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Journal Article

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Publication date:
2018-06

Permanent link:
https://doi.org/10.3929/ethz-b-000246240

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

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

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Abstract

Hemiparasitic plants are considered as ecosystem engineers because they can modify the interactions between hosts and other organisms. Thereby, they may affect vegetation structure, community dynamics and facilitate coexistence as they are able to reduce interspecific competition by parasitizing selectively on competitive species and promote subordinate ones. In agri-environmental schemes, introducing the hemiparasite *Rhinanthus* has therefore been suggested as a low-cost method to increase grassland plant diversity, which is still subject to debate.

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

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

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

Keywords

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

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

Similarly, while most studies found *Rhinanthus* to reduce community biomass (Ameloot et al., 2005, 2006), some studies found a biomass increase (Joshi et al., 2000). The intuitive expectation of many farmers is a reduction of yield by the presence of hemiparasites, which makes *Rhinanthus* very unpopular for them (Magda et al., 2004; Ameloot et al., 2006). Related to this, it is often presumed that *Rhinanthus* reduces the nutritional value of the yield with severe losses in fodder quality. Such fodder quality decreases might be driven by changes in the functional plant composition of infested grasslands and should then be reflected by changes in nitrogen, mineral and fibre contents in plant biomass. However, as

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

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

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

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

Vegetation and biomass data

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

whole meadow and that two plots of the same density class were not situated in the same *Rhinanthus* patch. We chose small sample quadrats of 400 cm^2 because the parasitic effects on host plants is limited to the close neighbourhood of the parasite (host plants are only affected within 10 cm of the parasite; Gibson and Watkinson, 1992) and this plot size has been already used in many previous studies (e.g., Pywell et al., 2004; Ameloot et al., 2006; Mudrak et al., 2016). In each of the resulting 423 plots, we identified all vascular plant species and estimated their percentage cover and the cover of bare ground.

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

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

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 Peppler-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 cm^2; 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 cm^2: 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; Mudrák 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

with altitude (Hargreaves et al., 2015), which might be a possible explanation for these regional differences. A possible explanation for the lowest density values in the meadows situated in the Valais might be the considerably lower mean annual precipitation in this region compared to the other two. Moreover, *Rhinanthus* densities are highly variable over time (Press and Phoenix, 2005; Ameloot et al., 2006; Cameron et al., 2009) and therefore one might expect a rather cyclic effect of *Rhinanthus* on plant diversity and the composition of the plant community. After reaching high densities and promoting subordinate plants, subsequent invasion by competitive species becomes more likely because *Rhinanthus* loses its advantage when suitable hosts are no longer available. The subsequent increase of rather competitive species with an extensive root system is then again beneficial for *Rhinanthus* as enough resources are again available. Thus, patches with high *Rhinanthus* densities appear to move through the meadow over time (Press and Phoenix, 2005; Cameron et al., 2009). However, spatially explicit monitoring over several years would be required to confirm whether *Rhinanthus* exhibits such cycles of temporal changes in patch density. Moreover, whether the distribution patterns of *Rhinanthus* populations vary along environmental or elevational gradients has not been tested, yet. In our study areas we had the impression that the distribution of *Rhinanthus* changes from aggregated to more random with increasing altitude. However, this needs to be tested in future studies. Until now, temporal dynamics in the community composition have not yet been monitored with permanent study plots. However, Cameron et al. (2009) calculated intransitive-competition networks between *Rhinanthus*, grasses and forbs based on pairwise competition experiments between *Rhinanthus minor* and three forbs as well as three grasses to simulate these changes over time. Their models suggested fluctuating abundances of the parasite and the other 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 Mudrák et al., 2016). We found a decrease in
405 community mean plant height with increasing *Rhinanthus* biomass. Similarly, Mudrák et al.
406 (2016), who compared plots with *Rhinanthus minor* to plots were 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 (Těšitel 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

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

Methodological implications and perspectives for future studies

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

Recommendations for restoration and agriculture

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

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

Funding

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

Acknowledgements

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

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671

Table 1: Summary of linear mixed effect models testing the effects of relative *Rhinanthus* biomass (including quadratic term when significant) on plant diversity in 47 grasslands in Switzerland. R^2 denotes the squared correlation coefficient between predicted and observed 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

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

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.

