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Interactions of farming and plant biodiversity in weed control related ecosystem service provision and weed conservation

Dissertation
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Für Eva und Benjamin

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1. General Introduction

1.1. Structure of the dissertation

This thesis consists of six chapters that contribute to the knowledge on the role of weed biodiversity in ecosystem service provision and the simultaneous influence of agricultural practices on both. Furthermore, the principles of ecosystem service provision by plant biodiversity were transferred to cover crops. In a comparison between pure stands and mixtures of cover crops, their respective weed control abilities were evaluated.

The scientific articles were arranged according to the ideas sparked by each other's actual or preliminary results. Chapter II is a review article that gives an introduction into the manifold positive ecosystem services that weeds can provide for practitioners in agriculture and identifies knowledge gaps to be addressed in future research. The idea for this review article was initiated during a working group meeting of the European Weed Research Society (EWRS) and realized by several of their members. In Chapter III influences of agricultural management were examined in regard to weed community composition, weed biodiversity and occurrence of rare arable weed species. One of the research gaps in Chapter II was the missing connection between weed biodiversity and ecosystem service provision. So, Chapter IV investigates bottom-up effects of weed biodiversity on weed seed predators and their performance of weed seed removal under a gradient of agricultural intensification. The link between plant biodiversity and ecosystem service provision can also be utilized to enhance biological weed control measures. In Chapter V the weed suppression potential of cover crop pure stands and cover crop mixtures was evaluated. Chapter VI comprises the general discussion of the research articles and a critical outlook for the topic's future challenges and opportunities.

1.2. Objectives

The specific objectives of this thesis were:

1. To summarize current knowledge and identify knowledge gaps in ecosystem service provision by weeds
2. To identify and understand the management factors shaping weed communities and affecting weed biodiversity and endangered weed species
3. To investigate the effects of weed biodiversity and farming intensity on weed seed predation and it's performing groups
4. To assess weed control abilities of cover crop species sown in pure stands and mixtures

2. Quantification of Regulating Ecosystem Services Provided by Weeds in Annual Cropping Systems Using a Systematic Map Approach

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Abstract: Ecosystem services have received increasing attention in life sciences, but only a limited amount of quantitative data is available concerning the ability of weeds to provide these services. Following an expert focus group on this topic, a systematic search for articles displaying evidence of weeds providing regulating ecosystem services was performed, resulting in 129 articles. The most common service regarded pest control and the prevailing mechanism was that weeds provide a suitable habitat for natural enemies. Other articles showed that weeds improved soil nutrient content, soil physical properties, and crop pollinator abundance. Weeds were found to provide some important ecosystem services for agriculture, but only a small amount of studies presented data on crop yield. Experimental approaches are proposed that can: 1) disentangle the benefits obtained from ecosystem services provisioning from the costs due to weed competition, and 2) quantify the contribution of diverse weed communities in reducing crop competition and in providing ecosystem services. Existing vegetation databases can be used to select weed species with functional traits facilitating ecosystem service provisioning while having a lower competitive capacity. However, for services such as pest control, there are hardly any specific plant traits that have been identified, and more fundamental research is needed.

Keywords: agroecology; functional traits; literature review; pest control; pollination; soil nutrient content; soil physical properties; soil quality; weed management

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2.1. Introduction

Weed research traditionally focuses on the adverse impact that weeds can have on economic, aesthetic, or environmental aspects of any system and on the approaches used to limit this. Recently, special attention has been paid to ecosystem services that natural vegetation can provide to society, and this may include species that are often classified as weeds. Ecosystem services can be described as the benefits obtained by the human population from an ecosystem (MEA, 2003). The communities that form (agro)ecosystems can provide services to humankind in terms of habitat, food and other goods, and clean resources (Daily 1997) thanks to the specific functional traits of the species. The diversity of species traits present in these communities can also provide an insurance against future changes by hosting organisms and genes that may become of fundamental importance to guarantee ecosystem processes under changing environmental conditions (Moonen & Bàrberi 2008). For example, insurance could derive from beneficial insect populations tolerant to extreme weather or from genes that can be used to grow drought-resistant crops. The Common International Classification of Ecosystem Services contains three main types of ecosystem services: provisioning services, regulating and maintenance services (hereafter referred to as regulating services), and cultural services (Haines-Young & Potschin 2011).

In light of current EU agricultural policies, and more specifically Directive 2009/128/EC on the sustainable use of pesticides and the 2014-2020 CAP reform including numerous proposals for 'greening', it becomes increasingly more important to provide farmers with concrete data regarding the benefits they can obtain from mixed farming, reduced herbicide use, inclusion of semi-natural habitats on their farms, and the use of cover crops. Agroecological farming approaches promote management of the weed community instead of its complete eradication inside cropped fields. Potentially, this could result in weed communities that do not negatively affect crop production while providing regulating services to the agroecosystem (Petit *et al.* 2015). These approaches can be combined with other management strategies. The management of agrobiodiversity surrounding cropped fields (e.g. in semi-natural habitat) can contribute to the provision of regulating ecosystem services such as increasing beneficial insects for pest control and pollination (e.g. Alignier *et al.* 2014, Sutter *et al.* 2017). However, the effect on actual pest control and crop yield are hardly measured (Holland *et al.* 2016).

In most reviews concerning weeds and ecosystem services, weeds are considered as pests (e.g. Oerke 2006; Shennan 2008). In others, potential benefits that weeds can have on ecosystem processes and functioning are discussed. These reviews focus on the role that weeds have in hosting beneficial arthropods (Petit *et al.* 2011) whether they be pollinators (e.g. Nicholls & Altieri 2013; Bretagnolle & Gaba 2015) or natural enemies of crop pests (e.g. Hillocks 1998; Norris & Kogan 2000). Weeds can exert an indirect effect on pest control by attracting beneficial insects that serve as crop pest predators. The effect of these beneficial insects on pest control and yield loss reduction is often difficult to establish and explanations for the lack of response can be similar to the ones hypothesised by Tscharntke *et al.* (2016) regarding the role of natural habitats in sustaining beneficial insects. On the other hand, weeds exert a direct effect on pest regulation by attracting or arresting certain pest species away from crops (Capinera 2005), by reducing the attractiveness of a crop (Altieri & Whitcomb 1979), or by making the crop less noticeable to the pest (Root's (1973) resource concentration hypothesis). Another mechanism through which weeds can reduce crop pest infestation is by creating an associational resistance within the crop. This occurs when weeds interact with a crop plant and increases the crop's resistance to pest infestation (Ninkovic *et al.* 2009).

The aforementioned review articles, however, are descriptive and present little quantitative data on the services provided by weeds. Assumptions extrapolate the role 'vegetation' plays in general in ecological processes, to the role 'weeds' may play. Based on discussions during a meeting of weed scientists interested in weed diversity conservation (Meeting of the Weeds and Biodiversity Working Group of the EWRS in Pisa, Italy, held from 18-20 November 2014), it was hypothesised that, in reality, little scientific evidence quantifying the services provided by weeds exists. Through a subsequent systematic literature mapping approach, quantitative information was extracted on regulating services provided by weeds (e.g. data on pest control enhancement) in arable or vegetable cropping systems. The search was restricted to regulating services in order to have a manageable number of articles in the search result, and coherent and quantitative results for analysis. At least in theory, it should be easier to quantify how weeds interact with ecosystem processes than to quantify their cultural services, which is a rather subjective matter. The objective of this work was to quantify the amount of empirical data available on weeds providing ecosystem services to identify perspectives for future research aimed at agroecological weed management by 1) giving a bibliometric overview of the articles that provided scientific evidence of regulating services (directly and indirectly) provided by weeds, and 2) identifying the weeds providing ecosystem services and quantifying the effect on crop yield.

2.2. Materials and Methods

Literature search

The systematic map approach consists of conducting a systematic review and collecting existing evidence on a broad topic (Haddaway *et al.* 2016). This approach allows for a more objective and transparent review compared to the traditional narrative review (Collins and Fauser 2005). It requires performing an initial search to define the relevant keywords in relation to the research topic. These terms are then used to perform a final search in an online database. The systematic map approach differs from a meta-analysis in that it gives an overview on a research topic as opposed to answering specific hypotheses. This tool has recently become popular in environmental sciences (e.g. Bernes *et al.* 2015; Fagerholm *et al.* 2016).

We followed a similar protocol to previously performed systematic map approaches (e.g. Holland *et al.* 2016). The online database Scopus® was used for searching articles. This search engine contains articles dating back to 1960. No year restriction was placed on the search. However, results were restricted to those in the field of 'agriculture and biological sciences', 'environmental science', and 'earth and planetary sciences'. The search was made on the 16th of January 2015. Preliminary searches were carried out to determine the terms associated with the research question. The search string used circumscribed the search results to papers focussing on plant species defined as weeds by including 'weed*' as a search term. Papers were then limited to studies relevant to arable or vegetable crops in the open field by including the terms 'agr*', 'field*' and 'crop*'. Finally, search terms that were included aimed at extracting papers focussing on at least one of the four key regulating ecosystem services: pest control, crop pollination, soil physical quality, and nutrient cycle regulation. Therefore, at least one of the following terms had to be present in the articles: 'ecosystem service*', 'ecological service*', nitr*, carbon, pollination, preda*, 'natural enem*', 'pest control', biocontrol, 'biological control', erosion, 'soil organic matter', 'temperature regulation', microclimate, 'nutrient cycle'.

In the preliminary searches, a high number of articles that did not contain information on weeds providing ecosystem services were found. Therefore, the following strategy was used to improve the focus of the search. Articles were excluded when the title, abstract or keywords contained the terms orchard*, forest*, tree*, as the habitat of interest was annual crops. Also, many unwanted articles appeared because the authors referred to 'weed control' as 'pest control' and, therefore, 'pest control' was not intended as an ecosystem service provided by weeds. By excluding the terms 'chemical control', 'mile-a-minute weed', and knapweed in the title, abstract, or keywords and the term herbicide* in the title, we were able to avoid collecting numerous articles that did not contain information on regulating ecosystem services in the final search. Finally, articles containing 'seed predat*' in the title, abstract or keywords were excluded as well because these articles focussed on the predation of weed seeds and did not contain information on weeds providing regulating ecosystem services. We did not extract data on the effect of scale on ecosystem provisioning as articles often did not contain such data and some reviews have already provided this information, although they did not focus on weeds (e.g. Mitchell *et al*. 2013, Veres *et al.* 2013, and Malinga *et al.* 2015).

Screening of the search results

In the second phase, abstracts of all retained articles were screened based on four predefined inclusion criteria. Firstly, the document should provide a quantitative result on at least one regulating ecosystem service provided by weeds. Secondly, the studied system should include arable or vegetable crops for human consumption. Thirdly, the document should be written in English, so that, in the event of an incongruent entry in the map, the article could be analysed by another author. Lastly, the result(s) of the study should not be obtained through the use of modelling as primary data was required to obtain values for the ecosystem services provided.

The abstracts of all the articles in the search result were scanned by the lead author to see if they met the set criteria. Whenever it was unclear if an article met all the criteria, the article was treated as if it did. Those that met the criteria were randomly distributed among the authors and read in full. Information was transcribed into the systematic map, a table constructed by the authors with issues deemed relevant to the research topic (Supplementary Information). Information retrieved was related to country of origin, type of experimentation (on-farm, on-station, controlled environment), ecosystem service targeted, weed species involved, ecosystem service measured, presence of other organisms benefitting from weed presence such as predators or pests, and comparison of crop yield in situations with and without weeds. Review articles that met the criteria were not included in the literature map. Instead, citations in the reviews that were related to the search topic but not yet included in the systematic map were collected. They then underwent the same process as the documents from the search result. Due to the wide variety of services presented, combined with the lack of uniform quantitative data, not all effect sizes could be analysed quantitatively. Pest control was the most abundant regulating service for which the range of minimum and maximum percentage values could be calculated. In thirty studies, the effect of weeds on yield was reported, however, in only seven of these was it possible to calculate the log response ratios (lnR) as an estimation of the effect size of the presence of weeds on crop yield.

2.3. Results

In total, 4,449 results were found in the literature search. The abstracts were scanned for the presence of empirical results on the relation between weeds and regulating ecosystem service. This yielded 189 articles. A second more thorough evaluation of the results led to the retention of 129 articles sixty of which did not contain detailed enough information to compile the systematic literature map despite the positive wording in the abstract.

Ecosystem services

The ecosystem service most often referred to was pest control (Fig. 2.1(A)). In all, 91 articles (71%) contained examples of weeds supporting pest control. Weeds were found to contribute to nutrient cycling in 28 articles (22%). In 7 articles (5%), weeds were shown to improve soil physical properties. Finally, benefits of weeds in enhancing crop pollination were only found in 5 articles (4%), while three articles were found showing evidence of weeds providing regulating services that were not directly targeted by the search (e.g. reduction of greenhouse gas emissions).

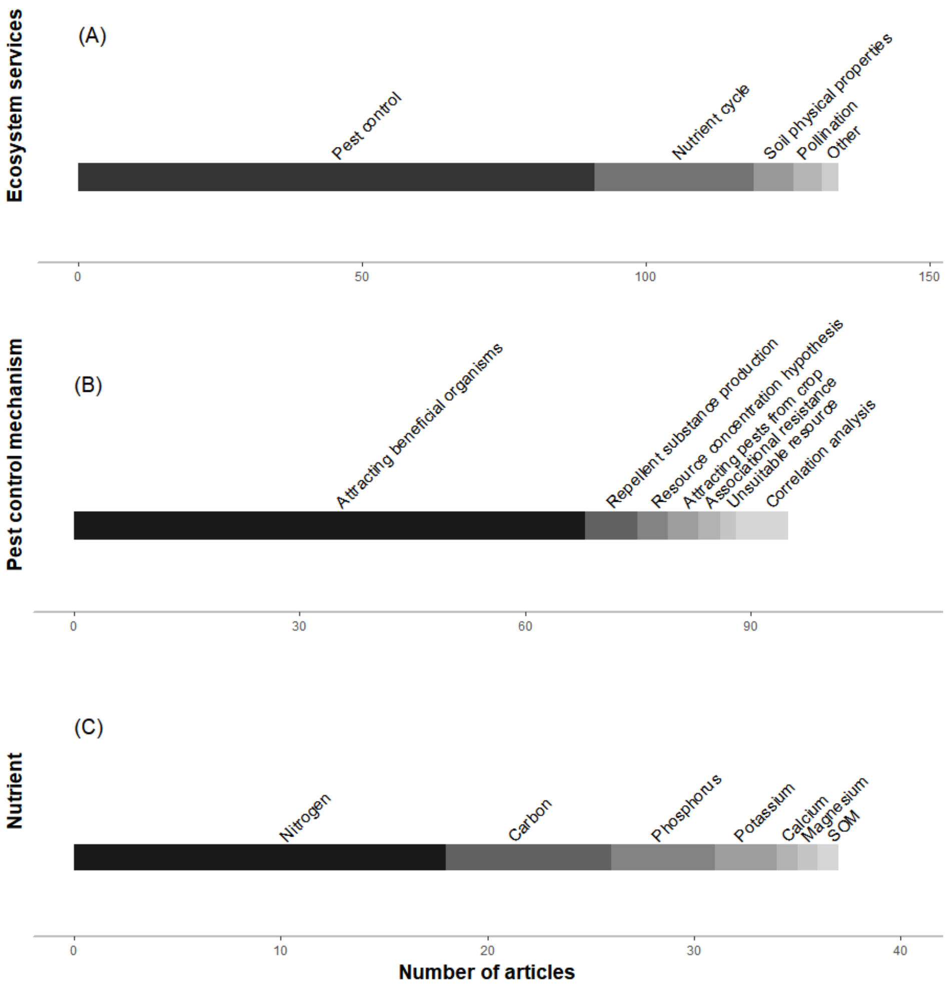

Figure 2.1 Partition of articles based on (A) ecosystem service type, (B) pest control mechanism type, and (C) soil nutrient type. In (A), 'Others': regulating ecosystem services that were not targeted by the search. In (B): 'Correlation analysis': no explanation was provided in the manner which weeds provided pest control.

Pest control

More than half of the articles contained examples of the presence of weeds benefitting pest control, although the mechanism through which this service was provided differed. In 38% of the studies documenting pest control, it was possible to acquire values for the reduction of pest abundance. An increase in the predation or parasitism of pests was calculated for 10% of the articles. Most commonly, however, studies calculated an increase in the abundance or diversity of natural pest enemies due to the presence of weeds (41% of studies). None of the above information was provided in 29% of the articles. In most cases, this was because the effects of weeds were not statistically tested either due to a lack of control or weeds not being directly investigated in the study. In other cases, the benefits of weeds were studied in a laboratory or in greenhouse experiments measuring the time beneficials spent foraging on flowers or by analysing their preference for flowers of specific species. For example, Belz *et al.* (2013) found a preference of *Microplitis mediator* Haliday for *Iberis amara* L. and *Cyanus segetum* Hill over *Fagopyrum esculentum* Moench and *Ammi majus* L.. Griffin and Yeargan (2002) demonstrated the preference of the lady beetle *Coleomegilla maculata* DeGeer to deposit eggs on *Abutilon theophrasti* Medik. over eight other broadleaf annual weeds (*Acalypha ostryaefolia* Riddell, *Acalypha virginica* L., *Amaranthus hybridus* L., *Chenopodium album* L., *Galinsoga ciliata* Ruiz & Pav., *Sida spinosa* L., *Solanum ptychanthum* Dunal, *Xanthium strumarium* L.). In a couple of cases, the presence of weeds was shown to decrease the number of damaged crop plants (Franck & Barone 1999; Gill *et al.* 2010). A few studies were based on mere correlation analysis. For example, Green (1980) showed that skylark predation on sugarbeet (*Beta vulgaris* L.) seedlings decreased with increasing abundance of weed seeds having a dry weight over 1 mg (e.g. *Polygonum* spp.). The mechanisms that explained how pest control was provided differed among studies (Fig. 2.1(B)). By far the most common means was by attracting or arresting natural enemies of pests (75% of the articles relating to pest control) by offering them a resource in or around cultivated fields. An increase in natural enemy abundance or diversity does not, however, necessarily mean that there is a reduction in pest abundance or, eventually, an increase in crop yield. Often this information was not provided. In seven cases (8%), weeds repelled pests by producing chemical substances (e.g. Glinwood *et al.* 2004). In three studies, weeds contributed to pest control through associational resistance (e.g. Ninkovic *et al.* 2009). Two studies found that weeds did not offer suitable resources to pests, which reduced their numbers (e.g. Alexander & Waldenmaier 2002). Four studies referred to the resource concentration hypothesis to explain an increase in pest control (e.g. Gill *et al.* 2010). In four other articles, weeds contributed to pest control by attracting or arresting pests away from crops (i.e. weed acting as a trap crop) (e.g. Green 1980). In seven articles, the mechanism with which weeds contributed to pest control was not explained and data were obtained from correlation analysis.

The range of values obtained for pest control varied considerably (Table 2.1). The highest value for pest reduction in the field was obtained from Atakan (2010) in which it was shown that infestation of the western flower thrips (*Frankliniella occidentalis* Pergande) on faba bean (*Vicia faba* L.) was reduced by a maximum of 98% due to weedy margins that hosted beneficial insects. For pest predation, the highest value was obtained in a laboratory experiment by Araj & Wratten (2015) in which they demonstrated that the predation of cabbage aphids *Brevicoryne brassicae* L. on *Capsella bursa-pastoris* L. increased by 255%. Powell *et al.* (1985) found that the rove beetle *Philonthus cognatus* Stephens was 1721% more abundant in plots containing weeds than in weed-free plots. As for natural enemy diversity, Albajes *et al.* (2009) reported that pest enemy diversity rose by a maximum of 213% in the presence of weeds.

Table 2.1 Range of values for all pest control measurements obtained in 90 articles retrieved. Negative values indicate a negative effect on pest control measures.

Pest control measurement	Mean lower range ± SD (in %)*	Mean upper range ± SD (in %)*
Reduction in pest abundance	19.4 ± 66.32	61.4 ± 29.39
Increase in predation/parasitism	49.9 ± 79.32	72.1 ± 74.16
Increase in pest enemies abundance	93.6 ± 211.97	423.3 ± 563.38
Increase in pest enemies diversity	15.0 ± 21.21	131.5 ± 115.26

*Mean lower/upper range ± SD: the average of all the minimum/maximum percentages of pest control enhancement reported in each study.

Soil nutrients

Twenty-three articles in the literature map provided information on weeds increasing the amount of nutrients in the soil. In 18 of these (78%), weeds were found to help improve both available and total nitrogen stock in agricultural soils (Fig. 2.1(C)) often as a consequence of their capacity to reduce nitrogen leaching by erosion control (available N) and by active N uptake and fixation (total N), which stabilised N levels in soil organic matter. For example, the presence of broad-leaved weeds (*Amaranthus viridis* L., *Richardia scabra* L., *Indigofera hirsuta* L.) led to less microbial immobilization of mineral N than grass weeds, which resulted in faster net release of mineral N in the following crop (Promsakha Na Sakonnakhon *et al.* 2006). Also, Ariosa *et al.* (2004) found that cyanobacteria in the common rice weed *Chara vulgaris* L. significantly improved soil fertility through their capacity to fix nitrogen in the weed biomass. Eight studies (35%) demonstrated that weed biomass increased carbon inputs in the soil (e.g. Arai *et al.* 2014). The same was shown to occur for phosphorus (e.g. Ojeniyi *et al.* 2012) as well as for potassium (e.g. Das *et al.* 2014), soil organic material (de Rouw *et al.* 2015), calcium, and magnesium (Swamy & Ramakrishnan 1988).

In seven out of the 13 articles, no values were given for the increase in nutrients due to weeds. In some cases, this was because there was no treatment factor without weeds (e.g. Ariosa *et al.* 2004). Mazzoncini *et al.* (2011) used correlation analysis to demonstrate the effect of weeds on soil organic carbon and soil total nitrogen. De Rouw and colleagues (2015) used carbon isotopes as a proxy for plant contribution to the soil organic pool. In these cases, it was not possible to accurately measure the contribution of weeds in providing ecosystem services.

Weeds were also shown to provide benefits to the nutrient cycle by promoting arbuscular mycorrhizal fungi (AMF). The presence of AMF in fields can facilitate nutrient acquisition in crops (Azaizeh *et al.* 1995). Vatovec *et al.* (2005) found that some weed species (e.g. *Ambrosia artemisiifolia* L.) were strong hosts to AMF and could potentially increase AMF abundance and diversity in an agricultural field. A correlation between weed diversity and spore numbers was also found (Miller & Jackson 1998). In another article weeds were found to promote rhizobacteria and, in turn, positively affect crop plant growth (Arun *et al.* 2012).

Soil physical properties

Weeds were found to enhance soil physical properties in seven articles. Most commonly, weeds had a positive effect by reducing soil loss and runoff (43%) (e.g. Pannkuk *et al.* 1997) or by reducing bulk density (29%) (e.g. Yagioka *et al.* 2014). In some cases, it was unclear if the positive effect on soil structure was caused by reduced tillage or by the increase in weeds often observed following reduced tillage (e.g. Arai *et al.* 2014). Weeds were also reported to benefit water storage in soil (e.g. Ojeniyi *et al.* 2012) while Kabir & Koide (2000) showed an increase in the proportion of water stable aggregates due to weeds hosting mycorrhizal fungi.

Crop pollination

In all five articles related to pollination, the effect that weeds had on crop pollination was not directly investigated. Instead, the attraction or arrestment of pollinators to dicotyledonous species was demonstrated (e.g. Hawes *et al.* 2003). Therefore, the extent to which weeds enhanced crop pollination remains unclear. All these studies were observational and were carried out on real farms. Pollinators belonged mostly to the insect family Hymenoptera. In some studies, pollinators from the orders Coleoptera, Diptera, Lepidoptera, and the suborder Heteroptera, were counted as well (Carvalheiro *et al.* 2011).

In three articles, weeds positively affected pollinator diversity (e.g. Carvalheiro *et al.* 2011) by offering a food resource and Hoehn *et al.* (2008) reported a positive impact of pollinator diversity on crop yield. Pettis *et al.* (2013) found that bees visited surrounding weeds as well as crops. Crop pollination increased near field margins where weeds offered the majority of alternative forage to pollinators (Gemmill-Herren & Ochieng 2008).

Other regulating and maintenance ecosystem services

Weeds can also play a part in reducing emissions linked to climate change. In rice paddy fields, weeds can reduce the emission of methane (CH_4) by improving the stimulation of CH_4 oxidation as well as by reducing methanogenesis rates compared to rice (Holzapfel-Pschorn *et al.* 1986). Yagioka *et al.* (2015) reported that weed cover mulching had a reduced net global warming potential compared to conventional tillage practices due to a greater soil organic carbon accumulation. Furthermore, they found that weeds altered the microclimate by increasing relative humidity.

Weed identity

In 23 studies, the focus was on one individual weed species. In small assemblages of less than 5 species, the ecosystem service provision was attributed to each of the species. For bigger assemblages, no single weed species effect was indicated. In 44 articles analysed (34%), the services were provided by a plant assemblage containing weeds but the main species were not specified. In these studies, the identity of the plant was not important. High plant diversity or the presence of vegetation was deemed to enhance the delivery of ecosystem services. Table 2.2 shows the list of weed species most often cited as providing an ecosystem service. *Chenopodium album* was the most frequently cited species, often in relation to enhanced pest control through offering resources, for example, oviposition sites to natural enemies (Smith 1976). Ninkovic *et al.* (2009) demonstrated that barley (*Hordeum vulgare* L.) exposed to volatiles from *C. album* reduced plant acceptance by aphids. Another study found that *C. album* dead mulch released nitrogen more quickly during the following growing season compared to the grass weed *Setaria faberi* Herrm. (Lindsey *et al.* 2013).

Table 2.2 Number of articles reporting the provision of ecosystem services by weed species.

	Pest control	Nutrient cycle	Soil physical properties	Others	Total articles
Chenopodium album L.	5	2	0	0	7
Ambrosia artemisifolia L.	3	2	0	0	5
Cirsium arvense L.	4	1	0	0	5
Acalypha ostryaefolia Riddell	4	0	0	0	4
Amaranthus retroflexus L.	2	2	0	0	4
Capsella bursa-pastoris (L.) Medik.	4	0	0	0	4
Sinapsis arvensis L.	4	0	0	0	4
Abutilon theophrasti Medik.	2	1	0	0	3
Echinochloa crus-galli (L.) Beauv.	2	0	0	1	3
Elytrigia repens (L.) Desv. ex Nevski	3	0	0	0	3
Solanum nigrum L.	2	1	0	0	3
Ageratum conyzoides L.	2	0	0	0	2
Bidens pilosa L.	2	0	0	0	2
Brassica rapa L.	2	0	0	0	2
Cirsium vulgare (Savi) Ten.	2	0	0	0	2
Commelina benghalensis L.	2	0	0	0	2
Imperata cylindrica (L.) Räusch.	1	1	1	0	2*
Lamium amplexicaule L.	2	0	0	0	2
Leersia hexandra Sw.	2	0	0	0	2
Sonchus oleraceus L.	2	0	0	0	2
Taraxacum officinale F.H.Wigg.	1	0	1	0	2
Urtica dioica L.	2	0	0	0	2

*= *Imperata cylindrica* was reported to have provided two different ecosystem services in one article.

Crops and yield

The most commonly studied crop was maize (*Zea mays* L.) (26% of studies), followed by wheat (*Triticum* spp.) (18%), and barley (11%) (Table 2.3). Cereals were the most studied crop type in the articles documenting improvement in soil nutrient and soil physical quality. However, legumes were more studied than cereals in pest control.

Table 2.3 Number of articles reporting ecosystem services provided by weeds for each crop.

	Pest control	Nutrient cycle	Soil physical properties	Pollination	Others	Total
Maize	16	13	4	1	0	33*
Wheat	15	5	2	1	1	23*
Barley	10	3	0	0	0	13
Rice	6	5	0	0	1	12
Rapeseed	7	0	0	1	0	7*
Bean	5	1	0	0	0	6
Soyabean	6	0	0	0	0	6
Tomato	5	1	1	0	0	6*
Lettuce	3	2	1	0	0	5*
Brussels sprout	4	0	0	0	0	4
Cucumber	2	1	0	1	0	4
Beet	2	0	0	1	0	3
Collard	3	0	0	0	0	3
Daikon/radish	1	2	2	0	0	3*
Eggplant	2	1	0	0	1	3*
Oat	3	0	0	0	0	3
Okra	2	1	0	0	1	3*
Pepper	2	1	0	0	1	3*
Potato	2	1	0	0	0	3
Pumpkin/squash	2	1	0	1	1	3*
Allium fistulosum L.	1	1	1	0	0	2*
Cabbage	2	0	0	0	0	2
Faba bean	2	0	0	0	0	2
Pea	1	1	0	0	0	2
Rye	2	0	0	0	0	2
Strawberry	1	0	1	0	0	2
Sunflower	0	1	0	1	0	2
Watermelon	1	0	0	1	0	2

*weeds in this crop were reported to have provided multiple ecosystem services in some articles.

