Non-random recruitment of invader species in experimental grasslands.

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Abstract

To assess potential effects of seed limitation, characteristics of invader species and characteristics of established plant communities on recruitment success, we conducted a split-plot experiment factorially combining three weeding treatments corresponding to increasing successional age (regular weeding < cessation of weeding after three years < never weeded since sowing) with two seed limitation treatments (control vs sowing a seed mixture of all experimental species = internal invaders) in experimental grasslands varying in species richness (1, 2, 4, 8, 16) and in functional group richness and composition (1, 2, 3, 4 functional groups: presence/absence of legumes x grasses x tall herbs x small herbs). Seed addition increased internal invader seedling densities and the probability of successful colonization per species. Legumes, tall herbs and species with large and long-lived seeds or a requirement for specific vectors for pollination and dispersal benefited from seed addition most. The number of successfully established internal invader species was highest in plots with low initial species richness and in the regularly weeded treatments and lowest in plots with high initial species richness and in the never weeded treatments, indicating decreased recruitment with increased successional age. Resident plant communities with legumes had mostly negative (legume and small- and tall-herb internal invaders, external invaders) or neutral (grass invaders) effects on seedling density and colonization probability of invader species whereas resident communities with grasses had positive effects on the colonization probability of invader species except grasses themselves. These results show that seed limitation, invader characteristics, and community characteristics all can affect recruitment success in predictable ways, suggesting non-random community assembly during succession starting from different initial species pools.

1   **Non-random recruitment of invader species in experimental grasslands**

2

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17   **MS details:** 263 words in abstract, 7419 words in full text, 5 figures, 4 tables, Supplementary

18   Material

19

20 **Abstract**

21 To assess potential effects of seed limitation, characteristics of invader species and

22 characteristics of established plant communities on recruitment success, we conducted a split-

23 plot experiment factorially combining three weeding treatments corresponding to increasing

24 successional age (regular weeding < cessation of weeding after 3 years < never weeded since

25 sowing) with two seed limitation treatments (control vs. sowing a seed mixture of all

26 experimental species = internal invaders) in experimental grasslands varying in species

27 richness (1, 2, 4, 8, 16) and in functional group richness and composition (1, 2, 3, 4 functional

28 groups: presence/absence of legumes × grasses × tall herbs × small herbs). Seed addition

29 increased internal invader seedling densities and the probability of successful colonization per

30 species. Legumes, tall herbs and species with large and long-lived seeds or a requirement for

31 specific vectors for pollination and dispersal benefited most from seed addition. The number

32 of successfully established internal invader species was highest in plots with low initial

33 species richness and in the regularly weeded treatments and lowest in plots with high initial

34 species richness and in the never weeded treatments, indicating decreased recruitment with

35 increased successional age. Resident plant communities with legumes had mostly negative

36 (legume and small- and tall-herb internal invaders, external invaders) or neutral (grass

37 invaders) effects on seedling density and colonization probability of invader species whereas

38 resident communities with grasses had positive effects on the colonization probability of

39 invader species except grasses themselves. These results show that seed limitation, invader

40 characteristics, and community characteristics all can affect recruitment success in predictable

41 ways, suggesting non-random community assembly during succession starting from different

42 initial species pools.

43 **Introduction**

44 The accelerated loss of species from ecosystems has motivated intensive research on

45 biodiversity–ecosystem functioning relationships (Hooper et al. 2005). A deeper insight into

46 the mechanisms that control community assembly, stability and resistance against invasion

47 are a prerequisite for understanding biodiversity and its effects on ecosystems. The ability of a

48 species to invade into a particular plant community is influenced by several factors: number

49 of available propagules (propagule pressure; seed limitation), invader characteristics, and

50 characteristics of the invaded plant community (Crawley et al. 1996, Lonsdale 1999, Shea and

51 Chesson 2002). A number of experimental studies have shown that invasibility is correlated

52 with the availability of unutilized resources such as nutrients and water by the resident species

53 in a community (e.g. Burke and Grime 1996, Davis et al. 2000, Thompson et al. 2001,

54 Houseman and Gross 2006). In addition to such environmental effects, there is an increasing

55 number of experimental studies supporting Elton`s hypothesis (Elton 1958) that communities

56 with high species diversity are more invasion-resistant. In contrast, some observational

57 studies reported positive relationships between the number of native and invasive exotic

58 species in natural plant communities, indicating that high native species richness may

59 promote the invasion of exotic species (see reviews in Herben et al. 2004, Fridley et al. 2007).

60 [Dieser Absatz ist so schwer zu sehen, kann man was machen dagegen?]

61 Niche differentiation among species has been suggested as main cause for a more complete

62 use of available resources in more diverse communities and thus higher invasion resistance

63 (complementarity effect). However, it also had been hypothesized that in experimental

64 communities, created by sowing different numbers of species, the probability to include a

65 particular invasion-suppressive resident species increases with a larger number of sown

66 species (sampling effect, Wardle 2001). Although experimental studies gave evidence that

67 both mechanisms can increase community invasion resistance (e.g. Levine and D`Antonio

68   1999, Fargione and Tilman 2005), it is still unclear if they affect the recruitment success of

69   different invader species in similar or different ways. Based on the "limiting similarity"

70   theory (Hutchinson 1959, MacArthur and Levins 1967, Abrams 1983) and rules of

71   community assembly (Fox 1987) it has been proposed that species already present in a

72   community suppress the recruitment of functionally similar species (Fargione et al. 2003,

73   Tilman 2004, Von Holle and Simberloff 2004), but results from experimental studies do not

74   consistently support this hypothesis (e.g. Symstad 2000, Emery 2007). Priority effects (Drake

75   1991) due to the sequence of species arrival may also affect recruitment and thus assembly

76   processes (e.g. Fukami et al. 2005) and final community composition and species richness

77   (Chase 2003) [Hier ev. noch Körners neues Paper in New Phytologist (?) zitieren?]. Finally

78   and obviously, only species whose propagules reach a community are potential invaders.

79   Accordingly, low propagule pressure, i.e. seed limitation, may also reduce recruitment

80   success of invader species (Kolar and Lodge 2001).

81   Here, we present results from an experiment which we designed to analyse the contributions

82   of seed limitation, characteristics of the invader species (species invasiveness), and

83   characteristics of the invaded community (community invasibility) to xxxx. We used a split-

84   plot approach where invasion treatments were factorially crossed with species richness and

85   functional group composition treatments in a large-scale biodiversity experiment (Jena

86   Experiment; Roscher et al. 2004). Our invasion treatments consisted of two crossed factors,

87   one simulating different successional ages of communities (regular weeding < cessation of

88   weeding 3 years after sowing < never weeded since sowing) and the other simulating presence

89   / absence of seed limitation (control vs. seed addition 4 years after sowing). We assessed the

90   effects of seed limitation, species invasiveness and community invasibility on the recruitment

91   success of all species belonging to the species pool of the experiment. Specifically, we wanted

92   to assess whether (i) seed limitation, (ii) the functional group or dispersial-related traits of the

93   invader species, (iii) initial species or functional group richness of resident species and

94   presence of particular functional groups of resident species in the invaded community, or (iv)

95   simulated age of the invaded community affect seed germination, density and subsequent

96   establishment of invader species. Points (iii) and (iv) could also be assessed for species which

97   did not belong to the species pool of the experiment (external invaders) but which invaded

98   spontaneously.

99

100   **Materials and methods**

101

102   **Site description and experimental design**

103   The study was implemented as part of the Jena Experiment, a large integrated biodiversity

104   experiment to investigate relationships between plant community diversity and ecosystem

105   functioning (Roscher et al. 2004). The experimental site is located in the floodplain of the

106   river Saale near the city of Jena (Thuringia, Germany, $50^o55'$ N, $11^o35'$ E, 130 m a.s.l.). The

107   area around Jena has a mean annual air temperature of 9.3 °C and mean annual precipitation

108   of 587 mm (Kluge and Müller-Westermeier 2000). The soil is a Eutric Fluvisol developed

109   from up to 2 m thick fluvial sediments that are almost free of stones. Due to fluvial dynamics,

110   the soil texture ranges from sandy loam in the vicinity of the river to silty clay with increasing

111   distance from the river. The site was used as fertilized agricultural field for more than 40

112   years prior to the establishment of the biodiversity experiment in 2002.

113   The compilation of a species pool for the experiment was based on species composition of

114   semi-natural Central European mesophilic grasslands typically mown twice a year

115   (Arrhenatherion alliance according to the vegetation classification of Ellenberg 1988). In

116   total, 60 species were chosen and categorized into four functional groups following the results

117   of a cluster analysis of a matrix of morphological and ecological traits (Roscher et al. 2004):

118 grasses (16 species), legumes (12 species), small herbs (12 species) and tall herbs (20

119 species). The Jena Experiment has a near-orthogonal design realizing all possible

120 combinations of the experimental factors species richness (from 1, 2, 4, 8 to 16 species) and

121 functional group richness (from 1, 2, 3, to 4 functional groups) as equal as possible with the

122 unavoidable restriction that functional group richness of a mixture cannot exceed species

123 richness. At each species-richness level, 16 replicates with different species compositions

124 were established, except for the 16-species level with only 14 replicates, because in two cases

125 species numbers within functional groups (legumes, small herbs) were too low to establish

126 16-species mixtures with species from only one functional group. Species for each mixture

127 were selected randomly with replacement. In total, 78 plots with a plot size of 20×20 m were

128 established. An even number of plots per species-richness level was assigned randomly to

129 four experimental blocks located parallel to the river. Blocking accounted for soil

130 heterogeneity, but management of the experiment and data collection was also organized

131 block-wise.

