1   **Hemiparasite-density effects on grassland plant diversity, composition and biomass**

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Abstract

17

18 Hemiparasitic plants are considered as ecosystem engineers because they can modify the

19 interactions between hosts and other organisms. Thereby, they may affect vegetation

20 structure, community dynamics and facilitate coexistence as they are able to reduce

21 interspecific competition by parasitizing selectively on competitive species and promote

22 subordinate ones. In agri-environmental schemes, introducing the hemiparasite *Rhinanthus*

23 has therefore been suggested as a low-cost method to increase grassland plant diversity,

24 which is still subject to debate.

25 The majority of previous studies simply compared sites with and without hemiparasites.

26 However, as hemiparasite effects are most likely density-dependent, we present a novel

27 approach assessing the effect of *Rhinanthus alectorolophus* density on grassland plant

28 diversity, yield and biomass quality. Moreover, we investigated whether functional plant

29 composition and community mean traits are affected, which has been largely neglected in

30 previous studies.

31 The relationship between species richness and relative *Rhinanthus* biomass followed an

32 optimum curve with highest values at 31% relative *Rhinanthus* biomass. At this *Rhinanthus*-

33 biomass level, species richness was increased by 12% and yield decreased by 26% compared

34 with plots without *Rhinanthus*. At relative *Rhinanthus* biomass > 60%, species richness was

35 even lower than in plots without *Rhinanthus*. Overall, the biomass of grasses and the

36 cumulative cover of legumes decreased linearly with increasing relative *Rhinanthus* biomass.

37 Community mean trait analysis revealed that an increasing *Rhinanthus* density shifts the

38 community composition towards smaller plant species. Biomass quality was not affected by

39 increasing relative *Rhinanthus* biomass.

40   In summary, our results of increased plant diversity – in line with a slightly lower yield but

41   similar biomass quality – indicate that *Rhinanthus* is a suitable biological tool for grassland

42   restoration.

43

44   **Keywords**

45   Biomass quality; community mean traits; Near Infrared Spectroscopy; *Rhinanthus*

46   *alectorolophus*; yield

Introduction

In Central Europe, land-use intensification has led to homogenous grassland communities with only few highly competitive species and a loss of the overall diversity and ecosystem functions (Wesche et al., 2012; Allan et al., 2014; Soliveres et al., 2016; Gossner et al., 2016). To reverse this trend, low intensity farming is currently promoted by agri-environmental schemes (e.g. Kleijn et al., 2009) to restore diverse and highly valuable grassland ecosystems. However, high residual soil fertility is a key factor limiting restoration success (Pywell et al., 2007, Klaus et al. 2011). Various attempts to overcome this problem have been suggested: Nutrient removal by frequent mowing or grazing tends to be slow and, particularly in the case of phosphorus, ineffective (Bullock and Pywell, 2005), whereas the more straightforward removal of top-soil is effective but costly (Hölzel & Otte 2003, Mudrák et al., 2014). An alternative and cost-effective tool for grassland restoration counteracting the inhibitive effects of dominant species is the introduction of native parasitic plants into these ecosystems (Davies et al., 1997; Smith et al., 2003; Mudrák et al., 2014).

The genus *Rhinanthus*, a member of the large parasitic Orobanchaceae family, is the most common root hemiparasitic genus throughout temperate Europe (Ameloot et al., 2005). Hemiparasites are photosynthetically active and consume water and nutrients from their hosts (Watson, 2009; Westwood et al., 2010), but also a considerable amount of assimilates and secondary compounds may be taken up (Adler, 2000; Těšitel et al., 2010). *Rhinanthus* spp. are generalists, parasitizing many different species (Gibson and Watkinson, 1991). Their roots form haustoria on any root they encounter (Cameron and Seel 2007). *Rhinanthus* is therefore more often successfully parasitizing hosts with a diffuse and wide spreading root system, such as grasses, than the ones with e.g. taproot during their whole lifecycle (Mudrák et al. 2016). Moreover, forbs with high nutrient contents, e.g. legumes, or forbs without

72   adequate defence mechanisms preventing penetration and access to the xylem have been

73   suggested to be better-suitable hosts (Seel and Press, 1993; Matthies, 1996; Ameloot et al.,

74   2005; Cameron et al., 2006). They are able to reduce interspecific competition by parasitizing

75   competitive species or by exerting density-dependent control of dominant plants, thereby

76   facilitating coexistence and promoting the stability of natural communities (Phoenix and

77   Press, 2005; Těšitel et al., 2015a). Moreover, it has been suggested that in particular annual

78   hemiparasites can create gaps after senescence, which in turn promotes the establishment

79   of other species (Joshi et al., 2000; Bullock and Pywell, 2005; but see also Davies et al.,

80   1997). *Rhinanthus* spp. have been recommended as tool for grassland restoration as they

81   are a natural part of European grasslands. In addition, because they are annuals, their

82   density can be controlled easily by mowing before seed ripening (Magda et al., 2004; Bullock

83   and Pywell, 2005; Westbury et al., 2006; Mudrák et al., 2014). Today, *Rhinanthus* spp. are

84   already part of seed mixtures for biodiversity promoting areas (BPA) in Switzerland.

85   However, whether effects on plant diversity are positive (e.g. Bardgett et al., 2006; Fibich et

86   al., 2016) or negative (Gibson and Watkinson, 1992) is still unclear (see also Ameloot et al.,

87   2005 for a meta-analysis).

88   Similarly, while most studies found *Rhinanthus* to reduce community biomass (Ameloot et

89   al., 2005, 2006), some studies found a biomass increase (Joshi et al., 2000). The intuitive

90   expectation of many farmers is a reduction of yield by the presence of hemiparasites, which

91   makes *Rhinanthus* very unpopular for them (Magda et al., 2004; Ameloot et al., 2006).

92   Related to this, it is often presumed that *Rhinanthus* reduces the nutritional value of the

93   yield with severe losses in fodder quality. Such fodder quality decreases might be driven by

94   changes in the functional plant composition of infested grasslands and should then be

95   reflected by changes in nitrogen, mineral and fibre contents in plant biomass. However, as

96   this has not been tested systematically, it remains dubious whether hemiparasites indeed

97   affect biomass quality.

98   Moreover, the functional role of hemiparasites in grasslands is still unclear (see Quested et

99   al., 2003). As they are known for their low nutrient and water-use efficiency (Phoenix and

100   Press, 2005) one can assume that they may affect the abiotic environment, which might be

101   reflected by changes in mean environmental indicator values of the vegetation, e.g. for

102   moisture and nutrient availability (e.g. Landolt, 2010). In addition, whether hemiparasites

103   affect plant community structure and composition, indicated by changes in functional groups

104   and community mean traits was also largely neglected in previous studies (but see Demey et

105   al., 2015; Mudrák et al., 2016). In particular, one can assume changes in resource related

106   community mean traits such as specific leaf area and leaf dry matter content as well as

107   competition relates ones such as mean plant height or dispersal and colonization related

108   ones such as seed mass.

109   So far, studies investigating hemiparasite effects on grasslands used an 'all or nothing'

110   approach, comparing sites with and without hemiparasites (e.g. Gibson and Watkinson,

111   1992; Stein et al., 2009; Mudrák and Lepš, 2010). However, this approach may not be fully

112   informative as it does not take the variation in *Rhinanthus* density into account, although

113   hemiparasite effects are most likely density-dependent. Thus, it is unclear whether there is a

114   *Rhinanthus*-density-grassland plant diversity optimum. In addition, different sites may not be

115   fully comparable as they might differ in environmental conditions and not only the presence

116   of the hemiparasite. It has been shown that the abiotic site conditions such as water and

117   nutrient availability have profound interactive effects on hemiparasite and host biomass and

118   fitness (Těšitel et al., 2015b). Thus, in studies showing decreases in productivity in the

119   presence of *Rhinanthus* (e.g. Davies et al., 1997) it remains unclear whether *Rhinanthus*

120   drives this decrease or simply prefers low-productive conditions (Ameloot et al., 2005;

121   Bullock and Pywell, 2005).

122   Here, we present results from an alternative approach testing whether varying *Rhinanthus*

123   *alectorolophus* densities affect the plant diversity, plant community composition,

124   productivity and biomass quality along *Rhinanthus*-density gradients within sites. Studying

125   density effects within a site instead of between sites ensures similar environmental

126   conditions among the replicates. Furthermore, to more explicitly explain plant community

127   patterns and test for individual species responses along the *Rhinanthus* gradient, we used

128   hierarchical Huisman-Olff-Fresco (HOF) models, a novel approach for modelling species

129   response curves.

