

1 **The biodiversity cost of reducing management intensity in**  
2 **species-rich grasslands: Mowing annually vs. every third**  
3 **year**

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16

17 **Abstract**

18 Mowing is an important management method for species-rich semi-  
19 natural grasslands in Europe. Since mowing is costly, it is important to  
20 find a balance between mowing frequency and conservation benefits. We  
21 compared vegetation data from eleven field trials situated in southern  
22 Sweden that involved two mowing regimes, annually and every third  
23 year, as well as a no-management control. After approximately 14 years,  
24 mowing every third year showed (i) a drop in species richness and  
25 Shannon and Gini-Simpson diversity indices, (ii) an increase in woody  
26 species, and (iii) increases in tall-grown species. However, there were no  
27 apparent changes in (iv) species that were indicative of poor  
28 management, nor (v) those indicating good management. For one of the  
29 trials, data after 38 years were also evaluated. Compared with annual  
30 mowing, there were strong negative changes in the number of species in  
31 the untreated control, while the results were conflicting for mowing every  
32 third year. In conclusion, the expected loss of conservation values from  
33 reduced mowing intensity was 50 to 60% of the loss after abandonment.  
34 The outcomes, however, varied among the eleven sites.

35 **Keywords:**

36 Cutting, Indicators, Meta-analysis, Mowing, Odds ratio, Response ratio,  
37 Semi-natural grassland, Sweden

38 **Nomenclature**  
39 Karlsson (1998)

## 40 **Introduction**

41 Ongoing changes in agriculture mean that it is a challenge for  
42 conservation efforts to maintain the rich biodiversity that is associated  
43 with traditionally managed semi-natural grasslands in Europe (Kull and  
44 Zobel 1991, Poschlod et al. 2009, D’Aniello et al. 2011, Wilson et al.  
45 2012, Habel et al. 2013, Babai & Molnár 2014). Grazing and mowing are  
46 the two options for exploiting the biomass of grass-dominated vegetation,  
47 and both seem relatively similar in regard to the benefit that they provide  
48 for preserving biodiversity (Tälle et al. 2015, 2016). However, the  
49 amount of available cattle for conservation-oriented grazing is decreasing  
50 (Kumm 2003), while the labour costs for annual mowing in most cases  
51 remain high (Schreiber et al. 2009, Török et al. 2011).

52 Although not the first choice, a reduction management intensity might  
53 allow more land to be managed. Managers can skip mowing every second  
54 year and thereby double the acreage that is mowed or reduce the stocking  
55 density (a limited number of animals spread over a larger area).  
56 Theoretically, there should be an optimal balance between the available  
57 resources (e.g., number of animals, or cost for labour), area covered and  
58 biodiversity benefits provided. Put another way, a larger area with

59 relaxed management (intensity or type) might be preferred over a smaller  
60 area under the best management option as long as the losses in  
61 biodiversity are acceptable. Hence, it is important to estimate the “cost”,  
62 in terms of lost biodiversity, for reducing the management intensity  
63 (Marriott et al. 2004).

64 As the grazing intensity is notoriously difficult to estimate,  
65 experiments that vary the stocking density are less suited to address this  
66 issue than experiments assessing the effect of different mowing  
67 intensities on biodiversity. The results from studies comparing the effect  
68 of higher and lower mowing intensities vary, with some in favour of  
69 higher mowing intensities (e.g., Köhler et al. 2005, Noordjik et al. 2009,  
70 and others in favour of lower mowing intensities (e.g., Everwand et al.  
71 2014, Körösi et al. 2014). However, few studies have examined the effect  
72 of mowing less than once per year (but see e.g., Bakker et al. 2002).  
73 Hence, the effect of different mowing intensities on biodiversity remains  
74 poorly understood, but could be expected to resemble secondary  
75 succession when management ceases, that is, woody species and tall-  
76 grown species increase while the diversity indices and richness decrease.

77 Here, we analyse data from eleven field trials in southern Sweden  
78 in which mowing every year was compared with mowing every third year  
79 as well as an unmanaged control. We intended to estimate the rate of loss of

80 conservation values from these eleven grasslands over 14 years. At one  
81 site, data were also available after 38 years. More specifically, when  
82 converting to more infrequent mowing, we expected:

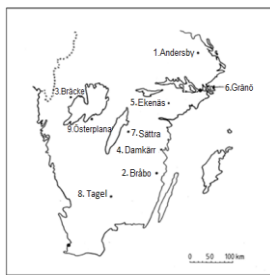
- 83 (i) a decrease in the number of species and diversity indices  
84 (Shannon, Gini-Simpson, Shannon evenness)
- 85 (ii) a decrease of species indicative of good management
- 86 (iii) an increase in species indicative of poor management
- 87 (iv) an increase in woody species
- 88 (v) an increase in tall-grown species

