

The effect of *Rhinanthus alectorolophus* on plant diversity in Swiss meadows

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Written by

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Abstract

Hemiparasitic plants can affect community composition and species diversity of grasslands. However, the magnitude and direction of the effect are contrarily discussed. This study focuses on the effect of varying *Rhinanthus alectorolophus* densities on species richness, effective diversity (e^H) and species evenness. To test this, we sampled all plant species in nine 20×20 cm plots in each of our 47 sites which were distributed across three regions of Switzerland. Moreover, we harvested above ground biomass, separated *Rhinanthus*, grasses and herbs and calculated the relative dry mass as indicator for the relative abundance of each group. In general, the effect of an increasing relative *Rhinanthus* biomass on diversity measures did not differ among regions. Species richness and effective diversity showed a hump-shaped relationship with an optimum at 31 % and 40 % of relative *Rhinanthus* biomass, respectively. Compared to plots without *Rhinanthus*, at these density levels the plant species richness (excluding *Rhinanthus*) increased by 12 % (1.4 species) and effective diversity by 24 %. Evenness increased linearly with increasing *Rhinanthus* densities. These results confirm the hypothesis of an “equalizing hemiparasite mechanism” promoting coexistence of species up to a certain density threshold. This study provides a practicable measure for maintaining maximum plant diversity in meadows by allowing approximately one third of *Rhinanthus* in the plant community.

Key words Effective diversity, ‘Gradient approach’, Root hemiparasite, Species diversity, Species evenness, Species richness

Preface

This 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 practice 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 Forschungsfragen Naturschutz” (www.kbnl.ch).

This thesis has been conducted in close collaboration with Nico Heer and Christoph Zwahlen who also studied *Rhinanthus*-related topics at the Institute of Plant Sciences (IPS), University of Bern in the framework of their bachelor thesis. Data collection, preparation and analysis have been performed together but the topics of the three theses differed. Nico Heer studied “The effect of *Rhinanthus alectorolophus* on community and functional diversity in Swiss meadows” (Heer 2015), and Christoph Zwahlen “The effect of *Rhinanthus alectorolophus* on plant biomass in Swiss meadows” (Zwahlen 2015).

Introduction

The evolution of parasitism in plants has multiple independent origins, meaning that the ability to meet a parasitic life style was present in many ancestral lineages of plants. This includes the recognition of suitable host plants, the development of an invasive organ and regulation of the molecule transfer between two plant individuals. The degree of host dependence and the photosynthetic status can vary a lot among parasitic families, genera and even species. Facultative parasites can live and reproduce even in the complete absence of suitable hosts while obligate parasites need a host to complete their life cycles (Westwood et al. 2010). Holoparasites lack completely the ability to make photosynthesis and are therefore non-green plants. In contrast, hemiparasites are able to make photosynthesis and obtain only water and solutes from their hosts (Press & Graves 1995; Irving & Cameron 2009). The central organ for all plant parasites is the haustorium (plural: haustoria). It is responsible for attachment, invasion and the physiological transport of host resources to the parasite (Kuijt 1969).

The family of Orobanchaceae is interesting because it includes species covering the whole range of host dependence from obligate to facultative parasites (Wolfe et al. 2005; Westwood et al. 2010). Members of Orobanchaceae are found worldwide in the New World as well as in

the Old World and on both hemispheres (Wolfe et al. 2005). The genus *Rhinanthus* includes in Switzerland five species: *R. alectorolophus* (Scop.) Pollich, *R. angustifolius* C. C. Gmel., *R. antiquus* (Sterneck) Schinz & Thell., *R. glacialis* Personnat and *R. minor* L. (Lauber & Wagner 1998). This study focuses on *Rhinanthus alectorolophus* (hereafter referred to as *Rhinanthus*). The plant is a facultative, hemiparasitic, annual root parasite occurring in grasslands of low to medium productivity in Central Europe (Meusel et al. 1978; Lauber & Wagner 1998). Host selectivity seems not to occur although some families are clearly preferred like Fabaceae and Poaceae (Gibson & Watkinson 1989; Matthies & Egli 1999).