130   We therefore conducted a multi-site study, investigating 47 sites in three distinct regions in

131   Switzerland allowing us to draw more general conclusions than investigating only a single

132   region. This may further allow us to draw recommendations on the suitability of *Rhinanthus*

133   in grassland restoration. In particular, we tested whether and how increasing *Rhinanthus*

134   *alectorolophus* density affects 1) plant diversity, 2) species composition reflected by

135   community mean functional traits and environmental indicator values, and 3) grassland

136   productivity and biomass quality.

137

138   **Methods**

139   *Study system*

140   To enhance representativeness and generality of results and conclusions, we conducted our

141   study in 47 meadows in three distinct regions in Switzerland: Bernese lowland (*N*=30), the

142   Bernese Oberland (*N*=13) and the Valais (*N*=4). Sites were selected by accurate point

143 coordinates on the occurrence of *Rhinanthus alectorolophus* provided by Info Flora

144 (www.infoflora.ch), the national data and information center of the Swiss flora, as well as by

145 own observations. All sites were non-intensively managed meadows which could be

146 assigned to communities of the Arrhenatherion alliance in the Bernese lowland and mainly

147 to communities of the Polygono-Trisetion alliance in the two regions in higher altitudes

148 (sensu Delarze et al., 2015). We considered a site to be suitable if it was well accessible, not

149 mown when the vegetation was assessed and when *Rhinanthus alectorolophus* was present

150 in varying densities. In addition, the site had to be visually homogeneous, e.g. that it could

151 be assigned to one vegetation type. Altitude ranged from 504 m.a.s.l. (Bernese lowland) to

152 1946 m.a.s.l. (Schynige Platte, Bernese Oberland). The maximum geographic distance

153 between the regions was approximately 80 km. Mean annual precipitation varies among the

154 regions with around 700 mm in the Valais, 1000 mm in the Bernese lowland and 2000 mm in

155 the Bernese Oberland.

156

157 *Vegetation and biomass data*

158 Between mid-May and beginning of June 2015, we sampled the meadows in the Bernese

159 lowland, in mid-June the ones in Valais and between mid and end of June the ones in the

160 Bernese Oberland, to account for the different developmental stages of the vegetation along

161 the altitudinal gradient. Within each meadow, we placed nine 20 cm × 20 cm plots along a

162 density gradient of *Rhinanthus alectorolophus* (named *Rhinanthus* hereafter). For this, we

163 first visually subdivided each grassland in zones with low, medium and high *Rhinanthus*

164 density and randomly placed three plots in each zone to maximize the range from a

165 minimum (mostly equivalent with the absence) to a maximum *Rhinanthus* density within

166 each meadow (up to 95% *Rhinanthus* cover), ensuring that plots were distributed across the

167 whole meadow and that two plots of the same density class were not situated in the same

168 *Rhinanthus* patch. We chose small sample quadrats of 400 cm^2 because the parasitic effects

169 on host plants is limited to the close neighbourhood of the parasite (host plants are only

170 affected within 10 cm of the parasite; Gibson and Watkinson, 1992) and this plot size has

171 been already used in many previous studies (e.g., Pywell et al., 2004; Ameloot et al., 2006;

172 Mudrak et al., 2016). In each of the resulting 423 plots, we identified all vascular plant

173 species and estimated their percentage cover and the cover of bare ground.

174 We then harvested the aboveground biomass, separated *Rhinanthus*, other herb and grass

175 species, dried the samples for 48 h at 80 °C and weighed them separately with 0.01 g

176 precision. After this, we again pooled the three biomass samples of each of the nine plots

177 per meadow and ground them to pass a 0.5 mm sieve to test for variation of biomass quality

178 along the *Rhinanthus*-density gradient.

179 As indications for biomass quality, we analysed the ground biomass samples for nitrogen (N),

180 phosphorus (P), calcium (Ca), magnesium (Mg), potassium (K), carbon (C), neutral detergent

181 fibre (NDF), acid detergent fibre (ADF), and lignin (ADL) by means of near infrared

182 reflectance (NIR) spectroscopy (Foley et al., 1998). We recorded the reflectance spectrum of

183 each sample between 1250 to 2350 nm at 1 nm intervals. Each sample scan consisted of 24

184 single measurements, which we averaged to one spectrum. Biomass nutrient concentrations

185 and fibre contents derived from calibration models previously established. For

186 methodological details on NIR spectral analyses, calibration models and the laboratory

187 reference measurements see Kleinebecker et al. (2011).

188

189 *Community weighted mean traits and environmental indicator values*

190   We requested data from the TRY – Plant Trait Database (Kattge et al., 2011) and the Seed

191   Information Database (SID; Royal Botanic Gardens Kew, 2016) to compute community mean

192   traits of seed mass, plant height, specific leaf area (SLA) and leaf dry matter content (LDMC).

193   Data was available for all herbaceous species (212 out of 231). We excluded woody species

194   (19 out of 231) from community mean trait calculations because they only occurred as

195   seedlings and play no significant role in mown grasslands but might strongly affect traits like

196   average plant height and seed mass. For each species trait, we computed the median value

197   of all data base records. We then used the abundance-weighted community mean of each

198   trait per plot for further analyses.

199   Moreover, we calculated abundance weighted indicator values for moisture and fertility

200   (values ranging from 1 to 5; see Landolt, 2010) of each plot. Indicator values give the

201   position of the realized niche of plant species and by averaging them over all species per

202   plot, these values yield information on the environmental conditions of the grasslands.

203

204   *Statistical analysis*

205   Data were analyzed using R (version 3.2.4, R Development Core Team, 2016). We first

206   calculated the biomass of *Rhinanthus*, grasses and herbs relative to the total biomass per

207   plot. As relative *Rhinanthus* biomass and *Rhinanthus* cover estimates were strongly

208   correlated ($r = 0.78$, $p < 0.001$), we used the measured relative *Rhinanthus* biomass values

209   for further analyses. Legumes are suggested to be well-suitable hosts for *Rhinanthus* (e.g.,

210   Cameron et al., 2006). However, as we did not separate the biomass of legumes from the

211   one of other herbs, we calculated the cumulative legume cover to test whether legumes as a

212   group are negatively affected by increasing *Rhinanthus* densities.

213   For each plot, we calculated species richness, effective diversity ($e^{H'}$, where H' denotes

214   Shannon diversity) and Pielou's evenness (J = H'/log[S]) using the vegan package (Oksanen et

215   al., 2015).

216   We then computed linear mixed effect models to account for the study design using the

217   nlme package (Pinheiro et al., 2014). Our response variables were the total plant diversity

218   measures and those separately for the functional groups grasses and herbs, community

219   mean traits and environmental indicator values for moisture and fertility, total biomass,

220   grass and herb biomass, and biomass quality measures. *Rhinanthus* was omitted from

221   calculations on diversity measures, community mean traits and environmental indicator

222   values. The models for biomass were calculated with and without *Rhinanthus*. Models on

223   biomass quality also included *Rhinanthus* as these measures were based on pooled total

224   biomass samples. As results for species richness and effective diversity were qualitatively

225   similar, we only show the ones for species richness. Fixed effects included region and the

226   relative *Rhinanthus* biomass and its interaction with region. We also included relative

227   *Rhinanthus* biomass as quadratic term because we suspected some non-linear relationships,

228   but omitted the quadratic term if not significant. As one of the three observers did not

229   sample the meadows in the Valais and to correct for individual differences of the observer in

230   species knowledge, we included the observer identity as a co-factor. Meadow was fitted as

231   random term to account for meadow-specific differences. Model assumptions were checked

232   visually by plotting residuals vs. predicted values and with normal-quantile plots.

233   To model species response curves along the *Rhinanthus* gradient, we used the package eHOF

234   (Jansen and Oksanen, 2013). Huisman-Olff-Fresco models (HOF models; Huisman et al.,

235   1993; see also Oksanen and Minchin, 2002) are five hierarchical models with increasing

236   complexity: I) no trend, II) monotone sigmoid with a maximum at one end of the gradient,

237   III) monotone sigmoid with a plateau, IV) unimodal symmetric and V) unimodal skewed.

238   Jansen and Oksanen (2013) further developed the models by adding model VI) bimodal with

239   equal maxima and VII) bimodal with different maxima. As species composition differed

240   strongly across the three regions, we modelled species response curves along the

241   *Rhinanthus*-density gradient separately for each region. For this, we used abundance data

242   (percentage cover) and a Gaussian error family distribution for species with at least 10

243   occurrences in all plots of the particular region (following Peppler-Lisbach and Kleyer, 2009;

244   Peper et al., 2011). Model selection was done by comparing Akaike information criterion

245   (AIC) and 100 bootstrapping runs tested model robustness. This resulted in a list of HOF

246   models for 36 species in the Bernese lowland, 30 species in the Bernese Oberland, and 16

247   species in the Valais (Tab. S3).

