6

7 **Title**

8 Carbon uptake changed but vegetation composition remained stable during transition from

9 grazing to mowing grassland management

10

11 **Names of the authors**

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Highlights

- Vegetation composition and diversity did not change for six years after the conversion from grazing to mowing.

- Even the detailed fine-scale analyses could not reveal differences.

- Carbon uptake differed between grazed vs. mowed sites due to biomass removal intensity.

- Returning from mowing to grazing would probably restore C uptake capacity at the mowed site because the vegetation composition remained stable.

Abstract

Grasslands could play an important role in supporting livestock, in carbon sequestration and in biodiversity conservation. Different grassland managements may change the vegetation composition of grasslands, which could alter these ecosystem services. We studied the effects of grazing vs. mowing on the vegetation composition (2012–2016) and on the carbon uptake (2011–2013) of sandy grasslands in Hungary to study if the vegetation composition differs and if it does, whether it affects carbon uptake. To observe differences in vegetation composition between the two types of management regimes we performed fine-scale vegetation survey in adjacent grazed and mowed sites. We compared species compositions and vegetation diversity indices between the management regimes based on permutational ANOVA, mixed effect model and information theory models. We used fine-scale vegetation survey because it has the potential to indicate vegetation changes within six years as changes in species richness and diversity are usually detected after 10-20 years. Carbon uptake was measured in parallel with eddy covariance technique at both sites. In spite of the contrasting management regimes the vegetation composition was stable (no differences observed in the diversity indices), while carbon uptake was significantly greater in the grazed

52 (sink: $+1\pm0.7$ t C ha^{-1} year^{-1}) compared to the mowed site (source: -0.3 ± 0.6 t C ha^{-1} year^{-1}).

53 The vegetation was heterogeneous (patchy) and had a high species richness at both sites

54 (grazed: 91 species ha^{-1}, mowed: 90 species ha^{-1}) which might have contributed to the stability

55 of the vegetation composition. We concluded that differences in carbon uptake existed

56 between the grazed vs. mowed sites due to biomass removal intensity with no differences in

57 the vegetation composition.

58 Keywords: community diversity; microcoenology; carbon uptake; grazing; mowing

59

60 **1. Introduction**

61

62 Grasslands could play an important role in providing feed for grazing livestock (Henwood,

63 2010), in carbon sequestration (Soussana et al., 2010) and in biodiversity conservation (in

64 case of natural, semi-natural grasslands) (Báldi et al., 2013; Tälle et al., 2016). Grasslands

65 store 20% of the world soil organic carbon (SOC) while sequestrating an average of 0.03 to 1

66 t of C (carbon) per ha per year (Smith el al., 2008). However, grasslands could be a source of

67 C, depending on the land type, soil parameters, climatic factors and management regimes

68 (Smith et al., 2008; Nagy et al., 2007). To maintain and enhance these ecosystem services

69 proper grassland management regimes and management intensities should be applied.

70 It was shown that different grassland managements (e.g. grazing vs. mowing) could change

71 the composition of the vegetation (Tälle et al., 2016), which can affect C sequestration of

72 grasslands (Klumpp et al., 2011; LeCain et al., 2002). However, little is known about how

73 changes in the management regimes (transition from grazing to mowing) affect C uptake and,

74 in parallel with this, how the fine-scale vegetation composition changes in response to a

75 switch in the management regimes and how this affects C uptake. It was found that intensified

76 grassland management e.g. sowing with legumes (Conant et al., 2017), fertilization (Senapati

77   et al., 2014) or increasing species richness (Cong et al., 2014) could enhance C sequestration.

78   It was shown in a 50-year-long experiment that vegetation composition changes due to

79   differences in grassland management regimes (grazing and grazing exclusion) influenced the

80   C sequestration capacity of the grassland (LeCain et al., 2002). Due to the exclusion of

81   grazing the ratio of plants with C3 photosynthetic pathway increased, while in the grazed site

82   the proportion of C4 plants increased. This example shows as how vegetation composition

83   affected C uptake (coupled with climatic condition) as grazing exclusion site had higher C

84   uptake in cold years (preferable to plants with C3 pathway), while the grazed site had higher

85   C uptake in warm years (preferable to plants with C4 pathway) compared to the other site

86   (LeCain et al., 2002).

87   Vegetation composition is under the influence of the management of biomass production. In

88   general, mowing is a sudden event when biomass is usually homogeneously removed, while

89   during grazing the biomass removal is patchy and prolonged (Adler et al., 2011). During

90   mowing the light penetration to the ground increases, the litter layer is reduced and due to the

91   lack of fertilization the soil nutrients are depleted. On the other hand, grazing leads to a higher

92   rate of nutrient turnover (due to urine and dung) compared to mowing. In many cases due to

93   either grazing or mowing, the vegetation composition and biodiversity is usually altered (Házi

94   et al., 2012; Jantunen, 2003; Moog et al., 2002; Socher et al., 2012; Vadász et al., 2016).

95   However, no differences were also observed in species richness (e.g. Hansson and Fogelfors,

96   2000; Stammel et al., 2003). Tälle et al., (2016) reviewed that grazing generally had a more

97   positive effect on the conservation value of grasslands, i.e. grazing led to higher biodiversity

98   compared to mowing but the magnitude of the positive effects was generally too small to

99   moderate. Vegetation composition was found to be rather stable under constant grazing or

100   mowing even during long-term (>15 years) (Hellström et al., 2006; Sullivan et al., 2017) or

101   mid-term time periods (cca. 10 years, Pavlů et al., 2011), although short term changes were

102 also observed (<5 years, Wan et al., 2016; Valkó et al., 2012). There is still little evidence

103 with regard to how grazing vs. mowing changes vegetation composition at fine-scale in short

104 or long time periods. Accurate knowledge on vegetation (type, composition, structure), soil,

105 climate and management parameters (stocking rate, mowing intensity, timing) are needed,

106 since due to the large differences obtained in these parameters (e.g. arid grassland vs. wet

107 meadows etc.) no general patterns can yet be identified.

108 Mowing in continental grasslands generally suppresses the dominant graminoid competitors,

109 favours forbs and decreases the mortality of light-demanding seedlings, while it is also

110 stressed that responses of plants to mowing can be highly species specific (Valkó et al., 2012).

111 It has been observed that due to mowing the frequency of drought tolerant species increased

112 (Socher et al., 2012), such as *Bromus inermis* or *Elymus repens* because of the increased light

113 and heat stress within the vegetation (Kovács and Csízi, 2004). On the other hand, due to the

114 selective grazing of cattle it can be observed that the frequency of unpalatable (*Eryngium*

115 *campestre*, *Ononis spinosa*) and trampling resistant species (*Festuca pseudovina*, *Cynodon*

116 *dactylon*) increased (Kovács and Csízi, 2004). Vegetation could react species-specifically to

117 either grazing or mowing. Thus, grazing provided clonal grasses and forbs with good

118 conditions (e.g. *Trifolium repens*), whereas grasses with below-ground storage organs were

119 better supported by mowing (e.g. *Molinia caerulea*) (Stammel et al., 2003). In general,

120 grazing and mowing could also contribute to high biodiversity (Tälle et al., 2016), provided

121 that the disturbance caused by the management regime is of intermediate level (Crawley,

122 1997; Török et al., 2018).