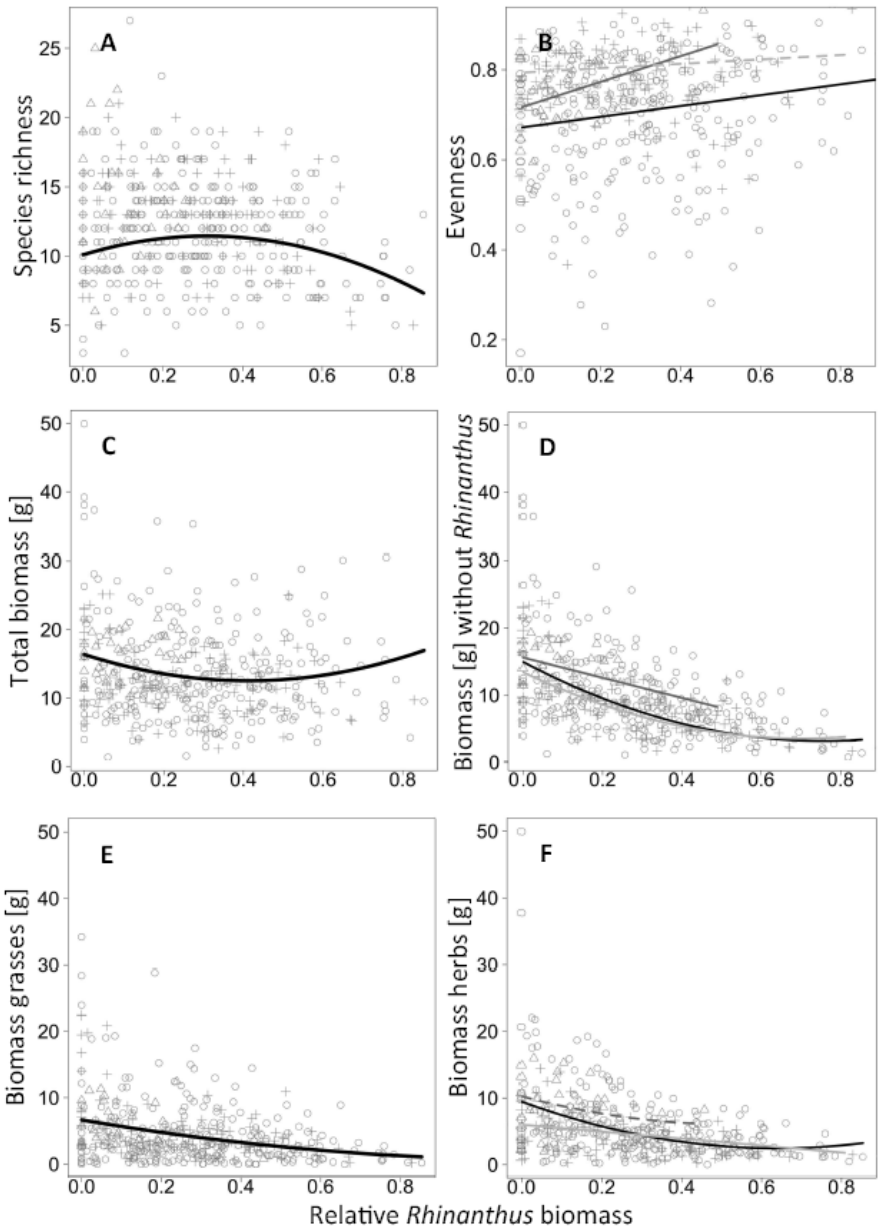
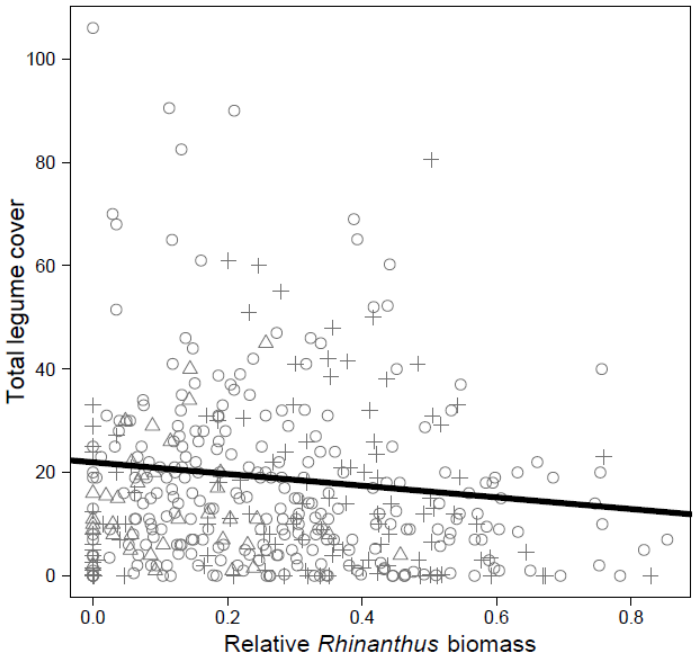