248   To obtain reliable species response curves, the whole extent of the distribution data of a

249   species must be covered along a gradient (Lawesson and Oksanen, 2002; Normand et al.,

250   2009). Therefore, we removed species described by model I) with no response to *Rhinanthus*

251   density and model II) with a monotone sigmoid response with a maximum at one end of the

252   gradient. For the remaining species, we extracted the optimum value from the HOF model,

253   represented by the maximum predicted abundance. For model III) we selected the mid-point

254   of the plateau, and for model VII) the higher of the two modes (Fig. S2).

255

256   **Results**

257   *Rhinanthus-density effects on plant diversity*

258   Although meadows in the Bernese lowland were less species rich (mean: 11.6 species per

259   400 cm^2; min: 3; max: 27) compared with the ones at higher altitudes in the Bernese

260   Oberland (mean: 12.8; min: 5; max: 21) and the Valais (mean: 14.4; min: 6; max: 25), and the

261   *Rhinanthus* densities never reached very high levels in the two regions at high altitudes

262   Bernese Oberland (mean: 0.26 rel *Rhinanthus* biomass; min: 0; max: 0.83) and the Valais

263   (mean: 0.12; min: 0; max: 0.45) compared to the lowland (mean: 0.33; min: 0; max: 0.85),

264   the effects of an increasing *Rhinanthus* density on all diversity measures were consistent

265   among regions in most cases (indicated by the non-significant *Rhinanthus* density-by-region

266   interactions, Table 1).

267   We found significant hump-shaped relationships of total, herb and grass species richness

268   with relative *Rhinanthus* biomass (Fig. 1a, Tab. 1), with highest values at 31%, 27.4% or

269   33.6% relative *Rhinanthus* biomass, respectively. Compared with plots without *Rhinanthus*,

270   total species richness increased by 12% (1.35 species per 400 cm^2: 0.32 grass and 1.03 herb

271   species on average) at this density level. At *Rhinanthus* densities >60%, species richness was

272   even lower than in plots without *Rhinanthus* (Fig. 1a).

273   In contrast, evenness (excluding *Rhinanthus*) increased linearly with increasing relative

274   *Rhinanthus* biomass (Fig. 1b, Tab. 1).

275

276   *Rhinanthus-density relationships with environmental indicator values and community mean*

277   *traits*

278   When excluding *Rhinanthus* from the community mean trait analysis, we found no

279   significant effects of increasing *Rhinanthus* densities on abundance weighted indicator

280   values for moisture and fertility and on seed mass and SLA (Tab. S1). This indicates that

281   *Rhinanthus* did not affect the abiotic conditions to such an extent that it would translate in a

282   shift in the community mean for these measures.

283   However, community mean plant height decreased with increasing relative *Rhinanthus*

284   biomass (the quadratic relationship was also significant and plant height tends to increase

285   again at the end of the *Rhinanthus* density gradient). In addition, the relationship of

286   community mean LDMC and relative *Rhinanthus* biomass was U-shaped (Fig. S1, Tab. S1).

287

288   *Rhinanthus-density effects on individual species responses*

289   We found species to respond differently to varying *Rhinanthus* densities (Tab. S3). However,

290   no consistent patterns to separate the effects of increasing *Rhinanthus* densities on

291   functional groups were evident. As the optima of different grass species (e.g. *Bromus*

292   *erectus, Cynosurus cristatus, Dactylis glomerata, Festuca* spp., *Phleum pratense, Poa* spp.),

293   legume species (e.g. *Lathyrus pratensis, Lotus corniculatus, Medicago lupulina, Trifolium*

294   spp.) or species with tap roots (e.g. *Leontodon hispidus, Taraxacum officinale*) were

295   distributed along the whole gradient (Tab. S3; Figs. S2, S3), we were not able to identify

296   consistent trends to point out functional groups which might be suitable hosts because they

297   suffer from high *Rhinanthus* densities. However, these results underline the rather unspecific

298   host selection of *Rhinanthus*.

299

300   *Rhinanthus-density effects on functional group abundances and biomass quality*

301   Excluding *Rhinanthus* led to a biomass decrease with increasing relative *Rhinanthus* biomass

302   (Fig. 1d; Tab. 2). Biomass of herbs followed a similar U-shaped pattern with increasing

303   relative *Rhinanthus* biomass (Fig. 1f, Tab. 2), whereas the biomass of grasses decreased

304   linearly (Fig. 1e). Overall, the cumulative cover of legumes decreased linearly with increasing

305   relative *Rhinanthus* biomass (Fig. 2, Tab. 2).

306 Including *Rhinanthus* led to a U-shaped relationship between the total biomass (including

307 *Rhinanthus*) and the relative *Rhinanthus* biomass (Fig. 1c, Tab. 2). At the density level with

308 the highest species richness (31% relative *Rhinanthus* biomass), yield was on average

309 reduced by 26%.

310 In addition, neither nutrient concentrations (N, P, K, Ca, Mg) nor fibre content (neutral

311 detergent fibre NDF, acid detergent fibre ADF or lignin) varied with *Rhinanthus* density (Tab.

312 S2). This indicates that the presence of *Rhinanthus* has no effect on biomass quality of these

313 meadows.

314

315 **Discussion**

316 *Rhinanthus density effects on plant diversity and biomass*

317 Using our new gradient approach showed that the species richness-*Rhinanthus*-density

318 relationship followed an optimum curve with highest values at intermediate densities, based

319 on corresponding increases in both grass and herb diversity. In contrast, studies using the 'all

320 or nothing' approach, like Fibich et al. (2016) simply found a positive effect of the presence

321 in 11 out of 16 hemiparasites on the plant diversity of grassland communities when

322 analyzing more than 30,000 plots of the Czech National Phytosociological Database.

323 Moreover, Joshi et al. (2000) experimentally showed that the presence of *Rhinanthus*

324 *alectorolophus* in newly created grasslands in Switzerland increased species richness of

325 unsown species. Similarly, the artificial introduction of *R. minor* also increased species

326 richness of sown grasslands in England (Pywell et al., 2004; Westbury et al., 2006). However,

327 results from studies using the 'all or nothing' approach may result in misleading

328   management recommendations as they do not account for changes along the *Rhinanthus*-

329   density gradient.

330   The major mechanism promoting plant diversity seems to be the mediation of competitive

331   balances in the community and the reduced productivity of grasslands (Davies et al., 1997;

332   Smith et al., 2003; Bullock and Pywell, 2005; Mudrák et al., 2016). According to Ameloot et

333   al. (2005; meta-analysis of experimental sowing studies) and Fisher et al. (2013; introduction

334   experiment) the average reduction of vegetation biomass by *Rhinanthus* is 26%. Our findings

335   partly confirm the positive *Rhinanthus* effects on plant diversity via reduced productivity as

336   we found an increase of species richness (+12%) coinciding with a maximum biomass

337   decrease (-26%). However, this changed along the *Rhinanthus*-density gradient with

338   maximum species richness at 31% relative *Rhinanthus* biomass. At *Rhinanthus* densities

339   >60%, we found species richness dropping below the average values of plots without

340   *Rhinanthus.* This is in accordance to Gibson and Watkinson (1992; observational study in

341   combination with a *Rhinanthus*-removal experiment), who found lower species richness in

342   patches with high *R. minor* densities in diverse British meadows. Interestingly, beyond this

343   threshold, *Rhinanthus* biomass even over-compensated the loss of total biomass. A reason

344   might be the relation of these high densities to optimal environmental conditions,

345   promoting nutritious hosts (e.g. Seel and Press, 1993; Cameron et al., 2006) and thereby

346   maximizing *Rhinanthus* biomass.