## 89 **Methods**

### 90 **Study sites**

91 In the early 1970s, a long-term experiment was established at eleven  
92 experimental sites at nine locations in southern Sweden (Figure 1). Two  
93 of the locations (Ekenäs, Tagel) had two experimental sites each. The  
94 mean annual temperature in southern Sweden is approximately 6 °C,  
95 mean annual precipitation is 500-1000 mm (Alexandersson et al. 1991)  
96 and growing period is 180-220 days (Sjörs 1999). Before the start of the  
97 experiment, most of the sites were managed using grazing. However, two  
98 of the sites (Dämkärr and Österplana) had been abandoned for a few  
99 years, and one site (Gränö) was mowed. Furthermore, two of the sites  
100 (Gränö and Tagel/former field) were fertilized prior to the start of the

101 experiment (Table 1, Hansson 1991). The sites differed in vegetation type  
102 and productivity, but the majority of the sites were of the mesic meadow  
103 type (Table 1), with medium productivity (Hansson 1991). If using the  
104 Council Directive 92/43/EEC on the conservation of natural habitats and  
105 of wild fauna and flora (Swedish Environmental Protection Agency  
106 2011), the sites are semi-natural dry grasslands (6210), hay meadows in  
107 submontane zones (6510), Fennoscandian wooded pastures (9070) or wet  
108 meadows (*Molinion caeruleae*) (6410).



109

110 *Figure 1. Study locations in southern Sweden. Ekenäs and Tagel had two*  
111 *experimental sites each.*

112 *Table 1. Description of the experimental sites established in southern*  
113 *Sweden for the comparison of the management methods in semi-natural*  
114 *grassland vegetation. X indicate that the data were used in the present*  
115 *study, while - indicates that existing data were not used (because of the*  
116 *design of data collection).*

Site	Year of inventory					Vegetation type	Soil category	Management at start of trial
	1973	1975	1980	1986	1987			
Andersby, Dannemora	X	X	X			Moist	Humus-rich light clay	Grazing
Bråbo, Oskarshamn	X	X	X			Mesic	Rock moraine	Grazing
Bräcke, Åmål	X	X	X			Mesic	Silt	Grazing
Dämkärr, Gamleby	-			X		Mesic	Humus-rich silt	Abandoned
Ekenäs, Flen								
Moist		X	X			Moist	Highly humus-rich light clay	Grazing
Mesic		-	X	X		Dry-mesic	Humus-rich loamy	Grazing
Gränö, Värmdö	-			X		Moist	Slightly humus-rich silt	Mowing, fertilized
Sättra Ödeshög	-		X	X		Mesic	Slightly clayey sand	Grazing
Tagel, Alvesta								
Mesic	-		X	X		Mesic	Rocky sand	Grazing
Former field	-				X	Mesic	-	Grazing, fertilized
Österplana, Götene	-		X	X		Dry	Gravelly clay loam	Abandoned

118 **Experimental design**

119 The experiment was set up with the aim of assessing vegetation changes  
120 as a result of the introduction of several management methods (Steen  
121 1976; Fogelfors 1982; Hansson 1991). For the present study, we used  
122 three management methods: annual mowing, mowing every third year,  
123 and an untreated control. Treatment plots (5 m × 20 m) were established  
124 in a randomized block design with two replicates. Mowing took place in  
125 late July or early August using a scythe or sickle bar mower. Because all  
126 of the experiments were surrounded by grazed grasslands, the plots were  
127 fenced.

128 **Vegetation sampling**

129 Fieldwork was conducted in July, before mowing took place. Initial  
130 vegetation assessments were conducted, but the protocol for data  
131 collection varied between sites (Steen 1976). Most experiments were  
132 assessed again after approximately 8 years (Fogelfors 1982), this time  
133 using a standard protocol. All of the sites were again visited in 1986-7  
134 using the standard protocol, which involved using five fixed 1 m<sup>2</sup>  
135 subplots per treatment plot (at Bräcke, three 1 m<sup>2</sup> fixed subplots were  
136 used).

137 We used the presence/absence of species in the subplots to  
138 generate a frequency per treatment plot. In some of the analyses, we used  
139 data as given in previous reports (Steen 1976, Fogelfors 1982, Hansson

140 1991), but corrected for numerous typing errors (see Tälle et al. 2015 for  
141 details on data retrieval and transcription). In some analyses, we first  
142 created a dataset with a species list that allowed analyses of species-wise  
143 data over the eleven trials. The latter meant deleting some records of only  
144 partially identified records (e.g., deleting *Luzula* sp., since the majority of  
145 *Luzula* records were identified at the species level). It also meant creating  
146 groups of species that had been identified with different levels of  
147 ambition (e.g., “other *Agrostis* spp.” i.e., all *Agrostis* recorded excluding  
148 *A. gigantea*). Finally, we merged the woody taxa, which were always  
149 infrequent, into “all woody species”.

150 One trial (Sättra ängar) has been continually managed since 1973,  
151 so here we used data collected in 1973 (Steen 1976), 1980 (Fogelfors  
152 1982), 1986 (Hansson 1991) and 2011 (unpublished). Data also exist for  
153 2000, but because a different methodology was used when assessing the  
154 vegetation and because the survey was conducted late in the season, well  
155 after mowing (Wahlman & Milberg 2002), we decided to not consider  
156 them in the present analysis.

