



**HAL**  
open science

## How do subordinate and dominant species in semi-natural grasslands relate to productivity and land-use change?

P. Mariotte, A. Buttler, F. Kohler, A.K. Gilgen, T. Spiegelberger

### ► To cite this version:

P. Mariotte, A. Buttler, F. Kohler, A.K. Gilgen, T. Spiegelberger. How do subordinate and dominant species in semi-natural grasslands relate to productivity and land-use change?. *Basic and Applied Ecology*, 2013, 14 (3), p. 217 - p. 224. 10.1016/j.baae.2013.02.003 . hal-00942284

**HAL Id: hal-00942284**

**<https://hal.science/hal-00942284>**

Submitted on 24 Feb 2014

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **How do subordinate and dominant species in semi-natural**  
2 **mountain grasslands relate to productivity and land-use change?**

3

4 Pierre Mariotte<sup>a,b,\*</sup>, Alexandre Buttler<sup>a,b,c</sup>, Florian Kohler<sup>a</sup>, Anna K. Gilgen<sup>d,e</sup>, Thomas  
5 Spiegelberger<sup>a,b,f</sup>

6

7 <sup>a</sup> Ecole Polytechnique Fédérale de Lausanne EPFL, School of Architecture, Civil and  
8 Environmental Engineering (ENAC), Laboratory of Ecological Systems (ECOS), Station 2,  
9 1015 Lausanne, Switzerland

10 <sup>b</sup> Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Site Lausanne,  
11 Station 2, 1015 Lausanne, Switzerland

12 <sup>c</sup> Laboratoire de Chrono-Environnement, UMR CNRS 6249, UFR des Sciences et  
13 Techniques, 16 route de Gray, Université de Franche-Comté, F-25030 Besançon, France

14 <sup>d</sup> ETH Zurich, Institute of Agricultural Sciences, Universitätstrasse 2, 8092 Zurich,  
15 Switzerland.

16 <sup>e</sup> University of Bern, Institute of Plant Sciences and Oeschger Centre for Climate Change  
17 Research, Altenbergrain 21, 3013 Bern, Switzerland

18 <sup>f</sup> Irstea, UR EMGR Mountain Ecosystems, 2 rue de la Papeterie, BP 76, 38402 Saint-Martin-  
19 d'Hères, France

20

21 \*Corresponding author. Tel.: +41 21 693 39 05; fax: + 41 21 693 39 13.

22 E-mail address: pierre.mariotte@epfl.ch

23

24

25 Running title: Abandonment of pasturing reduces subordinate species

26 **Abstract**

27 Changes in agricultural practices of semi-natural mountain grasslands are expected to modify  
28 plant community structure and shift dominance patterns. Using vegetation surveys of 11 sites  
29 in semi-natural grasslands of the Swiss Jura and Swiss and French Alps, we determined the  
30 relative contribution of dominant, subordinate and transient plant species in grazed and  
31 abandoned communities and observed their changes along a gradient of productivity and in  
32 response to abandonment of pasturing.

33 The results confirm the humpbacked diversity-productivity relationship in semi-natural  
34 grassland, which is due to the increase of subordinate species number at intermediate  
35 productivity levels. Grazed communities, at the lower or higher end of the species diversity  
36 gradient, suffered higher species loss after grazing abandonment. Species loss after  
37 abandonment of pasturing was mainly due to a higher reduction in the number of subordinate  
38 species, as a consequence of the increasing proportion of dominant species.

39 When plant biodiversity maintenance is the aim, our results have direct implications for the  
40 way grasslands should be managed. Indeed, while intensification and abandonment have been  
41 accelerated since few decades, our findings in this multi-site analysis confirm the importance  
42 of maintaining intermediate levels of pasturing to preserve biodiversity.

43

44

45

46

47

48

49

50

51 **Zusammenfassung**

52 Änderungen in der Bewirtschaftung naturnaher Bergwiesen können die Struktur von  
53 Pflanzengesellschaften und deren Dominanzmuster verändern. Anhand von  
54 Vegetationsaufnahmen 11 naturnaher Wiesen des Schweizer Juras und der Schweizer und  
55 Französischen Alpen erfassten wir den Anteil der dominanten, untergeordneten und  
56 transienten Pflanzenarten in beweideten und aufgelassenen Pflanzengemeinschaften,  
57 beobachteten ihre Veränderungen entlang eines Produktivitätsgradienten und ihre Antwort auf  
58 die Aufgabe der Beweidung.

59 Die Ergebnisse bestätigen den glockenförmigen Zusammenhang zwischen Artenreichtum und  
60 Produktivität in naturnahem Grünland, insbesondere aufgrund der Zunahme von  
61 untergeordneten Arten bei mittlerer Produktivität. Beweidete Pflanzengesellschaften am  
62 unteren oder oberen Ende des Pflanzenvielfalts-Gradienten verloren nach Aufgabe der  
63 Beweidung mehr Arten. Der Artenverlust nach der Beweidungsaufgabe war vor allem ein  
64 Resultat der höheren Reduktion von untergeordneten Arten als Folge des steigenden Anteils  
65 hochwachsender Arten.

66 Unsere Ergebnisse haben direkte Auswirkungen auf die Art und Weise, wie Grünland  
67 bewirtschaftet werden sollte. Während die Intensivierung und die Aufgabe beweideter  
68 Flächen seit Jahrzehnten schneller vorangehen, bestätigen die Ergebnisse dieser Multi-Site-  
69 Analyse die Bedeutung einer mittleren Beweidungsintensität für den Erhalt der Artenvielfalt.

70

71

72

73

74 **Keywords:** diversity-productivity relationship, grazing, land-use management, plant  
75 community structure, species coexistence.

## 76 **Introduction**

77 Semi-natural mountain grasslands are widespread components of north-temperate landscapes  
78 and play an important role by providing fodder for livestock and acting as reservoirs for both  
79 carbon (Follett & Reed 2010) and biodiversity (Mariotte et al. 2013a). These ecosystems host  
80 species-rich communities with up to 40 plant species per square meter but are among the most  
81 endangered ecosystems in Europe, threatened by both land-use (Silva et al. 2008, Fava et al.  
82 2010) and climate change (Jentsch et al. 2009; Mariotte et al. 2013b). Indeed, changes in  
83 agricultural practices, which have been accelerated since the 1950 in Central Europe are  
84 leading to either agricultural intensification or abandonment (Gillet & Galandat 1996, Buttler  
85 et al. 2012). While plant community structure (species diversity and composition) is largely  
86 the result of management (regular grazing) of semi-natural grasslands, land-use changes are  
87 likely to modify this structure and, as a consequence, perturb community stability and  
88 ecosystem functioning. Therefore, it seems essential to understand which structural  
89 components of plant communities contribute most to species diversity and how they are  
90 affected by land-use changes.

