than in the past. We should add that the largest remaining
352 unburnt juniper-poplar stand in Bugac region burnt down in 2012, ignited by the surrounding
353 *Pinus nigra* plantations.

354

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356

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363

364

365 **Refereces**

366

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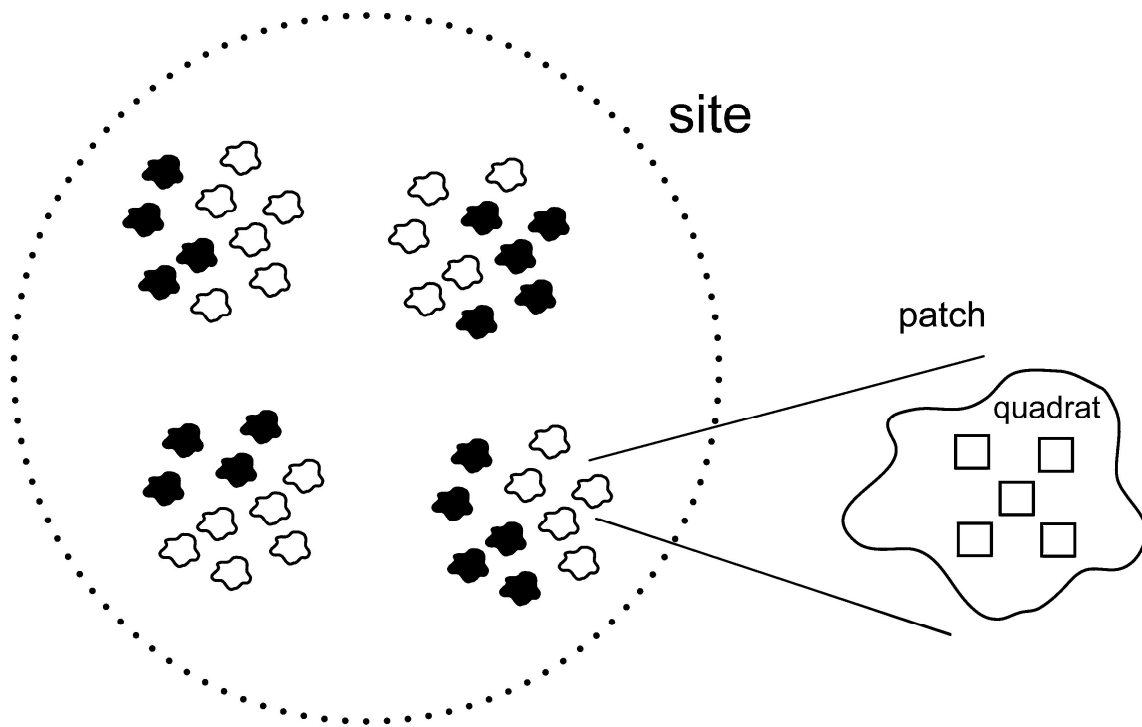
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Years	Treatments	Sites		
		Bugac	Bócsa	Orgovány
1997-2001	unburnt	26	6	
	burnt	10	10	
2002-2008	unburnt	28	6	20
	burnt	12	14	20