### 157 **Classification of plant species**

158 To enable a comparison of data collected from different sites that differ in  
159 species composition, we simplified the data in some analyses by  
160 classifying grassland species as indicators. Based on previous experience

161 (Milberg et al. 2014, Tälle et al. 2014, 2015), we chose a well-  
162 documented indicator system that targeted species-rich semi-natural  
163 grasslands in southern Sweden (Ekstam & Forshed 1992). In this  
164 indicator system, which is widely used by practitioners, species are  
165 classified according to the rate at which a species is lost during secondary  
166 succession from grassland to forest (four classes) and according to a  
167 nitrogen availability gradient (three classes). We classified species as (i)  
168 indicators of good management for species richness if they decrease in  
169 early succession stages (classes A and B) and grow in sites poor under  
170 nitrogen (N1); (ii) indicator species of poor management if they do not  
171 decrease until later successional stages (classes C and D) and grow in  
172 nutrient-poor sites or sites with moderate levels of nitrogen (classes N1  
173 and N2).

#### 174 **Statistical analyses**

##### 175 *Species richness and diversity*

176 The treatment effect on the number of species recorded in the 5 (or 3) m<sup>2</sup>  
177 sampled per treatment were calculated as ln-transformed response ratios  
178 (RR). To avoid bias in the RR due to small sample sizes, Lajeunesse's  
179 (2011) method of calculating ln(RR) was used:

$$180 \ln(\text{RR}) = \ln((X_T/X_C) + 1/2[SD_T^2/N_T X_T^2 - SD_C^2/N_C X_C^2]) \quad (\text{eqn. 1})$$

181 where  $X$  is the mean,  $T$  is mowing every third year,  $C$  is annual mowing,  
182  $SD$  is the standard deviation and  $N$  is the sample size. Corresponding  
183  $\ln(RR)$  values were calculated for two diversity indices (Shannon, Gini-  
184 Simpson) and for evenness (Shannon). Using a meta-analysis tool  
185 (Comprehensive Meta-analysis version 2; Biostat, Inc. 2006; [www.meta-](http://www.meta-analysis.com)  
186 [analysis.com](http://www.meta-analysis.com)), we then calculated the weighted average, based on the  
187 random effects model, for the eleven trials. A positive value of  $\ln(RR)$   
188 signifies a more positive effect of mowing every third year.

189 To estimate the rate of change, we used trial-wise estimates of  
190 species numbers and diversity, where comparable, to follow the  
191 development of  $\ln(RR)$  over time. Three trials had data from three time  
192 points, five from two (the remaining three had only been surveyed once  
193 with the standard protocol). The slopes of the trial-wise regressions for  
194 these eight trials were then used to calculate the average and weighted  
195 average (giving the three sites with the best data more weight).

#### 196 *Species indicating good or poor management*

197 We analysed the data using an odds ratio as a way of overcoming  
198 differences in the vegetation composition and the differing number of  
199 subplots. This analysis method compared the odds of a species recorded  
200 being an indicator, contrasting two different treatments. For each type of  
201 indicator, we first calculated the total number of indicators and non-

202 indicators (i.e., all other species) per subplot or per treatment plot if  
203 subplots were not used. We then summed the number of indicators and  
204 non-indicators per treatment plot (if subplots were surveyed). This  
205 measure reflects the frequency of the indicator species and non-indicator  
206 species in each treatment plot.

207 To compare annual mowing with mowing every third year, or the  
208 untreated control, a random effects meta-analysis was performed using  
209 Comprehensive Meta-analysis.

210 The effect sizes were measured as log odds ratio (logOR):

$$211 \quad \log\text{OR} = \log [(A \times D) / (B \times C)] \quad (1)$$

212 where A = the frequency of indicators in the annual mowing treatment; B  
213 = the frequency of non-indicators in the annual mowing treatment; C =  
214 the frequency of indicators in the alternative treatment; and D = the  
215 frequency of non-indicators in the alternative treatment. A positive  
216 logOR signifies higher odds of finding indicators in plots with annual  
217 mowing. Since each trial contained two blocks, each trial contributed two  
218 entries to the meta-analysis.

219 *Woody species and tall-grown species*

220 Since the majority of woody species were observed only once or twice,  
221 we based these calculations on the occurrence of woody species in

222 subplots, irrespective of species identity. Because these data contained  
223 several zeros,  $\ln(\text{RR})$  was deemed to be less suited for the analysis, and  
224 we instead calculated the difference in occurrence after 11-14 years over  
225 the eleven trials between mowing every third year and annual mowing.  
226 For comparison, differences between the untreated control and annual  
227 mowing were also calculated.

228 In a similar manner, we calculated species-wise differences between  
229 mowing every third year, or the untreated control, and annual mowing.  
230 Only species occurring in at least seven of the 22 experimental blocks  
231 were considered (fewer occurrences were not considered to appropriately  
232 reflect between-site variation), which meant 56 species in total. For these  
233 species, we extracted information on plant height from the LEDA  
234 traitbase (Kleyer et al. 2008; [http://www.uni-](http://www.uni-oldenburg.de/en/biology/landeco/research/projects/leda/)  
235 [oldenburg.de/en/biology/landeco/research/projects/leda/](http://www.uni-oldenburg.de/en/biology/landeco/research/projects/leda/), accessed August  
236 2016), using averages when there was more than one entry for a species.  
237 Plant height was then used in a regression analysis to predict the  
238 treatment differences.