123 In this study we used microcoenological methodology (fine-scale vegetation survey) to study

124 the effect of transition from grazing to mowing on the fine-scale vegetation composition of

125 the grazed and mowed grasslands. This method was used because fine-scale (5×5 cm

126 quadrates) diversity changes could be detected earlier compared to cover estimations in larger

127 quadrats (traditionally 2×2 m in these grasslands) (Bartha et al., 1995, 2004). Microcoenology

128 provides a well-documented and precise tool (high resolution, spatially explicit, multi-scale

129 sampling design) to indicate changes in the vegetation composition of grasslands early under

130 varying management regimes (Bartha et al., 2004; Matus and Tóthmérész, 1990; Virágh et al.,

131 2008). It is a tool not only for nature conservation (indication of degradation) but also for

132 ecosystem management purposes (when vegetation composition and its changes are linked to

133 ecosystem services) (Loreau et al., 2003; Wilcox et al., 2017). It was proved that behind the

134 apparent larger scale stability (invariance) of vegetation there could be intensive fine-scale

135 dynamics operating (Herben et al., 1993), suggesting that multidirectional and uncorrelated

136 fine-scale local transitions stabilize the larger scale patterns (Wang and Loreau 2016). Any

137 forces that synchronize the fine-scale processes will destabilize the community and will result

138 finally in larger scale transitions. The information theory models (Juhász-Nagy and Podani

139 1983, Juhász-Nagy 1993) offer a methodology to describe and understand details of fine-scale

140 patterns, therefore we used the compositional diversity (CD) index as a sensible tool for

141 detecting initial stages of vegetation changes (Bartha et al., 1998, 2011).

142 Our goal was to investigate the effects of grazing and mowing on the fine-scale pattern of

143 plant species diversity in sandy, semi-arid grasslands in Hungary (Bugac) and to relate

144 vegetation composition changes to C sequestration measured (and published; Koncz et al.,

145 2017) at both sites. We hypothesized that the contrasting management regimes (grazing vs.

146 mowing) had an effect on vegetation composition.

147

148 We expected that;

149 1) switching the management from grazing to mowing would change the fine-scale

150 vegetation composition which could be detected after five years,

151   2) diversity of vegetation composition would decrease while homogeneity would

152   increase in the mowed site, although we do not expect changes (besides inter-annul

153   variability) at the grazed site.

154   3) vegetation composition changes would influence C sequestration and C sink activity.

155   4) C sequestration in the mowed site will be lower compared to grazed site.

156 In our previous study we found that changing the management from grazing to mowing in

157 2011 did not change the microcoenological composition between the grazed and mowed sites

158 in the first year (2012) (Koncz et al., 2014). In the present study we analyze the results

159 obtained since then (2012–2016). The measurements of the vegetation composition and

160 functional parameters (C uptake) together provide an understanding about the role of

161 contrasting grassland managements on the plant diversity and ecosystem function.

162

163 **2. Materials and Methods**

164

165 **2.1. Study area**

166 To investigate the effect of grazing and mowing on the vegetation composition we performed

167 repeated microcoenological surveys (high resolution vegetation monitoring) in a closed, sandy

168 grassland (Fig. 1) in Hungary near Bugac (N46°41'28", E19°36'42"). The soil type is sandy

169 chernozem (Calcic Chernozem according to the World Reference Base classification; see

170 http://www.fao.org/nr/land/soils/ soil/en/), with high sand and low clay contents (Nagy et al.,

171 2010). Total organic carbon content in the upper 10 cm soil layer is 5.2% (Nagy et al., 2010).

172 The vegetation is classified as closed sand steppes (H5b) (Bölöni et al., 2011) and Pannonic

173 sand steppe (6260) (Šefferová Stanová et al., 2008). Based on the 19th Century Military

174 Surveys of the area both grazed (1 ha) and mowed grassland sites (1 ha) has been grazed in

175 the last 150 years (Web references: MAPIRE-1; MAPIRE-2). The total grazing area is around

176   500 ha at the present. The average annual precipitation in the area was 575 mm and the annual

177   mean temperature was 10.4 °C (2004-2013). Grazing period of cattle usually lasted from 15th

178   May to 15th July and from 15th October to the first of December (0.65±0.15 livestock unit,

179   LSU ha^{-1}, 2010–2016). The mowed area (1 ha) was fenced from the grazed area in March

180   2011 (Fig. 1). Thus, before the fencing both sites had the same history. The mowed site was

181   cut once per year between June and August (except in 2014, when it was cut twice). Mowing

182   height was 6 centimetres. After drying for a few days the hay was removed from the mowed

183   site. No other treatments (e.g. irrigation, fertilization, or burning) were applied on the sites

184   (these are banned in these protected grasslands according to the *Law of Nature Protection,*

185   *1996. LIII., 5§ (2) 269/2007. (X. 18.) Parliament Decision*). For more details on stocking rate,

186   mowing intensity, grazed and mowed biomass, herbage use efficiency see Koncz et al.,

187   (2017).

188   The mowed and the grazed study areas were adjacent to each other (250 m) therefore

189   precipitation rates and air temperatures were assumed to be similar. Precipitation (ARG 100

190   Tipping Bucket Raingauges, Waterra Ltd.) and air temperature (HMP35AC, Vaisala) were

191   recorded by the meteorological station in the grazed site (Fig. 1) between 2011–2018. The

192   weather conditions of the months were described with the Gaussen-Bagnouls index.

193

194   **2.2. Experimental design**

195   Microcoenological surveys were performed at both grazed and mowed sites (Fig 1). We used

196   permanent transects for the microcoenological survey because it provides an objective and

197   precise baseline record to follow fine-scale changes in species frequencies and composition

198   (Bartha et al., 2004; Virágh et al., 2008). Plant presences were recorded in small 5×5 cm

199   quadrates along 5-meter transects (100 quadrates per transect). Species abundances were

200   represented by the number of presences to avoid subjective bias from cover estimates (%).

201   This type of sampling was used successfully in previous comparative studies in various

202   grassland types from tall-grass prairie to semi-deserts (Margóczi 1993; Bartha et al., 1995,

203   2004, 2008, 2011; Virágh et al., 2008; Bakacsy 2019). Alternative methods, e.g. line-intercept

204   method (Collins and Xie, 2015) could not be used because of the relatively high species

205   density (majority of 5×5 cm quadrates had more than 4 species, cf. Supplementary Material 1.

206   Fig S1) and the presence of clonal species in our data.

207   Microcoenological surveys were done parallel on both sites at the peak of the vegetation

208   period (13–14th June 2012, 11–12th June 2013, 29–30th May 2014, 4–5th June 2015, 30–31th

209   May 2016). Permanent transects started at 40 meters from the eddy-covariance (EC) stations

210   at both sites (Fig. 1). Transects were at an angle of 60 degrees to each other (Fig. 1). In each

211   transect the presence of all rooting plant species was recorded in 100 contiguous 5×5 cm

212   micro-quadrates to determine species frequencies and composition. Identification to species

213   level was not always possible due to the lack of flowers, seeds or due to the lack of the main

214   part of the stem; therefore, for the analysis we combined certain species at genus level (e.g.