347   As both grass and herb biomass decreased along the gradient and their diversity was

348   enhanced at intermediate *Rhinanthus* densities, our results indicate that *Rhinanthus*

349   parasitizes rather density-dependent than selectively. Given the rather unspecific behaviour

350   of *Rhinanthus*, which is supported by our analysis on individual species responses along the

351   *Rhinanthus* gradient where we found no consistent patterns, it might well be that the

352   belowground abundance of a host species, e.g. of species with a diffuse and wide spreading

353   root system, at least partly influences the probability of being parasitized. Accordingly, Press

354   and Phoenix (2005) stated that a parasite's host specificity might simply be an artefact of

355   host abundance, meaning that the probability of being encountered by a parasite is higher

356   for abundant host species than for less abundant ones and that parasitism is often

357   proportional to the belowground presence of a host species. However, our findings of the

358   overall linear reduction of grass biomass and legume cover support the idea that some hosts

359   with a diffuse and wide spreading root system and high nutrient content, and at the same

360   time lacking adequate defence mechanisms are better suited (e.g., Cameron et al., 2006;

361   Sandner and Matthies, 2016). This might in turn reduce the abundance of the whole

362   functional group of suitable hosts, when *Rhinanthus* densities are increasing.

363   The positive response in evenness with increasing *Rhinanthus* densities also confirm the

364   resource-availability theory and suggests that suitable host species are parasitized over-

365   proportionally, given that these hosts have a diffuse and wide spreading root system and

366   lack adequate defence mechanisms preventing penetration. Thereby competitive exclusion

367   could be prevented and coexistence with subordinate species might be promoted (Gibson

368   and Watkinson, 1992; Press, 1998; Phoenix and Press, 2005). Similar to our findings, Fibich et

369   al. (2016) found hemiparasite presence to be positively related with the evenness of plant

370   communities. In addition, Demey et al. (2015) reported a decrease in evenness after the

371   removal of *Rhinanthus*. It seems that hemiparasitic plants can play key roles in mediating the

372   competitive relationships and the stability in a plant community (Press, 1998; Pennings and

373   Callaway, 2002). Chesson (2000) described this effect as an "equalizing mechanism".

374   *Rhinanthus* densities varied among our study regions with highest mean and maximum

375   densities in the Bernese lowland. It has been shown that *Rhinanthus* performance decreases

376   with altitude (Hargreaves et al., 2015), which might be a possible explanation for these

377   regional differences. A possible explanation for the lowest density values in the meadows

378   situated in the Valais might be the considerably lower mean annual precipitation in this

379   region compared to the other two. Moreover, *Rhinanthus* densities are highly variable over

380   time (Press and Phoenix, 2005; Ameloot et al., 2006; Cameron et al., 2009) and therefore

381   one might expect a rather cyclic effect of *Rhinanthus* on plant diversity and the composition

382   of the plant community. After reaching high densities and promoting subordinate plants,

383   subsequent invasion by competitive species becomes more likely because *Rhinanthus* loses

384   its advantage when suitable hosts are no longer available. The subsequent increase of rather

385   competitive species with an extensive root system is then again beneficial for *Rhinanthus* as

386   enough resources are again available. Thus, patches with high *Rhinanthus* densities appear

387   to move through the meadow over time (Press and Phoenix, 2005; Cameron et al., 2009).

388   However, spatially explicit monitoring over several years would be required to confirm

389   whether *Rhinanthus* exhibits such cycles of temporal changes in patch density. Moreover,

390   whether the distribution patterns of *Rhinanthus* populations vary along environmental or

391   elevational gradients has not been tested, yet. In our study areas we had the impression that

392   the distribution of *Rhinanthus* changes from aggregated to more random with increasing

393   altitude. However, this needs to be tested in future studies. Until now, temporal dynamics in

394   the community composition have not yet been monitored with permanent study plots.

395   However, Cameron et al. (2009) calculated intransitive-competition networks between

396   *Rhinanthus*, grasses and forbs based on pairwise competition experiments between

397   *Rhinanthus minor* and three forbs as well as three grasses to simulate these changes over

398   time. Their models suggested fluctuating abundances of the parasite and the other

399   functional groups resulting in "shifting clouds" of *Rhinanthus* within a grassland (Cameron et

400   al., 2009). The lack of information on *Rhinanthus* densities in previous seasons is therefore a

401   limitation of our study and all other previous ones investigating the effect of *Rhinanthus* on

402   diversity and composition in only one year.

403

404   *Rhinanthus-density effects on community composition*

405   The effects of hemiparasites on vegetation structure and community mean traits were rarely

406   considered in previous studies (but see Mudrák et al., 2016). We found a decrease in

407   community mean plant height with increasing *Rhinanthus* biomass. Similarly, Mudrák et al.

408   (2016), who compared plots with *Rhinanthus minor* to plots were they had experimentally

409   removed *Rhinanthus*, also found a reduced community mean plant height in plots with

410   *Rhinanthus* present. These shifts in the community composition towards smaller plant

411   species might be explained by the stronger parasitization of rather large and competitive

412   species with large root volumes or by exerting *Rhinanthus* density-dependent control of

413   dominant plants facilitating coexistence and promoting smaller plants (Phoenix and Press,

414   2005). *Rhinanthus* performance, e.g. the individual biomass and seed production is better

415   when suitable host groups are present (Sandner and Matthies, 2016) likely leading to a

416   stronger suppression of the host in the next year. This might facilitate the establishment of

417   less competitive, e.g. smaller plant species. In addition, hemiparasitic plants are in general

418   considered to be rather weak light competitors (Matthies, 1995), especially sensitive to

419   shading during the seedling stage (Těšitel et al., 2011). Together with the dominance and

420   productivity reducing effects (Ameloot et al., 2005), smaller species and also the

421   establishment of *Rhinanthus* itself are thus likely promoted under these *Rhinanthus-*

422   engineered conditions. However, the significant quadratic relationship with plant height

423   tending to increase again at the end of the *Rhinanthus* density gradient is biologically

424   doubtful because at these high *Rhinanthus* densities only few species have a large effect on

425   the community mean plant height.

426   In contrast to Mudrák et al. (2016), who found a decrease of LDMC with *Rhinanthus minor*

427   present, we found a U-shaped LDMC vs. *Rhinanthus* density relationship. Mudrák et al.

428   (2016) assumed that this decrease might be due to the reduced grass abundance as grasses

429   have distinct trait values compared to forbs. However, as they used the 'all or nothing'

430   approach, comparing sites with and without hemiparasite the results might be not fully

431   comparable to ours. Moreover, the other investigated community mean traits such as seed

432   mass indicating colonization ability and SLA, related to fertilization and resource utilization

433   of plants (e.g. Pfestorf et al., 2013), did not differ along the *Rhinanthus*-density gradient. This

434   suggests that predominantly height as an indicator of light competition, and LDMC as an

435   indicator for changed resource use, are directly affected by *Rhinanthus*. The minor effect of

436   *Rhinanthus* on community composition is further substantiated by the absence of changes in

437   the abundance-weighted indicator values. Although hemiparasites have high transpiration

438   rates and low water use efficiencies (Phoenix and Press, 2005), this seems not to translate

439   into higher abundance or number of species that prefer drier conditions.

440

441   *Rhinanthus-density effects on biomass quality*

442   Given the small impact of *Rhinanthus* on species composition and community mean traits,

443   the absence of effects on fodder quality may not be surprising. As we are not aware of any

444   other study addressing how the quality of biomass changes with an increasing abundance of

445   (hemi-)parasitic plants, further studies are required to test whether our results hold for

446   other types of grasslands or other parasitic plants. Also testing for density effects on the

447   quality of herb and grass biomass separately might be very interesting to investigate.

448

449   *Methodological implications and perspectives for future studies*

450   Our results clearly support the use of the gradient approach instead of the 'all or nothing'

451   approach in order to account for the density-dependent role of hemiparasitic plants for the

452   functioning of plant communities. Our findings further suggest that studies using the 'all or

453   nothing' approach may result in misleading conclusions and management recommendations.

454   However, the limitation of our study and all other previous ones investigating the effect of

455   *Rhinanthus* on diversity and composition is that we captured only a snapshot of the dynamic

456   *Rhinanthus* invasion. As we only investigated one year, we cannot distinguish between

457   recently invaded plots and the ones where the parasite density had already declined

458   because of the decreasing abundance of suitable hosts. We therefore suggest establishing

459   permanent plots to monitor the dynamics of *Rhinanthus* populations over time. This would

460   further allow analysing compositional and functional changes of the host community.

461   Moreover, this might also help to find more consistent patterns of increasing *Rhinanthus*

462   densities on particular plant species. Such an observational monitoring approach might also

463   be combined with experimentally controlling *Rhinanthus* densities by seed addition in

464   established plant communities in meadows. Furthermore, including varying environmental

465   and elevational gradients in future studies would allow testing for differences in distribution

466   patterns of *Rhinanthus* populations and their effects on plant community composition along

467   these gradients in addition to changing *Rhinanthus* densities.