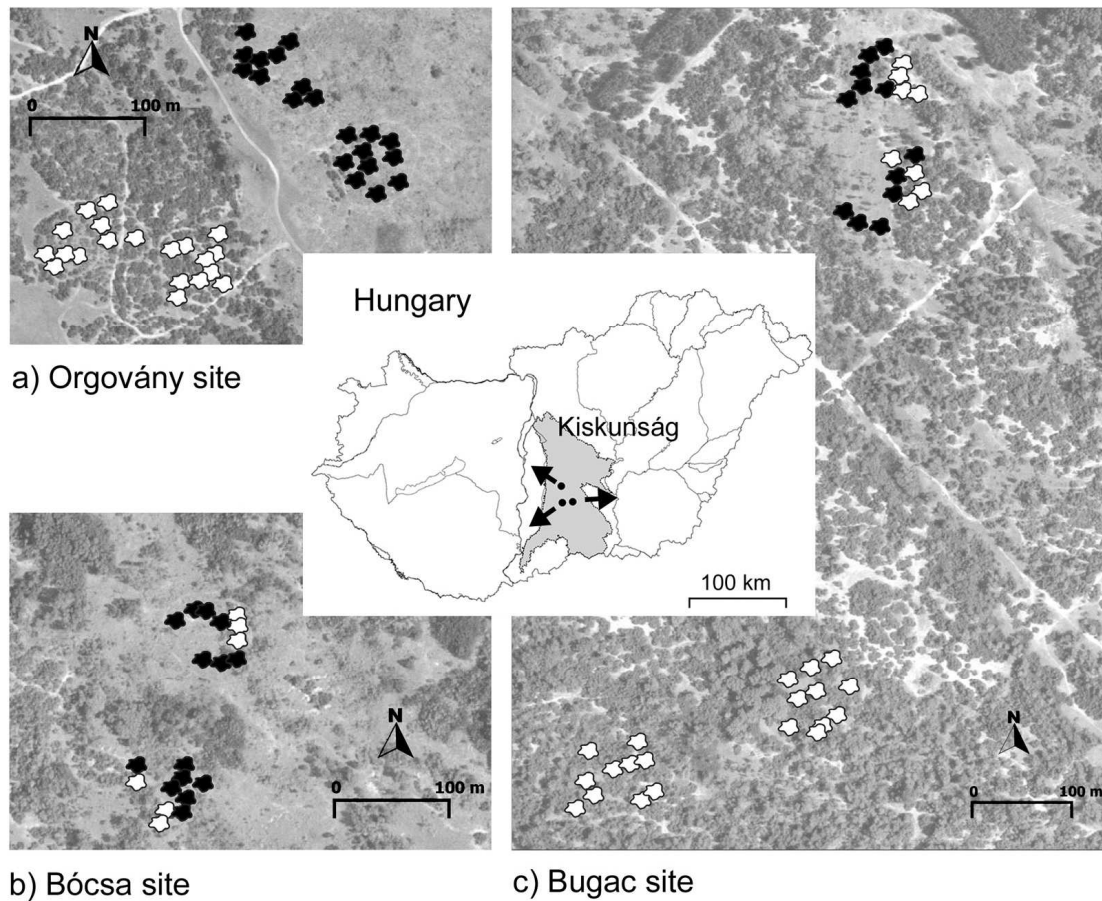
508

509 **Table 1** Number of unburnt and burnt grassland patches in the experimental sites



510

511 **Fig 1** Levels of the sampling design: (1) 1 by 1 meter quadrats; (2) five quadrats are grouped
 512 in one grassland patch; (3) burnt (black filled) and unburnt (white filled) patches are arranged
 513 in the burnt and unburnt areas of the sites (dotted line)