Of all the articles included in the literature map, only 30 (23%) measured the effect of weeds on crop yield. In 13 (43%) of these articles, the effect of weeds on yield was significantly negative, in nine (30%) no significant change in yield was reported, while eight (27%) demonstrated a positive effect of weeds on yield. There was no relation between the effect on yield and crop type and the relation with weed species could not be analysed because all the studies contained different species. The log response ratios (lnR) representing an estimation of the effect size of the presence of weeds on crop yield is shown in Fig. 2.2 (15 cases provided by seven articles). No clear pattern of the effect size distribution emerged. However, we found more effect sizes with positive values than with negative values.

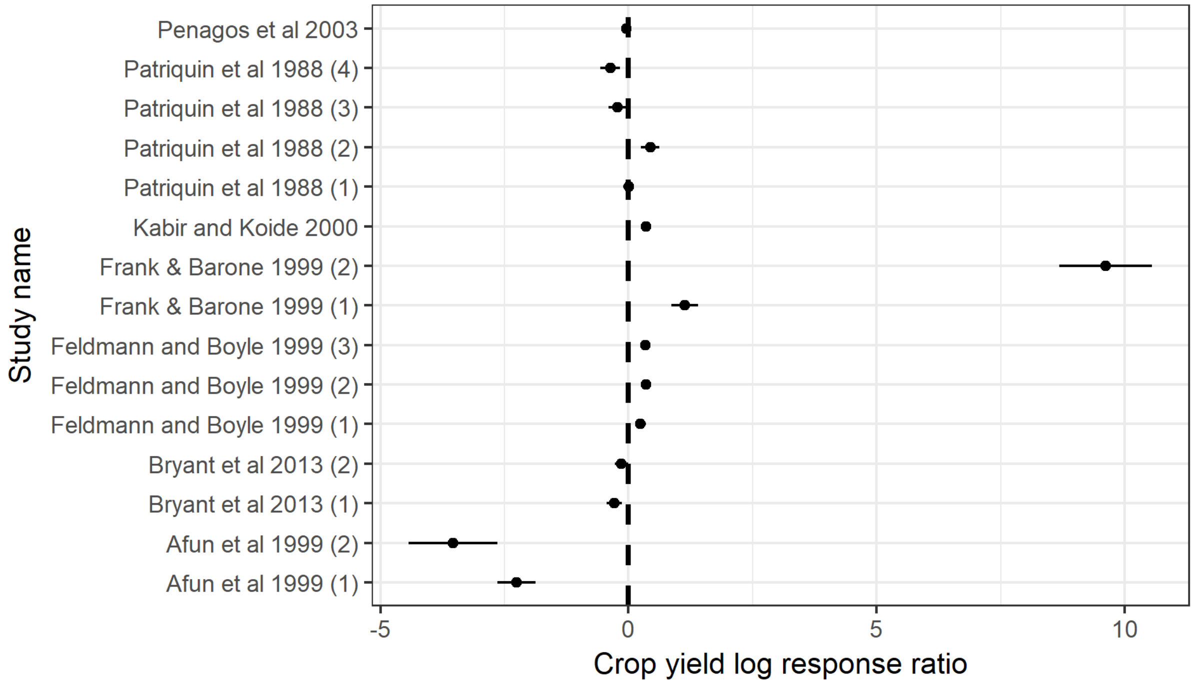

Figure 2.2 Log response ratio (lnR) estimating the effect size of the presence of weeds on crop yield in different studies. Whiskers indicate 95 % confidence intervals. The dashed vertical line indicates 0 effect. Some studies contain more than one entry due to multiple yield data (e.g. yield data for multiple years). A positive lnR indicates that crop yield was higher when weeds were present while a negative lnR indicates that it was lower.

2.4. Gaps in knowledge and future perspectives

The number of articles retained in the systematic map was low considering that the original search yielded 4,449 results. This reduction is in line with results from other reviews based on the systematic map approach, such as Holland *et al.* (2016) who found 2252 references of which only 152 were retained in the final map. The systematic map has clarified the amount of scientific evidence that is available on regulating ecosystem services provided by weeds. Data retrieved in the map also allowed for the quantification of the services provided and, in some cases, gave an indication of the effects weeds had on crop yield. However, the list of articles found containing information on regulating ecosystem services provided by weeds is not exhaustive. This is partly due to the methodology that prescribes only one literature search. Furthermore, the search was inevitably restricted to articles in which the authors considered the plant providing the regulating ecosystem service as a weed. For example, Smith and colleagues (2009) demonstrated that *Bassia hyssopifolia* (Pall.) Kuntze attracted natural enemies to various species of tumbleweed. Although *B. hyssopifolia* is often considered a weed, the authors did not refer to it as a weed. Furthermore, our search was restricted to the English language but there are articles written in other languages that contain evidence of weeds providing regulating ecosystem services (e.g. Cochereau 1976).

Regulating ecosystem services

From this systematic map analysis, a substantial gap in knowledge emerged regarding two of the four key regulating services that are relevant to farmers; soil properties and crop pollination. Among the few articles dealing with weed effects on soil properties, over half of the studies were performed in Asia. This may be due to the observed stagnation in crop production in that continent (Ray *et al.* 2012), which has been attributed to the depletion of nutrient pools (Bhandari *et al.* 2002; Manna *et al.* 2005). Soil erosion rates also tend to be higher in Asia than elsewhere (Pimentel *et al.* 1995; Lal 2003). Similarly, not many articles were found to demonstrate the benefits of weeds in supporting crop pollination. Since agricultural land often offers low amounts of nectar compared to other habitats (Baude *et al.* 2016), it stands to reason that the presence of weeds would diversify and augment nectar availability, which could attract more pollinators. In fact, a review published on the pollination services offered by weeds supports this view (Bretagnolle & Gaba 2015). The review, however, only demonstrated the potential of weeds in offering floral resources to pollinators but did not give quantitative data on the consequences for crop pollination or for pollinator abundance and diversity.

Although the pest control service provided by weeds has been described abundantly, the articles did not provide much insight into the mechanisms responsible for the beneficial effects, or for the lack of increased crop yield despite the presence of ecosystem service providers. More fundamental research aimed at elucidating the complex trophic interactions between crops, weeds, beneficials, and pests would help to provide more precise management guidelines for farmers and would possibly also reduce uncertainty in the response of agroecosystems to manipulation of weed communities.

Research needs at crop yield level

It is difficult to draw a conclusion about the effect of weeds on yield because only 30 papers quantified crop yield in relation to weed abundances. Articles including a measure of the variability in crop yield are even fewer (seven articles, Fig. 2.2). Therefore, studies that quantify the effect of weeds on crop yield with a measure of the variability are required. Despite the common view that weeds have a negative effect on crop yield, over half the articles that measured yield did not report a significant decrease due to the presence of weeds. However, this is only true for articles from the systematic map where weeds were supposed to provide a regulating ecosystem service. The vast majority of studies on weeds, not included in this systematic map, focus on weed competition with the crop and on their negative effect on crop production. Furthermore, it is possible that some studies focussing on regulating ecosystem services provided by weeds did not publish the negative effects weeds had on crop yield. Looking at the effect sizes (Fig 2.2), we see that they tend to be centred around zero. There were two cases were the effect sizes were larger than 1 or -1. In Frank & Barone (1999), there was one unusually large effect size due to total crop failure in the plots without weeds. In Afun *et al.* (1999), the service provided by weeds in hosting natural enemies of pests was completely negated by the strong competition of weeds with the crop. In this case, the yield loss due to competition was greater than the benefit obtained from service provisioning. A possible explanation for the small effect size found on crop yield could be that the studies were performed under optimal external input conditions leaving no margin for measuring a yield increase. For example, if the aim was to measure the contribution of weeds to soil fertility, in a system characterised by high soil fertility levels, the weed contribution would not be detected.

In an agroecological perspective, the role of weeds would be to partly compensate for reduced external inputs such as fertilisers, pesticides or tillage, with the ecosystem services they can provide while maintaining competition with the crop at a minimum through optimisation of resource use efficiency. This means that the yield measured is the result of a series of parameters as formulated in (Eqn 1):

$$\text{Yield} = Y_{max} - Y_{loss.comp} - Y_{ext.inp} + Y_{gain.ES} \quad (1)$$

where Y_{max} is the maximum yield that can be obtained for the crop in the optimal growth condition, $Y_{loss.comp}$ is the yield loss due to competition with the crop, $Y_{ext.inp}$ is the yield loss due to reduced use of the external input that the weed is hypothesised to provide, and $Y_{gain.ES}$ is the yield increase due to ecosystem service provisioning by the weed(s). In order to calculate $Y_{gain.ES}$, a series of four experiments needs to be set up as indicated in Table 2.4. This system allows to estimate Y_{max}, $Y_{loss.comp}$ and $Y_{ext.inp}$,. The yield (Y) in the system with weeds providing ecosystem services is measured and from Eqn 1 $Y_{gain.ES}$ is calculated.

In such a system, the research objective is to select for weed communities that minimise competition with the crop while providing an ecosystem service that can help to reduce the use of external inputs. Therefore, two more treatments could be added where the spontaneous weed community could be replaced by a weed community managed with the aim to increase service provisioning while decreasing competition by, for example, accepting legume weeds while suppressing grass species. In that case, $Y_{loss.comp}$ in the system with selected weeds is hypothesised to be lower while $Y_{gain.ES}$ is hypothesised to be higher than that in the system with the spontaneous weed community. Ideally, $Y_{gain.ES}$ would equal the yield loss if all external inputs were avoided. Since we are dealing with weeds this is rather improbable and this situation can probably only be created by using functional living mulches or inter cropping.

Table 2.4 Experimental plots needed to calculate the yield gain provided by a predefined ecosystem service provided by weeds ($Y_{gain.ES}$) in cropping systems, where the reduced input level refers to a reduction in those external inputs that are supposed to be replaced by the ecosystem service provided by the weeds. Y is the yield measured in the four experimental treatments needed to determine the parameters in Eqn. 1.

	No weeds	**Weeds**
Optimal input	Y_1 $Y_1=Y_{max}$	Y_2* $Y_{loss.comp}=Y_1-Y_2$
Reduced input	Y_3 $Y_{ext.inp}=Y_{max}-Y_3$	Y_4 $Y_{gain.ES}=Y_4-Y_{max}+Y_{loss.com}+Y_{ext.inp}$

*Y_2 is the result of weed competition with the crop where, due to the optimal input level, the ecosystem service provided cannot result in a yield increase and the only measurable effect is the yield reduction due to competition.

Research needs at weed species level

The list of weeds providing ecosystem services (Table 2.2) must be interpreted with caution. The fact that a species is more often cited than others does not necessarily mean that it is the most beneficial species. Many species listed in Table 2.2 are very common weeds and their high frequency in literature might simply be related to the higher likelihood of being studied. In the majority of articles, weeds were studied as an assemblage rather than investigating the ecosystem services provided by individual species. Norris & Kogan (2000) warned about this generalisation of weeds and claimed that to describe and elucidate the complex mechanisms regulating pest control, the weed species identity and their relevant functional traits must be known. Furthermore, this information is crucial for the development of agroecological weed management aimed at reducing competition with the crop while optimising service provisioning. This means that more effort should be spent on the identification of weed species with effective functional traits for ecosystem service provisioning. It would be desirable to select these traits from species that have a low competitive ability with the crop, a limited seed production capacity, and limited seed longevity in order to avoid uncontrollable weed problems in the cropped field. At the moment, there are functional trait databases that contain information on spontaneous vegetation including many plant species that are considered weeds in the main cropping systems. An R package has been developed that enables the extraction of information on functional traits for a list of species from nine publically available databases (Bocci 2015). However, many of the available traits are response traits (*sensu* Lavorel & Garnier 2002) while the effect traits available are mostly limited to provisioning of floral resources to arthropods. Furthermore, it must also be taken into consideration that traits measured from the spontaneous vegetation may be slightly different from the traits observed in the same species grown in cropped systems (Storkey *et al.* 2015) and, therefore, fundamental research on weed species traits in relation to ecosystem service provisioning potential would be recommended.

Research needs at weed community diversity level

The hypothesis that an increase in weed diversity may increase ecosystem service provisioning and that this effect is stronger in systems with low weed diversity is illustrated in Figure 2.3a. At high levels of weed diversity, with higher levels of redundant functional traits among the weed species, there will be a higher resilience of the service provisioning especially under changing environmental or cropping system conditions (Hooper *et al.* 2005; Tscharntke *et al.* 2005). Although weed community diversity was often mentioned as a positive aspect, none of the studies included weed diversity as a factor for determining its effect on service provisioning nor did they quantify or explain how diversity reduced competition with the crop. Smith *et al.* (2010) formulated the Resource Pool Diversity Hypothesis, which predicts that, in diversified cropping systems, having a diverse weed community increases resource use efficiency and, therefore, competition between weeds and crops is expected to decrease. As far as we know, only Cierjacks *et al.* (2016) and Ferrero *et al.* (2017) provided results from research aimed at testing this relationship. However, they did not manipulate weed densities and simple correlation analyses were the only means with which weed diversity-crop yield relationships were tested.

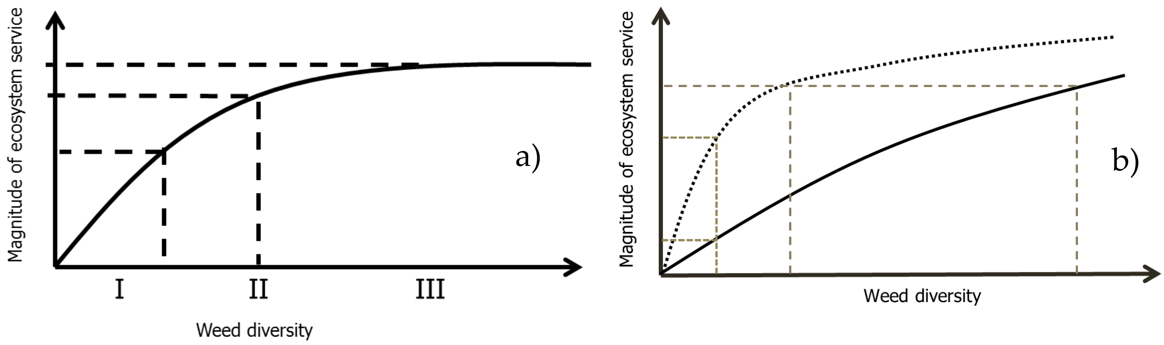

Figure 2.3 Theoretical relationship between increase of weed diversity and the increase in magnitude of ecosystem service provisioning (e.g. increase in beneficial abundance). a) At low levels of diversity (I), there is a high potential for affecting ecosystem processes. At medium levels of diversity (II), the magnitude of increase of ecosystem processes is reduced. In diverse weed communities (III) the increase in diversity increases the resilience of the ecosystem service under changing environmental or farming system conditions but it will not affect the magnitude of the service provisioning. b) The continuous function shows the increase in magnitude of the service when weed diversity is randomly increased. The dashed function shows the increase when management is aimed at conserving those weed species that are most effective for the desired service while at the same time being little competitive with the crop.

As the objectives for increased weed species diversity should be to minimise competition with the main crop while maximising profitability in terms of ecosystem service provisioning, a multi-criteria assessment of weed communities should be performed based on weed species traits in order to determine the most effective weed management strategies. From a research point of view, stimulating species diversity may provide satisfactory solutions but, from a management point of view, diversification may result in an exponential increase in complexity. Therefore, guided diversification by stimulating a few species with the desired traits is recommended in order to obtain maximum results with a minimum increase in vegetation complexity in the cropped fields. In theory (comparison of the light grey and dashed lines in Fig 2.3b), a higher increase in diversity is needed to reach the maximum functionality if species diversity increases randomly instead of managing it based on the functional traits of weed species. Equation 1 and the experimental layout proposed in Table 2.4 may be used to compare the efficacy of these diversified systems while the layout of the Jena Experiment, aimed at establishing plant diversity in relation to ecosystem functioning (Weisser *et al.* 2017), is a stimulating example to design experiments testing the effect of weed diversity on ecosystem services provisioning.

The types of ecosystem services that are most suitable for investigation are services directly provided by the weeds, such as nitrogen accumulation, amelioration of the physical soil structure, stimulation of soil arbuscular mycchorhizal fungi, and production of pest repellent chemicals. Both the weed traits and the service provided can be measured and quantified, and this can be directly related to crop yield. The indirect services provided by weeds, such as pest control through supporting pest predators or crop pollination through supply of nectar and pollen resources to pollinators, occur in successive steps where the potential benefits derived from the weeds on yield increase can easily be disrupted by external factors at each step. For example, weeds attract beneficial insects, but if there are many predators of these beneficial insects, there will be no increase in pest control. In cases where pest control increases due to the presence of beneficial insects, yield increases may not be verified due to, for example, adverse weather conditions or diseases. The lack of actual service provisioning in terms of pest control and crop yield has also been identified in studies focussing on promotion and conservation of semi-natural habitats around cropped field with the aim of increasing pest control and, subsequently, crop yield (Tscharntke *et al.* 2016). Studies investigating how weeds sustain ecosystem service providers (ESP) should, therefore, focus on the interactions between the weeds and the ESP by comparing diversity and abundance of ESP communities in crops with and without weed communities. In the case of weed support to pest predators, the review by Norris and Kogan (2000), could be a helpful start to plan a weed management strategy, and care should be taken to evaluate the potential pest species response to the weed community.

The magnitude of the impact that can be expected from single management tactics for agroecosystem service provisioning is limited and the 'many little hammers' approach for Integrated Weed Management proposed by Liebmann & Gallant (1997) should be applied. This means that, in order to increase agroecosystem service provisioning by vegetation, weed management strategies should be used in conjunction with other vegetation management strategies, such as intercropping or the establishment of semi-natural habitats, to maximise the provision of the desired services. By having a low but homogeneous distribution of weeds in a cropped field we should obtain a homogenous distribution of a service provided by the weeds. This would complement the services provided by the vegetation present in field margins and adjacent semi-natural habitats because their influence tends to decline as the distance from the field edge increases (e.g. Pisani Gareau *et al.* 2013).

2.5. Conclusion

In conclusion, this review highlights how few studies have specifically investigated and quantified the ecosystem services provided by weeds. We proposed an experimental design able to disentangle the benefits obtained from ecosystem service provisioning from the costs due to weed competition. The proposed approach can be useful in other studies aiming at the quantification of the role of weed community diversity in the reduction of competition with the crop and in determining the magnitude of ecosystem services provisioning by weed communities with different levels of diversity. Existing vegetation databases can be used to select weed species with functional traits facilitating ecosystem service provisioning while having a low competitive ability. However, for services such as pest control there are hardly any specific plant traits that have been identified, and more fundamental research is needed.

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3. How Management Factors Influence Weed Communities of Cereals, Their Diversity and Endangered Weed Species in Central Europe

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Abstract: The loss of weed biodiversity in agricultural fields is a global issue that needs to be counteracted to preserve their supported ecosystem services and food webs. Many short-term efforts are undertaken to conserve weed species, especially already endangered ones, but several years after expiration, eventually result in species-poor communities. Understanding drivers of community composition is key to prevent biodiversity loss. To understand the factors that shape weed communities and influence weed diversity and endangered weed species, we monitored conventional and organic cereal fields in two regions of southwestern Germany. A redundancy analysis was performed on vegetation recordings and data from a farmer survey. Crop species, herbicide use, farming system, nitrogen, and light availability had the strongest impact on weed diversity. The weed communities were dominated by *Alopecurus myosuroides*, *Galium aparine*, *Viola arvensis*, *Polygonum convolvulus*, and *Veronica persica*, and were mainly shaped by crop species, tillage, location in the field, and timing of herbicide application. *Bromus grossus* and *Bromus secalinus*, two endangered weed species, survived in conventional field margins as a result of the use of herbicides with gaps for *Bromus* species. Conservation efforts are not restricted to organic farming and should consider the major drivers of weed communities. Precision farming techniques are available to create networks of habitats for endangered and common weed species and subsequently increase agro-biodiversity *per se*.

Keywords: *Bromus grossus*; *Bromus secalinus*; rare arable weed species; redundancy analysis (RDA); species conservation; weed community; weed diversity

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3.1. Introduction

The Convention on Biological Diversity (CBD) is an international treaty dedicated to the conservation of biological diversity, its sustainable use, and the sharing of genetic resources. So far, 168 countries have signed this treaty, which highlights the global importance of biodiversity (CBD 2018a). The Global Strategy for Plant Conservation (GSPC) within the CBD aims specifically at stopping the loss of further plant species, conserving their natural habitats, and using plant diversity in a sustainable manner. As plants are the lowest trophic level, they support the whole food chain within an ecosystem. Conservation of plant species thus means also conserving animal species of higher trophic levels (Power *et al.* 1992, Scherber *et al.* 2010). As large areas within countries are naturally used for food production, the tradeoff between production and conservation becomes a controversial issue (Holt *et al.* 2016). However, agro-ecosystems in particular have suffered from species loss in the last decades (Flynn *et al.* 2009). Not only plant species (Meyer *et al.* 2013), but also insects (Hallmann *et al.* 2017) and larger vertebrate animals such as birds (Donald *et al.* 2001), have decreased in population size and species numbers in agricultural fields. The reasons for this species decline in agro-ecosystems are manifold; intensification of the production system, excessive use of water, nutrients and chemicals, as well as pollution of the environment (CBD 2018b). Weeds in particular represent one of the most important biological constraints for crop production as they affect quantity and quality of the harvest product as a result of competition (Oerke 2006). On the other hand, they are the basis for the whole food chain in the agro-ecosystem and provide a range of important ecosystem services (Blaix *et al.* 2018). The decline of weed species in agro-ecosystems is inter alia attributed to high fertilizer inputs, the use of efficient weed control measures like herbicides, improvements in soil tillage, and the increased competitive abilities of crop plants since the middle of the 20th century (Marshall *et al.* 2003, Meyer *et al.* 2013). Until today, the number of weed species has declined by 64% (Gerhards *et al.* 2013). Many of the species became highly endangered or even extinct (Meyer *et al.* 2013). A once diverse weed flora is nowadays dominated by those few species that were able to cope with the agricultural intensification process.

Conserving weed species, and endangered ones in particular, not only adds to the conservation of food webs and animals of higher trophic levels (Marshall *et al.* 2003, Scherber *et al.* 2010), it further supports beneficial insects that combat major pests (Atakan 2010) and preserves potential genetic resources in the gene pool (Brütting *et al.* 2012). Eventually, these species represent cultural assets of former agricultural production systems and have an intrinsic aesthetic value for humans (Gerowitt *et al.* 2003). In order to protect endangered weed species (EWS), a wide spectrum of conservation measures has evolved, from in situ conservation under actual farming to field margin concepts and floral nature reserves (Meyer *et al.* 2014). As weeds have co-evolved with the crop plants, they often need specific farming operations to survive; for example, *Agrostemma githago* propagates with contaminated crop seeds (Firbank 1998). Therefore, many in situ conservation strategies give monetary compensation to farmers in return for particular management restrictions. These restrictions comprise higher row distances to lower the light competition of the crop, less nitrogen fertilization and abandonment of herbicides, and other non-chemical weed control methods. Moreover, they are in line with special requirements of the endangered species like late stubble tillage to enable species that flower very late to produce seeds or a higher proportion of winter cereals in the crop rotation, because most endangered species germinate in autumn (Van Elsen *et al.* 2009, Meyer *et al.* 2010). The fields should also be ploughed on a regular basis to prevent the spread of competitive grass weeds and perennials (Van Elsen *et al.* 2009). These measures aim to increase the chances of survival and propagation of EWS and ultimately increase their population sizes.

Although conservation measures are used, most of the fields have suffered from the species decline and display a very low diversity of weed species (Waldhardt *et al.* 2003, Meyer *et al.* 2013). Although, not only the species number, but also their respective coverage and genetic diversity, have decreased over the years (Fried *et al.* 2009, Meyer *et al.* 2013), which in the long run leads to lower amounts of seeds in the soil seed bank, and ultimately to the disappearance of species. The resulting modern weed community is impoverished and exhibits only a handful of species that occur almost everywhere throughout Germany. *Chenopodium album*, *Viola arvensis*, *Polygonum convolvulus*, *Polygonum aviculare*, and *Galium aparine* are typically among these species (Meyer *et al.* 2013), as well as *Alopecurus myosuroides*, which experienced a dramatic increase due to its development of herbicide resistance (Heap 2014) and higher percentages of winter cereals in the rotation.

Conservation contracts with famers in Germany are normally effective in preserving the occurring endangered species (Albrecht 2003), but are also unfortunately subject to time limitations. Fields whose contracts have expired often display weed communities similar to conventionally farmed fields after several years (Schumacher 2018). Additionally, there is only little information about the habitat and management requirements of EWS (Torra *et al.* 2018), as well as of common ones. This lack of knowledge diminishes the success of the conservation efforts themselves and leads to further impoverishment of the weed community. Identifying key drivers of weed community composition and EWS is urgently needed to derive effective measures and strategies for successful species conservation.

Within this study, we performed weed vegetation recordings and farmer surveys in two regions of southwestern Germany where EWS were protected during the last decade, but are currently not under conservation contracts. The aim of this work was to detect driving factors of weed community assembly, weed diversity, and particularly of the occurrence of EWS. The resulting knowledge can be used to improve conservation measures for EWS and the enhancement of in-field biodiversity. We thus determined the agronomic and environmental factors in cereal crops that (i) shape the present weed community, and identified those factors that positively affect (ii) weed species diversity and (iii) the occurrence of EWS.

3.2. Materials and Methods

Experimental areas and field selection

Vegetation recordings were performed in the regions “Gäu” and “Swabian Alps” in the southwestern part of Germany. The “Gäu” region is located between the Black Forest and the Swabian Alps. Soils in the region can range from sandy clay to heavy clay soils. Muschelkalk (shellbearing limestone) or Unterer Keuper (sandstone or clay) were the parent rocks for these soils. The long-term mean (1960–1990) of temperature is 7.1–8.0 °C and the mean precipitation is 900–1000 mm. The Swabian Alps originated to a large extent from Jurassic limestone (limestone with clay marl and mudstone) that turned into rendzina soils, Terra fusca, vertic cambisols, or (chromic) luvisols. The long-term mean of temperature on the Swabian Alps is 6.1–7.0 °C and the precipitation ranges from 1000 to 1200 mm.

In 2017, cereal fields were selected in the Gäu region on the basis of former recordings of *Bromus grossus*, which is an almost extinct species in Germany, by the regional nature conservation authority (2004–2015). We wanted to determine if this species was still present in the region. Therefore, fields surrounding the formerly confirmed areas of the occurrence of

B. grossus were chosen for the recording. We mapped 33 fields, of which 28 were conventionally farmed and 5 were organically farmed. In 2018, we carried out the same search pattern in the Swabian Alps region. The recordings of a private nature conservation organization from 2006 had documented the occurrence of rare weed species such as *Bromus secalinus*, *Neslia paniculata*, *Legousia hybrid*, and *Vaccaria hispanica*. In total, 33 fields, consisting of 30 conventionally farmed and 3 organically farmed, were mapped.

Vegetation recordings and farmer surveys

The vegetation recordings were performed according to van Elsen (1989), who used a 2 m by 50 m area along the field margin and a second strip, parallel to the first, in the middle of the field. All occurring plant species were noted according to the extended Braun–Blanquet scale by Wilmanns (1998). The obtained data were afterwards transformed according to Van der Maarel (2007).

To be able to relate the recorded weed community or the occurrence of rare arable weed species to farming practices, we performed a farmer survey. The survey retrieved information about crop species, fertilization, soil tillage, and weed control measures. However, not all farmers were willing to or could share all their available information. Therefore, we used only variables that were consistent for all vegetation recordings within a region for the statistical analysis. Additionally, we measured crop height, nitrate (NO_3) and ammonium (NH_4) content in the soil, and photosynthetic active radiation (PAR) at soil level between the crop rows, and assessed the soil type. Table 3.1 shows the obtained variables in each region and their levels.

Table 3.1 Levels and ranges of categorical and metric variables assessed by a farmer survey in the Gäu region and the Swabian Alps.

Variable	Gäu Region	Swabian Alps
	Levels	Levels
Location in the field	Field margin; field middle	Field margin; field middle
Farming system	Organic; conventional	Organic; conventional
Crop species	winter mix [1]; spelt; winter barley; winter wheat; triticale	Oat; rye; spring barley; triticale; winter barley; winter wheat
Photosynthetic active radiation (PAR) at soil level (%)	1.3–18.4	2.8–70.0
Crop cover (%)	55.0–95.0	30.0–97.0
Nitrate in the soil in June (NO_3) ($kg*ha^{-1}$)	1.7–115.9	-
NH_4 in the soil in June ($kg*ha^{-1}$)	0.0–17.5	-
Soil type	lT, tL, t'L, uL, tU [2]	-
Timing of herbicide application	Spring appl.; autumn appl.; spring + autumn appl.[3]	Spring appl.; autumn appl.; spring + autumn appl.
Total nitrogen fertilization ($kg*ha^{-1}$)	0.0–271.5	44.0–110.0
Crop row distance (cm)	12.0–17.0	12.2–15.0
Seeding density ($kg*ha^{-1}$)	140.0–260.0	100.0–250.0
Number of applied herbicides	0–3	-
Number of tillage operations	2–4	2–4
Tillage	Plough; reduced tillage	Plough; reduced tillage
Crop height (cm)	51–153	45–150
Field size (ha)	-	0.15–5.00
Nitrogen fertilization	-	Mineral; organic; mineral + organic

[1] winter mix consists of triticale, rye, winter oat, winter barley, and winter pea; [2] lT = loamy clay, tL = clayey loam, t'L = weakly clayey loam, uL = silty loam, tU = loamy silt; [3] appl. = application.