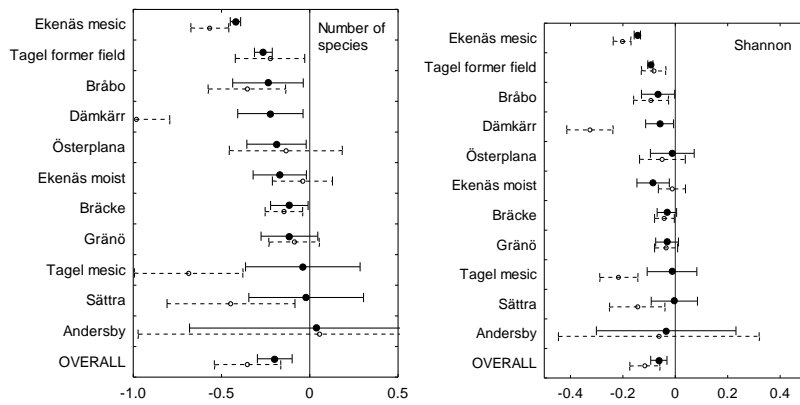
## 239 **Results**

### 240 **Effect on species richness and diversity**

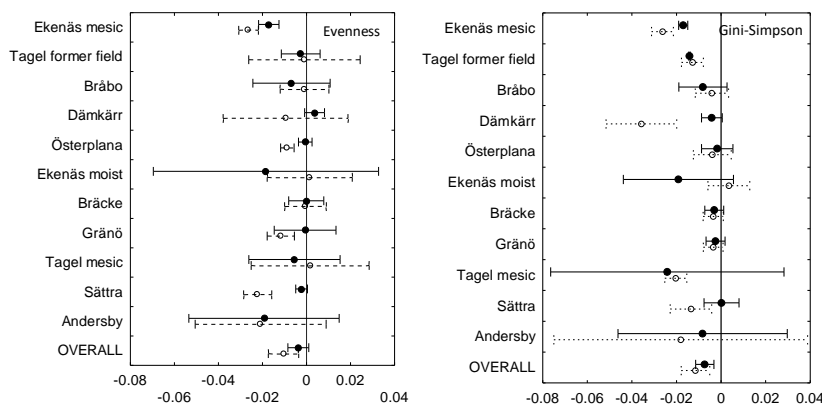
241 As expected, there was an overall drop in  $\ln(\text{RR})$  for the number of  
242 species when mowing every third year was compared with annual

243 mowing, but with considerable variation between sites (Figure 2a). In line  
 244 with this, the two diversity indices also decreased, albeit the Gini-  
 245 Simpson decreased only very modestly (Figures 2b, 2c), while there were  
 246 no apparent change in evenness (Figure 2d). Generally, after 11-14 years,  
 247 the losses were approximately twice the magnitude when comparing the  
 248 untreated control with mowing every third year (estimates of Overall in  
 249 Figure 2).

250



251



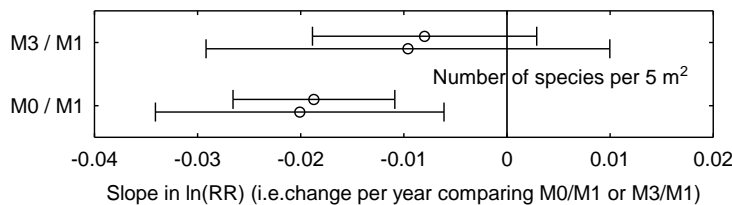
252 *Figure 2. ln(RR) for the 2a) number of species, 2b, 2d) two diversity*  
 253 *indices (Shannon and Gini-Simpson) and 2c) index on evenness*  
 254 *(Shannon). A negative value means smaller diversity or evenness in*  
 255 *mowing every third year (filled symbol with solid bars) or in the*  
 256 *untreated control (unfilled symbol with broken bars), compared with*  
 257 *annual mowing. The trials had been running for 13 years, eleven years*  
 258 *(Ekenäs moist, Ekenäs mesic) or 14 years (Tagel former field). Note the*  
 259 *differences in scale on the x-axes.*