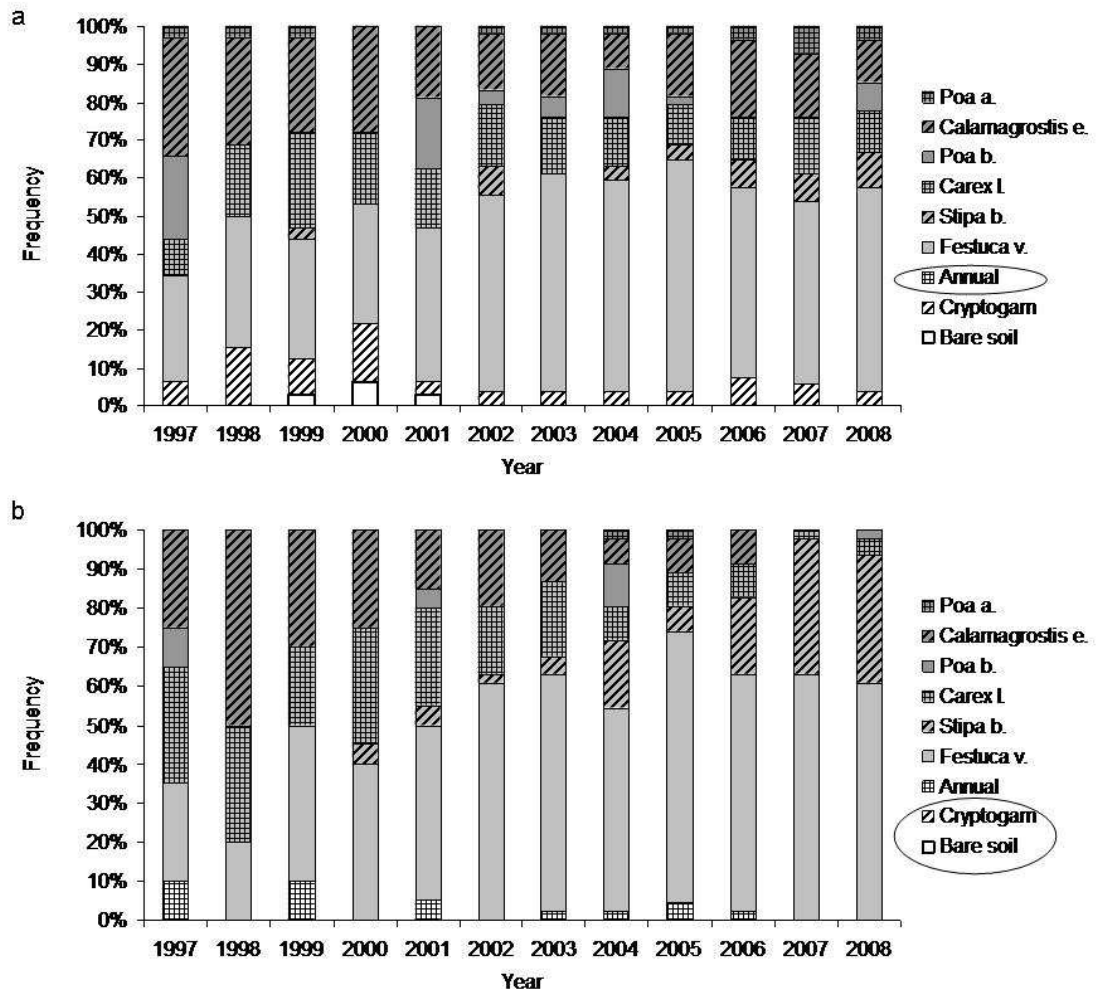
 - burnt patches
  - unburnt patches

514

515 **Fig 2** The study area: (a) the Orgovány site, (b) the Bócsa site, (c) the Bugac site. The

516 sampled burnt (black filled) and unburnt (white filled) grassland patches of juniper-poplar

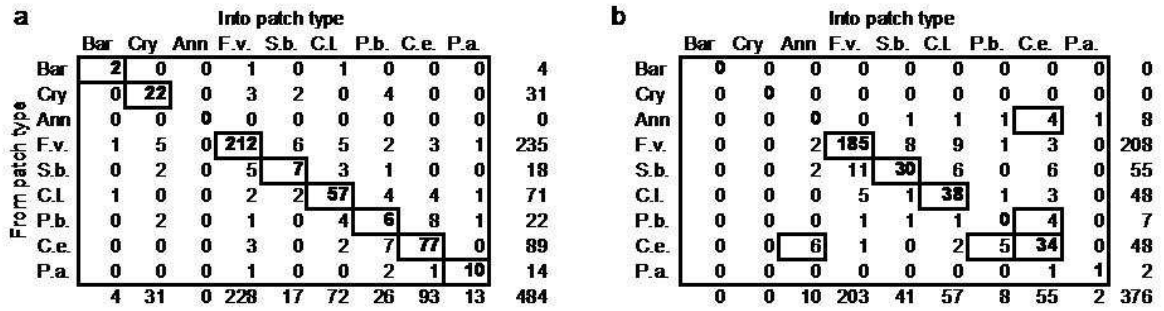
517 forest-steppe mosaics are shown on aerial photographs in 2005.