Data analysis

Statistical analysis was performed with the software R (version 3.4.3, R Foundation for Statistical Computing, Vienna,Austria). Species numbers were analyzed with the standard analysis of variance (ANOVA) and means compared with a Tukey-HSD-test ($p \leq 0.05$).

To detect influences of farming or environmental variables on the weed species composition, we performed a redundancy analysis (RDA). Species were transformed by the Hellinger approach (Legendre & Gallagher 2001) prior to analysis. The final model with environmental and farming variables was selected by a stepwise forward selection with a threshold of $p \leq 0.05$. The generalized variance inflation factor (GVIF) for the variables were between 1.1 and 6.7 most of the time, except for two levels of the variable "crop", which were between 10 and 20. Values of GVIF above 20 indicate collinearity between variables (Fox & Monette 1992). To detect the effects of single explanatory variables we calculated gross and net effects of each variable according to Lososova *et al.* (2004). The gross effect represents the explained variation of the target variable under a univariate RDA, while the net effect represents the explained variation under a partial RDA (pRDA) with the target variable as explanatory variable and the other variables of the model as covariables. The fit for the models of net effect was tested afterwards using a permutation test with 999 permutations of the constrained axis for each model.

3.3. Results

Weed species diversity

In total, 140 different weed species were found in the Gäu region and 93 weed species in the Swabian Alps. The average number of weed species in each recorded plot typically ranged between 10 and 30. We found six variables that significantly affected the weed species number in the Gäu region. These variables were location in the field, crop species, number of herbicide applications, farming system, total nitrogen fertilization, and the amount of PAR at soil level (Figure 3.1). Meanwhile, there were only three variables in the Swabian Alps that affected weed diversity significantly, namely, location in the field, number of different crops in the crop rotation, and farming system (Figure 3.2).

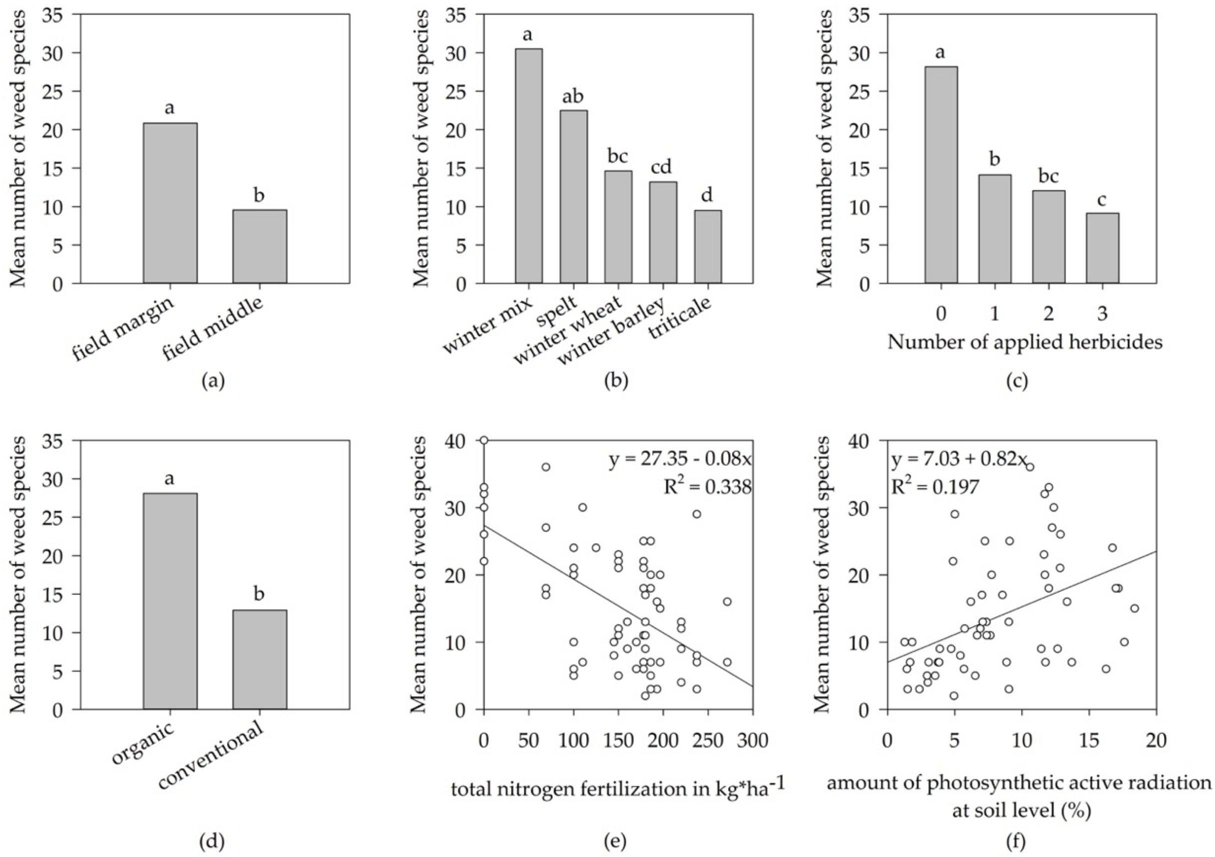


Figure 3.1 Factors influencing the mean number of weed species in the Gäu region (a) location in the field; (b) crop species; (c) number of applied herbicides; (d) farming system; (e) total nitrogen fertilization (y = 27.35 − 0.08x; R^2 = 0.338); and (f) amount of photosynthetic active radiation at soil level (y = 7.03 + 0.82x; R^2 = 0.197). Means with different letters represent significant differences according to the Tukey HSD test ($p \leq 0.05$).

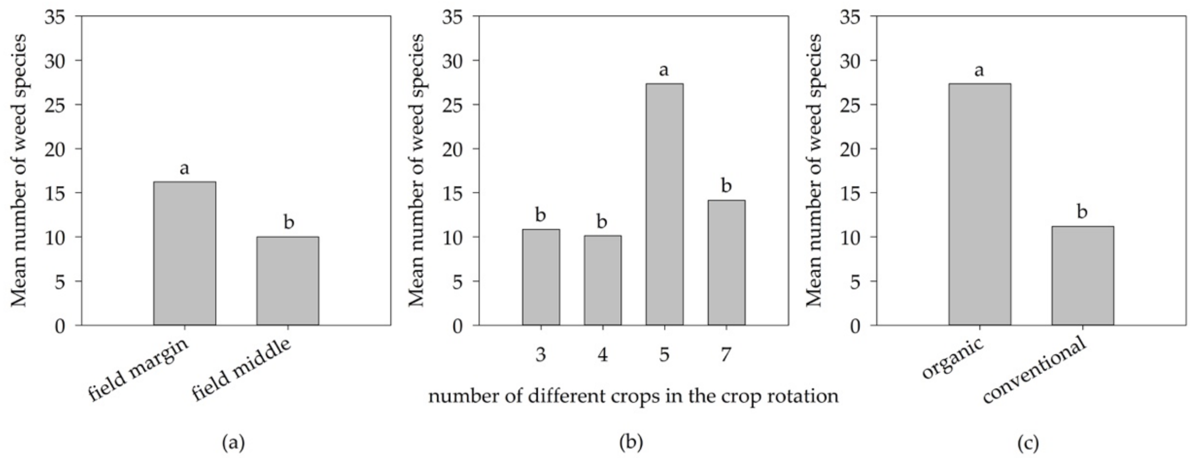


Figure 3.2 Factors influencing the mean number of weed species in the Swabian Alps (a) location in the field; (b) number of different crops in the crop rotation; and (c) farming system. Means with different letters represent significant differences according to the Tukey HSD test ($p \leq 0.05$).

Species numbers in the Gäu region and the Swabian Alps were higher in organic (28.1 and 27.3, respectively) compared with conventional farming (12.9 and 11.2, respectively), and were always higher at the field margin (20.8 and 16.2, respectively) in comparison with the middle of the field (9.5 and 10.0, respectively). In the Gäu region, a prominent effect of the different crop species was present, while in the Swabian Alps, the number of crops in the crop rotation significantly influenced the weed species numbers. Moreover, in the Gäu region, total nitrogen fertilization was negatively correlated with weed species diversity, while the amount of PAR was positively correlated (See Figure 3.1e,f). A significantly higher number of weed species was present if any herbicide application was omitted (28.2 species). However, sprayed plots also showed rather high species numbers (10.1 to 13.4), although not significantly different from each other.

Weed species community

The weed species communities in both locations were very similar in terms of weed species occurrence (Figure 3.3). *Alopecurus myosuroides*, *Galium aparine*, *Viola arvensis*, *Polygonum convolvulus*, and *Veronica persica* were the most frequent species and were present in more than 50% of the recorded plots. These five species were also within the top ten species in regard to mean soil cover at both locations. The weed species coverage was generally lower in the Swabian Alps compared with the Gäu region. The majority of species, 73% of all species in the Gäu region and 52% in the Swabian Alps, were not very frequent (<10% occurrence). More than 75% of the weed species also showed a mean soil cover that was below 0.5% (78% for the Gäu region and 82% for the Swabian Alps).

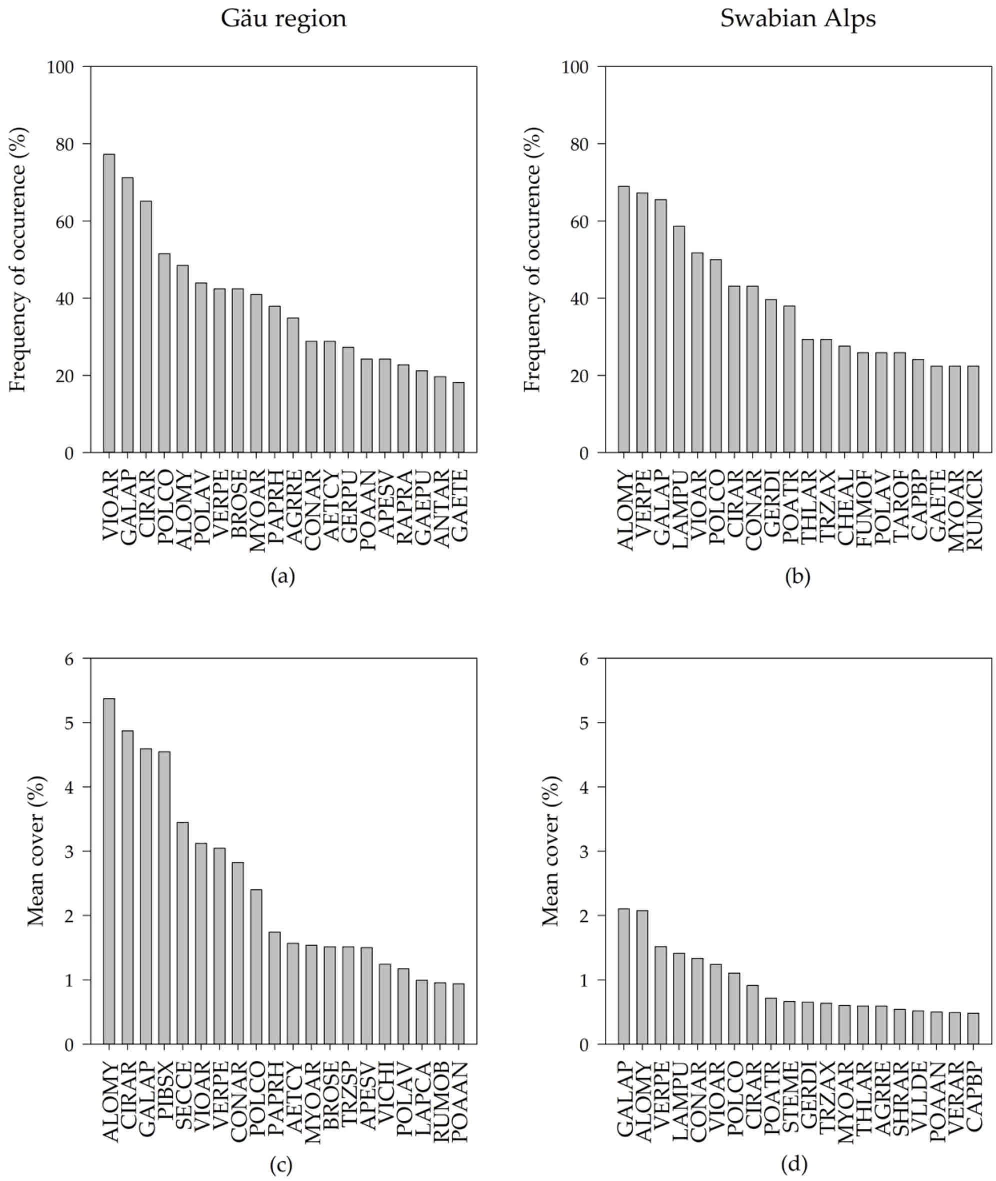


Figure 3.3 Values of (a,b) frequency of occurrence (%) and (c,d) mean cover (%) for those 20 weed species with the highest occurrence or soil cover in the (a,c) Gäu region or the (b,d) Swabian Alps. Abbreviation of weed species according to the EPPO (European and Mediterranean Plant Protection Organization) Code.

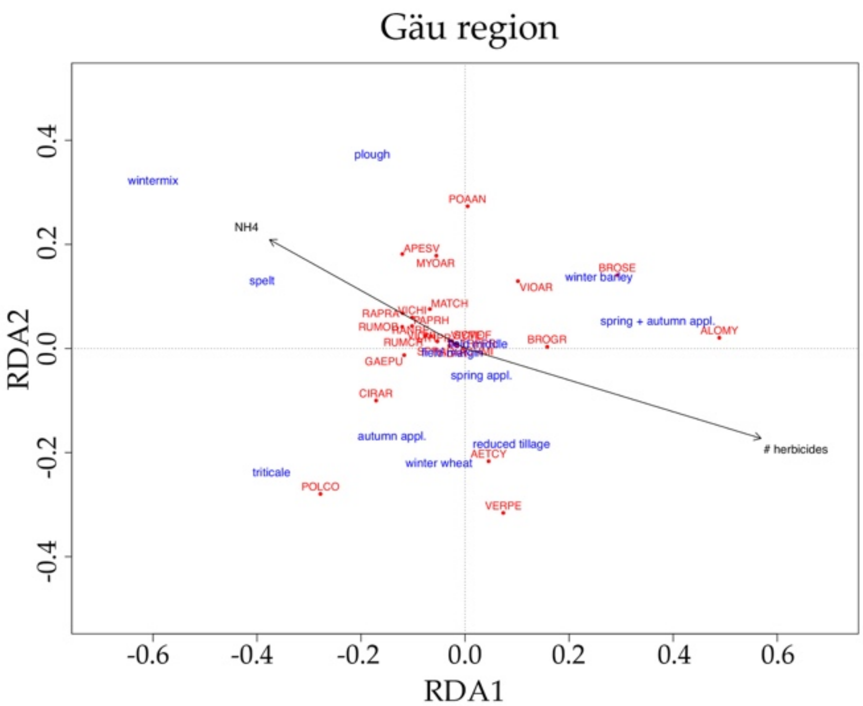
The stepwise forward selection of the model in the RDA analysis selected six variables for the Gäu region and eight for the Swabian Alps that significantly affected the composition of the weed communities (Table 3.2). The full model was able to explain more than 40% of the total variation in the species composition in both locations. The models of both regions share four variables, namely, crop species, tillage, location in the field, and timing of the herbicide application. Of these four variables, crop species and timing of herbicide application were the two variables explaining the biggest part of the species community.

Table 3.2 Explained variation (%) of the full model, as well as the gross (redundancy analysis (RDA) with single explanatory variable) and net ((partial) RDA with single explanatory variable and additional variables held constant) effects of the explanatory variables on weed species composition and their F-values from the permutation test for the Gäu region and the Swabian Alps.

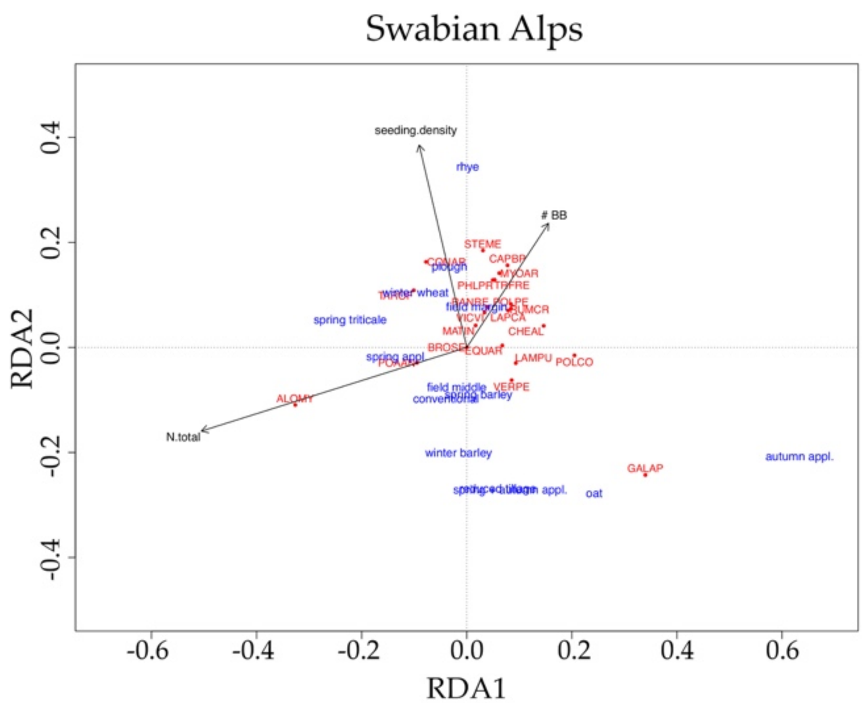
Variables	Gäu Region			Swabian Alps		
	Gross Effect	Net Effect	F-Value	Gross Effect	Net Effect	F-Value
Full model [1]	42.54		3.634 ***	46.63		2.185 ***
Crop species	21.92	12.61	2.963 ***	19.05	20.83	2.276 ***
Tillage	7.79	5.37	5.049 ***	3.39	3.31	2.174 **
Number of herbicide applications	7.13	2.60	2.441 **	-	-	-
Location in the field	2.77	2.63	2.471 ***	3.20	3.20	2.101 **
Herbicide timing	16.51	5.93	1.857 ***	11.44	7.51	2.463 ***
NH_4	4.56	2.37	2.235 **			
Total N				4.21	4.53	2.968 ***
Farming system				5.59	NA	NA
Number of tillage operations				3.11	2.76	1.812 **
Seeding density				2.87	2.53	1.659 *

[1] Full model selected by stepwise forward selection with an adjusted R^2 of 0.3083 at the Gäu region and 0.2529 at the Swabian Alps. (*** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$, NA = not available).

The RDA plots in Figure 3.4 show the association of the respective weed species in each location to the selected variables from the model. In the Gäu region, the first RDA axis was associated with the number of applied herbicides, the timing of application, and NH_4 content in the soil. The second axis was associated with the tillage and the location of records in the field. *Polygonum convolvulus* and *Veronica persica* were associated with reduced tillage and winter wheat or triticale, while *Bromus secalinus* and *Bromus grossus*, two endangered species, were associated with a low content of ammonia in the soil and combined spring and autumn herbicide applications. *Rumex* species on the contrary were associated with higher values of ammonia in the soil. The first axis of the RDA in the Swabian Alps was associated with the total nitrogen fertilization of the farmer, whereas the second axis was associated with seeding density, number of tillage operations, crop species, and timing of herbicide application. *Galium aparine* had a higher association with oats and winter barley than any other weed species. *Alopecurus myosuroides* was present under higher values, while *Galium aparine* was more abundant at medium values of nitrogen fertilization. Additionally, *Alopecurus myosuroides* was more frequent if the number of tillage operations was low. *Polygonum convolvulus* and *Veronica persica* in the Swabian Alps were also associated with a low number of tillage operations.



(a)



(b)

Figure 3.4 Ordination diagram of the partial redundancy analysis (RDA) from (a) the Gäu region and (b) the Swabian Alps containing (a) six and (b) eight significant explanatory variables. Only species with the highest fit on the first two axes are displayed. Eigenvalues for (a) the Gäu region are 0.083 for RDA1 and 0.058 for RDA2 with total inertia of 0.703 and 0.299 for all constrained axes. Eigenvalues for the (b) Swabian Alps are 0.057 for RDA1 and 0.045 for RDA2 with total inertia of 0.689 and 0.321 for all constrained axes. Abbreviation of weed species according to the EPPO Code.

Endangered weed species (EWS)

In the Swabian Alps, only two EWS, namely *Bromus secalinus* and *Neslia paniculata*, were found. *Bromus secalinus* was discovered in three conventional fields with a population size of around 10–30 plants, while *Neslia paniculata* occurred only once inside a conventional field. In the Gäu region, we found *Bromus grossus* and *Bromus secalinus* in relatively high numbers, so that we were able to analyze possible variables affecting the occurrence of these two species. Figure 3.5 displays the variables affecting the abundance of these two species. Both were found with significantly higher soil coverage at field margins and under the influence of combined spring and autumn herbicide applications. *Bromus secalinus* was mainly present in those fields, which were not sprayed with Atlantis (0.3 $kg*ha^{-1}$; a.i. iodosulfuron and mesosulfuron; Bayer Crop Science, Langenfeld, Germany) or Broadway (0.22 $kg*ha^{-1}$; a.i. pyroxsulam and florasulam, Dow AgroSciences, Munich, Germany) in autumn and spring, respectively. The coverage of *Bromus grossus* was half as much as that of *Bromus secalinus* in both cases. A correlation test between the two species was significant ($R^2 = 0.572$). *Bromus secalinus* displayed a significant reaction to soil type, with higher values at heavy soils with high clay content (lT and tL) and decreasing values towards soils with a higher portion of silt (tU). *Bromus grossus* was mainly present in winter barley fields, although not significantly different from the other crop species. In addition, *Bromus arvensis* and *Galium spurium* were found at four field margins of conventional fields; *Veronica triphyllos* once at a conventional field margin; and *Camelina alyssum* and *Ranunculus arvensis* once and twice, respectively, restricted to organic fields. The number of individuals of these species was rarely higher than 5–20 plants.

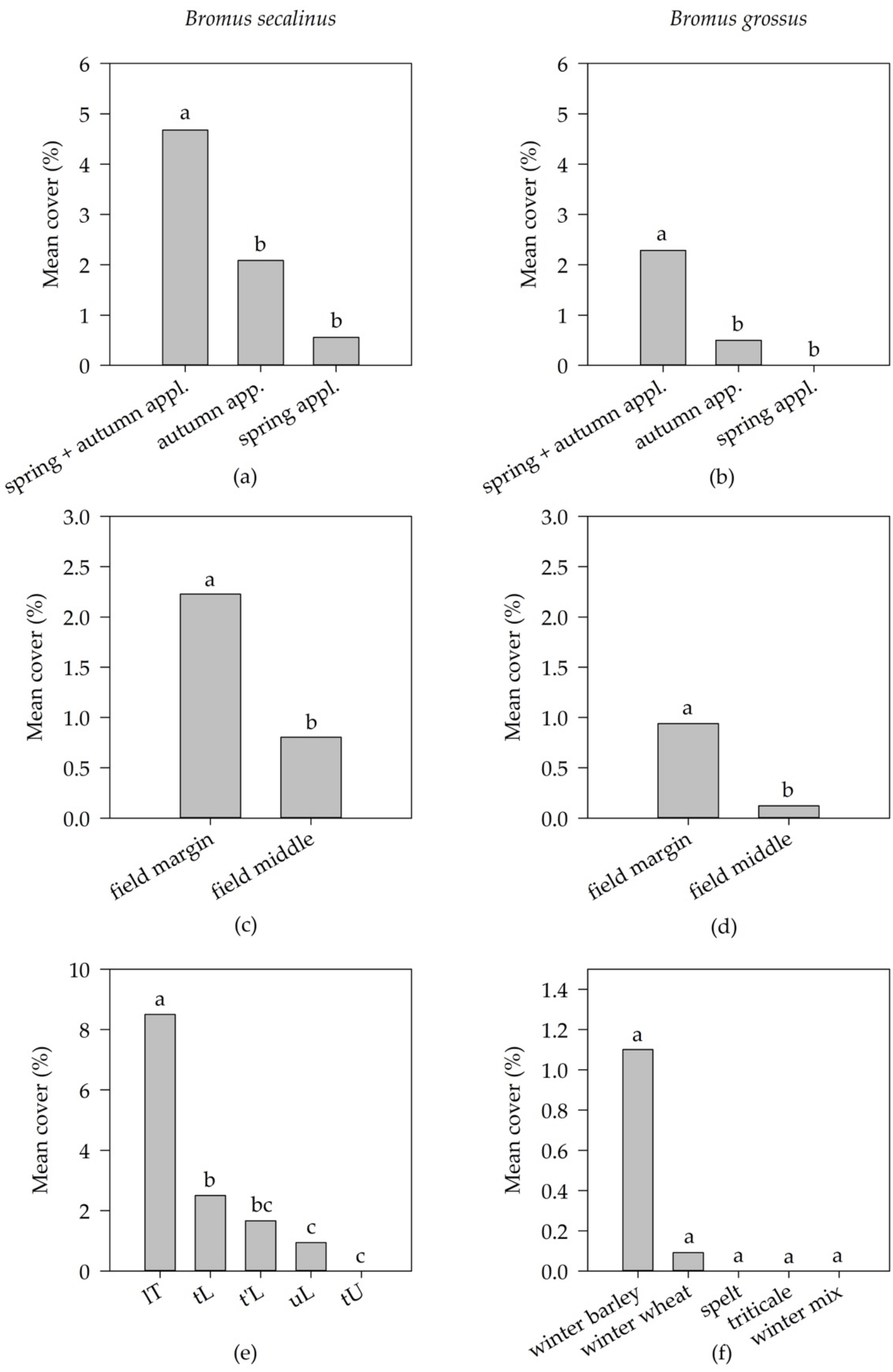


Figure 3.5 Factors influencing the mean cover (%) of (a,c,e) Bromus secalinus and (b) Bromus grossus in the Gäu region. (a,b) Timing of herbicide application; (c,d) location in the field; (e) soil type (lT = loamy clay, tL = clayey loam, t'L = weakly clayey loam, uL = silty loam, tU = loamy silt); and (f) crop species. Means with different letters represent significant differences according to the Tukey HSD test ($p \leq 0.05$).

3.4. Discussion

Most of the EWS that were once present in the Gäu region and the Swabian Alps have either decreased in their numbers or even disappeared. *Camelina alyssum* and *Bromus grossus* in particular are supposed to be extinct in many regions of Germany. The two regions, Gäu and Swabian Alps, thus have a high responsibility to ensure their conservation and promotion. *Bromus secalinus* was the only rather frequent EWS in the Gäu region. As it is presumed to have descended from *Bromus grossus* (Koch *et al.* 2016), the identified factors influencing *Bromus secalinus* might also help to develop better conservation measures for *Bromus grossus*. The two *Bromus* species were positively affected by herbicide applications, which may be because of the fact that the applied herbicides in the respective locations are known to have a gap in effectiveness against *Bromus* species. Therefore, it might be possible to promote species conservation not only in organic farming (Van Elsen 2000), but even with the use of herbicides in conventional farming, at least for these particular species. In contrast, it was assumed that *Bromus grossus* was only able to survive in fields if it is reintroduced using uncleaned crop seeds from previous years (Piqueray *et al.* 2018). However, the control of other, more competitive species needs also to be concerned, as this might interfere greatly with the success of facilitating endangered species. In particular, measures affecting a whole group of weeds, like the promotion of grassy weeds by conservation tillage (Peigné *et al.* 2007), might not aid in conservation. To facilitate the propagation of EWS is of paramount importance, as their genetic variability is quite low (Brütting *et al.* 2012) and needs to be increased, if necessary, even by reintroduction of new seeds (Lang *et al.* 2018).