A
B
C
D
E
F
Species richness
Evenness
Total biomass [g]
Biomass [g] without *Rhinanthus*
Biomass grasses [g]
Biomass herbs [g]
Relative *Rhinanthus* biomass

Figure 1.

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 *Rhinanthus*													
		Moisture value		**Nutrient value**		**Seed mass**		**Plant height**		**SLA**		**LDMC**	
	df	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*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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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.

		C		N		P		Ca		K		Mg		ADF		ADL		NDF	
	df	*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

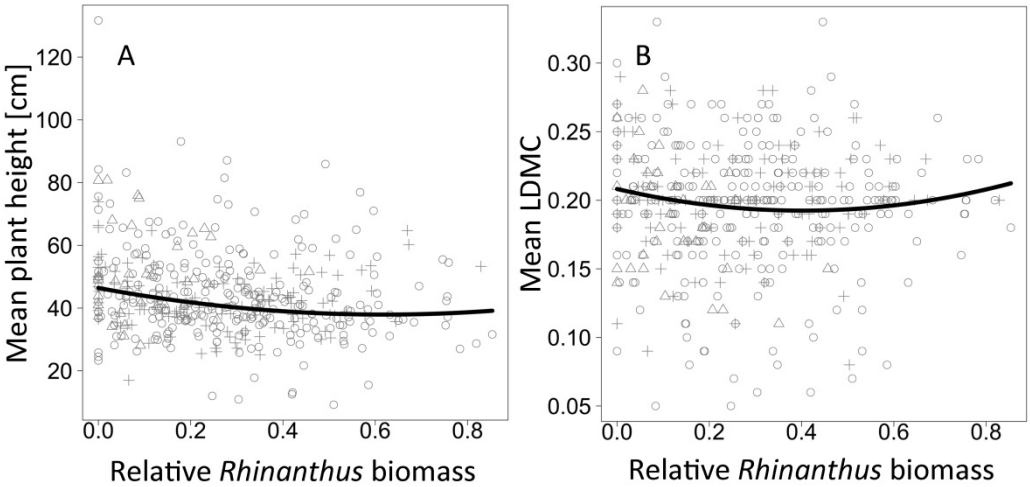
723 **Table S3.** Parameters of the response curves (optimum, minimum, maximum, range and
724 mean), the applied eHOF model (III monotone sigmoid with a plateau, IV unimodal symmetric,
725 V unimodal skewed, VI bimodal with equal maxima, VII bimodal with different maxima) and
726 its parameters (a-d), 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										
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	VI	-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	VI	-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	VII	-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	0.2	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

Figure S1. The relationship between A) community mean plant height and B) community mean leaf dry matter content (LDMC) 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.

