„The effect of *Rhinanthus alectorolophus* on community composition and structure in Swiss meadows"

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Written by
Nico Heer

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Supervisors: Dr. Steffen Boch, Dr. Daniel Prati, Prof. Dr. Markus Fischer,
Institute of Plant Sciences (IPS)

Preface

The presented bachelor thesis is part of a larger project from the "Marktplatz für Forschungsfragen Naturschutz" led by the "Forum Biodiversität Schweiz der Akademien der Naturwissenschaften (SCNAT)" and the "Konferenz der Beauftragten Natur und Landschaft (KBNL)". This platform aims at enhancing the connection and exchange between practice and research in conservation biology. For this purpose, questions from conservation practitioners are collected and mediated to research with the aim to develop evidence-based solutions for practical problems. The results will be published on the website of the "Marktplatz für Forschunsgfragen Naturschutz" (www.kbnl.ch/).

This bachelor thesis was conducted in close collaboration with Christoph Zwahlen and Fabian Klimmek who also studied a *Rhinanthus*-related topic at the Institute of Plant Sciences (IPS), University of Bern in the framework of their bachelor thesis. Data collection, preparation and analyses were performed together but the topics of the three theses differed. Christoph Zwahlen studied "The effect of *Rhinanthus alectorolophus* on productivity of Swiss meadows" (Zwahlen 2015) and Fabian Klimmek "The effect of *Rhinanthus alectorolophus* on plant biodiversity in Swiss meadows" (Klimmek 2015). Accordingly I will cite my colleagues when referring to their results.

Abstract

Intensification of agriculture promoted monotonous, species poor meadows throughout Europe. The implementation of agri-environmental schemes aims to reverse this dramatic trend. Various methods were proposed to restore intensively managed meadows into extensive grasslands. Because the hemiparasite *Rhinanthus* is assumed to promote the coexistence of dominant and subordinate plant species and thereby increases diversity, it has been introduced in grasslands of different European countries.

However, the effects on pant diversity have only rarely been monitored and are controversially discussed. Notably, other studies used observational presence-absence, sowing and removal approaches, which can be criticised because the effects of *Rhinanthus* on the plant community are most likely density-dependent. Furthermore, the effects on functional diversity, community mean traits and vegetation structure were largely neglected.

Here, we present a novel approach, where we performed 427 vegetation assessments in 47 meadows in three distinct regions of Switzerland along a *Rhinanthus alectorolophus* density gradient. We assessed the effect of an increasing relative *Rhinanthus* biomass on species richness, effective diversity and evenness of the functional groups grasses and herbs, the community means of selected plant traits and the abundance-weighted mean Landolt indicator values.

We found a hump-shaped relationship for grass and herb diversity and the relative *Rhinanthus* biomass with diversity maxima at intermediate biomass values of about 30-40%. The abundance-weighted indicator values did not change along the *Rhinanthus* gradient, indicating that *Rhinanthus* does not change the abiotic environment markedly. Further, the community mean trait analysis revealed that *Rhinanthus* promotes smaller plant species. Although previous observations indicated that *Rhinanthus* reaches high densities in low vegetation patches, our results demonstrate for the first time that this is due to *Rhinanthus* and that community composition is shifted towards smaller plant species.

Overall, our results highlight that intermediate *Rhinanthus* densities indeed promote plant diversity in grasslands. We therefore suggest to use *Rhinanthus* in grassland restoration programs. Since *Rhinanthus* spp. are all annuals, intermediate densities can be promoted if heavily infested patches are mown before fruit ripening. Thus, grassland restoration using hemiparasitic *Rhinanthus* could become more applicable in future.

Introduction

The current trend of land-use intensification is one of the main drivers of biodiversity decline worldwide (Sala et al. 2000). In Central Europe, semi-natural grasslands are threatened mainly by increasing nutrient inputs which promote few highly competitive species thriving under such conditions at the cost of overall plant species richness and functional diversity (Wesche et al. 2012). This trend is alarming because vascular plant diversity can be extremely high in such grasslands compared to other vegetation types of similar size (Wilson et al. 2012). Moreover, the loss of plant diversity is likely linked to species losses in higher trophic levels, dooming many other taxa as victims of land-use intensification (Haddad et al. 2009, Wesche et al. 2012, Allan et al. 2014). In the worst case, the balance of agricultural ecosystems is altered to such an extent, that essential biotic services on which we human depend are no longer maintained (Foley et al. 2005, Kleijn et al. 2009).

Therefore, extensive farming practices, the maintenance of (semi-)natural landscape elements and the conversion of highly intensified agricultural grasslands to more extensive grasslands are currently promoted under the agri-environmental framework (e.g. Kleijn et al. 2009). The aim is to maintain and restore highly valuable grassland ecosystems. However, the effectiveness of these programs appears context-dependent and can vary between taxa (Kleijn and Sutherland 2003). High residual soil fertility is a key factor limiting the success of extensification and can explain why an increase in plant diversity is often not achieved (Pywell et al. 2007). Various attempts to overcome this problem have been suggested. For example, extracting nutrients in plant biomass through frequent mowing or grazing tends to be slow or ineffective (Bullock and Pywell 2005) while the more straightforward removal of top-soil is effective but costly (Mudrak et al. 2014). Due to these constraints, an alternative aim could be to control the ultimate effects of high soil fertility, namely the vast growth of few competitive species (Bullock and Pywell 2005). Hence, a cost-effective tool for grassland restoration could be the introduction of native parasitic plants in these ecosystems (Davies et al. 1997, Smith et al. 2003).

We know about 4000 parasitic plant species in 16 different families (Westwood et al. 2010). This life strategy evolved many times independently and seems to be highly successful. Two major groups can be distinguished: Holoparasites are fully dependent on assimilates from their hosts and consequently do not produce chlorophyll for photosynthesis. Hemiparasites however, comprising most parasitic plants, are photosynthetic active themselves and take only water and nutrients from their hosts (Watson 2009, Westwood et al. 2010). Furthermore, root and shoot parasites can be distinguished, depending on the site of attachment to the host via specific organs called haustoria (Press and Phoenix 2005).