132 Seeds for the experiment were purchased from commercial suppliers. The anticipated initial

133 sowing density was 1000 viable seeds per m^2 distributed equally among species following a

134 substitutive design (Joliffe 2000). Preliminary tests under standardized temperature and light

135 regime (16 h day at 20 °C and a night temperature of 12 °C) served to determine germination

136 rates and to adjust seed numbers. Fifty seeds were placed in Petri dishes (three replicates per

137 species) on moistened filter paper and checked every second day over a period of 50 days.

138 Seeds of several legume species (*Lathyrus pratensis*, *Lotus corniculatus*, *Medicago lupulina*,

139 *Trifolium campestre*, *T. dubium*, *Vicia cracca*) and *Geranium pratense* were scarified, and

140 seeds of *Ajuga reptans*, *Carum carvi*, *Cirsium oleraceum*, *Pastinaca sativa*, *Pimpinella*

141 *major*, *Primula veris*, *Ranunculus acris* and *R. repens* were pre-treated with gibberellic acid

142 (500 mg l^{-1}, 24 h) to break dormancy prior to germination tests as well as for seed addition in

143   the field. All plots were sown from 11-16 May 2002 (for further details see Roscher et al.

144   2004).

145   Three pairs of 2.00×2.25 m subplots were established at the margin of each main plot

146   (excluding the outer 50 cm). The pairs were separated by 0.3 m distance from each other. One

147   pair of subplots was never weeded since the establishment of the experiment in 2002, and two

148   pairs of subplots were weeded regularly twice a year. One pair of the regularly weeded

149   subplots was selected randomly to stop weeding three years after the establishment of the

150   experiment. At the same time, one subplot of each weeding treatment was chosen at random

151   for seed addition, resulting in the following treatments:

152   (i)   regular weeding treatment, no seed addition (w-),

153   (ii)   regular weeding treatment, seed addition (w+),

154   (iii)   cessation of weeding after three years, no seed addition (c-),

155   (iv)   cessation of weeding after three years, seed addition (c+),

156   (v)   late succession treatment, never weeded, no seed addition (s-), and

157   (vi)   late succession treatment, never weeded, seed addition (s+).

158   A mixture containing seeds of all species of the experimental species pool at equal

159   proportions was assembled for the seed addition treatment. Aimed sowing density amounted

160   to 1000 viable seeds per m^2. The usage of the same seed mixture for all plots irrespective of

161   plot species number and composition ensured that each potential internal invader was sown

162   with equal density in all plots, but reduced the number of sown invader seeds with increasing

163   species richness (e.g. 938 seeds out of 1000 seeds sown per m^2 were potential invaders in

164   monocultures, but only 733 out of 1000 were potential invaders in 16-species mixtures). Seed

165   material was prepared following the same protocol as used during the establishment of the

166   plots in 2002 including viability tests, pre-treatments of seeds and adjustment for germination

167   rates. All subplots were sown from 13-18 April 2005. Seeds were mixed with groats of soya

168   as bulking agent to guarantee an even distribution of seeds over the subplot area because of

169   highly heterogeneous seed shapes and sizes. Groats of soya only were distributed in subplots

170   without seed addition treatment. The topsoil was scratched slightly, a border was placed

171   around the subplots during sowing to avoid drift into neighboring subplots and after hand-

172   sowing the surface was raked to ensure that no seed material get caught on the established

173   vegetation.

174   Plots of the regular weeding treatment were weeded twice a year in early April and July. In

175   the seed addition treatment, only species not belonging to the experimental species pool (=

176   external invaders) were weeded, while all species not belonging to the originally sown species

177   combinations were removed in the subplot without seed addition. All plots were mown twice

178   a year (early June, September) and the mown plant material was removed.

179

180   **Data collection**

181   All seedlings (plant individuals with cotyledons) were determined to species level as far as

182   possible and counted twice in 2005 (early July after first mowing, early October after second

183   mowing) and three times in 2006 (early April, July, October). In each subplot, three quadrats

184   of 30 × 30 cm size per subplot were placed at random positions for each census of all

185   seedlings present in each time period. All counts were summed up to account for temporal

186   differences among species to germinate and seedling densities per m^2 were calculated for each

187   subplot, although we are aware that it is not possible to quantify the number of emerging

188   seedlings exactly with this schedule because we cannot exclude completely that further

189   seedlings appeared in between (underestimation of seedling densities) or that seedlings

190   persevered for a longer period in this stage (overestimation of seedling densities). Species

191   inventories based on cover estimates with a modified Londo scale (Londo 1976) were made

192   four times a year in 2006, before weeding (early April, July) and before mowing (at estimated

193   peak biomass: May, August). Occurrences of each species in each subplot were pooled over

194   all census dates in 2006 to assess established invader species numbers per treatment one year

195   after seed addition. These numbers were used to calculate the proportion of successfully

196   invaded plots per species as well as the proportion of invader species per functional group,

197   excluding those species that already occurred as residents in the originally sown plant

198   communities. This allowed us to account for the fact that the number of potential internal

199   invaders decreased with increasing plant species richness.

200

201   **Data analyses**

202   For all analyses we used the statistical software R 2.6.2 (R Development Core Team 2005).

203   Data on invader seedling densities and species numbers (separated into external and internal

204   invader species), seedling numbers and proportions of established invader species per

205   functional group of internal invaders were analysed with general linear models. Proportion

206   data were arcsine-square root transformed, and count data were log-transformed in most cases

207   to account for heteroscedasticity and non-normality of errors. The Jena Experiment has a

208   factorial design based on different levels of species and functional group richness. The design

209   is not fully balanced because it is not possible to vary species and functional group numbers

210   completely independently (e.g. functional group number cannot be higher than species

211   number in a given plant community). Analysis of variance with sequential sum of squares

212   (type I sum of squares) allows for assessing the effects of the experimental factors on a

213   response variable although changing the order of terms in these models may affect the

214   outcome of data analysis (Schmid et al. 2002). Analysis was based on the split-(split-)plot

215   design with weeding treatments as split-plot factor to be tested at the level of subplot pairs

216   and seed addition treatments as split-split-plot factor to be tested at the level of subplots, both

217   factorially crossed with each other and with the main-plot factors of species and functional-

218   group richness mentioned above. In all analyses, we fitted block first. In the following steps

219   we entered the experimental factors of the main experiment, e.g. sown species number (log-

220   linear) and functional group number (linear), followed by factors for the split-plot variables

221   weeding treatment and seed addition and their interactions with the main experimental

222   factors. Separate models were calculated to test for effects of particular functional groups

223   (presence/absence of legumes, grasses, tall herbs and small herbs).

224   Binary data on the occurrence of each internal invader species were analysed with generalized

225   linear mixed-effects models using the *lmer* function in the R package LME4 (Bates and Saker

226   2006) because of the unbalanced occurrence of species in the experimental plots that violates

227   the assumption of independence of errors. Plots where a particular species already belonged to

228   the originally sown species composition were excluded in analyses of individual invader

229   species because newly arriving invaders could not be differentiated from established plants of

230   the same species. Stepwise series of models with a binomial error distribution were fitted

231   including the above-mentioned treatments as fixed effects and block, plot and subplot pair as

232   random effects in a nested sequence. Chi-square statistics were used to assess model

233   improvement and the statistical significance of the fixed effects.

234   To get further insight into which traits allow species to be successful invaders or may indicate

235   source- or dispersal-limitation of recruitment (Clark et al. 2007), we compiled a matrix of

236   species characteristics supposed to be relevant for invasion based on literature (Fitter and Peat

237   1994; http://www.ecoflora.co.uk: time of germination; Rothmaler 2002: mechanisms of

238   pollination and dispersal, flowering phenology, seed longevity, germination requirements as

239   chilling and light) and our own measurements (seed mass). Spearman rank correlations were

240   calculated to test for relationships between the selected plant traits and species invasion

241   probability either spontaneously or the increment after seed addition and the dependence of

242   invasion probability on the occurrence of particular functional groups (difference between

243   invasion probability in plots with a particular functional group and without this functional

244   group) in the resident communities. We restricted these analyses to internal invaders because

245   the inclusion of external invaders would be biased by a lack of knowledge about the

246   occurrence of potential unsuccessful invaders, i.e. species with available propagules that

247   never became established. In contrast, the seed addition/non-seed addition treatment of

248   internal invaders allowed us to assess the relative role of propagule availability.

249

250   **Results**

251

252   **Invader seedling density**

253   Averaged over all three weeding treatments, seedlings were made up of 82 % internal and

254   18 % external invader seedlings. Seedlings of two invader species were particularly frequent

255   and together made up about 73 % of all internal invader seedlings (*Taraxacum officinale*

256   43 %, *Poa trivialis* 30 %). Therefore, we analysed these species separately. Seedling densities

257   of the other internal invader species were pooled for analyses because no species contributed

258   more than 5 % to the total number of recorded internal invader seedlings.

259   Both seedling densities of pooled internal and external invaders as well as seedling densities

260   of *T. officinale* and *P. trivialis* decreased with a log-linear increase of originally sown species

261   in the experimental communities (Table 1, Fig. 1). While the presence of particular functional

262   groups among the originally sown species did not affect seedling densities of external

263   invaders, significantly fewer internal invader seedlings emerged in communities containing

264   legumes among the residents. Higher numbers of internal invader seedlings were counted in

265   communities with resident tall herbs. In contrast, the presence of legumes among the residents

266   had positive effects and the presence of resident grasses had negative effects on seedling

267   densities of *T. officinale* and *P. trivialis*. Seedling densities of external invaders and

268   *T. officinale* increased with successional age and were highest in the never weeded subplots,

269   but seedling densities of *P. trivialis* and the remaining pooled internal invader species were

270   not significantly different among weeding treatments.