Most parasitic plants have a broad host range and can parasitize a large number of different species (e.g. Gibson & Watkinson 1989; Press & Phoenix 2005). Although, hemiparasites of the genus *Rhinanthus* are no exception (*R. minor* is known to parasitize over 50 different species from 18 families (Gibson & Watkinson 1991)) they can still alter the competitive balance between host plants by selecting “good” hosts over “bad” hosts (Gibson & Watkinson 1989, 1991; Matthies 1996). This means that parasites are no true generalists but act more as specialists despite their broad host range by selecting favourable species with a high nitrogen content (Seel & Press 1993; Matthies 1996) or a readily reduced defence system (Cameroon et al. 2005). Some species, especially pioneers on bare ground, might benefit indirectly from the free space that annual hemiparasites leave when dying after their life cycle has been completed (Joshi et al. 2000; Ameloot et al. 2006). This can increase species diversity during the following years if invading species successfully establish in the community (Joshi et al. 2000). Already today, *Rhinanthus* spp. are part of seed mixtures for biodiversity promoting areas (BPA) in Switzerland. However, several experimental studies, mainly with other hemiparasitic species, have shown positive, negative or neutral effects of hemiparasites on diversity (e.g. Gibson & Watkinson 1992; Pennings & Callaway 1996; Pywell et al. 2004; Stein et al. 2009; Mudrak & Lepš 2010). Thus, this topic remains controversial.

Some studies used a ‘space for time substitution’ approach comparing sites with and without hemiparasite (e.g. Gibson & Watkinson 1992; Stein et al. 2009; Mudrak & Lepš 2010). However, this approach allows only the comparison between two extremes and cannot tell anything about effects along a density gradient. Additionally, sites may not be fully comparable since they can also differ in other environmental conditions than just the presence of the hemiparasite. Alternatively, we used a ‘gradient approach’ where we investigated plots on single meadows that vary in the density of our target hemiparasite *Rhinanthus* which allowed us to quantify how varying densities affect community diversity. This approach has already been used by other

authors (e.g. Davies et al. 1997; Matthies 2003; Bardgett et al. 2006; Westbury & Dunnett 2007) but mainly in experimental studies where they established artificial density gradients. Thus, it is largely unknown how hemiparasites in natural communities with inherent density variations affect plant diversity.

One main question provided by the “Marktplatz für Forschungsfragen Naturschutz” related to *Rhinanthus* is how an increase in abundance influences the diversity in the resident plant community. We can expect an upper limit to the beneficial effect on diversity because it is obvious that a community consisting almost only of *Rhinanthus* cannot harbour many other species. Our research questions are:

- 1) How do varying *Rhinanthus* densities affect species richness, effective diversity and evenness?
- 2) Are there regional differences in the response of the diversity measures to varying *Rhinanthus* densities?

These questions are especially interesting in the light of making recommendations for the practice and how these may vary in implementation among different regions and altitudes.

Material and methods

We selected 47 meadows across the western part of Switzerland (30 around Bern, 4 in Valais and 13 in the Bernese uplands) to cover an altitudinal gradient (altitude ranged from 504 m.a.s.l. (Bern) to 1'946 m.a.s.l. (Schynige Platte, Bernese uplands)). Maximum geographic distance between the regions was about 80 km. From May to end of June 2015, we sampled all plant species in nine randomly stratified selected 20×20 cm plots per meadow covering a relative density gradient of *Rhinanthus*: Three plots were set randomly in patches with a relatively high density, three in intermediate dense patches, two in low density patches and one where no *Rhinanthus* occurred. We identified all plant species and estimated their relative cover. Identification was done to species level and we were as conservative as possible, using species aggregates and species names “sensu lato” (s.l.) rather than identifying them to taxonomically lower levels. In addition, we recorded the cover of bare ground, the altitude of each meadow and took three 1.5×10 cm soil samples per plot for later investigation. Moreover, we harvested the complete above ground biomass from each plot excluding litter and mosses. The plant material and the soil samples were dried at 75-80°C for at least 48 hours in a compartment drier. Afterwards, the plant biomass was weighed and the soil samples stored for further analyses.