As a result of the rapid disappearance of ever more weed species, the weed community is becoming less diverse and uniform across Germany. This uniform weed community consists of well adapted dominant species that cause high yield losses, such as *Alopecurus myosuroides* and *Galium aparine* (Keller *et al.* 2014). These two species were also the most frequently found weeds in the present study and those displaying the highest soil coverage. Moreover, *Alopecurus myosuroides*, *Galium aparine*, *Polygonum convolvulus*, and *Viola arvensis* were associated with low soil disturbance and higher values of nitrogen. This is in line with other studies that found weed communities dominated by these species under intensive conventional farming (Dessaint *et al.* 2001, Keller *et al.* 2014). With regard to climate change, weed communities will further evolve. EWS will become even more vulnerable to the new weather conditions (Rühl *et al.* 2015) and difficult to control, and invasive weed species might spread into more agricultural fields (McDonald *et al.* 2009). This can shift the weed community further to one with a higher frequency of dominant species.

The main drivers found in this study that shaped the weed community were crop species, herbicide use, nitrogen fertilization, and tillage operations. Of these, crop species and timing of herbicides were the most influential in determining the weed composition. The influence of crops can be explained by the major differences in cultivation (Nowak *et al.* 2015), ultimately leading to the typical weed communities of spring or autumn sown crops (Nagy *et al.* 2018). Other authors also found cropland type and surrounding habitats to be major drivers of weed composition (Nagy *et al.* 2018). Herbicide use leads to a massive selection pressure upon the weeds, resulting in very low densities of species per se or the evolution of herbicide resistance (Heap 2014). They are even potent enough to mask effects of tillage on weed community composition by leading to uniform weed communities (Derksen 1995). In our study, timing of herbicides was also identified as a major factor, however, no consistent association between weeds and the herbicide application timing was found. This might be due to the wide range of available herbicides, each with its uniquely targeted weed species spectrum. Further studies should investigate the influence of herbicides and their active ingredients in more detail. Nitrogen fertilization was associated with higher abundance of *Rumex* species and *Alopecurus myosuroides*. The reaction of weed species to nitrogen content in the soil is common knowledge (Chadwigk 1963), however, there are still gaps in knowledge when it comes to its contribution to weed community composition. In regard to soil tillage, a regular disturbance of the soil promotes the emergence of more weed species and can also aid in conservation of EWS (Torra *et al.* 2018). Apart from management factors, environmental and site conditions have a huge impact on the weed community composition (De Mol *et al.* 2015, Pinke *et al.* 2016, Nagy *et al.* 2018), which were not available in detail for the present study.

To increase the biodiversity in agricultural fields, the number of different weed species first of all needs to be raised in order to gain further increases in animal species. In this process, obviously most of the species will first be present in quite low numbers or coverages. Especially endangered species can contribute substantially to increasing agro-biodiversity, as they were once well integrated into the weed community. Their associated insect species might also benefit from the promotion of these weed species and will become more frequent.

Organic farming is promising in terms of biodiversity conservation (Van Elsen 2000), as no chemical plant protection agents are used and a more diverse crop rotation is practiced. These are two of the factors that we also found affecting the weed diversity positively. In terms of crop rotation, a higher diversity of crops seems to enhance weed diversity until a certain point (De Mol *et al.* 2015, Zarina *et al.* 2015). In our study, this was highlighted by a medium number of crops in the crop rotation. Simple crop rotations promote those species that occur within the specific crop, thus resulting in one similar simple weed spectrum over the years. Very diverse rotations on the other hand make use of the weed suppressive effects exerted by particular timing of farming operations (e.g., tillage, sowing) and available weed control measures within each crop species. This diverse set of operations in the long-term might be able to diminish the soil seed bank in general, and species that have a low seed longevity in particular. Thus, a medium number of crops in the crop rotation might represent a maximum turning point for weed species diversity. Another important factor for higher diversity is the field margin, where fertilization, weed control, and sowing are often not as accurate as in the crop stand. Therefore, more light reaches the ground and gives many competition-weak weeds a chance to grow (Kleijn & van der Voort 1997). It would thus be suitable to start increasing weed diversity at the field margin to help in the conservation of species (Schumacher 1980). Moreover, field margins are associated with a higher diversity of fauna, including pollinators, beneficial insects, and farmland birds (Marshall & Moonen 2002). Field margins are a good start for conservation efforts and more diverse weed communities, but more area with suitable habitat conditions for a wide spectrum of weeds should be generated. Increasing weed diversity while simultaneously controlling problematic weeds and ensuring food security is a process in which every alteration needs to be carefully tested and evaluated. As a potential solution, there are already some techniques available to successively replace herbicide applications by mechanical treatments (Kunz *et al.* 2015), or to manipulate the competitiveness of the crop by altering seeding patterns (Kristensen *et al.* 2008). Furthermore, fertilizers can be placed quite accurately to the crop roots only (Blackmer & White 1998), so that weeds need to cope with lower fertilizer levels, which in turn might lead to an increasing species richness if dominant, nitrogen-loving species decline (Storkey *et al.* 2010).

In this context, field margin strips or entire fields farmed under nature conservation regulations and contracts can add a lot to increase biodiversity (Denys & Tscharntke 2002, Meek *et al.* 2002, Krompa & Steinberger 2012) and the goals set by the GSPC. This needs to be coordinated in order to gain a dense network of these programs and to provide the species with enough habitats linked by corridors, which ensures their future propagation and spread (Meyer *et al.* 2008). The disappearance of EWS and the low diversity of weed communities, especially in the Swabian Alps, emphasizes the need to make long-term contracts between farmers and nature conservation authorities. In fields, where the soil seed bank is highly depleted in terms of species diversity, it might be reasonable to reintroduce weed species by sowing (Lang *et al.* 2018), otherwise weed diversity is hard to restore. On the other hand, it might be problematic to introduce weed seeds from completely random areas, as they might not fit well into the regional weed community and might contain very dominant species. This approach must thus be executed with caution. Historical assessments of weed communities are available for many sites and should be taken into consideration for restoration of weed diversity. Moreover agri-environmental schemes and national strategies help to provide habitats for species in every type of farming. Furthermore, increasing the diversity in and around the field by intercropping, mixed cropping, and deliberately manipulating landscape structures can further assist in the recovery of agro-biodiversity (Landis 2017). To reach this goal, policy makers, nature conservation authorities, and farmers need to come (and stay) together to develop practical and sustainable solutions for both crop production and species conservation (Holt *et al.* 2016).

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4. Effects of Weed Biodiversity on the Ecosystem Service of Weed Seed Predation Along a Farming Intensity Gradient

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Abstract Weed biodiversity plays a key role in supporting food webs and ecosystem services in agroecosystems. One important service, reducing the abundance of weeds, is the predation of weed seeds by invertebrates and vertebrates. Weed biodiversity may be supportive in maintaining seed predator prevalence, this however, can be highly influenced by farming systems. In the present study we examined the connections between weed diversity, Carabid beetle diversity and weed seed predation (WSP) rate. Additionally, the influence of a farming intensity gradient on WSP rate and predator groups was evaluated. An on-farm experiment on the Eastern Swabian Alps was set up from 2015 – 2017, where we determined the weed diversity, Carabid beetle diversity using pitfall traps and WSP rates and predator groups by utilizing seed cards and exclosure cages. There was a linear correlation between weed diversity and Carabid beetle diversity as well as a pattern showing that medium diversity of Carabid beetles (3-8 species) exhibited the highest WSP rates by invertebrates. However, a direct connection between weed diversity and WSP was not detected. Farming intensity had no consistent influence on WSP, rather year and specific agronomic measures like cover cropping most presumably affected WSP. Carabid beetle communities were similar in 2016 and 2017 with omnivorous species dominating in the conventional fields and granivorous species in extensively managed fields. The most efficient seed predator group were vertebrates. The promotion of beneficial predators and ecosystem services like WSP is possible by designing appropriate management strategies. Key components of these strategies should be the conservation of plant diversity and the utilization of weed control strategies such as cover cropping that provide suitable habitats for beneficial predators.

Keywords: agricultural intensity**;** Carabid beetle community; ecosystem service; food web; seed predation

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4.1. Introduction

All food webs are built on the first trophic level of producers, which are plants. Primary producers are supporting all other higher levels including herbivores, their predators and other top predators (*Power 1992*, *Macfadyen et al. 2009*, *Scherber et al. 2010*, *Evans et al. 2011*). The importance of plants in food webs is emphasized by studies examining plant species declines in natural and agricultural systems (Marshall et al. 2003). In agroecosystems weeds provide food, shelter (mainly by cover), oviposition and mating sites (Norris & Kogan 2000). Therefore, the decline of weed species affects higher trophic levels (Donald et al. 2001, Seibold et al. 2019). Especially invertebrate species closely associated with particular weed species have vanished along with their resources (Marshall et al. 2003). Conservation of weed species diversity therefore is key to the conservation of higher order taxa (invertebrates and vertebrates) in the food web (Bàrberi et al. 2010.

In this context, weeds are not only supporting overall species diversity and food webs, but they also provide several ecosystem services (ES) (Blaix et al. 2018). These services are beneficial for the farmer and the agroecosystem. They rely on the species and the diversity of the species performing the respective service (Hooper et al. 2005, Storkey et al. 2013) and their functional interactions to work properly (Wall and Nielsen 2012, Birkhofer et al. 2015). This assumption is based on the "sampling effect" (Tilman et al. 1997) and the "niche complementarity" (Macarthur & Levins 1967) in ecological theory leading to more resilient or productive services if communities are more diverse (Wall & Nielsen 2012). This connection between biodiversity and ES provision in agricultural systems has been described for grasslands (Sanderson et al. 2007, Scherber et al. 2010) and cover crops (Storkey et al. 2015, Baraibar et al. 2018), but rarely for weed communities (Blaix et al. 2018). Weeds are indirectly supporting crop pollination and enhancing pest control by attracting pollinators and beneficials or by diverting pest species (Norris & Kogan 2000, Blaix et al. 2018).

One of the most examined and most important services in the agricultural context is pest control (Blaix et al. 2018). Among pests, especially weeds can cause substantial yield losses (Oerke 2006). Although the majority of weed species has little influence on yield quality and quantity, there are problematic weed species that impact yield parameters considerably. One ecosystem service providing weed control is weed seed predation (WSP). Weed seed predation although is not a service that affects weed plants in the current cropping season, but it prevents weed seeds from entering the soil seed bank and therefore reduces the potential weed infestation in the following crops (Westerman et al. 2003a). As WSP occurs mainly after seed shed of weeds, it is complementary to the weed control measures of the farmer, because the newly built seeds of the remaining weed plants are consumed. Seed predators are able to consume up to 90% of the freshly produced weed seeds (Westerman et al. 2003, Davis et al. 2011). The service of WSP is carried out by several species belonging to different taxa. They can be classified into the group of vertebrates, including birds (Holmes & Froud-Williams 2005) and mice (Daedlow et al. 2014, Tschumi et al. 2018), and the group of invertebrates with crickets (White et al. 2007), ants (Torra et al. 2016) and beetles (Kulkarni et al. 2015).

The disturbances exerted by agricultural practices are a major factor influencing not only weed species, but also higher trophic levels as well as the ES performed by both. The weed community in agricultural fields is the results of several agricultural measures like crop type, tillage or herbicide use, that select a specific set of weed species from the soil seed bank (Ryan et al. 2010, Schumacher et al. 2018). In addition, direct weed control and other agronomic measures in the crop impact weed species composition (Hawes et al. 2010, Ryan et al. 2010), leading for example to 15 - 40% more species rich weed communities in organic compared to conventional farming systems (Ryan et al. 2010). Therefore, management decisions of the farmer are reflected by the weed community composition and diversity and are often linked to a certain agricultural intensity (Hawes et al. 2010, Flohre et al. 2011). Some of these measures, like soil tillage (Shearin et al. 2008, Menalled et al. 2007, Baraibar et al. 2009) with no-till systems exhibiting 5 – 40 % higher WSP rates and harrowing (Navntoft et al. 2016) with more frequent harrowing negatively impacting the arthropod diversity through direct lethal effects and habitat disruptions as well as the farming system in general (Navntoft et al. 2009) can furthermore affect the populations of seed predators. Herbicide use has been documented to cause a decrease in seed removal of 10 – 20 % (Sanguankeo & León al. 2011) most presumably through removal of aboveground vegetation. Seed predation rate has been shown to decrease by 8 % if chisel ploughing instead of no-till or moldboard ploughing was used (Cromar et al. 1999). WSP rates are therefore influenced by particular farming practices and their intensity. It is presumed that the resulting impact of farming measures is more pronounced if the food web depends on few strong links in contrast to many weak links (Wall & Nielsen 2012).

A diverse weed flora provides a wide spectrum of different seeds for seed predators. The food preferences of the predators can differ significantly already at the species level (Honek et al. 2007, Petit et al. 2014, Saska et al. 2014, Kulkarni et al. 2016). Therefore, an increased food resource diversity has most likely a positive effect on food web interactions (Harvey et al. 2008) with pronounced effects on lower trophic levels (Scherber et al. 2010) sustaining a larger spectrum of seed predators. A diverse seed predator community should in turn be able to perform WSP more efficiently or be more resilient to agricultural and environmental disturbances. Previous studies revealed that there is a link between weed density and carabid beetle activity-density (Kulkarni et al. 2017), as well as a close connection between carabid beetle diversity and WSP rate (Gaines and Gratton 2010). However, the link between weed species diversity and carabid beetle diversity to the performance of WSP has never been investigated.

Within this study, we recorded weed vegetation, carabid beetles and the rate of weed seed consumption in an on-farm experiment with cereal fields in Southwestern Germany between 2015 and 2017. Farming types comprised conventional, organic and extensive (nature conservation fields) farming, that displayed a gradient of farming intensity and a broad range of associated weed diversity. Our work is aimed at determining if there are positive effects of weed diversity on carabid beetle diversity and the performance of WSP along a gradient of farming intensity. Findings could be utilized to promote and enhance ecosystem services based on weeds and to preserve in-field biodiversity. The objectives of this study were to determine (i) if there is a connection between weed species diversity, carabid beetle diversity and the rate of weed seed consumption, (ii) if the rate of WSP is influenced by year and the type of farming system and decreasing as farming becomes more intensive and (iii) if the groups performing weed seed predation are affected by year and the type of farming.

4.2. Material and Methods

We conducted on-farm field trials from 2015 to 2017 on eight (2015 and 2016) and nine (2017) different cereal fields on the Eastern Swabian Alb, Germany. The region is characterized by high differences in altitude (450 – 600 m above NN), a mean temperature of 7.5 °C and a yearly amount of precipitation of 800 - 900 mm. The fields were grouped into three different blocks with a conventional (CF), an organic (OF) and an extensively (EF) managed field, each. Each field (replicate) contained four (pseudo) replicates (5 m x 12 m plots) that were set up randomly inside the field with at least 10 m distance from the field margin. The plots were located in the field centre to avoid edge effects and inhomogeneous agronomic measures that are often observed at field margins. The third block was lacking the EF in 2015 and 2016. The fields represented an increasing farming intensity gradient from EF to OF to CF, with EF representing the lowest possible input. Grouping into blocks was based on soil characteristics, inclination of the field, landscape context and field history. Extensively farmed fields (nature conservation fields) are part of a national conservation program for endangered weed species. The management of these fields is designed to promote occurrence and abundance of rare arable weed species. No management is carried out on these fields between sowing and harvest. Crop rotation is diverse, including summer and winter crops as well as grass-clover-mixtures to suppress noxious weeds, if deemed necessary. Extensive fields are scarce. Therefore, in terms of geological base substrate and surrounding landscape structure, these fields set the search standards for the fields of the other farming types. Due to the crop rotation, the experimental fields switched from year to year. However, examined fields were not more than 300 m away from the fields examined in the previous year and still fit into the initially determined block characteristics.

Questionnaire for farming operations

Farming operations and their timings were assessed each year by a questionnaire filled in by the participating farmers. The questionnaire recorded management measures (crop protection, tillage, fertilization) as well as crop selection and harvest dates. Agronomic measures performed by the farmers were very heterogeneous in application time and use of equipment. For comparison between farming types Table 1 gives a summary of operations and weed control measures in a very basic form.

Table 4.1 Agronomic measures performed by the farmers in the years 2015 – 2017 in conventional (CF), organic (OF) and extensively (EF) managed fields at the Eastern Swabian Alb, Germany. Farmer code represents individual fields; tillage operations gives the number of repeated stubble tillage operations plus plough use before crop sowing; mechanical weed control and herbicide application indicate the number of applications of the respective operation in the crop.

year	farming	farmer code	crop	fertilization	tillage operations	mechanical weed control	herbicide application	cover crop / living mulch	yield [t/ha]
2015	CF	HM-N	triticale	mineral and organic	2	-	2	cover crop	7.6
		HM-S	triticale	mineral and organic	2	-	2	-	7.5
		SZ-C	winter wheat	mineral and organic	2	-	2	-	5.6
	OF	VW	winter wheat	organic	2	1	-	-	2.2
		SH	spelt	organic	3	2	-	-	2.0
		WM	oat	organic	2	-	-	-	3.4
	EF	HM-I	winter wheat	organic	3	-	-	-	1.5
		HM-II	winter wheat	organic	3	-	-	-	1.9
2016	CF	HM-N	triticale	mineral	2	-	2	-	7.0
		HM-S	winter wheat	mineral	2	-	2	cover crop	4.9
		SZ-C	winter barley	mineral	2	-	2	-	4.9
	OF	VW	winter wheat	organic	2	1	-	-	5.2
		SH	spelt	organic	3	1	-	-	1.5
		WM	winter wheat	organic	2	1	-	-	2.1
	EF	HM-I	winter wheat	organic	3	-	-	-	0.9
		HM-II	triticale	organic	3	-	-	-	3.1
2017	CF	HM-N	winter barley	mineral and organic	2	-	2	cover crop	7.1
		HM-S	winter wheat	mineral and organic	2	-	2	-	6.0
		SZ-C	winter barley	mineral	2	-	1	-	5.8
	OF	VW	oat	organic	2	1	-	living mulch	2.8
		SH	spelt	organic	4	1	-	-	2.4
		WM	triticale	organic	2	2	-	-	4.7
	EF	HM-I	oat	organic	2	-	-	-	1.1
		HM-II	oat	organic	2	-	-	-	1.3
		SZ-E	spring barley	organic	2	-	-	-	1.4

Weed diversity and density

To assess weed species diversity and abundance we performed relevées (vegetation recordings) according to a modified Braun-Blanquet scale (Wilmanns 1998) within each replicate (4 relevées of a field). The Braun-Blanquet scale is a cover-abundance measure, providing a species specific combination of soil cover and population size (for details see supplementary table S1). Vegetation recordings took place in April and July each year to ensure a complete recording of the weed species spectrum. Weed species were determined to the species level. First all weed species present within a plot were recorded and then the cover-abundance of each species was estimated according to the modified Braun-Blanquet scale.

Weed seed predation (WSP)

Within each plot, we studied WSP by monitoring weed seed removal using openly displayed seed cards and exclosure cages with seed cards (Westerman 2003b). The exclosure cages were made of metal and had a mesh width of 10 mm to exclude larger vertebrates. Additionally, control cages with 1 mm mesh width were used to exclude any predator and account for the seed loss due to weather conditions and handling of the cards. The seed cards were made of high-quality sand paper (45mm x 115mm, grain size 60 or 80) and sprayed with repositionable glue (Lyreco, Switzerland, art.no. 3.047.832). The high quality of the sand paper ensured that it did not bend or soak under moist conditions. 50 weed seeds composed of 4 - 5 different species, each field specific and thus representing the actual resources present in the field, were glued to the sand paper and the remaining glue was covered with fine sand to prevent insects from sticking to it. Weed seeds were either purchased (Herbiseed, Twyford, England) or obtained directly from the specific field. The field-specific seed set-up was chosen due to most closely address the research question to assess if there is a relation between weed biodiversity and WSP (Table 2). To reflect the naturally occurring weed seed consumption, weed seed species offered on the seed cards to the endemic weed seed predator community have to mirror the resources that are actually present in the field. With the hypothesis being based on weed species diversity, the assessment of WSP through one particular weed species across treatments would not respect the initial research question and could measure seed consumption that might not occur naturally. The weed community for each field was assessed in March/April of the respective year and the 4 - 5 most abundant weed species were utilized to reflect the "naturally" present weed seeds. Moreover, the endemic seed predator species are adapted to a certain spectrum of weed seeds that serve as their food source. A field-specific set-up of weed seeds additionally takes this food spectrum of the seed predators into account. During the experimental period, the seed cards were replaced every two days. In the field, seed cards as well as exclosure cages were fastened to the ground using nails. WSP measurements were performed four times: in May, June and July and 4 weeks after harvest in the mid of September. In 2015, we did not record WSP in May and June, but additionally assessed WSP directly after harvest at the beginning of August. In the following years 2016 and 2017, the timing of the soil disturbance by repeated stubble tillage was too heterogeneous between farmers to allow assessments of WSP in August. In general, seed cards were exposed to predators for 8 days during each assessment period.

Table 4.2 Setup of seed cards in the years 2015 – 2017 with weed species names and the respective number of seeds on the seed cards. Seed choice and numbers reflect the four to five most abundant weed species in each experimental field and year. Farming type abbreviations are: conventional farming (CF), organic farming (OF) and extensive farming (EF). Farmer code represents abbreviations for individual fields.

		2015		2016		2017	
farming type	farmer code	weed species	number of seeds	weed species	number of seeds	weed species	number of seeds
	HM-N	*Galeopsis tetrahit*	12	*Galium aparine*	18	*Veronica persica*	15
		Convolvulus arvensis	12	*Stellaria media*	18	*Convolvulus arvensis*	15
		Thlaspi arvense	13	*Veronica persicaria*	8	*Viola arvensis*	12
		Polygonum convolvulus	13	*Viola arvensis*	6	*Lamium purpureum*	8
	HM-S	*Alopecurus myosuroides*	12	*Galium aparine*	18	*Veronica persica*	15
CF		*Veronica hederifolia*	12	*Stellaria media*	18	*Lamium purpureum*	15
		Chenopodium album	13	*Veronica persicaria*	8	*Stellaria media*	12
		Polygonum convolvulus	13	*Viola arvensis*	6	*Thlaspi arvense*	8
	SZ-C	*Viola arvensis*	12	*Viola arvensis*	18	*Viola arvensis*	12
		Stellaria media	13	*Geranium dissectum*	10	*Stellaria media*	13
		Veronica hederifolia	13	*Stellaria media*	14	*Veronica hederifolia*	13
		Polygonum convolvulus	12	*Galium aparine*	8	*Polygonum convolvulus*	12
	VW	*Viola arvensis*	12	*Stellaria media*	14	*Alopecurus myosuroides*	14
		Myosotis arvensis	12	*Veronica hederifolia*	12	*Stellaria media*	12
		Alopecurus myosuroides	13	*Galium aparine*	10	*Veronica hederifolia*	10
		Stellaria media	13	*Ranunculus repens*	7	*Ranunculus repens*	7
				Viola arvensis	7	*Lamium amplexicaule*	7
	SH	*Galeopsis tetrahit*	13	*Stellaria media*	15	*Ranunculus repens*	15
OF		*Thlaspi arvense*	13	*Veronica hederifolia*	15	*Veronica hederifolia*	15
		Polygonum convolvulus	12	*Geranium dissectum*	12	*Polygonum aviculare*	8
		Geranium dissectum	12	*Viola arvensis*	8	*Alopecurus myosuroides*	12
	WM	*Viola arvensis*	13	*Alopecurus myosuroides*	14	*Centaurea cyanus*	14
		Viccia tetrasperma	13	*Centaurea cyanus*	12	*Lamium purpureum*	12
		Centaurea cyanus	12	*Geranium dissectum*	7	*Viola arvensis*	8
		Polygonum convolvulus	12	*Thlaspi arvense*	7	*Galeopsis tetrahit*	8
				Stellaria media	10	*Veronica persica*	8
	HM-I	*Convolvulus arvensis*	13	*Alopecurus myosuroides*	15	*Sinapis arvensis*	15
		Rhinantus alectorolophus	12	*Viccia tetrasperma*	13	*Alopecurus myosuroides*	13
		Consolida regalis	13	*Consolida regalis*	8	*Viccia tetrasperma*	8
		Alopecurus myosuroides	12	*Polygonum convolvulus*	7	*Rhinantus alectorolophus*	7
				Rhinantus alectorolophus	7	*Consolida regalis*	7
	HM-II	*Convolvulus arvensis*	13	*Alopecurus myosuroides*	15	*Sinapis arvensis*	15
		Rhinantus alectorolophus	13	*Viccia tetrasperma*	13	*Alopecurus myosuroides*	13
EF		*Viccia tetrasperma*	12	*Consolida regalis*	8	*Viccia tetrasperma*	8
		Alopecurus myosuroides	12	*Polygonum convolvulus*	7	*Rhinantus alectorolophus*	7
				Rhinantus alectorolophus	7	*Consolida regalis*	7
	SZ-E					*Centaurea cyanus*	15
						Alopecurus myosuroides	12
						Viola arvensis	9
						Polygonum convolvulus	7
						Spergula arvensis	7

WSP rates were calculated according to Westerman *et al.* (2003b) as following:

$$M_{invertebr.} = \frac{\frac{R_c}{N_c} - \frac{R_e}{N_e}}{\frac{R_c}{N_c}}$$

$$M_{vertebr.} = \frac{\frac{R_e}{N_e} - \frac{R_o}{N_o}}{\frac{R_c}{N_c}}$$

where $M_{invertebr.}$ describes the proportion of weed seeds consumed by invertebrates and $M_{vertebr.}$ the proportion by vertebrates in each assessment period. R represents the number of remaining seeds and *N* the number of initial seeds in the control (*c*), under exclosure cages (*e*) or openly displayed (*o*).

To determine the dominant predator group, we generated an index that reflects the ratio between WSP of vertebrates and WSP of invertebrates. This index was calculated as:

$$I_{VI} = log_{10}\left(\frac{M_{vertebr.}}{M_{invertebr.}}\right)$$

The logarithm of the ratio is necessary to gain equal distances of the index values towards the zero line, which represents equal removal rates of both groups.

Assessment of Carabid beetle diversity

Each year in July and September, we simultaneously assessed the activity-density of carabid beetles using barber traps. Traps consisted of a plastic beaker (diameter: 8 cm; total volume: 0.3 L) that was buried into the soil so that the top rim lay flush with the soil surface. We added 40 mL of a mixture of water and ethylene glycol (50:50) to each barber trap. The top of each trap was covered with the same metal mesh as used for the exclosure cages (10 mm mesh width). This ensured recording only those species that were actually able to feed on the weed seeds and additionally prevented larger animals from damaging the trap. Traps were emptied every two days and carabid beetles stored in "Scheerpeltz-solution" (70% ethanol, 25% destilled water, 5% acetic acid) for a later counting and determination of the species according to Freude et al (1976). When determination of species was ambiguous, experts from the department of applied entomology of the university of Hohenheim were consulted. The determination of species level within the genus *Amara*, was performed using the collection of *Amara* of the State Museum of Natural History of Stuttgart as comparison, as well as consultation of the museum's experts on Coleoptera.

Statistical Analysis

The analysis was carried out using the statistical software R© (Version 3.4.3, R Foundation for Statistical Computing, Vienna, Austria). WSP data was analysed with a linear model containing farming type, year and month as fixed effects as well as their respective interactions and a normal distributed error term with zero mean and homogenous variance. A standard analysis of variance (ANOVA) revealed that interactions year by month, year by farming type and month by farming type are significant (see supplementary table S2). To separate the temporal effects from the farming type, analyses were carried out within each year.

The WSP data for the farming types (EF, OF, CF) in each month was then analyzed using a linear mixed model (package "nlme") with a correlation structure to account for repeated measurements in the field within each year. If y_{ijk} denotes the observation of the total WSP rate in the *i*th (*i*=1,…, *I*) month for the *k*th (*k*=1,…, *K*) farming type in the *j*th (*j*=1,…, *J*) block, then the model is written as

$$y_{ijk} = \mu + \alpha_k + \beta_i + b_j + (\beta.b)_{ij} + (\alpha.b)_{jk} + (\alpha.\beta)_{ik} + (\alpha.\beta.b)_{ijk} + e_{ijk}$$

where μ denotes the general mean and α_k and β_i are the fixed effect of the *k*th farming type in the *i*th month. The block effect of *j*th block b_j, month x block interaction, block x farming type interaction, month x farming type interaction and month x block x farming type interaction are taken as random effect. The error term e_{ijk} was taken as normal distributed with zero mean and homogenous variance σ^2. Since the data includes repeated measures, errors are correlated. Therefore, a correlation structure for errors is required. Several correlation structures *e.g.* Gaussion, Linear, Exponential and Compound symmetry were considered. Normality of data distribution and homogeneity of variance were checked through residual plots ("residual vs. predicted" plot and a quantile-quantile-plot). The residual plots revealed that a data transformation is required to achieve the assumptions of error term. The square root transformation achieved the normality and variance homogeneity of errors. Optimal model fitting and covariance structure were selected according to Akaike's Information Criterion (AIC), yielding a Compound symmetry correlation structure.