271   Seed addition did not affect seedling densities of the most frequent internal invaders

272   *T. officinale* and *P. trivialis*, but had positive effects on seedling densities of internal invader

273   seedlings in total. Sown species richness of the recipient communities did not influence the

274   effects of seed addition on seedling densities of internal invaders (non-significant interaction

275   "SR (log-linear) × ADD") although the number of added invader seeds decreased slightly in

276   plots of originally higher species richness (see "Material and methods"). The positive effect of

277   seed addition on internal invader seedling densities varied among weeding treatments (see

278   interaction "WT × ADD"). Separate analyses indicated that seed addition had positive effects

279   on the number of internal invader seedlings in the regularly weeded subplots only ($F_{1,75}$ =

280   40.33, p < 0.001). There was no effect of seed addition on internal invader seedling densities

281   in the treatment where weeding was stopped after three years ($F_{1,75}$ = 0.87, p = 0.354) and in

282   the never weeded treatment ($F_{1,75}$ = 0.16, p = 0.695). Seed addition (of internal invaders) had

283   negative effects on seedling densities of external invaders, and these negative effects were

284   more pronounced in communities of originally low species richness (significant interaction

285   "SR (log-linear) × ADD", Table 1).

286   Internal invader seedling densities per functional group (after exclusion of *T. officinale* and

287   *P. trivialis* in the respective functional groups) decreased in three functional groups (invading

288   grasses, small herbs and tall herbs) with increasing number of originally sown species in the

289   recipient plant communities, while seedling density of invading legumes did not depend on

290   species richness of the originally sown plant communities (Table 1). Seed addition had

291   positive effects on invader seedling densities in all functional groups and increased

292   particularly densities of legume and tall herb invader seedlings (Fig. 1). In addition, the

293   presence of species of their own functional group in the resident plant communities

294   diminished seedling densities of invading legumes and grasses, while similar effects did not

295   occur in both groups of non-legume herbs. However, the presence of legumes in the recipient

296   communities also reduced seedling density of invading non-legume small and tall herbs.

297   Density of legume invader seedlings was increased in communities with resident grasses,

298   while we found positive effects of resident tall herbs on densities of emerging grass and small

299   herb invader seedlings (Table 1).

300

301   **Invader species richness**

302   One year after the establishment of the split-plot experiment combining different weeding and

303   seed addition treatments, the number of established internal and external invader species

304   decreased with a log-linear increase of resident species richness (Table 2, Fig. 2). Increasing

305   functional group richness of the resident communities fitted after species richness tended to

306   have additional negative effects on the number of established internal and external invader

307   species. The presence of resident legumes affected species numbers of both internal and

308   external invader species negatively, while the presence of resident grasses and tall herbs in the

309   originally sown communities had positive effects on the number of internal invader species.

310   The effect of weeding treatments on species numbers of internal invaders depended on the

311   number of originally sown species, while we generally observed more external invader

312   species in regularly weeded subplots (significant contrast for the regular weeding treatment

313    $F_{1,150} = 4.87$, $p = 0.029$). Seed addition increased average numbers of internal invader species

314   from 9 ($\pm$ 4 s.d.) to 21 ($\pm$ 9 s.d.) per subplot. Seed addition was particularly efficient in plant

315   communities of originally low species richness (significant interaction "SR (log-linear) $\times$

316   ADD"). The effect of seed addition differed to some degree among weeding treatments

317   (significant interaction "WT $\times$ ADD"; Table 2). The presence of resident legumes strongly

318   reduced the success of seed addition (significant interaction "LEG × ADD": $F_{1,225} = 23.59$,

319   $p < 0.001$), while we found positive effects of resident grasses on internal invader species

320   numbers after seed addition ("GRA × ADD": $F_{1,225} = 11.63$, $p = 0.001$). Additional analyses

321   (not shown) of species numbers of internal invader seedlings led to similar results and

322   confirmed that resident legumes and grasses influenced the number of germinating internal

323   invader species and that effects of these functional groups in the resident plant communities

324   were not a result of species interactions during later stages of plant individual development.

325   Seed addition reduced the number of external invader species from 8 (± 5 s.d.) to 7 (± 4 s.d.)

326   per subplot (averaged across all weeding treatments) irrespective of weeding treatments

327   (Table 2).

328

329   **Species-specific pattern of internal invaders**

330   Seed addition increased the invasion probability (= number of invaded plots) in all functional

331   groups of internal invader species (Table 3) and 49 out of 60 species (Appendix, Table S1).

332   Seed addition resulted in a higher invasion probability of all legume and non-legume herb

333   species (except for one small and two tall herbs) and 8 out of 16 grass species (Table S1).

334   However, the proportion of communities where species could invade successfully after seed

335   addition varied greatly (Fig. 3). While species invasion probability through spontaneous

336   invasion did not differ among functional groups (Kruskall-Wallis ANOVA: $H_3 = 2.69$, $p =$

337   0.441), seed addition increased the invasion probability of legumes and tall herbs more

338   strongly than that of grasses and small herbs ($H_3 = 12.71$, $p = 0.005$). Invasion probability of

339   legume invaders varied among weeding treatments, but the effect of weeding treatments on

340   invasion probability depended on the number of originally sown species in the resident

341   communities not only for legumes, but also for grass and tall herb invaders. The effect of seed

342   addition on invasion probability differed among weeding treatments in all functional groups

343   (Table 3) and in fourteen individual species (see significant interactions "WT × ADD" in

344   Table S1). Increasing species richness of the originally sown communities reduced invasion

345   probability in all functional groups and this was particularly evident in the seed addition

346   treatment (Table 3, Fig. 4). Per-species analyses showed that the invasion success of 24

347   internal invader species decreased with increasing resident species richness (Table S1).

348   Functional group richness of the resident communities fitted after species richness did not

349   lower invasion probability in any functional group and influenced only ten species negatively.

350   Analyses of functional group composition indicated that two particular functional groups,

351   resident grasses and legumes, affected the invasion probability of internal invaders, but their

352   effect varied depending on functional group identity of the invader species. The occurrence of

353   resident legumes had negative effects on the invasion probability of 28 internal invader

354   species, most of them legumes themselves or non-legume small and tall herbs (Table S1), and

355   on the proportion of successful invaders from these functional groups (Table 3, Fig. 5).

356   Resident grasses in the recipient communities had positive effects on the invasion probability

357   of 9 out of 13 legume species and 13 out of 32 non-legume herb species, respectively

358   (Table S1) and increased the proportion of invading legumes, as well as of invading non-

359   legume small and tall herbs (Table 3, Fig. 5). The proportion of invading grass species

360   (Table 3, Fig. 5) and the invasion probability of four grass species (Table S1) were

361   significantly reduced when the recipient plant community already contained grasses. The

362   proportion of invading small herbs increased in communities with resident tall herbs (Table 3,

363   Fig. 5). Analyses of cover values of invaders largely confirmed results from analyses of per-

364   species occurrences. Contrary to many internal invader species that were negatively affected

365   by resident legumes, the most successful invaders, *P. trivialis* and *T. officinale*, reached

366   particularly high cover abundances as invaders in plant communities with resident legumes.

367

Invasion success of internal invaders related to plant functional characteristics

Invasion probability without seed addition was higher for species with adhesive fruits. These species may be dispersed by small mammals such as common voles (*Microtus arvalis* L.) frequently occurring at the field site. Invasion probability also tended to be higher in wind-pollinated species. Spontaneous invasion was also positively correlated with germination immediately after seed release without specific germination requirements as for instance chilling (Table 4). The proportional increase of invasion success after seed addition was positively related with insect- and self-pollination, and negatively with wind-pollination. Species that benefited from seed addition often had heavier, long-lived seeds, did not depend on light during germination, flowered late in the growing season, and germinated in spring. Species for which negative effects of resident legumes on their invasion probability were less likely had short-lived seeds and a short flowering period restricted to early summer, did not need particular vectors for pollination and dispersal (wind pollination and dispersal), but depended on light availability during germination. Species with an increased invasion probability in plant communities with resident grasses had a longer flowering period, more specific requirements for pollination and dispersal (e.g. insect-pollination), needed more often a period with low temperatures for germination (chilling), but were not dependent on light for germination. Although traits describing requirements for pollination, dispersal and germination were often correlated with species assignment to particular functional groups (Table 4), species within functional groups differed in their specific combinations of these characteristics.

Discussion

Processes that determine community assembly and finally the composition and number of co-occurring plant species in a community have been discussed controversially (see Chase 2003).

393   Although it has been repeatedly suggested that the close interaction between characteristics of

394   potential invaders and those of the recipient community control the outcome of invasion

395   under similar environmental conditions, different assembly histories due to source- or

396   dispersal-limitation of particular species and different sequences of species arrival at potential

397   sites for invasion may result in a divergent community composition [Hier wäre es gut, wenn

398   du eine Schlüsselreferenz ("initial floristic composition"?) oder einige Beispielsreferenzen

399   angeben könntest.]. In this experiment we tested the effects of resident species and functional

400   group richness, presence/absence of particular functional groups of resident species and

401   successional age of experimental grasslands on number and identity of species that could

402   invade either spontaneously or after seed addition. We focused our analyses on the first year

403   after initiating the seed addition treatment because processes causing mortality at early life

404   cycle stages may disproportionally affect community composition, structure and dynamics.

405   A number of authors studying artificially assembled plant communities found negative effects

406   of species and functional group richness of residents on invasibility after seed addition (e.g.

407   Tilman 1997, Symstad 2000), although some of them also observed that the presence of

408   particular resident species is more important for community invasibility (Crawley et al. 1999,

409   van Ruijven et al. 2003). Several studies reported that introduced species were most strongly

410   inhibited in plant communities already containing species from the same functional group

411   among the resident species (Fargione et al. 2003, Turnbull et al. 2005, Mwangi et al. 2007).

