


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

Journal Article**Author(s):**

Heer, Nico; Klimmek, Fabian; Zwahlen, Christoph; Fischer, Markus; Hölzel, Norbert; [Klaus, Valentin](#) ; Kleinebecker, Till; Prati, Daniel; Boch, Steffen

Publication date:

2018-06

Permanent link:

<https://doi.org/10.3929/ethz-b-000246240>

Rights / license:

[Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International](#)

Originally published in:

Perspectives in Plant Ecology, Evolution and Systematics 32, <https://doi.org/10.1016/j.ppees.2018.01.004>

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

2

3 Nico Heer¹, Fabian Klimmek¹, Christoph Zwahlen¹, Markus Fischer^{1,2}, Norbert Hölzel³,

4 Valentin H. Klaus^{3,5}, Till Kleinebecker³, Daniel Prati¹, Steffen Boch^{1,2,4}

5 1 Institute of Plant Sciences, University of Bern, 3013 Bern, Switzerland

6 2 Botanical Garden, University of Bern, 3013 Bern, Switzerland

7 3 Institute of Landscape Ecology, University of Münster, 48149 Münster, Germany

8 4 Swiss Federal Institute for Forest, Snow and Landscape Research WSL, 8903 Birmensdorf, Switzerland

9 5 ETH Zürich, Institute of Agricultural Sciences, 8092 Zürich, Switzerland

10

11 Corresponding author:

12 Steffen Boch, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, 8903

13 Birmensdorf, Switzerland, e-mail: steffen.boch@wsl.ch

14

15 **Abstract**

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

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

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

19 interspecific competition by parasitizing selectively on competitive species and promote

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

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

22 which is still subject to debate.

23 The majority of previous studies simply compared sites with and without hemiparasites.
24 However, as hemiparasite effects are most likely density-dependent, we present a novel
25 approach assessing the effect of *Rhinanthus alectorolophus* density on grassland plant
26 diversity, yield and biomass quality. Moreover, we investigated whether functional plant
27 composition and community mean traits are affected, which has been largely neglected in
28 previous studies.

29 The relationship between species richness and relative *Rhinanthus* biomass followed an
30 optimum curve with highest values at 31% relative *Rhinanthus* biomass. At this *Rhinanthus*-
31 biomass level, species richness was increased by 12% and yield decreased by 26% compared
32 with plots without *Rhinanthus*. At relative *Rhinanthus* biomass > 60%, species richness was
33 even lower than in plots without *Rhinanthus*. Overall, the biomass of grasses and the
34 cumulative cover of legumes decreased linearly with increasing relative *Rhinanthus* biomass.
35 Community mean trait analysis revealed that an increasing *Rhinanthus* density shifts the
36 community composition towards smaller plant species. Biomass quality was not affected by
37 increasing relative *Rhinanthus* biomass.

38 In summary, our results of increased plant diversity – in line with a slightly lower yield but
39 similar biomass quality – indicate that *Rhinanthus* is a suitable biological tool for grassland
40 restoration.

41

42 **Keywords**

43 Biomass quality; community mean traits; Near Infrared Spectroscopy; *Rhinanthus*
44 *alectorolophus*; yield

45

46 **Introduction**

47 In Central Europe, land-use intensification has led to homogenous grassland communities
48 with only few highly competitive species and a loss of the overall diversity and ecosystem
49 functions (Wesche et al., 2012; Allan et al., 2014; Soliveres et al., 2016; Gossner et al., 2016).
50 To reverse this trend, low intensity farming is currently promoted by agri-environmental
51 schemes (e.g. Kleijn et al., 2009) to restore diverse and highly valuable grassland ecosystems.
52 However, high residual soil fertility is a key factor limiting restoration success (Pywell et al.,
53 2007, Klaus et al. 2011). Various attempts to overcome this problem have been suggested:
54 Nutrient removal by frequent mowing or grazing tends to be slow and, particularly in the
55 case of phosphorus, ineffective (Bullock and Pywell, 2005), whereas the more
56 straightforward removal of top-soil is effective but costly (Hölzel & Otte 2003, Mudrak et al.,
57 2014). An alternative and cost-effective tool for grassland restoration counteracting the
58 inhibitive effects of dominant species is the introduction of native parasitic plants into these
59 ecosystems (Davies et al., 1997; Smith et al., 2003; Mudrak et al., 2014).

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

70 adequate defence mechanisms preventing penetration and access to the xylem have been
71 suggested to be better-suitable hosts (Seel and Press, 1993; Matthies, 1996; Ameloot et al.,
72 2005; Cameron et al., 2006). They are able to reduce interspecific competition by parasitizing
73 competitive species or by exerting density-dependent control of dominant plants, thereby
74 facilitating coexistence and promoting the stability of natural communities (Phoenix and
75 Press, 2005; Těšitel et al., 2015a). Moreover, it has been suggested that in particular annual
76 hemiparasites can create gaps after senescence, which in turn promotes the establishment
77 of other species (Joshi et al., 2000; Bullock and Pywell, 2005; but see also Davies et al.,
78 1997). *Rhinanthus* spp. have been recommended as tool for grassland restoration as they
79 are a natural part of European grasslands. In addition, because they are annuals, their
80 density can be controlled easily by mowing before seed ripening (Magda et al., 2004; Bullock
81 and Pywell, 2005; Westbury et al., 2006; Mudrak et al., 2014). Today, *Rhinanthus* spp. are
82 already part of seed mixtures for biodiversity promoting areas (BPA) in Switzerland.
83 However, whether effects on plant diversity are positive (e.g. Bardgett et al., 2006; Fibich et
84 al., 2016) or negative (Gibson and Watkinson, 1992) is still unclear (see also Ameloot et al.,
85 2005 for a meta-analysis).

86 Similarly, while most studies found *Rhinanthus* to reduce community biomass (Ameloot et
87 al., 2005, 2006), some studies found a biomass increase (Joshi et al., 2000). The intuitive
88 expectation of many farmers is a reduction of yield by the presence of hemiparasites, which
89 makes *Rhinanthus* very unpopular for them (Magda et al., 2004; Ameloot et al., 2006).

90 Related to this, it is often presumed that *Rhinanthus* reduces the nutritional value of the
91 yield with severe losses in fodder quality. Such fodder quality decreases might be driven by
92 changes in the functional plant composition of infested grasslands and should then be
93 reflected by changes in nitrogen, mineral and fibre contents in plant biomass. However, as

94 this has not been tested systematically, it remains dubious whether hemiparasites indeed
95 affect biomass quality.

96 Moreover, the functional role of hemiparasites in grasslands is still unclear (see Queded et
97 al., 2003). As they are known for their low nutrient and water-use efficiency (Phoenix and
98 Press, 2005) one can assume that they may affect the abiotic environment, which might be
99 reflected by changes in mean environmental indicator values of the vegetation, e.g. for
100 moisture and nutrient availability (e.g. Landolt, 2010). In addition, whether hemiparasites
101 affect plant community structure and composition, indicated by changes in functional groups
102 and community mean traits was also largely neglected in previous studies (but see Demey et
103 al., 2015; Mudrak et al., 2016). In particular, one can assume changes in resource related
104 community mean traits such as specific leaf area and leaf dry matter content as well as
105 competition related ones such as mean plant height or dispersal and colonization related
106 ones such as seed mass.

107 So far, studies investigating hemiparasite effects on grasslands used an ‘all or nothing’
108 approach, comparing sites with and without hemiparasites (e.g. Gibson and Watkinson,
109 1992; Stein et al., 2009; Mudrak and Lepš, 2010). However, this approach may not be fully
110 informative as it does not take the variation in *Rhinanthus* density into account, although
111 hemiparasite effects are most likely density-dependent. Thus, it is unclear whether there is a
112 *Rhinanthus*-density-grassland plant diversity optimum. In addition, different sites may not be
113 fully comparable as they might differ in environmental conditions and not only the presence
114 of the hemiparasite. It has been shown that the abiotic site conditions such as water and
115 nutrient availability have profound interactive effects on hemiparasite and host biomass and
116 fitness (Těšitel et al., 2015b). Thus, in studies showing decreases in productivity in the
117 presence of *Rhinanthus* (e.g. Davies et al., 1997) it remains unclear whether *Rhinanthus*

118 drives this decrease or simply prefers low-productive conditions (Ameloot et al., 2005;
119 Bullock and Pywell, 2005).

120 Here, we present results from an alternative approach testing whether varying *Rhinanthus*
121 *alctorolophus* densities affect the plant diversity, plant community composition,
122 productivity and biomass quality along *Rhinanthus*-density gradients within sites. Studying
123 density effects within a site instead of between sites ensures similar environmental
124 conditions among the replicates. Furthermore, to more explicitly explain plant community
125 patterns and test for individual species responses along the *Rhinanthus* gradient, we used
126 hierarchical Huisman-Olff-Fresco (HOF) models, a novel approach for modelling species
127 response curves.