Statistical analysis

The vegetation survey data was digitalized using Vegedaz (Küchler 2014). Statistical analysis was done using R (R Development Core Team 2008). We used the R packages “vegan” (Oksanen et al. 2015) to calculate species richness and “nlme” (Pinheiro et al. 2014) to run linear mixed effect models. We first calculated species richness per plot taken as the total number of species recorded excluding *Rhinanthus*. The Shannon index H' was calculated following the formula in figure 1 for each plot excluding *Rhinanthus*. To get a comparable and more graspable measure we took the effective diversity which is represented by $e^{H'}$. This measure

$$H' = - \sum_i p_i \cdot \ln p_i \quad \text{mit } p_i = \frac{n_i}{N}$$

yields whole numbers which can be more easily interpreted as the original Shannon index. Evenness describes how even abundance is distributed among all present species. It ranges from 0 to 1. If evenness is 1 then each occurring species has exactly the same abundance

Figure 1: Formula for calculating the Shannon index H' where N is the total cover of all species, n is the cover per species i , and p_i is the relative abundance of species i .

(in our case “cover”). The nearer the measure gets to 0, fewer species are dominating the community. Evenness was calculated as Shannon evenness by dividing the Shannon index H' by the logarithm of the species number excluding *Rhinanthus*. Species richness, effective diversity and species evenness were analyzed with the same linear mixed effect model. The three diversity measures were used as response variable, respectively. Fixed factors comprised of ‘region’ and the interaction with ‘relative *Rhinanthus* biomass’. As there was a significant observer effect on species number ($R^2=0.03$, Tab. 1), we included ‘observer’ as a co-variable in our final model. The factor ‘meadow’ was included as a random factor to account for the study design.

Results

In general, the effect of an increasing relative *Rhinanthus* biomass on diversity measures did not differ among regions. We found a significant hump-shaped relationship of species richness and relative *Rhinanthus* biomass ($R^2=0.47$, Tab. 1) with a highest species richness value at 31 % relative *Rhinanthus* biomass (Appendix Fig. 2). Compared to plots without *Rhinanthus*, we found an increase in species richness by 12 % (1.4 species; without counting *Rhinanthus*) at this density level.

Table 1: Coefficients of the best model for species richness, effective diversity $e^{H'}$ and evenness. Significant values ($p<0.05$) are depicted in bold.

	Y ~ region* (rel.Rhinanthus.biomass + I(rel.Rhinanthus.biomass^2)) + observer, random = ~1 meadow)								
	Y = Species richness			Y = Effective diversity $e^{H'}$			Y = Evenness		
	df	F	<i>p</i>	df	F	<i>p</i>	df	F	<i>p</i>
Intercept	368	1358.61	<0.0001	368	1191.86	<0.0001	371	2309.15	<0.0001
Region	44	3.00	0.0598	44	9.99	0.0003	44	12.19	0.0001
rel. <i>Rhinanthus</i> biomass	368	2.24	0.1352	368	1.38	0.2415	371	4.69	0.0309
I(rel. <i>Rhinanthus</i> biomass ²)	368	16.45	0.0001	368	9.51	0.0022	-	-	-
Observer	368	6.11	0.0025	368	3.92	0.0207	371	2.81	0.0615
Region:rel. <i>Rhinanthus</i> biomass	368	2.30	0.1018	368	1.87	0.1553	371	1.48	0.2277
Region:I(rel. <i>Rhinanthus</i> biomass ²)	368	0.23	0.7957	368	0.82	0.4404	-	-	-

In addition, the effective diversity-relative *Rhinanthus* biomass relationship also followed an optimum curve ($R^2=0.37$, Tab. 1) with highest effective diversity values at a relative *Rhinanthus* biomass of 40 %, which was an increase of 24 % compared to sites without *Rhinanthus* (Appendix Fig. 3).