While research often focused on parasitic plants as agricultural pests (e.g. Parker 2009), their role in natural systems is often ignored in community theory. Like herbivores, parasitic plants possess host preferences, reduce host biomass and reproduction, modify the interactions between hosts and other organisms and ultimately affect vegetation structure and community dynamics (Pennings and Callaway 2002). As a key difference they do not only parasitize but compete with their hosts at the same time. Notably, parasitic plants can be considered as keystone species because they can reduce competition when parasitizing selectively or density-dependent, e.g. dominant plants. Thereby they facilitate coexistence and promote the stability of natural communities. Moreover, due to their effects on the abiotic environment, mostly the availability of nutrients, parasitic plants are considered as ecosystem engineers (Press and Phoenix 2005).

Rhinanthus spp.*,* a member of the large parasitic *Orobanchaceae* family*,* is the most common root hemiparasitic genus throughout temperate Europe (Ameloot et al. 2005). Due to several reasons, *Rhinanthus* species were recommended as an appropriate tool for grassland restoration: *Rhinanthus* is a natural part of European grasslands, seeds are easy to gather and are therefore cheap, *Rhinanthus* can be sown under fertile conditions, its density

can be controlled easily and most important, it presumably promotes coexistence and diversity of grasslands (Bullock and Pywell 2005, Westbury et al. 2006, Mudrak et al. 2014). While there is evidence that *Rhinanthus* has marked effects on natural communities, we do not yet understand the mechanistic basis of how diversity is promoted and if this prevails under all conditions. Nevertheless, three non-exclusive mechanisms were proposed: i) *Rhinanthus* facilitates coexistence by mediating competition between competitive dominants and subordinates, ii) vegetation productivity and height are reduced, resulting in higher diversity and iii) the formation of gaps after early senescence of *Rhinanthus* promotes colonization by exterior species and recruitment by present species (Bullock and Pywell 2005).

It could be shown that competitive balances can be mediated by the presence of *Rhinanthus* (Gibson and Watkinson 1991) and also other hemiparasitic plants (Matthies 1996). The consequence for plant diversity depends on host-preference because only if competitive dominant species are parasitized over-proportionally compared to subordinate species, coexistence is promoted and diversity enhanced (Phoenix and Press 2005). However, *Rhinanthus* had both positive (e.g. Bardgett et al. 2006) and negative (Gibson and Watkinson 1992) effects on plant diversity. Due to the low number and methodological differences between studies, the meta-analysis by Ameloot et al. (2005) highlighted that we do not know enough yet to draw general conclusions about diversity promoting effects of *Rhinanthus* via mediating competitive relationships.

Also the effects on productivity are still rather unclear. Although farmers are very unpopular with *Rhinanthus* because they fear less productive meadows with lower yield, the reduction in host biomass can potentially be compensated by the hemiparasite (Pennings and Callaway 2002). However, resource inefficiency is characteristic to many parasites (Press and Phoenix 2005), suggesting that compensation is only minimal. Accordingly, a decrease in productivity by on average 26% was found (Ameloot et al. 2006). However, a long-term study revealed no effect of *Rhinanthus* on productivity (Ameloot et al. 2006) and others reported even increases in productivity (Joshi et al. 2000, Spasojevic and Suding 2011). Hemiparasites clearly decrease the biomass of their hosts (Cameron et al. 2005), but they can be seen as mutualists on community level (Phoenix and Press 2005). Evidence is growing that hemiparasites have positive effects on nitrogen cycling and availability and the structure of microbial communities in the soil (Quested et al. 2003, Bardgett et al. 2006, Spasojevic and Suding 2011). Thus, effects on productivity are rather context-dependent. Moreover, it remains unclear whether less productive meadows are actually more diverse and whether there is indeed a link between plant productivity and diversity overall (Adler et al. 2011).

Ultimately, the effect of gap formation after senescence of *Rhinanthus* was shown to increase bare ground availability, promote colonization and recruitment (Joshi et al. 2000) and was positively associated with established phases of less competitive species (Pywell et al. 2004). However, this mechanism works only after die back of *Rhinanthus*. By then, grasslands have reached a considerable biomass and species are already established (personal observation). Thus, the importance of gap formation as a mechanism promoting coexistence might be rather low (see also Davies et al. 1997).

There is evidence for all of these three mechanisms but their relative importance and context-specific role remains rather unclear (Bullock and Pywell 2005). In addition, other aspects such as the effects of hemiparasites on community structure and composition were largely neglected (Quested et al. 2003, Ameloot et al. 2005). Traditional correlation studies depicting decreases in productivity where *Rhinanthus* was present (e.g. Davies et al. 1997) are problematic because one cannot conclude whether *Rhinanthus* decreases productivity or whether *Rhinanthus* thrives particularly well under low-productive conditions (Ameloot et al. 2005, Bullock and Pywell 2005). If *Rhinanthus* should be used successfully in grassland restoration, the mechanistic effects on grassland diversity, productivity, composition and structure need

to be further elucidated. Moreover, while it was shown that functional groups are more important for ecosystem functioning than species richness per se (Tilman et al. 1997), only few studies examined the effects of *Rhinanthus* on functional diversity (but see Demey et al. 2015).

Therefore, we present a novel approach investigating the effect of *Rhinanthus* on the functional groups grasses and herbs and the community structure and mean traits along a density gradient. Thereby we can reveal the mechanistic relationships more precisely and try to fill prevailing knowledge gaps. Moreover, this approach might allow us to draw recommendations on the suitability of *Rhinanthus* in grassland restoration. We are interested in the following three questions: how does increasing *Rhinanthus* density affect i) the diversity in terms of species richness, effective diversity and evenness of herbs and grasses, ii) the community structure and functional traits, and iii) the abundance-weighted mean Landolt indicator values?

Material and methods

Study system

In this observational study, we collected data from 47 meadows in three distinct regions located in the western part of Switzerland: the vicinity of Bern, the Bernese uplands and the Valais. Altitude ranged from 504 (Bern) to 1946 m.a.s.l. (Schynige Platte, Bernese uplands). The maximum geographic distance between the regions was approximately 80 km. In Bern we investigated 30, in the Bernese uplands 13 and in the Valais 4 meadows. The sampling period lasted from mid-May to the end of June 2015.