260 **The rate of change**

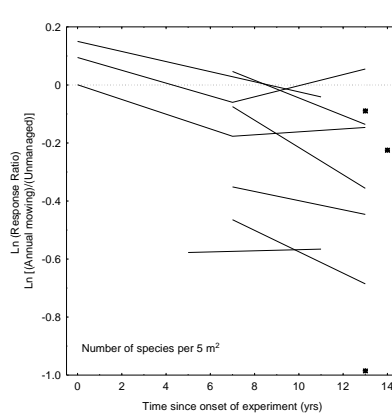
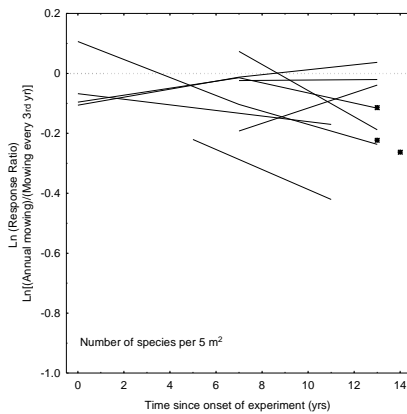
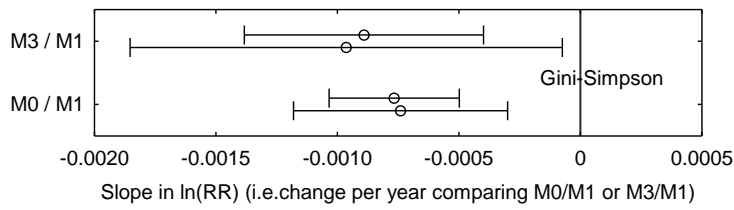
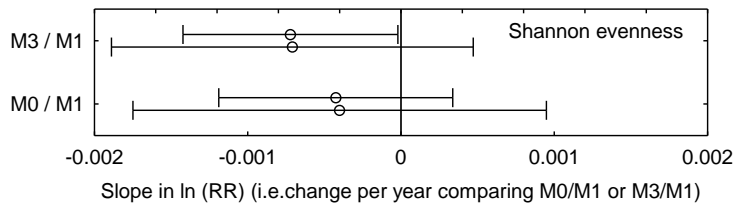
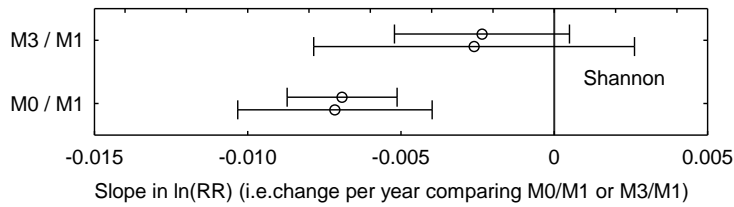
261 The estimates of change in ln(RR) for the species number and Shannon  
 262 diversity index suggested that the loss was slower, approximately half the  
 263 rate, when mowing every third year compared with the untreated control  
 264 (Figure 3a, 3b). For the Gini-Simpson and evenness indexes, there were  
 265 much smaller, but still clear losses, and if anything, the untreated control  
 266 performed better than mowing every third year (Figure 3c, 3d).

267 Trial-wise trajectories in ln(RR) for the species number varied greatly  
 268 among sites: in some trials, there were increases when mowing every  
 269 third year compared with annual mowing (Figure 3e), and in some trials,  
 270 there were increases in ln(RR) in the untreated control (Figure 3f).

271



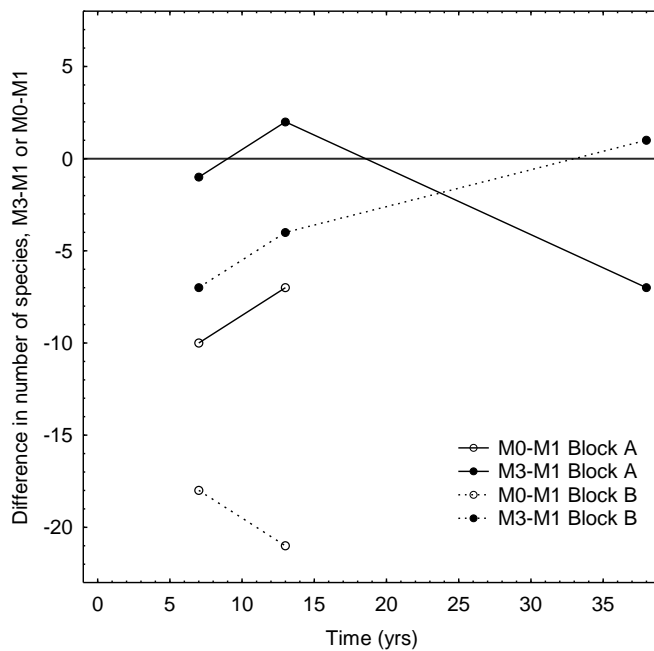
272



277 *Figure 3. Development of ln(RR) over time. 3a-3d) Averages for the eight*  
 278 *trials with comparable data. In the pairs, the bottom value is an average*  
 279 *and the top value is a weighted average (weighted based on whether*  
 280 *there were two or three time points). Note the differences in scale on the*  
 281 *x-axes 3e) ln(RR) for the species number when mowing every third year*  
 282 *compared with annually and 3f) untreated control compared with annual*  
 283 *mowing. Stars in 3e and 3f indicate trials that only had one time point*

284 using the standard protocol for vegetation sampling. A negative value  
285 means that the number of species, biodiversity or evenness is higher in  
286 annual mowing than in the alternative treatment.