412   While increasing resident species richness decreased the invasion probability of newly

413   arriving species in our study, the assumption that resident species prevent the invasion of

414   functionally similar species was only partly supported. Only resident grasses and legumes

415   reduced the successful invasion of further species of their own functional group. However, the

416   presence of particular functional groups generally either reduced (legumes: negative effects

417   on the invasion of legume and small- and tall-herb invaders) or increased (grasses: positive

418   effects on legume and tall- and small-herb invaders; tall herbs: positive effects on grass and

419   small-herb invaders) the invasion of other species. This contradicts in part previous studies of

420   spontaneously occurring invaders in the Jena Experiment during the first three years after

421   sowing, in which species numbers of external invaders were higher in communities with

422   resident legumes and lower in those with resident grasses, while resident legumes and grasses

423   did not affect species numbers of internal invaders (Roscher et al. 2009a). In addition, other

424   studies in the Jena Experiment have shown that transplanted individuals of species belonging

425   to the experimental species pool (*Rumex acetosa*: Scherber et al. 2006, *Plantago lanceolata*,

426   *Knautia arvensis*, *Festuca pratensis*, *Trifolium pratense*: Mwangi et al. 2007) had a higher

427   survival rate and achieved a better performance in plots with legumes, which had facilitative

428   effects on these transplants (Temperton et al. 2007), while resident grasses affected them

429   negatively.

430   The contrasting results of the seed addition experiment presented here could have several

431   reasons. We cannot exclude the possibility that invasibility of the experimental plots changed

432   with increasing age of the experiment. However, because we observed that the effects on

433   invasion resistance of the sown richness of resident species or the presence of particular

434   functional groups of resident species became stronger through time (Roscher et al. 2009a) it

435   seems more likely that differences in the available invader species pool caused our divergent

436   observations. Arable weeds were predominant external invaders, while *T. officinale* and

437   *P. trivialis* were the most frequent internal invaders during the first three years after sowing

438   (Roscher et al. 2009a). While the occurrence of external invaders emerging from the seed

439   bank became less important through time, we observed in the present study significantly

440   higher seedling densities of the most frequent internal invaders *T. officinale* and *P. trivialis* in

441   plots with legumes, which is in accordance with previous results. In contrast, resident legumes

442   generally had negative or neutral effects on seedling densities and species numbers of other

443   internal invaders. Since *Taraxacum officinale* and *P. trivialis* accounted for about 60 % of

444   invader seedlings in total and reached high cover abundances as invaders particularly in plots

445   with legumes, we included cover values of these species as covariates in analyses of other

446   internal invaders to appraise whether the observed negative effects of resident legumes are

447   indirectly due to competition with these particularly successful invaders. While the cover of

448   *T. officinale* as an invader generally did not influence the invasion probability of other

449   species, the cover of *P. trivialis* as an invader often correlated with a lower invasion

450   probability of other species. The negative effect of this grass invader may be due to its ability

451   to form dense swards via the production of numerous creeping shoots.

452   The negative effects of legumes among the resident species on the invasion of other species

453   may at least in part also be due to increased site fertility and plant productivity. Biodiversity

454   experiments have repeatedly shown that soil nitrate concentrations (Oelmann et al. 2007),

455   aboveground productivity and canopy density are increased when the experimental

456   communities contain legumes (e.g. Symstad et al. 1998, Spehn et al. 2000a). Although it is

457   known that germination of several species may be stimulated by nitrate (Pons 1989, Hilhorst

458   and Karssen 2000), seed germination may also be reduced by high soil fertility (Kitajima and

459   Tilman 1996). Seed addition experiments along fertility gradients have indicated that

460   "competitive filtering" prevents the establishment of new colonizers with increasing

461   productivity of the established vegetation (Foster et al. 2004, Stevens et al. 2004, Houseman

462   and Gross 2006). Increased root respiration in response to higher nutrient availability and

463   resulting higher CO_2 concentrations may inhibit germination of some species (Egley 1986,

464   Hilhorst and Karssen 2000).

465   Although seed addition reduced seed source and dispersal limitation of most species in our

466   experiment, secondary seed dispersal through horizontal and vertical seed movement or seed

467   predation may have operated as further control of plant seed survival and invader

468   establishment (Chambers and MacMahon 1994). Soil heterotrophic activity (e.g. earthworm

469   density, vole activity) is known to be increased in plots with legumes and decreased in those

470   with grasses (Spehn et al. 2000b, Milcu et al. 2008). Vertical transport of seeds in the soil and

471   increased seed mortality due to ingestion might cause lower seedling densities and species

472   numbers of invaders in communities with resident legumes, while we found opposite patterns

473   in communities with resident grasses. Effects of soil heterotrophic activity on invader

474   establishment as recently shown in experimental microcosms (Milcu et al. 2006, Eisenhauer

475   and Scheu 2008) are probable in our experiment. Species with long-lived seeds are more

476   prone to post-dispersal mortality through seed predation and species with specific

477   requirements for pollination and dispersal are more likely to be seed source- or dispersal-

478   limited (Clark et al. 2007). In particular, these species had a lower invasion probability in

479   plots with legumes in contrast to wind-pollinated or -dispersed species, as many grasses or

480   *T. officinale* are.

481   The invasion history of the experimental subplots affected invasibility to some degree, but not

482   very strongly. Whereas seedling densities of external invaders were higher in subplots that

483   were never weeded since sowing (longest invasion history), the effect of seed addition was

484   stronger in plots where spontaneously occuring invaders were removed before adding seeds in

485   spring 2005 (shortest invasion history). This result supports other studies showing that the

486   timing of arrival affects the process of invasion (Ejrnæs et al. 2006, Körner et al. 2008). In an

487   earlier study we have shown that species richness and relative abundances of sown species did

488   not vary between regularly and never weeded plots during the first three years of our

489   experiment (Roscher et al. 2009b). Thus, previously arrived spontaneous invaders apparently

490   reduced niche availability for the establishment of species after artificial seed addition in

491   subplots that were either never weeded or where weeding was stopped after three years

492   (intermediate length of invasion history). The findings that particular invader species had little

493   effect on the invasion of further species (see above) and that increasing successional age had

494   relatively minor effects on invasion (Table S1) suggest that community-specific effects (see

495   previous paragraphs) are more important in determining the recruitment success of invaders.

496   [Ich würde den Satz so oder ähnlich umstellen, damit er mehr als Diskussion denn als Resultat

497   wirkt.]

498   Although the establishment of seedlings is known to be a crucial life stage in plant population

499   ecology (Silvertown et al. 1993), the percentage of studies where introduced species became

500   adult is lower than those where seedlings have been observed after seed sowing (Harper 1977,

501   Turnbull et al. 2000). Seedlings from species with larger seeds usually have a better potential

502   for survivorship in established vegetation, but species with larger seeds often produce a

503   smaller number of seeds (Westoby et al. 1996) which are also less well dispersed (Turnbull

504   1999, Moles and Westoby 2002). Therefore, species with larger seeds are more likely to

505   establish successfully after seed addition (Turnbull et al. 2000, Moles and Westoby 2002). In

506   accordance with this, we found that species with higher seed mass benefitted more from seed

507   addition and thus removal of dispersal limitation than did species with lower seed mass.

508   Additionally, species that benefited from seed addition were often insect- or self-pollinated

509   instead of wind-pollinated, tended to have long-lived seeds and not to depend on light

510   availability during germination. [Der vorgehende Satz ist wieder zu Resultat-artig. Kannst du

511   ihn so umformulieren, dass er Diskussion wird, z.B. mit dem Hinweis, dass andere

512   Eigenschaften offensichtlich ebenfalls wichtig sind, obwohl wir keine Erklärungen dafür

513   haben? Reviewers könnten bösartig fragen, weshalb wir diese Merkmale untersucht haben,

514   ohne dafür eine Hypothese gehabt zu haben.]

515   In conclusion, although seed addition generally increased invader recruitment in our

516   experiment, seedling establishment was non-random among invading species or among

517   invaded communities. The often positive effects of resident grasses and the frequently

518 negative effects of resident legumes on invader establishment demonstrate that "limiting

519 similarity" among species was not the only driver of these patterns. It is conceivable that the

520 specificity of biotic interactions in the recipient communities modulated species invasion

521 success dependent on their seed characteristics. Thompson et al. (2001) reported that

522 generative plant traits (e.g. seed mass, germination characteristics) are important for a short-

523 term advantage as invaders, while over a longer course of succession these traits may not

524 serve as good predictors of invasiveness. Whether the beneficial effects of seed addition allow

525 for the establishment of viable invader populations and how invasion affects the structure of

526 the recipient community can only be assessed with a longer run of this experiment. However,

527 our study gave clear evidence for non-random processes during invader establishment caused

528 by the characteristics of the invaded communities and the invaders themselves that finally

529 may result in a divergent species number and composition of the newly assembled

530 communities.

531

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Figure captions

Figure 1: Invader seedling densities as a function of originally sown plant species richness. Values are arithmetic means per species-richness level (± s.e.) for subplots with and without seed addition averaged across weeding treatments based on the sum of five censuses in 2005/2006. *Poa trivialis* (grass) and *Taraxacum officinale* (small herb) were not included in the calculation of seedling densities of internal invaders, grass and small herb invaders. Note different scales of y-axes.

Figure 2: Species number of external and internal invaders as a function of originally sown plant species richness. Values are arithmetic means per species-richness level for each combination of weeding and seed addition treatments based on species inventories in 2006 on subplots of 2.00 × 2.25 m size. Abbreviations are: (w) = regular weeding, (c) = cessation of weeding, (s) = never weeded, (-) = no seed addition, and (+) = seed addition.

Figure 3: Proportion of plots where internal invader species occurred without and with seed addition. Species are arranged according to their invasion probability without seed addition. Values are means per weeding treatment (+ s.e.). Species belonging to different functional groups are symbolised with white bars = grasses, grey bars = small herbs, hatched grey bars = tall herb, black bars = legumes.

Figure 4: Proportion of successful invader species from each functional group as a function of originally sown plant species richness. Values are arithmetic means (± s.e.) per species-richness level for subplots with and without seed addition averaged across weeding treatments

based on species inventories in 2006. Symbols are (●) subplots without seed addition, (○) subplots with seed addition.

