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35 **Abstract**

36

37 Conservation status of hay meadows highly depends on their management. The main goal of this
38 study was to assess the efficiency of different mowing regimes in maintenance of plant species
39 richness and diversity of mesic hay meadows. The field experiment was carried out on a species
40 rich, mesic hay meadow in Western Hungary. We evaluated the effects of four alternative types of
41 management on the plant community after 7 years of continuous treatment: (1) mowing twice a
42 year, typical traditional management, (2) mowing once a year in May, most practised currently by
43 local farmers, (3) mowing once a year in September, often proposed for conservation management
44 and (4) abandonment of mowing. Both cutting frequency and timing had significant effects on
45 species richness and diversity of vegetation. Traditional mowing resulted in significantly higher
46 number and higher diversity of vascular plant species than other mowing regimes. Mowing twice a
47 year was the only efficient way to control the spread of the invasive *Solidago gigantea*, and mowing
48 in September was more successful in it than mowing in May. We conclude that the traditional
49 mowing regime is the most suitable to maintain botanical diversity of mesic hay meadows, however
50 other regimes should also be considered if certain priority species are targeted by conservation.

51

52 **Keywords:** *plant species richness, plant diversity, meadow management, plant invasion, Solidago*
53 *gigantea, temperate mesic grasslands*

54 **Introduction**

55 Although the majority of recent mesic hay meadows have been formed by human deforestation
56 and classified as semi-natural habitats, they harbour an outstanding diversity of plant and animal
57 species (Veen et al. 2009; Hejcman et al. 2013). The maintenance of biodiversity in these secondary
58 grasslands depends on their appropriate management and thus holds a high interest in conservation
59 planning. In a global assessment, Uchida and Ushimaru (2014) demonstrated that highest plant and
60 herbivore species richness can be reached by mowing twice per year, defined as intermediate
61 mowing frequency by them. Other studies, however, could not reveal distinctive effect of timing
62 and frequency of mowing on species richness (Oomes & Mooi 1981; Ilmarinen & Mikola 2009).
63 Moreover, in a large variety of grasslands located in three regions of Germany, Socher et al. (2012)
64 found a higher species richness in case of mowing once per year, than in case of mowing twice.
65 Although it is known that European mesic hay meadows are seriously threatened by invasion of
66 *Solidago gigantea* (Weber & Jacobs 2005) and regular mowing may be able to largely reduce its
67 stands, only a little experimental evidence is available on this process.

68 Due to the contradictory results of previous empirical studies, in spite of the long history of
69 studies on meadow management for conservation, it is still not entirely clear how intensive mowing
70 is necessary for maintaining the high species richness and diversity of Central European mesic hay
71 meadows. To reveal consequences of different mowing regimes on the vegetation of mesic hay
72 meadows, we set up a field experiment in the region of Órség National Park (Western Hungary).
73 We have chosen alternative management regimes that are either widely used and feasible, or are
74 recommended by conservationists.

75 The first alternative to be tested was traditional management. As we know from previous studies
76 (Vörös 1986) and recent personal interviews with old farmers (Babai et al. 2015), in the area of
77 Órség National Park mesic hay meadows had been mown two times per year for centuries, first in
78 May-June and then in August-September.

79 In the last few decades, mowing once a year became general in our study region (Hahn et al.
80 2012). Farmers typically manage a large number of widely scattered areas, therefore mowing twice
81 a year is not always technically feasible or simply not profitable. Mowing twice a year is not
82 encouraged by agri-environmental schemes either, since subsidies are already available for cutting
83 once a year (Babai et al. 2015). As animal husbandry has dramatically declined since the 1980's,
84 there is a surplus of hay meadows and there is no need for more intensive mowing. Since farmers
85 optimise for the highest ratio of yield and effort, they most often choose mowing in early summer.
86 Therefore, the second management scheme tested in our study was mowing once a year in May-
87 June.

88 The third management alternative to be tested was mowing once a year in August-September.
89 This way of grassland management is justified by the habitat requirements of numerous endangered
90 animal species. Several previous studies have shown that some rare species would benefit from
91 delayed first cut or only one late cut (Wakeham-Dawson & Smith 2000; Green 2002; Buri et al.
92 2013; Kőrösi et al. 2014). Hence, local nature conservation regulations often allow only one
93 mowing per year late in the season.

94 The fourth management type was abandonment, which is a frequently observed phenomenon in
95 Hungarian and other European farmlands. Although lack of management obviously leads to
96 spontaneous afforestation of secondary grasslands in the long term, it may have positive
97 consequences in the short term, especially for certain invertebrates (e.g. Fenner & Palmer 1998;
98 Cattin et al. 2003).