468

469   *Recommendations for restoration and agriculture*

470   Overall, our results highlight that the density rather than the pure presence of hemiparasites

471   is particularly important to understand and control their functional role. In summary, our

472   findings of increased plant diversity in line with a slightly lower yield but similar biomass

473   quality clearly show that *Rhinanthus* is a suitable tool for grassland restoration if its density

474   can be maintained at intermediate levels. We therefore recommend introducing *Rhinanthus*

475   into meadows for which high hay production is not the only goal, e.g. in course of agri-

476   environmental schemes aiming at a reduction of management intensity and the

477   enhancement of biodiversity.

478   But, how can intermediate *Rhinanthus* densities be maintained after successful

479   establishment? A suitable management action to control the abundance of *Rhinanthus*

480   without eradicating the whole population is early mowing before fruit ripening during one

481   year (more than one year of early mowing will likely eradicate the population; Magda et al.,

482   2004). However, Blažek and Lepš (2015) and Mudrák et al. (2014) demonstrated that

483   *Rhinanthus* abundance can be drastically reduced when a meadow is mown before seed

484   ripening and that the population depends on annual seed production. We therefore suggest

485   late mowing of strips or even leave uncut strips until the next year on 10–20% of a meadow,

486   as it has been suggested to support invertebrate diversity without detrimental effects on

487   plant diversity (van Klink et al., 2017). These uncut strips might act as refuge to preserve the

488   seed source and thereby maintain the *Rhinanthus* population in a meadow.

489

490   **Funding**

502

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674 **Table 1**: Summary of linear mixed effect models testing the effects of relative *Rhinanthus*

675 biomass (including quadratic term when significant) on plant diversity in 47 grasslands in

676 Switzerland. R^2 denotes the squared correlation coefficient between predicted and observed

677 values.

| | | Species richness | | | | | | Evenness | |
| | | Total | | Herbs | | Grasses | | Total | |
	df	F	p	F	p	F	p	F	p
(Intercept)	1	1358.6	**< 0.001**	1054.7	**< 0.001**	619.2	**< 0.001**	8348.1	**< 0.001**
Region	2	3.0	0.060	2.9	**0.064**	0.9	0.426	10.5	**< 0.001**
Observer	2	6.1	**0.003**	6.7	**0.001**	1.2	0.292	1.2	0.313
rel. *Rhinanthus* biomass linear	1	2.2	0.135	0.3	0.597	6.1	**0.014**	12.4	**< 0.001**
rel. *Rhinanthus* biomass quadratic	1	16.5	**< 0.001**	11.0	**0.001**	7.3	**0.007**	–	–
Region × rel. *Rhinanthus* biomass linear	2	2.3	0.102	0.9	0.396	2.8	0.063	1.0	0.364
Region × rel. *Rhinanthus* biomass quadratic	2	0.2	0.796	0.2	0.789	0.1	0.926	–	–
		R^2=0.47		R^2=0.43		R^2=0.39		R^2=0.25	

678

679

680 **Table 2**: Summary of linear mixed effect models testing the effects of relative *Rhinanthus*

681 biomass (including quadratic term when significant) on biomass and cumulative percentage

682 cover of legumes in 47 grasslands in Switzerland. R^2 denotes the squared correlation

683 coefficient between predicted and observed values.

| | | Biomass | | | | | | | | Cover | |
| | | Total | | Excl. *Rhinanthus* | | Herbs | | Grasses | | Legumes | |
	df	F	p	F	p	F	p	F	p	F	p
(Intercept)	1	494.9	**< 0.001**	540.6	**< 0.001**	323.5	**< 0.001**	140.4	**< 0.001**	146.435	**< 0.001**
Region	2	1.4	0.255	3.9	**0.028**	7.8	**0.001**	0.6	0.560	2.381	0.104
rel. *Rhinanthus* biomass linear	1	6.0	**0.015**	186.9	**< 0.001**	64.1	**< 0.001**	62.1	**< 0.001**	4.052	**0.045**
rel. *Rhinanthus* biomass quadratic	1	11.7	**< 0.001**	13.4	**< 0.001**	4.3	**0.040**	4.1	0.044	-	-
Region × rel. *Rhinanthus* biomass linear	2	0.8	0.470	1.2	0.305	2.9	0.056	1.1	0.327	0.994	0.371
Region × rel. *Rhinanthus* biomass quadratic	2	0.1	0.899	0.1	0.873	1.4	0.242	2.0	0.142	-	-
		R^2= 0.42		R^2= 0.52		R^2= 0.35		R^2= 0.40		R^2= 0.33	

684

Figures

Figure 1. Relationships between A) species richness, B) evenness C) total biomass, D) biomass without *Rhinanthus*, E) biomass of grasses, and F) biomass of herbs and relative *Rhinanthus* biomass in nine plots in each of 47 meadows in three regions in Switzerland. Open circles indicate plots from Bernese lowland, triangles from Valais and plus signs from Bernese Oberland. Linear or curve-linear regressions are indicated for all data (bold black) and the three study regions Bernese lowland (thin black), Bernese Oberland (dark grey), Valais (light grey), separately. The regions were only fitted separately when they differed significantly from each other. In these cases, the lines/curves are limited to the maximum extent of *Rhinanthus* density in the particular regional data set.

Figure 2. Relationship between the cumulative percentage cover of legumes and the relative *Rhinanthus* biomass in nine plots in each of 47 meadows in three regions in Switzerland. Open circles indicate plots from Bernese lowland, triangles from Valais and plus signs from Bernese Oberland.

702

703 **Figure 1.**
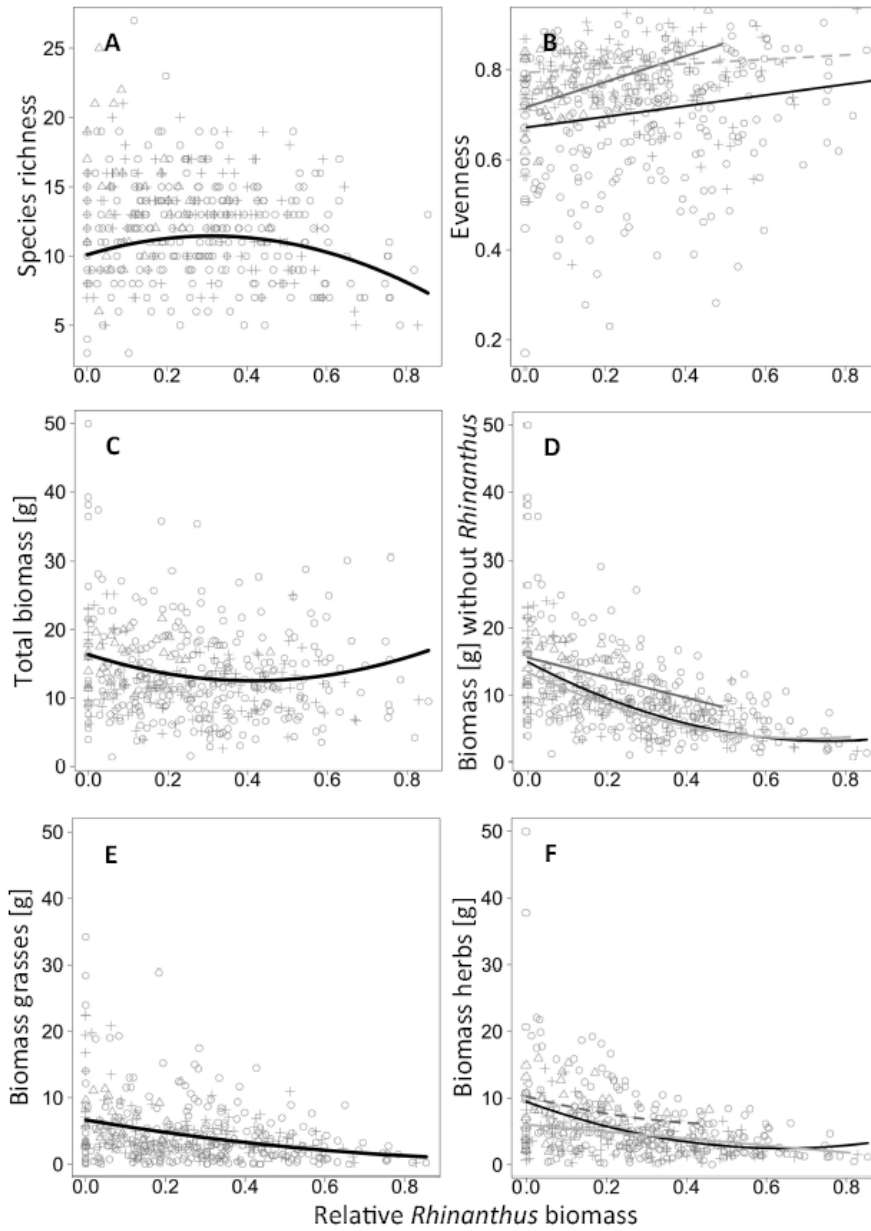
Figure 2.
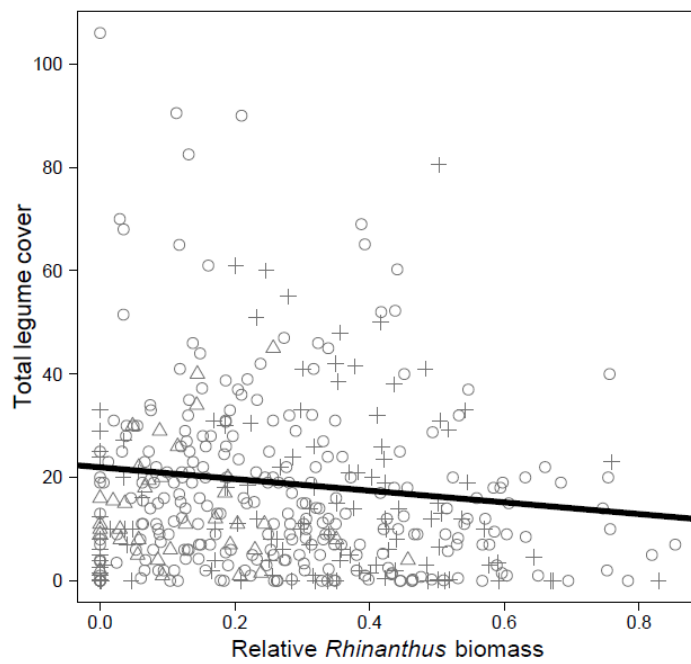
708 **Appendix**