Figure 5: Proportion of successful invader species from each functional group in plots where species of a particular functional group in the resident community were absent (abs) or present (pres). Values are averaged across all species-richness levels and present means per weeding treatment (+ s.e.) with and without seed addition.
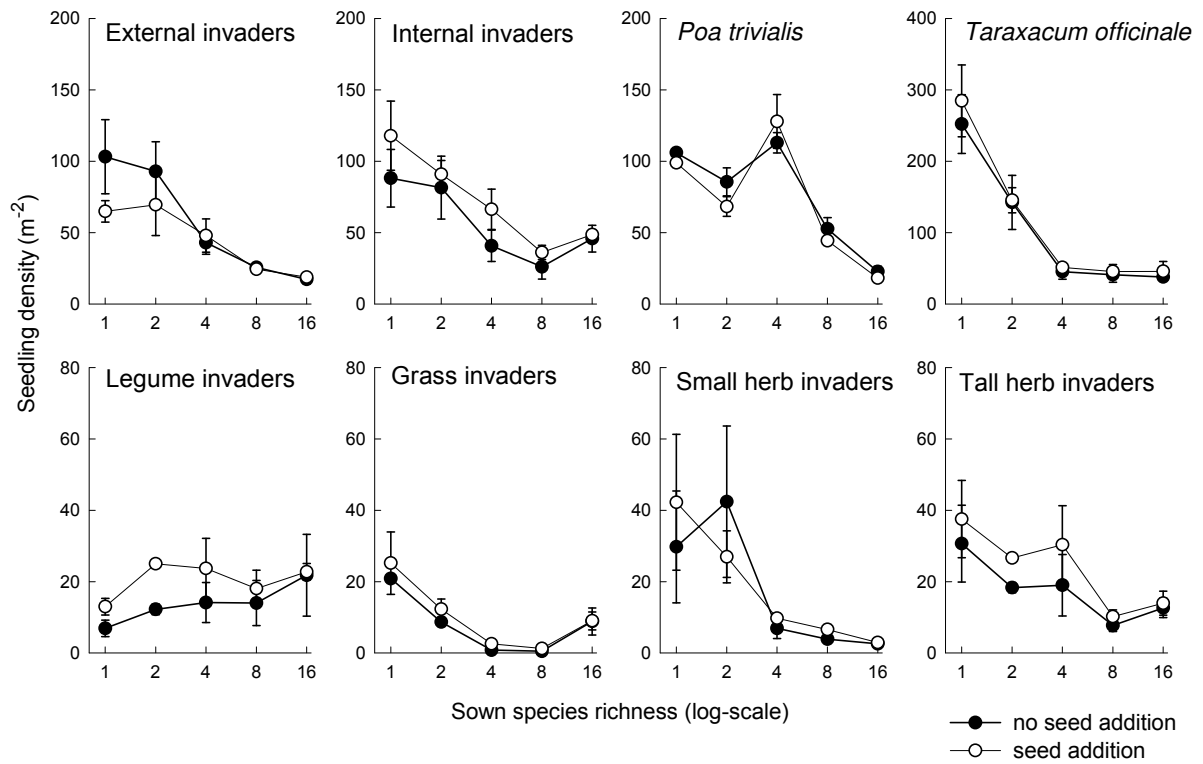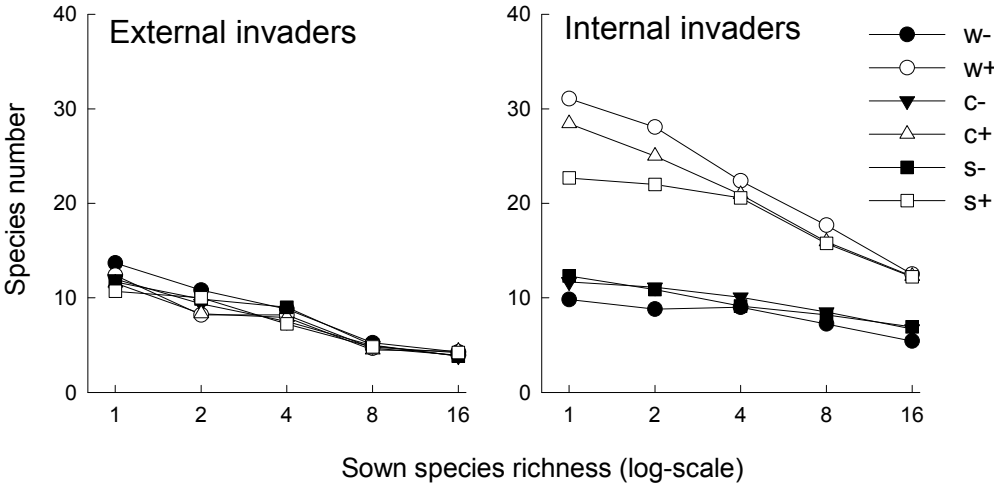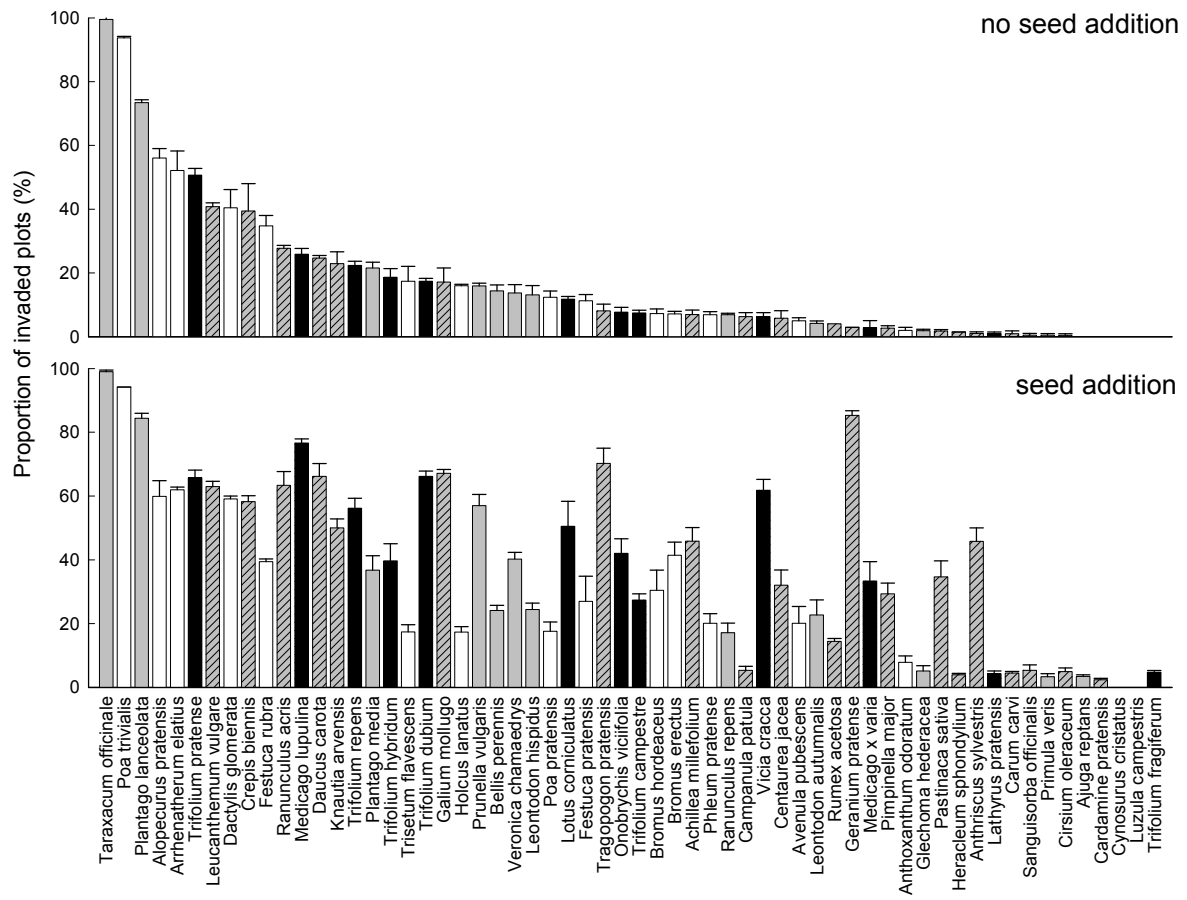
Figure 1