The significance of factors was tested using analysis of variance (ANOVA) on final fitted model. Pairwise comparisons of farming type within each month were tested with least-square means ($p \leq 0.05$) (package "emmeans"). WSP results represent the back-transformed values.

Correlations between assessed parameters (number of carabid beetle species vs. number of weed species, seed predation rate of invertebrates vs. carabid species diversity, proportion of weed seeds predated vs. number of weed species) were determined using Pearson's product momentum correlation coefficient. The method of least square means was used to estimate regression lines.

Diversity indices for carabid beetles were calculated using the package "vegan". Analysis of variance (ANOVA) was used to analyse diversity indices of carabid beetles as well as species numbers of weeds and carabid beetles. Means were compared with a Tukey-HSD-test ($p \leq 0.05$).

4.3. Results

Weed diversity, Carabid beetle diversity and weed seed predation (WSP)

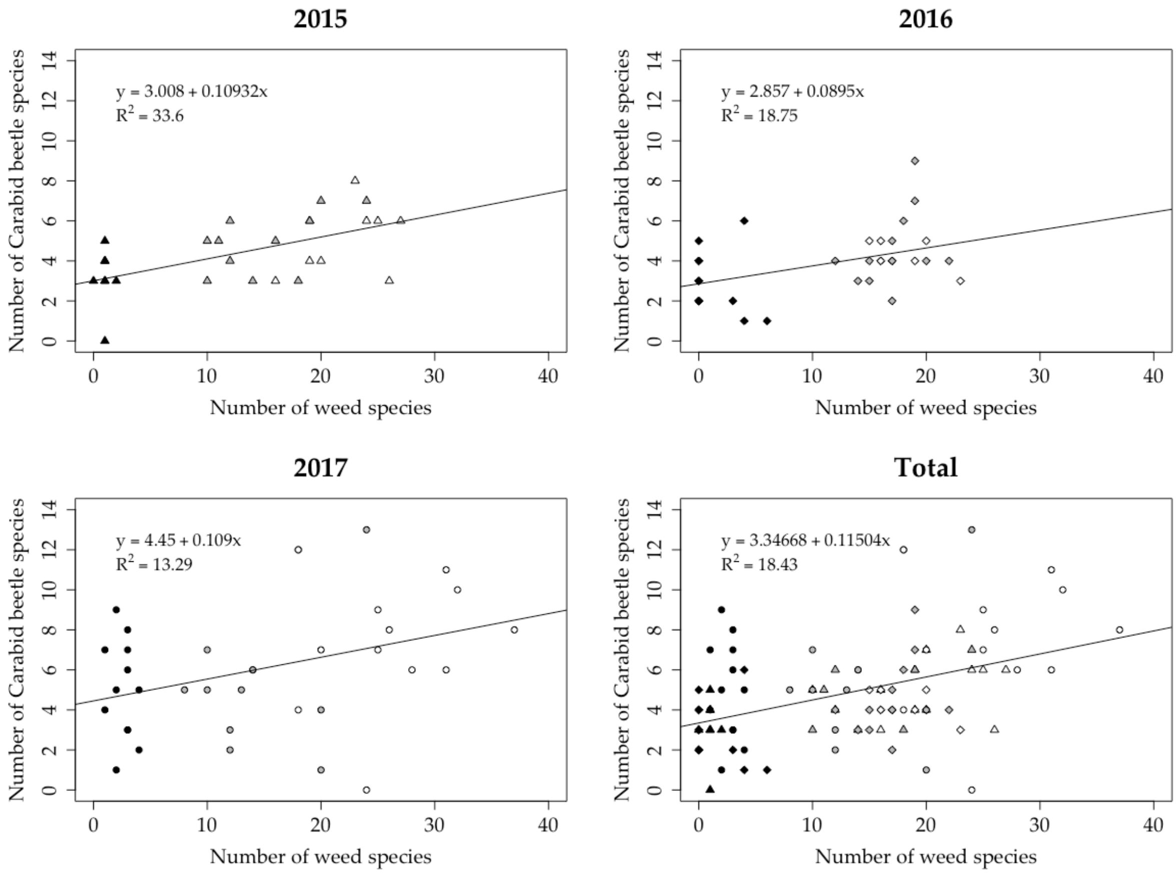

Figure 4.1 Correlations between the number of weed species and the number of Carabid beetle species. Correlation according to Pearson is significant ($p < 0.001$) in 2015 (triangle), 2016 (diamond) and 2017 (circle) and across years. Farming types are represented by colors: conventional farming (black), organic farming (grey) and extensive farming (white).

Weed species diversity was significantly different between farming types in general, with EF exhibiting the highest mean species diversity (22.75 species/relevée). Diversity in OF systems was intermediate (15.69 species/relevée) and CF showed the lowest mean diversity (2.25 species/relevée). Weed species diversity was positively correlated to carabid beetle diversity (Pearson's product-momentum correlation, significant, $p < 0.001$) (Figure 1). A tenfold increase in weed species numbers roughly elevated the carabid species diversity by one species. The R^2 values ranged from 13.29 to 33.6, in 2017 and 2015 respectively. In 2017, a higher diversity of carabid beetles (see also Table 4) and weed species was present (see supplementary table S3) compared to 2015 and 2016.

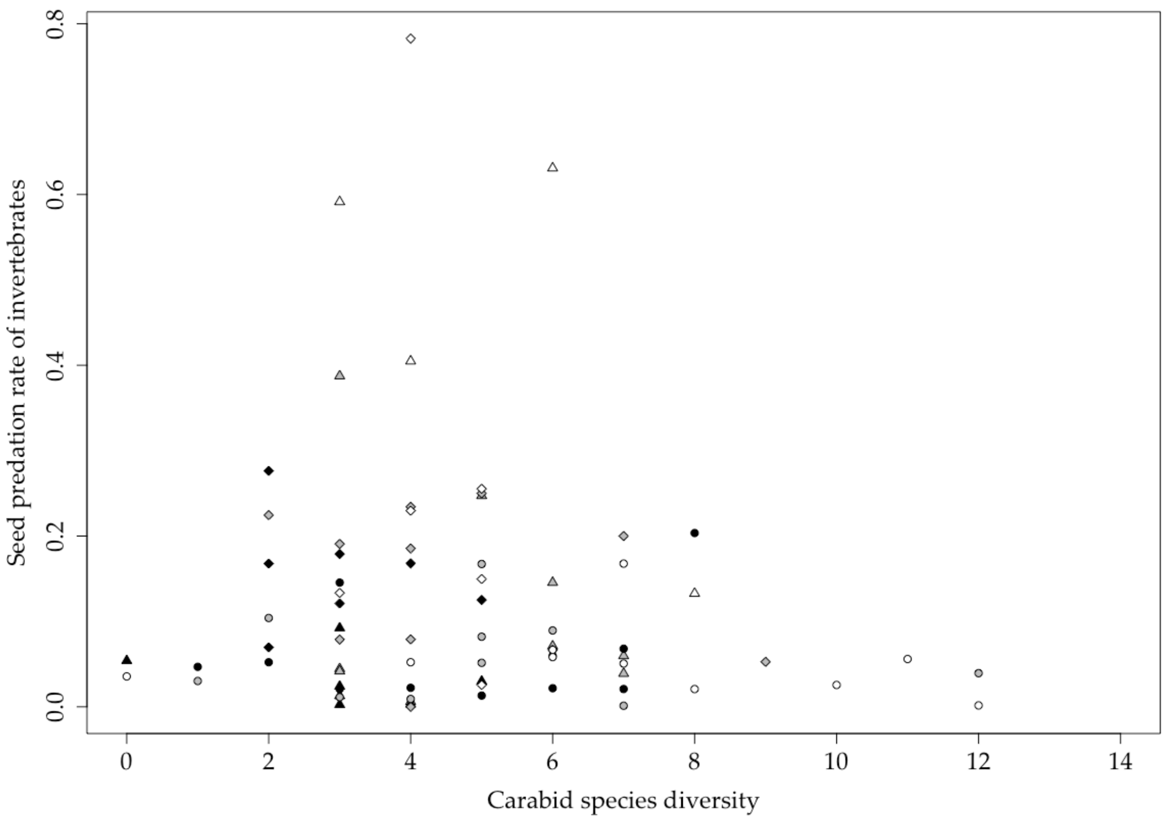

Figure 4.2 Correlation between the number of Carabid beetle species and the proportion of weed seed predation by invertebrates. Correlation according to Pearson is not significant (*p* = 0.3101) in 2015 (triangle), 2016 (diamond) and 2017 (circle). Farming types are represented by colors: conventional farming (black), organic farming (grey) and extensive farming (white).

The correlation of carabid species diversity and WSP rate of invertebrate species was not significant (Pearson's product-momentum correlation not significant, p=0.3101), but exhibits a distinct pattern (Figure 2). Very low (<2 species) and very high (>9 species) diversity in the carabid community showed low WSP rates of below 10 % seed removal (except the outliers at 1 species with 60 –80 % removal). Higher WSP rates were observed if species numbers of carabid beetles ranged between 2 to 8 species with rates between 10 –50 %. In total we found 15, 36 and 48 different carabid beetle species across farming types in 2015, 2016 and 2017, respectively.

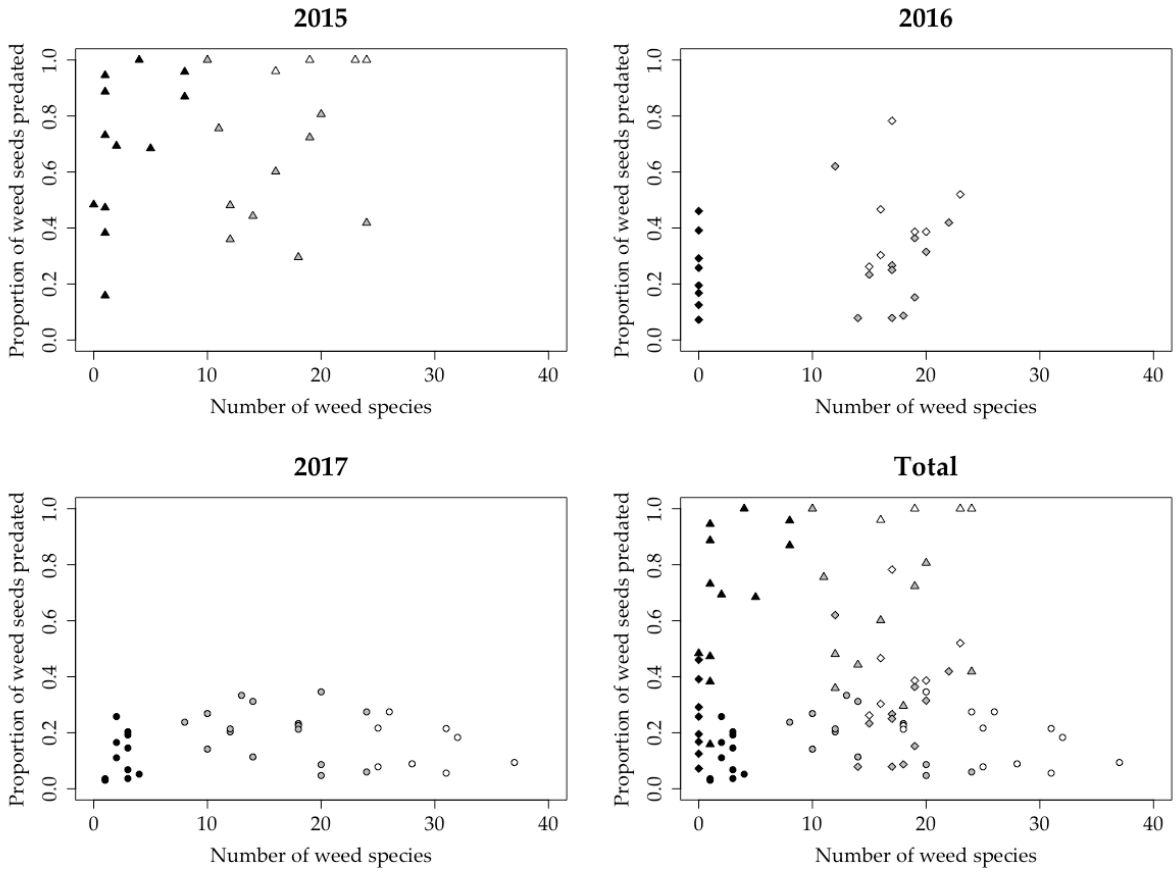

Figure 4.3 Correlation between weed species number and the proportion of weed seeds predated in 2015 (triangle), 2016 (diamond) and 2017 (circle). Farming types are represented by colors: conventional farming (black), organic farming (grey) and extensive farming (white). Correlation according to Pearson was not significant (p=0.6435).

In total, from 2015 to 2017, we recorded 100 weed species across the farming types. The correlation analysis revealed no significant influence of weed species number on WSP in any year (Figure 3). The year 2015 showed high WSP rates up to total consumption of weed seeds independent from weed species diversity, while in 2016 and 2017 the mean WSP rate was generally low to medium (42 to 18 %, respectively). Across the years, the proportion of weed seeds removed in CF ranged from 0 to 1 while exhibiting a very low number of weed species (below 10). OF and EF also covered the whole range of the scale, but with substantially higher weed species numbers (up to 24 and 37 weed species, respectively). There were no significant differences between farming types.

Weed seed predation (WSP) rates

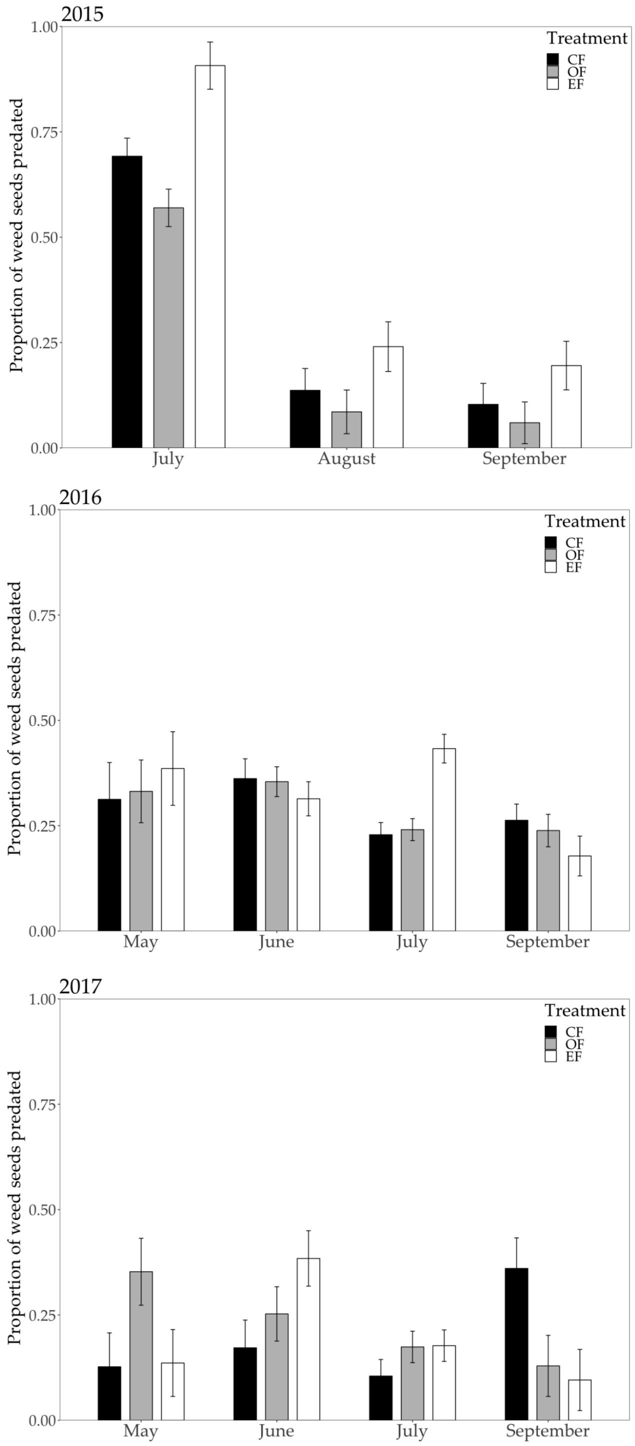

Figure 4.4 Proportion of weed seeds predated in July, August and September of the year 2015 and May, June, July and September of the years 2016 and 2017 in conventional (CF, black), organic (OF, grey) and extensively (EF, white) farmed fields.

The WSP rates were significantly influenced by the year (Figure 4a). In 2015, we found a distinct and significant separation between the three farming types. In July 2015, the highest WSP rate was observed in EF (91 %), followed by CF (70 %) and OF (57 %). This pattern was also present in the following months, however at a level below 30 % seed removal.

In 2016, we found no significant influence of farming type on the WSP rate (Figure 4b). The WSP rate also remained quite stable across the months (May and June 34 % and September

24 %) with one significantly higher value from EF in July (43 %, compared to CF (23 %) and OF 24 %). The year 2017 showed a continuous decline of WSP in the organically farmed fields, dropping from 35 % to 13 % from May to September (Figure 4c). The predation rate in OF was significantly higher in May than within any of the other farming types (35 % compared to 13 % (CF) and 14 % (EF)). In EF, we found the significantly highest WSP rate in June at 38 %. In CF the highest weed seed removal was 36 % in September. The WSP rates for the other months and farming types were quite low, ranging between 10 % (EF in September) and 25 % (OF in June).

Seed predator groups and Carabid beetle communities

We found significant differences between both seed predation groups, but always in combination with either the particular year, the farming type or both. When the field exhibited a low level of WSP, we found no significant impact of the predator group on the WSP ratio. Under high seed predation pressure, as in the year 2015, we found that vertebrates were the dominant predators. The interaction between the months and farming types showed similar index patterns in the years 2016 and 2017 (Figure 5). Differences in index values between farming types within each month and year were mostly not significant.

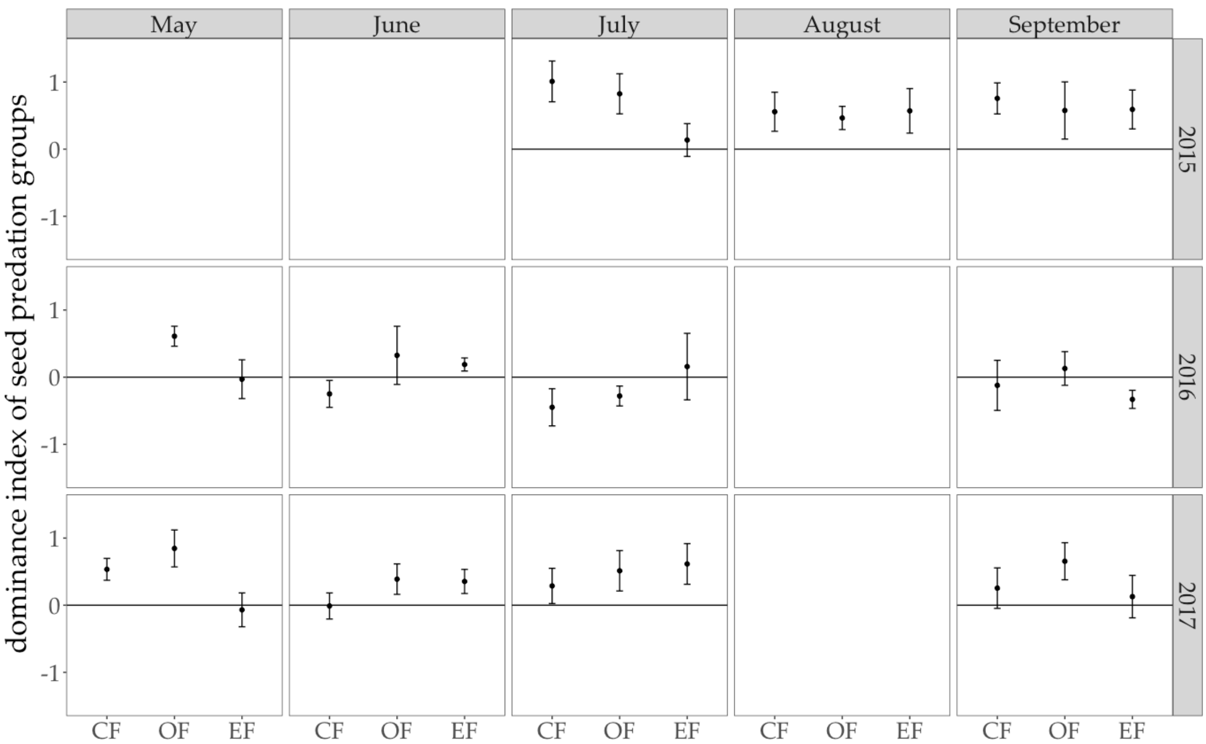

Figure 4.5 Dominance index of seed predation groups from May to September in 2015 – 2017 in conventional (CF), organic (OF) and extensively (EF) managed fields. Values above zero represent relative dominance of vertebrates, while values below zero represent relative dominance of invertebrates. The higher the values are above or below zero, the higher is the relative dominance of the respective seed predator group.

Table 4.3 Mean activity density (±SE) of the five most abundant Carabid beetle species as well as mean number of Carabid beetles per plot in July 2015 – 2017 separated by farming type. Farming types are abbreviated: conventional farming (CF), Organic farming (OF) and extensive farming (EF). Letters that are not identical within rows indicate significant differences according to Tukey HSD test (p < 0.05). Root transformation of data prior to the analysis of variance is indicated by #

year	Carabid beetle spectrum	diet type	CF	OF	EF	p value
2015	*Pterostichus melanarius*	omnivorous	34.17 (±11.36) a	2.08 (±0.82) b	1.88 (±1.01) b	**<0.001#**
	Pterostichus niger	carnivorous	0.00 (±0.00) b	11.67 (±5.63) a	11.88 (±5.37) a	**0.0480#**
	Harpalus rufipes	granivorous	0.33 (±0.19) b	4.17 (±2.97) b	20.88 (±5.09) a	**<0.001**
	Nebria brevicolis	carnivorous	0.33 (±0.22) b	7.67 (±3.42) a	0.00 (±0.00) b	**0.0314**
	Poecilus cupreus	omnivorous	1.75 (±0.65) b	4.83 (±1.15) a	1.00 (±0.27) b	**0.0095**
	Mean number of Carabids		38.50 (±11.31) a	34.58 (±8.34) a	42.75 (±8.92) a	0.8584
2016	*Poecilus cupreus*	omnivorous	5.13 (±2.17) b	34.58 (±8.59) a	10.88 (±3.59) b	**0.0085**
	Harpalus rufipes	granivorous	1.38 (±0.65) b	7.17 (±1.22) ab	10.13 (±2.81) a	**0.0073**
	Brachinus crepitans	carnivorous	0.00 (±0.00) b	0.58 (±0.50) b	14.88 (±6.76) a	**0.0084**
	Pterostichus niger	carnivorous	3.63 (±1.05) a	1.08 (±0.29) b	0.13 (±0.13) b	**0.0016#**
	Amara ovata	granivorous	0.00 (±0.00) b	0.42 (±0.34) b	3.63 (±0.65) a	**<0.001#**
	Mean number of Carabids		11.75 (±2.80) b	48.67 (±9.46) a	42.50 (±12.95) ab	**0.030**
2017	*Poecilus cupreus*	omnivorous	7.67 (±1.43) a	22.17 (±10.27) a	9.67 (±2.54) a	0.2125
	Harpalus rufipes	granivorous	2.75 (±0.81) a	6.33 (±2.11) a	6.42 (±1.28) a	0.1583
	Brachinus crepitans	carnivorous	0.17 (±0.11) b	0.42 (±0.42) b	13.75 (±5.03) a	**0.0027**
	Harpalus affinis	granivorous	0.75 (±0.66) b	0.83 (±0.34) b	5.92 (±1.55) a	**<0.001#**
	Pterostichus melanarius	omnivorous	3.17 (±1.60) a	2.58 (±0.82) a	1.08 (±0.47) a	0.3757
	Mean number of Carabids		19.33 (±3.18) a	39.25 (±14.47) a	50.00 (±9.89) a	0.1172

The total number of carabid beetles caught differed considerably between the years and farming types. The total activity-density (sum of catches across all fields per treatment) of carabid beetles in 2015 was 462 (CF), 415 (OF) and 342 (EF). In 2016, the total activity density was significantly higher in OF (904) than in CF (481) and in EF (503). Activity-density in 2017 showed huge differences in numbers following the intensity gradient from CF (655) to OF (1445) to EF (2140). However, these differences were not significant. Within the carabid beetle communities we found *Harpalus rufipes* (granivorous), *Pterostichus melanarius* (omnivorous) and *Pterostichus niger* (carnivorous) to be the dominant species in 2015 and 2016, while *Poecilus cupreus* (omnivorous), *H.rufipes* and *Brachinus crepitans* (likely carnivorous) dominated the community in 2017 (Table 3). Between the farming types, the composition of the five most abundant species differed considerably in 2015 and 2016. In 2015, *P. melanarius* was most common in conventional fields and *H. rufipes* in organic and extensively managed fields. The dominant species in 2016 was *P. cupreus* in conventional and organic fields and *H. rufipes* in extensively managed fields.

Table 4.4 Carabid beetle diversity per plot expressed as mean species numbers (±SE), Shannon index (±SE) and Simpson's index of diversity (1-D) (±SE) in 2015 – 2017 separated by farming type. Farming types are abbreviated: conventional farming (CF), organic farming (OF) and extensive farming (EF). Different letters show significant differences within rows according to Tukey HSD test ($p < 0.05$).

year	Carabid beetle diversity	CF	OF	EF	p value
2015	Mean species number of Carabid beetles	3.25 (±0.52) a	3.75 (±0.22) a	4.38 (±0.32) a	0.179
	Shannon index	0.50 (±0.15) b	1.06 (±0.07) a	1.02 (±0.12) a	**0.0023**
	Simpson's index of diversity (1-D)	0.26 (±0.07) b	0.59 (±0.03) a	0.54 (±0.06) a	**0.0006**
2016	Mean species number of Carabid beetles	2.92 (±0.45) b	3.83 (±0.21) ab	4.25 (±0.25) a	**0.0323**
	Shannon index	0.46 (±0.14) b	1.08 (±0.06) a	1.03 (±0.11) a	**0.0005**
	Simpson's index of diversity (1-D)	0.24 (±0.07) b	0.60 (±0.03) a	0.55 (±0.06) a	**0.0002**
2017	Mean species number of Carabid beetles	5.00 (±0.72) a	5.75 (±1.04) a	7.33 (±0.93) a	0.1931
	Shannon index	1.14 (±0.17) a	1.12 (±0.13) a	1.52 (±0.16) a	0.1311
	Simpson's index of diversity (1-D)	0.56 (±0.07) b	0.55 (±0.06) b	0.77 (±0.03) a	**0.0156**

Mean species numbers in the carabid beetle community differed significantly only between farming types in 2016. Shannon index and Simpson's index of diversity showed similar results in 2015 and 2016 with significantly lower index values for CF compared to OF and EF. In 2017, only Simpson's index of diversity indicated significant differences between farming types. Overall, EF displayed in most cases the highest index values, though not always significant (Table 4). There was also a temporal pattern with higher index values and species numbers in 2017 compared to 2015 and 2016.

4.4. Discussion

Weed diversity, Carabid beetle diversity and weed seed predation (WSP)

Weed species diversity and carabid beetle diversity did significantly correlate in this study. This agrees with the first part of our hypothesis, that an increasing spectrum of different weed seeds supports a higher diversity of carabid beetles, that consume weed seeds either as part of their diet or are completely dependent on them. Saska et al. (2014) already hypothesized a positive influence of a diverse weed community on carabid beetle diversity and the subsequent ecosystem services performed. A positive correlation between weed or plant diversity with carabid beetles or other invertebrates in the order Coleoptera has been described for natural and agricultural systems (Crisp et al. 1998, Liu et al. 2015, Koricheva & Hayes 2018). In the present study, weed diversity was also strongly associated with the farming system (intensity), which was utilized to create a gradient of increasing weed species diversity for the initial hypotheses. Flohre et al. (2011) discovered that contrary to plant and bird diversity, carabid beetle diversity was not affected by a gradient of agricultural intensification. This was explained by the broad range of realized farming operations already on a local scale and the ability of beetles to effectively colonize fields from surrounding habitat structures. This effect might also explain the unexpectedly low, but still significant correlation between weed diversity and carabid beetle diversity identified in this study.