709 **Table S1.** Summary of linear mixed effect models testing the effects of relative *Rhinanthus*

710 biomass (including quadratic term when significant) on mean environmental indicator values

711 and on the community mean traits specific leaf area (SLA) and leaf dry matter content

712 (LDMC) in 47 grasslands in Switzerland. R^2 denotes the squared correlation coefficient

713 between predicted and observed values.

Community excluding *Rhinanthus*

	df	Moisture value F	p	Nutrient value F	p	Seed mass F	p	Plant height F	p	SLA F	p	LDMC F	p
(Intercept)	1	10806.0	**< 0.001**	6949.8	**< 0.001**	285.5	**< 0.001**	1219.4	**< 0.001**	7310.1	**< 0.001**	2518.7	**< 0.001**
Region	2	2.3	0.116	0.0	0.986	1.5	0.234	1.6	0.214	3.7	**0.032**	0.6	0.539
rel. *Rhinanthus* biomass linear	1	0.1	0.742	0.9	0.355	3.4	0.067	14.0	**< 0.001**	2.0	0.160	2.5	0.116
rel. *Rhinanthus* biomass quadratic	1	-	-	-	-	-	-	4.8	**0.029**	-	-	4.5	**0.035**
Observer	2	0.4	0.646	0.3	0.710	1.2	0.288	1.2	0.309	1.2	0.294	0.3	0.724
Region × rel. *Rhinanthus* biomass linear	2	1.1	0.319	0.2	0.795	0.3	0.732	1.5	0.217	1.2	0.313	0.4	0.699
Region × rel. *Rhinanthus* biomass quadratic	2	-	-	-	-	-	-	1.3	0.264	-	-	0.8	0.459
		R^2 =0.36		R^2 =0.38		R^2 =0.21		R^2 =0.43		R^2 =0.42		R^2 =0.34	

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718   **Table S2.** Summary of linear mixed effect models testing the effects of relative *Rhinanthus*

719   biomass on measures of biomass quality in 47 grasslands in Switzerland. C (carbon), nitrogen

720   (N), phosphorus (P), Ca (calcium), K (potassium), Mg (magnesium), ADF (acid detergent

721   fibre), ADL (lignin), and NDF (neutral detergent fibre). Quadratic terms were excluded

722   because they were not significant. R^2 denotes the squared correlation coefficient between

723   predicted and observed values.

	df	C		N		P		Ca		K		Mg		ADF		ADL		NDF	
		F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p
(Intercept)	1	856087.9	**<0.001**	2428.6	**<0.001**	3104.3	**<0.001**	2385.8	**<0.001**	6893.7	**<0.001**	20793.2	**<0.001**	5444.4	**<0.001**	7313.6	**<0.001**	5054.2	**<0.001**
Region	2	8.3	**0.001**	6.6	**0.003**	12.1	**<0.001**	5.9	**0.006**	3.5	**0.040**	6.2	**0.004**	9.3	**<0.001**	3.6	**0.034**	5.6	**0.007**
rel. *Rhinanthus* biomass linear	1	1.3	0.256	1.1	0.293	0.1	0.776	0.3	0.566	2.3	0.133	0.1	0.703	0.4	0.506	2.9	0.092	1.5	0.228
Region × rel. *Rhinanthus* biomass linear	2	1.0	0.376	2.1	0.111	1.4	0.245	1.3	0.270	0.5	0.617	1.0	0.370	1.0	0.985	0.6	0.560	0.6	0.524
		$R2 = 0.61$		$R2 = 0.61$		$R2 = 0.66$		$R2 = 0.42$		$R2 = 0.19$		$R2 = 0.52$		$R^2 = 0.74$		$R2 = 0.45$		$R2 = 0.51$	

726   **Table S3.** Parameters of the response curves (optimum, minimum, maximum, range and

727   mean), the applied eHOF model (III monotone sigmoid with a plateau, IV unimodal

728   symmetric, V unimodal skewed, VI bimodal with equal maxima, VII bimodal with different

729   maxima) and its parameters (a-d), using percentage cover (abundance) data of the species

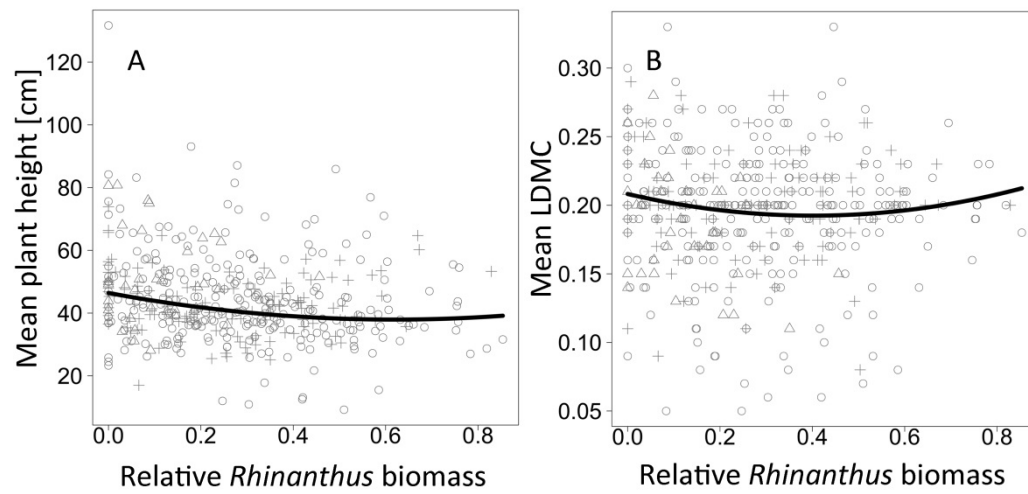730   with at least 10 occurrences in each of the three study regions.