128 We therefore conducted a multi-site study, investigating 47 sites in three distinct regions in
129 Switzerland allowing us to draw more general conclusions than investigating only a single
130 region. This may further allow us to draw recommendations on the suitability of *Rhinanthus*
131 in grassland restoration. In particular, we tested whether and how increasing *Rhinanthus*
132 *alctorolophus* density affects 1) plant diversity, 2) species composition reflected by
133 community mean functional traits and environmental indicator values, and 3) grassland
134 productivity and biomass quality.

135

136 **Methods**

137 *Study system*

138 To enhance representativeness and generality of results and conclusions, we conducted our
139 study in 47 meadows in three distinct regions in Switzerland: Bernese lowland ($N=30$), the
140 Bernese Oberland ($N=13$) and the Valais ($N=4$). Sites were selected by accurate point

141 coordinates on the occurrence of *Rhinanthus alectorolophus* provided by Info Flora
142 (www.infoflora.ch), the national data and information center of the Swiss flora, as well as by
143 own observations. All sites were non-intensively managed meadows which could be
144 assigned to communities of the Arrhenatherion alliance in the Bernese lowland and mainly
145 to communities of the Polygono-Trisetion alliance in the two regions in higher altitudes
146 (sensu Delarze et al., 2015). We considered a site to be suitable if it was well accessible, not
147 mown when the vegetation was assessed and when *Rhinanthus alectorolophus* was present
148 in varying densities. In addition, the site had to be visually homogeneous, e.g. that it could
149 be assigned to one vegetation type. Altitude ranged from 504 m.a.s.l. (Bernese lowland) to
150 1946 m.a.s.l. (Schynige Platte, Bernese Oberland). The maximum geographic distance
151 between the regions was approximately 80 km. Mean annual precipitation varies among the
152 regions with around 700 mm in the Valais, 1000 mm in the Bernese lowland and 2000 mm in
153 the Bernese Oberland.

154

155 *Vegetation and biomass data*

156 Between mid-May and beginning of June 2015, we sampled the meadows in the Bernese
157 lowland, in mid-June the ones in Valais and between mid and end of June the ones in the
158 Bernese Oberland, to account for the different developmental stages of the vegetation along
159 the altitudinal gradient. Within each meadow, we placed nine 20 cm × 20 cm plots along a
160 density gradient of *Rhinanthus alectorolophus* (named *Rhinanthus* hereafter). For this, we
161 first visually subdivided each grassland in zones with low, medium and high *Rhinanthus*
162 density and randomly placed three plots in each zone to maximize the range from a
163 minimum (mostly equivalent with the absence) to a maximum *Rhinanthus* density within
164 each meadow (up to 95% *Rhinanthus* cover), ensuring that plots were distributed across the

165 whole meadow and that two plots of the same density class were not situated in the same
166 *Rhinanthus* patch. We chose small sample quadrats of 400 cm² because the parasitic effects
167 on host plants is limited to the close neighbourhood of the parasite (host plants are only
168 affected within 10 cm of the parasite; Gibson and Watkinson, 1992) and this plot size has
169 been already used in many previous studies (e.g., Pywell et al., 2004; Ameloot et al., 2006;
170 Mudrak et al., 2016). In each of the resulting 423 plots, we identified all vascular plant
171 species and estimated their percentage cover and the cover of bare ground.

172 We then harvested the aboveground biomass, separated *Rhinanthus*, other herb and grass
173 species, dried the samples for 48 h at 80 °C and weighed them separately with 0.01 g
174 precision. After this, we again pooled the three biomass samples of each of the nine plots
175 per meadow and ground them to pass a 0.5 mm sieve to test for variation of biomass quality
176 along the *Rhinanthus*-density gradient.

177 As indications for biomass quality, we analysed the ground biomass samples for nitrogen (N),
178 phosphorus (P), calcium (Ca), magnesium (Mg), potassium (K), carbon (C), neutral detergent
179 fibre (NDF), acid detergent fibre (ADF), and lignin (ADL) by means of near infrared
180 reflectance (NIR) spectroscopy (Foley et al., 1998). We recorded the reflectance spectrum of
181 each sample between 1250 to 2350 nm at 1 nm intervals. Each sample scan consisted of 24
182 single measurements, which we averaged to one spectrum. Biomass nutrient concentrations
183 and fibre contents derived from calibration models previously established. For
184 methodological details on NIR spectral analyses, calibration models and the laboratory
185 reference measurements see Kleinebecker et al. (2011).

186

187 *Community weighted mean traits and environmental indicator values*

188 We requested data from the TRY – Plant Trait Database (Kattge et al., 2011) and the Seed
189 Information Database (SID; Royal Botanic Gardens Kew, 2016) to compute community mean
190 traits of seed mass, plant height, specific leaf area (SLA) and leaf dry matter content (LDMC).
191 Data was available for all herbaceous species (212 out of 231). We excluded woody species
192 (19 out of 231) from community mean trait calculations because they only occurred as
193 seedlings and play no significant role in mown grasslands but might strongly affect traits like
194 average plant height and seed mass. For each species trait, we computed the median value
195 of all data base records. We then used the abundance-weighted community mean of each
196 trait per plot for further analyses.

197 Moreover, we calculated abundance weighted indicator values for moisture and fertility
198 (values ranging from 1 to 5; see Landolt, 2010) of each plot. Indicator values give the
199 position of the realized niche of plant species and by averaging them over all species per
200 plot, these values yield information on the environmental conditions of the grasslands.

201

202 *Statistical analysis*

203 Data were analyzed using R (version 3.2.4, R Development Core Team, 2016). We first
204 calculated the biomass of *Rhinanthus*, grasses and herbs relative to the total biomass per
205 plot. As relative *Rhinanthus* biomass and *Rhinanthus* cover estimates were strongly
206 correlated ($r = 0.78$, $p < 0.001$), we used the measured relative *Rhinanthus* biomass values
207 for further analyses. Legumes are suggested to be well-suitable hosts for *Rhinanthus* (e.g.,
208 Cameron et al., 2006). However, as we did not separate the biomass of legumes from the
209 one of other herbs, we calculated the cumulative legume cover to test whether legumes as a
210 group are negatively affected by increasing *Rhinanthus* densities.

211 For each plot, we calculated species richness, effective diversity ($e^{H'}$, where H' denotes
212 Shannon diversity) and Pielou's evenness ($J = H'/\log[S]$) using the vegan package (Oksanen et
213 al., 2015).

214 We then computed linear mixed effect models to account for the study design using the
215 nlme package (Pinheiro et al., 2014). Our response variables were the total plant diversity
216 measures and those separately for the functional groups grasses and herbs, community
217 mean traits and environmental indicator values for moisture and fertility, total biomass,
218 grass and herb biomass, and biomass quality measures. *Rhinanthus* was omitted from
219 calculations on diversity measures, community mean traits and environmental indicator
220 values. The models for biomass were calculated with and without *Rhinanthus*. Models on
221 biomass quality also included *Rhinanthus* as these measures were based on pooled total
222 biomass samples. As results for species richness and effective diversity were qualitatively
223 similar, we only show the ones for species richness. Fixed effects included region and the
224 relative *Rhinanthus* biomass and its interaction with region. We also included relative
225 *Rhinanthus* biomass as quadratic term because we suspected some non-linear relationships,
226 but omitted the quadratic term if not significant. As one of the three observers did not
227 sample the meadows in the Valais and to correct for individual differences of the observer in
228 species knowledge, we included the observer identity as a co-factor. Meadow was fitted as
229 random term to account for meadow-specific differences. Model assumptions were checked
230 visually by plotting residuals vs. predicted values and with normal-quantile plots.

231 To model species response curves along the *Rhinanthus* gradient, we used the package eHOF
232 (Jansen and Oksanen, 2013). Huisman-Olff-Fresco models (HOF models; Huisman et al.,
233 1993; see also Oksanen and Minchin, 2002) are five hierarchical models with increasing
234 complexity: I) no trend, II) monotone sigmoid with a maximum at one end of the gradient,

235 III) monotone sigmoid with a plateau, IV) unimodal symmetric and V) unimodal skewed.
236 Jansen and Oksanen (2013) further developed the models by adding model VI) bimodal with
237 equal maxima and VII) bimodal with different maxima. As species composition differed
238 strongly across the three regions, we modelled species response curves along the
239 *Rhinanthus*-density gradient separately for each region. For this, we used abundance data
240 (percentage cover) and a Gaussian error family distribution for species with at least 10
241 occurrences in all plots of the particular region (following Pepler-Lisbach and Kleyer, 2009;
242 Peper et al., 2011). Model selection was done by comparing Akaike information criterion
243 (AIC) and 100 bootstrapping runs tested model robustness. This resulted in a list of HOF
244 models for 36 species in the Bernese lowland, 30 species in the Bernese Oberland, and 16
245 species in the Valais (Tab. S3).