91 The easiest way to classify components of floristic biodiversity is to order species  
92 according to their relative abundance and to define their functional role (Grime 1998). This  
93 approach was further developed by using dominance-diversity profiles, which allowed to  
94 distinguish three components: dominant, subordinate and transient species (Grime 1987,  
95 1998). Those elements may vary in species richness, functional traits and functional groups.  
96 According to Grime, dominant species are few in number, tall and more expansive in  
97 morphology and produce high quantities of biomass. Therefore, immediate influence of plant  
98 communities on the ecosystem properties is expected to be primarily determined by traits of  
99 dominant species (“mass ratio theory”, Grime 1998). Subordinate species are generally more  
100 numerous, but smaller in stature and form a low proportion of the total community biomass.

101 By contrast, transient species, which generally do not persist after years and appear only  
102 briefly as seedlings, may replace the other species or colonize new areas after disturbance  
103 (“founder effects”).

104 Species-rich ecosystems, such as semi-natural grasslands, are driven by coexisting  
105 species in a strict dominance hierarchy where superior competitors (dominants) can displace  
106 inferior competitors (subordinates) from occupied patches whereas inferior competitors  
107 cannot displace superior competitors (Amarasekare 2003). Subordinate species have no access  
108 to patches occupied by dominants, but their better resource efficiency (“filter effects”, Grime  
109 1998) allows them to establish in patches that dominants are not able to colonize. This  
110 mechanism leads towards spatial niche differentiation between the two species-groups and  
111 resource complementarity instead of resource competition. Species coexistence, through niche  
112 partitioning, is mainly the result of differences in light availability, soil fertility and  
113 disturbance which all contribute to ecosystem productivity. Productivity has been  
114 demonstrated to be a function of species diversity in artificially created grasslands (Hooper et  
115 al. 2005) but a meta-analysis suggested that, in natural grasslands, diversity is a function of  
116 productivity (Grace et al. 2007). Diversity-productivity relationships of species-rich  
117 communities follow in general a humpback model (Grime 1973) where species diversity is  
118 higher at intermediate levels of productivity, fertility and disturbance (Odum 1963, Hughes et  
119 al. 2007). However, the humpbacked pattern has generated strong debate in ecology and  
120 recent meta-analytical syntheses concluded that various patterns can occur (Gillman & Wright  
121 2006). Indeed, based on standardized samples from 48 herb-dominated plant communities on  
122 five continents, the productivity-diversity relationship shows different patterns depending on  
123 land-use history and management of the sites (Adler et al. 2011). Nevertheless, evidence of a  
124 humpback relationship was found when including restored prairies, pastures and old fields in  
125 the analysis (Adler et al. 2011), confirming findings of Grime (1973) for species-rich

126 communities. According to the theory, productive grasslands with high soil fertility and/or  
127 light availability are sites of competitive exclusion, which allows dominance of some species,  
128 while low productive grasslands with low soil fertility and/or light availability are stressful  
129 environments for plant species (Al-Mufti et al. 1977). Therefore, higher species richness  
130 should be observed at intermediate productivity levels, which represent the equilibrium  
131 between disturbance and dominance. Concerning the role of subordinate species it is further  
132 suggested (Grime 1987) that subordinate species represent a higher proportion of species  
133 within the hump of the diversity-productivity model but this statement has not been confirmed  
134 by field experiments and calls for verification.

135         In semi-natural mountain grasslands, grazing by large herbivores is an important  
136 driver for creating and maintaining biodiversity and many studies showed that species  
137 diversity decreases after abandonment of pasturing (Kohler et al. 2006a,b, Sebastià et al.  
138 2008, Marion et al. 2010, Parolo et al. 2011). In these ecosystems, the persistence of  
139 subordinate species seems to be closely related to the activity of large herbivores, which  
140 reduce competition from dominant species through gap creation (Mariotte et al. 2012a, Kohler  
141 et al. 2006b) or grazing (Tahmasebi Kohyani et al. 2009, Gillet et al. 2010). Inversely, the  
142 exclusion of cattle can lead to the dominance of competitive tall-growing species (Tasser &  
143 Tappeiner 2002, Mayer et al. 2009), which reduces light availability for small-stature ground  
144 layer species. These findings confirm the hypothesis that intermediate disturbance through  
145 cattle activity may over-proportionally benefit small-stature subordinate species while cattle  
146 abandonment is expected to reduce the abundance of these species.

147         In this multi-site study, we aim at describing the structure of plant communities in  
148 semi-natural mountain grasslands along a productivity gradient. The study includes eleven  
149 sites of the Swiss Jura and the Swiss and European Alps, which differ in their aboveground  
150 biomass production. The abundance of dominant, subordinate and transient species (species-

151 groups) is determined and related to species diversity. We then compare the abundance of  
152 these species-groups in paired grazed and abandoned plots from nine sites to test whether the  
153 abundance of subordinate species decreases after abandonment and how this impacts plant  
154 species diversity.

## 155 **Materials and methods**

### 156 *Study sites*

157 In order to have a large productivity gradient, we brought together results of eleven similar  
158 studies carried out in semi-natural grasslands of the Jura and the Alps (Kohler et al. 2006a,b,  
159 Spiegelberger et al. 2006, Vandenberghe et al. 2008, Gilgen & Buchmann 2009, Mariotte et  
160 al. 2013a, see Appendix A: Table 1). The sites, situated between the montane and the  
161 subalpine belt, were floristically similar and dominated by *Festuca nigrescens*, *Agrostis*  
162 *capillaris*, *Dactylis glomerata*, *Trifolium repens* and *Taraxacum officinale*. The eleven sites  
163 were extensively grazed by cattle (summer grazing, see Appendix A: Table 1) and nine of  
164 them included also 3- to 5-years-old abandoned plots. Grazed and abandoned communities  
165 were situated either in the same place (sites 1, 4, 6, 7 & 10) or with a maximum of 5 km  
166 between them but in similar conditions of exposition and inclination (sites 2, 5, 8 & 9, see  
167 Spiegelberger et al. (2006) for a more detailed description). Each site included five very  
168 homogeneous plots except for sites 1, 4 and 6 where three plots were available. Aboveground  
169 community biomass production was measured at peak biomass by harvesting standing crop  
170 above 5-7 cm in each plot, drying at 60 °C for 72 hours and weighing. Vegetation surveys  
171 were done in mid-summer using different methods: Braun-Blanquet index (site 3), biomass  
172 sorting (sites 7, 10 & 11), point quadrats (sites 1, 4 & 6) or estimated to the nearest per cent  
173 (sites 2, 5, 8 & 9). The sampled surface corresponded to 1 m<sup>2</sup>, except in site 11 where it was  
174 0.2 m<sup>2</sup>. Smaller quadrats were justified here because no further species were expected to be  
175 included by a 1 m<sup>2</sup> sample, and the species number was used without correcting for quadrat



176 size. Proportion of species assessed in the field as Braun-Blanquet index, cover or biomass  
177 was transformed in relative proportion (%) to allow comparison between sites.