Species evenness increased linearly with increasing relative *Rhinanthus* biomass ($R^2=0.23$, Tab. 1); the quadratic term was no longer significant and therefore excluded from the model. This trend would have been even more obvious when plotting all meadows separately (Appendix Fig 4).

Discussion

We showed that *Rhinanthus* indeed affected plant diversity in meadows. Species richness and effective diversity showed an optimum curve with highest values at intermediate *Rhinanthus* densities. Species evenness had a linear positive trend meaning that the plant community becomes more even the more *Rhinanthus* is growing. Species richness was increased by 12 % or

1.4 species at an intermediate *Rhinanthus* density of 31 %. The effective diversity takes into account species richness and the relative abundance of each species and the increase there amounts to 24 %. The effect was achieved at a relative abundance of 40 % of *Rhinanthus*. This difference tells us that *Rhinanthus* has a bigger effect on equalizing species abundances than on only increasing overall species richness. A look at the results of the evenness measure confirms this issue. However, we have to be careful not to overestimate this result: the evenness measure tells us only about how equally abundant species are regardless of total species number. At a high relative *Rhinanthus* density there may be only few other competitive species coexisting with the hemiparasite but with similar abundances which does not improve diversity.

Our results of higher plant diversities at intermediate *Rhinanthus* densities can be explained by the fact that *Rhinanthus* spp. are rather generalist hemiparasites (Gibson & Watkinson 1989; Press & Phoenix 2005) and host selection depends strongly on available species in the near surrounding. Therefore, common species get parasitized disproportionately frequent, which reduces asymmetric above ground competition by reducing the growth of dominants, leading to a better growth of weaker species (Press & Phoenix 2005). Chesson (2000) described this effect as an “equalizing mechanism” promoting coexistence which minimizes average fitness differences between species and therefore leads to the observed pattern of increased evenness. In other words, one can say that *Rhinanthus* steals resources from the ones that have plenty and redistributes them among the community when finishing its life cycle, acting somehow like Robin Hood as first stated by Press (1998).

Gibson & Watkinson (1992) conducted a removal experiment with *R. minor* just before seed fall in July to test the effects on species diversity in the following year. There were no changes in species richness and rank abundance of species but significant changes in the abundance of some species. Unsurprisingly, the species that benefitted most from the removal were preferred hosts and the ones that suffered most were avoided hosts (see also Gibson & Watkinson 1989). The authors showed that *R. minor* was growing in low diversity patches within highly diverse meadows (Gibson & Watkinson 1992). They quoted several explanations for this pattern: a) the hemiparasite might reduce the local diversity by suppressing parasitized non-dominant species, b) it might preferentially germinate in low diversity patches and/or c) it might be an artefact of the sampling method. Our findings, which show an optimum curve, suggest rather that *R. alectorolophus* reduces at high abundances the diversity locally just by the fact that it demands itself the space other species would. Below its optimal density the effect of the hemiparasite seems to be too weak to increase diversity significantly.

A severe disadvantage of the study of Gibson & Watkinson (1992) was its ‘all-or-nothing’ treatment of removing the hemiparasite completely. Comparisons with undisturbed control plots yielded no effect on plant diversity which would have also been the case for our data if we had not sampled along a gradient. The diversity promoting effect of *Rhinanthus* is only present at intermediate densities. If we would have only considered the extremes in relative *Rhinanthus* biomass in our data (Appendix Fig. 2 and 3) species richness would have seemed to decline and effective diversity would have shown no difference. Nevertheless, comparable to our results, Gibson & Watkinson (1992) found a higher evenness with *Rhinanthus* present than without *Rhinanthus* (Appendix Fig. 4). Several other studies using the same or similar approaches with artificially created density gradients could also not prove an increase in diversity (Westbury & Dunnett 2007; Stein et al. 2009; Mudrak & Lepš 2010).