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

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



744

745 **Figure S1.**

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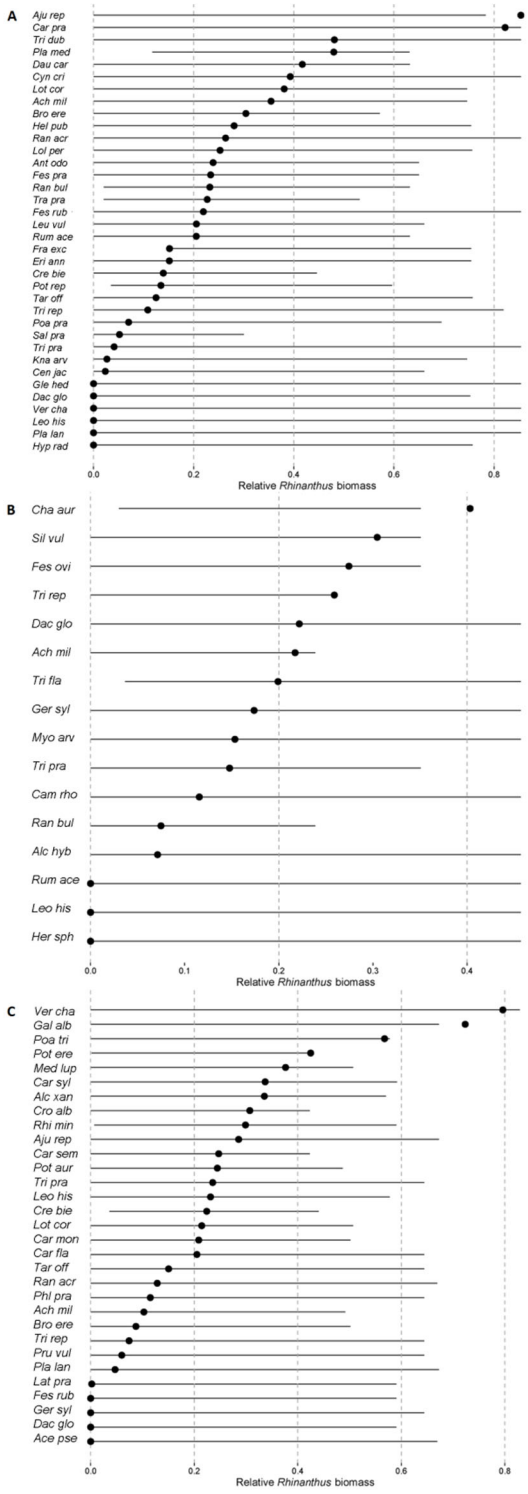
A
Aju rep
Car pra
Tri dub
Pla med
Dau car
Cyn cri
Lot cor
Ach mil
Bro ere
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Fes pra
Ran bul
Tra pra
Fes rub
Leu vul
Rum ace
Fra exc
Eri ann
Cre bie
Pot rep
Tar off
Tri rep
Poa pra
Sal pra
Tri pra
Kna arv
Cen jac
Gle hed
Dac glo
Ver cha
Leo his
Pla lan
Hyp rad
0.0
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Relative Rhinanthus biomass
B
Cha aur
Sil vul
Fes ovi
Tri rep
Dac glo
Ach mil
Tri fla
Ger syl
Myo arv
Tri pra
Cam rho
Ran bul
Alc hyb
Rum ace
Leo his
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Relative Rhinanthus biomass
C
Ver cha
Gal alb
Poa tri
Pot ere
Med lup
Car syl
Alc xan
Cro alb
Rhi min
Aju rep
Car sem
Pot aur
Tri pra
Leo his
Cre bie
Lot cor
Car mon
Car fla
Tar off
Ran acr
Phl pra
Ach mil
Bro ere
Tri rep
Pru vul
Pla lan
Lat pra
Fes rub
Ger syl
Dac glo
Ace pse
0.0
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Relative Rhinanthus biomass

Figure S2.