518

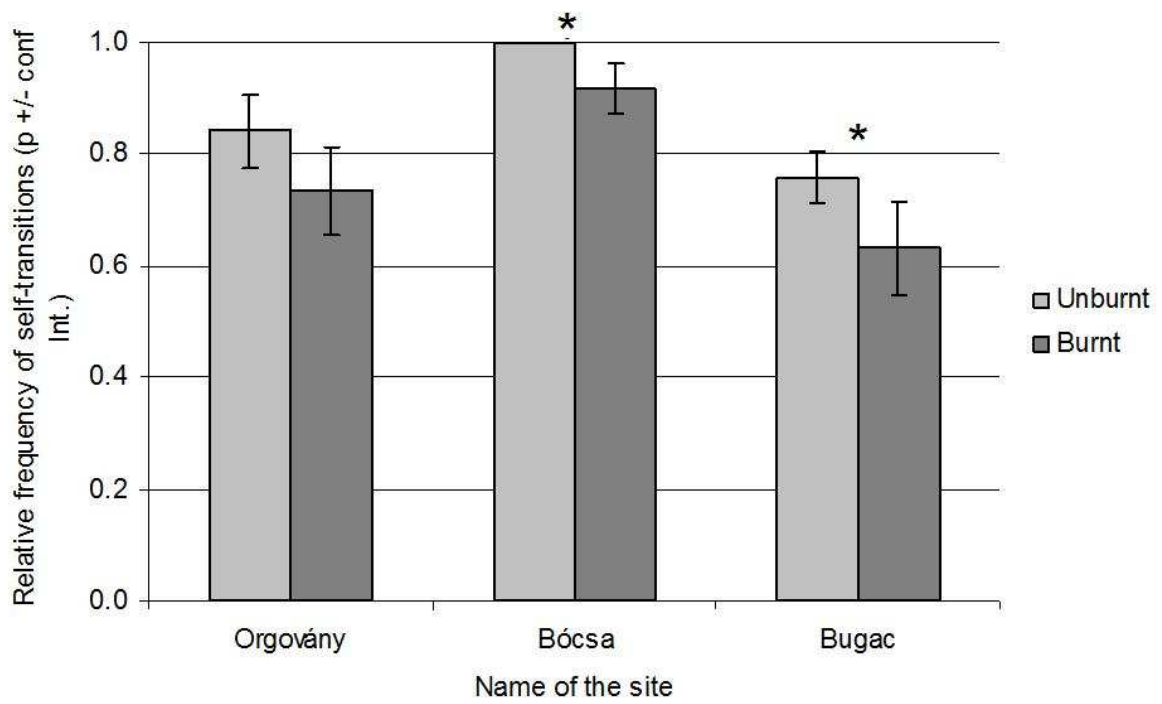
519 **Fig 3** Relative frequency of the patch types in the unburnt (a) and burnt (b) grassland patches.