215   *Carex* spp., in which case three-quarter of the *Carex* spp. were *Carex stenophylla* and the rest

216   were *C. divisa*, *C. praecox* and *C. liparicarpos*).

217   We surveyed two sites (1 ha each) because the experiment was originally designed to be used

218   by the carbon uptake surveys (because of the labour work and expenses required for EC

219   measurement it was not feasible to have more replicates or performing a landscape scale

220   survey). Carbon uptake was studied by net ecosystem exchange measurements (NEE) by

221   eddy-covariance systems at both sites (described in our previous study; Koncz et al., 2017).

222   This experimental design tried to cover the heterogeneity of the vegetation in both sites

223   surrounding the meteorological stations in an area of one hectare, where the NEE

224   measurements were performed (Fig. 1).

225
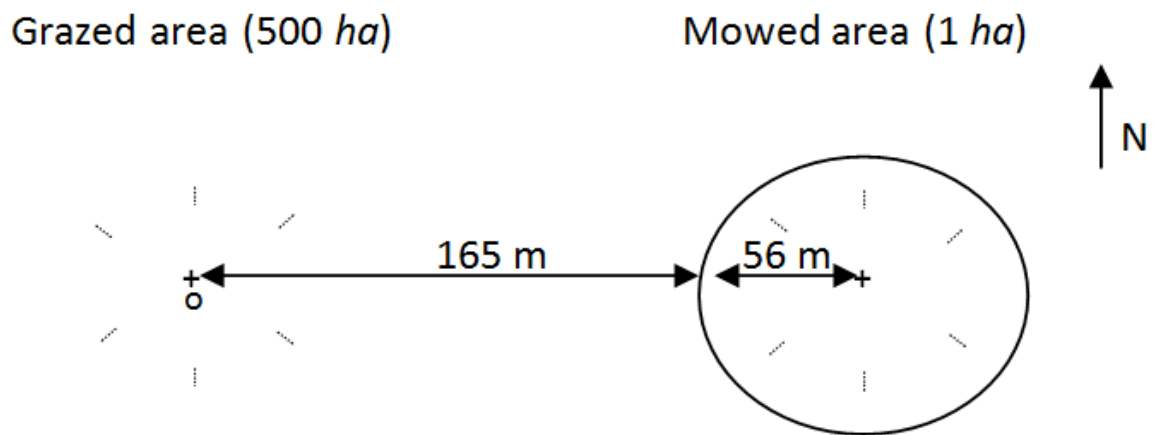
Figure 1. The experimental design of the microcoenological survey conducted in the grasslands of Bugac, Hungary (eddy covariance measurements: +; meteorological station: o; microcoenological transects: ····).

2.3. Diversity indices

Vegetation patterns were characterized at the level of transects and also at finer scale (representing vegetation patterns within transects). Alpha diversity (species richness and Shannon diversity index) and species frequency were measured at each transects. Species frequency was calculated based on the occurrence (counts) of a species in the quadrates along the transects (100 quadrates). Plant species were grouped into functional groups (monocotyledons, forbs – dicotyledons except legumes –, legumes, bryophytes), and into disturbance resistance and annual species. The frequencies (%) of the different functional groups at site level were calculated as the ratio of the counts of a given functional group to the total counts of all functional groups (2012-2016 average).

Beta diversity indices were used to characterize composition variability within transects. Each transect was subdivided into five (20 units long) sub-transects and species abundances were calculated in each sub-transects (summarizing presences of species ranging from 0 to 20).

244 Based on these abundance scores, composition variability (beta diversity) within a transect

245 was characterized by the mean Bray–Curtis dissimilarity between sub-transects. Variability of

246 these indices (based on the 6 transects per site) was compared between the grazed and mowed

247 sites.

248

249 **2.4. Indicators for fine-scale species coexistence, compositional diversity index**

250 Fine–scale spatial variability of species co-occurrences was further analysed by information

251 theory models (Juhász-Nagy, 1993). The Compositional Diversity index (CD) describes the

252 diversity of realized species combinations (where a particular combination is formed by the

253 species which co-occur in the same sampling unit). It is calculated as the Shannon entropy for

254 the frequency distribution of the observed species combinations within the sampling units:

255

$$CD = - \sum_{k=1}^{\omega} p_k \log_2 p_{\mathbf{k}}$$

256

257 where $\omega = 2^N$ is the number of possible species combinations, N is the number of species and

258 $p_{\mathbf{k}}$ is the frequency of the kth species combinations in the sample. In contrast to beta diversity

259 indices based on pairwise comparisons of plots (e.g. Bray–Curtis index), CD considers all

260 plots (a multiple-site beta diversity measure, Bartha et al., 1998, 2011). As the number of

261 realized species combinations depends on the spatial scale (Juhász-Nagy, 1993; Podani et al.,

262 1993; Bartha et al., 2004), CD is calculated at a series of plots of increasing sizes (gradually

263 merging   2,   3,   4   etc.   adjacent   micro-quadrats   along   the   transects)

264 (cf. Supplementary Material 2., Fig. S2-S6). Spatial scaling was performed by computerized

265 resampling of the base-line transects (Podani 1987) with sampling units of gradually

266 increasing sizes (changing resolution, i.e. grain sizes) from 5 cm to 100 cm. CD showed a

267 unimodal maximum curve if it was plotted against the grain size (for detailed explanation cf.

268 Supplementary Material 2., Fig. S2-S6). We usually present only the maximum of this

269   function (Bartha et al., 1998) that appeared in this data set at very fine scales at 5 cm and 10

270   cm (Supplementary Material 2., Fig. S5, Fig. S7, Fig. S9).

271   The length of the transects (100 quadrates) determines the possible detectable number of

272   realized species combinations (100 combinations), thus to calculate unbiased CD (Tóthmérész

273   and Erdei, 1992) only those species were kept which had at least 20 occurrences along one

274   transect (for detailed reasoning cf. Supplementary Material 2. Fig. S7, Fig S8).

2.5. Statistics

During the statistical analysis the dependent variables were diversity indices (1-4, see explanation below), plant groups (5-10, see explanation below), and the nine most frequent species (11-19). Diversity indices were 1) species richness, 2) Shannon index, 3) Bray–Curtis dissimilarity index, and 4) compositional diversity. Plant groups were: 5) disturbance resistance species (Poptcheva et al., 2009), 6) annual species, 7) monocotyledons, 8) forbs (Dumont et al., 2012), 9) legumes, and 10) bryophytes. Finally, dependent variables included the frequency of the nine most frequent species (or their agglomeration) as well as the 11) *Achillea millefolium* agg., 12) *Arenaria serpyllifolia*, 13) *Bromus hordeaceus*, 14) *Carex* spp., 15) *Cynodon dactylon*, 16) *Elymus repens*, 17) *Festuca pseudovina*, 18) *Medicago falcata*, 19) *Poa angustifolia*. Differences of these dependent variables were compared with mixed effects models (Pinheiro et al., 2018) between years and managements. To perform mixed effects models we used the *lme* function from the *nlme* package (Pinheiro et al., 2018) in R (R Core Team 2018). Random effects were the transects. Independent variables included the years (2012–2016) and the managements (with interaction).