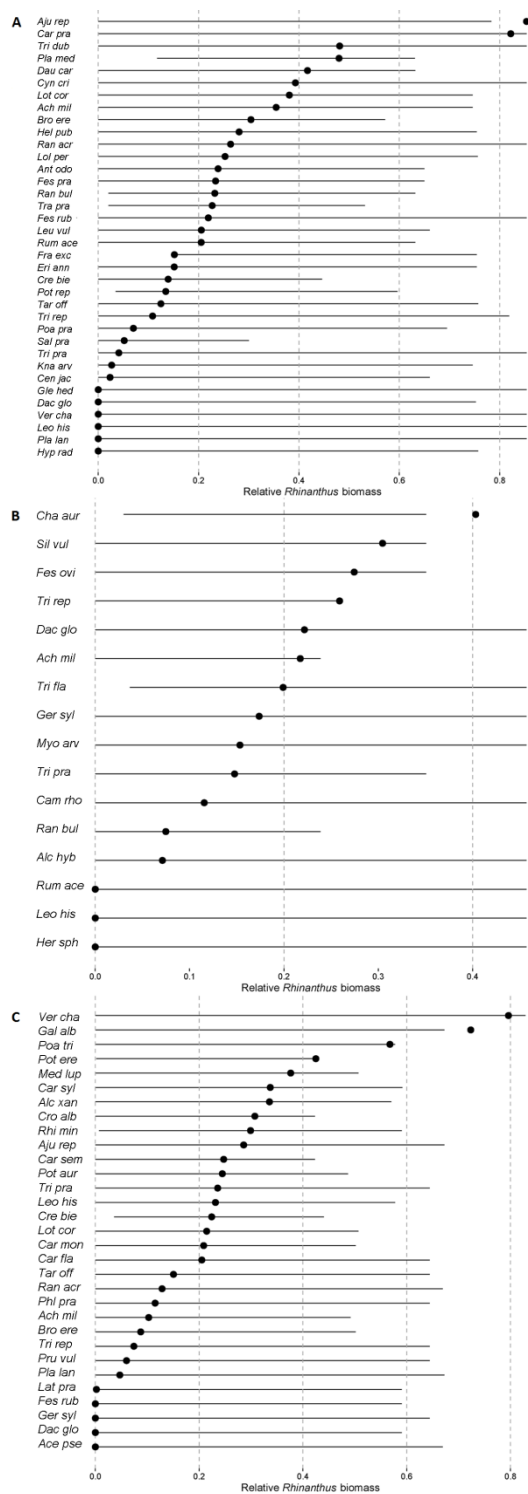| Species	Opt	Min	Max	Range	Mean	Model	a	b	c	d
Bernese lowland										
Dactylis glomerata	0.0	0.0	0.8	0.8	0.3	III	-32.9	100.0	3.9	-
Glechoma hederacea	0.0	0.0	0.9	0.9	0.3	VII	-45.9	100.0	48.6	14.8
Hypochaeris radicata	0.0	0.0	0.8	0.8	0.3	VII	-3.3	8.3	7.3	0.2
Leontodon hispidus	0.0	0.0	0.9	0.9	0.3	III	-4.5	8.9	2.8	-
Plantago lanceolata	0.0	0.0	0.9	0.9	0.3	VII	-2.2	6.1	4.6	-0.9
Veronica chamaedrys	0.0	0.0	0.9	0.9	0.3	VII	-17.8	0.2	4.6	0.9
Centaurea jacea	0.0	0.0	0.7	0.7	0.2	VII	-1.9	100.0	3.5	0.0
Knautia arvensis	0.0	0.0	0.7	0.7	0.2	V	2.6	7.7	0.6	100.0
Trifolium pratense	0.0	0.0	0.9	0.9	0.3	V	1.9	1.3	0.4	100.0
Salvia pratensis	0.1	0.0	0.3	0.3	0.1	IV	0.3	13.6	2.0	-
Poa pratensis	0.1	0.0	0.7	0.7	0.2	IV	-3.2	59.1	6.5	-
Trifolium repens	0.1	0.0	0.8	0.8	0.3	VII	1.5	1.1	59.3	-1.6
Taraxacum officinale agg.	0.1	0.0	0.8	0.8	0.3	V	1.8	4.5	1.5	19.1
Potentilla reptans	0.1	0.0	0.6	0.6	0.3	VI	-0.9	21.2	5.8	0.5
Crepis biennis	0.1	0.0	0.4	0.4	0.2	IV	-14.8	100.0	17.9	-
Erigeron annuus	0.2	0.0	0.8	0.8	0.3	IV	-16.2	100.0	19.2	-
Fraxinus excelsior	0.2	0.1	0.8	0.6	0.3	IV	-15.7	100.0	19.8	-
Leucanthemum vulgare agg.	0.2	0.0	0.7	0.7	0.2	IV	-22.9	100.0	25.2	-
Rumex acetosa	0.2	0.0	0.6	0.6	0.3	IV	0.8	7.3	4.3	-
Festuca rubra agg.	0.2	0.0	0.9	0.9	0.3	VI	-0.2	6.1	2.9	1.0
Tragopogon pratensis	0.2	0.0	0.5	0.5	0.2	IV	-1.6	15.7	6.8	-
Ranunculus bulbosus	0.2	0.0	0.6	0.6	0.3	IV	-0.3	10.8	5.5	-
Festuca pratensis	0.2	0.0	0.7	0.7	0.3	V	-26.6	100.0	28.2	100.0
Anthoxanthum odoratum	0.2	0.0	0.7	0.7	0.3	IV	0.5	6.8	4.3	-
Lolium perenne	0.3	0.0	0.8	0.8	0.3	IV	4.9	-8.2	0.0	-
Ranunculus acris	0.3	0.0	0.9	0.9	0.3	V	-2.3	9.0	4.7	5.8
Helictotrichon pubescens	0.3	0.0	0.8	0.8	0.3	VI	-30.9	100.0	34.9	0.5
Bromus erectus	0.3	0.0	0.6	0.6	0.3	VI	-21.6	63.9	24.0	-0.4
Achillea millefolium agg.	0.4	0.0	0.7	0.7	0.3	IV	-1.4	7.2	4.6	-
Lotus corniculatus	0.4	0.0	0.7	0.7	0.3	V	-0.8	7.1	5.2	10.5
Cynosurus cristatus	0.4	0.0	0.9	0.9	0.4	IV	-18.6	45.0	22.9	0.5
Daucus carota	0.4	0.0	0.6	0.6	0.3	VII	-6.2	16.4	10.0	-0.4
Plantago media	0.5	0.1	0.6	0.5	0.3	VII	-56.2	100.0	56.2	-0.3
Trifolium dubium	0.5	0.0	0.9	0.9	0.3	IV	0.1	3.0	3.5	-
Cardamine pratensis	0.8	0.0	0.9	0.9	0.4	IV	-96.2	100.0	96.5	-
Ajuga reptans	0.9	0.0	0.8	0.8	0.3	VII	-100.0	4.5	7.6	17.7
Valais										
Heracleum sphondylium	0.0	0.0	0.5	0.5	0.1	VII	1.6	0.4	-1.6	0.1
Leontodon hispidus	0.0	0.0	0.5	0.5	0.1	VII	-6.8	17.4	6.9	1.0
Rumex acetosa	0.0	0.0	0.5	0.5	0.1	VI	3.0	29.9	-28.0	2.0
Alchemilla hybrida agg.	0.1	0.0	0.5	0.5	0.1	III	-33.4	100.0	2.8	-
Ranunculus bulbosus	0.1	0.0	0.2	0.2	0.1	IV	-16.3	100.0	16.5	-
Campanula rhomboidalis	0.1	0.0	0.5	0.5	0.1	V	-4.6	16.9	4.2	7.6
Trifolium pratense	0.1	0.0	0.4	0.4	0.1	VII	-8.5	26.5	8.7	-0.2
Myosotis arvensis	0.2	0.0	0.5	0.5	0.2	VII	-66.7	65.3	67.9	-0.7
Geranium sylvaticum	0.2	0.0	0.5	0.5	0.1	V	-1.3	40.0	1.6	0.3
Trisetum flavescens	0.2	0.0	0.5	0.4	0.2	VI	-3.9	12.0	6.6	0.7
Achillea millefolium agg.	0.2	0.0	0.2	0.2	0.1	IV	-0.2	3.6	3.2	-
Dactylis glomerata	0.2	0.0	0.5	0.5	0.1	VII	-17.1	36.6	18.4	9.3
Trifolium repens	0.3	0.0	0.3	0.3	0.1	IV	-57.4	100.0	55.9	-
Festuca ovina agg.	0.3	0.0	0.4	0.4	0.1	VII	-1.3	11.8	1.8	0.5
Silene vulgaris	0.3	0.0	0.4	0.4	0.1	VII	-47.0	64.5	39.0	69.8
Chaerophyllum aureum	0.4	0.0	0.4	0.3	0.2	V	-91.9	100.0	4.6	5.3
Bernese Oberland										
Dactylis glomerata	0.0	0.0	0.6	0.6	0.2	VI	2.2	5.2	-18.0	4.9
Geranium sylvaticum	0.0	0.0	0.6	0.6	0.2	VI	2.5	4.4	-10.2	4.1
Festuca rubra agg.	0.0	0.0	0.6	0.6	0.2	VII	2.9	1.7	-3.6	0.5
Lathyrus pratensis	0.0	0.0	0.6	0.6	0.3	III	-1.6	100.0	2.4	-
Plantago lanceolata	0.0	0.0	0.7	0.7	0.3	VII	3.4	2.0	-48.4	0.5
Prunella vulgaris	0.1	0.0	0.6	0.6	0.3	V	3.7	6.4	4.6	100.0
Trifolium repens	0.1	0.0	0.6	0.6	0.3	V	2.4	3.6	2.5	58.7
Bromus erectus	0.1	0.0	0.5	0.5	0.2	III	-4.4	11.0	3.3	-
Achillea millefolium agg.	0.1	0.0	0.5	0.5	0.2	V	-2.4	36.4	6.9	51.1
Phleum pratense	0.1	0.0	0.6	0.6	0.2	VII	-3.0	-100.0	2.8	0.2
Ranunculus acris	0.1	0.0	0.7	0.7	0.3	V	-0.8	7.7	2.8	5.1
Taraxacum officinale agg.	0.2	0.0	0.6	0.6	0.2	VI	-2.7	18.5	4.1	0.4
Carex flacca	0.2	0.0	0.6	0.6	0.3	VII	-4.0	19.4	5.6	0.3
Carex montana	0.2	0.0	0.5	0.5	0.2	IV	-1.7	14.6	5.7	-
Lotus corniculatus	0.2	0.0	0.5	0.5	0.3	VII	-3.4	17.3	5.4	0.3
Crepis biennis	0.2	0.0	0.4	0.4	0.3	III	-56.3	100.0	4.5	-
Leontodon hispidus	0.2	0.0	0.6	0.6	0.2	IV	-0.9	5.6	2.2	-
Trifolium pratense	0.2	0.0	0.6	0.6	0.3	III	-13.5	19.9	2.9	-
Potentilla aurea	0.2	0.0	0.5	0.5	0.2	VII	-3.2	16.9	6.8	-0.5
Carex sempervirens	0.2	0.0	0.4	0.4	0.2	V	-30.8	100.0	11.6	34.7
Ajuga reptans	0.3	0.0	0.7	0.7	0.3	IV	0.2	4.1	3.1	-
Rhinanthus minor	0.3	0.0	0.6	0.6	0.3	V	-2.2	11.7	8.1	23.0
Crocus albiflorus	0.3	0.0	0.4	0.4	0.2	VII	-6.4	22.0	10.1	2.0
Alchemilla xanthochlora agg.	0.3	0.0	0.6	0.6	0.3	V	-2.1	7.9	4.3	-0.8
Carex sylvatica	0.3	0.0	0.6	0.6	0.3	IV	-1.9	9.1	5.5	-
Medicago lupulina	0.4	0.0	0.5	0.5	0.2	IV	-2.0	8.1	5.4	-
Potentilla erecta	0.4	0.0	0.4	0.4	0.2	V	-49.9	100.0	52.6	100.0
Poa trivialis	0.6	0.0	0.6	0.6	0.3	III	34.8	-100.0	3.7	-
Galium album	0.7	0.0	0.7	0.7	0.3	IV	-92.2	100.0	82.3	-
Veronica chamaedrys	0.8	0.0	0.8	0.8	0.3	VII	-10.6	12.0	12.5	29.1