In contrast to the findings of Gibson & Watkinson (1992) and in accordance with ours, Joshi et al. (2000) showed that the presence of *Rhinanthus* in newly created grasslands in Switzerland increased species richness of unsown species. The introduction of *R. minor* also increased species richness and Shannon diversity in a young *Lolium perenne* sward (Westbury et al. 2006). A greater number of experimentally sown species has also been observed in grasslands in association with *R. minor* (Pywell et al. 2004).

Deduced from the results of Gibson & Watkinson (1992) and ours, another crucial factor when investigating the effects of parasites on community diversity, is the plot size. Our plot size of 20×20 cm is quite established to study effects of hemiparasites on plant diversity (Gibson & Watkinson 1992; Ameloot et al. 2006; Mudrak & Lepš 2010). Therefore it should not have had any confounding effects on our results and we can recommend it for later studies on this subject. We found no regional differences in the response of the diversity measures to relative *Rhinanthus* biomass, highlighting the generality of our findings. However, a more equally distributed number of investigated sites among the regions (we investigated 4 sites in Valais, 17 in the Bernese uplands and 30 around Bern) might have resulted in differences in the effect size among regions. Interestingly, the regions did not differ significantly in their native species richness which was surprising since we covered an altitudinal gradient of roughly 1’400 m. Perhaps, meadows harbouring *Rhinanthus* are very similar concerning their species richness regardless of altitude meaning that *Rhinanthus* cannot occur in a wide range of habitats. Indeed, *Rhinanthus* is listed as characteristic species only for the Arrhenatherion communities (Delarze et al. 2015). However, the three regions differed significantly in terms of native plant community evenness and effective diversity.

Our findings can be of great practical importance for conservation purposes: we suggest promoting meadows consisting of roughly one third of *Rhinanthus* biomass. So far, there was no study reporting the optimal proportion of hemiparasites to maximize plant diversity. This study thus provides a practicable measure for farmers and conservationists for maintaining maximum diversity in meadows by having assessed the proportion of *Rhinanthus* needed. Unfortunately, this high level of diversity promoted by *Rhinanthus* comes together with a reduction in yield (Davies et al. 1997). In our case, yield was reduced by approximately 25 % at the optimal *Rhinanthus* density of 31 % (Zwahlen 2015). It is now up to conservation biologists and farmers to decide individually if the increase in diversity can compensate for the reduction in productivity.

Interesting for future studies would be to analyse the hay quality (with *Rhinanthus* biomass) in terms of carbon-nitrogen ratio, fibre content and concentration of essential nutrients for livestock such as phosphorus, sulphur and calcium. Such analyses would give additional information about how severe the detriments in yield are. In addition, for practitioners the question how to maintain an optimal density of *Rhinanthus* over several years would be interesting. I suggest testing various approaches in manipulative experiments on field scale under real-world conditions. Testable (and for the farmers later practicable) approaches could e.g. be delayed mowing, leaving of unmown refuges of different sizes and spatial patterns, annual re-sowing of *Rhinanthus* or applying grazing regimes with various intensities. The investigation of patch dynamics of *Rhinanthus* within meadows could shed light on the best measures to maintain an optimal density. Additionally, the soil parameters could be analysed to examine soil chemistry and how these factors change over a density gradient.

The results shown in this paper could also be applicable to other hemiparasitic species such as *Melampyrum* spp., *Pedicularis* spp. or *Bartsia* spp. which are more common than *Rhinanthus* spp. in other grasslands of the world and may have similar effects on diversity and therefore might be even better suited for particular habitats. *Rhinanthus* is surely not the “saviour” for plant diversity in Swiss meadows but according to our findings it can be another little step in the conservation of species-rich meadows and the promotion of a more natural agricultural management system.