178 *Plant community structure (analysis A)*

179 For each site, species diversity was calculated as the mean species number in grazed plots (n  
180 = 3 or 5). We averaged relative species proportion observed in replicated plots (n = 3 or 5) to  
181 obtain the mean relative species proportion per site. Species were classified in competitive  
182 hierarchical groups (Grime 1998, Mariotte et al. 2013a,b) for each site according to a  
183 frequency-proportion curve (see Appendix A. Figure 1) based on species frequency and  
184 cumulative proportion. Species were ranked by proportion in ascending order and cumulated  
185 to obtain cumulative proportion value for each species. 100% frequency means that the  
186 species is present in all plots and 100% cumulative proportion corresponds to the most  
187 abundant species. A species was classified as dominant if its frequency was greater than 50%  
188 and its cumulative relative proportion greater than 12%. A species was classified as  
189 subordinate if its frequency was greater than 50% and its cumulative relative proportion  
190 between 2 and 12% (adapted from Grime 1998). The other species were classified as transient  
191 plants. Vegetation surveys were done during several years (except in sites 2, 5, 8 & 9) and we  
192 confirmed that our species-groups selection was consistent over these years. Moreover,  
193 further analysis on plant functional traits in sites 7 and 10 showed that selected species-groups  
194 differed (Mariotte et al. 2013a), with dominant species linked to high specific leaf area (SLA)  
195 and plant height whereas subordinate species are associated to low SLA and small-stature  
196 traits. We determined the relative contribution (%) of the three species-groups to the diversity  
197 along a productivity gradient containing the 11 sites. The relative contributions of dominant,  
198 subordinate and transient species correspond to the number of species per species-group  
199 divided by the total number of species in the respective plot.

200 *Abandonment of pasturing (analysis B)*

201 In a second analysis, we analysed the effect of cattle abandonment on the structure of plant  
202 communities and put this in relation to changes in species diversity. Species diversity was  
203 calculated as the mean species number in abandoned plots (n = 3 or 5) and compared with the  
204 productivity of abandoned communities and with the species diversity of nearby grazed  
205 communities at the same location. As previously, dominant, subordinate and transient species  
206 were determined in abandoned communities and changes in the relative contribution of the  
207 three species-groups (plant community structure) in abandoned plots were plotted against the  
208 diversity in grazed communities. For each site, proportional changes in dominant species  
209 (subordinate or transient) were calculated as the difference in log between the number of  
210 dominant species (respectively subordinate or transient) in abandoned plots and in grazed  
211 plots. The use of log allows to account for the effect of initial species diversity and highlights  
212 the negative, neutral or positive effects of abandonment. In addition, to test whether  
213 abandonment of pasturing benefits tall-growing species at the expense of small-stature  
214 species, we classified all species from vegetation surveys in one of those two groups and  
215 calculated their relative proportion in grazed and abandoned communities. Species growing  
216 taller than 15-20 cm were classified as tall-growing species while the others were classified as  
217 small-stature species. Data on canopy height was taken from “Flora Helvetica” (Lauber &  
218 Wagner 2007) and the “LEDA trait database” (Kleyer et al. 2008).

### 219 *Statistical analysis*

220 In the analysis (A), we first focused on the relationship between species diversity and  
221 productivity and then on the relative importance of species-groups in this relationship. Species  
222 diversity, productivity and abundance of species-groups were summarized into mean values  
223 per site. In the second analysis (B), we explored the relationship between the species diversity  
224 in abandoned and grazed communities and observed the effect of abandonment on species-  
225 groups contribution at 9 sites (see Appendix A: Table 1). Polynomial models (degree 2) were

226 calculated with the orthogonal polynomial function (poly {stats}) in R version 2.14.1 (R  
227 Development Core Team, 2011). Statistical significance of models (p-value) and multiple  $R^2$   
228 values were obtained using ANOVAs to estimate the goodness-of-fit. The differences in the  
229 relative contribution of tall-growing versus small-stature species between grazed and  
230 abandoned communities were analysed using linear mixed-effects models specifying plot (n =  
231 3 or 5) nested into site (n = 9) as random factors.

## 232 **Results**

### 233 *Diversity-productivity relationship in grazed plots*

234 The mean species diversity per site ranged from  $13.2 \pm 0.6$  species to  $36.8 \pm 1.1$  species along  
235 the productivity gradient, which ranged from  $99 \pm 7$  to  $590 \pm 77$  g dwt.m<sup>-2</sup>. Species diversity  
236 was clearly linked to productivity (Fig. 1A) and best explained by a polynomial function ( $F_{2,8}$   
237 = 11.525,  $P < 0.01$ ,  $R^2 = 0.75$ ). Dominant species represented between 41 and 61% of species  
238 but their contribution to the total diversity remained similar along the productivity gradient  
239 (Fig. 1B). By contrast, subordinate species, representing 15 to 36% of species (Fig. 1C),  
240 followed a polynomial distribution along the productivity gradient ( $F_{2,8} = 10.065$ ,  $P < 0.01$ ,  $R^2$   
241 = 0.72). The contribution of subordinate species to total species diversity was less important  
242 at low and high productive sites but higher at intermediate productivity. The transient species,  
243 which contributed from 9 to 41% (Fig. 1D), followed an inverse pattern, fitted by a significant  
244 polynomial function ( $F_{2,8} = 6.671$ ,  $P < 0.05$ ,  $R^2 = 0.63$ ). Soil dissolved inorganic nitrogen,  
245 which had been measured in four sites (see Appendix A: Table 1), was positively correlated to  
246 productivity ( $F_{1,2} = 119.792$ ,  $P < 0.01$ ,  $R^2 = 0.98$ ).

### 247 *Abandonment of pasturing*

248 In abandoned plots, productivity did not affect species diversity (see Appendix A: Figure 2;  
249 Polynomial:  $F_{2,6} = 0.332$ ,  $P = 0.73$ ,  $R^2 = 0.09$ ; Linear:  $F_{1,7} = 0.766$ ,  $P = 0.41$ ,  $R^2 = 0.10$ ).