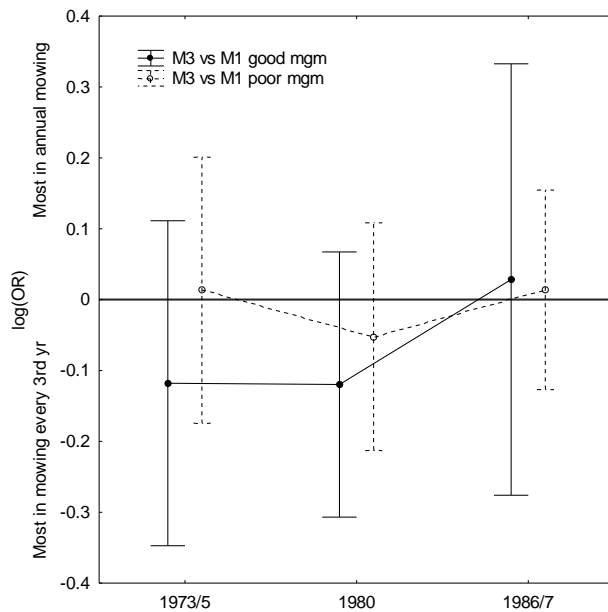
287 The site at Sättra, which had been followed for 38 years, showed a clear  
288 negative trend over time when mowed every third year in one of the two  
289 blocks. In the other block, however, there was no negative trend (Figure  
290 4). In both blocks, the untreated control had lost species over time (Figure  
291 4; no assessment was performed after 38 years because the dense tree  
292 canopy that had developed in the plots had recently been thinned to  
293 eliminate the shading of adjacent plots).



295 *Figure 4. The development of the species number recorded in the long-*  
296 *term trial at Sättra and expressed as the difference between M1 (annual*  
297 *mowing) and M3 (mowing every third year) or M0 (untreated control).*

298 **Change in species indicating good or poor management**

299 The odds of finding indicators of good management showed no apparent  
300 change over time, nor did the odds of finding indicators of poor  
301 management (Figure 5).

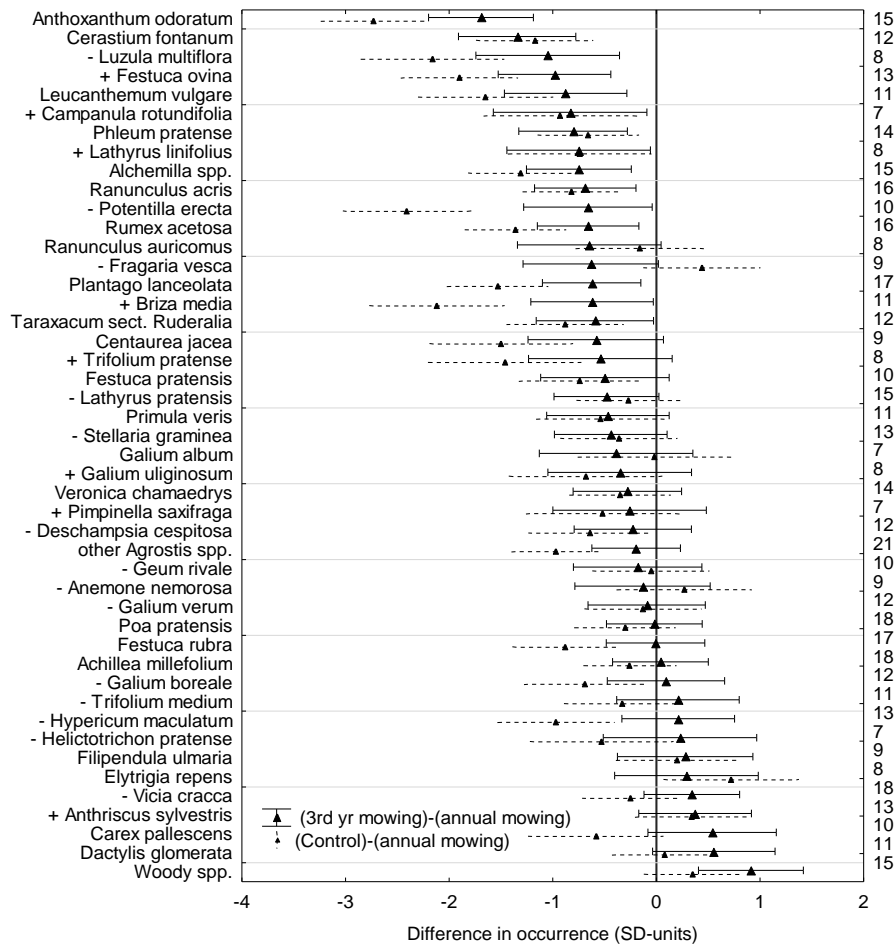


302

303 *Figure 5. ln(OR) contrasting mowing yearly with every third year for*  
304 *indicators of good management and/or poor management.*