246 To obtain reliable species response curves, the whole extent of the distribution data of a
247 species must be covered along a gradient (Lawesson and Oksanen, 2002; Normand et al.,
248 2009). Therefore, we removed species described by model I) with no response to *Rhinanthus*
249 density and model II) with a monotone sigmoid response with a maximum at one end of the
250 gradient. For the remaining species, we extracted the optimum value from the HOF model,
251 represented by the maximum predicted abundance. For model III) we selected the mid-point
252 of the plateau, and for model VII) the higher of the two modes (Fig. S2).

253

254 **Results**

255 *Rhinanthus*-density effects on plant diversity

256 Although meadows in the Bernese lowland were less species rich (mean: 11.6 species per
257 400 cm²; min: 3; max: 27) compared with the ones at higher altitudes in the Bernese

258 Oberland (mean: 12.8; min: 5; max: 21) and the Valais (mean: 14.4; min: 6; max: 25), and the
259 *Rhinanthus* densities never reached very high levels in the two regions at high altitudes
260 Bernese Oberland (mean: 0.26 rel *Rhinanthus* biomass; min: 0; max: 0.83) and the Valais
261 (mean: 0.12; min: 0; max: 0.45) compared to the lowland (mean: 0.33; min: 0; max: 0.85),
262 the effects of an increasing *Rhinanthus* density on all diversity measures were consistent
263 among regions in most cases (indicated by the non-significant *Rhinanthus* density-by-region
264 interactions, Table 1).

265 We found significant hump-shaped relationships of total, herb and grass species richness
266 with relative *Rhinanthus* biomass (Fig. 1a, Tab. 1), with highest values at 31%, 27.4% or
267 33.6% relative *Rhinanthus* biomass, respectively. Compared with plots without *Rhinanthus*,
268 total species richness increased by 12% (1.35 species per 400 cm²: 0.32 grass and 1.03 herb
269 species on average) at this density level. At *Rhinanthus* densities >60%, species richness was
270 even lower than in plots without *Rhinanthus* (Fig. 1a).

271 In contrast, evenness (excluding *Rhinanthus*) increased linearly with increasing relative
272 *Rhinanthus* biomass (Fig. 1b, Tab. 1).

273

274 *Rhinanthus*-density relationships with environmental indicator values and community mean
275 traits

276 When excluding *Rhinanthus* from the community mean trait analysis, we found no
277 significant effects of increasing *Rhinanthus* densities on abundance weighted indicator
278 values for moisture and fertility and on seed mass and SLA (Tab. S1). This indicates that
279 *Rhinanthus* did not affect the abiotic conditions to such an extent that it would translate in a
280 shift in the community mean for these measures.

281 However, community mean plant height decreased with increasing relative *Rhinanthus*
282 biomass (the quadratic relationship was also significant and plant height tends to increase
283 again at the end of the *Rhinanthus* density gradient). In addition, the relationship of
284 community mean LDMC and relative *Rhinanthus* biomass was U-shaped (Fig. S1, Tab. S1).

285

286 *Rhinanthus*-density effects on individual species responses

287 We found species to respond differently to varying *Rhinanthus* densities (Tab. S3). However,
288 no consistent patterns to separate the effects of increasing *Rhinanthus* densities on
289 functional groups were evident. As the optima of different grass species (e.g. *Bromus*
290 *erectus*, *Cynosurus cristatus*, *Dactylis glomerata*, *Festuca* spp., *Phleum pratense*, *Poa* spp.),
291 legume species (e.g. *Lathyrus pratensis*, *Lotus corniculatus*, *Medicago lupulina*, *Trifolium*
292 spp.) or species with tap roots (e.g. *Leontodon hispidus*, *Taraxacum officinale*) were
293 distributed along the whole gradient (Tab. S3; Figs. S2, S3), we were not able to identify
294 consistent trends to point out functional groups which might be suitable hosts because they
295 suffer from high *Rhinanthus* densities. However, these results underline the rather unspecific
296 host selection of *Rhinanthus*.

297

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

299 Excluding *Rhinanthus* led to a biomass decrease with increasing relative *Rhinanthus* biomass
300 (Fig. 1d; Tab. 2). Biomass of herbs followed a similar U-shaped pattern with increasing
301 relative *Rhinanthus* biomass (Fig. 1f, Tab. 2), whereas the biomass of grasses decreased
302 linearly (Fig. 1e). Overall, the cumulative cover of legumes decreased linearly with increasing
303 relative *Rhinanthus* biomass (Fig. 2, Tab. 2).

304 Including *Rhinanthus* led to a U-shaped relationship between the total biomass (including
305 *Rhinanthus*) and the relative *Rhinanthus* biomass (Fig. 1c, Tab. 2). At the density level with
306 the highest species richness (31% relative *Rhinanthus* biomass), yield was on average
307 reduced by 26%.

308 In addition, neither nutrient concentrations (N, P, K, Ca, Mg) nor fibre content (neutral
309 detergent fibre NDF, acid detergent fibre ADF or lignin) varied with *Rhinanthus* density (Tab.
310 S2). This indicates that the presence of *Rhinanthus* has no effect on biomass quality of these
311 meadows.

312

313 **Discussion**

314 *Rhinanthus* density effects on plant diversity and biomass

315 Using our new gradient approach showed that the species richness-*Rhinanthus*-density
316 relationship followed an optimum curve with highest values at intermediate densities, based
317 on corresponding increases in both grass and herb diversity. In contrast, studies using the ‘all
318 or nothing’ approach, like Fibich et al. (2016) simply found a positive effect of the presence
319 in 11 out of 16 hemiparasites on the plant diversity of grassland communities when
320 analyzing more than 30,000 plots of the Czech National Phytosociological Database.
321 Moreover, Joshi et al. (2000) experimentally showed that the presence of *Rhinanthus*
322 *alectorolophus* in newly created grasslands in Switzerland increased species richness of
323 unsown species. Similarly, the artificial introduction of *R. minor* also increased species
324 richness of sown grasslands in England (Pywell et al., 2004; Westbury et al., 2006). However,
325 results from studies using the ‘all or nothing’ approach may result in misleading

326 management recommendations as they do not account for changes along the *Rhinanthus*-
327 density gradient.

328 The major mechanism promoting plant diversity seems to be the mediation of competitive
329 balances in the community and the reduced productivity of grasslands (Davies et al., 1997;
330 Smith et al., 2003; Bullock and Pywell, 2005; Mudrak et al., 2016). According to Ameloot et
331 al. (2005; meta-analysis of experimental sowing studies) and Fisher et al. (2013; introduction
332 experiment) the average reduction of vegetation biomass by *Rhinanthus* is 26%. Our findings
333 partly confirm the positive *Rhinanthus* effects on plant diversity via reduced productivity as
334 we found an increase of species richness (+12%) coinciding with a maximum biomass
335 decrease (-26%). However, this changed along the *Rhinanthus*-density gradient with
336 maximum species richness at 31% relative *Rhinanthus* biomass. At *Rhinanthus* densities
337 >60%, we found species richness dropping below the average values of plots without
338 *Rhinanthus*. This is in accordance to Gibson and Watkinson (1992; observational study in
339 combination with a *Rhinanthus*-removal experiment), who found lower species richness in
340 patches with high *R. minor* densities in diverse British meadows. Interestingly, beyond this
341 threshold, *Rhinanthus* biomass even over-compensated the loss of total biomass. A reason
342 might be the relation of these high densities to optimal environmental conditions,
343 promoting nutritious hosts (e.g. Seel and Press, 1993; Cameron et al., 2006) and thereby
344 maximizing *Rhinanthus* biomass.

345 As both grass and herb biomass decreased along the gradient and their diversity was
346 enhanced at intermediate *Rhinanthus* densities, our results indicate that *Rhinanthus*
347 parasitizes rather density-dependent than selectively. Given the rather unspecific behaviour
348 of *Rhinanthus*, which is supported by our analysis on individual species responses along the
349 *Rhinanthus* gradient where we found no consistent patterns, it might well be that the

350 belowground abundance of a host species, e.g. of species with a diffuse and wide spreading
351 root system, at least partly influences the probability of being parasitized. Accordingly, Press
352 and Phoenix (2005) stated that a parasite's host specificity might simply be an artefact of
353 host abundance, meaning that the probability of being encountered by a parasite is higher
354 for abundant host species than for less abundant ones and that parasitism is often
355 proportional to the belowground presence of a host species. However, our findings of the
356 overall linear reduction of grass biomass and legume cover support the idea that some hosts
357 with a diffuse and wide spreading root system and high nutrient content, and at the same
358 time lacking adequate defence mechanisms are better suited (e.g., Cameron et al., 2006;
359 Sandner and Matthies, 2016). This might in turn reduce the abundance of the whole
360 functional group of suitable hosts, when *Rhinanthus* densities are increasing.