99 From former experimental studies, rich knowledge is available about the effect of timing and
100 frequency of mowing on restored grasslands that were fertilized or grazed before the experiment
101 (Oomes & Mooi 1981; Bobbink & Willems 1993; Poptcheva et al. 2009). However, there is a lack
102 of practical knowledge regarding optimal mowing strategies to maintain plant diversity of species
103 rich meadows within real environmental and socio-economic conditions. Accordingly, the research

104 goals of this study were (1) to evaluate effects of different mowing regimes on plant species
105 richness and diversity of mesic hay meadows in a medium term (7 years), (2) to determine
106 correlations between invasive *S. gigantea*, management and species richness and (3) to provide
107 practical recommendations for nature conservation.

108

109 **Materials and methods**

110 *Study site*

111 The study site was a mesic hay meadow located next to the Slovenian-Hungarian border, in
112 Órség National Park, in the valley of Szentgyörgyvölgyi stream (N46.46°, E16.19°) (Figure 1). The
113 vegetation of the area can be identified as an *Alopecuro-Arrhenatheretum* (Máthé & Kovács 1960)
114 Soó 1971 grassland, which community (syntaxon) corresponds to Natura 2000 habitat type 6510
115 “Lowland hay meadows” (European Commission 2013). Soil conditions can be characterised with
116 rich alluvial sediments and slightly acidic pH (between pH H₂O 5.3 and 5.8), and the groundwater
117 table is usually close to the soil surface. The average annual temperature is 9.5 °C, and the average
118 annual precipitation is about 800 mm (Dövényi 2010). The mean elevation is 210 m, but the surface
119 gently slopes towards the stream with a nearly flat section in the middle. Parallel to the stream,
120 there is no perceptible difference in elevation. The stream bordered by a 5 m wide and 15 m high
121 alder grove flows approx. 10 m far from the experimental site. On the opposite, northern side, a dirt
122 road can be found in a similar distance. The northern part of the study site is waterlogged for
123 several months during the spring and autumn period, contrary to the southern, 20 m wide belt,
124 where the 1.5 m deep running stream has an intense water suction effect. The specific heterogeneity
125 in environmental conditions allows us to study the effect of various types of timing and intensity of
126 mowing in more stressed (drier and shady) and more balanced conditions as well.

127 Before 1990s, the study site was usually mown twice per year by local farmers and no chemicals
128 or overseeding were applied. Until the 1960s the second aftergrass was even grazed. From the late

129 1990s a single mowing was carried out in June or July. Since 2002 the management of the area has
130 been carried out by the Órség National Park Directorate, using tractor driven RK-165 type drum
131 mowers. Due to the unified management history and topographical conditions, the original
132 vegetation of the area was quite similar before the onset of the experimental treatment in 2007. The
133 initial similarity of vegetation was also shown by former studies (Kőrösi et al. 2014; Szépligeti et
134 al. 2015) carried out on this study site.

135

136 *Experimental design and data collection*

137 The study site was divided into four adjacent 20 m × 80 m stripes, each assigned to one of the
138 following management types (going from east to west): mowing once a year in May (henceforward
139 May-mown), mowing once a year in September (September-mown), mowing twice a year in both
140 May and September (twice-mown), and abandonment. Every treatment stripe was further split into
141 four 20 m × 20 m plots (Figure 1). This experimental design was motivated by two main
142 considerations: (1) the current mowing practice is normally implemented by large tractors, which
143 need place to turn around and are not able to manage smaller patches (e.g. in a Latin square design);
144 (2) treatment stripes placed perpendicular to the stream bordering our study site made it possible to
145 control for the potential confounding effect of environmental stress factors suspected near the
146 stream.

147 For botanical survey, we placed 10 pieces of 2 m × 2 m sampling quadrats in all plots (n = 160
148 quadrats) randomly. In each quadrat, we recorded (visually estimated) cover of every vascular plant
149 species, with an accuracy of 1 percent. Below 1 percent, we used decimal precision. In all samples,
150 we also measured mean height of *S. gigantea* with an accuracy of 1 cm. All data were collected by
151 the same person in the second half of May 2014, before the first cut.

152

153 *Statistical analyses*

154 We aimed to test the effects of different types of management on plant species richness, plant
155 diversity and *S. gigantea* coverage. In models of plant species richness, management and *S.*
156 *gigantea* cover were both included as explanatory variables. We also calculated Pearson's
157 correlation coefficients between mean height and coverage of *S.gigantea*, species richness and
158 Shannon diversity index.

159 Since environmental stress factors can seriously modify features of equally treated vegetation
160 (Moeslund et al. 2013), we intended to control for them. Assuming the water suction effect of the
161 Szentgyörgyvölgyi stream and the modifying effect of shading of alder grove, we used the distances
162 of sampling quadrats from the stream as a proxy of environmental stress. This approach was
163 justified by the fact that the proportion of drought-tolerant plant species (Borhidi 1995) was
164 noticeably higher near the stream (Appendix 1). We used generalized linear models (GLM) with
165 appropriate error distributions (Poisson distribution for species richness and normal distribution for
166 species diversity) or general additive models (GAM). First, a full model was constructed including
167 all predictors that we aimed to test and then an AICc-based model selection was performed
168 (Burnham & Anderson 2002). Parameter estimates of the best models are presented (Table I). Note
169 that we did not perform post-hoc tests for multiple comparisons, but repeatedly ran the model with
170 the nominal variable 'management' re-levelled (see Appendix 2).