To compare the effects of managements on the vegetation composition we also performed Redundancy Analysis (RDA). During RDA communities that have similar species composition appear as points near each other, whereas communities that have different species compositions are further away from each other on the plot. Following RDA, permutational ANOVA (PERMANOVA) was performed to test significant differences among managements. RDA, PERMANOVA were performed in R (R Core Team 2018).

3. Results

3.1. Meteorological conditions

The climatic conditions differed considerably between the years. Year 2011 and 2012 were dry (Psum<512 mm, T average 10.45 °C, based on Bagnouls-Gaussen index six months were arid), year 2013 and 2015 could be regarded as average years (P sum=562±50 mm, T average=10.97°C, based on Bagnouls-Gaussen index three months were arid in both years), whereas year 2014 and 2016 were wet (Psum>612 mm, T average= 10.99 °C, based on Bagnouls-Gaussen index only one month was arid in 2014 and two in 2016) (Fig. 2). Shortly before the study period climatic conditions probably greatly affected the general vegetation compositions at both sites, since 2010 was an extremely wet year (960 mm), while 2011 was a dry year (471 mm).
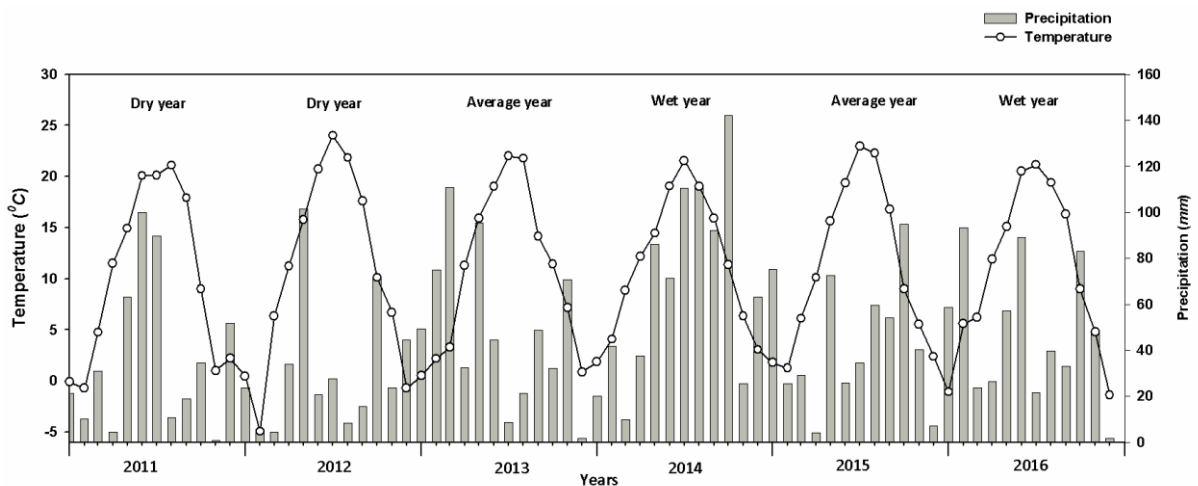
Figure 2. Mean monthly temperature (black line with dots) and the amount of precipitation (grey columns) in the study area.
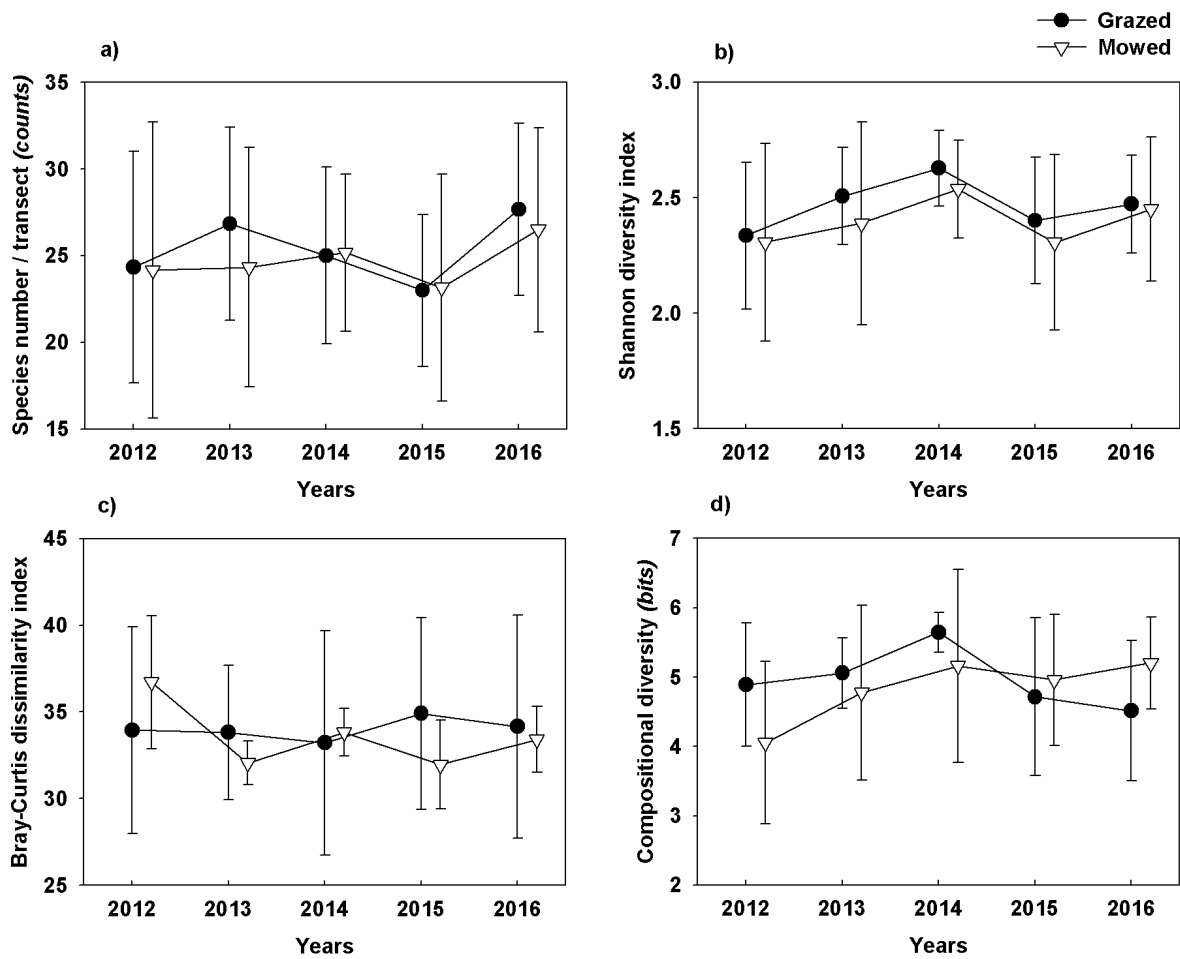
3.2. Diversity indices at the grazed vs. mowed sites

During the survey we found a total of 114 species, 91 on the grazed and 90 on the mowed site. The experimental design represents one hectare for both sites, thus the grasslands were species rich.