361 The positive response in evenness with increasing *Rhinanthus* densities also confirm the
362 resource-availability theory and suggests that suitable host species are parasitized over-
363 proportionally, given that these hosts have a diffuse and wide spreading root system and
364 lack adequate defence mechanisms preventing penetration. Thereby competitive exclusion
365 could be prevented and coexistence with subordinate species might be promoted (Gibson
366 and Watkinson, 1992; Press, 1998; Phoenix and Press, 2005). Similar to our findings, Fibich et
367 al. (2016) found hemiparasite presence to be positively related with the evenness of plant
368 communities. In addition, Demey et al. (2015) reported a decrease in evenness after the
369 removal of *Rhinanthus*. It seems that hemiparasitic plants can play key roles in mediating the
370 competitive relationships and the stability in a plant community (Press, 1998; Pennings and
371 Callaway, 2002). Chesson (2000) described this effect as an "equalizing mechanism".

372 *Rhinanthus* densities varied among our study regions with highest mean and maximum
373 densities in the Bernese lowland. It has been shown that *Rhinanthus* performance decreases

374 with altitude (Hargreaves et al., 2015), which might be a possible explanation for these
375 regional differences. A possible explanation for the lowest density values in the meadows
376 situated in the Valais might be the considerably lower mean annual precipitation in this
377 region compared to the other two. Moreover, *Rhinanthus* densities are highly variable over
378 time (Press and Phoenix, 2005; Ameloot et al., 2006; Cameron et al., 2009) and therefore
379 one might expect a rather cyclic effect of *Rhinanthus* on plant diversity and the composition
380 of the plant community. After reaching high densities and promoting subordinate plants,
381 subsequent invasion by competitive species becomes more likely because *Rhinanthus* loses
382 its advantage when suitable hosts are no longer available. The subsequent increase of rather
383 competitive species with an extensive root system is then again beneficial for *Rhinanthus* as
384 enough resources are again available. Thus, patches with high *Rhinanthus* densities appear
385 to move through the meadow over time (Press and Phoenix, 2005; Cameron et al., 2009).
386 However, spatially explicit monitoring over several years would be required to confirm
387 whether *Rhinanthus* exhibits such cycles of temporal changes in patch density. Moreover,
388 whether the distribution patterns of *Rhinanthus* populations vary along environmental or
389 elevational gradients has not been tested, yet. In our study areas we had the impression that
390 the distribution of *Rhinanthus* changes from aggregated to more random with increasing
391 altitude. However, this needs to be tested in future studies. Until now, temporal dynamics in
392 the community composition have not yet been monitored with permanent study plots.
393 However, Cameron et al. (2009) calculated intransitive-competition networks between
394 *Rhinanthus*, grasses and forbs based on pairwise competition experiments between
395 *Rhinanthus minor* and three forbs as well as three grasses to simulate these changes over
396 time. Their models suggested fluctuating abundances of the parasite and the other
397 functional groups resulting in “shifting clouds” of *Rhinanthus* within a grassland (Cameron et

398 al., 2009). The lack of information on *Rhinanthus* densities in previous seasons is therefore a
399 limitation of our study and all other previous ones investigating the effect of *Rhinanthus* on
400 diversity and composition in only one year.

401

402 *Rhinanthus*-density effects on community composition

403 The effects of hemiparasites on vegetation structure and community mean traits were rarely
404 considered in previous studies (but see Mudrak et al., 2016). We found a decrease in
405 community mean plant height with increasing *Rhinanthus* biomass. Similarly, Mudrak et al.
406 (2016), who compared plots with *Rhinanthus minor* to plots where they had experimentally
407 removed *Rhinanthus*, also found a reduced community mean plant height in plots with
408 *Rhinanthus* present. These shifts in the community composition towards smaller plant
409 species might be explained by the stronger parasitization of rather large and competitive
410 species with large root volumes or by exerting *Rhinanthus* density-dependent control of
411 dominant plants facilitating coexistence and promoting smaller plants (Phoenix and Press,
412 2005). *Rhinanthus* performance, e.g. the individual biomass and seed production is better
413 when suitable host groups are present (Sandner and Matthies, 2016) likely leading to a
414 stronger suppression of the host in the next year. This might facilitate the establishment of
415 less competitive, e.g. smaller plant species. In addition, hemiparasitic plants are in general
416 considered to be rather weak light competitors (Matthies, 1995), especially sensitive to
417 shading during the seedling stage (Teřitel et al., 2011). Together with the dominance and
418 productivity reducing effects (Ameloot et al., 2005), smaller species and also the
419 establishment of *Rhinanthus* itself are thus likely promoted under these *Rhinanthus*-
420 engineered conditions. However, the significant quadratic relationship with plant height
421 tending to increase again at the end of the *Rhinanthus* density gradient is biologically

422 doubtful because at these high *Rhinanthus* densities only few species have a large effect on
423 the community mean plant height.

424 In contrast to Mudrák et al. (2016), who found a decrease of LDMC with *Rhinanthus minor*
425 present, we found a U-shaped LDMC vs. *Rhinanthus* density relationship. Mudrák et al.
426 (2016) assumed that this decrease might be due to the reduced grass abundance as grasses
427 have distinct trait values compared to forbs. However, as they used the ‘all or nothing’
428 approach, comparing sites with and without hemiparasite the results might be not fully
429 comparable to ours. Moreover, the other investigated community mean traits such as seed
430 mass indicating colonization ability and SLA, related to fertilization and resource utilization
431 of plants (e.g. Pfestorf et al., 2013), did not differ along the *Rhinanthus*-density gradient. This
432 suggests that predominantly height as an indicator of light competition, and LDMC as an
433 indicator for changed resource use, are directly affected by *Rhinanthus*. The minor effect of
434 *Rhinanthus* on community composition is further substantiated by the absence of changes in
435 the abundance-weighted indicator values. Although hemiparasites have high transpiration
436 rates and low water use efficiencies (Phoenix and Press, 2005), this seems not to translate
437 into higher abundance or number of species that prefer drier conditions.

438

439 *Rhinanthus*-density effects on biomass quality

440 Given the small impact of *Rhinanthus* on species composition and community mean traits,
441 the absence of effects on fodder quality may not be surprising. As we are not aware of any
442 other study addressing how the quality of biomass changes with an increasing abundance of
443 (hemi-)parasitic plants, further studies are required to test whether our results hold for

444 other types of grasslands or other parasitic plants. Also testing for density effects on the
445 quality of herb and grass biomass separately might be very interesting to investigate.

446

447 *Methodological implications and perspectives for future studies*

448 Our results clearly support the use of the gradient approach instead of the ‘all or nothing’
449 approach in order to account for the density-dependent role of hemiparasitic plants for the
450 functioning of plant communities. Our findings further suggest that studies using the ‘all or
451 nothing’ approach may result in misleading conclusions and management recommendations.
452 However, the limitation of our study and all other previous ones investigating the effect of
453 *Rhinanthus* on diversity and composition is that we captured only a snapshot of the dynamic
454 *Rhinanthus* invasion. As we only investigated one year, we cannot distinguish between
455 recently invaded plots and the ones where the parasite density had already declined
456 because of the decreasing abundance of suitable hosts. We therefore suggest establishing
457 permanent plots to monitor the dynamics of *Rhinanthus* populations over time. This would
458 further allow analysing compositional and functional changes of the host community.
459 Moreover, this might also help to find more consistent patterns of increasing *Rhinanthus*
460 densities on particular plant species. Such an observational monitoring approach might also
461 be combined with experimentally controlling *Rhinanthus* densities by seed addition in
462 established plant communities in meadows. Furthermore, including varying environmental
463 and elevational gradients in future studies would allow testing for differences in distribution
464 patterns of *Rhinanthus* populations and their effects on plant community composition along
465 these gradients in addition to changing *Rhinanthus* densities.

466

467 *Recommendations for restoration and agriculture*

468 Overall, our results highlight that the density rather than the pure presence of hemiparasites
469 is particularly important to understand and control their functional role. In summary, our
470 findings of increased plant diversity in line with a slightly lower yield but similar biomass
471 quality clearly show that *Rhinanthus* is a suitable tool for grassland restoration if its density
472 can be maintained at intermediate levels. We therefore recommend introducing *Rhinanthus*
473 into meadows for which high hay production is not the only goal, e.g. in course of agri-
474 environmental schemes aiming at a reduction of management intensity and the
475 enhancement of biodiversity.

476 But, how can intermediate *Rhinanthus* densities be maintained after successful
477 establishment? A suitable management action to control the abundance of *Rhinanthus*
478 without eradicating the whole population is early mowing before fruit ripening during one
479 year (more than one year of early mowing will likely eradicate the population; Magda et al.,
480 2004). However, Blažek and Lepš (2015) and Mudrak et al. (2014) demonstrated that
481 *Rhinanthus* abundance can be drastically reduced when a meadow is mown before seed
482 ripening and that the population depends on annual seed production. We therefore suggest
483 late mowing of strips or even leave uncut strips until the next year on 10–20% of a meadow,
484 as it has been suggested to support invertebrate diversity without detrimental effects on
485 plant diversity (van Klink et al., 2017). These uncut strips might act as refuge to preserve the
486 seed source and thereby maintain the *Rhinanthus* population in a meadow.