171 Due to the spatial arrangement of the sampling plots, we had to take a possible spatial
172 autocorrelation into account (Dormann et al. 2007). When significant spatial autocorrelation was
173 revealed in model residuals by a Moran's I-test (Moran 1948), then we applied Moran eigenvector
174 filtering to remove it (Dray et al. 2006; Griffith & Peres-Neto 2006). Neighbouring matrix was
175 constructed using row-standardised spatial weights in 0-10 m distance (Bivand et al. 2009).

176 All analyses were performed with R statistical software (version 3.1.2, R Core Team 2015) using
177 packages 'mgcv' (Wood 2006), 'MuMIn' (Barton 2014) and 'spdep' (Bivand 2014).

178

179 **Results**

180 Species richness was significantly influenced by management type, and there was no spatial
181 autocorrelation in model residuals. Species richness was significantly higher in twice-mown plots
182 than in other treatments. Furthermore, it was significantly higher in September-mown plots than in
183 abandoned ones or May-mown ones (Table I, Figure 2). Although *S. gigantea* cover related to
184 species richness negatively (see below), it did not show up in the best model (Table I). In the second
185 best model, both management and *S. gigantea* cover were included, but the effect of the latter was
186 not significant (results not shown). This means that *S. gigantea* cover was not significantly related
187 to plant species richness within each management type separately (Figure3).

188 Shannon diversity index was analysed by fitting a linear model, and then removing significant
189 spatial autocorrelation from model residuals. Plant diversity was significantly influenced by the
190 interaction between management and distance from the stream (Table I, Figure 4). Model output
191 indicates that diversity at distance = 0 was significantly higher in twice-mown sampling quadrats
192 than in quadrats in abandoned stripe, whereas it did not significantly differ from diversity in May-
193 or September-mown plots. Interaction terms suggest that diversity in twice-mown plots
194 significantly increased with distance from the stream. By re-levelling the model, we found that
195 diversity also increased with distance in September-mown plots, although in a significantly smaller
196 degree than in twice-mown plots. Such a relationship could not be observed in abandoned and May-
197 mown plots. Diversity was significantly higher in May-mown quadrats than in September-mown
198 ones close to the stream, but this difference disappeared by increasing distance from the stream
199 (Figure 4, Appendix 2).

200 *S. gigantea* cover was close to zero in all of twice-mown plots, hence these plots were omitted
201 from the analysis (to meet the assumption of homogeneity). According to the best GAM model, *S.*
202 *gigantea* cover was significantly lower in September-mown plots than in May-mown and
203 abandoned plots, but there was no significant difference between the two latter treatments. *S.*

204 *gigantea* cover increased in a significantly different and non-linear way with distance from stream
205 in these three treatments (Figure 5). We found highly significant negative correlations between mean
206 *S. gigantea* height and either species richness ($r=-0.68$, $p<<0.001$) or Shannon diversity ($r=-0.58$,
207 $p<<0.001$). In these tests we included only those quadrats where *S. gigantea* was present. When all
208 quadrats were included, correlations between *S. gigantea* cover and species richness ($r=-0.40$,
209 $p<<0.001$) and Shannon diversity ($r=-0.36$, $p<<0.001$) were weaker, but still highly significant.

210

211 **Discussion**

212 *Species richness and diversity*

213 Our results revealed that both frequency and timing of mowing had significant effects on species
214 richness and diversity of vegetation. Mowing a meadow twice, in May and September, resulted in
215 the highest species richness and diversity of plants, whereas both variables were lowest in
216 abandoned plots, and intermediate in plots mown once either in May or in September. This outcome
217 is consistent with other studies (Moog et al. 2002; Poptcheva et al. 2009; Házi et al. 2011) and
218 suggests that meadows' vegetation adapted to the management that have been applied through
219 centuries in our study region, i.e. mowing first in May-June and the second in August-September
220 (Babai et al. 2015). This result is also in accordance with a number of studies demonstrating that
221 traditional management practices are the most suitable tools to maintain biological diversity of
222 species rich grasslands (WallisDeVries et al. 2002; Schmitt & Rákósy 2007; Middleton 2012; Babai
223 & Molnár 2014). However, they should be supported in agri-environmental schemes to avoid the
224 risk of diversity loss and the increasing rate of land abandonment (Babai et al. 2015). Several
225 studies showed an inverse relationship between biomass production and species richness on highly
226 productive temperate secondary grasslands (Zobel & Liira 1997; Crawley et al. 2005; Hejcman et
227 al. 2010; Kelemen et al. 2013), and pointed out that regular removal of biomass is necessary to
228 maintain plant diversity (Köhler et al 2005; Ruprecht et al. 2009). [The primary impact of mowing](#)

229 twice a year on mesic hay meadows vegetation is the effective suppression of all dominant species,
230 thereby providing space and light for less competitive species. Twice-mown, shorter sward allows
231 more light to reach the ground surface than denser and taller sward of once-mown meadows (Jutila
232 & Grace 2002). Furthermore, the amount of litter and nutrient replenishment of the soil is also
233 reduced by more intensive mowing (Oelmann et al. 2009). These conditions together facilitate
234 seedlings germination and development of less competitive plant species in twice-mown meadows
235 (Bissels et al. 2006).