In each meadow, we selected nine 20×20cm plots according to the density of our focal plant species *Rhinanthus alectorolophus* (Scop.) Pollich (named *Rhinanthus* hereafter). We aimed to cover a gradient from minimum (mostly equivalent with absence) to maximum *Rhinanthus* densities in each meadow. In each plot, we identified all plant species and estimated their percentage cover and the one of bare ground. Where species identification was problematic, we chose species aggregates

and species names with the notation *sensu lato* (s.l.) rather than identifying to taxonomically lower levels. In addition, we recorded GPS coordinates, altitude, slope and exposition of each plot. Moreover, we harvested the total aboveground biomass, separated *Rhinanthus*, herbs and grasses, dried the samples at 80°C for at least 48 hours and weighted them with 0.01g precision. Thus, we could estimate not only the total biomass per plot but also the biomass of the three distinguished groups and their relative biomass per plot.

Data base research

We requested data from the TRY – Plant Trait Database (www.try-db.org/) and the Seed Information Database (SID) from the Kew Royal Botanical Gardens (www.data.kew.org/sid/) to compute mean traits of seed weight, plant height, specific leaf area (SLA) and leaf dry matter content (LDMC) for all species recorded in the field. Data was available for >80% of the species. For each species we computed the overall mean, mostly by using the median values of all the data base records of the traits. We then used the abundance-weighted community mean traits for further analyses.

Statistical analysis

The statistical analysis was performed using R (version 3.1.1, R Development Core Team 2014). We used the package *vegan* (Oksanen et al. 2015) to calculate species richness S, effective diversity ($e^{H'}$, where H' denotes Shannon index) and Pielou's evenness ($J = H'/\log[S]$) with the cover estimates from the vegetation surveys. With the package *nlme* (Pinheiro et al. 2014) we computed a linear mixed effect model including as fixed effects the relative *Rhinanthus* biomass per plot as a linear and quadratic term and region and observer as covariates. The different meadows were included as a random term to account for meadow specific differences. To investigate the effect of *Rhinanthus* on composition, we applied the model to the cover values of the two functional groups grasses and herbs separately. Our response variables included the diversity estimates per functional group as well as the community mean traits and

weighted indicator values of light, moisture, nutrient level and soil pH (Landolt 2010). *Rhinanthus* was omitted for the calculations of all response variables except community mean traits, where we run a model on the response when including and when excluding the values of our focal species.

Results

The effect of Rhinanthus on grass and herb diversity

We found a significant curved-linear relationship for species richness of grasses and herbs along the relative *Rhinanthus* biomass gradient (Fig. 1a, b, Table 1) with highest values of grass and herb species richness at intermediate *Rhinanthus* densities of 27.4 or 33.6% respectively. The net increase encompassed 0.32 grass species and 1.03 herb species at this optimum *Rhinanthus*-density level.

The effective diversity of grasses and herbs also followed this hump-shaped relationship (Fig. 1c, d, Table 1). Highest effective diversity values were obtained at a *Rhinanthus* density of 33.8% for grasses and 42.3% for herbs. At these densities, the net increase in effective diversity was 21.2% for grasses and 17.2% for herbs compared to control plots without *Rhinanthus.*

For Pielou's evenness, we found a curved-linear relationship for grasses and a linear relationship for herbs (Fig. 1e, f, Table 1).

Overall, the meadows in the vicinity of Bern were less species rich compared to the ones at higher altitudes in the Bernese uplands and the Valais. The effects of an increasing *Rhinanthus* density on all diversity measures were consistent among regions in four out of six cases (indicated by the non-significant *Rhinanthus* density – by – region interactions, Table 1) underlining the generality of our results. There was a significant region effect

Table 1. Model outputs (anova table) for species richness, effective diversity and Pielou's evenness of grasses and herbs. We performed the following linear mixed effect model (lme) for all three measures: Y ~ Region*(*Rhinanthus* density + I(*Rhinanthus* density ^2)) + Observer, with Meadow as random term. In each case we computed models with *Rhinanthus* density as a quadratic or as a linear parameter and selected the best model according to *p*-values.

Grasses

	df	Species richness		Effective diversity		Evenness	
		F-value	p-value	F-value	p-value	F-value	p-value
(Intercept)	1	619.175	**< 0.001**	862.682	**< 0.001**	1479.874	**< 0.001**
Region	2	0.871	0.426	1.331	0.275	0.891	0.417
rel. *Rhinanthus* biomass linear	1	-	-	-	-	-	-
rel. *Rhinanthus* biomass quadratic	1	7.304	**0.007**	10.782	**0.001**	4.455	**0.036**
Observer	2	1.234	0.292	2.631	0.073	2.353	0.097
Region × rel. *Rhinanthus* biomass linear	2	-	-	-	-	-	-
Region × rel. *Rhinanthus* biomass quadratic	2	0.077	0.926	0.082	0.922	0.585	0.558
			R^2: 0.39		R^2: 0.30		R^2: 0.24