250 However, species diversity of abandoned communities was linked to the species diversity of  
251 paired grazed communities (Fig. 2A), which was assumed to represent the initial species  
252 diversity before pasturing of the sites was abandoned. Mean species diversity in abandoned  
253 plots was either similar or lower compared to mean species diversity in grazed plots (Fig. 2A).  
254 The loss of species due to abandonment was remarkably pronounced in initially low (e.g. 10  
255 species less in abandoned site 9 compared to the grazed site 9) and highly diverse sites (e.g.  
256 24 species less in site 5) resulting in a significant polynomial relationship between initial  
257 species diversity and current diversity ( $F_{2,6} = 62.606$ ,  $P < 0.001$ ,  $R^2 = 0.95$ ).

258 At the species-group level, the differences in number of dominant ( $F_{2,6} = 12.616$ ,  $P <$   
259  $0.01$ ,  $R^2 = 0.81$ ) and subordinate species ( $F_{2,6} = 11.501$ ,  $P < 0.01$ ,  $R^2 = 0.79$ ) showed the  
260 similar polynomial pattern as observed for species diversity whereas the difference in number  
261 of transient species (Fig. 2D) was similar in grazed and abandoned communities (-12% to  
262 +19%). The difference in number of dominant species (Fig. 2B) was similar in four sites,  
263 higher in one site (+14%) and lower in four sites (respectively -58% and -45% in lower and  
264 higher initial species diversity). In abandoned communities, the difference in number of  
265 subordinates (Fig. 2C) was high in eight of the nine plots (-6% to -94%) and much higher than  
266 the difference in number of dominants, especially in sites with high species diversity. The  
267 analysis of vegetation surveys showed that the identity of dominant species was almost  
268 similar in grazed and abandoned communities, while the identity of subordinate and transient  
269 species showed more variation between both communities. Indeed, some transient species  
270 observed in grazed plots became subordinates in abandoned plots and vice versa.

271 The relative contribution of tall-growing species was significantly higher ( $F_{1,38} =$   
272  $31.788$ ,  $P < 0.001$ ) in abandoned plant communities (81%) compared to grazed communities  
273 (63%) at the expense of small-stature species.

274 **Discussion**

275 *Plant community structure and the diversity-productivity relationship*

276 This multi-sites analysis, including 11 semi-natural mountain grasslands, determined plant  
277 community structure along a productivity gradient. In analysis A, we highlighted a diversity-  
278 productivity relationship, which was best fit by a polynomial model. These results confirm the  
279 diversity-productivity dependency suggested by various authors (Al-Mufti et al. 1977, Grime  
280 1973, Grace et al. 2007, Adler et al. 2011). In pastures, plant communities are continuously  
281 disturbed by cattle activities (Gillet et al. 2010, Kohler et al. 2006a,b), and disturbance due to  
282 grazing was constant and similar for the eleven sites (see Appendix A: Table 1). Here, we  
283 suggest that the productivity gradient is more related to soil fertility as concentrations of  
284 dissolved inorganic nitrogen in soil increase along this gradient. In our study, the maximum  
285 diversity (30-35 species) occurred at intermediate productivity (between 180 and 420 g dwt.m<sup>-2</sup>  
286 <sup>2</sup>) and supports the humpback model of Grime (1973, 1987), where species diversity is  
287 predicted to be higher at intermediate productivity and fertility (Odum 1963). Our findings  
288 therefore confirm that intermediate productivity favours species coexistence in semi-natural  
289 grasslands.

290 Interestingly, the contribution of species-groups differed along the diversity-  
291 productivity relationship. Grime (1987) proposed that low productivity favours transient  
292 species, intermediate productivity favours subordinate species and high productivity favours  
293 dominant species. Indeed, in our analysis, the proportion of subordinates peaked at  
294 intermediate productive sites and we confirm that intermediate productivity favours the  
295 presence of subordinate species through coexistence, and thus increases species diversity. In  
296 contrast to Grime's hypothesis (1987), the proportion of transient species increased in our  
297 multi-sites study at low and high productivity sites, whereas dominant species did not change  
298 along the productivity gradient, representing about 50% of the species diversity. In contrast

299 with Grime's work, which included a wide range of herbaceous vegetation, we based our  
300 analysis only on semi-natural mountain grasslands. In these ecosystems, cattle activities such  
301 as grazing and trampling, even at low intensity, tend to prevent potentially competitive  
302 species from attaining maximum size at high productive sites (Grime 1973, Augustine &  
303 McNaughton 1998). Therefore, we suggest that large herbivores may stabilize the proportion  
304 of dominant species along the productivity gradient, whereas subordinate species prevent low  
305 competitive transient species to appear at intermediate productivity.

### 306 *Abandonment of pasturing in semi-natural grasslands*

307 In the second analysis (B), we showed that, in 7 out of 9 cases, species diversity was lower in  
308 abandoned communities compared to grazed communities which confirms previous  
309 observations in species-rich pastures (Sebastià et al. 2008, Marion et al. 2010, Parolo et al.  
310 2011). Interestingly, the difference of species diversity associated with land abandonment was  
311 a function of the initial species diversity of the site (species diversity when plots were still  
312 grazed) with high and low diverse sites being more affected by abandonment. Plant  
313 productivity differed in abandoned communities but we did not find a clear relationship  
314 between the loss of species diversity and/or the differences in plant community structure.

315 Plant community structure differed in abandoned plots, with a loss of species diversity,  
316 and these differences can be interpreted here as a function of initial species diversity (e.g.  
317 diversity of the grazed plots). The loss of subordinate species was higher than the loss of  
318 dominants, showing that abandonment of pasturing over-proportionally affects subordinates.  
319 The mechanisms underlying this pattern are difficult to explain as various components of  
320 cattle activity, such as grazing, trampling and dunging, may influence plant community  
321 (Kohler et al. 2006b). Selective grazing is especially high at low cattle density (Klapp 1971)  
322 as was the case in the sites included in our study. Selective grazing is expected to increase  
323 species diversity when dominant species are grazed (reduction of dominance), and to decrease