236

237 *Solidago gigantea*

238 Our results highlight that mowing two times per year is necessary to prevent effectively the
239 invasion of *S. gigantea*. In plots infested by *S. gigantea*, many species were displaced owing to its
240 shoot height and clonal, rhizomatous growth strategy (Prach & Pyšek 1999). This outcome explains
241 the landscape-level expansion of *S. gigantea* and the retreat of characteristic meadow species due to
242 land use changes, i.e. with the exchange from the traditional mowing frequency to mowing once a
243 year and abandonment of mowing. Therefore more intensive mowing is necessary to stop invasion
244 and to restore meadow vegetation, as proposed by Hartmann and Konold (1995).

245 In cases when mowing twice a year is not feasible, our results suggest that late mowing is more
246 efficient to prevent invasion of *S. gigantea*. In May-mown plots, *S. gigantea* started a vigorous
247 vegetative spread after mowing and was able to continue it during the entire growing season. In
248 September-mown plots, stands of *S. gigantea* grew thinner, although remained permanent. This
249 result suggests that it is more sensitive to mowing during the flowering period when most nutrients
250 are invested in sprout and florescence. Late mowing therefore weakens polycormons more
251 efficiently. In addition, late mowing favours the spread of native competitor species. This is in
252 agreement with findings of Meyer and Schmid (1999), which showed that shoot density of *Solidago*
253 *altissima* is reduced by competition.

254

255

256 **Recommendations for conservation**

257 Our results indicate that the highest botanical richness and diversity of mesic hay meadows can
258 be reached by the traditional mowing frequency. Mowing regularly twice a year is necessary to
259 prevent spreading of *S. gigantea*, and control native competitive species, which hinder the growth
260 of many rare and less competitive species, often being of conservation importance. That means,
261 reduced mowing intensity could not maintain diversity, not even in those regions, which are not
262 threatened by invasion of *S. gigantea*. Mowing both in May and in September does not just
263 correspond to traditional meadow management, but it provides both the highest quantity and quality
264 of hay (Kun 2014). Therefore, it could be applied widespread in the region, though there are some
265 counterarguments. First, mowing twice a year is not always feasible. For instance, there is often no
266 need or no resource for the second cut or weather conditions make hay making difficult in
267 September. Second, there are threatened species, such as *Phengaris alcon* butterfly and its host
268 plant *Gentiana pneumonanthe*, or the ground-nesting bird *Crex crex*, which do not tolerate mowing
269 in May or mowing twice a year. Moreover, some studies underlined that decreasing plant species
270 richness of untreated spots is often combined with an increased diversity of the arthropod fauna
271 (Southwood et al. 1979; Fenner & Palmer 1998; Cattin et al. 2003), which means that efforts to
272 promote plant diversity can lead to reduced diversity of certain invertebrates. In addition, various
273 types of timing and frequency of mowing have different effects on numerous individual plant
274 species as well (Bissels et al. 2006; Leng et al. 2011).

275 To overcome these problems, conservation goals must be clearly defined on each single site, and
276 conservation efforts should be concentrated on most valuable grasslands. Mowing once a year in
277 May-June could be applied on those meadows, where competitive species are already limited by
278 some additional environmental stress (e.g. in xeromesophilous grasslands). Late mowing in August-

279 September is recommended in those meadows, which harbour invertebrates or birds of conservation
280 concern (Wakeham-Dawson & Smith 2000; Kőrösi et al. 2014); and which are invaded by *S.*
281 *gigantea* but only one mowing per year is feasible. Alternatively, mosaic type mowing could be
282 applied, by splitting the same meadow into twice and once mown parts, or leaving uncut refuge
283 areas at every mowing. This mowing regime might be appropriate to maximize zoological and
284 botanical values of mesic hay meadows (Fenner & Palmer 1998; Cizek et al. 2012; Kőrösi et al.
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286

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427 Appendix 1

428 Mean moisture indicator values (Borhidi 1995) of plant species weighted with cover. Higher values
 429 indicate higher water demands.

	Row Nr.	MS	M	S	A
road	1	5.48	7.1	7.06	6.18
	2	6.18	6.56	6.79	7.18
	3	5.59	5.46	5.87	6.09
stream	4	4.65	4.78	4.98	4.76

430

431 Appendix 2

432 Parameter estimates of best models for each response variable with management as a nominal
 433 variable re-levelled. Re-levelled models are identical; re-levelling shows pairwise differences
 434 between management types without multiple comparisons. Significant terms are in bold. "d" means
 435 distance from the stream.