Herbs

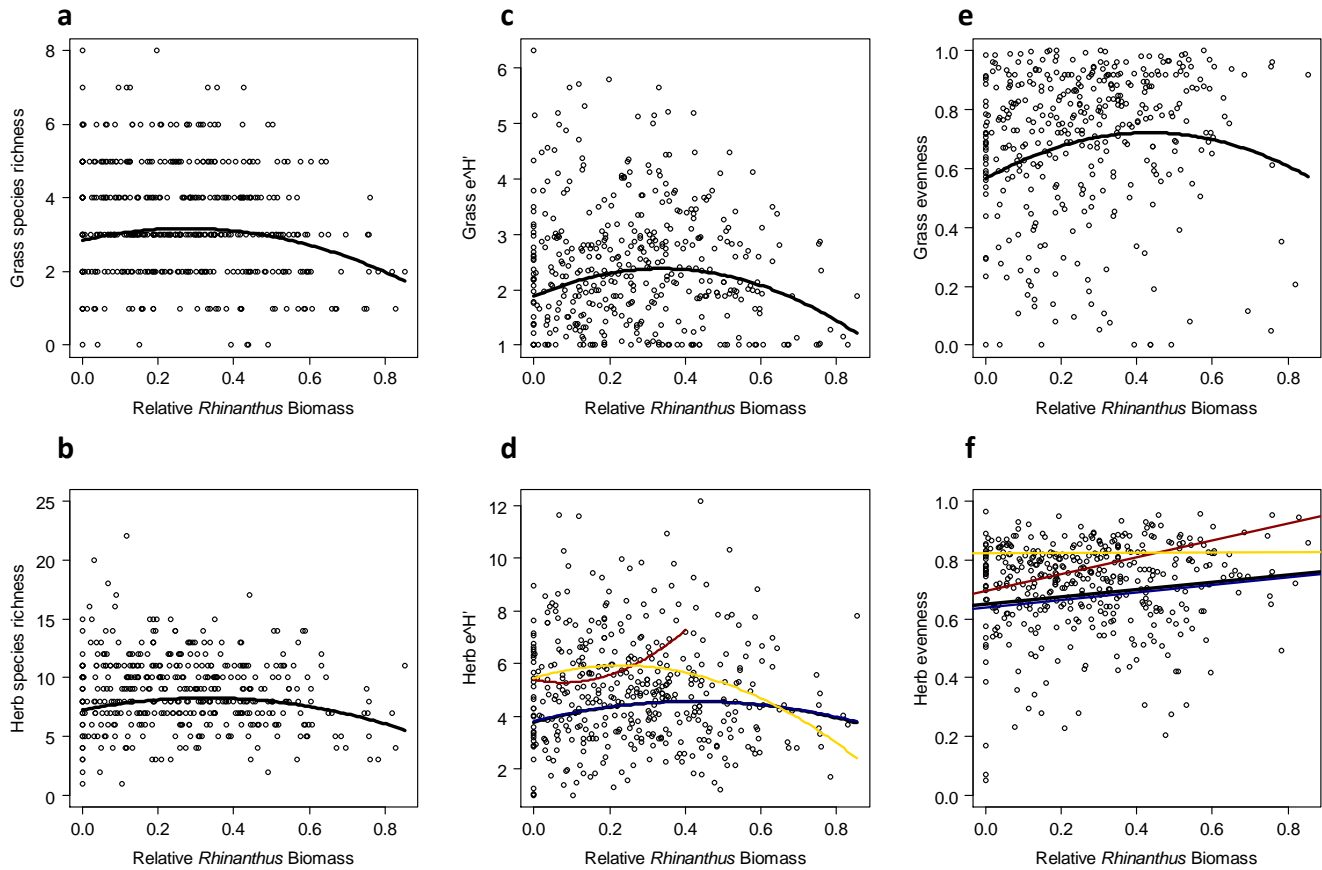|	df	Species richness		Effective diversity		Evenness	
		F-value	p-value	F-value	p-value	F-value	p-value
(Intercept)	1	1054.655	**< 0.001**	1329.933	**< 0.001**	7671.941	**< 0.001**
Region	2	2.925	0.064	10.238	**< 0.001**	11.077	**< 0.001**
rel. *Rhinanthus* biomass linear	1	-	-	-	-	7.042	**0.008**
rel. *Rhinanthus* biomass quadratic	1	11.010	**0.001**	4.142	**0.043**	-	-
Observer	2	6.719	**0.001**	7.470	**0.001**	3.526	**0.030**
Region × rel. *Rhinanthus* biomass linear	2	-	-	-	-	1.470	0.231
Region × rel. *Rhinanthus* biomass quadratic	2	0.238	0.789	0.993	0.371	-	-
			R^2: 0.43		R^2: 0.32		R^2: 0.17

Figure 1 (a-f). Relationships of species richness (a, b), effective diversity (c, d) and Pielou's evenness (e, f) of grasses and herbs and the relative *Rhinanthus* biomass gradient. Accentuated black lines represent the regression of the complete model. Coloured lines indicate the relationships in the three study regions Bern (blue), Valais (red) and Bernese uplands (yellow). They are only shown where we found a significant difference among regions. In all cases, both curved and linear relationships were tested. For regression coefficients and additional information see tables S1–S3 in the appendix.

Table 2. Model outputs (anova table) for the community weighted Landolt indicator values (light, moisture, pH and nutrient level). We performed linear mixed effect models (lme) for all measures: Y ~ Region*(*Rhinanthus* density + I(*Rhinanthus* density ^2)) + Observer, with Meadow as random term. The values of *Rhinanthus* were excluded from this analysis in order to test the effect on the community solely.

	df	Light index F-value	Light index p-value	pH index F-value	pH index p-value
(Intercept)	1	13752.587	**< 0.001**	16168.295	**< 0.001**
Region	2	0.393	0.678	0.807	0.453
rel. *Rhinanthus* biomass linear	1	0.023	0.880	1.873	0.172
rel. *Rhinanthus* biomass quadratic	1	0.076	0.783	0.828	0.363
Observer	2	0.052	0.949	0.048	0.954
Region × rel. *Rhinanthus* biomass linear	2	0.014	0.986	0.034	0.967
Region × rel. *Rhinanthus* biomass quadratic	2	1.358	0.259	1.166	0.313

	df	Moisture index F-value	Moisture index p-value	Nutrient index F-value	Nutrient index p-value
(Intercept)	1	10874.83	**< 0.001**	6954.457	**< 0.001**
Region	2	2.276	0.115	0.014	0.986
rel. *Rhinanthus* biomass linear	1	0.109	0.742	0.853	0.356
rel. *Rhinanthus* biomass quadratic	1	0.647	0.422	0.274	0.601
Observer	2	0.473	0.623	0.335	0.716
Region × rel. *Rhinanthus* biomass linear	2	0.953	0.387	0.159	0.853
Region × rel. *Rhinanthus* biomass quadratic	2	0.197	0.822	0.527	0.591

for effective diversity and evenness of herbs. However, due to low sample size in the Bernese uplands and the Valais and the low coverage of the density gradient in the Valais we are not very confident in these region specific differences. Also, the overall trends appear mostly consistent (see Fig. 1).