324 species diversity when subordinates are grazed (increase of dominance). In our study, species  
325 diversity was lower in the absence of grazing (abandoned plots), suggesting that selective  
326 herbivory on dominants occurred in grazed communities. A major response to grazing is the  
327 promotion of ground-layer species due to the vertical defoliation (Dupré & Diekmann 2001).  
328 This adaptation favours small subordinate species, which are expected to be less affected,  
329 whereas dominant plants, which are often characterised by higher nutrient requirements and  
330 growth rate, are vulnerable to foliage losses (Augustine & McNaughton 1998). Subordinate  
331 species have shown to regrow better after grazing than dominants due to their physiological  
332 plasticity or because they benefit from reduced competition from grazed dominants  
333 (Tahmasebi Kohyani et al. 2009, Mariotte et al. 2012a,b). However, although grazing  
334 significantly favours subordinate species, increasing nutrient levels may counteract the  
335 negative effect of grazing on dominant species (Tahmasebi Kohyani et al. 2009). Indeed, the  
336 fertilizing effect of dung favours competitive dominants (nutrient demanding tall species) at  
337 the expense of stress-tolerant or perturbation-resistant subordinates (Gillet et al. 2010).  
338 Trampling by cattle must also be considered as it provides spatial heterogeneity (gaps), which  
339 may benefit subordinate species (Kohler et al. 2006b, Mariotte et al. 2012a). Moreover, while  
340 the number of dominant species was lower, our observations on canopy height showed that  
341 the proportion of tall-growing species was higher in abandoned plots at the expense of small-  
342 stature species (less light availability or nutrient resources), which confirms that dominance  
343 increased after abandonment of pasturing. Therefore, we suggest that the higher loss of  
344 subordinate species may be due to the absence of both grazing and trampling but also to the  
345 increase of dominance, which impedes their development, while dominant species are only  
346 reduced by the absence of dunging. By contrast, transient species were not affected by  
347 abandonment of pasturing but they are generally colonizer species (“founder effect”, Grime  
348 1998) and very resistant to disturbance.

349           In this study, we showed that subordinate species are an important component of plant  
350 species diversity, which is favoured by intermediate productivity and the presence of cattle at  
351 low density (extensive management). Considering that subordinate species may have a larger  
352 influence on ecosystem processes (plant productivity, nutrient cycling, decomposition) than  
353 their relative abundance would suggest (Mariotte et al. 2013a,b), favouring these species  
354 seems to be very important for ecosystem functioning in semi-natural grasslands. Our results  
355 have direct implications for the way grasslands should be managed, when management aims  
356 at maintenance of plant biodiversity value. Indeed, while intensification and abandonment  
357 have been accelerated since the 1950s in Central Europe, findings of this study confirm the  
358 necessity to maintain intermediate levels of pasturing to preserve biodiversity and ecosystem  
359 integrity.

## 360 **Acknowledgments**

361 We acknowledge funding by the Swiss National Science Foundation (PM: project n°31003A-  
362 114139, FK: project n°3100-064116, and TS: project n°4048-064424), the NCCR Climate  
363 (AKG) and the Competence Centre in Environmental Science (CCES) of the ETH Domain  
364 through the CCES-project Mountland (AB and TS). We thank also Charlotte Vandenberghe  
365 and Aurélie Thébault for their help in this study.

366

## 367 **Appendix A. Supplementary data**

368 Supplementary data associated with this article can be found, in the online version, at  
369 XXXXX."

## 370 **References**

371 Adler, P.B., Seebloom, E.W., Borer, E.T., Hillebrand, H., Hautier, Y., Hector, A., Harpole,  
372 W.S., O'Halloran, L.R., Grace, J.B., Anderson, T.M., Bakker, J., Biederman, L.A.,



- 373 Brown, C.S, Yvonne M. Buckley, Y., Calabrese, L.B., Chu, C-J. Cleland, E.E.,  
374 Collins, S.L., Cottingham, K.L., Crawley, M.J., Damschen, E.I., Davies, K.F.,  
375 DeCrappeo, N.M., Fay, P.A., Firn, J., Frater, P., Gasarch, E.I., Gruner, D.S.,  
376 Hagenah, N., Lambers, J.H.R., Humphries, H., Jin, V.L., Kay, A.D., Kirkman, K.P.,  
377 Klein, J.A., Knops, J.M.H., La Pierre, K.J., Lambrinos, J.G., Li, W., MacDougall,  
378 A.S., McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Morgan, J.W.,  
379 Mortensen, B., Orrock, J.L., Prober, S.M., Pyke, D.A, Risch, A.C., Schuetz, M. ,  
380 Smith, M.D., Stevens, C.J., Sullivan, L.L., Wang, G., Wragg, P.D., Wright, J.P. &  
381 Yang, L.H. (2011). Productivity is a poor predictor of plant species richness. *Science*,  
382 333, 1750-1752.
- 383 Al-Mufti, M.M., Sydes, C.L., Furness, S.B., Grime, J.P. & Band, S.R. (1977). A quantitative  
384 analysis of shoot phenology and dominance in herbaceous vegetation. *Journal of*  
385 *Ecology*, 65, 759-791.
- 386 Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: a  
387 synthesis. *Ecology Letters*, 6, 1109–1122.
- 388 Augustine, D.J. & McNaughton, S.J. (1998). Ungulate effects in the functional species  
389 composition of plant communities: herbivore selectivity and plant tolerance. *Journal*  
390 *of Wildlife Management*, 2, 1165–1183.
- 391 Buttler, A., Gavazov, K., Peringer, A., Siehoff, S., Mariotte, P., Wettstein, J.-B., Chételat, J.,  
392 Huber, R., Gillet, F. & Spiegelberger, T. (2012). Preservation of Wooded pastures in  
393 the Jura: climatic and agricultural Policy challenges. *Agrarforschung Schweiz*, 3,  
394 346-353.
- 395 Dupré, C. & Diekmann, M., (2001). Differences in species richness and life-history traits  
396 between grazed and abandoned grasslands in southern Sweden. *Ecography*, 24, 275–  
397 286.

- 398 Fava, F., Parolo, G., Colombo, R., Gusmeroli, F., Della Marianna, G., Monteiro, A.T. &  
399 Bocchi, S. (2010). Fine-scale assessment of hay meadow productivity and plant  
400 diversity in the European Alps using field spectrometric data. *Agriculture,*  
401 *Ecosystems and Environment*, 137, 151–157.
- 402 Follett, R.F. & Reed, D.A. (2010). Soil Carbon Sequestration in Grazing Lands: Societal  
403 Benefits and Policy Implications. *Rangeland Ecology & Management*, 63, 4-15.
- 404 Gilgen, A.K. & Buchmann, N. (2009). Response of temperate grasslands at different altitudes  
405 to simulated summer drought differed but scaled with annual precipitation.  
406 *Biogeosciences*, 6, 2525-2539.
- 407 Gillet, F. & Gallandat, J.D. (1996). Wooded pastures of the Jura Mountains. In: M. Etienne  
408 (Eds.) *Western European silvopastoral systems* (pp. 37-53). INRA, Paris.
- 409 Gillet, F., Kohler, F., Vandenberghe, C. & Buttler, A. (2010). Effect of dung deposition on  
410 small-scale patch structure and seasonal vegetation dynamics in mountain pastures.  
411 *Agriculture, Ecosystems & Environment*, 135, 34-41.
- 412 Gillman, L.N. & Wright, S.D. (2006). The influence of productivity on the species richness of  
413 plants: A critical assessment. *Ecology*, 87, 1234-1243.
- 414 Grace, J.B., Anderson, T.M., Smith, M.D, Seabloom, E., Andelman, S.J., Meche G., Weiher,  
415 E.; Allain, L.K., Jutila, H., Sankaran, M., Knops, J., Ritchie, M. & Willig, M.R.  
416 (2007). Does species diversity limit productivity in natural grassland communities?  
417 *Ecology Letters*, 10, 680-689.
- 418 Grime, J.P. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, 242, 344-347.
- 419 Grime, J.P. (1987). Dominant and subordinate components of plant communities –  
420 implications for succession, stability and diversity. In: A. Gray, P. Edwards & M.  
421 Crawley (Eds.) *Colonisation, Succession and Stability* (pp. 413-428). Blackwell,  
422 Oxford.