Species number differed between years (due to annual fluctuations) but not between the managements (grazed: 25.4 ± 1.9 species; mowed 24.7 ± 1.2 per 0.25 m^2) (Fig. 3a, Table 1).

316   Shannon diversity index varied considerably between the years but the course of the change

317   was similar in both sites (Fig. 3b) and no differences were observed between the

318   managements (grazed: 2.5 ± 0.1; mowed 2.4 ± 0.1 per 0.25 m^2) (Table 1). Throughout the

319   years the grazed (34 ± 0.6) and mowed (33.6 ± 1.9) sites remained similar as is shown by the

320   Bray–Curtis dissimilarity (grazed: 34 ± 0.6; mowed 33.6 ± 1.9) (Fig. 3c) and compositional

321   diversity index (grazed: 5 ± 0.4; mowed 4.8 ± 0.5) (Fig. 3d) and the results of the mixed

322   effect model (Table 1). The different management regimes (grazing vs. mowing, i.e. the

323   management change from grazing to mowing) had no effect on the diversity indices (Table 1).

324   The effects of the management regimes were not manifest in the interaction term either (Table

325   1). Within each management regime (site) the diversity indices greatly differed among

326   transects as seen by the large standard deviations (Fig. 3), which indicated that the vegetation

327   composition in both the grazed and the mowed sites were heterogeneous (patchy).

328

329

Figure 3. Diversity indices of grazed and mowed sites; a) species richness, b) Shannon diversity, c) Bray–Curtis dissimilarity index, and d) compositional diversity along the transects. Average and standard deviations values are based on six transects per year per management (one transect was 500 cm long and 5 cm wide, i.e. 0.25 m^2).

3.3. Plant groups and frequency of species

Based on the mixed effect model the different managements had no effect on the plant groups and on the most frequent species (Table 1). The frequencies of the functional groups were the following (2012-2016) in the grazed and mowed sites, respectively: monocotyledons (53% 56%), forbs (30%, 34%), legumes (13%, 8%), and bryophytes (4%, 2%). All plant groups except bryophytes were greatly affected by the years (Table 1). Yearly fluctuations can also

342   be seen in Fig 4, especially in case of annuals and forbs in 2014 (Fig 4b, 4d). In case of these

343   two groups the effects of years may have caused a difference between the two sites in 2014

344   (the post hoc analysis of ANOVA was significant in case of annuals at p=0.02 level and in

345   case of forbs but only at p=0.07 level), but these differences did not persist, thus there were

346   not the consequences of the different managements (Table 1).

347   The nine most frequents species were always the same and the managements (sites) had no

348   effect on the frequencies of these species, except on *Arenaria serpyllifolia* and *Cynodon*

349   *dactylon* (Table 1). The frequency of *Arenaria serpyllifolia* became higher by 2014 at the

350   mowed site, while the frequency of *Cynodon dactylon* decreased constantly at the mowed site

351   (data not shown). Besides these two species the frequency of *Bromus hordeaceus* and *Elymus*

352   *repens* was affected by the years (Table 1).
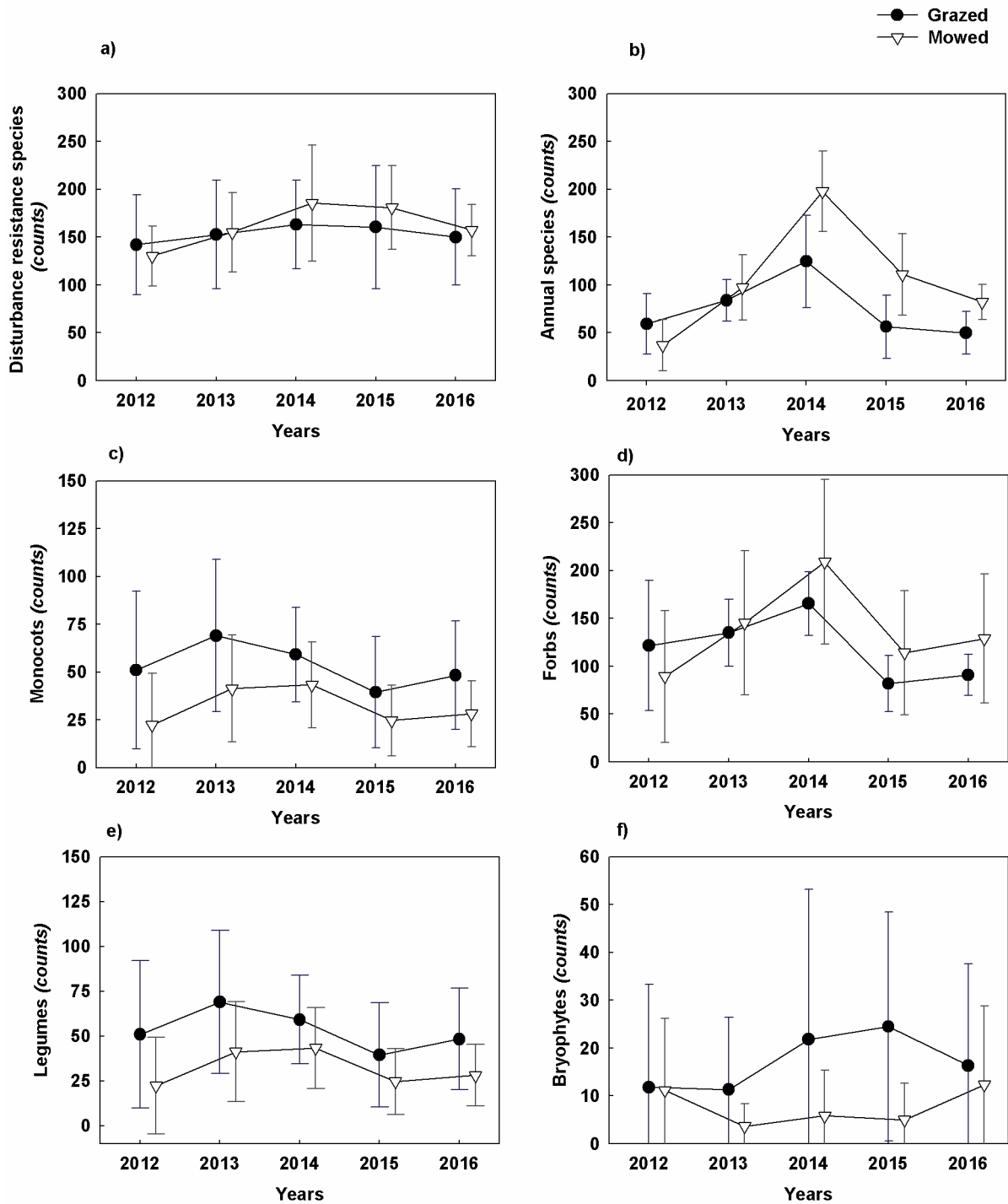
Figure 4. Frequencies of the functional groups (monocotyledons, forbs, legumes, and bryophytes), as well as the disturbance resistance and annual species in the grazed and mowed sites (number of occurrence transect^{-1}). One transect consisted of 100 contiguous 5×5 cm micro-quadrates.