Effects on the mean Landolt indicator values and on the community mean traits

We could not detect any significant effect of *Rhinanthus* density on weighted Landolt indicator values for moisture, light, nutrient and soil pH (Table 2). This indicates that *Rhinanthus* did not affect the abiotic conditions to such an extent that it would translate in a shift in the community mean for these indices.

For seed weight, SLA and LDMC there was no significant effect of relative *Rhinanthus* biomass when *Rhinanthus* was excluded from the community mean trait analysis. However, we found a negative linear relationship between plant height and relative *Rhinanthus* biomass (Fig. 2, Table 3). This shift in community mean height indicates that higher *Rhinanthus* densities promote smaller species in plant communities.

Not surprisingly, if we included *Rhinanthus* in the analysis, all four traits showed significant linear or curved-linear relationships (Table 3) approaching the particular values of *Rhinanthus* as its density increased. The community mean SLA decreased, seed weight increased and plant height and LDMC followed a u-shaped curve.
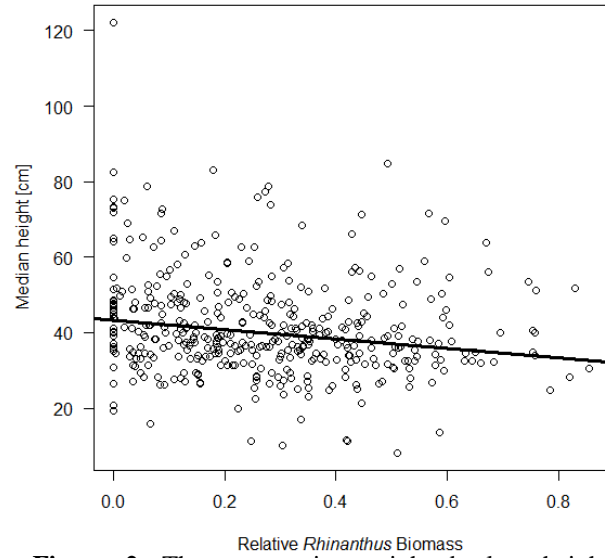

Figure 2. The community weighted plant height along the relative *Rhinanthus* biomass gradient. Plant height decreased linearly, indicating that *Rhinanthus* promotes smaller plant species in species number and/or abundance. The accentuated black line represents the regression of the complete model.

Table 3. Model outputs (anova table) for the community mean traits seed weight, plant height, specific leaf area (SLA) and leaf dry matter content (LDMC). We performed linear mixed effect models (lme) for all measures: Y ~ Region*(*Rhinanthus* density + I(*Rhinanthus* density ^2)) + Observer, with Meadow as random term. For each community trait, we ran two models; one where we excluded and one where we included the values for *Rhinanthus*.

Community excluding *Rhinanthus*

	df	Seed weigth F-value	Seed weigth p-value	Plant height F-value	Plant height p-value	SLA F-value	SLA p-value	LDMC F-value	LDMC p-value
(Intercept)	1	285.475	**< 0.001**	1170.678	**< 0.001**	7310.138	**< 0.001**	2518.698	**< 0.001**
Region	2	1.504	0.234	1.536	0.227	3.729	**0.032**	0.627	0.539
rel. *Rhinanthus* biomass linear	1	3.384	0.067	13.790	**< 0.001**	1.983	0.160	-	-
rel. *Rhinanthus* biomass quadratic	1	-	-	-	-	-	-	4.484	**0.035**
Observer	2	1.248	0.288	1.192	0.305	1.229	0.294	0.324	0.724
Region × rel. *Rhinanthus* biomass linear	2	0.312	0.732	0.607	0.546	1.165	0.313	-	-
Region × rel. *Rhinanthus* biomass quadratic	2	-	-	-	-	-	-	0.781	0.459

R^2: 0.42

Community including *Rhinanthus*

	df	Seed weigth F-value	Seed weigth p-value	Plant height F-value	Plant height p-value	SLA F-value	SLA p-value	LDMC F-value	LDMC p-value
(Intercept)	1	588.573	**< 0.001**	1831.286	**< 0.001**	10707.85	**< 0.001**	3828.950	**< 0.001**
Region	2	0.742	0.482	1.927	0.158	3.756	**0.031**	0.735	0.485
rel. *Rhinanthus* biomass linear	1	13.843	**< 0.001**	-	-	4.553	**0.034**	-	-
rel. *Rhinanthus* biomass quadratic	1	-	-	8.656	**0.004**	-	-	6.051	**0.014**
Observer	2	0.721	0.487	1.381	0.253	0.451	0.637	0.339	0.713
Region × rel. *Rhinanthus* biomass linear	2	0.165	0.848	-	-	1.891	0.152	-	-
Region × rel. *Rhinanthus* biomass quadratic	2	-	-	0.471	0.625	-	-	0.621	0.538

Discussion

Our results indicate that the increase in overall plant species richness and effective diversity at intermediate *Rhinanthus* densities (Klimmek 2015) is based on corresponding increases in both grass and herb diversity. These findings are interesting for grassland restoration, because functional composition and diversity are more important for ecosystem processes than diversity per se (Tilman et al. 1997).