- 423 Grime, J.P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder  
424 effects. *Journal of Ecology*, 86, 902-910.
- 425 Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H.,  
426 Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J.,  
427 Vandermeer, J. & Wardle, D.A. (2005). Effects of biodiversity on ecosystem  
428 functioning: A consensus of current knowledge. *Ecological Monographs*, 75, 3-35.
- 429 Hughes, A.R., Byrnes, J.E., Kimbro, D.L. & Stachowicz, J.J. (2007). Reciprocal relationships  
430 and potential feedbacks between biodiversity and disturbance. *Ecology Letters*, 10,  
431 849-864.
- 432 Jentsch, A., Kreyling, J., Boettcher-Treschkow, J. & Beierkuhnlein, C. (2009). Beyond  
433 gradual warming: extreme weather events alter flower phenology of European  
434 grassland and heath species. *Global Change Biology*, 15, 837-849.
- 435 Klapp, E. (1971) *Wiesen und Weiden, eine Grünlandlehre*. Hamburg, Parey, Berlin.
- 436 Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P, Thompson, K., Sonnenschein, M.,  
437 Poschlod, P., Van Groenendael, J.M., Klimes, L., Klimesová, J., Klotz, S., Rusch,  
438 G.M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels,  
439 P., Götzenberger, L., Hodgson, J.G., Jackel, A-K., Kühn, I., Kunzmann, D., Ozinga,  
440 W.A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg,  
441 O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E. & Peco, B. (2008).  
442 The LEDA Traitbase: A database of life-history traits of Northwest European flora.  
443 *Journal of Ecology* 96, 1266-1274.
- 444 Kohler, F., Gillet, F., Reust, S., Wagner, H.H., Gadallah, F., Gobat, J.M. & Buttler, A.  
445 (2006a). Spatial and seasonal patterns of cattle habitat use in a mountain wooded  
446 pasture. *Landscape Ecology*, 21, 281-295.

- 447 Kohler, F., Gillet, F., Gobat, J.M. & Buttler, A. (2006b). Effect of cattle activities on gap  
448 colonization in mountain pastures. *Folia Geobotanica*, 41, 289-304.
- 449 Lauber, K. & Wagner, G. (2007). *Flora Helvetica. Flore illustrée de Suisse*. 2<sup>nd</sup> Edition.  
450 Belin.
- 451 Marion, B., Bonis, A. & Bouzille, J.B. (2010). How much does grazing-induced heterogeneity  
452 impact plant diversity in wet grasslands? *Ecoscience*, 17, 229-239.
- 453 Mariotte, P., Buttler, A., Johnson, D., Thébault, A. & Vandenberghe, C. (2012a). Exclusion of  
454 root competition increases competitive abilities of subordinate plant species through  
455 root-shoot interactions. *Journal of Vegetation Science*, 23, 1148-1158.
- 456 Mariotte, P., Meugnier, C., Johnson, D., Thébault, A., Spiegelberger, T. & Buttler, A.  
457 (2012b). Arbuscular mycorrhizal fungi reduce the differences in competitiveness  
458 between dominant and subordinate plant species. *Mycorrhiza*, DOI: 10.1007/s00572-  
459 012-0465-8. In press.
- 460 Mariotte, P., Vandenberghe, C., Meugnier, C., Rossi, P., Bardgett, R.D. & Buttler, A.  
461 (2013a). Subordinate plant species impact on soil microbial communities and  
462 ecosystem functioning in grasslands: findings from a removal experiment.  
463 *Perspectives in Plant Ecology, Evolution and Systematics*, DOI:  
464 10.1016/j.ppees.2012.12.003. In press.
- 465 Mariotte, P., Vandenberghe, C., Kardol, P., Hagedorn, F. & Buttler, A. (2013b). Subordinate  
466 species enhance community resistance against drought in semi-natural grasslands.  
467 *Journal of Ecology*, DOI: 10.1111/1365-2745.12064. In press.
- 468 Mayer, R., Kaufmann, R., Vorhauser, K. & Erschbamer, B. (2009). Effects of grazing  
469 exclusion on species composition in high altitude grasslands of the Central Alps.  
470 *Basic and Applied Ecology*, 10, 447–455.
- 471 Odum, E.P. (1963). *Ecology*. Holt, Rinehart & Winston, New York.

- 472 Parolo, G., Abeli, T., Gusmeroli, F. & Rossi, G. (2011). Large-scale heterogeneous cattle  
473 grazing affects plant diversity and forage value of Alpine species-rich *Nardus*  
474 pastures. *Grass and Forage Science*, 66, 541-550.
- 475 R Development Core Team (2011) R: A Language and Environment for Statistical  
476 Computing. R Foundation for Statistical Computing, Vienna, Austria.
- 477 Sebastià, M.T., De Bello, F., Puig, L. & Taull, M. (2008). Grazing as a factor structuring  
478 grasslands in the Pyrenees. *Applied Vegetation Science*, 11, 215-222.
- 479 Silva, J.P., Toland, J., Jones, W., Eldridge, J., Thorpe, E. & O'Hara, E. (2008). *LIFE and*  
480 *Europe's grasslands: restoring a forgotten habitat*. Luxembourg: European  
481 Communities.
- 482 Spiegelberger, T., Matthies, D., Müller-Schärer, M. & Schaffner, U. (2006). Scale-dependent  
483 effects of land use on plant species richness of mountain grassland in the European  
484 Alps. *Ecography*, 29, 541-548.
- 485 Tahmasebi Kohyani, P., Bossuyt, B., Bonte, D. & Hoffmann, M. (2009). Differential  
486 herbivory tolerance of dominant and subordinate plant species along gradients of  
487 nutrient availability and competition. *Plant Ecology*, 201, 611-619.
- 488 Tasser, E. & Tappeiner, U. (2002). Impact of land use changes on mountain vegetation.  
489 *Applied Vegetation Science*, 5, 173-184.
- 490 Vandenberghe, C., Frelechoux, F. & Buttler, A. (2008). The influence of competition from  
491 herbaceous vegetation and shade on simulated browsing tolerance of coniferous and  
492 deciduous saplings. *Oikos*, 117, 415-423.
- 493
- 494
- 495
- 496

497 **Figures**

498

499 Fig. 1. Relationships between site productivity (mean biomass production) and (A) the species  
500 diversity (mean species number per site), (B) the proportion of dominant species, (C) the  
501 proportion of subordinate species, and (D) the proportion of transient species for eleven semi-  
502 natural grassland sites. Curves represent significant polynomial models fitted to the  
503 relationships.