520 Unobserved patch types are marked by circles



521

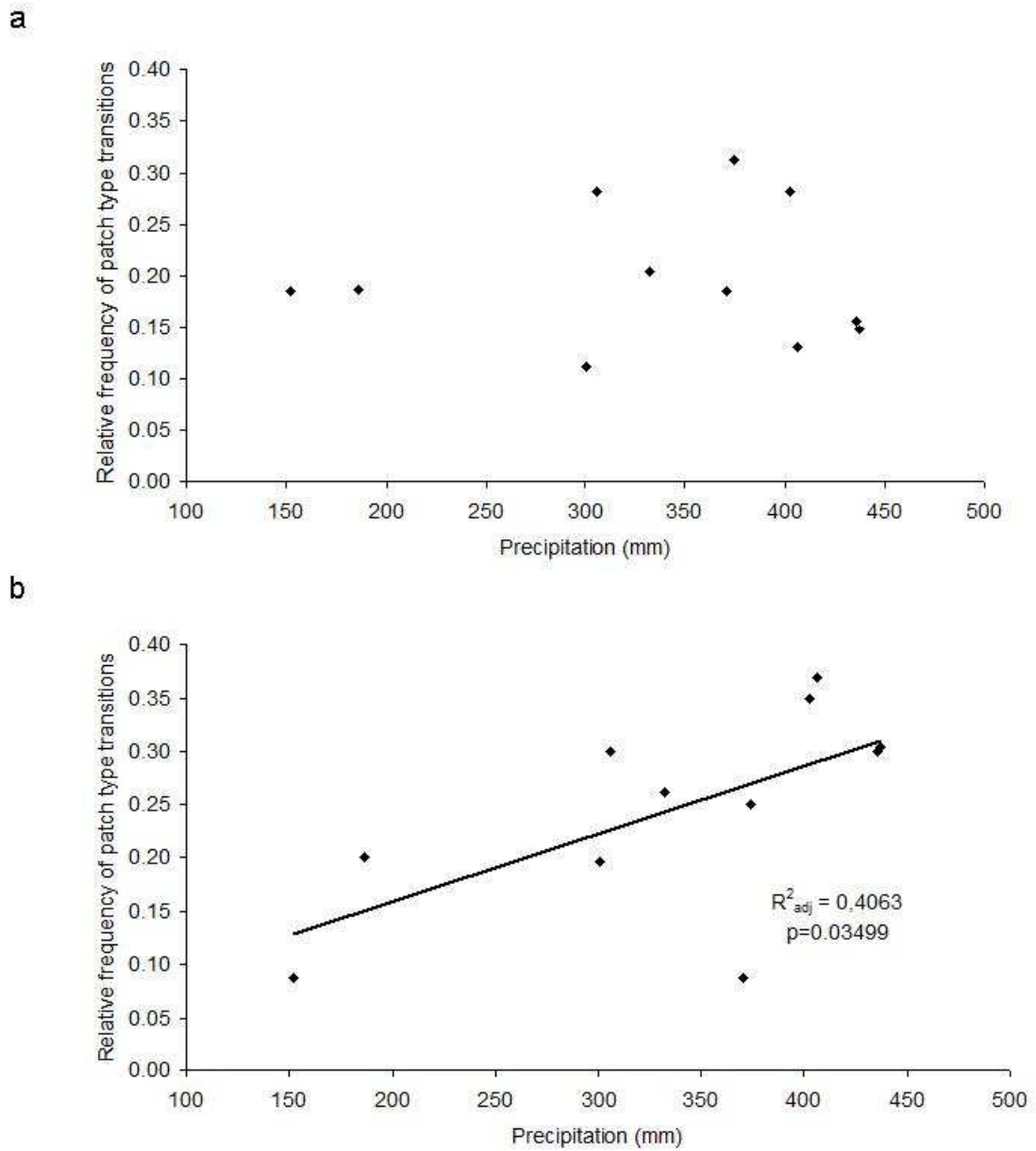
522 **Fig 4** Transition matrix (a) for unburnt patches and (b) for burnt patches. Bold frames denote
 523 transitions which significantly higher than the expected values based on the frequencies of the
 524 patch types. The marked significant deviations are positive ones. Abbreviations: Bar - bare
 525 soil, Cry - cryptogam, Ann - annual, F.v. - *Festuca vaginata* group, S.b. - *Stipa borysthenica*
 526 group, C.l. - *Carex liparicarpos* group, P.b. - *Poa bulbosa* group, C.e. - *Calamagrostis*
 527 *epigeios* group, P.a. - *Poa angustifolia* group