358   Table 1. Summary of the results of mixed effect model (p-values) performed for the grazed

359   vs. mowed sites by diversity indices (1–4), plant groups (5–10), and by the most frequent

360   species (or their agglomeration) (11–19). Independent variables include the years and

361   managements with interaction.

362   * indicates significant differences at level=0.05.

Dependent variables	year	management	year× management
Diversity indices			
1 Species richness	0.01*	0.96	0.83
2 Shannon index	<0.0001*	0.67	0.79
3 Bray–Curtis dissimilarity index	0.55	0.65	0.35
4 Compositional diversity	0.25	0.60	0.35
Plant groups			
5 Disturbance resistance species	0.0002*	0.76	0.21
6 Annual species	<0.0001*	0.06	0.0003*
7 Monocotyledons	0.01*	0.77	0.49
8 Forbs	<0.0001*	0.59	0.008*
9 Legumes	0.0001*	0.23	0.49
10 Bryophytes	0.20	0.16	0.57
Frequent species			
11 *Achillea millefolium* agg.	0.69	0.42	0.52
12 *Arenaria serpyllifolia*	<0.0001*	0.34	0.00*
13 *Bromus hordeaceus*	<0.0001*	0.11	0.38
14 *Carex* spp.	0.08	0.65	0.60
15 *Cynodon dactylon*	0.02*	0.19	0.049*
16 *Elymus repens*	0.007*	0.52	0.29
17 *Festuca pseudovina*	0.61	0.55	0.19
18 *Medicago falcata*	0.08	0.55	0.26

| 19 | *Poa angustifolia* | | 0.30 | 0.83 | 0.86 |

3.4. Results of PERMANOVA

According to the PERMANOVA the vegetation remained similar between the grazed and mowed sites i.e. there was no compositional differences (p>0.05) (Fig. 5). Grazed and mowed plant communities had similar species composition.
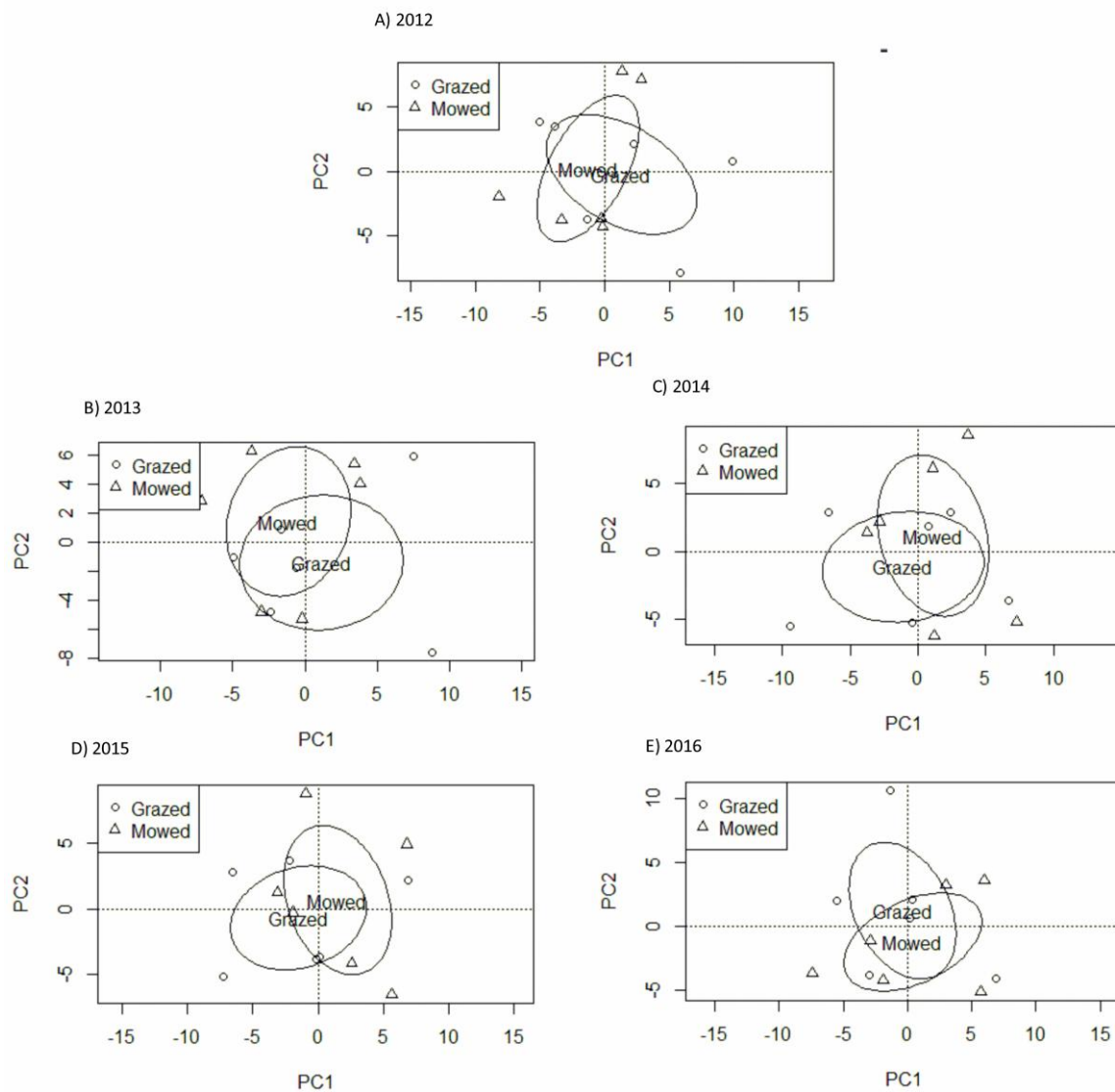

Figure 5. Results of Redundancy Analysis (RDA) and permutational ANOVA (PERMANOVA).