Carabid beetle diversity showed a pattern regarding WSP rates with highest seed removal at a medium diversity level. The low WSP rate at higher diversity levels might be attributed to additional species in the carabid beetle community that are carnivorous. These may have preyed on the granivorous beetles, which in turn might have decreased their populations or affected their feeding behaviour (Charalabidis et al. 2017). The majority of beetle species recorded in the current study were, however, either omnivorous or granivorous species with weed seeds constituting the major source of their diet (Frei et al. 2019). Trichard et al. (2013) found a significant positive correlation between WSP and species diversity of strictly granivorous carabid beetles as well as the activity-density of omnivorous species. A positive effect of carabid beetle diversity on the WSP rate has been reported before (Gaines and Gratton 2010, Jonason et al. 2013). Gaines and Gratton (2010) explained this effect with a better ability in service performance by a functionally diverse beetle community. Accordingly, ecosystem services provided by species-poor communities are more prone to disturbances (Wall & Nielsen 2012). For this reason, WSP might strongly fluctuate if carabid beetle diversity is very low. In the present study, this was indicated by huge differences in invertebrate WSP rates if only one carabid beetle species was recorded in the pitfall traps. Another reason might be the pre-selection of carabid beetles by the limited weed seed spectrum on the seed cards yielding improper accounts of seed predation potentials. Petit et al. (2014) found that in field experiments two out of the five weed seed species offered were particularly preferred by the endemic invertebrate seed predators. Moreover, the size of a potentially consumed weed seed is linked to the carabid beetle's size and their taxonomic division (Honek et al. 2007).

We found no direct connection between weed species diversity and WSP rate. In contrast, several authors describe positive correlations between plant species diversity and the performance of ecosystem services (Isbell et al. 2011, Balvanera et al. 2006, Harrison et al. 2014). Storkey et al. (2015) showed that the provision of ecosystem services by plants in an agricultural context was optimal at a low to intermediate diversity level. They assumed that functional contrasts of specific plant traits were the decisive factor for ES provision in their study system. Therefore, functional diversity rather than weed diversity *per se* might give more insights into the link between biological diversity and ecosystem services such as WSP.

Farming impact

The farming system had no consistent impact on WSP rate. Rather, the study year determined weed consumption. Furthermore, we presume that other factors like cover cropping affected the predation rate (Gallandt et al. 2005). Other authors examining WSP found seasonal patterns of crop growth or harvest to be more relevant than farming type (Heggenstaller et al. 2006). Moreover, landscape mosaic may have a larger influence on WSP than local management (Trichard et al. 2013). Thus, promotion of ecosystem services or beneficial predators should start with designing management strategies at a scale larger than fields or single farms.

Contrary to our initial assumption, CF did not exhibit the lowest WSP rates. This may have resulted from changes in the food web structure. The chemical control of weeds by herbicides might have removed the major food source for granivors and favored omnivorous carabids instead. With no naturally available seeds, the seed predators might have responded to the additional seed input via seed cards over-proportionally (Frank et al. 2011). This might explain the high WSP rates in conventional fields, even if only one seed predator species was present. Additionally, the use of insecticides can negatively affect carabid beetles (Labruyere et al. 2016). In organic farming the mechanical weed control by harrowing during the vegetation phase is common practice. Frequent soil disturbance can also lower the activity of carabids and thereby lowering the WSP rate (Blubaugh & Kaplan 2015). Navntoft et al. (2009) showed that there was no significant difference in seed removal between conventional and organic fields. Rather, interactions linked to the distance of sampling sites from the field margin and total plant cover influenced WSP rates. Extensive farming, exhibiting no disturbances between sowing and harvest, showed predominantly high WSP rates, although not always significantly different from the other farming types.

The positive response of mice and carabid beetles, in particular, to plant cover is quite prominent (Navntoft et al. 2016, Meiss et al. 2010). This might explain the seed predation pattern in 2017, when peaks in WSP rates can be attributed to vegetation cover. In May living mulch (Davis & Liebman 2003) was grown in the majority of the organic fields, in June weed cover was high in the extensive fields (Kulkarni et al. 2017) and in September the presence of a cover crop mixture (Shearin et al. 2008, Blubaugh et al. 2016) in conventional farming provided quite dense coverage for seed predators. The temporal pattern of June and July exhibiting the highest WSP rates might be explained by the provision of weed cover (Heggenstaller et al. 2006) and the availability of weed seeds. This further suggests that WSP can be positively influenced by biological weed control strategies involving living mulch and cover crops (Gallandt et al. 2005) and is not limited to extensive or organic farming management.

Predominant weed seed predator group

The measured predation rates in this study were higher for vertebrates than for invertebrates. In contrast, it was initially presumed that the temporal coincidence between food demand and seed shed in cereals is attributing a higher potential of weed control in favour of invertebrates (Westerman et al. 2003b). Also, the amount of seed rain by weed plants is affecting WSP by carabid beetles positively (Bohan et al. 2011). Therefore, WSP by invertebrates should have been very high in EF and very low in CF, according to the weed coverage. However, there was no such trend in the present study.

The dominant seed predators in this study were vertebrates, most presumably mice, that exhibited also quite high predation rates of weed seeds. If WSP was low, both predator groups were similarly efficient in weed seed consumption. Vertebrates are able to consume much more seeds per individual, while invertebrates may compensate their low seed intake per individual through their high population sizes. A consistently positive correlation between ground beetle abundance and WSP rate has not been shown yet. However, the majority of studies report high correlations (e.g. Menalled et al. 2007, Trichard et al. 2013), while others disagree with this (Saska et al. 2008). Therefore, WSP of both groups can be rather similar. Actual dominance of seed predator groups in overall seed consumption may ultimately be determined by environmental factors such as temperature (Saska et al. 2010) or initial population sizes. In 2015, for example, we had high populations of mice, indicated by feces in close vicinity to the seed cards and a huge number of nests. The same was experienced in 2015 by Pannwitt et al. 2017 in Northern Germany. This year exhibited the highest recorded WSP rates and dominance indices for vertebrates. However, the present study did not differentiate between different types of vertebrate predators. Other vertebrate seed predators such as birds might also have consumed the offered weed seeds (Orlowski & Czarnecka 2009), although their role in post-dispersal WSP has been found to be quite low (Holmes & Froud-Williams 2005).

The most abundant and active predators in the group of invertebrates were omnivorous carabid beetles like *Pterostichus melanarius* and *Poecilus cupreus*. Granivorous beetles such as *Harpalus rufipes* and *Amara ovata* were common, but mainly in the extensive or organically farmed fields. Kromp (1989) described a correlation of two granivorous carabid beetles, namely *Amara consularis* and *Harpalus rufipes*, with weed vegetation independent of the farming type. They also found a high abundance of *Pterostichus melanarius* in conventional fields (Kromp 1989). Because omnivorous species can switch between plant and animal food, their contribution to WSP is difficult to quantify and might also negatively affect WSP by consumption of granivorous species (Trichard et al. 2013, Charalabidis 2017).

The diversity indices and abundances of carabid beetles were low in 2015 and 2016, but high in 2017. We presume that the massive number of mice in 2015 might have consumed a large portion of carabid beetles as additional food, reducing their population sizes tremendously. Therefore, the group of vertebrates and especially mice, were not only performing positive services (WSP) but also disservices (Tschumi et al. 2018). Due to less predation pressure by vertebrates, the carabid beetle species recovered over time, which was reflected in elevated index values in 2017. The population reductions might also help explain the overall low WSP rates in the years following 2015.

The Eastern Swabian Alb is characterized by small fields and high landscape complexity. Thus, exchange of species between habitats (grassland, field, woody structures) is more likely than in simplified landscapes. Accordingly, a higher species diversity is present *per se* and could have masked the effect of farming type on WSP and the carabid beetle spectrum. Also, Jonason et al. (2013) discovered that landscape context explains the variation in WSP of carabid beetles better than local farming practices. However, they also found that WSP was higher in simplified landscapes with a high proportion of annual crops. The last point is controversial, as increasing environmental heterogeneity favours the diversity of seed predators (Diekötter et al. (2010)) and landscape complexity and farming type are often influencing carabid communities and WSP simultaneously and in conjunction (Fischer et al. 2011).

4.5. Conclusion

Weed diversity was positively correlated to carabid beetle diversity and this in turn contributed to WSP if diversity was intermediate (2-8 species). Although there was no indication of a direct relation between weed diversity and WSP, we were able to shed some light on the effects of weed diversity on carabid beetles and the effectuated WSP. In total, farming intensity did not affect WSP rates consistently, rather year and provision of cover were more important determinants of WSP. Extensive farming exhibited the highest weed and carabid beetle diversity in all experimental years. Omnivorous carabid species were the most common diet type in every farming type and in every year. This in turn means that the carabid beetles present were not only performing the ecosystem service of weed control, but also of (arthropod) pest control (Pretorius et al. 2018). This makes the promotion of beneficial predators also attractive for conventional farming. The results highlight weed seed predation as an important component of integrated weed management. Management strategies should aim at preserving weed diversity and consider weed control measures such as living mulch and cover crops that also provide suitable habitats for beneficial predators.

4.6. Acknowledgements

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Supplementary table S1: Modified Braun-Blanquet scale according to Wilmanns (1998)

code	abundance	coverage
r	1 - 2 individuals	rare
+	2 - 5 individuals	≤ 5 %
1	6 - 50 individuals	≤ 5 %
2m	> 50 individuals	≤ 5 %
2a	very abundant	5 - 15 %
2b	very abundant	16 - 25 %
3	very abundant	25 - 50 %
4	very abundant	51 - 75 %
5	very abundant	76 - 100 %

Supplementary table S2: Output of the analysis of variance (ANOVA) of weed seed predation rate explained by year (2015, 2016, 2017), month (May, June, July, August, September) and farming type (conventional, organic, extensive farming) as well as their interactions. Weed seed predation rate was square root transformed prior to analysis. ns= not significant

explanatory variable	df	F value	p value
year	2	11.84	**<0.001**
month	4	9.48	**<0.001**
farming type	2	0.90	ns
year:month	4	11.95	**<0.001**
year:farming type	4	3.34	**0.01**
month:farming type	8	3.78	**<0.001**
year:month:farming type	8	1.53	ns

Supplementary table S3: Total species richness and mean species numbers of weeds (±SE) per relevée in 2015 – 2017 separated by farming type. Farming types are abbreviated: conventional farming (CF), organic farming (OF) and extensive farming (EF). Different letters show significant differences within rows according to Tukey HSD test ($p < 0.05$).

year	weed species diversity	CF	OF	EF	p value
2015	Total species richness	15	43	100	
	Mean species number of weeds	2.75 (±1.32) c	15.42 (±1.35) b	22.50 (±0.82) a	**<0.001**
2016	Total species richness	8	34	100	
	Mean species number of weeds	1.42 (±0.80) b	17.08 (±0.96) a	17.75 (±0.63) a	**<0.001**
2017	Total species richness	12	37	61	
	Mean species number of weeds	2.58 (±1.41) c	14.58 (±1.70) b	26.25 (±0.29) a	**<0.001**

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5. Weed Control Ability of Single Sown Cover Crops Compared to Species Mixtures

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Abstract: To achieve efficient weed control through cover cropping, the plant species chosen needs particular consideration. Combing different cover crop (CC) species in mixtures may increase the number of provided ecosystem services, including reliable suppression of weeds. We tested the weed suppression ability of single CC species and CC mixtures in a field trial during the autumn-to-winter growing season of 2016 and 2017. *Anethum graveolens* L. (dill), *Raphanus sativus* var. *oleiformis* Pers. (oilseed radish), *Avena strigosa* Schreb. (black oat), *Carthamus tinctorius* L. (safflower), *Vicia sativa* L. (vetch) and *Phacelia tanacetifolia* Benth. (phacelia) were sown in monocultures, as well as in mixtures with three or six species. Treatments with favorable establishment and above-average biomass yields tended to suppress weeds by showing lower weed dry matter and weed numbers. The highest weed control efficacy within the monocultures was reached in 2017 by black oat and oilseed radish with 72 and 83 %, respectively. The mixture treatments reached a generally lower soil cover, aboveground dry matter and weed control efficacy (with an average of 57 % in 2017). Even though mixtures were not as effective as the best performing single sown CCs, species combinations increased resilience against adverse weather conditions, an advantage to achieving efficient weed control over a long-term period. Therefore, species composition within mixtures is more relevant than the number of species included.

Keywords: biological; catch crop; plant diversity; weed management

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5.1. Introduction

The incorporation of cover crops (CCs) into crop rotations has become a practical strategy by producers. The European Union further promotes the use of CCs in agriculture by their "greening" strategy (EU Regulation 1307/2013). The increasing interest of producers and researchers in CCs might have been encouraged by the manifold positive aspects which are attributed to cover cropping. CCs are normally grown between two main crops to reduce erosion and to improve soil characteristics like nitrogen content, phosphor availability and soil structure (Hartwig & Ammon 2002). Additionally, they serve as a pollen and nectar source for pollinators and overwintering habitat for beneficials (Ellis & Barbercheck 2015, Dunbar *et al.* 2017). They also provide services that reduce pests, pathogens and weeds (Farooq *et al.* 2011, Fourie *et al.* 2016). CCs offer different temporal and spatial (niche) possibilities as well as physical and biochemical mechanisms to control weeds.

After sowing, CCs provide direct weed control during their establishment by releasing allelochemical compounds into the environment (Gfeller *et al.* 2018) and competing with weeds for light, water, nutrients and space (Blanco-Canqui *et al.* 2015). This can severely hamper the development of weeds (Brennan & Smith 2005) or even prevent them from emerging. Some cover crop (CC) species are able to survive the harsh conditions over winter and continue to provide this service in early spring. CCs are normally terminated by mechanical or chemical methods before sowing of the next main crop. In any case, CC residues are either incorporated into the soil or retained on the soil surface (Creamer *et al.* 1996). Under both strategies, plant residues continue to release the remaining allelochemicals that are contained in the dead plant material (Putnam *et al.* 1983, Tabaglio *et al.* 2013). If CC residues are left on the soil surface, they additionally act as a physical layer that small weed seedlings need to penetrate (Teasdale *et al.* 1991, Teasdale & Mohler 1993). This slows down the development of the weed populations in spring after the main crop has already been sown (Wayman *et al.* 2015). Therefore, CCs are able to affect weed populations from their sowing date until a certain time after the subsequent main crop is established (Falquet *et al.* 2015). Naturally, the weed suppressive ability of a CC depends on several environmental influences that determine, e.g., the level and activity of allelochemicals (Belz 2007), the speed of CC development and the build-up of biomass (Hiltbrunner *et al.* 2007). Under unfavorable conditions, a single sown CC might not be able to provide a sufficient level of weed suppression.

Crop stands of single CC species are not able to buffer rapidly changing environmental conditions. Therefore, many studies have investigated the adaptability of mixtures (Finckh *et al.* 2000, Tilman *et al.* 2001, Hajjar *et al.* 2008). Higher species diversity increases the likelihood that some of the species in a mixture are more productive, because they are better adapted to a certain set of environmental conditions (sampling effect) (Huston 1997, Tilman *et al.* 1997). The CC species *Vicia sativa* L. and *Phacelia tanacetifolia* Benth. were not germinating well under high temperatures, whereas *Guizotia abyssinica* (L.f.) Cass. performed well (Tribouillois *et al.* 2016). Combinations of contrasting species in regard to environmental conditions, therefore, might provide resilience to weather conditions and provide stability in their service provision. The conditions that drive CC species performance are also dependent on agronomic measures such as sowing date and termination method (Constantin *et al.* 2015). CC mixtures might not only be resilient to environmental conditions, but also to failures in the conductance of agronomic measures by the producer. One of the upcoming major challenges will be the handling of climate change and extreme weather events in agriculture (Stott *et al.* 2004) and the question of how to design appropriate CC mixtures to deal with them.

Additionally, more diverse mixtures host species that have different acquisition and competition strategies. The "niche complementarity" (MacArthur & Levins 1967) describes the actual function of a mixture based on the traits of the single species. The more diverse or different the setup of these traits for every single species within a mixture, the more likely it is that they occupy different niches and are more productive. CC species with different plant canopy features might intercept and use light more efficiently and therefore reduce the availability of light on the soil surface, leading to a reduced emergence of weeds. The unique root growth patterns and abilities to take up and mobilize nutrients in the soil by CC species in mixtures might be able to use nutrients more efficiently and consequently leave fewer resources for weeds (Abraham & Singh 1984, Tribouillois *et al.* 2015). Regarding weed suppressive abilities, cereal species are often more effective than legume species (Ofori & Stern 1987, Brainard *et al.* 2011, Baraibar *et al.* 2018), which makes the former preferable components of CC mixtures dedicated to controlling weeds while the latter can add value by fixing nitrogen. It might also be possible to combine CC species with predominant physical or biochemical effects to further enhance the weed control abilities of these mixtures. Poaceae and Brassicaceae species have proven to be allelopathic (Hartwig & Ammon 2002, Belz 2007), while others like vetch (*Vicia villosa* Roth) seem to act predominantly via competition (Inderjit 2001). As the weed control efficiency is dependent on both of these effects, the use of CC mixtures was already advised and examined by several authors (Kunz *et al.* 2016, Baraibar *et al.* 2018). One, yet unsolved, issue is how to separate between competition and biochemical effects and their contribution to weed control in the field (Tschuy *et al.* 2014, Sturm *et al.* 2018). Another important question is: which traits of CCs are affecting their level of weed control? The usual reasoning that higher biomass production leads to a higher competitive ability and therefore more efficient weed control (Teasdale 1996) might not hold true in all cases. Several recent studies reported no correlation between biomass and weed reduction (Kunz *et al.* 2016, Baraibar *et al.* 2018). There might be other or additional factors that may determine the level of weed control.

Sampling effect and niche complementarity have been examined well in natural plant communities (Tilman 1999, Hooper *et al.* 2005), but also to some extend for agricultural systems (Hector *et al.* 1999, Prieto *et al.* 2015). All these systems, natural and agricultural alike, perform ecosystem services based on the functions that the plants provide and these are often enhanced if species diversity is increased. A combination of the effects of species mixtures with the multiple advantages that CCs offer, can result in a very productive CC stand. This productivity does not normally lead to a harvest good, but might enhance the services provided by the CCs (Blesh 2018). How many CC species or which particular traits are necessary to ensure weed control is still under investigation (Wortman *et al.* 2012, Holmes *et al.* 2017, Finney & Kaye 2017, Baraibar *et al.* 2018). Ultimately, carefully designed species mixtures may be more stable in terms of weed control efficiency and reaction to changing weather conditions than single sown CCs, providing reassurance for the producer. Recognizing this great potential of CC mixtures along with the still scarce knowledge on service provision and reaction to climate, this study investigated the weed control ability of single sown CCs and CC mixtures in two very contrasting years. Within the study, the following hypotheses were investigated: i) CC dry matter does not determine the weed suppression ability; ii) mixtures have a better ability to suppress weeds in comparison to CC monocultures; iii) species-rich mixtures suppress weeds more efficiently than species-poor mixtures.

5.2. Materials and Methods

Experimental sites

The experimental field trials were conducted at the research station of the University of Hohenheim (48.74° N, 8.92° E, 475 m a.s.l.) in Southwest-Germany from August until December 2016 and 2017. After CC sowing in 2016 a long dry period followed. During the cover cropping season in 2017 the frequency and the amount of water provided ideal growing conditions for the CCs (Figure 5.1).

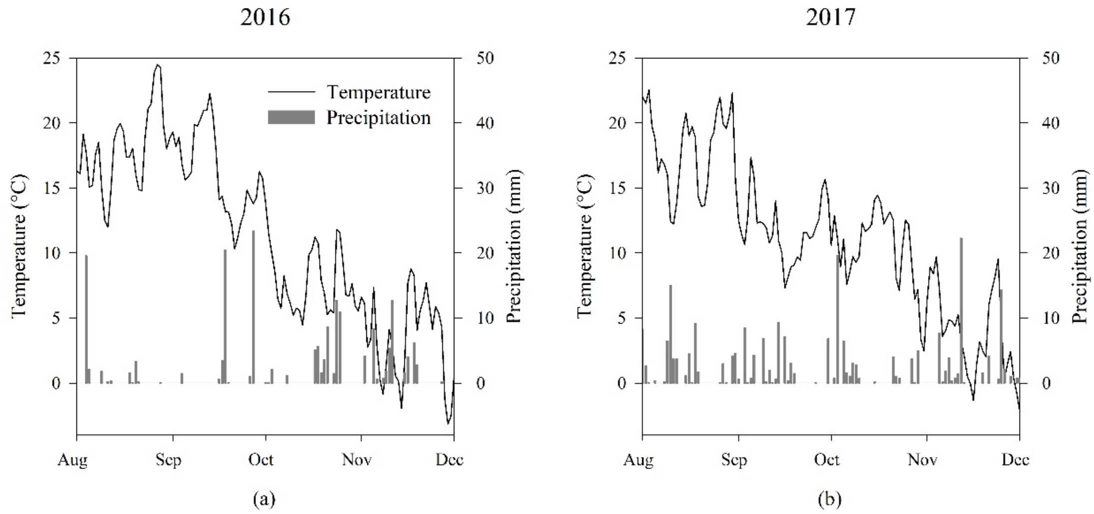

Figure 5.1 Temperature and precipitation from August to December 2016 (a) and 2017 (b).

The soil type at the field site during the season 2016 was classified as a silty clay (6% sand, 53% silt and 41% clay). During the 2017 season, the field site was classified as a silty loamy soil (27% sand, 48% silt and 25% clay). Table 5.1 shows details about the crop rotation and field preparations.

Table 5.1 Experimental set-up and conditions for the field trials in Southwest Germany in 2016 and 2017.

Management	2016	2017
Crop rotation	Winter wheat - cover crop	Winter barley - cover crop
Cereal harvest date	8 August 2016	5 August 2017
Soil preparation (depth)	Stubble cultivator + deep tillage (15 cm) + power harrow (6–8 cm)	Stubble cultivator + deep tillage (15 cm) + power harrow (6–8 cm)
Sowing date	19 August 2016	25 August 2017
Sowing depth	2 cm	2 cm

Six CCs (provided by Deutsche Saatveredelung AG (DSV)): *Anethum graveolens* L. (*A. graveolens*), *Raphanus sativus* var. *oleiformis* Pers. (*R. sativus*), *Avena strigosa* Schreb. (*A. strigosa*), *Carthamus tinctorius* L. (*C. tinctorius*), *Vicia sativa* L. (*V. sativa*) and *Phacelia tanacetifolia* Benth. (*P. tanacetifolia*) were sown in both years (Table 5.2) in monocultures and in five mixtures including the same species as for the monocropping treatments. The untreated control treatment was left as a weed fallow without CCs. The mixing ratios refer to the seed weight and recommend seeding densities as for the single sown CCs.

Table 5.2 Twelve treatments including an untreated control treatment without cover crops, six single sown cover crops and five cover crop mixtures.

Treatment	Crop species	Seed density (kg ha^{-1})
Control	Without cover crops	-
A. graveolens	Single sown *Anethum graveolens* L.	25
R. sativus	Single sown *Raphanus sativus* var. *oleiformis* Pers.	25
A. strigosa	Single sown *Avena strigosa* Schreb.	120
C. tinctorius	Single sown *Carthamus tinctorius* L.	40
V. sativa	Single sown *Vicia sativa* L.	100
P. tanacetifolia	Single sown *Phacelia tanacetifolia* Benth.	10
Mixture 1	Mixture with 33% *A. graveolens*, 33% *R. sativus*, 33% *A. strigosa*	57
Mixture 2	Mixture with 33% *P. tanacetifolia*, 33% *C. tinctorius*, 33% *V. sativa*	50
Mixture 3	50% Mixture 1, 50% Mixture 2	53
Mixture 4	20% Mixture 1, 80% Mixture 2	51
Mixture 5	80% Mixture 1, 20% Mixture 2	55

Data collection

Percent of soil coverage by CCs was estimated four times in a 0.1 m^2 area randomly selected in each plot. Soil coverage was recorded seven (2016) and four times (2017) after sowing until 12 weeks after sowing (WAS). Seven and 12 WAS the weed density and community were determined. Fresh matter of CCs and weeds was cut 7 and 12 WAS within an area of 0.25 m^2. The fresh matter was cleaned with water and afterwards placed in the oven at 100 °C for 24 hours to obtain biomass on a dry matter basis.

Data analysis

The data were analyzed with the software R (Version 3.5.1). Normal distribution and homogeneity of variance were visually checked before analyzing the data. Linear regression was used to test for correlations. A log data transformation, prior to using an analysis of variance (ANOVA), was necessary for the weed density (12 WAS 2017) data. Means of different treatments were compared using the Tukey-HSD test ($p \leq 0.05$). According to Rasmussen (1991), the weed control efficacy (WCE) based on the weed density was calculated as

$$\text{WCE (\%)} = 100 - wt\ (0.01 \times wc)^{-1}$$

whereby wt is the weed density (weeds m^{-2}) of the weed management treatments and wc the weed density (weeds m^{-2}) of the untreated control.

5.3. Results

Cover crop and weed development

At the beginning of the CC growing season in 2016, the *R. sativus* and *P. tanacetifolia* treatments displayed the highest soil cover among the single sown CCs (Figure 5.2). The *P. tanacetifolia* treatment had the highest soil cover (79%) during the beginning of November while *R. sativus* reached a maximum of 50% soil cover during this same period. In 2017, the *A. strigosa* and the *P. tanacetifolia* treatments reached the highest soil cover among all treatments with a maximum of 92 and 83%, respectively, in late November. The mixtures generally showed less soil cover than the best performing single sown CC treatments in both years. The soil cover of the mixtures was generally quite homogeneously distributed and ranged between 39–67 % (4 November) in 2016 and 68–79% (15 November) in 2017.

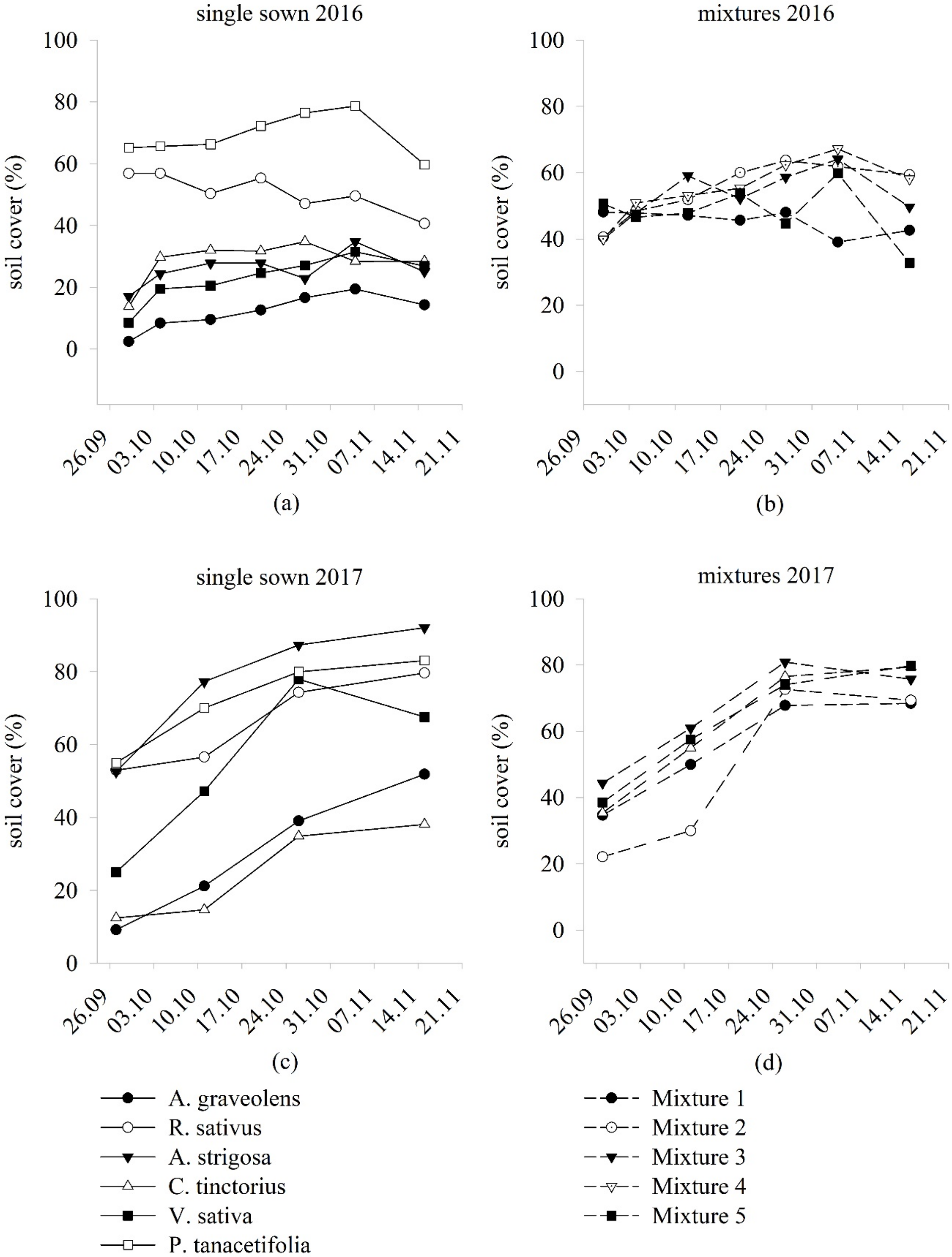

Figure 5.2 Cover crop soil cover (%) for the six single sown cover crops (a, c) and the five mixtures (b, d) from the end of September until the end of November in 2016 (a, b) and 2017 (c, d). Dates in the x-axis in the format dd.MM.