487

488 **Funding**

489 This research did not receive any specific grant from funding agencies in the public,
490 commercial, or not-for-profit sectors.

491

492 **Acknowledgements**

493 We thank the editor Diethart Matthies as well as Renate A. Wesselingh and two further
494 anonymous reviewers for their constructive comments and their efforts with our
495 manuscript. The study has been supported by the TRY initiative on plant traits
496 (<http://www.try-db.org>). The TRY initiative and database is hosted, developed and
497 maintained by Jens Kattge and Gerhard Bönisch (Max Planck Institute for Biogeochemistry,
498 Jena, Germany). TRY is currently supported by DIVERSITAS/Future Earth and the German
499 Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig.

500

501 **References**

502 Adler, L.S., 2000. Alkaloid uptake increases fitness in a hemiparasitic plant via reduced
503 herbivory and increased pollination. *Am. Nat.* 156, 92–99.

504 Allan, E., Bossdorf, O., Dormann, C.F., Prati, D., Gossner, M.M., Tschardtke, T., Bluethgen, N.,
505 Bellach, M., Birkhofer, K., Boch, S. et al., 2014. Interannual variation in land-use intensity
506 enhances grassland multidiversity. *Proc. Natl. Acad. Sci. U.S.A.*, 111, 308–313.

507 Ameloot, E., Verheyen, K., Bakker, J.P., De Vries, Y., Hermy, M., 2006. Long-term dynamics of
508 the hemiparasite *Rhinanthus angustifolius* and its relationship with vegetation structure. *J.*
509 *Veg. Sci.* 17, 637–646.

510 Ameloot, E., Verheyen, K., Hermy, M., 2005. Meta-analysis of standing crop reduction by
511 *Rhinanthus* spp. and its effect on vegetation structure. *Folia Geobot.* 40, 289–310.

512 Bardgett, R.D., Smith, R.S., Shiel, R.S., Peacock, S., Simkin, J.M., Quirk, H., Hobbs, P.J., 2006.
513 Parasitic plants indirectly regulate below-ground properties in grassland ecosystems. *Nature*
514 439, 969–972.

515 Blažek, P., Lepš J., 2015. Victims of agricultural intensification: Mowing date affects
516 *Rhinanthus* spp. regeneration and fruit ripening. *Agric. Ecosyst. Environ.* 211, 10–16.

517 Bullock, J.M., Pywell, R.F., 2005. *Rhinanthus*: A tool for restoring diverse grassland? *Folia*
518 *Geobot.* 40, 273–288.

519 Cameron, D.D., Coats, A.M., Seel, W.E., 2006. Differential resistance among host and non-
520 host species underlies the variable success of the hemi-parasitic plant *Rhinanthus minor*.
521 *Ann. Bot.* 98, 1289–1299.

522 Cameron, D.D., Seel, W.E., 2007. Functional anatomy of haustoria formed by *Rhinanthus*
523 *minor*: linking evidence from histology and isotope tracing. *New Phytol.* 174, 412–419.

524 Cameron, D.D., White, A., Antonovics, J. 2009. Parasite-grass-forb interactions and rock-
525 paper-scissor dynamics: predicting the effects of the parasitic plant *Rhinanthus minor* on
526 host plant communities. *J. Ecol.* 97, 1311–1319.

527 Chesson, P., 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*
528 31, 343–358.

529 Davies, D.M., Graves, J.D., Elias, C.O., Williams, P.J., 1997. The impact of *Rhinanthus* spp. on
530 sward productivity and composition: implication for the restoration of species-rich
531 grasslands. *Biol. Cons.* 82, 87–93.

532 Delarze, R., Gonseth, Y., Eggenberg, S., Vust, M. 2015. Lebensräume der Schweiz. 3rd edn.,
533 hep Verlag AG, Bern.

534 Demey, A., De Frenne, P., Baeten, L., Verstraeten, G., Hermy, M., Boeckx, P., Verheyen, K.
535 2015. The effects of hemiparasitic plant removal on community structure and seedling
536 establishment in semi-natural grasslands. *J. Veg. Sci.* 26, 409–420.

537 Fibich, P., Lepš, J., Chytrý, M., Těšitel, J., 2016. Root hemiparasitic plants are associated with
538 high diversity in temperate grasslands. *J. Veg. Sci.* Doi: 10.1111/jvs.12472

539 Fisher, J.P., Phoenix, G.K., Childs, D.Z., Press, M.C., Smith, S.W., Pilkington, M.G., Cameron,
540 D.D., 2013. Parasitic plant litter input: a novel indirect mechanism influencing plant
541 community structure. *New Phytol.* 198, 222–231.

542 Foley, W.J., McIlwee, A., Lawler, I., Aragones, L., Woolnough, A.P., Berding, N., 1998.
543 Ecological applications of near infrared reflectance spectroscopy – a tool for rapid, cost-
544 effective prediction of the composition of plant and animal tissues and aspects of animal
545 performance. *Oecologia* 116, 293–305.

546 Gibson, C.C., Watkinson, A.R., 1991. Host selectivity and the mediation of competition by the
547 root hemiparasite *Rhinanthus minor*. *Oecologia* 86, 81–87.

548 Gibson, C.C., Watkinson, A.R., 1992. The role of the hemiparasitic annual *Rhinanthus minor*
549 in determining grassland community structure. *Oecologia* 89, 62–68.

550 Gossner, M.M., Lewinsohn, T., Kahl, T., Grassein, F., Boch, S., Prati, D., Birkhofer, K., Renner,
551 S.C., Sikorski, J., Arndt, et al. 2016. Land-use intensification causes homogenization of
552 grassland communities across trophic levels. *Nature* 540, 266–269.

553 Hargreaves, A.L., Weiner, J.L., Eckert, C.G. 2015. High-elevation range limit of an annual herb
554 is neither caused nor reinforced by declining pollinator service. *J. Ecol.* 103, 572–584.

555 Hölzel, N., Otte, A. 2003. Restoration of a species-rich flood-meadow by topsoil removal and
556 diaspore transfer with plant material. *Appl. Veg. Sci.* 6, 131–140.

557 Huisman, J., Olf, H., Fresco L.F.M. 1993. A hierarchical set of models for species response
558 analysis. *J. Veg. Sci.* 4, 37–46.

559 Jansen, F., Oksanen, J. 2013. How to model species responses along ecological gradients –
560 Huisman-Olf-Fresco models revisited. *J. Veg. Sci.* 24, 1108–1117.

561 Joshi, J., Matthies, D., Schmid, B., 2000. Root hemiparasites and plant diversity in
562 experimental grassland communities. *J. Ecol.* 88, 634–644.

563 Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M.,
564 Reich, P.B., Wright, I.J., et al., 2011. TRY – a global database of plant traits. *Glob. Chang. Biol.*
565 17, 2905–2935.

566 Kleijn, D., Kohler, F., Baldi, A., Batary, P., Concepcion, E.D., Clough, Y., Diaz, M., Gabriel, D.,
567 Holzschuh, A., Knop, E., et al., 2009. On the relationship between farmland biodiversity and
568 land-use intensity in Europe. *Proc. Biol. Sci.* 276, 903–909.

569 Klaus, V.H., Kleinebecker, T., Hölzel, N., Blüthgen, N., Boch, S., Müller, J., Socher, S.A., Prati,
570 D., Fischer, M. 2011. Nutrient concentrations and fibre contents of plant community biomass
571 reflect species richness patterns along a broad range of land-use intensities among
572 agricultural grasslands. *Perspect. Plant Ecol. Evol. Syst.* 13, 287–295.

573 Kleinebecker, T., Klaus, V.H., Hölzel, N., 2011. Reducing sample quantity and maintaining
574 high prediction accuracy of quality parameters in grassland biomass with near-infrared
575 reflectance spectroscopy (NIRS). *J. Near Infrared Spec.* 19, 495–505.

576 Landolt, E. 2010. *Flora indicativa*. Haupt Verlag, Bern.

577 Lawesson, J.E., Oksanen, J. 2002. Niche characteristics of Danish woody species as derived
578 from coenoclines. *J. Veg. Sci.* 13, 279–290.

579 Magda, D., Duru, M., Theau, J.-P., 2004. Defining management rules for grasslands using
580 weed demographic characteristics. *Weed Sci.* 52, 339–345.

581 Matthies, D., 1995. Parasitic and competitive interactions between the hemiparasites
582 *Rhinanthus serotinus* and *Odontites rubra* and their host *Medicago sativa*. *J. Ecol.* 83, 245–
583 251.