3.5. Carbon uptake

Details of carbon uptake and greenhouse gas balance of the managements (sites) have been analysed in details and published elsewhere (Koncz et al., 2017). We found that the grazed site had higher C sink capacity ($+1\pm0.7$ t C ha^{-1} year^{-1}) compared to the mowed site, which was C source (-0.3 ± 0.6 t C ha^{-1} year^{-1}) (Fig. 6). The average difference in C uptake between the grazed and mowed site was 1.3 ± 0.2 t C ha^{-1} year^{-1}. Vegetation composition did not differ between the grazed and mowed sites, thus it could not have been the reason behind the differences in C uptake.
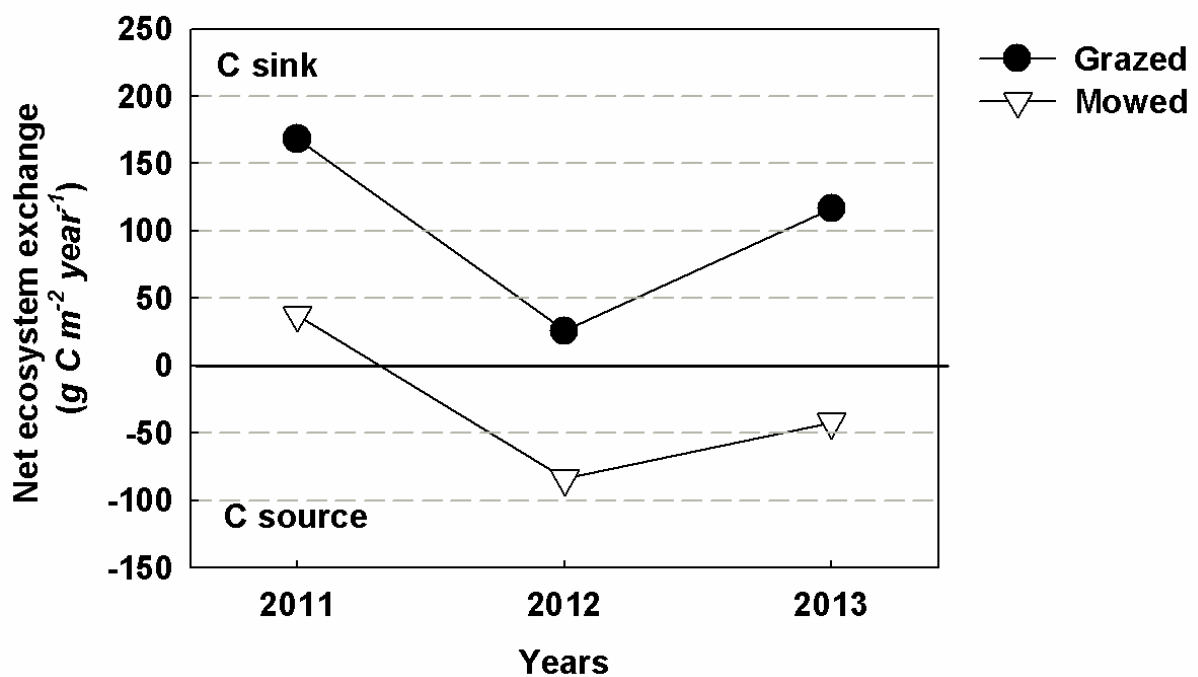
Figure 6. Net ecosystem exchange (NEE, carbon uptake) of the grazed and mowed sites. Calculations were based on data published in Koncz et al., (2017).

4. Discussion

4.1. Vegetation composition and grassland managements

In general, grazing causes a gradual and patchy decrease in the vegetation height, compacts and re-fertilizes the soil, while mowing causes a sudden and homogeneous drop in the vegetation height and depletes the soil minerals provided there is no fertilization. In consequence, vegetation composition is assumed to be altered by management differences. However, due to contrasting management regimes (grazing vs. mowing) the vegetation composition showed no differences in our study in adjacent grazed and mowed grassland sites during the six years of the experiment. At the scale of individual vegetation patches (represented by total species richness of transects and Shannon diversity calculated from transect-level relative abundances), we did not observe diversity changes of the vegetation. At finer scales (within individual patches), in contrast to our expectations, beta diversity measures (Bray–Curtis dissimilarity index and the diversity of species combinations) were also similar throughout the years between the grazed and mowed sites (Table 1). PERMANOVA (Fig. 5) did not reveal any differences either in the vegetation composition between grazed vs. mowed managements. Thus, the fine-scale composition and spatial organization of vegetation remained unchanged, which showed high stability of the studied sandy grasslands. High stability might be the consequence of the high species number belonging to various functional types as we observed 91 species in the grazed (1 ha) and 90 species in the mowed site (1 ha), a total of 114 species. However, species diversity and vegetation stability is not necessarily linked, as e.g. grasslands with long term reservation were found to have lower biodiversity but higher stability in a study in a steppe site of Mongolia compared to an enclosed grassland with or without mowing, which had higher biodiversity but lower stability (Zhang, 2016).

407   Remarkable yearly changes in the vegetation composition in our study were observed in case

408   of the frequency of two plant groups (annual species and forbs) and in the frequency of two

409   frequent species (*Arenaria serpyllifolia*, *Cynodon dactylon*) during the six years of the

410   experiment (Table 1). Due to mowing (the mowed site was fenced in 2011 to exclude grazing)

411   the frequency of annual species apparently increased possibly due to the appearance of small

412   openings in the grassland caused by the hay harvesting, although after 2014 these differences

413   disappeared. The apparent increase of forbs was unexpected and should further be studied as

414   in contrast to our study, mowing was found to suppress tall growing forbs (Billeter et al.,

415   2007; Valkó et al., 2012). Due to mowing the vegetation before seeding would reduce the

416   seed germination capability of plants, which was expected to decrease the frequency of forbs.

417   However, it is possible that the forbs simply survived under the blades of the cutting machine

418   and further forbs emerged from the soil seed bank (as space became available). In other study,

419   due to intensive grazing the cover of tall grasses such as *Bromus inermis* or *Elymus repens*

420   decreased, while due to mowing the frequency of drought and disturbance tolerant species

421   increased (Grime, 2001; Kovács and Csízi, 2004).

422   High stability/resilience in species richness and diversity was also observed in other studies.

423   There were no changes found in species richness and diversity at fine-scale even after 25

424   years of grazing vs. mowing in mesotrophic grasslands (Sullivan et al., 2017). In another

425   study no shift was observed to a different plant community despite 10 years of contrasting

426   management (mowing vs. abandonment) of a mountain hay meadow (Pavlů et al., 2011). In a

427   mountainous grassland plot Csergő and Demeter (2011) found that long term mowing

428   increased the persistence of the dominant *Festuca* species, and allowed the co-existence of

429   several other species adapted to low nutrient content of soil, rapid nutrient recycling, and open

430   microsites. On the other hand, short-term rapid vegetation changes were observed in a few

431   studies, e.g. Wan et al., (2016) found that within three years mowing management regime

432 (twice per year) reduced the abundance of semi-xeric and xeric forbs (Wan et al., 2016). Also,

433 yearly mowing in a mountain fen and dry-mesophilous hay meadow in Hungary increased the

434 species richness of forbs and target forbs between 2006 and 2007 (Valkó et al., 2012). In mid-

435 term, after seven years of experiment, grazing supported the dominance of grasses, while

436 mowing enhanced non-leguminous forbs in a species rich grassland of the White Carpathian

437 Mountains (Mládková et al., 2015). There is a great need for long-term (10-20 years)

438 comparative (comparing managements) micro-coenological experiments (to be more detailed

439 as using only species cover) taking into consideration the local conditions and legacy effects.

440

441 **4.2. Inter-annual and spatial variability of vegetation composition**

442 In our study the inter-annual variability of the vegetation composition was high for both

443 grazed and mowed sites, which is a characteristic of numerous grasslands (Loeser, 2001).