The major mechanism promoting grass and herb diversity seems to be the mediation of competitive balances in the community. The positive response in evenness of both herbs and grasses at favourable *Rhinanthus* densities suggests that highly dominant species are parasitized over-proportionally. Thereby competitive exclusion is prevented and coexistence with subordinate species promoted (Press 1998, Phoenix and Press 2005). In accordance with these findings, Demey et al. (2015) reported a decrease in species evenness after removal of *Rhinanthus.* It seems that, similarly to herbivores, hemiparasitic plants like *Rhinanthus* can play key roles in mediating the competitive relationships and the stability in a community (Press 1998, Pennings and Callaway 2002). In this regard, an important determinant is not only parasite virulence but also host selection. Studies investigating host specificity of *Rhinanthus* include the counting of haustoria on neighbouring plant roots (Weber 1976) or frequency analyses of plants commonly associated with *Rhinanthus* (Gibson and Watkinson 1989). These approaches are problematic because the results do not reveal whether the identified hosts are truly used as hosts. Observations along a *Rhinanthus* density gradient allow us to draw more general conclusions. As both grass and herb diversity and evenness was enhanced at intermediate *Rhinanthus* densities, our results indicate that *Rhinanthus* parasitizes rather density-dependent than selectively. Accordingly, Press and Phoenix (2005) stated that a parasite's host specificity might simply be an artefact of host abundance, meaning that abundant host species are more parasitized because the chance is higher that they encounter the parasite. However, *Rhinanthus* decreased grass and legume biomass but increased forb biomass and plant diversity in some studies (Davies et al. 1997, Joshi et al. 2000, Ameloot et al. 2005, Cameron et al. 2005, Bardgett et al. 2006). It was concluded that the biomass decrease of highly dominant grasses and/or legumes and the resulting increase in herbs translated into higher diversity. In contrast, we found positive effects on diversity of both grasses and herbs. Furthermore, according to Zwahlen (2015), the productivity of grasses and herbs similarly decreased along the *Rhinanthus* density gradient. Although we did not separate herbs and legumes, this further implies a lack of host preference in *Rhinanthus.*

As an alternative mechanism, *Rhinanthus* was considered to increase plant diversity by reducing the overall productivity of communities (Davies et al. 1997, Smith et al. 2003, Bullock and Pywell 2005). The decrease in community productivity in the study of Zwahlen (2015) at favourable *Rhinanthus* densities was around 25%, which matches well the average productivity decline in the meta-analysis of Ameloot (2005) of 26% for field experiments. A reduction in overall productivity could therefore also partly explain the increase in diversity of grasses and herbs. However, the relationship between productivity and diversity is still rather poorly understood (Adler et al. 2011) and indirect effects via vegetation structure, e.g. plant height, can perhaps reveal better insight than productivity.

Ultimately, we cannot conclude from our data whether the promotion of colonization and recruitment after die back of *Rhinanthus* could explain our findings. *Rhinanthus* abundance can vary greatly between years and follows typically a cyclic pattern (Press and Phoenix 2005). Therefore, we could only speculate about connections between *Rhinanthus* density in the current year and gap size in the previous year at a particular location.

The effects of hemiparasites on vegetation structure and community mean traits were rarely considered. Farmers have noted long ago that patches dominated by *Rhinanthus*

have low vegetation height and are open (Gibson and Watkinson 1992) and *Rhinanthus* is frequently seen as a weed because of its negative effects on productivity (Bullock and Pywell 2005). However, it was never tested whether there are more small plants in the community and vegetation is open due to *Rhinanthus*, or whether *Rhinanthus* reaches high densities only under such conditions. We found a decrease in community mean plant height, which reveals for the first time that *Rhinanthus* shifts community composition towards smaller plant species. Hemiparasitic plants are in general considered to be rather weak light competitors (Matthies 1995) and together with the productivity reducing effects of *Rhinanthus* (Ameloot et al. 2005, Zwahlen 2015), smaller plants are more likely to be maintained in the community. However, hemiparasites can also increase productivity and therefore enhance light competition under some conditions (Joshi et al. 2000, Spasojevic and Suding 2011). Furthermore, *Rhinanthus* densities are highly variable over time (Press and Phoenix 2005, Ameloot et al. 2006). Consequently, one might see a rather cyclic effect of *Rhinanthus* on vegetation height. After reaching high densities and promoting smaller plants, invasion by competitive species is likely because *Rhinanthus* loses its advantage if suitable hosts are no longer available. The subsequent increase in competitive species, mostly grasses and legumes, is then again beneficial for *Rhinanthus*. Thus, patches of high *Rhinanthus* density appear to move through the meadow over time (Press and Phoenix 2005), which might serve as source pools for small, subordinate plant species.

Despite the effect on plant height, the community (excluding *Rhinanthus*) did not change in its abundance-weighted Landolt indicator values. We found no significant shift in the mean Landolt indicator value for light, indicating that not only poor light competitors benefit from *Rhinanthus.* In addition, the mean Landolt indicator value for moisture was not affected in our study, which differs to the results of Spasojevic et al. (2011) who found a 25% decrease in soil moisture levels associated with the hemiparasitic *Castilleja*

occidentalis. Although we know that hemiparasites have high transpiration rate and low water use efficiencies (Phoenix and Press 2005), this seems not to translate into higher abundance or number of species which prefer drier conditions. Our results therefore suggest that negative effects on soil water levels are not as pronounced as sometimes feared.

When the values for *Rhinanthus* were included in the community mean trait analysis, the relationships for plant height, seed mass, SLA and LDMC along the density gradient appeared significant and approached the values of *Rhinanthus* itself. Although these findings are not interesting from a mechanistic perspective, the changes are relevant for practical purposes. It might for example translate into shifts in hay nutrient quality. Therefore, a subsequent hay quality analysis on fibre content and levels of important nutrients with our biomass samples is in process.

Altogether, our results indicate that *Rhinanthus alectorolophus* is suitable for promoting plant diversity if its density can be maintained at intermediate levels of about 30 to 40%. Thereby, both grass and herb diversity could benefit. Thus, we confirm the findings of previous studies suggesting the use of *Rhinanthus* species in restoration of semi-natural grasslands (Smith et al. 2003, Bullock and Pywell 2005, Pywell et al. 2007). Our results and recommendations for *R. alectorolophus* are presumably also representative for other *Rhinanthus* species, because the demographic characteristics and the community impacts of at least the most widely distributed *R. angustifolius, R. alectorolophus* and *R. minor* are largely similar (Bullock and Pywell 2005). Therefore, depending on the regions and grassland type, different *Rhinanthus* species could be chosen for restoration.