584 Matthies, D., 1996. Interactions between the root hemiparasite *Melampyrum arvense* and
585 mixtures of host plants: Heterotrophic benefit and parasite-mediated competition. *Oikos* 75,
586 118–124.

587 Mudrák, O., de Bello, F., Doležal, J., Lepš, J., 2016. Changes in the functional trait
588 composition and diversity of meadow communities induced by *Rhinanthus minor* L. *Folia*
589 *Geobot.* 51, 1–11.

590 Mudrák, O., Lepš, J., 2010. Interactions of the hemiparasitic species *Rhinanthus minor* with
591 its host plant community at two nutrient levels. *Folia Geobot.* 45, 407–424.

592 Mudrák, O., Mládek, J., Blažek, P., Lepš, J., Doležal, J., Nekvapilová, E., Těšitel, J., 2014.
593 Establishment of hemiparasitic *Rhinanthus* spp. in grassland restoration: lessons learned
594 from sowing experiments. *Appl. Veg. Sci.* 17, 274–287.

595 Normand, S., Treier, U.A., Randin, C., Vittoz, P., Guisan, A., Svenning, J.C. 2009. Importance
596 of abiotic stress as a range-limit determinant for European plants: insights from species
597 responses to climatic gradients. *Glob. Ecol. Biogeogr.* 18, 437–449.

598 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L.,
599 Solymos, P., Wagner, H., 2015. *Vegan: Community ecology package*. R package version 2.3-
600 0., <http://CRAN.R-project.org/package=vegan>.

601 Pennings, S.C., Callaway, R.M., 2002. Parasitic plants: parallels and contrasts with herbivores.
602 *Oecologia* 131, 479–489.

603 Peper, J., Jansen, F., Pietzsch, D., Manthey, M. 2011. Patterns of plant species turnover along
604 grazing gradients. *J. Veg. Sci.* 22, 457–466.

605 Peppler-Lisbach, C., Kleyer, M. 2009. Patterns of species richness and turnover along the pH
606 gradient in deciduous forests: testing the continuum hypothesis. *J. Veg. Sci.* 20, 984–995.

607 Pfestorf, H., Weiß, L., Boch, S., Socher, S.A., Müller, J., Prati, D., Schöning, I., Weisser, W.W.,
608 Fischer, M., Jeltsch, F., 2013. Community mean traits as additional indicators to monitor
609 effects of land-use intensity on grassland plant diversity. *Perspect. Plant Ecol. Evol. Syst.* 15,
610 1–11.

611 Phoenix, G.K., Press, M.C., 2005. Linking physiological traits to impacts on community
612 structure and function: the role of root hemiparasitic Orobanchaceae (ex-Scrophulariaceae).
613 *J. Ecol.* 93, 67–78.

614 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R-Core-Team., 2014. *nlme: Linear and nonlinear*
615 *mixed effects models*. R package version 3.1-117. <http://CRAN.R-project.org/package=nlme>.

616 Press, M.C., 1998. Dracula or Robin Hood? A functional role for root hemiparasites in
617 nutrient poor ecosystems. *Oikos* 82, 609–611.

618 Press, M.C., Phoenix, G.K., 2005. Impacts of parasitic plants on natural communities. *New*
619 *Phytol.* 166, 737–751.

620 Pywell, R.F., Bullock, J.M., Tallowin, J.B., Walker, K.J., Warman, E A., Masters, G., 2007.
621 Enhancing diversity of species-poor grasslands: an experimental assessment of multiple
622 constraints. *J. Appl. Ecol.* 44, 81–94.

623 Pywell, R.F., Bullock, J.M., Walker, K.J., Coulson, S.J., Gregory, S.J., Stevenson, M.J., 2004.
624 Facilitating grassland diversification using the hemiparasitic plant *Rhinanthus minor*. *J. Appl.*
625 *Ecol.* 41, 880–887.

626 Quested, H.M., Cornelissen, J.H.C., Press, M.C., Callaghan, T.V., Aerts, R., Trosien, F.,
627 Riemann, P., Gwynn-Jones, D., Kondratchuk, A., Jonasson, S.E., 2003. Decomposition of sub-
628 arctic plants with differing nitrogen economies: A functional role for hemiparasites. *Ecology*
629 84, 3209–3221.

630 R Development Core Team, 2016. R: a language and environment for statistical computing. R
631 Foundation for Statistical Computing, Vienna.

632 Royal Botanic Gardens Kew, 2016. Seed Information Database (SID). Version 7.1. Available
633 from: <http://data.kew.org/sid/> (October 2016).

634 Sandner, T.M., Matthies, D., 2016. Interactions of inbreeding and stress by poor host quality
635 in a root hemiparasite. *Ann. Bot.* 119, 143–150.

636 Seel, W.E., Press, M.C., 1993. Influence of the host on three sub-Arctic annual facultative
637 root hemiparasites. *New Phytol.* 125, 131–138.

638 Smith, R.S., Shiel, R.S., Bardgett, R.D., Millward, D., Corkhill, P., Rolph, G., Hobbs, P.J.,
639 Peacock, S., 2003. Soil microbial community, fertility, vegetation and diversity as targets in
640 the restoration management of a meadow grassland. *J. Appl. Ecol.* 40, 51–64.

641 Soliveres, S., van der Plas, F., Manning, P., Prati, D., Gossner, M.M., Renner, S.C., Alt, F.,
642 Arndt, H., Baumgartner, V., Binkenstein, J., et al., 2016. Biodiversity at multiple trophic levels
643 is needed for ecosystem multifunctionality. *Nature* 536, 456–459.

644 Stein, C., Rissmann, C., Hempel, S., Renker, C., Buscot, F., Prati, D., Auge, H., 2009. Interactive
645 effects of mycorrhizae and a root hemiparasite on plant community productivity and
646 diversity. *Oecologia* 159, 191–205.

647 Těšitel, J., Fibich, P., de Bello, F., Chytrý, M., Lepš, J., 2015a. Habitats and ecological niches of
648 root-hemiparasitic plants: an assessment based on a large database of vegetation plots.
649 *Preslia* 87, 87–108.

650 Těšitel, J., Lepš, J., Vráblová, M., Cameron, D.D., 2011. The role of heterotrophic carbon
651 acquisition by the hemiparasitic plant *Rhinanthus alectorolophus* in seedling establishment
652 in natural communities: a physiological perspective. *New Phytol.* 192, 188–199.

653 Těšitel J, Plavcová L, Cameron DD., 2010. Heterotrophic carbon gain by the root
654 hemiparasites, *Rhinanthus minor* and *Euphrasia rostkoviana* (Orobanchaceae). *Planta* 231,
655 1137–1144.

656 Těšitel, J., Těšitelová, T., Fisher, J.P., Lepš, J., Cameron, D.D., 2015b. Integrating ecology and
657 physiology of root-hemiparasitic interaction: interactive effects of abiotic resources shape
658 the interplay between parasitism and autotrophy. *New Phytol.* 205, 350–360.

659 van Klink, R., Boch, S., Buri, P., Rieder, N.S., Humbert, J.Y., Arlettaz, R., 2017. No detrimental
660 effects of delayed mowing or uncut grass refuges on plant and bryophyte community
661 structure and phytomass production in low-intensity hay meadows. *Basic Appl. Ecol.* 20, 1–9.

662 Watson, D.M., 2009. Parasitic plants as facilitators: more Dryad than Dracula? *J. Ecol.* 97,
663 1151–1159.

664 Wesche, K., Krause, B., Culmsee, H., Leuschner, C., 2012. Fifty years of change in Central
665 European grassland vegetation: Large losses in species richness and animal-pollinated plants.
666 *Biol. Cons.* 150, 76–85.

667 Westbury, D.B., Davies, A., Woodcock, B.A., Dunnett, N.P., 2006. Seeds of change: The value
668 of using *Rhinanthus minor* in grassland restoration. *J. Veg. Sci.* 17, 435–446.

669 Westwood, J.H., Yoder, J.I., Timko, M.P., de Pamphilis, C.W., 2010. The evolution of
670 parasitism in plants. *Trends Plant Sci.* 15, 227–235.

671

672 **Table 1:** Summary of linear mixed effect models testing the effects of relative *Rhinanthus*
673 biomass (including quadratic term when significant) on plant diversity in 47 grasslands in
674 Switzerland. R^2 denotes the squared correlation coefficient between predicted and observed
675 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. <i>Rhinanthus</i> biomass linear	1	2.2	0.135	0.3	0.597	6.1	0.014	12.4	< 0.001
rel. <i>Rhinanthus</i> biomass quadratic	1	16.5	< 0.001	11.0	0.001	7.3	0.007	-	-
Region × rel. <i>Rhinanthus</i> biomass linear	2	2.3	0.102	0.9	0.396	2.8	0.063	1.0	0.364
Region × rel. <i>Rhinanthus</i> biomass quadratic	2	0.2	0.796	0.2	0.789	0.1	0.926	-	-
		$R^2=0.47$		$R^2=0.43$		$R^2=0.39$		$R^2=0.25$	

676

677

678 **Table 2:** Summary of linear mixed effect models testing the effects of relative *Rhinanthus*
679 biomass (including quadratic term when significant) on biomass and cumulative percentage
680 cover of legumes in 47 grasslands in Switzerland. R^2 denotes the squared correlation
681 coefficient between predicted and observed values.