In both years, volunteer crops like *Brassica napus* L. (2016), *Triticum aestivum* L. (2016) and *Hordeum vulgare* L. (2017) belonged to the dominant weeds. Dicotyledonous weeds were the dominant weed species in addition to volunteer crops. In 2016, the dominant weed species were *Galium aparine* L., *Chenopodium album* L., *Veronica persica* Poir. and *Capsella bursa-pastoris* (L.) Medik.. In 2017, there was a broader species diversity, including species like *Matricaria spp*., *Lamium purpureum* L., *Capsella bursa-pastoris* (L.) Medik., *Veronica persica* Poir., *Stellaria media* Vill., *Chenopodium album* L. and *Cirsium arvense* (L.) Scop. The untreated control treatment in 2016 showed a mean weed infestation of 62.5 plants m^{-2} (Table 5.3). In 2017, the untreated control showed a 10-times higher (678.8 plants m^{-2} 12 WAS) weed density than in 2016. In 2016, the significantly lowest number of weeds was counted in the *R. sativus* (13.1 plants m^{-2}) and Mixture 4 (14.4 plants m^{-2}) treatments. In 2017, the significantly lowest number of weeds was observed in the *A. strigosa* treatment with 112.5 plants m^{-2}. Similarly, high weed densities as in the untreated control were counted in the *A. graveolens*, *C. tinctorius* and *V. sativa* treatments, which had shown a generally weak performance within the two years regarding CC soil cover and CC dry matter. There were no significant differences between any treatments concerning total weed density 7 WAS in 2017.

The weed densities 12 WAS in 2016 and 2017 showed a correlation with an R^2 of 0.58. The regression between those two parameters was significant (p = 0.004), which shows that the occurrence of weeds within the treatments was not random within both years.

Table 5.3 Total weed density for the six single sown and five cover crop mixtures 12 weeks after sowing in 2016 and 2017. Different capital letters within one column show significant differences according to Tukey-HSD test (p ≤ 0.05).

Treatments	Total weed density (plants m^{-2})	
	2016	**2017**
Control	62.5 ^{A}	678.8 ^{A}
A. graveolens	49.9 ^{AB}	433.8 ^{ABC}
R. sativus	13.1 ^{C}	196.6 ^{BC}
A. strigosa	29.4 ^{BC}	112.5 ^{C}
C. tinctorius	41.9 ^{ABC}	452.5 ^{ABC}
V. sativa	37.5 ^{ABC}	483.8 ^{AB}
P. tanacetifolia	20.0 ^{BC}	382.5 ^{ABC}
Mixture 1	30.0 ^{BC}	168.8 ^{BC}
Mixture 2	25.6 ^{BC}	370.0 ^{ABC}
Mixture 3	28.8 ^{BC}	326.3 ^{ABC}
Mixture 4	14.4 ^{C}	237.5 ^{ABC}
Mixture 5	27.5 ^{BC}	272.5 ^{ABC}

Due to the four weeks of drought after sowing in 2016, the CCs were only sparsely developed 7 WAS (Figure 5.3a). The *R. sativus* treatment reached the significantly highest aboveground dry matter (1210 kg ha^{-1}) 7 WAS in 2016. Except for the *A. graveolens* and Mixture 2 treatment, all treatments were able to significantly reduce the dry matter amount of weeds (7 WAS) compared to the untreated control. The generally low weed infestation and the poor growing conditions in 2016 season led to a maximum weed dry matter of 206 kg ha^{-1}.

None of the CC treatments were able to show a significantly lower weed dry matter than the untreated control 12 WAS in 2016 (Figure 5.3b). The *R. sativus* and *P. tanacetifolia* treatments reached the significantly highest amount of CC dry matter within the single sown species with

1626 and 2068 kg ha^{-1}, respectively. Among all treatments, Mixture 2 and 3 achieved with 2396 and 2350 kg ha^{-1} the highest amount of CC dry matter.

The amount of weed dry matter of the untreated control 7 WAS in 2017 was, with 467 kg ha^{-1}, almost twice as high as 7 WAS in 2016 (Figure 5.3c). Among the single sown CCs, only the treatments *R. sativus* and *A. strigosa*, with 1247 and 1450 kg ha^{-1} aboveground dry matter, respectively, were able to significantly reduce the amount of weed dry matter compared to the untreated control 7 WAS in 2017. Compared to the untreated control all mixtures, except for Mixture 2, significantly reduced the weed dry matter.

In 2017, the *P. tanacetifolia* treatment had the highest amount of CC dry matter with 2247 kg ha^{-1} but did not significantly reduce the amount of weed dry matter compared to the untreated control 12 WAS (Figure 5.3d). The treatment *A. strigosa* showed the lowest amount of weed dry matter with 97 kg ha^{-1} among all treatments and reached an aboveground dry matter of 2197 kg ha^{-1}. The mixtures, except for Mixture 4, were able to significantly reduce the dry matter of weeds compared to the untreated control, but showed generally lower numbers of CC dry matter compared to the previous year, reaching a maximum of 1674 kg ha^{-1} (Mixture 1).

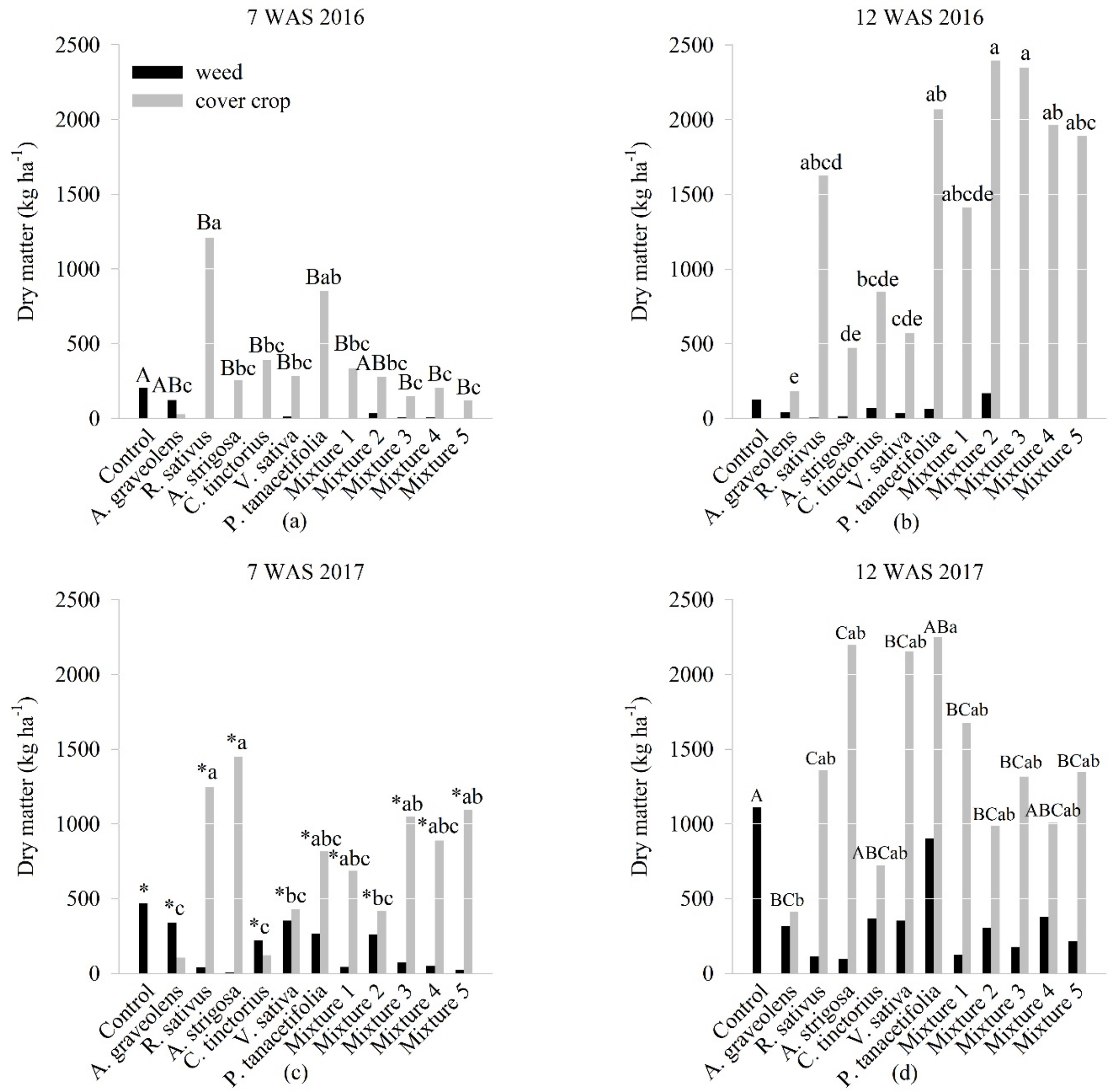

Figure 5.3 Cover crop (grey) and weed (black) aboveground dry matter in kg ha-1 for the six single sown and five cover crop mixtures 7 weeks after sowing (WAS) in 2016 (a) / 2017 (c) and 12 WAS in 2016 (b) / 2017 (d). Different small letters within one graph show significant differences concerning the cover crop dry matter according to Tukey-HSD test ($p \leq 0.05$). Different capital letters within one graph show significant differences concerning the weed dry matter according to Tukey-HSD test ($p \leq 0.05$). Means for weed dry matter with no capital letters do not differ significantly. * Due to space limitations in the graph (c): Control A, A. graveolens ABC, R. sativus BCD, A. strigosa D, C. tinctorius ABCD, V. sativa AB, P. tanacetifolia ABCD, Mixture 1 BCD, Mixture 2 ABCD, Mixture 3 BCD, Mixture 4 BCD, Mixture 5 CD.

Weed control efficacy

In 2016, among the mixtures, the highest WCE was reached 12 WAS by the Mixture 4 treatment with 47% (Figure 5.4). Across all treatments, the *R. sativus* treatment had the highest WCE with 60%. The highest WCE 12 WAS in 2017 among all treatments was reached by the *A. strigosa* treatment with 83% followed by the treatments Mixture 1 and *R. sativus* with 75% and 72%, respectively. The differences in WCE between the treatments were not significant in 2016 and 2017 (12 WAS).

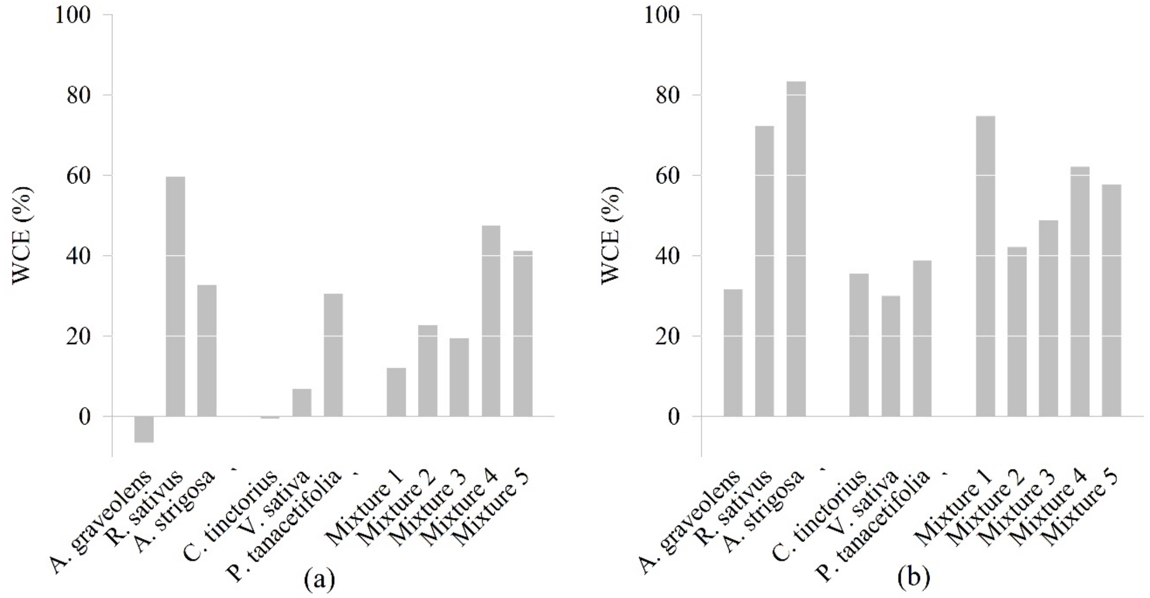

Figure 5.4 Weed control efficacy (WCE) of the six single sown and five cover crop mixtures 12 weeks after sowing in 2016 (a) and 2017 (b). Means with no letters do not differ significantly according to Tukey-HSD test ($p \leq 0.05$).

5.4. Discussion

The highest WCE within both years was achieved by the *A. strigosa* treatment with 83% (12 WAS in 2017). Brust and Gerhards (2012) showed a similarly high weed suppression ability of *A. strigosa* with 90%. CCs seem to be able to significantly reduce the number of weeds but have not shown complete weed control within this study due to a severe drought period after sowing in 2016 and the generally high weed infestation in the 2017 season.

As expected, the CC dry matter is not necessarily a predictor of the weed suppression ability. No correlations between CC biomass and weed dry matter/density were determined. This agrees with Kunz *et al.* (2016) and Baraibar *et al.* (2018) who also did not find correlations between CC dry matter and weed density. Finney *et al.* (2016) pointed out that biomass driven CCs do generally have a more effective weed suppression potential. However, it seems like this is only relevant to a certain extent. Gfeller *et al.* (2018) name the threshold of 3 t ha^{-1}, until which the CC biomass and the suppression of *Amaranthus retroflexus* L. were negatively correlated. Onwards, other parameters, like chemical or other physical parameters might have a higher importance to contribute to an efficient weed control. Within their study, also some CCs with low biomass yields, like Brassicaceae and *A. strigosa*, were able to achieve an efficient weed control against *Amaranthus retroflexus* L. (Gfeller *et al.* 2018). This agrees with the data presented for the season 2016, whereby the *A. strigosa* treatment reached a WCE of 33% (average WCE across all treatments: 24%), with a simultaneously low amount of dry matter. This might be attributed to the allelopathic potential of *A. strigosa* (Rueda-Ayala 2015, Gfeller *et al.* 2018). *R. sativus* was, within the experiment, one of the most efficient single sown CC, reaching an average WCE within the two seasons of 66% (12 WAS). *R. sativus* is able to reach weed suppression efficacies of more than 90% (Brust *et al.* 2014, Sturm *et al.* 2017) under ideal conditions and sowing dates. This is probably caused by the relatively high dry matter production (negative correlation between weed and brassica CC biomass (Baraibar *et al.* 2018) and the well-reported allelopathic potential of Brassicaceae species (Petersen *et al.* 2001, Haramoto & Gallandt 2005).

Additionally, Brennan and Smith (2005) and Dorn *et al.* (2015) suggest that rapid plant development after sowing is more important than the final CC biomass (Baraibar *et al.* 2018). For some examples, these results can be referred to the data presented. In late September 2017, the treatments *R. sativus*, *A. strigosa* and *P. tanacetifolia* showed the highest soil cover with 52–55%. Both, the *R. sativus* and the *A. strigosa* treatment achieved the highest WCE among the single sown CCs with 72% and 83%, respectively. In contrast, the *P. tanacetifolia* treatment, even though biomass and soil cover were well developed, performed as poorly as the very weak established treatments *A. graveolens* and *C. tinctorius* with less than 13% of soil cover.

The mixtures were not more efficient at suppressing weeds than the monocultures, which agrees with several studies (Brust *et al.* 2014, Smith *et al.* 2014, Finney *et al.* 2016, Baraibar *et al.* 2018). The most efficient single sown CCs showed a higher suppression ability than the most efficient mixture in both years, which is also shown by Smith *et al.* (2014). According to Baraibar *et al.* (2018), CC mixtures containing grasses are more efficient to suppress weeds than monocultures with Brassicaceae species or legumes. Within both years, all mixtures were clearly more efficient at suppressing weeds than *V. sativa*. This can be inferred from the studies of Baraibar *et al.* (2018) and Hayden *et al.* (2012), who conclude that CCs with early canopy closing, to which vetch does not belong, generally show better weed suppression. In 2016, the *R. sativus* treatment reached the highest WCE with 60%, while in 2017 the Mixture 1 and the *R. sativus* treatment showed a similar WCE of 75% and 72%, respectively. All other mixtures only reached a WCE between 42% and 62%. Finney *et al.* (2016) state as a reason that highly productive single sown CCs may produce as much biomass as diverse species mixtures. In October 2016 and 2017, particularly the single sown treatments like *R. sativus* and *P. tanacetifolia* were achieving higher dry matter yields than the mixtures. However, as discussed, the biomass of CC monocultures and mixtures is not, or only weakly, related to the weed suppression potential. Generally, species-specific mechanisms for weed suppression are still not well understood. How different mechanisms of weed suppression act or interact also need further investigation (Baraibar *et al.* 2018). Even though mixtures might not be an improved tool for weed management in cover cropping systems, many other benefits are attributed to CC mixtures. In consideration of the dry matter, soil cover and the reduction of weeds during the 2016 season, the mixtures showed the ability to withstand unfavorable weather conditions better than many of the single sown CCs. The resilience of mixtures towards severe weather conditions or management errors (Wortman *et al.* 2012), might compensate their less efficient weed control compared to monocultures. However, only high crop densities are an effective tool for weed suppression (Weiner *et al.* 2010). As species mixtures follow the idea to be able to buffer the failure of other species, increasing the sowing density of all species included in the mixture should be considered. This might be relevant in order to achieve similar crop stands under unfavorable conditions than within well-performing single sown treatments, resulting in an improved weed suppression potential.

The six species mixtures (Mixture 3–5) did not show a more efficient weed suppression potential than the three species mixtures (Mixture 1–2). As demonstrated by Kunz *et al.* (2017), a five species mixture was not better than a mixture with seven species in terms of weed control. This leads to the conclusion that the quantity of plant species within a mixture is less relevant than the mixture composition. Brassicaceae and Poaceae species, for example, respond well to dry conditions, while Fabaceae species do not (Tribouillois *et al.* 2016). Mixture 1, with *R. sativus*, *A. strigosa* and A. *graveolens* showed the best weed control performance and was able to significantly reduce the weed density in both years compared to the control. Baraibar *et al.* (2018) concluded that a high proportion of grass species achieves a large reduction of weed biomass, as grass species are also highly suppressive in monocultures.

Mixtures with an increasing proportion of rye were able to decrease the weed biomass as observed by Akemo *et al.* (2000). This might be the reason why Mixture 1 with the highest proportion of *A. strigosa* performed best, while Mixture 2, as the only mixture without grass species, showed a comparably slow soil cover and weak WCE in 2017. Mixture 3–5 with different proportions of *A. strigosa* showed a reliable establishment and an adequate weed suppression ability. Sufficient weed control might already be provided by low proportions of grass species within mixtures, meanwhile other species may fulfill important ecosystem services (Baraibar *et al.* 2018).

5.5. Conclusions

Out of the two years of data presented, *R. sativus* and *A. strigosa* are the two most promising single sown CCs, because they showed a fast establishment along with the highest weed suppression potential. In order to fulfill the requirements of diverse ecosystem services and weed control, CC mixtures like Mixture 1 seem to be suitable for cover cropping. In general, mixtures need to be composed reasonably in order to avoid weed problems caused by poorly competitive species (McLaren *et al.* 2019). Combing CC species with physical and chemical weed suppression mechanisms may increase the weed control success. Species with chemical mechanisms thereby, for example, contribute to an efficient weed control under unfavorable circumstances when CC development and biomass yield is low. CC mixtures might substantially contribute to the success of biological weed control if the weed suppression mechanisms of different plant species and their ideal composition within mixtures can be identified.

5.6. Acknowledgments

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6. General Discussion and future perspectives

In this chapter, the main results of the preceding chapters are accentuated and discussed in a general overview of the thesis. The presented research papers have contributed knowledge to species conservation known as the A to B (agriculture contributes to biodiversity) approach and gained insights into the B to A (biodiversity important for agriculture) approach (Bàrberi *et al.* 2010) by examining weed seed predation. Moreover, the general principles underlying B to A were transferred to enhance weed control by cover crop mixtures. The results obtained in this work are helpful to further optimize conservation effectiveness and weed control strategies and to understand interdependencies between farming practice, plant biodiversity and ecosystem service provision. Insights into current and future challenges and opportunities for the examined topics are given as well as potential future research topics.

Political background and basics

"Biodiversity" is currently a very popular term used in politics and has raised public awareness for species conservation. We currently are in the "United Nations Decade on Biodiversity", which runs from 2011 to 2020 and aims at implementing the strategic plan for biodiversity set by the Aichi biodiversity targets (CBD 2019). These targets include, among others, raising public awareness on the topic of biodiversity, reducing the pressure on biodiversity while simultaneously promoting its sustainable use and enhancing the benefits from biodiversity and ecosystem services. In Germany, the "Nationale Strategie zur Biologischen Vielfalt" (NBS) was passed by the Federal Government in 2007 in accordance to their commitment at the "Convention on Biological Diversity" (CBD) in 1993 to achieve the Aichi goals (CBD 2019). Actual implementations are conservation of endemic species, payments for ecosystem services and promotion of biological "hotspot regions" (BMUB 2007). Although conservation measures are predominantly aiming at vertebrate and invertebrate species, plants play a major role in supporting biodiversity, as they represent the basis of the food chain in terrestrial ecosystems (Power *et al.* 1992, Scherber *et al.* 2010). This connection is especially affected in ecosystems that are characterized by a high amount of disturbances such as agroecosystems (Evans *et al.* 2011). There, the primary producers, that are the foundation of food webs, are, along with the crop, weeds. As weeds exist in highly disturbed ecosystems, weed biodiversity *per se* and any ecosystem service directly or indirectly provided by them, is affected by agricultural management practices (Petit *et al.* 2011).

Status quo: Rare weed species and biodiversity of weed communities

The form and intensity of agricultural practices have severely changed during the last decades, impacting particular weed species negatively and driving some of them to the brink of extinction (Meyer *et al.* 2013). Currently 20% of all endemic plant species, including weeds, are on the red list of vascular plants in Germany (Ludwig & Schnittler 1996). This list was last updated in 1996, but is currently revised and will most likely reveal a higher number of species in need of conservation (personal communication Stefan Meyer, University of Göttingen). In the course of a decline in spatial and temporal occurrence of particular species, a reduction in population sizes is inevitable and subsequent genetic erosion is the consequence (Brütting *et al.* 2012). This in turn leads to further susceptibility to environmental and management disturbances. Not only particular species are affected, but also weed communities, once quite diverse, have undergone a major structural change along with the loss of multiple species due to the trends in agricultural intensification (Storkey *et al.* 2012). Nowadays weed communities in Germany are often quite uniform within the major crops and dominated by a few competitive weed species (Waldhardt *et al.* 2003, Meyer *et al.* 2013).

To prevent a further decline, the conservation of weed species diversity in general and endangered weed species (EWS) in particular is of paramount importance to conserve the associated food webs and animals of higher orders (Scherber *et al.* 2010, Marshall *et al.* 2003). Furthermore, several positive aspects are provided by weeds. Attracting beneficial insects to enhance biological pest control (Atakan 2010 and see Chapter IV) or utilizing potential genes to breed crops that are more resilient to extreme environmental conditions (Moonen & Bàrberi 2008) are just some of them. In order to put conservation efforts into action effectively, the key drivers behind weed biodiversity and occurrence of weed species need to be identified and understood.

6.1. Weed communities and endangered weed species (EWS)

In Chapter III we examined the effects of farming practice on weed biodiversity, EWS and weed community composition. Using multivariate statistic procedures on vegetation and management data of On-farm experiments in Southwestern Germany, we were able to determine major factors affecting weed biodiversity and community composition. Among these factors crop species, herbicide use, nitrogen fertilization as well as tillage operations had the highest influence on the weed community and in parts also on weed biodiversity. Moreover, weed biodiversity was significantly higher in field margins compared to the field center and increased with an increasing amount of light at the soil level. These findings were in line with several authors and highlighted the overall decline of weed species diversity and the subsequent simplification of weed communities. Particular factors influencing the EWS *Bromus grossus* and its descendant *Bromus secalinus* were, clay content in the soil, location in the field and the timing of herbicide application. Additionally, we presume that these two EWS only occurred because herbicides with effectivity gaps against *Bromus* species were used.

By utilizing the knowledge about driving factors in community composition, it is possible to adjust farming techniques to enhance biodiversity and EWS conservation. Moreover, if integrated into mechanistic models, predictions about weed pressure and the occurrence of problematic species are possible (González-Díaz *et al.* 2015) and can aid in adapting farming strategies accordingly.

Farming strategies in weed conservation

Weeds have co-evolved with the crop plant and are thus adapted to specific disturbances exerted by farming (management) within particular crops (Firbank 1988). Executing management practices is therefore of paramount importance for the conservation of EWS. Conservation strategies often comprise less fertilization and omitted pest control practices, lowering the competitiveness of the crop and reflecting farming strategies of the mid 20th century (Schumacher 1980, Albrecht 2003). The same recommendations, of reduced nitrogen fertilization and seeding rate, as well as a reduction in herbicide input, were deduced from Chapter III. Although these conservation measures are often effective, they are simultaneously time-limited. Therefore, we are currently studying weed communities and the occurrence of particular EWS in agricultural fields along a temporal conservation gradient. The methods are the same as applied in Chapter III. Vegetation recordings document the development of the weed flora in specific time intervals since the withdrawal of subsidies from conservation fields. This is based on a preliminary study (Schumacher *et al.* 2018) that indicated a rapid conversion of former conservation field flora to similar communities as in conventional fields. A reduction of weed diversity and loss of EWS were recorded in this conversion process. A comparable trend is discussed in Chapter III, where the majority of EWS populations were found to consist only of a small number of individuals. As this is not the goal of conservation efforts, more permanent conservation solutions should be pursued.

Factors for successful conservation

From the view of a conservation biologist, three prerequisites have to be fulfilled to ensure the conservation of species (Haddad 2019). At first, knowledge on the biology of species is crucial to understand the basic requirements of habitat factors, the competitive ability and vulnerable stages in the life cycle. Secondly, adequate habitat disturbances need to be identified and applied. Finally, the conservation habitats should be connected to ensure migration of individuals or propagules in order to achieve genetic exchange between populations. Experiments conducted in Chapter III contributed knowledge for the first and second point for the conservation of *Bromus grossus*.

From personal experience and communication with farmers during the experiments in Chapters III and IV, we can additionally derive two more prerequisites, namely economic and social/psychological aspects, for the implementation of conservation. Although there are several sources of money for agri-environmental schemes, ranging from EU to national to the federal state level, farmers are often cautious about applying (Gatto *et al.* 2019). Farmers sometimes view these contracts as a burden and are anxious about unfair sanctions. If the farmer is granted a fair amount of money along with a certain degree of management freedom or has good guidance by nature conservation authorities, the conservation projects are more likely to come into existence and to be continued.

Precision farming technology

A set of novel and proven techniques in farming is available to take further steps in targeted conservation of species and biodiversity in every farming system. Novel techniques involve the use of precision agriculture tools, such as sensor-based (Peteinatos *et al.* 2014) and neural-network evaluated recognition of individual weed plants along with site-specific adjustments of weed control implements (Gerhards & Christensen 2003). Although weed recognition is currently not precise enough to identify all weed species, the recent development of neural networks and deep learning promises a big leap forward in this regard (dos Santos Ferreira *et al.* 2019, Yu *et al.* 2019). This precision farming technique holds great potential to identify EWS in the field and spare them from weed control measures. In the future, it may be possible to utilize unmanned aerial vehicles (UAVs) in an offline procedure to map the weed vegetation before actually driving into the field and setting specific species-related thresholds (Mink *et al.* 2018). That way, one might reduce weed abundance to a level below the economic threshold while protecting weed species richness and EWS.

Field margin strips

Field margin strips are a quite common method in EWS and biodiversity conservation (Marshall & Moonen 2002, Holland *et al.* 2016). The results of the study presented in Chapter III showed significantly higher weed biodiversity and occurrence of EWS in field margins compared to the center of the field. In field margins, species, plants and animals alike, are able to migrate from semi-natural or natural habitats to agricultural production areas. As they represent transition areas, species occurrence and abundance are also influenced by landscape structure and connectivity of these habitat types (Marshall & Moonen 2002). Moreover, pest control, fertilization and sowing are often not as accurately achieved as in the field center. This makes margins a habitat with less intense disturbance and competition by the crop. Field margins have also been studied in relation to beneficial insect promotion (Thomas & Marshall 1999). Especially diversity and abundance of pollinators and Carabid beetles increase at the field margin (Fusser *et al.* 2018). Cover by weeds (Heggenstaller *et al.* 2006, Blubaugh *et al.* 2011) and increased or continuous food availability (Diehl *et al.* 2012, Schellhorn *et al.* 2015) and diversity might be attracting factors for beneficial species. Moreover, ecosystem services such as pollination, reduced run-off and biological pest control can emanate from field margins (Olson & Wäckers 2007, Nicholls & Altieri 2013) and extend into the field. Taking all these aspects together, field margins are destined to serve as a conservation measure.