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Appendix

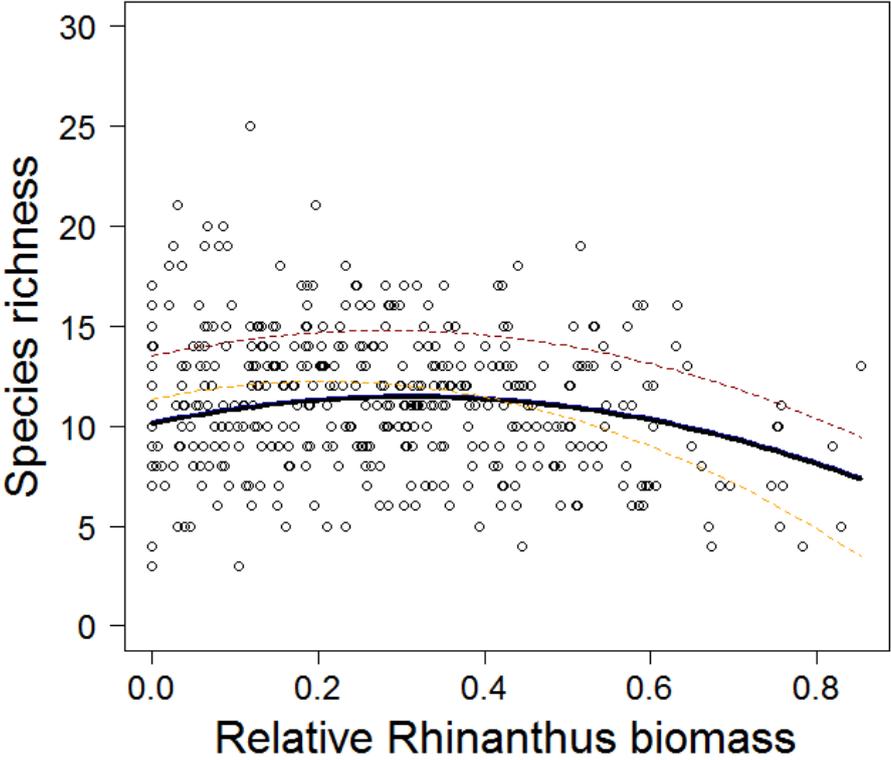


Figure 2: Relationship between species richness and relative *Rhinanthus* biomass. **Black**=overall relationship, **blue**=Bern, **red**=Valais, **yellow**=Bernese uplands. Non-significant slopes are depicted with dashed lines.