Response variable	Predictors	Estimate (±SE)	p-value
Species richness	mowing in May & Sept (intercept)	3.59 (±0.026)	<< 0.001
	abandoned	-0.399 (±0.042)	<< 0.001
	mowing in May	-0.317 (±0.041)	<< 0.001
	mowing in Sept	-0.186 (±0.039)	<< 0.001
	abandoned (intercept)	3.19 (±0.032)	<< 0.001
	mowing in May	0.082 (±0.045)	0.065
	mowing in May & Sept	0.399 (±0.042)	<< 0.001
	mowing in Sept	0.213 (±0.043)	<< 0.001
	mowing in May (intercept)	3.27 (±0.031)	<< 0.001
	abandoned	-0.082 (±0.045)	0.065
	mowing in May & Sept	0.317 (±0.041)	<< 0.001
	mowing in Sept	0.131 (±0.042)	0.002
	mowing in Sept (intercept)	3.40 (±0.029)	<< 0.001
	abandoned	-0.213 (±0.043)	<< 0.001
	mowing in May	-0.131 (±0.042)	0.002
	mowing in May & Sept	0.186 (±0.039)	<< 0.001
Shannon index	mowing in May & Sept (intercept)	1.86 (±0.081)	<< 0.001
	abandoned	-0.263 (± 0.114)	0.022
	mowing in May	0.135 (±0.111)	0.226
	mowing in Sept	-0.219 (±0.121)	0.071

	d: May-Sept	0.013 (±0.002)	<< 0.001
	d: abandoned	-0.013 (±0.002)	<< 0.001
	d: May	-0.011 (±0.002)	<< 0.001
	d: Sept	-0.009 (±0.002)	< 0.001
	abandoned (intercept)	1.60 (±0.078)	<< 0.001
	mowing in May	0.398 (± 0.112)	< 0.001
	mowing in May & Sept	0.263 (±0.114)	0.022
	mowing in Sept	0.044 (±0.111)	0.692
	d: abandoned	-0.001 (±0.002)	0.612
	d: May	0.002 (±0.002)	0.335
	d: May-Sept	0.013 (±0.002)	<< 0.001
	d: Sept	0.005 (±0.002)	0.061
	mowing in May (intercept)	1.99 (±0.079)	<< 0.001
	abandoned	-0.398 (± 0.112)	< 0.001
	mowing in May & Sept	-0.135 (±0.111)	0.226
	mowing in Sept	-0.355 (±0.116)	0.003
	d: May	0.002 (±0.002)	0.392
	d: abandoned	-0.002 (±0.002)	0.335
	d: May-Sept	0.011 (±0.002)	<< 0.001
	d: Sept	0.002 (±0.002)	0.353
	mowing in Sept (intercept)	1.64 (±0.082)	<< 0.001
	abandoned	-0.044 (±0.111)	0.692
	mowing in May	0.355 (±0.116)	0.003
	mowing in May & Sept	0.219 (±0.121)	0.071
	d: Sept	0.004 (±0.002)	0.032
	d: abandoned	-0.005 (±0.002)	0.061
	d: May	-0.002 (±0.002)	0.353
	d: May-Sept	0.009 (±0.002)	< 0.001
	abandoned (intercept)	46.96 (± 4.13)	<< 0.001
	mowing in May	-9.50 (± 5.84)	0.107
	mowing in Sept	-22.18 (± 5.84)	<< 0.001
<i>S. gigantea</i> coverage	mowing in May (intercept)	37.47 (± 4.13)	<< 0.001
	abandoned	9.50 (± 5.84)	0.107
	mowing in Sept	-12.68 (± 5.84)	0.032
	mowing in Sept (intercept)	24.79 (± 4.13)	<< 0.001
	abandoned	22.18 (± 5.84)	< 0.001
	mowing in May	12.68 (± 5.84)	0.032