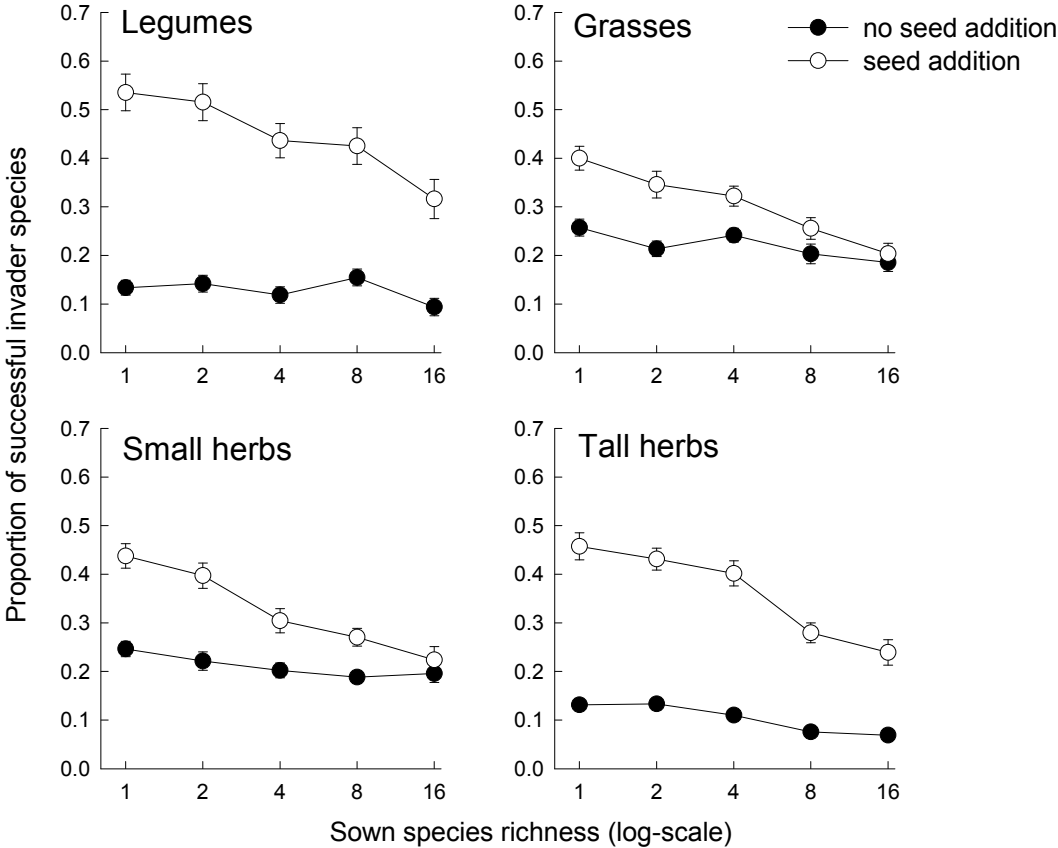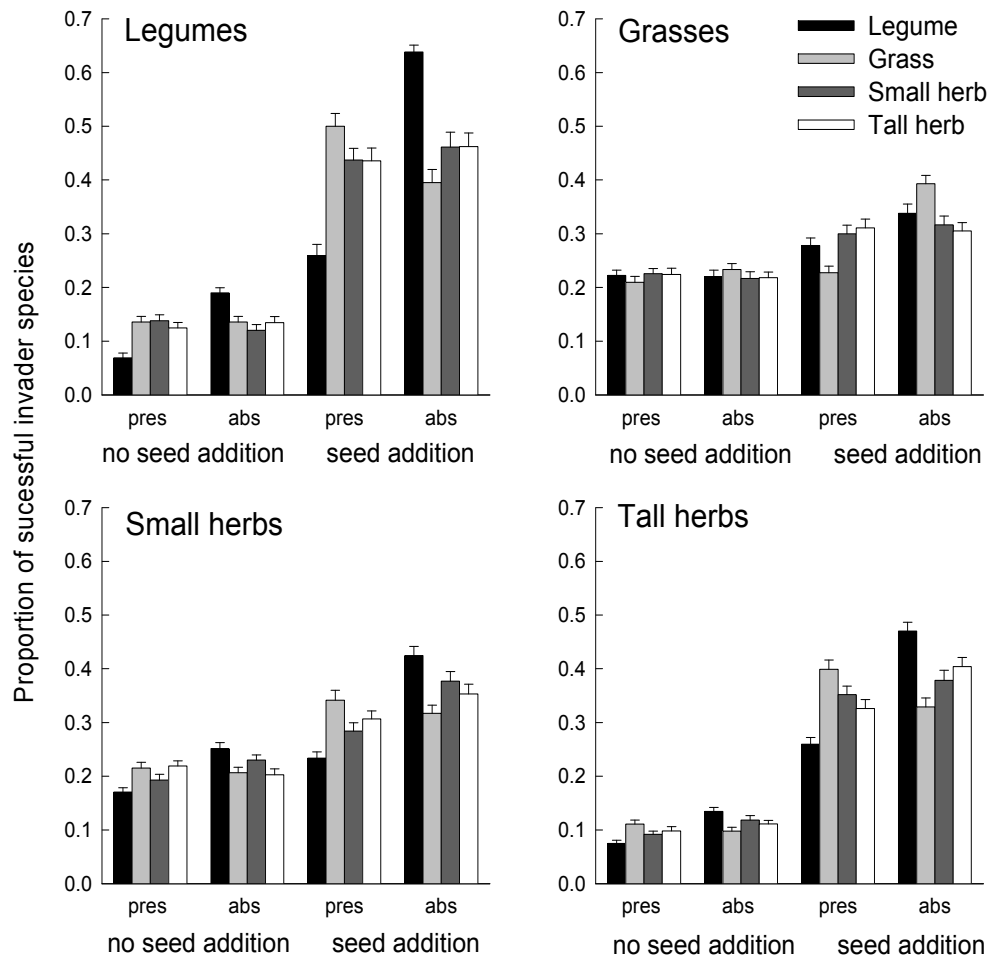Figure 2

Figure 3

Figure 4

Figure 5

Table 1: Summary of analyses of variance (ANOVA) for seedling densities of external and internal invaders, *Poa trivialis*, *Taraxacum officinale* and for each functional group of internal invaders; *P. trivialis* (grass) and *T. officinale* (small herb) were excluded in the calculation of seedling densities of internal invaders and the respective functional groups. Plots where *T. officinale* and *P. trivialis* occurred as resident species were not included in analyses of invader seedling densities of these species. Model terms were fitted sequentially and tested against the respective residuals. Note that contrasts for functional group identities were fitted separately in a series of analyses. Listed are degrees of freeedom (df), mean sums of squares (MS), F ratios (F) and p values (p). Arrows indicate significant increase (↑) or decrease (↓) of the variables with increasing species richness, the presence of a particular functional group, successional age or after seed addition; SR = species richness, FG = functional group richness, GRA = grasses, LEG= legumes, SHE = small herbs, THE = tall herbs, WT = weeding treatment, ADD = seed addition.

	External invaders				Internal invaders				Poa trivialis				Taraxacum officinale			
	df	MS	F	p	df	MS	F	p	df	MS	F	p	df	MS	F	p
Block	3	1.543	1.55	0.208	3	1.434	0.90	0.445	3	8.259	**3.09**	**0.033**	3	4.297	**3.03**	**0.036**
SR (log-linear)	1	20.828	**20.95**	**<0.001**↓	1	12.335	**7.75**	**0.007**↓	1	14.636	**5.47**	**0.022**↓	1	21.334	**15.06**	**<0.001**↓
FG (linear)	1	3.613	3.63	0.061	1	7.201	**4.52**	**0.037**↓	1	5.068	1.89	0.173	1	2.712	1.92	0.171
LEG	1	0.448	0.45	0.506	1	26.596	**21.45**	**<0.001**↓	1	19.36	**8.02**	**0.006**↑	1	8.667	**6.69**	**0.012**↑
GRA	1	0.006	0.01	0.941	1	1.137	0.71	0.402	1	46.61	**23.43**	**<0.001**↓	1	5.362	3.97	0.051
SHE	1	0.013	0.01	0.909	1	0.377	0.23	0.630	1	0.925	0.34	0.561	1	1.900	1.35	0.250
THE	1	0.237	0.24	0.628	1	12.59	**8.76**	**0.004**↑	1	9.221	3.58	0.063	1	0.375	0.26	0.611
Composition	72	0.994			72	1.592			65	2.676			61	1.416		
WT	2	0.437	**3.44**	**0.035**↑	2	0.396	2.19	0.116	2	0.011	0.09	0.913	2	1.703	**16.79**	**<0.001**↑
SR (log-linear) x WT	2	0.049	0.39	0.681	2	0.487	2.69	0.071	2	0.026	0.21	0.807	2	0.107	1.05	0.352
FG (linear) x WT	2	0.026	0.21	0.812	2	0.254	1.40	0.249	2	0.058	0.48	0.619	2	0.003	0.03	0.972
Composition x WT	150	0.127			150	0.181			136	0.120			128	0.101		
ADD	1	0.549	**4.56**	**0.034**↓	1	11.008	**73.00**	**<0.001**↑	1	0.043	0.52	0.470	1	0.024	0.34	0.562
SR (log-linear) x ADD	1	0.723	**6.01**	**0.015**	1	0.014	0.09	0.759	1	0.238	2.88	0.091	1	<0.001	<0.01	0.946
FG (linear) x ADD	1	<0.001	<0.01	0.968	1	<0.001	<0.01	0.989	1	0.039	0.47	0.492	1	0.140	2.01	0.158
WT x ADD	2	0.038	0.31	0.731	2	0.617	**4.09**	**0.018**	2	0.055	0.66	0.516	2	0.021	0.31	0.737
SR (log-linear) x WT x ADD	2	0.156	1.30	0.276	2	0.003	0.02	0.982	2	0.143	1.73	0.179	2	0.129	1.85	0.160
FG (linear) x WT x ADD	2	0.088	0.73	0.484	2	0.089	0.59	0.557	2	0.075	0.91	0.405	2	0.062	0.88	0.416
Residuals	225	0.120			225	0.151			204	0.083			192	0.070		

Table 1 continued:

	Legume invaders				Grass invaders				Small herb invaders				Tall herb invaders			
	df	MS	F	p	df	MS	F	p	df	MS	F	p	df	MS	F	p
Block	3	0.547	0.31	0.821	3	8.019	**6.23**	**0.001**	3	1.086	0.90	0.447	3	8.871	**7.26**	**<0.001**
SR (log-linear)	1	1.508	0.84	0.362	1	9.123	**7.10**	**0.009**↓	1	19.274	**15.91**	**<0.001**↓	1	16.771	**13.72**	**<0.001**↓
FG (linear)	1	6.978	3.90	0.052	1	0.009	0.01	0.933	1	0.678	0.56	0.457	1	3.457	2.83	0.097
LEG	1	61.563	**65.02**	**<0.001**↓	1	1.641	1.28	0.261	1	15.438	**15.27**	**<0.001**↓	1	6.322	**5.49**	**0.022**↓
GRA	1	13.995	**8.66**	**0.004**↑	1	10.457	**9.05**	**0.004**↓	1	2.755	2.32	0.132	1	0.161	0.13	0.720
SHE	1	4.580	2.62	0.110	1	3.444	2.74	0.102	1	1.468	1.22	0.274	1	3.847	3.25	0.076
THE	1	4.626	2.65	0.108	1	13.553	**12.18**	**0.001**↑	1	12.327	**11.69**	**0.001**↑	1	0.051	0.04	0.840
Composition	72	1.789			72	1.285			72	1.121			72	1.222		
WT	2	0.014	0.08	0.928	2	0.113	1.02	0.363	2	0.620	2.66	0.073	2	0.083	0.45	0.638
SR (log-linear) x WT	2	0.181	0.95	0.389	2	0.104	0.94	0.393	2	0.560	2.40	0.094	2	0.492	2.68	0.072
FG (linear) x WT	2	0.258	1.35	0.261	2	0.093	0.84	0.433	2	0.069	0.30	0.744	2	0.019	0.11	0.900
Composition x WT	150	0.190			150	0.111			150	0.233			150	0.184		
ADD	1	15.955	**82.72**	**<0.001**↑	1	1.275	**12.27**	**0.001**↑	1	7.100	**36.35**	**<0.001**↑	1	10.263	**59.63**	**<0.001**↑
SR (log-linear) x ADD	1	0.380	1.97	0.162	1	0.106	1.02	0.314	1	1.523	**7.79**	**0.006**	1	0.031	0.18	0.670
FG (linear) x ADD	1	0.434	2.25	0.135	1	0.010	0.09	0.761	1	0.586	3.00	0.085	1	0.586	3.40	0.066
WT x ADD	2	0.308	1.60	0.205	2	0.075	0.72	0.487	2	0.459	2.35	0.098	2	0.494	2.87	0.059
SR (log-linear) x WT x ADD	2	0.023	0.12	0.887	2	0.451	**4.34**	**0.014**	2	0.020	0.10	0.902	2	0.012	0.07	0.931
FG (linear) x WT x ADD	2	0.037	0.19	0.825	2	0.002	0.02	0.983	2	0.154	0.79	0.456	2	0.483	2.80	0.063
Residuals	225	0.193			225	0.104			225	0.195			225	0.172		

Table 2: Summary of analyses of variance (ANOVA) of species numbers of external and internal invader species. Model terms were fitted sequentially and tested against the respective residuals. Note that contrasts for functional group identities were fitted separately in a series of analyses. Listed are the mean sums of squares (MS), F ratios (F) and p values (p). Arrows indicate significant increase (↑) or decrease (↓) of invader species numbers with increasing species richness, the presence of a particular functional group or after seed addition; for abbreviations of predictor variables see Table 1.

		External invaders			Internal invaders		
	df	MS	F	p	MS	F	p
Block	3	0.161	1.22	0.309	0.061	0.54	0.657
SR (log-linear)	1	**10.126**	**76.62**	**<0.001**↓	4.478	**39.49**	**<0.001**↓
FG (linear)	1	0.480	3.63	0.061	0.416	3.67	0.059
LEG	1	0.821	**6.70**	**0.012**↓	3.484	**52.84**	**<0.001**↓
GRA	1	0.011	0.09	0.766	0.825	**7.98**	**0.006**↑
SHE	1	0.420	3.28	0.074	0.111	0.98	0.326
THE	1	0.030	0.22	0.637	0.442	**4.07**	**0.048**↑
Composition	72	0.132			0.113		
WT	2	0.038	2.77	0.066	0.009	1.25	0.290
SR (log-linear) x WT	2	0.008	0.55	0.580	0.027	**3.58**	**0.030**
FG (linear) x WT	2	0.007	0.49	0.614	<0.001	0.02	0.981
Composition x WT	150	0.014			0.007		
ADD	1	0.089	**7.17**	**0.008**↓	11.528	**970.494**	**<0.001**↑
SR (log-linear) x ADD	1	0.020	1.61	0.206	0.264	**22.19**	**<0.001**
FG (linear) x ADD	1	0.002	0.17	0.681	0.026	2.21	0.139
WT x ADD	2	0.015	1.19	0.308	0.191	**16.07**	**<0.001**
SR (log-linear) x WT x ADD	2	<0.001	0.01	0.989	0.022	1.82	0.164
FG (linear) x WT x ADD	2	0.012	0.98	0.378	0.003	0.29	0.749
Residuals	225	0.012			0.012		

Table 3: Summary of analyses of variance (ANOVA) of proportions of successfully established internal invader species per functional group. Model terms were fitted sequentially and tested against the respective residuals. Note that contrasts for functional group identities were fitted separately in a series of analyses. Listed are the mean sums of squares (MS), F ratios (F) and p values (p). Arrows indicate significant increase (↑) or decrease (↓) of the respective variables with increasing species richness, the presence of a particular functional group or after seed addition; for abbreviations of predictor variables see Table 1.

		Grass invaders			Legume invaders			Small herb invaders			Tall herb invaders		
	df	MS	F	p	MS	F	p	MS	F	p	MS	F	p
Block	3	0.243	2.14	0.103	0.133	0.38	0.770	0.021	0.17	0.919	0.093	0.88	0.454
SR (log-linear)	1	**1.669**	**14.67**	**<0.001** ↓	1.422	**4.03**	**0.048** ↓	**2.002**	**15.57**	**<0.001** ↓	2.562	**24.29**	**<0.001** ↓
FG (linear)	1	0.005	0.05	0.829	0.760	2.15	0.146	0.314	2.45	0.122	0.046	0.44	0.509
LEG	1	0.006	0.05	0.817	14.396	**92.83**	**<0.001** ↓	1.829	**17.48**	**<0.001** ↓	2.608	**37.15**	**<0.001** ↓
GRA	1	1.303	**13.43**	**<0.001** ↓	3.746	**12.28**	**0.001** ↑	0.926	**7.89**	**0.006** ↑	1.759	**21.40**	**<0.001** ↑
SHE	1	0.203	1.80	0.184	1.166	3.42	0.069	0.172	1.34	0.250	0.167	1.60	0.210
THE	1	0.357	3.24	0.076	0.761	2.19	0.143	0.679	**5.62**	**0.020** ↑	0.005	0.05	0.830
Composition	72	0.114			0.353			0.129			0.105		
WT	2	0.017	1.42	0.244	0.054	**3.34**	**0.038**	0.038	2.53	0.083	0.009	0.94	0.394
SR (log-linear) x WT	2	0.043	**3.67**	**0.028**	0.056	**3.44**	**0.034**	0.023	1.55	0.216	0.053	**5.37**	**0.006**
FG (linear) x WT	2	0.017	1.49	0.230	0.006	0.40	0.671	0.019	1.30	0.276	0.008	0.83	0.440
Composition x WT	150	0.016			0.016			0.015			0.010		
ADD	1	1.150	**71.79**	**<0.001** ↑	19.31	**637.64**	**<0.001** ↑	1.981	**133.81**	**<0.001** ↑	13.581	**738.03**	**<0.001** ↑
SR (log-linear) x ADD	1	0.278	**17.37**	**<0.001**	0.524	**17.31**	**<0.001**	0.628	**42.40**	**<0.001**	0.192	**10.45**	**0.001**
FG (linear) x ADD	1	0.179	**11.17**	**0.001**	0.012	0.38	0.537	0.042	2.82	0.095	0.005	0.30	0.584
WT x ADD	2	0.111	**6.92**	**0.001**	0.163	**5.37**	**0.005**	0.058	**3.91**	**0.021**	0.198	**10.77**	**<0.001**
SR (log-linear) x WT x ADD	2	0.068	**4.23**	**0.016**	0.018	0.60	0.549	0.010	0.68	0.507	0.014	0.78	0.459
FG (linear) x WT x ADD	2	0.004	0.24	0.787	0.010	0.32	0.723	0.030	2.00	0.138	0.001	0.07	0.929
Residuals	225	0.016			0.030			0.015			0.018		

Table 4: Spearman rank correlation coefficients between plant functional characteristics and the proportion of plant communities per internal invader species colonized spontaneously, as proportional increment after seed addition or dependent on the occurrence of resident legumes or grasses (difference between invasion probability after seed addition in plots with these functional groups and without this functional groups) observed five years after the establishment of the biodiversity experiment and one year after seed addition (2006). All values were averaged across weeding treatments. The last columns shows results of Kruskal-Wallis-ANOVA (for continuous and ordinal data: seed mass, phenology) or Chi-square test (for binary data) to test whether the analysed functional characteristics differ significantly among species assigned to different functional groups (Gr = grasses, Sh = small herbs, Th = tall herbs, Le = legumes).