	Biomass						Cover				
	Total			Excl. <i>Rhinanthus</i>		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. <i>Rhinanthus</i> biomass linear	1	6.0	0.015	186.9	< 0.001	64.1	< 0.001	62.1	< 0.001	4.052	0.045
rel. <i>Rhinanthus</i> biomass quadratic	1	11.7	< 0.001	13.4	< 0.001	4.3	0.040	4.1	0.044	-	-
Region × rel. <i>Rhinanthus</i> 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. <i>Rhinanthus</i> biomass quadratic	2	0.1	0.899	0.1	0.873	1.4	0.242	2.0	0.142	-	-
		$R^2=0.42$		$R^2=0.52$		$R^2=0.35$		$R^2=0.40$		$R^2=0.33$	

682

683

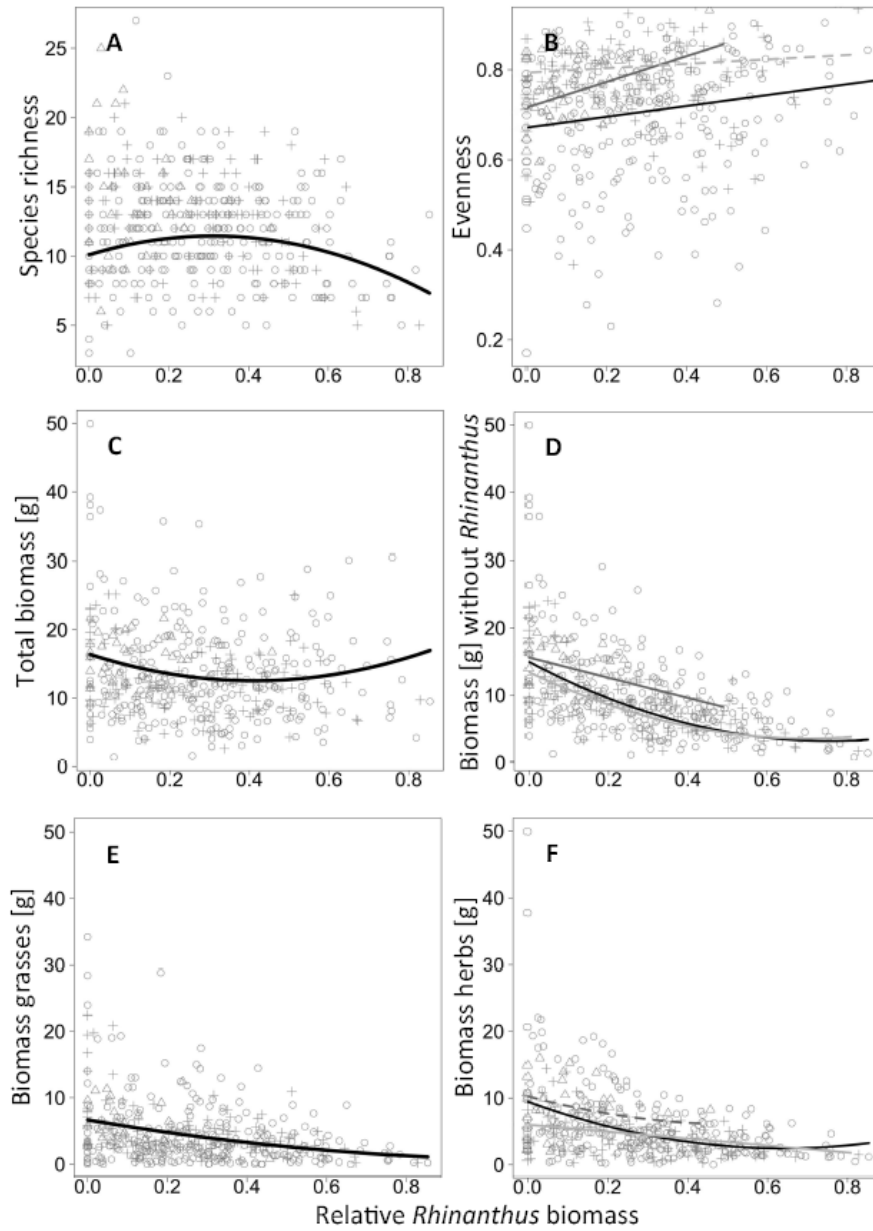
684 **Figures**

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

694

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

699

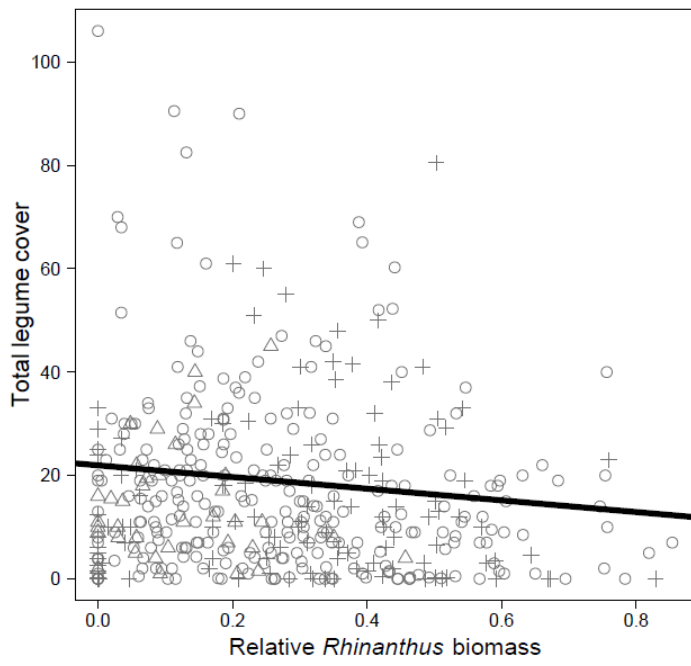


700

701 **Figure 1.**

702

703 **Figure 2.**



704

705

706 **Appendix**

707 **Table S1.** Summary of linear mixed effect models testing the effects of relative *Rhinanthus*
 708 biomass (including quadratic term when significant) on mean environmental indicator values
 709 and on the community mean traits specific leaf area (SLA) and leaf dry matter content
 710 (LDMC) in 47 grasslands in Switzerland. R^2 denotes the squared correlation coefficient
 711 between predicted and observed values.

Community excluding <i>Rhinanthus</i>													
	<i>df</i>	Moisture value		Nutrient value		Seed mass		Plant height		SLA		LDMC	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
(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. <i>Rhinanthus</i> 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. <i>Rhinanthus</i> 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. <i>Rhinanthus</i> 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. <i>Rhinanthus</i> biomass quadratic	2	-	-	-	-	-	-	1.3	0.264	-	-	0.8	0.459
		$R^2 = 0.36$		$R^2 = 0.38$		$R^2 = 0.21$		$R^2 = 0.43$		$R^2 = 0.42$		$R^2 = 0.34$	

712

713

714

715 **Table S2.** Summary of linear mixed effect models testing the effects of relative *Rhinanthus*
716 biomass on measures of biomass quality in 47 grasslands in Switzerland. C (carbon), nitrogen
717 (N), phosphorus (P), Ca (calcium), K (potassium), Mg (magnesium), ADF (acid detergent
718 fibre), ADL (lignin), and NDF (neutral detergent fibre). Quadratic terms were excluded
719 because they were not significant. R^2 denotes the squared correlation coefficient between
720 predicted and observed values.

721

722

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. <i>Rhinaranthus</i> 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 x rel. <i>Rhinaranthus</i> 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
			$R^2=0.61$		$R^2=0.61$		$R^2=0.66$		$R^2=0.42$		$R^2=0.19$		$R^2=0.52$		$R^2=0.74$		$R^2=0.45$		$R^2=0.51$

723 **Table S3.** Parameters of the response curves (optimum, minimum, maximum, range and
724 mean), the applied eHOF model (III monotone sigmoid with a plateau, IV unimodal symmetric,
725 V unimodal skewed, VI bimodal with equal maxima, VII bimodal with different maxima) and
726 its parameters (a-d), using percentage cover (abundance) data of the species with at least 10
727 occurrences in each of the three study regions.

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

729 **Figure S1.** The relationship between A) community mean plant height and B) community mean
730 leaf dry matter content (LDMC) and relative *Rhinanthus* biomass in nine plots in each of 47
731 meadows in three regions in Switzerland. Open circles indicate plots from Bernese lowland,
732 triangles from Valais and plus signs from Bernese Oberland.