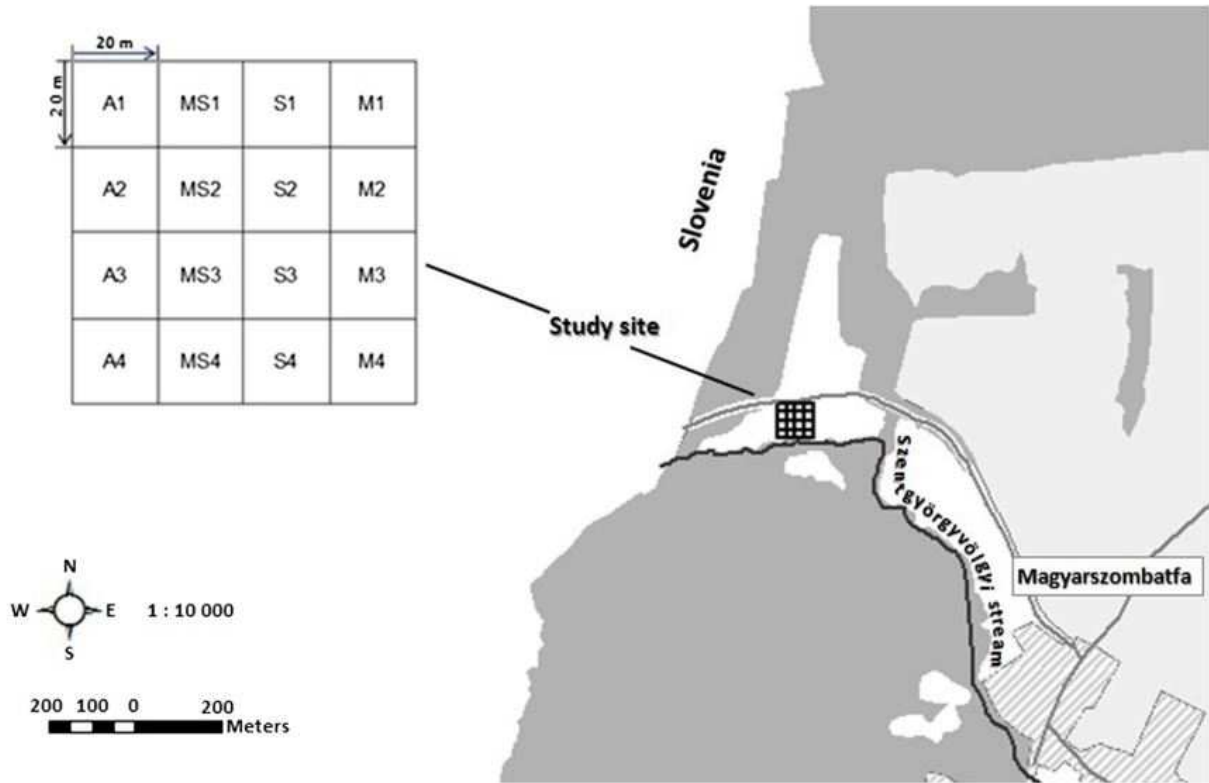
436 Table I. Estimates of best models for each response variable. Mowing in May and September was
437 the reference level of management (intercept in GLMs and GAMs). 'd' denotes distance from the
438 stream. Significant terms are in bold.

439

440

441 **Figure captions**

442



443 Figure 1. Location of study site, and the experimental design. Codes of treatment bands: *A* – abandoned, *MS* – mown in May and September, *S* – mown in September, *M* – mown in May. White: grassland; dark grey: woodland; light grey: plough land; streaked: built-in area; dark grey line: road; black line: stream.

444

444 Figure 1. Location of study site, and the experimental design. Codes of treatment bands: *A* –

445 abandoned, *MS* – mown in May and September, *S* – mown in September, *M* – mown in May.