Functional characteristics	Spontaneous invasion		Increase after seed addition		Negative legume effect		Positive grass effect		Trait differences among functional groups	
	R	p	R	p	R	p	R	p	X^2/H	p
Seed mass	-0.199	0.128	**0.315**	**0.015**	-0.146	0.266	-0.024	0.858	3.98	0.263
Seed longevity	0.112	0.394	*0.240*	*0.065*	**-0.378**	**0.003**	*0.242*	*0.063*	7.24	0.065
Pollination										
Self pollination	0.062	0.637	**0.293**	**0.023**	-0.382	0.003	0.145	0.268	8.25	0.041 Le = Sh = Th > Gr
Wind-pollination	*0.236*	*0.070*	**-0.332**	**0.010**	**0.412**	**0.001**	**-0.599**	**<0.001**	44.40	<0.001 Gr > Le = Sh = Th
Insect-pollination	-0.199	0.128	**0.397**	**0.002**	**-0.497**	**<0.001**	**0.650**	**<0.001**	55.45	<0.001 Le = Sh = Th > Gr
Dispersal mode										
Self dispersal	*-0.223*	*0.087*	0.124	0.345	0.014	0.915	*0.230*	*0.077*	6.98	0.072
Wind-dispersal	0.041	0.753	*-0.224*	*0.085*	*0.234*	*0.072*	**-0.433**	**<0.001**	12.47	0.006 Gr > Le = Sh = Th
Ant-dispersal	-0.101	0.441	-0.016	0.902	-0.070	0.593	-0.034	0.797	1.93	0.588
Dispersal by adhesion	**0.355**	**0.005**	-0.074	0.572	0.127	0.322	**-0.362**	**0.005**	24.00	<0.001 Gr > Le = Sh = Th
Dispersal by digestion	-0.072	0.582	0.149	0.253	**-0.271**	**0.036**	**0.276**	**0.033**	17.40	0.001 Le > Sh = Th = Gr
Shock-dispersal	-0.163	0.211	-0.038	0.775	-0.021	0.873	0.090	0.493	4.76	0.190
Germination requirements										
Light	0.213	0.102	**-0.275**	**0.034**	*0.241*	*0.064*	**-0.272**	**0.036**	15.41	0.001 Sh = Gr > Th = Le
Chilling	**-0.273**	**0.035**	0.035	0.791	-0.044	0.738	**0.279**	**0.031**	13.44	0.004 Th > Sh = Le = Gr
Time of germination										
Spring	-0.078	0.554	*0.230*	*0.077*	-0.061	0.642	0.197	0.132	14.03	0.003 Th = Sh > Le = Gr
Summer	0.192	0.140	-0.189	0.147	0.048	0.717	0.015	0.912	9.61	0.022 Sh = Gr > Th = Le
Autumn	0.141	0.283	0.022	0.870	-0.205	0.116	0.095	0.470	9.05	0.029 Gr = Le > Th = Sh
Phenology										
Start of flowering	-0.022	0.866	0.244	0.060	-0.203	0.119	0.101	0.443	7.22	0.065
End of flowering	0.145	0.268	**0.493**	**<0.001**	**-0.585**	**<0.001**	**0.371**	**0.004**	14.90	0.002 Le = Sh = Th > Gr

Supplementary Material

Table S1: Summary of mixed-effects model analyses for internal invader species occurrences including all communities where these species were not present in the originally sown plant communities. Models were fitted by stepwise inclusion of variables. Listed are the results of Chi square statistics that were applied to assess model improvement and the statistical significance of the variables, where ns = non-significant, *: $p \leq 0.05$, **: $p < 0.01$, and ***: $p < 0.001$. Arrows indicate a significant increase (↑) or decrease (↓) of invader species occurrences with increasing species richness, functional group richness, the presence of a particular functional group, successional age or after seed addition; for abbreviations of predictor variables see Table 1. Abbreviations for plant families are Ast = Asteraceae, Api = Apiaceae, Bra = Brassicaceae, Cam = Campanulaceae, Dip = Dipsacaceae, Fab = Fabaceae, Ger = Geraniaceae, Jun = Juncaceae, La = Lamiaceae, Pla = Plantaginaceae, Poa = Poaceae, Pol = Polygonaceae, Pri = Primulaceae, Ran = Ranunculaceae, Ros = Rosaceae, Rub = Rubiaceae, Scr = Scrophulariaceae. Nomenclature follows Rothmaler (2002).

Species	Family	SR	FG	LEG	GRA	SHE	THE	WT	ADD	WT x ADD
Grasses										
Alopecurus pratensis L.	Poa	***↓	ns	ns	***↓	ns	**↑	*↓	ns	ns
Anthoxanthum odoratum L.	Poa	ns	ns	ns	ns	ns	ns	ns	***↑	*
Arrhenatherum elatius (L.) J. et C. Presl	Poa	ns	ns	ns	ns	ns	ns	ns	**↑	ns
*Avenula pubescens (*Huds.) Dum.	Poa	*↓	ns	ns	ns	ns	*↑	ns	***↑	ns
Bromus erectus Huds.	Poa	***↓	*↓	ns	ns	ns	ns	ns	***↑	ns
Bromus hordeaceus L.	Poa	**↓	***↓	ns	**↓	ns	ns	ns	***↑	*
Cynosurus cristatus L.	Poa	ns	ns	ns	ns	ns	ns	ns	ns	ns
Dactylis glomerata L.	Poa	*↓	**↓	ns	ns	*↓	*↓	ns	***↑	ns
Festuca pratensis Huds.	Poa	ns	ns	*↑	***↓	ns	*↑	*↓	***↑	**
Festuca rubra L.	Poa	**↓	ns	***↓	ns	ns	ns	ns	ns	ns
Holcus lanatus L.	Poa	ns	ns	ns	*↑	ns	ns	ns	ns	ns
Luzula campestris (L.) Dc.	Jun	ns	ns	ns	ns	ns	ns	ns	ns	ns
Phleum pratense L.	Poa	ns	ns	ns	*↓	ns	ns	ns	***↑	ns
Poa pratensis L.	Poa	ns	ns	ns	ns	**↑	ns	ns	ns	ns
Poa trivialis L.	Poa	ns	ns	ns	ns	ns	ns	ns	ns	ns
Trisetum flavescens (L.) P. Beauv.	Poa	**↓	ns	ns	ns	ns	ns	ns	ns	*
Legumes										
Lathyrus pratensis L.	Fab	ns	ns	ns	ns	ns	ns	ns	***↑	ns
Lotus corniculatus L.	Fab	ns	ns	***↓	***↑	ns	ns	*↓	***↑	*
Medicago lupulina L.	Fab	ns	ns	***↓	*↑	**↑	ns	ns	***↑	ns
Medicago x varia Martyn	Fab	**↓	ns	***↓	*↑	ns	ns	*↓	***↑	*
Onobrychis viciifolia Scop.	Fab	ns	ns	**↓	**↑	ns	ns	ns	***↑	ns
Trifolium campestre Schreb.	Fab	ns	**↓	***↓	ns	ns	ns	ns	***↑	ns
Trifolium dubium Sibth.	Fab	ns	ns	***↓	*↑	ns	ns	ns	***↑	ns
Trifolium fragiferum L.	Fab	ns	ns	ns	ns	ns	ns	ns	***↑	ns
Trifolium hybridum L.	Fab	ns	ns	***↓	***↑	ns	ns	ns	***↑	**
Trifolium pratense L.	Fab	ns	**↓	***↓	*↑	ns	ns	ns	***↑	ns
Trifolium repens L.	Fab	*↓	**↓	***↓	**↑	*↑	ns	ns	***↑	ns
Vicia cracca L.	Fab	ns	ns	***↓	**↑	ns	ns	ns	***↑	ns
Small herbs										
Ajuga reptans L.	Lam	ns	ns	ns	ns	ns	ns	ns	***↑	ns
Bellis perennis L.	Ast	ns	ns	***↓	*↑	ns	ns	ns	**↑	ns
Glechoma hederacea L.	Lam	ns	ns	ns	ns	ns	ns	ns	**↑	ns

Leontodon autumnalis L.	Ast	***↓	ns	***↓	***↑	ns	ns	ns	***↑	ns
Leontodon hispidus L.	Ast	**↓	ns	**↓	ns	ns	ns	ns	***↑	ns
Plantago lanceolata L.	Pla	ns	*↓	***↓	ns	ns	**↑	ns	**↑	ns
Plantago media L.	Pla	**↓	ns	***↓	***↑	ns	ns	ns	***↑	ns
Primula veris L.	Pri	ns	ns	ns	ns	ns	ns	ns	***↑	**
Prunella vulgaris L.	Lam	***↓	ns	***↓	***↑	ns	ns	ns	***↑	ns
Ranunculus repens L.	Ran	ns	ns	ns	ns	ns	ns	ns	***↑	*
Taraxacum officinale Wiggers	Ast	ns	ns	ns	ns	ns	ns	ns	ns	**
Veronica chamaedrys L.	Scr	*↓	ns	**↓	*↑	ns	ns	ns	***↑	ns
Tall herbs										
Achillea millefolium L.	Ast	***↓	ns	***↓	*↑	ns	ns	ns	***↑	ns
Anthriscus sylvestris (L.) Hoffm.	Api	ns	ns	***↓	***↑	ns	ns	ns	***↑	ns
Campanula patula L.	Cam	ns	ns	**↓	ns	ns	ns	ns	ns	ns
Cardamine pratensis L.	Bra	ns	ns	ns	ns	ns	ns	ns	***↑	ns
Carum carvi L.	Api	ns	ns	ns	ns	ns	ns	ns	***↑	**
Centaurea jacea L.	Ast	***↓	*↓	*↓	ns	ns	*↑	ns	***↑	**
Cirsium oleraceum (L.) Scop.	Ast	ns	ns	ns	ns	ns	ns	ns	ns	ns
Crepis biennis L.	Ast	*↓	ns	ns	ns	ns	ns	**↑	***↑	**
Daucus carota L.	Api	**↓	ns	***↓	*↑	ns	ns	ns	***↑	ns
Galium mollugo Mill.	Rub	ns	ns	ns	ns	ns	ns	ns	***↑	*
Geranium pratense L.	Ger	ns	ns	ns	ns	ns	ns	ns	***↑	ns
Heracleum sphondylium L.	Api	ns	ns	ns	ns	ns	ns	ns	***↑	ns
Knautia arvensis (L.) J.M. Coult.	Dip	***↓	ns	***↓	**↑	ns	ns	ns	***↑	ns
Leucanthemum vulgare Lam.	Ast	***↓	ns	***↓	**↑	ns	ns	ns	***↑	ns
Pastinaca sativa L.	Api	ns	ns	***↓	***↑	ns	ns	ns	***↑	ns
Pimpinella major (L.) Huds.	Api	**↓	ns	ns	*↑	ns	ns	ns	***↑	ns
Ranunculus acris L.	Ran	***↓	*↓	***↓	**↑	ns	ns	ns	***↑	ns
Rumex acetosa L.	Pol	ns	ns	ns	ns	ns	ns	ns	***↑	ns
Sanguisorba officinalis L.	Ros	ns	ns	ns	ns	ns	ns	ns	***↑	ns
Tragopogon pratensis L.	Ast	*↓	*↓	***↓	ns	ns	ns	ns	***↑	ns