444 Climatic conditions affected both sites simultaneously, e.g. when the precipitation was

445 relatively high during the springs of 2013 and 2016 species richness and Shannon diversity

446 indices were also high at both the grazed and the mowed sites. Climatic conditions appeared

447 to be even stronger drivers than the effects of the management regime; as the yearly

448 differences were larger than the differences between the managements. Of the 19 dependent

449 variables analysed with the mixed effect model, the effects of years were found to be

450 significant, while the type of management regime (sites) had no effect at all and year-

451 management interaction was significant in four cases (Table 1). It was noticeable that the

452 frequency of *Bromus hordeaceus*, a drought tolerant species, greatly increased at both sites in

453 2014 (with no differences between sites). Most probably it was the results of drought in the

454 previous years. This showed the adaptive capability of grasslands to changing climatic

455 conditions and highlighted the need for species rich grasslands (as there could be years which

456 favour some species better than others).

457 Besides temporal variability we found that both the grazed and the mowed grassland sites

458 were highly heterogeneous (patchy) spatially. This is also characteristic for species-rich

459 grasslands, especially for grasslands under long-term grazing, as grazing usually leads to

460 patchy vegetation due to differences in grazing intensity as well as to selective grazing by

461 livestock in contrast to mowing (Bakker et al., 1983). Heterogeneous vegetation could

462 contribute to functional stability (Loreau et al., 2003; Wilcox et al., 2017). For example at our

463 site the spatial pattern of soil respiration and nitrous oxide fluxes become spatially more

464 homogenous but temporally more variable due to mowing in contrast to grazing (Fóti et al.,

465 2018).

466

467 **4.3. Carbon uptake and vegetation composition**

468 In the studied grassland parallel to the vegetation (microcoenological) survey we investigated

469 the C uptake and the net ecosystem carbon exchange as well. We observed large differences

470 in the net C uptake between the grazed and mowed sites (Koncz et al., 2017). Mowed site was

471 a source for C in dry years, while the grazed site remained C sink. Loss of C was due to high

472 herbage use intensity in the mowed site, which resulted in a low gross primary production and

473 high rates of ecosystem respiration after mowing. Based on the yearly course of C fluxes there

474 was a sudden drop in C uptake and a large loss of C after mowing due to the respiration of the

475 ecosystem. Vegetation composition did not change, thus differences in C uptake between the

476 grazed and mowed sites could not be attributed to the expected differences in the vegetation

477 composition. We assumed that the effect of contrasting managements affected the

478 functionality of the grassland (mowed site became a source for C), without vegetation

479 composition changes. Although functional changes may have an effect on the structure in the

480 long run. In our study the vegetation patches remained stable and spatially heterogeneous also

481 at the mowed site even at the finest scale. Therefore, we can conclude that functional

482 differences can occur independently of composition changes. This showed the stability of the

483 vegetation composition to contrasting managements. We found evidence for fast functional

484 degradation, a phenomenon in which mowed site turns to be a C source. However, we assume

485 that it could be restored provided that grazing will be reintroduced because the vegetation

486 structure remained the same. It was shown in a study that differences in the vegetation due to

487 difference in stocking rates influenced net C uptake of the ecosystem (Klumpp et al., 2011),

488 thus vegetation differences played a key role in carbon balance. However, according to other

489 researches, changing plant community structure induced by grazing did not lead to changes in

490 soil C storage (Frank et al., 1995), thus it is the question of what role vegetation changes play

491 in maintaining C balance.

492

493 **4.4. Management recommendations**

494 Grazing or mowing alone does not necessarily secure that the management regime will

495 favourably affect vegetation composition i.e. to sustain or increase diversity, stability.

496 However, managing semi-natural grasslands is usually better than no management at all (i.e.

497 abandonment) as it was found that species were more frequent in grazed sites compared to

498 abandoned ones (Pykälä 2005). Management is recommended in Hungary as large grasslands

499 became abandoned, however it could be utilized to support livestock (Koncz et al 2017).

500 Depending on the timing and intensity both grazing and mowing could alter vegetation

501 composition but, in general, extensive grazing and extensive mowing were found to maintain

502 or increase plant diversity (Házi et al., 2012; Jantunen, 2003; Fritch et al., 2011; Socher et al.,

503 2012; Török et al., 2018). Based on our study we also recommend that extensive grazing

504 should be supported and extended in space and time (where possible). Annually grazed and

505 mowed plots were found to have higher species number compared to untreated (abandoned)

506 plots in semi-natural grasslands of Southern Sweden after 28 years of experiment (Wahlman

507 and Milberg, 2002). Grazing has proved to be a successful management tool in terms of

508 maintenance and restoration of biodiversity (Benthien et al 2018; Vadász et al., 2016). In a

509 22-year-long experiment with different management types of dry limestone grasslands it was

510 found that a mixture of varying cutting regimes is required to sustain high species diversity

511 (Köhler et al., 2005). Long-lived forbs (*Trifolium medium*, *Salvia pratensis*, *Primula veris*)

512 tended to be favoured by annual mowing in October and by controlled annual burning at the

513 end of winter in contrast to annual mowing in July (as in the latter case no nutrients were

514 stored) (Köhler et al., 2005). In general, to improve vegetation composition and species

515 richness mowing date, stocking rate, grazing period should be tailored to specific local

516 conditions (Smith et al., 2000), keeping in mind that management alone is just one of the

517 many other driving factors (climate, soil, topography, hydrology) shaping vegetation

518 composition (Wellstein et al., 2007). It is recommended to design agri-environmental

519 measures that will encourage alternating mowing and grazing, because this promotes the

520 coexistence of multiple forbs and grasses, balances the nutrient limitation and ensures stable

521 biomass production (Mládková et al., 2015).

522 In summary, our study shows that a species rich, well preserved, closed steppe grassland

523 could turn to be a C source when changing the management from grazing to mowing.

524 However, it is important to emphasize that vegetation composition and diversity of the

525 grassland remained stable, thus changing the management regime back from mowing to

526 extensive grazing could potentially recover the C sink activity of grassland.

527

528 **5. Conclusion**

529 We compared the effect of grazing and mowing on fine-scale diversity of sandy grasslands in

530 Hungary. We found that both grassland sites were heterogeneous and the vegetation diversity

531 indices and compositional parameters showed large inter-annual variability. We found no

532   differences in the fine-scale vegetation composition between the two management regimes

533   analysed by mixed effect model, information theory model and PERMANOVA. The studied

534   grassland sites had been grazed with traditional extensive methods in the last 150 years thus

535   we expected to find some significant changes in the vegetation patterns in response to

536   changing the management regime from grazing to mowing after five years (the mowed site

537   was fenced in 2011). The stand-scale composition stability might be attributed to the

538   spatiotemporal heterogeneity of the grasslands. On the other hand, C uptake showed large

539   differences between grazed vs. mowed site unrelated to vegetation composition. The

540   reintroduction of grazing at the mowed site would probably restore C uptake capacity of the

541   mowed site as the vegetation composition remained unchanged.

542

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