Recommendations on the successful introduction of *Rhinanthus* into meadows are increasing (Pywell et al. 2004, Mudrak et al. 2014). However, how can intermediate densities be maintained after successful establishment? Blazek et al. (2015) and Mudrak et al. (2014) recently demonstrated that *Rhinanthus* abundance can be drastically

reduced, if it is mown before fruit ripening and when regeneration is minimal. They pointed out that the seed bank of *Rhinanthus* persists only for a short time and the population therefore depends on a yearly seed production. In accordance, earlier studies stated that the density of *Rhinanthus* can be controlled relatively easily by pulling, ploughing or cutting (Bullock and Pywell 2005). Furthermore, as the long-term study by Ameloot et al. (2006) revealed, population dynamics of *Rhinanthus* are highly variable over time with no persistent impacts on productivity, suggesting that *Rhinanthus* density might be controlled by itself. The observation that highly infested patches seem to move through the meadow (Press and Phoenix 2005) further supports this notion. Anyway, a recommendation for the practice could be the early cutting of heavily infested patches before fruit ripening, whilst intermediate density patches should be mown later to serve as sources for recruitment. Subsequent monitoring of species diversity and grassland productivity would allow us to improve the successful application of *Rhinanthus* in grassland restoration.

In summary, at favourable densities, *Rhinanthus* seems to promote the diversity of both grasses and herbs. As the increase in evenness in both functional groups indicates, the underlying mechanism is the mediation of competitive balances between dominant and subordinate species. *Rhinanthus* seems to play a key role in promoting their coexistence. Furthermore, there were no marked effects on community mean traits except for the decrease in plant height, indicating that *Rhinanthus* promotes smaller plant species. As Zwahlen (2015) showed, the increase in diversity comes with a cost in productivity reduction by 25%. Nevertheless, we encourage the use of *Rhinanthus* in grassland restoration where the ultimate goal should not be maximizing hay production but the maintenance of high biodiversity at landscape scales and the promotion of diversity-related services in such valuable agricultural ecosystems. This is largely in accordance with agri-environmental frameworks including direct payments to farmers for promoting extensively managed grasslands in which high yield is not the main purpose.

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Appendix

Table S1. Model outputs (summary table) for species richness, effective diversity and Pielou's evenness of grasses and herbs. Indicated are the deviations of each parameter in respect to the reference parameter (intercept), the standard errors (SE) and the p-values.

Grasses

	Species richness			Effective diversity			Evenness		
	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value
(Intercept) Region Bern	2.85	0.27	< 0.001	1.88	0.19	< 0.001	0.56	0.05	< 0.001
Region Oberland	0.76	0.42	0.075	0.71	0.28	0.016	0.13	0.07	0.051
Region Wallis	0.18	0.65	0.783	0.13	0.43	0.772	0.07	0.11	0.548
rel. *Rhinanthus* biomass linear	2.35	1.27	0.065	2.98	0.94	0.002	0.73	0.24	0.002
rel. *Rhinanthus* biomass quadratic	-4.28	1.78	0.017	-4.40	1.32	0.001	-0.84	0.33	0.012
Observer 2	0.28	0.19	0.133	0.09	0.14	0.521	-0.02	0.03	0.621
Observer 3	0.28	0.19	0.142	0.29	0.14	0.033	0.04	0.03	0.238
Region Oberland × rel. *Rhinanthus* biomass linear	-1.26	2.29	0.583	-2.08	1.70	0.223	-0.59	0.48	0.213
Region Wallis × rel. *Rhinanthus* biomass linear	1.47	5.76	0.799	-0.43	4.27	0.921	-0.53	1.10	0.628
Region Oberland × rel. *Rhinanthus* biomass quadratic	-1.00	3.59	0.781	1.04	2.65	0.695	0.76	0.83	0.363
Region Wallis × rel. *Rhinanthus* biomass quadratic	-4.23	14.42	0.769	1.26	10.71	0.906	1.67	2.66	0.531

Herbs

	Species richness			Effective diversity			Evenness		
	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value
(Intercept) Region Bern	7.24	0.53	< 0.001	3.79	0.34	< 0.001	0.65	0.02	< 0.001
Region Oberland	0.98	0.82	0.239	1.63	0.50	0.002	0.12	0.03	0.000
Region Wallis	2.51	1.28	0.056	1.67	0.76	0.033	0.05	0.04	0.271
rel. *Rhinanthus* biomass linear	6.34	2.44	0.010	3.72	1.73	0.032	0.13	0.04	0.004
rel. *Rhinanthus* biomass quadratic	-9.74	3.43	0.005	-4.40	2.42	0.070	-	-	-
Observer 2	0.25	0.36	0.493	-0.09	0.25	0.712	-0.02	0.02	0.378
Observer 3	1.14	0.36	0.002	0.65	0.25	0.010	0.02	0.02	0.212
Region Oberland × rel. *Rhinanthus* biomass linear	0.81	4.41	0.854	-0.18	3.12	0.954	-0.12	0.08	0.134
Region Wallis × rel. *Rhinanthus* biomass linear	-4.17	11.09	0.708	-6.83	7.83	0.383	0.16	0.23	0.505
Region Oberland × rel. *Rhinanthus* biomass quadratic	-4.59	6.92	0.507	-3.30	4.85	0.496	-	-	-
Region Wallis × rel. *Rhinanthus* biomass quadratic	3.99	27.75	0.886	23.37	19.65	0.235	-	-	-

Table S2. Model outputs (summary table) for the Landolt indicator values light index, moisture index, pH index and nutrient index. Indicated are the deviations of each parameter in respect to the reference parameter (intercept), the standard errors (SE) and the p-values.