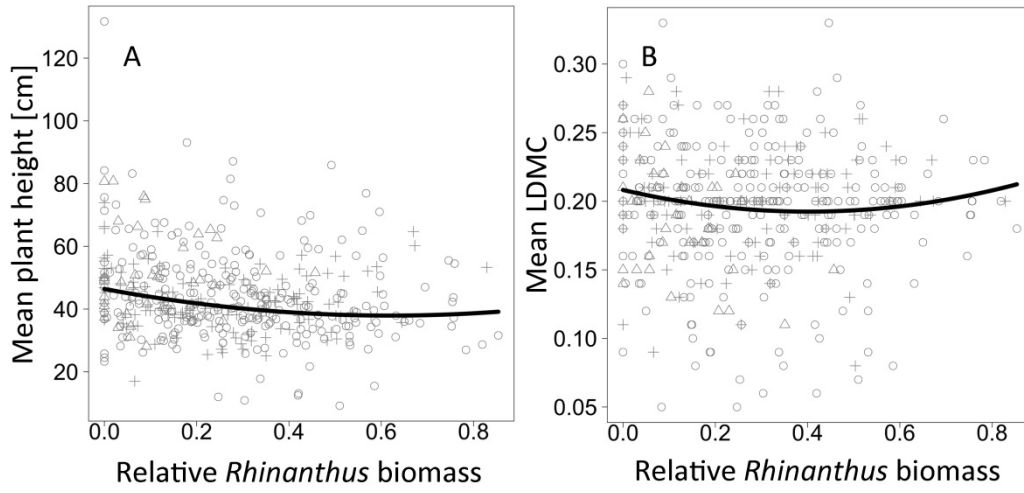
733

734 **Figure S2.** Species ranges and optima along the *Rhinanthus*-density gradient for the species
735 with at least 10 occurrences in each of the three study regions (A) Bernese lowland, (B) Valais
736 and (C) Bernese Oberland, and a species response curve different from model I (no response)
737 or model II (monotone sigmoid).

738

739 **Figure S3.** Response curves of species with at least 10 occurrences in each of the three study
740 regions (A) Bernese lowland, (B) Valais and (C) Bernese Oberland along the *Rhinanthus*-density
741 gradient. The parameters of the species response curves and the eHOF model are summarized
742 in Table S3.

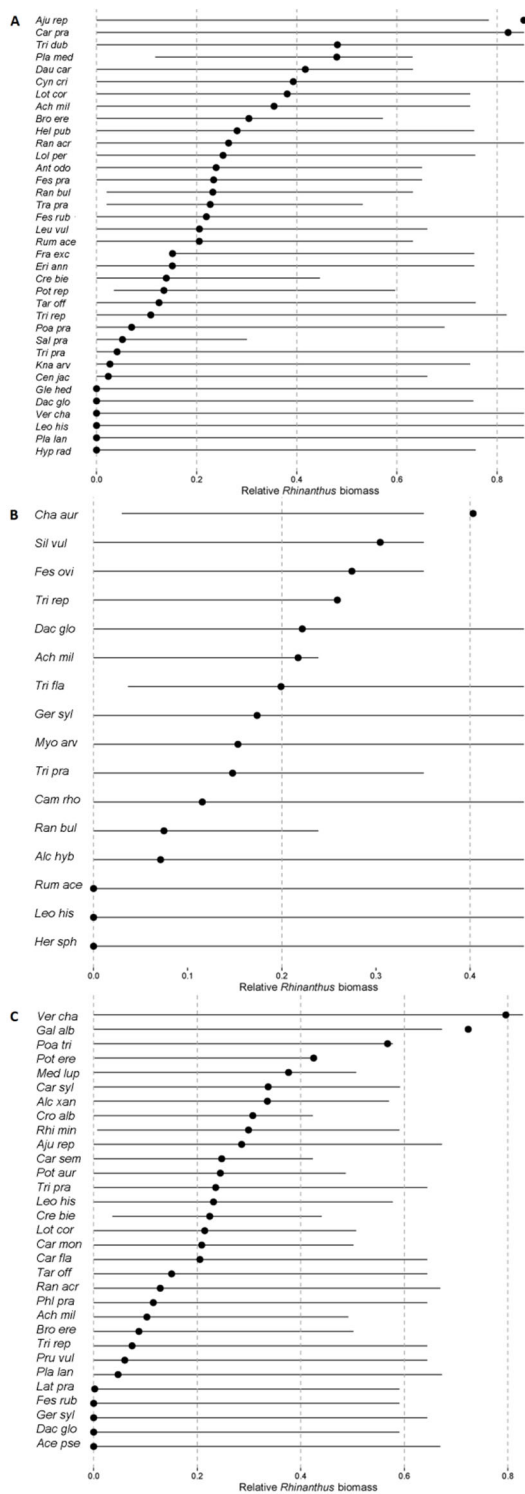
743



744

745 **Figure S1.**

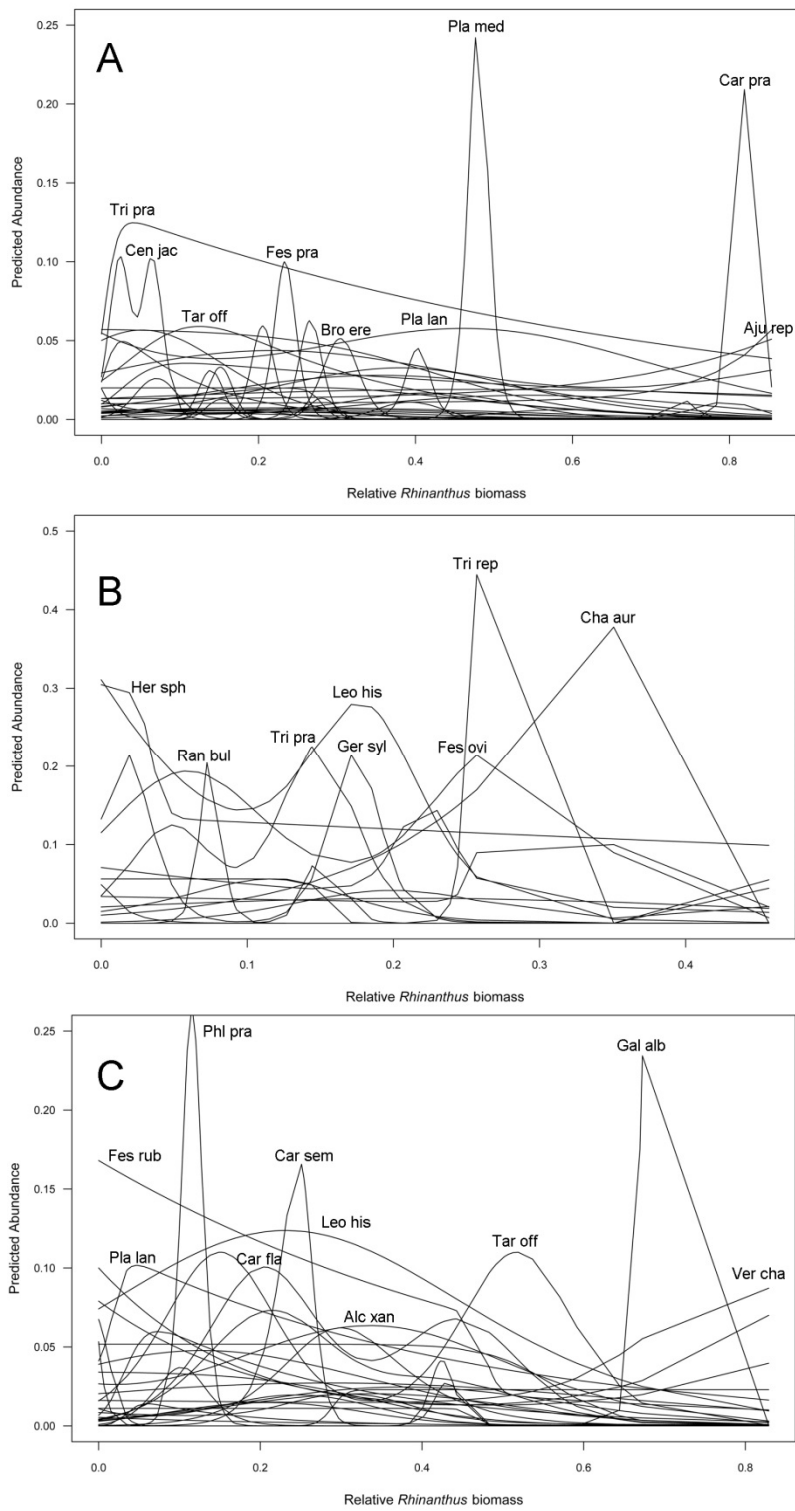
746



747

748 **Figure S2.**

749



750

751 **Figure S3.**