731

732 **Figure S1.** The relationship between A) community mean plant height and B) community

733 mean leaf dry matter content (LDMC) and relative *Rhinanthus* biomass in nine plots in each

734 of 47 meadows in three regions in Switzerland. Open circles indicate plots from Bernese

735 lowland, triangles from Valais and plus signs from Bernese Oberland.

736

737 **Figure S2.** Species ranges and optima along the *Rhinanthus*-density gradient for the species

738 with at least 10 occurrences in each of the three study regions (A) Bernese lowland, (B)

739 Valais and (C) Bernese Oberland, and a species response curve different from model I (no
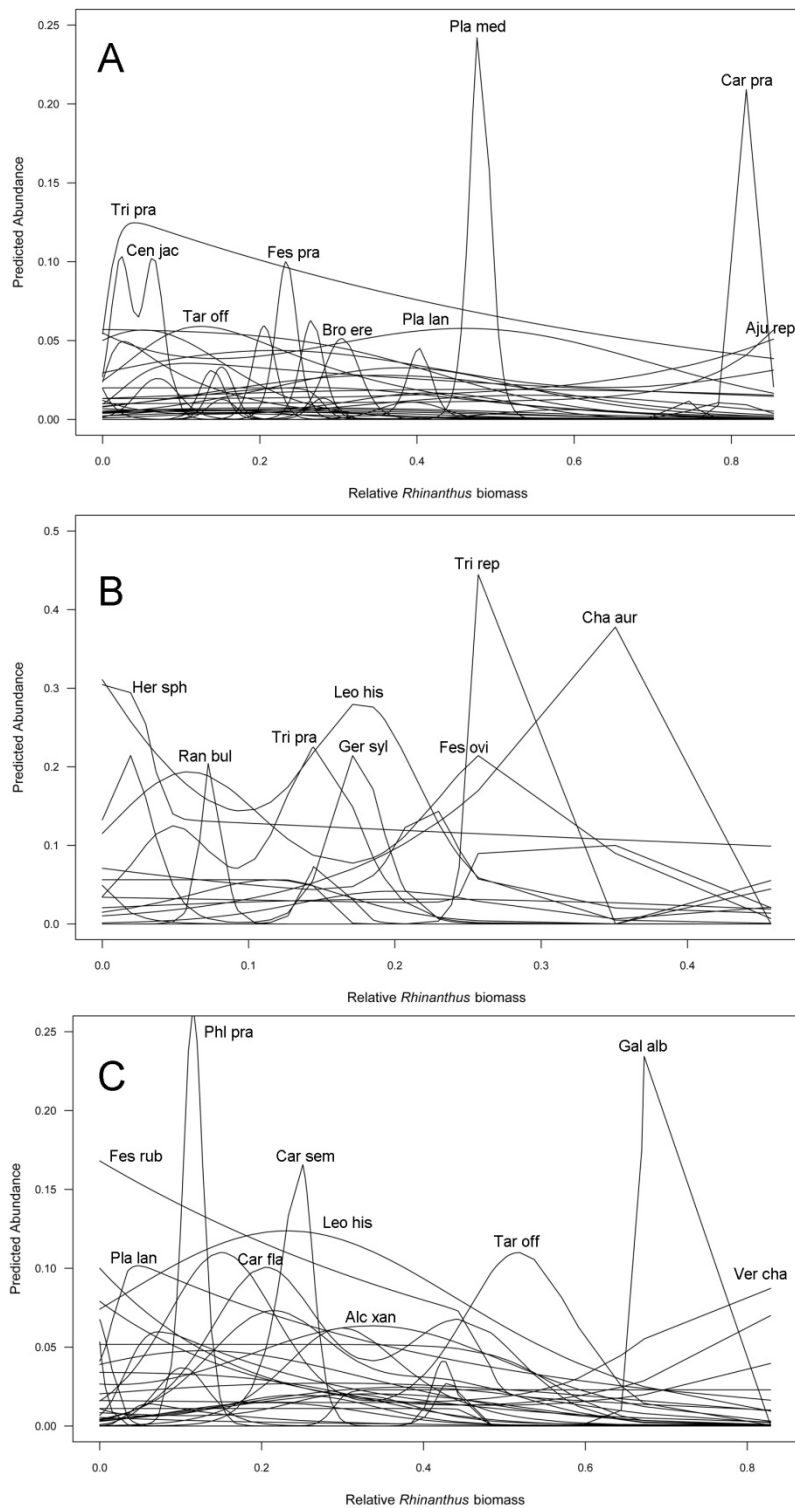
740 response) or model II (monotone sigmoid).

741

742 **Figure S3.** Response curves of species with at least 10 occurrences in each of the three study

743 regions (A) Bernese lowland, (B) Valais and (C) Bernese Oberland along the *Rhinanthus*-

744 density gradient. The parameters of the species response curves and the eHOF model are

745 summarized in Table S3.

747

748 **Figure S1.**

750

751   **Figure S2.**

753

Figure S3.