504

505 Fig. 2. Relationship between species diversity in grazed plots and (A) species diversity (mean  
506 species number per plot) in abandoned plots, (B) difference in number of dominant species,  
507 (C) difference in number of subordinates, and (D) difference in number of transients in  
508 abandoned plots compared to grazed plots for nine semi-natural grassland sites. Polynomial  
509 curves represent the significant models fitting the relationships. Straight lines indicate neutral  
510 effects of abandonment.

511

512

513

514

515

516

517

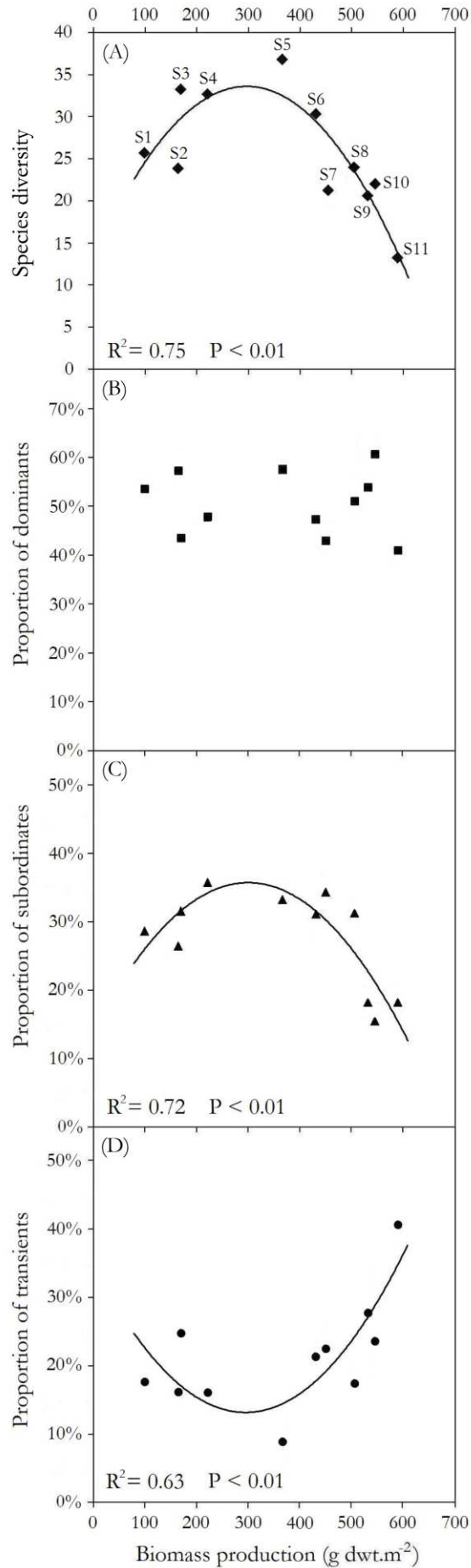
518

519

520

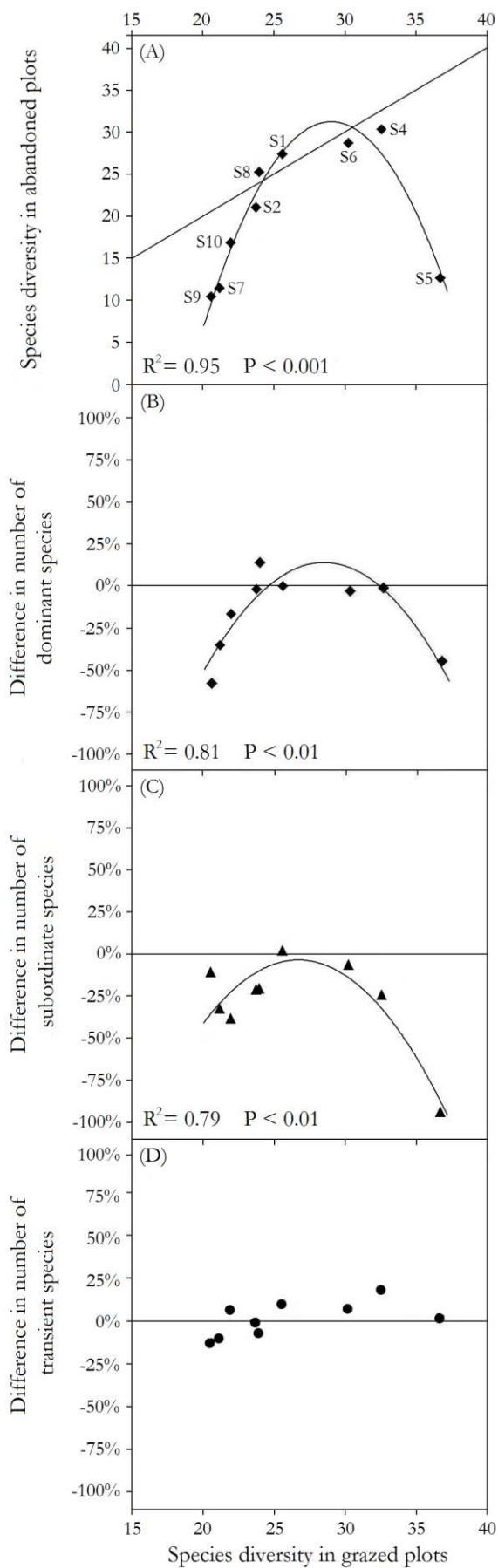
521

522 **Fig.1**



547 **Fig. 2**

548  
549  
550  
551  
552  
553  
554  
555  
556  
557  
558  
559  
560  
561  
562  
563  
564  
565  
566  
567  
568  
569  
570  
571





572 **Appendix A. Supplementary data**

573 Appendix A: Table 1. General description of the study sites ordered by increasing  
 574 productivity. In site 5, 8 and 9, the first altitude corresponds to grazed communities and the  
 575 second to abandoned communities. DIN (= Dissolved inorganic nitrogen).