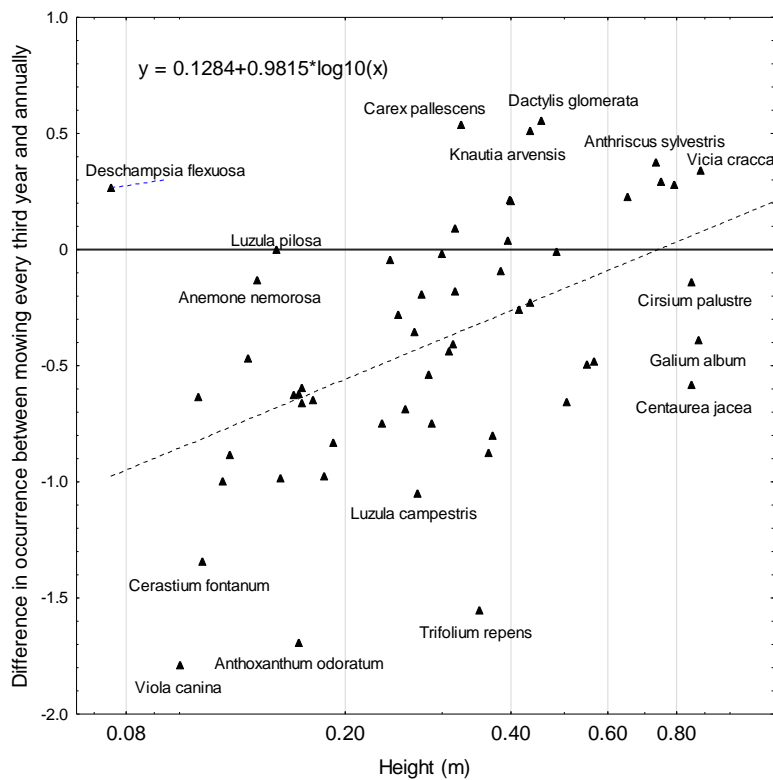
305 **Effects on woody and tall-grown species**

306 Species-wise analyses showed that a majority of species occurred less  
307 frequently when mowing was performed every third year, and for many  
308 of these species, the negative trend was stronger in the untreated control  
309 treatment (Figure 6). While there were 15 species that showed a  
310 significant decrease with relaxed management, there was only one  
311 species group with a significant increase, woody species (Figure 6),  
312 hence confirming our hypothesis.



313  
 314 *Figure 6. Species-wise responses after 11, 13 or 14 years of differing*  
 315 *treatments. A negative value means that a species is decreasing when the*  
 316 *mowing frequency decreases compared with annual mowing. The*  
 317 *indicator status of species is shown with a + or -, for good and poor*  
 318 *management indicators, respectively (based on Ekstam & Forshed 1992).*  
 319 *Numbers to the right are the number of blocks that had an occurrence*  
 320 *(max 22); species with <7 are not shown.*

321 Comparing the height of species with the values shown in Figure 6,  
 322 there was a strong positive relationship ( $F_{(1,54)}=16.759$ ;  $R^2= 0.2368$ ;  
 323  $P=0.000143$ ), i.e., short-grown species mainly became less frequent with  
 324 relaxed mowing (Figure 7).



325  
 326 *Figure 7. Differences between the two mowing treatments (annual and*  
 327 *every third year) per species (N=57) as a function of the species' plant*  
 328 *height. The latter was according to the LEDA traitbase, while differences*  
 329 *were according to eleven field trials after 11-14 years (see Figure 6).*  
 330 *Species names are shown for a selection of the species.*

## 331 **Discussion**

332 By using data from eleven replicated field trials, we showed that relaxed  
333 management, in this case mowing every third year, means losing  
334 biodiversity attributes in vegetation after 11-14 years compared to annual  
335 mowing. This was most clearly seen in data on the species number  
336 (Figure 2a) as well as for some of the species (Figure 6) but also in one  
337 diversity index (Figure 2b). However, it is important to note that the  
338 effect sizes were quite small (an  $\ln(RR)$  of -0,1 represents e.g. comparing  
339 species richness of ten and eleven species), despite the management trials  
340 running between 10 and 15 years. That the evenness index (Figure 2d)  
341 seemed unaffected suggests that the balance among the species resilient  
342 to relaxed management does not change much. More surprising was the  
343 lack of treatment effects in the odds of finding indicator species (Figure  
344 5). This particular system of indicator species has previously been shown  
345 to be relatively sensitive to management effects in grasslands in the area  
346 in which these trials were conducted (Milberg et al. 2014, Tälle et al.  
347 2015). Using indicator species has sometimes been subject to criticism  
348 (Siddig et al. 2016), and their usefulness is known to vary in reliability  
349 along environmental gradients (e.g., Jansson et al. 2009, Zettler et al.  
350 2013). Hence, some caution is always needed, and validation for a  
351 particular scenario is important.

352 As hypothesized, short-grown species were most likely to decrease when  
353 the mowing frequency was relaxed, confirming previous findings  
354 (Hejcman et al. 2007, but see also Milberg et al. in prep.) and suggesting  
355 one or several possible mechanisms: impaired seed regeneration due to a  
356 denser canopy or litter accumulation (e.g., Laborde & Thompson 2013,  
357 Loydi et al. 2013, Kladviová & Münzbergová 2016), impaired growth  
358 due to litter accumulation (Kelemen et al. 2013), or species being  
359 outcompeted by more tall-grown species through shading or root  
360 interactions (Lamb et al. 2009, Kiær et al. 2013). From the point of view  
361 of management, our finding might suggest the allocation of parts of a  
362 grassland – preferably with low grass sward – to an annual mowing  
363 regime, while performing more extensive management of more tall-  
364 grown areas (e.g., every second year).