	Light index			Moisture index			pH index			Nutrient index		
	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value
(Intercept) Region Bern	3.44	0.06	< 0.001	2.73	0.05	< 0.001	3.13	0.05	< 0.001	3.18	0.07	< 0.001
Region Oberland	0.00	0.09	0.997	0.20	0.08	0.020	-0.03	0.07	0.719	-0.02	0.11	0.893
Region Wallis	0.12	0.14	0.411	0.11	0.13	0.387	-0.19	0.11	0.103	-0.04	0.18	0.813
rel. *Rhinanthus* biomass linear	0.21	0.27	0.441	-0.01	0.26	0.965	0.03	0.22	0.892	-0.31	0.34	0.364
rel. *Rhinanthus* biomass quadratic	-0.33	0.38	0.391	0.08	0.36	0.827	-0.18	0.30	0.542	0.38	0.47	0.422
Observer 2	0.00	0.04	0.961	0.03	0.04	0.450	0.01	0.03	0.776	0.02	0.05	0.679
Observer 3	-0.01	0.04	0.811	0.01	0.04	0.885	0.01	0.03	0.795	0.04	0.05	0.392
Region Oberland × rel. *Rhinanthus* biomass linear	-0.52	0.49	0.293	-0.46	0.47	0.326	0.03	0.39	0.942	0.45	0.61	0.463
Region Wallis × rel. *Rhinanthus* biomass linear	-1.48	1.24	0.233	-0.40	1.18	0.736	1.30	0.98	0.187	0.44	1.53	0.774
Region Oberland × rel. *Rhinanthus* biomass quadratic	0.84	0.77	0.282	0.40	0.73	0.588	0.00	0.61	1.000	-0.92	0.96	0.337
Region Wallis × rel. *Rhinanthus* biomass quadratic	4.08	3.11	0.191	1.03	2.94	0.728	-3.73	2.45	0.128	-1.61	3.83	0.675

Table S3. Model outputs (summary table) for the community mean traits seed weight, plant height, specific leaf area (SLA) and leaf dry matter content (LDMC). Indicated are the deviations of each parameter in respect to the reference parameter (intercept), the standard errors (SE) and the p-values.

Community excluding *Rhinanthus*

	Seed weight			Plant height			SLA			LDMC		
	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value
(Intercept) Region Bern	2.02	0.22	< 0.001	43.41	2.09	< 0.001	233.88	4.60	< 0.001	0.21	0.01	< 0.001
Region Oberland	-0.02	0.33	0.946	-2.74	3.28	0.408	-15.99	7.20	0.032	0.00	0.01	0.719
Region Wallis	0.33	0.50	0.510	2.13	5.11	0.678	-23.59	11.21	0.041	-0.02	0.02	0.403
rel. *Rhinanthus* biomass linear	-0.62	0.45	0.169	-12.63	3.50	0.000	3.32	7.81	0.670	-0.08	0.04	0.045
rel. *Rhinanthus* biomass quadratic	-	-	-	-	-	-	-	-	-	0.10	0.05	0.075
Observer 2	-0.03	0.20	0.898	1.61	1.59	0.312	-5.44	3.54	0.125	0.00	0.01	0.449
Observer 3	-0.25	0.20	0.216	2.34	1.57	0.137	-4.47	3.51	0.204	0.00	0.01	0.835
Region Oberland × rel. *Rhinanthus* biomass linear	-0.30	0.84	0.720	3.86	6.55	0.556	21.17	14.63	0.149	0.01	0.07	0.872
Region Wallis × rel. *Rhinanthus* biomass linear	1.62	2.44	0.508	18.90	19.17	0.325	26.97	42.78	0.529	0.14	0.18	0.415
Region Oberland × rel. *Rhinanthus* biomass quadratic	-	-	-	-	-	-	-	-	-	-0.01	0.11	0.909
Region Wallis × rel. *Rhinanthus* biomass quadratic	-	-	-	-	-	-	-	-	-	-0.55	0.44	0.212

Community including *Rhinanthus*

	Seed weight			Plant height			SLA			LDMC		
	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value
(Intercept) Region Bern	1.93	0.19	< 0.001	45.41	1.99	< 0.001	233.66	3.82	< 0.001	0.21	0.01	< 0.001
Region Oberland	0.02	0.28	0.940	-2.17	3.05	0.480	-15.48	5.93	0.012	0.00	0.01	0.773
Region Wallis	0.48	0.43	0.272	-0.06	4.72	0.990	-24.63	9.22	0.011	-0.02	0.02	0.308
rel. *Rhinanthus* biomass linear	1.32	0.39	0.001	-31.71	9.33	0.001	-18.49	6.65	0.006	-0.08	0.03	0.016
rel. *Rhinanthus* biomass quadratic	-	-	-	32.67	13.09	0.013	-	-	-	0.11	0.05	0.027
Observer 2	-0.13	0.18	0.457	1.56	1.39	0.260	-2.73	3.01	0.365	0.00	0.01	0.536
Observer 3	-0.21	0.17	0.239	2.16	1.37	0.117	-2.03	2.98	0.498	0.00	0.00	0.987
Region Oberland × rel. *Rhinanthus* biomass linear	-0.34	0.73	0.645	-5.52	16.85	0.744	22.10	12.45	0.077	0.02	0.06	0.726
Region Wallis × rel. *Rhinanthus* biomass linear	0.62	2.12	0.770	44.92	42.36	0.290	35.39	36.40	0.332	0.13	0.15	0.405
Region Oberland × rel. *Rhinanthus* biomass quadratic	-	-	-	18.14	26.39	0.492	-	-	-	-0.03	0.10	0.740
Region Wallis × rel. *Rhinanthus* biomass quadratic	-	-	-	-67.94	106.02	0.522	-	-	-	-0.42	0.38	0.280

Erklärung
Gemäss Art. 28 Abs. 2 RSL 05

Name/Vorname: Heer Nico
Matrikelnummer: 12-105-227
Studiengang: Biologie

Bachelor Titel der Arbeit: „The effect of *Rhinanthus alectorolophus* on community composition and structure in semi-natural Swiss meadows"

Leiter der Arbeit: S. Boch, D. Prati und M. Fischer

Ich erkläre hiermit, dass ich diese Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen benutzt habe. Alle Stellen, die wörtlich oder sinngemäss aus Quellen entnommen wurden, habe ich als solche gekennzeichnet. Mir ist bekannt, dass andernfalls der Senat gemäss Artikel 36 Absatz 1 Buchstabe r des Gesetztes vom 5. September 1996 über die Universität zum Entzug des auf Grund dieser Arbeit verliehenen Titels berechtigt ist. Ich gewähre hiermit Einsicht in diese Arbeit.

Ort/Datum: Hinterkappelen 20.12.2015
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