Code	Site	Region	Altitude (m)	Community aboveground biomass (g dwt/m <sup>2</sup> ) and year of sampling	Soil fertility (DIN in µg/g dry soil)	Cattle density (per ha)	Dominant species	Analysis	Duration of abandonment (years)	References
1	Orvin	Jura, CH	1210	99 ± 7 (2002)	-	0.8	<i>Festuca nigrescens</i> , <i>Dactylis glomerata</i> , <i>Luzula sylvatica</i> , <i>Geranium sylvaticum</i>	A, B	3	Kohler et al. 2006a,b
2	Chablais	Alps, FR	1470	164 ± 15 (2004)	12.5 ± 1.7	1	<i>Festuca nigrescens</i> , <i>Cynosurus cristatus</i> , <i>Deschampsia caespitosa</i> , <i>Taraxacum officinale</i>	A, B	5	Spiegelberger et al. 2006
3	La Frétaz	Jura, CH	1200	169 ± 10 (2004)	-	0.9	<i>Festuca nigrescens</i> , <i>Agrostis capillaris</i> , <i>Taraxacum officinale</i> , <i>Dactylis glomerata</i>	A	-	Vandenberghé et al. 2008
4	Métairie d'Evillard	Jura, CH	1210	221 ± 16 (2002)	-	0.8	<i>Festuca nigrescens</i> , <i>Agrostis capillaris</i> , <i>Trifolium repens</i> , <i>Alchemilla monticola</i>	A, B	3	Kohler et al. 2006ab
5	Bauges	Alps, FR	1607-1755	366 ± 14 (2004)	22.2 ± 1.6	0.8	<i>Festuca nigrescens</i> , <i>Agrostis capillaris</i> , <i>Anthoxanthum odoratum</i> , <i>Arnica montana</i>	A, B	5	Spiegelberger et al. 2006
6	Le Haut des Joux	Jura, CH	1240	431 ± 17 (2002)	-	0.8	<i>Festuca nigrescens</i> , <i>Agrostis capillaris</i> , <i>Trifolium repens</i> , <i>Alchemilla monticola</i>	A, B	3	Kohler et al. 2006a,b
7	Les Amburnex	Jura, CH	1300	455 ± 29 (2011)	-	0.8	<i>Festuca nigrescens</i> , <i>Agrostis capillaris</i> , <i>Trifolium repens</i> , <i>Taraxacum officinale</i>	A, B	4	Mariotte et al. 2012a,2013a
8	Chablais	Alps, CH	1409-1517	506 ± 29 (2004)	27.3 ± 3.8	0.9	<i>Festuca nigrescens</i> , <i>Cynosurus cristatus</i> , <i>Poa pratensis</i> , <i>Taraxacum officinale</i>	A, B	5	Spiegelberger et al. 2006
9	Lac de Dix	Alps, CH	1507-1646	546 ± 99 (2004)	27.5 ± 2.9	0.8	<i>Festuca nigrescens</i> , <i>Cynosurus cristatus</i> , <i>Trifolium repens</i> , <i>Agrostis capillaris</i>	A, B	5	Spiegelberger et al. 2006
10	La Frétaz	Jura, CH	1200	532 ± 33 (2011)	-	0.9	<i>Festuca nigrescens</i> , <i>Cynosurus cristatus</i> , <i>Trifolium repens</i> , <i>Taraxacum officinale</i>	A, B	4	Mariotte et al.2013b
11	Früebüel	Alps, CH	980	590 ± 77 (2005)	-	-	<i>Festuca nigrescens</i> , <i>Allopecurus pratensis</i> , <i>Phleum pratense</i> , <i>Rumex acetosa</i>	A	-	Gilgen & Buchmann 2009

597 Appendix A: Figure 1. Frequency-proportion curve used for the selection of competitive  
598 hierarchical groups. Dominant and subordinate species are always present in the community  
599 and was distinguished from transient species (3), which do not persist in the vegetation, by a  
600 frequency higher than 50%. The distinction between dominant (1, grey area) and subordinate  
601 species (2, darkgrey area) is based upon cumulative proportion (%) and has been set at an  
602 arbitrary value of 12%.

603

604

605

606

607

608

609

610

611

612

613

614

615

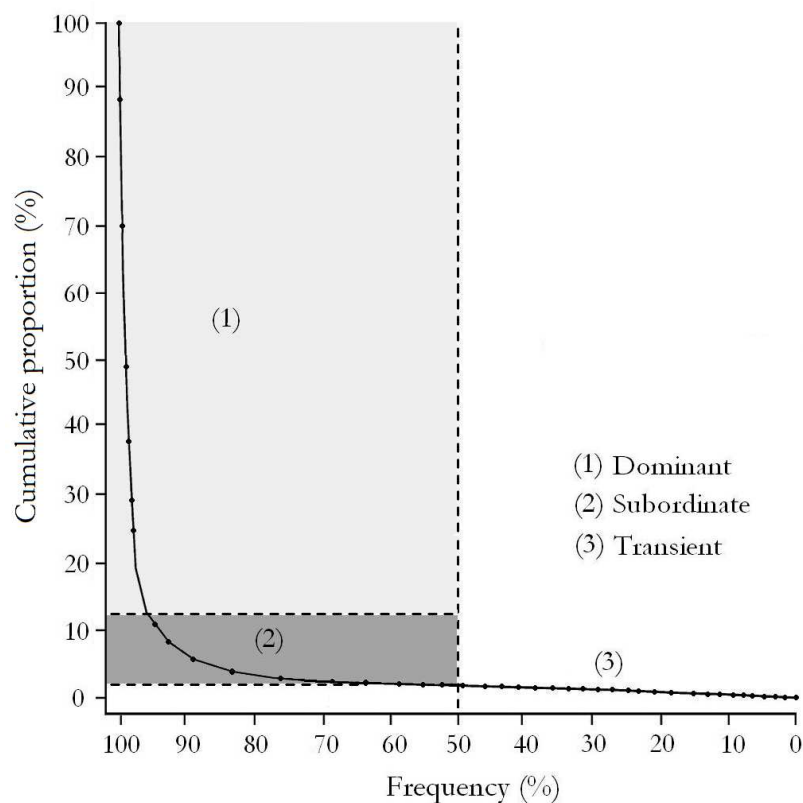
616

617

618

619

620



621 Appendix A: Figure 2. Relationship between the diversity (mean species number per plot) and  
622 the productivity (mean biomass production per plot) of abandoned plots in 9 sites of semi-  
623 natural grasslands. No significant linear ( $F_{1,7} = 0.766$ ,  $P = 0.41$ ,  $R^2 = 0.10$ ) or polynomial  
624 model ( $F_{2,6} = 0.332$ ,  $P = 0.73$ ,  $R^2 = 0.09$ ) was found to link diversity and productivity.

625

626

627