365 As hypothesized, the occurrence of woody species increased with relaxed  
366 management. Even if these woody perennials are cut every third year,  
367 they seem to have secured enough resources to re-sprout – or have more  
368 chances for successful seed establishment – despite the more dense and  
369 tall-grown vegetation with relaxed management. Whether these small  
370 woody plants are benign or will create an increasing obstacle for mowing  
371 remains to be seen. Shoots might be larger when grown from older  
372 stumps than from younger stumps or from seed, hence requiring more

373 force to be cut by a scythe or being more likely to remain after the  
374 passage of a sickle-bar mower.

375 By comparing the eleven trials, it is apparent that changes can occur at  
376 different rates (Figure 3) and even differ in direction (Figure 3e, Figure  
377 4). Hence, basing conclusions on a single field trial involves a degree of  
378 risk of reaching false conclusions (cf Ioannidis 2005). The false discovery  
379 rate in science seems to generally be underrated (Button et al. 2013,  
380 Nosek et al. 2015), particularly so within ecology, where studies often  
381 have low power and there is a reluctance to repeat studies (Parker et al.  
382 2016). Within conservation biology, the total research budget is limited,  
383 leading to a data deficiency (Milberg 2014). It was particularly  
384 noteworthy that the outcome after 38 years – when a potential treatment  
385 effect should have had plenty of time to manifest itself – differed between  
386 the two blocks (Figure 4). Therefore, apart from the experimental error  
387 that manifested in between-site differences, there was also substantial  
388 variation within sites, despite sharing identical land use histories and  
389 edafic factors.

390 The majority of studies on effects of different mowing intensities focus  
391 on comparing annual mowing with mowing at a higher intensity (e.g.  
392 mowing two times a year). Studies comparing annual mowing with  
393 mowing at a lower intensity are more rare, and results are often varying.

394 While some studies reveal similar results as in the present study, with a  
395 more positive effect of the higher mowing frequency (e.g. Köhler et al.  
396 2005), others reveal results in favour of mowing every second year  
397 (Gosteli 1996, Bakker et al. 2002, Ameloot et al. 2006). A study by Ryser  
398 et al. (1995) revealed similar effect of annual mowing and mowing every  
399 second year but a negative effect of mowing every fifth year.  
400 Consequently, this might suggest that from a conservation perspective it  
401 is sufficient with mowing every second year, while mowing more seldom  
402 can have a more negative effect. However, we expect that the most  
403 suitable mowing intensity also depends on specific site conditions, e.g.  
404 more productive grasslands requiring a higher management intensity to  
405 facilitate biomass and nutrient removal (Al-Mufti et al. 1977; Oelmann et  
406 al. 2009)

#### 407 **Rate of change**

408 There is no apparent unit by which to assess biodiversity changes  
409 (Milberg 2014), but indices might be more universal than the number of  
410 species and so on. In the present study, we chose a palette of different  
411 outcomes, several expressed as a response ratio (Figure 3) or odds ratio  
412 (Figure 5). For others, the nature of the data forced us to use the  
413 difference between the treatment (mowing every third year) and control  
414 (annual mowing) (Figure 4, Figure 6). The odds and response ratios are  
415 transferable and comparable with other such estimates (e.g., Tälle et al.

416 2016), while raw treatment differences are context-specific. Furthermore,  
417 to aid interpretation, we added corresponding data contrasting the  
418 untreated control with annual mowing because this approach hopefully  
419 allows more comparisons with other studies.

420 The loss of biodiversity when turning to mowing every third year was  
421 approximately half of that seen in abandonment for the two clearly  
422 affected response ratios (number of species, Shannon). The median for  
423 the species-wise reductions was 62% of that seen after abandonment, but  
424 with large differences among species, confirming previous reports from  
425 two of the experimental sites (Hansson and Fogelfors 2000, Wahlman  
426 and Milberg 2002), where the outcome of mowing every third year was  
427 intermediate between annual mowing and abandonment.

#### 428 **Implications**

429 Mowing every third year resulted in biodiversity losses, and a more  
430 realistic frequency might therefore be mowing every second year (Bakker  
431 et al. 2002; Köhler et al. 2005) or skipping one year in three. Such  
432 relaxed management might not be perfect for grassland plants, but could  
433 be beneficial for many insects, most notably pollinators and butterflies  
434 (e.g., Littlewood et al., 2012; van Klink et al., 2015, Milberg et al. 2016).

435 There are subsidies available for farmers in the EU, e.g., to support the  
436 management of semi-natural grasslands. Because these subsidies

437 represent a substantial societal investment, it is important that funds be  
438 used in the best possible way. They should function as an incentive for  
439 farmers to maintain management that might otherwise not be justified  
440 economically. If adjusting subsidies to the actual cost of maintaining  
441 mowing, one method is to halve the subsidy if converting to mowing  
442 every second year, but such a move is likely to decrease farmers'  
443 incentive for maintaining management.

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