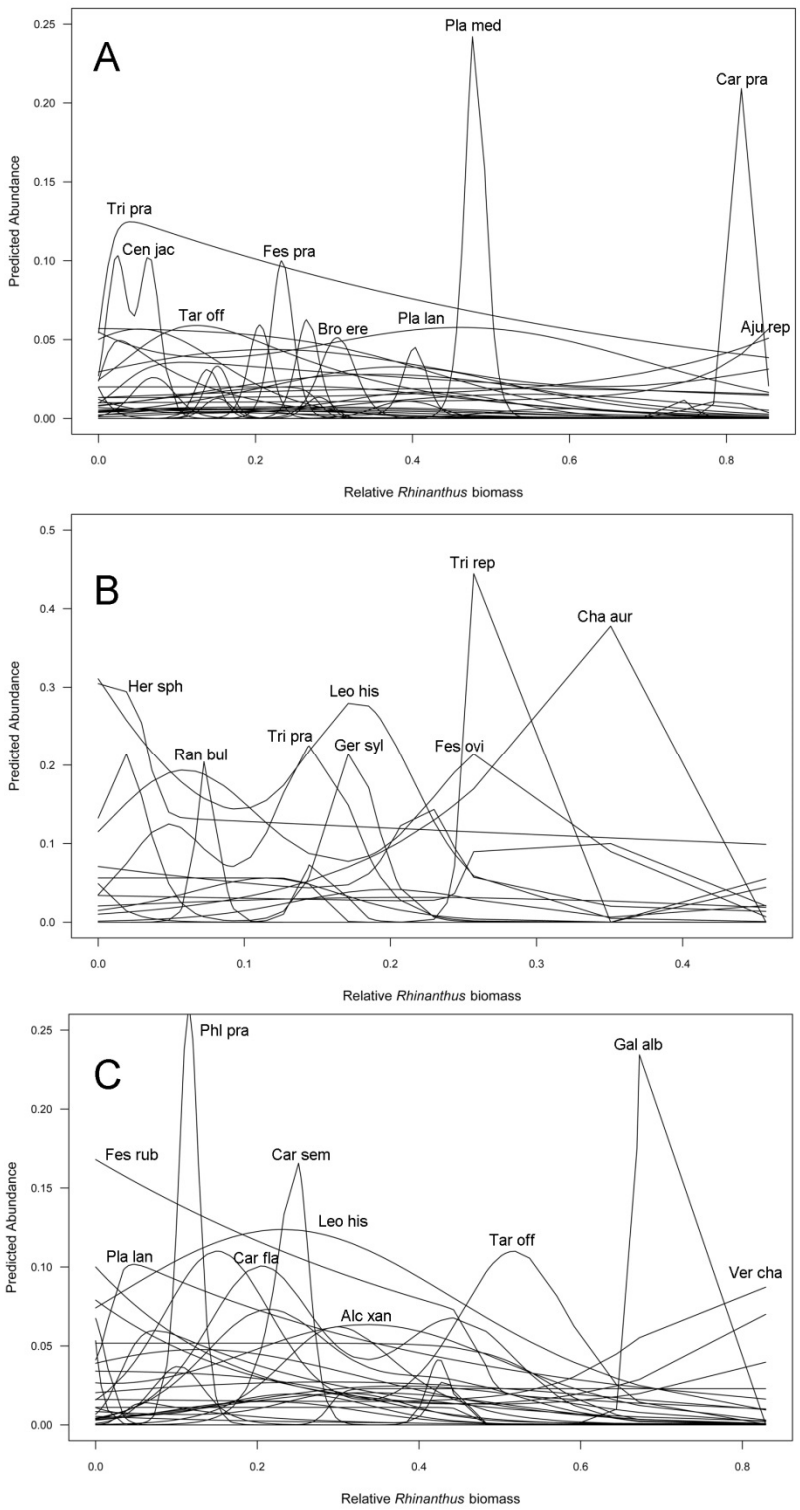
A
Pla med
Car pra
Tri pra
Cen jac
Fes pra
Tar off
Bro ere
Pla lan
Aju rep
Predicted Abundance
Relative Rhinanthus biomass
B
Tri rep
Cha aur
Her sph
Leo his
Tri pra
Ger syl
Fes ovi
Ran bul
Predicted Abundance
Relative Rhinanthus biomass
C
Phl pra
Gal alb
Fes rub
Car sem
Leo his
Tar off
Pla lan
Car fla
Ver cha
Alc xan
Predicted Abundance
Relative Rhinanthus biomass

Figure S3.