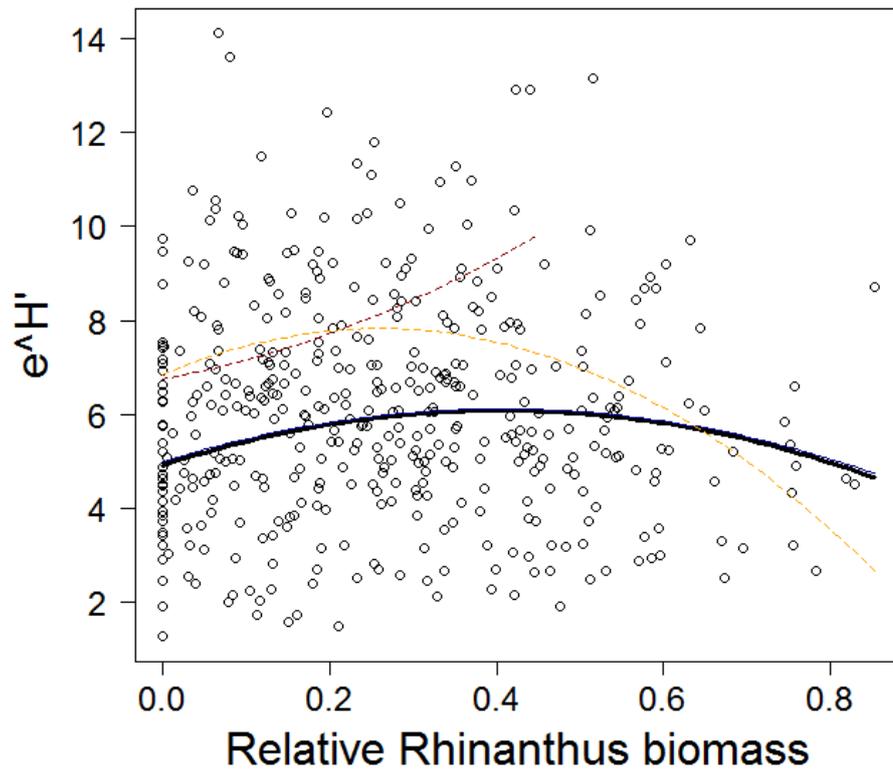


Figure 3: Relationship between effective diversity (depicted as e^H') and relative *Rhinanthus* biomass. **Black**=overall relationship, **blue**=Bern, **red**=Valais, **yellow**=Bernese uplands. Non-significant slopes are depicted with dashed lines.

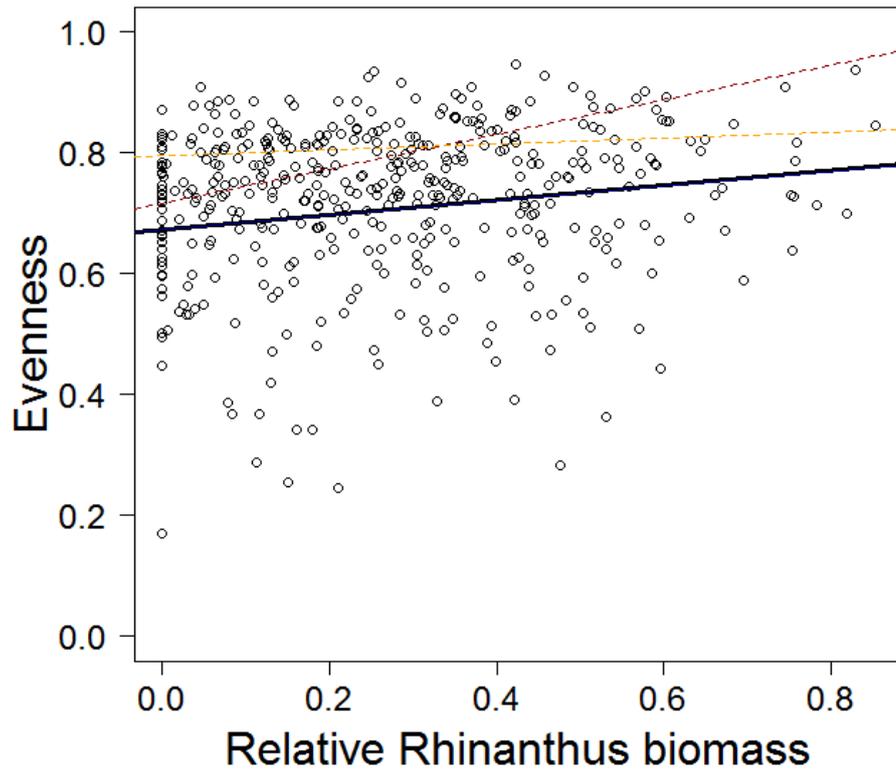


Figure 4: Relationship between species evenness and relative *Rhinanthus* biomass. **Black**=overall relationship, **blue**=Bern, **red**=Valais, **yellow**=Bernese uplands. Non-significant slopes are depicted with dashed lines.

Erklärung

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Bachelor Master Dissertation

Titel der Arbeit: The effect of *Rhinanthus alectorolophus*
on plant diversity in Swiss meadows

LeiterIn der Arbeit: Dr. S. Boch, Dr. D. Prati, Prof. Dr. H. Fischer
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Ich gewähre hiermit Einsicht in diese Arbeit.

Krauchthal, 01.12.2015

Ort/Datum

J. Klimmek

Unterschrift