446 White: grassland; dark grey: woodland; light grey: plough land; streaked: built-in area; dark grey

447 line: road; black line: stream

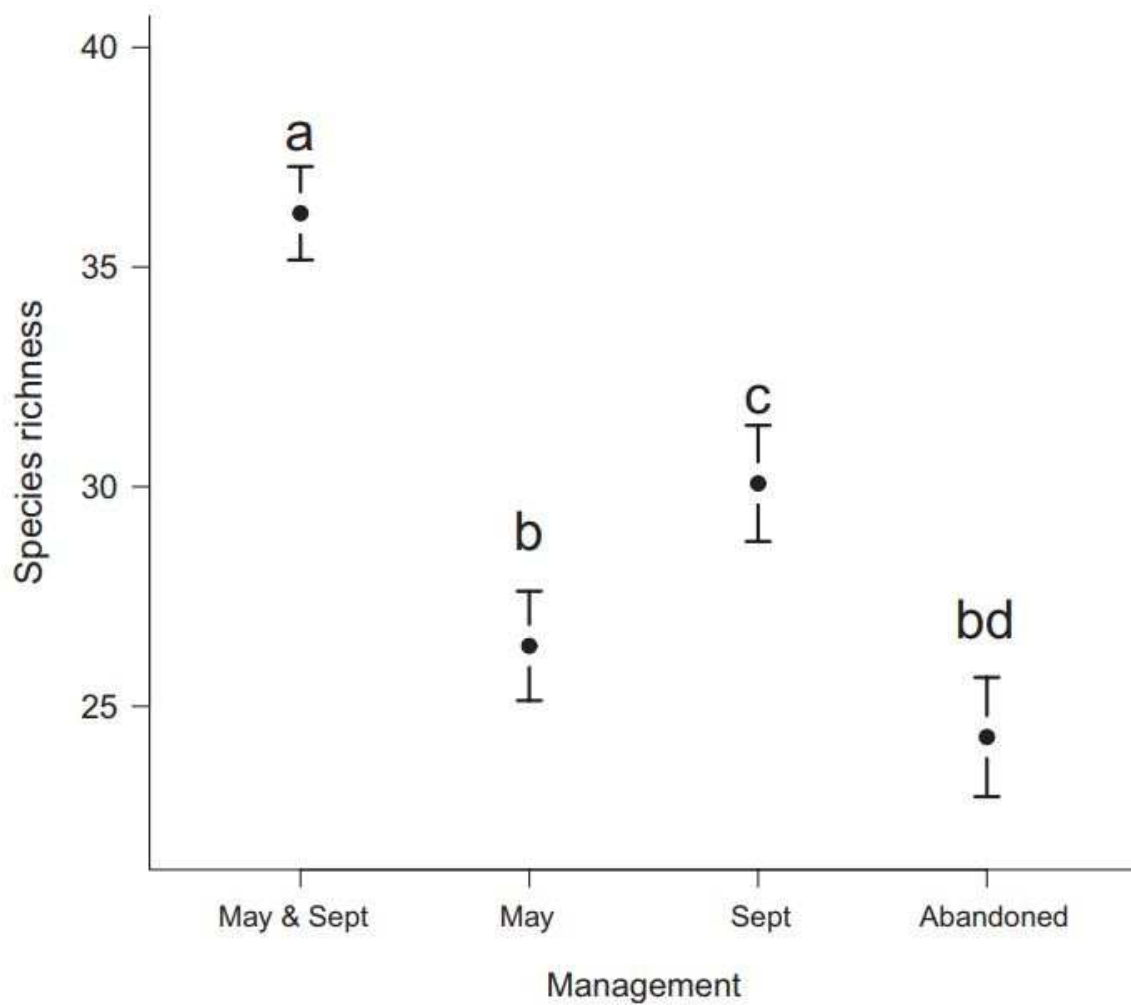


Figure 2. Mean species richness in each management type. Error bars indicate 95% confidence intervals. Letters indicate significant differences.

448

449 Figure 2. Mean species richness in each management type. Error bars indicate 95% confidence
 450 intervals. Letters indicate significant differences.

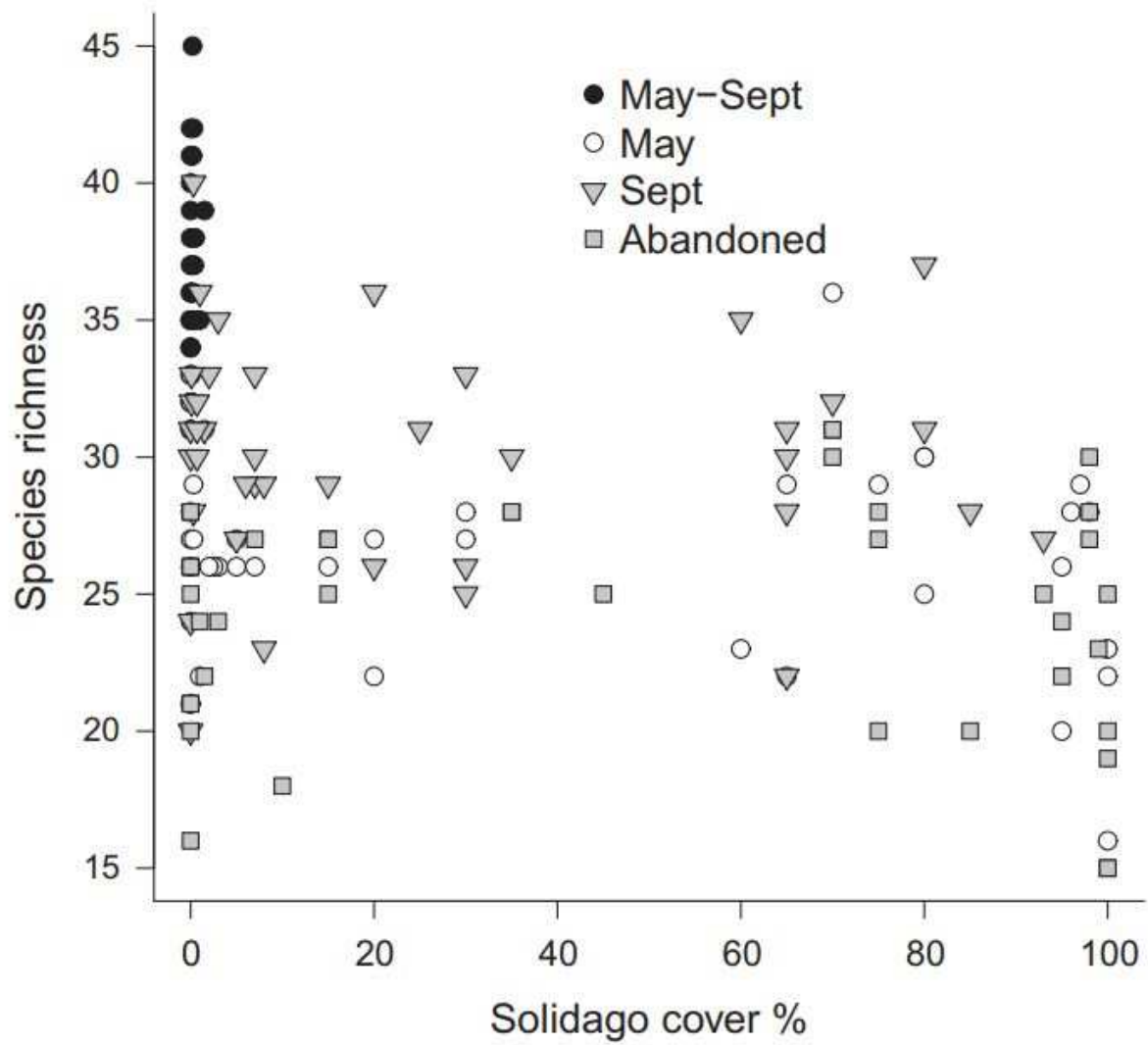


Figure 3. Relationship between species richness and coverage of *Solidago gigantea* in each management type.