528

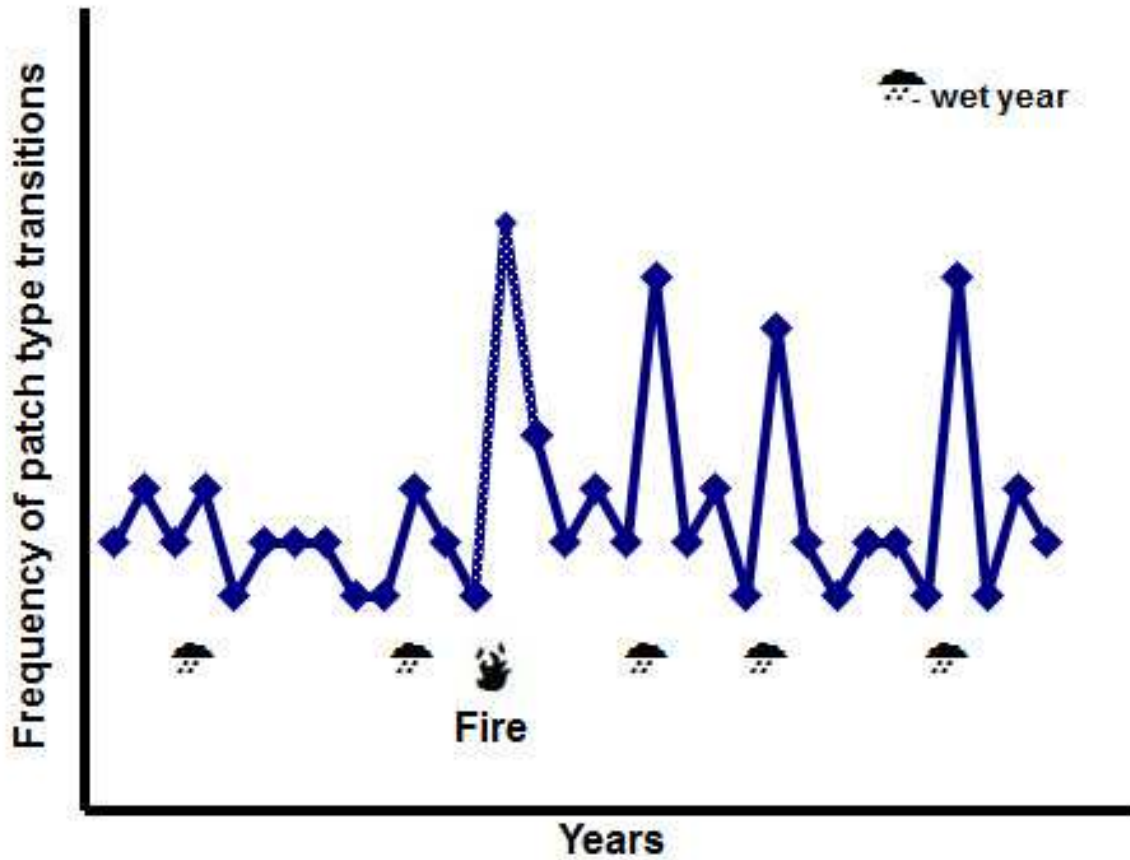
529 **Fig 5** Self-transitions of unburnt and burnt open sand grassland patches. Asterisks indicate

530 significantly decreased self-transitions in the burnt patches



531

532 **Fig 6** The relationship between the precipitation (from April to September) and the relative
 533 frequency of the patch type changes (the ratio is calculated by dividing the number of the
 534 changed patches compared to the former year by the total number of the patches) in the
 535 unburnt (a) and burnt (b) patches



536

537 **Fig 7** Conceptual scheme of the impact of wet years on vegetation dynamics before and after

538 fire