451

452 Figure 3. Relationship between species richness and coverage of *Solidago gigantea* in each

453 management type.

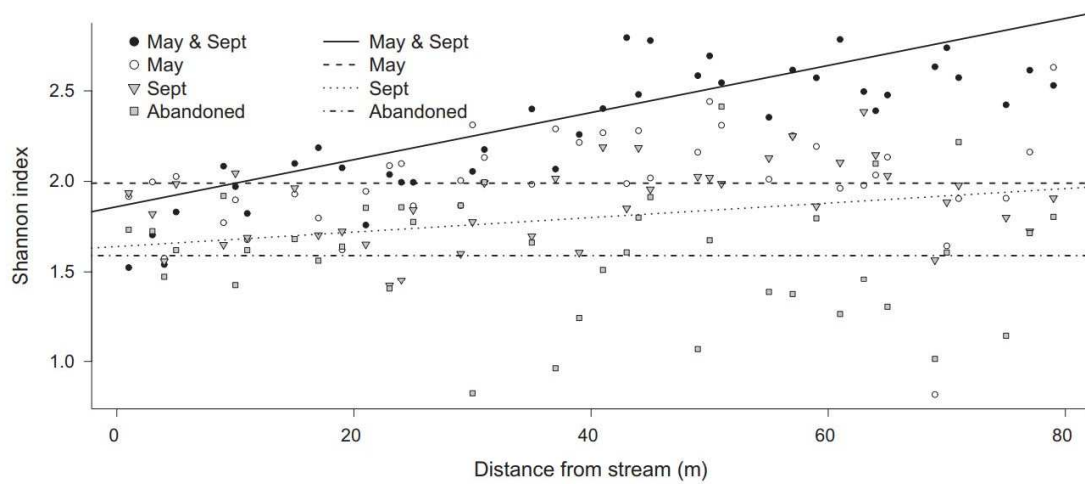


Figure 4. Relationship between Shannon's diversity index and distance from stream in each management type. Lines represent regression slopes.

454

455 Figure 4. Relationship between Shannon's diversity index and distance from stream in each

456 management type. Lines represent regression slopes.

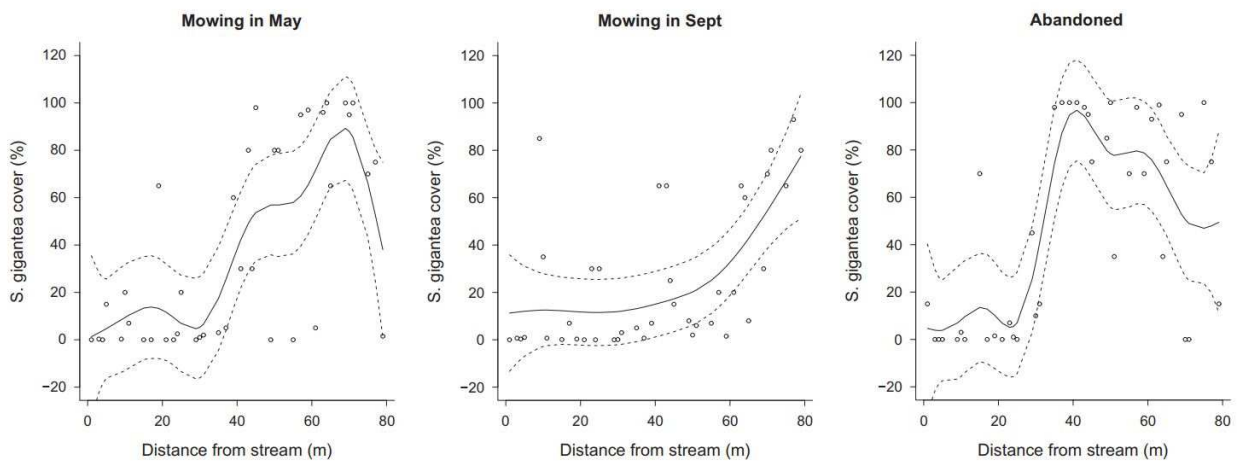


Figure 5. Relationship between *Solidago gigantea* coverage and distance from the stream. Estimated smoothing curves (thin plate regression splines) with point-wise 95% confidence bands and observed values in three treatments.

457

458 Figure 5. Relationship between *Solidago gigantea* coverage and distance from the stream.

459 Estimated smoothing curves (thin plate regression splines) with point-wise 95% confidence bands

460 and observed values in three treatments.

461

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