Combining technology and agroecology

The combination of precision agriculture with conservation strategies holds a great potential to expand and connect habitats of EWS at field margins and within the field. If applied to a larger scale, it aids in connecting habitats of species to ensure genetic exchange. This melt might be particularly important as the current trend in agricultural structure is for larger fields and more area per producer. This in turn means fewer margins, but simultaneously a more intense reliance on technology. The landscape level plays a crucial role in biodiversity research as it determines the dimension of habitats and thus connections for exchange of species or propagules (Tambosi *et al.* 2014). Also, environmental conditions like drought periods, altered vegetation periods and occurrence of frost events during winter can affect species on all trophic levels quite considerably. The combination of agroecology with technology can lead to a more sustainable weed management strategy that ensures resilience against weed adaptation, weed invasions and climate change (Neve *et al.* 2018). The utilization and implementation of precision agriculture in field margin management for species conservation gains even more in importance when considering challenges like climate change and food security ahead.

6.2. Weed diversity, Carabid beetles and weed seed predation

The positive effects of increased weed diversity along with less agricultural input at field margins might also enhance weed seed predation as presented in Chapter IV. With the help of seed cards and exclosure cages we measured weed seed predation (WSP) along a farming intensity gradient and simultaneously assessed the weed vegetation and Carabid beetle community. This study aimed to find connections between weed biodiversity and the ecosystem service of WSP mediated by Carabid beetles as well as to evaluate the role of agricultural intensity in this context. A positive correlation between weed biodiversity and Carabid beetle diversity was discovered along with a pattern indicating highest weed seed removal by a medium diversity of Carabid beetles (2-8 species). However, there was no evidence for a direct connection between weed biodiversity and WSP. Farming intensity did not affect WSP consistently, but weed diversity and Carabid beetle community composition. Omnivorous Carabid beetles were the most abundant species and especially dominated the communities of conventional fields, while granivorous species were more abundant in extensive fields. We determined that WSP was more affected by year and particular farming practices like presumably cover cropping, than by farming intensity itself. Diversity of weed species and Carabid beetles was on the other hand tendentially higher in extensive compared to intensive farming strategies. Weed diversity is important to support the food web in agroecosystems and also the subsequent ecosystem service provision. Management strategies that comprise cover cropping (Shearin *et al.* 2008, Ward *et al.* 2011) and facilitate weed biodiversity (Saska *et al.* 2014), can hence substantially contribute to natural pest control.

Improving weed seed predation

The service of WSP is performed by a spectrum of different species from different taxa, like beetles (Kulkarni *et al.* 2015), crickets (White *et al.* 2007), ants (Westerman *et al.* 2012, Torra *et al.* 2016), slugs, mice (Daedlow *et al.* 2014) and birds (Holmes & Froud-Williams 2005). When examining the effects of farming on WSP, these species might be affected by particular management operations quite differently. Beetles can, for instance, be severely disturbed by tillage operations (Blubaugh & Kaplan 2015), while birds might not be affected at all. Beside management practices, seed predators and their WSP performance are influenced by environmental conditions (Saska *et al.* 2010), landscape characteristics (Labruyere *et al.* 2016) and food distribution (Daedlow *et al.* 2014). It is therefore difficult to predict the influence of single factors (like management operations) on the performance of WSP, especially if weed seeds are consumed by several different species simultaneously.

However, there are two major factors that can be used to improve weed seed predation. At first, all weed seed predators, irrespective of their taxa, rely in parts or entirely on weed seeds in their diet (Saska *et al.* 2014, Kulkarni *et al.* 2016). Increasing weed diversity, for example by methods described earlier in this chapter or the previous ones, also increases food resource diversity and availability for seed predators. This has most likely a positive effect on WSP by sustaining a larger spectrum and abundance of weed seed predators (Harvey *et al.* 2008, Scherber *et al.* 2010). The second factor is the availability of cover. Especially Carabid beetles, but also mice respond positively to plant cover (Meiss *et al.* 2010, Navntoft *et al.* 2016). By providing cover, for example by a denser weed vegetation (Heggenstaller *et al.* 2006, Kulkarni *et al.* 2017) in field margin strips or by sowing living mulches (Davis & Liebman 2003) and cover crops (Blubaugh *et al.* 2016), it may be possible to attract or retain seed predators in the field. Both approaches might be viable to improve WSP in the field, however also disservices, like crop seed consumption, can arise from unspecific facilitation of insect or vertebrate groups (Tschumi *et al.* 2018).

We examine in a current study, that is not included in this dissertation, the combination of these two major factors. In a field experiment, several cover crops and living mulches are sown in non-tilled and tilled plots to determine the influence of weed seed availability on the soil surface and the provision of plant cover on WSP and weed emergence after cereal harvest. Preliminary results indicate that living mulches are able to keep the WSP rates at a level similar to pre-harvest of the cereals. We aim to derive recommendations for farmers with this study to improve biological weed control via WSP and cover crops.

6.3. Weed suppression ability of cover crops and species mixtures

A range of positive aspects and ecosystem services is attributed to cover crops, such as reduced erosion and N leaching, promotion of pollinators and weed control. The use of mixtures in cover cropping, is currently facilitated by the European Union's "greening" strategy. The combination of different species in mixtures might increase the number of provided services and their resilience towards external influences. According to the underlying ecological principles and results of Chapter IV, we examined six single sown cover crops and created species mixtures to test their effects on weed control efficacy and reliability in Chapter V. Cover crop mixtures contained either three or six species in varying proportions.

Single sown *Raphanus sativus* var. *oleiformis* (oilseed radish) and *Avena strigosa* (black oat) were the most efficient species in terms of density and dry matter reduction of weeds. In general, cover crop mixtures reached a lower soil cover, dry matter and weed control efficacy compared to the two before mentioned single sown species. Nevertheless, weed control was performed more reliable by mixtures than by single sown cover crops, albeit not always as effective. The cover crop mixtures performed much more homogeneous in terms of soil cover, dry matter and weed control efficacy than the single sown cover crop species. This indicates an increased resilience of species mixtures towards adverse weather conditions and is an advantage for long-term weed control. However, cover crop diversity *per se* was in this study not related to the efficacy of weed control, we presume that species composition within the mixtures had a much bigger influence on service provision.

Florence *et al.* (2018) argued that productive single sown cover crops are also very productive in cover crop mixtures. A logical choice for cover crop mixtures, according to the results of Chapter IV, would therefore be *A. strigosa* or *R. sativus*. Increasing the proportion of *Poaceae* species in a mixture was found to enhance weed control efficacy (Baraibar *et al.* 2018, McLaren *et al.* 2018). This concurs with the contrasting performances of the highly weed suppressive mixture 1 that contained *A. strigosa* and mixture 2 without it, which exhibited also a high dry matter production but a significantly lower weed control efficacy. Likewise, ecosystem functioning in natural ecosystems largely depends on a certain number of dominant species, while the subordinate species do not greatly contribute to the actual functioning (Schwartz *et al.* 2000). Their importance, however, might increase if environmental conditions change (Muillot *et al.* 2013, Grime 1998). If dominant species fail to provide a particular function, their role can be taken over by functionally redundant species. This is called "risk spreading" (MacArthur 1955) or "insurance hypothesis" (Yachi & Loreau 1999). To gain stable performance of an ecosystem service thus requires a set of species providing the same ecosystem service (effect trait) but differing in their response to environmental conditions (response trait) (Lavorel & Garnier 2002).

Functional biodiversity

In Chapters III and IV we focused predominantly on the community level of Carabid beetles and weeds and their response to farming practices. As already indicated in Chapter II, the knowledge of effect traits of weeds is so far limited to the provision of floral resources (Gaba *et al.* 2017). The use of response- and effect-traits from functional biodiversity might therefore reveal more details about weed community composition and its connection to the provision of ecosystem services (Bàrberi *et al.* 2018). If applied to Chapter IV, seed size, seed coat thickness and number of seeds available could be effect traits of the different weed species impacting Carabid beetle diversity or their WSP performance. The results from Chapter III could be re-evaluated with a functional approach as well (Storkey *et al.* 2013).

In Chapter V pure cover crop stands and cover crop mixtures were analysed exclusively regarding their effect traits like soil cover, biomass production and weed density reduction. However, weed control ability can arise from several more effects like early emergence, time of canopy closure and level of produced allelochemicals, which in turn are also a response to environmental conditions (Belz *et al.* 2007). In general, species-specific mechanisms for weed suppression and their interactions are still not well understood (Baraibar *et al.* 2018). We presumed for example in Chapter V that weed suppression of *R. sativus* was mainly due to high biomass production, while *A. strigosa* acted predominantly via allelopathy. However, both species are able to produce a large amount of biomass and are said to be allelopathic. The predominant weed control mechanism exerted by a species might therefore be dependent on their response to environmental conditions. Applying the concepts of functional ecology to investigate the connection of response and effect traits of single species might aid in designing cover crop mixtures (Blesh 2018) with enhanced weed control abilities. To gain reliable weed control, mixture composers should furthermore take into account the "insurance hypothesis" and utilize functionally redundant species that differ in environmental responses. This partially validates the conclusion from Chapter V that species composition of cover crop mixtures is more important than species numbers alone. Also, Finney and Kaye (2017) found that functional diversity was a much better predictor of multifunctionality in cover crops than species richness. Cover crops are not exclusively grown to suppress weeds, but to reduce erosion and retain nitrogen. Focusing on one aspect, like weed control might compromise other important services. Mixtures should therefore be designed carefully to increase their productivity and ecosystem service provision.

In a current study, which is not included in this dissertation, we examine the effect and response traits of ten single sown cover crops and several mixtures arising from this species pool. The aim is to evaluate the resilience and flexibility of the species in mixtures in comparison to their single sown counterparts in response to weather conditions. Furthermore, their effects on weed control and the subsequent yield of the spring crop are determined. We hope to identify traits (and species) that are complementary in mixtures and provide successful weed control under a range of weather conditions.

6.4. Future challenges

Climate change

Especially EWS exhibit traits that morphologically explain their vulnerability to intensive management, such as large seeds, late flowering and short growth, commonly regarded as "rare weed trait syndrome". Atop of that, they are more prone to changes in weather conditions such as more frequent drought events and higher temperatures (Rühl *et al.* 2015, Rühl *et al.* 2016). The currently projected climate scenarios for Europe under climate change (IPCC 2015), may, therefore, affect the already small EWS populations dramatically. As a consequence, species decline will continue or even accelerate in the future. An even bigger issue is the invasion of weed communities by new, competitive weed species due to shifted temperature contour lines (isotherms) (Zhu *et al.* 2007, Sheppard *et al.* 2014). The removal of weed species by agricultural measures or weather conditions results in open niches (or niche gaps) (Erikson 2013), creating opportunities for invaders. In diverse weed communities these gaps can be filled by species from the species pool (Booth and Swanton 2002), while in species-poor communities this might not be the case (Rejmanek 1989). The latter are therefore more prone to invasion. There is already an indication that the current weed communities have changed in regard to temperature by higher abundances of weeds that are adapted to warm and dry summers (Peters *et al.* 2014). Invasive species often outcompete native species and are able to trigger huge changes in biodiversity by altering the original food webs of agroecosystems (Froud-Williams 1997) not to mention their severe influence on crop yield (Vilà *et al.* 2004).

Also, arthropod pest species are promoted by increased mean temperature and prolonged vegetation period. Some species might even be able to complete several life cycles instead of only one, thereby increasing the pest pressure on the crop (Delgado *et al.* 2011). In contrast, a diverse weed community might also help to mitigate negative effects of climate change by hosting beneficial insect populations that are tolerant to extreme weather conditions.

However, increased pest pressure will most likely lead to heavy use of insecticides, affecting Carabid beetles and their performance of WSP as well as other beneficial insects and their provided ecosystem services negatively (Biondi *et al.* 2012). As extreme weather events will be more likely, cover cropping needs to be adapted to changing weather conditions. It might therefore be reasonable to combine species that are effectively suppressing weeds under dry and moist conditions. Moreover, agronomic measures like sowing date and technique can be used to improve cover crop establishment (Sturm *et al.* 2017).

Food production vs. conservation

As the majority of agricultural land within countries is normally utilized to produce food, the trade-off between food production and species conservation creates an area of conflict. Especially the conservation of weeds is a controversial issue. On the one hand, they affect crop yield quantity and quality severely (Oerke 2006). On the other hand, they support higher-order diversity and can provide positive services that enhance crop productivity such as pollination (Carvalheiro *et al.* 2011). As mentioned earlier, conservation methods rely to a large extent on omitting pesticides and fertilizer inputs, thus reducing the potential productivity of the crop. The cropping of plants for bioenergy purposes further intensifies this issue, as agricultural production areas have to fulfill three potential assignments. Let alone the increasing area requirements for infrastructure, settlements and renewable energy. The last issue creates further area consumption as construction projects need to have functional compensation areas that often use agricultural land.

We already hypothesized that precision farming technologies are able to create more suitable habitats for weeds while supporting the crop more precisely. In combination with field margin conservation strategies, this might lead to a better habitat connection and partially alleviates the pressure on food production. To enhance weed diversity and overall biodiversity of agro-ecosystems, we need to re-evaluate and adjust our current cropping systems. The desired solution would be systems that manage the weed vegetation in a way that diversity is maximized while weed abundance is reduced below the economic thresholds. Many ideas have been proposed to serve this ideal. Intercropping to create niches for endangered weed species (Brooker *et al.* 2016) and the use of crop cultivar mixtures are just some examples. Others propose solutions that target the landscape scale instead of the farm scale (Holt *et al.* 2016).

To reduce the adverse effects of pesticides on species and other ecosystems is probably one of the most obvious steps that needs to be taken. In Germany, the "Nationale Aktionsplan Pflanzenschutz" (BMEL 2013) that was set up in 2013 is dealing with the legal implementation of this step. The concept to use herbicides as a last possible measure if all other options cannot reduce the weed pressure is quite old and comprised in the Integrated Weed Management (IWM) concept. However, the low costs for herbicides, or pesticides in general, compared to other control measures, led to an intensive use that created resistance problems along the way (Heap 2014). Finally utilizing the knowledge of ecological weed management principles (Bastiaans *et al.* 2008) and the "many little hammers" approach (Liebman & Gallandt 1997) would help to manage the weed vegetation more sustainably without the use of herbicides. Besides legal regulations to reduce herbicide use, financial incentives are provided for farmers to implement agri-environmental schemes. These schemes entail conservation of particular species (Aavik & Liiraa 2009) up to species diversity *per se* (Ulber *et al.* 2009).

6.5. Conclusion

Many concepts are available to adjust cropping systems in order to enhance biodiversity in agroecosystems and to conserve EWS. This chapter highlighted approaches such as the combination of precision agriculture technology with conservation strategies or the utilization of functional biodiversity for future research. However, to find a balance between the necessity of weed control to ensure food production and the conservation of weed diversity remains a challenge. Deliberately integrating weed biodiversity into agricultural production systems in order to utilize the ecosystem services provided by weeds, might be a first step to reconcile these contrasting positions. Identifying weed species with functional traits that facilitate ecosystem services while being weak competitors for the crop, is still an ongoing research goal. Promoting biodiversity, either of weeds or cover crops, through suitable management decisions, might even enhance WSP and weed control. Designing the landscape to include more semi-natural habitats and to increase connectivity will help to increase biodiversity in agroecosystems and on the landscape level (Landis 2017). To realize these steps, farmers, nature conservation authorities, landscape architects and policy makers must act together to develop practical and sustainable solutions. This serves to create more diverse agroecosystems, utilize provided ecosystem services and to reach some of the Aichi biodiversity targets. How climate change will impact weed community compositions, their diversity and provided services in the future, remains to be seen. Most likely arable farming systems will need to evolve to mitigate the effects of adverse weather conditions by creating more resilient and sustainable crop production strategies.

6.6. References

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7. Summary

7.1. Abstract

In terrestrial ecosystems plants represent the basis of food webs and provide important ecosystem services. There is evidence that diverse plant communities are either more stable or more productive in terms of food web support and ecosystem service provision. In agro-ecosystems, characterized by high disturbance and external inputs, plant diversity and their services can only be provided by weeds. Weeds, however, are a major constraint for crop production and need to be managed in order to produce adequate yield quality and quantity. Conserving weeds and biodiversity on the other hand means conserving food webs and utilizing the potential of ecosystem services including weed control. The current study comprises three experiments focusing mainly on the interactions between farming management factors, plant diversity and weed control related ecosystem service provision in agroecosystems.

In the first study, vegetation recordings and farmer surveys were conducted in on-farm experiments in two regions of Southwestern Germany. The aim was to examine the effects of agricultural management on weed community composition, weed biodiversity and occurrence of rare arable weed species in cereal fields. Weed biodiversity was influenced mainly by crop species, herbicide use and farming system as well as nitrogen and light availability. Moreover, field margins exhibited a higher diversity than the center of fields. Weed communities were quite similar in both study regions and dominated by *Alopecurus myosuroides*, *Galium aparine*, *Viola arvensis*, *Polygonum convolvulus* and *Veronica persica*. A redundancy analysis revealed that the weed community was mainly shaped by crop species, tillage, location in the field and timing of herbicide application. The dominating weed species were furthermore positively affected by medium to high nitrogen fertilization and a low number of tillage operations. The only rare arable weed species occurring in sufficient number for analysis were *Bromus grossus* and *Bromus secalinus*. Both were present in field margins of conventional fields as a result of the use of herbicides with gaps for *Bromus* species. Additional rare weed species such as *Neslia paniculata*, *Camelina alyssum* and *Veronica triphyllos* were found but their total population was rarely larger than 5-20 plants. The results highlight the erosion of weed communities due to intensive agricultural practices and emphasize the conservation of weed biodiversity *per se* and rare arable weed species in particular. Conservation efforts need not to be restricted to organic farming but should rather take the biologic requirements of species and the major drivers of weed community composition into consideration. Agro-biodiversity in total would profit from the utilization of precision farming techniques to create habitat connections on a larger scale.

Having identified major factors in weed biodiversity determination, the next aim was to examine if this biodiversity is able to support weed control related ecosystem services in the field. An important regulating ecosystem service originating from the food chain is the predation of weed seeds by invertebrate and vertebrate species. The objectives of this study were to investigate the connection between weed biodiversity, Carabid beetle diversity and weed seed predation as well to evaluate the role of farming intensity in this sequence. On-farm experiments were performed on the Eastern Swabian Alps measuring weed seed predation, Carabid beetle diversity and weed biodiversity by utilizing seed cards, pitfall traps and vegetation recordings, respectively. Measurements were taken from 2015 to 2017 along a farming intensity gradient represented by conventionally, organically and extensively farmed cereal fields to create a gradient of weed biodiversity. A positive correlation between weed

biodiversity and Carabid beetle diversity was identified as well as a pattern of medium Carabid beetle diversity (2-8 species) providing the highest weed seed predation. Carabid beetle communities were similar in the last two experimental years with granivorous species more abundant in extensive fields and omnivorous species dominating the conventional farming type. A direct connection between weed biodiversity and weed consumption rates was not detected. There was no consistent influence of farming intensity on weed seed predation, rather year and particular farming practices, such as cover cropping, affected seed consumption. In total vertebrate seed predators were more efficient in consuming weed seeds than invertebrates. The revealed connection between weed diversity, Carabid beetle diversity and weed seed predation highlights the role of plants in food web support and subsequent ecosystem service provision. The utilization of these services depends on the promotion of biodiversity by designing appropriate management strategies. Key components of these systems are integration of cover cropping and facilitation of weed biodiversity.

In the next step, the general principles underlying ecosystem service provision by biodiversity, namely niche complementarity and sampling effect, were conveyed to a cover cropping system. The aim was to test single sown cover crops and species mixtures in terms of weed suppression efficacy and reliability. For this purpose, six cover crop species, *Anethum graveolens*, *Raphanus sativus* var *oleiformis*, *Avena strigosa*, *Carthamus tinctorius*, *Vicia sativa* and *Phacelia tanacetifolia*, were sown singly and as mixtures in a field experiment during the autumn-to-winter growing season. The mixtures contained either three or six of the species in varying proportions. Lower weed dry matter and weed densities were found predominantly in treatments with favorable establishment and above-average biomass production. In 2017 *A. strigosa* and *R. sativus* exhibited the highest weed control efficacy of 72% and 83%, respectively. In contrast, mixtures were generally lower in regard to soil cover, aboveground dry matter and weed control efficacy, reaching average values of 57% in 2017. But then again mixtures performed much more homogeneous in regard to the measured parameters compared to single sown cover crops. This observed resilience towards adverse weather conditions provides an insurance for the farmer in terms of weed suppression over a long-term period. The results suggest that, although particular single sown cover crops are more effective to control weeds than mixtures, mixtures are more reliable under changing conditions. Additionally, the composition of the mixtures seems to be more relevant than number of species included. Altering the species composition of cover crop mixtures according to more complementary traits might further improve their weed control efficacy.

The results of this thesis demonstrate the importance of plant biodiversity in the provision and reliability of weed control related ecosystem services, either by weeds themselves or by specifically designed cover crop mixtures. Furthermore, management factors influencing weed biodiversity were determined, which can aid in the creation of more sustainable management strategies for a diverse agroecosystem and the conservation of rare arable weed species. This work aims to understand the interactions of farming practice, plant biodiversity and ecosystem service provision and to use this knowledge in optimizing conservation effectiveness and creating (ecology inspired) biological weed control strategies. Future challenges in this regard will be the reconciliation of food production and security with conservation efforts as well as the large-scale impacts of climate change. Advancing technologies in precision agriculture and increasing knowledge of multi-functional biodiversity provide an opportunity to create more sustainable and economically sound, yet diverse, agricultural systems in the future.

7.2. Zusammenfassung

In terrestrischen Ökosystemen sind Pflanzen die Grundlage für Nahrungsnetze und stellen wichtige Ökosystemdienstleistungen bereit. Man nimmt weiterhin an, dass artenreichere Pflanzengesellschaften eine stabilere Unterstützung des Nahrungsnetzes gewährleisten und produktiver in der Bereitstellung von Ökosystemdienstleistungen sind. In Agrarökosystemen, die sich durch hohe Störungsfrequenzen und externe Inputs auszeichnen, können Pflanzenvielfalt und deren Leistungen nur durch Unkräuter bereitgestellt werden. Unkräuter sind jedoch ein limitierender Faktor für die Pflanzenproduktion und müssen bekämpft werden, um eine angemessene Ertragsqualität und -quantität zu erzielen. Die Erhaltung von Unkräutern und Biodiversität im Feld kann dazu führen Nahrungsnetze zu erhalten und das Potenzial von Ökosystemdienstleistungen, einschließlich dem der Unkrautbekämpfung, zu nutzen. Die vorliegende Dissertation umfasst drei Experimente, die sich hauptsächlich auf die Wechselwirkungen zwischen landwirtschaftlichen Bewirtschaftungsfaktoren, Pflanzenvielfalt und deren Bereitstellung von Ökosystemdienstleistungen zur Unkrautbekämpfung in Agrarökosystemen konzentrieren.

In der ersten Studie wurden Vegetationsaufnahmen in On-Farm-Experimenten und Umfragen unter Landwirten in zwei Regionen Südwestdeutschlands durchgeführt. Ziel war es, die Auswirkungen der landwirtschaftlichen Bewirtschaftung auf die Zusammensetzung der Unkrautgesellschaften, die Unkraut-Biodiversität und das Vorkommen seltener Ackerunkräuter in Getreidefeldern zu untersuchen. Die Biodiversität von Unkräutern wurde hauptsächlich durch die Kulturpflanzenart, den Einsatz von Herbiziden und das Anbausystem sowie Stickstoff- und Lichtverfügbarkeit beeinflusst. Darüber hinaus zeigten die Feldränder eine höhere Vielfalt an Unkräutern als die Feldmitte. Die Unkrautgesellschaften waren in beiden Studienregionen sehr ähnlich zusammengesetzt und wurden von *Alopecurus myosuroides*, *Galium aparine*, *Viola arvensis*, *Polygonum convolvulus* und *Veronica persica* dominiert. Eine Redundanzanalyse ergab, dass die Unkrautgesellschaft hauptsächlich durch Kulturpflanzenart, Bodenbearbeitung, Lage der Aufnahmefläche im Feld und Zeitpunkt der Herbizidanwendung geprägt wurde. Dabei wurden die dominierenden Unkrautarten durch eine mittlere bis hohe Stickstoffdüngung und eine geringe Anzahl von Bodenbearbeitungsvorgängen gefördert. Die einzigen gefährdeten Unkrautarten, die in ausreichender Anzahl für die Analyse vorzufinden waren, waren *Bromus grossus* und *Bromus secalinus*. Beide kamen überwiegend in den Feldrändern konventioneller Felder als Folge des Einsatzes von Herbiziden mit Wirkstofflücken für Trespenarten vor. Weitere seltene Unkrautarten wie *Neslia paniculata*, *Camelina alyssum* und *Veronica triphyllos* waren zwar vorhanden, aber ihre Gesamtpopulationen waren selten größer als 5-20 Individuen. Die erzielten Ergebnisse weisen auf einen Rückgang der Diversität von Unkrautgesellschaften durch intensive landwirtschaftliche Praktiken hin. Weiterhin verdeutlichen sie die Notwendigkeit der Erhaltung der Unkrautbiodiversität an sich und den Schutz seltener Unkrautarten im Besonderen. Die Schutzbemühungen dürfen sich jedoch nicht auf den ökologischen Landbau beschränken, sondern sollten vielmehr die biologischen Anforderungen der Arten und die wichtigsten Faktoren für die Zusammensetzung der Unkrautgesellschaften berücksichtigen. Die Biodiversität in Agrarökosystemen würde von der Anwendung von Precision Farming Techniken profitieren, um damit eine Vernetzung von Lebensräumen in größerem Maßstab herzustellen.

Nachdem die wichtigsten Faktoren für das Zustandekommen von Unkrautbiodiversität identifiziert wurden, sollte untersucht werden, ob diese biologische Vielfalt in der Lage ist, Ökosystemdienstleistungen, die zur Unkrautbekämpfung beitragen, zu unterstützen. Eine wichtige regulierende Ökosystemdienstleistung, die durch die Nahrungskette bereitgestellt wird, ist der Verzehr von Unkrautsamen durch wirbellose Tiere und Wirbeltiere. Die Studie hatte zum Ziel, den Zusammenhang zwischen Unkrautbiodiversität, Laufkäferdiversität und Unkraut-Samenprädation zu untersuchen sowie die Rolle der landwirtschaftlichen Intensität in dieser Abfolge zu bewerten. Zu diesem Zweck wurden im Ostalbkreis On-Farm-Experimente angelegt und, unter Verwendung von Vegetationsaufnahmen, Bodenfallen und Samenkarten, die Unkrautbiodiversität, Laufkäferdiversität und Unkraut-Samenprädation gemessen. Diese Messungen fanden von 2015 bis 2017 entlang eines landwirtschaftlichen Intensitätsgradienten statt. Dieser Gradient enthielt konventionell, ökologisch und extensiv bewirtschaftete Getreidefelder und stellte zudem eine zunehmende Unkrautbiodiversität dar. Es wurde ein positiver Zusammenhang zwischen der Unkrautbiodiversität und der Laufkäferdiversität festgestellt. Die Ergebnisse zeigten, dass eine mittlere Laufkäferdiversität (2-8 Arten) das höchste Level an Unkraut-Samenprädation aufwies. Die Laufkäfergemeinschaften waren in den letzten beiden Untersuchungsjahren sehr ähnlich, wobei granivore Arten häufiger unter extensiver Bewirtschaftung vorhanden waren und omnivore Arten im konventionellen Anbau dominierten. Ein direkter Zusammenhang zwischen Unkrautbiodiversität und der Verzehrsrate von Unkrautsamen wurde nicht festgestellt. Die Bewirtschaftungsintensität hatte keinen einheitlichen Einfluss auf die Unkraut-Samenprädation, viel eher waren das Jahr und bestimmte Bewirtschaftungsmethoden, wie z.B. der Anbau von Zwischenfrüchten, maßgebend für die Rate der Samenprädation. Insgesamt waren Wirbeltiere effizienter im Verzehr von Unkrautsamen als wirbellose Tiere. Der festgestellte Zusammenhang zwischen Unkrautvielfalt, Laufkäferdiversität und Unkraut-Samenprädation verdeutlicht die Rolle von Pflanzen in Nahrungsnetzen und deren Bereitstellung von Ökosystemdienstleistungen. Um diese Dienstleistungen zu nutzen, muss Biodiversität durch die Gestaltung geeigneter Bewirtschaftungssysteme gefördert werden. Schlüsselkomponenten dieser Systeme sind die Einbindung von Zwischenfrüchten in die Fruchtfolge und der Erhalt der biologischen Vielfalt von Unkräutern.

In der dritten Studie wurden die grundlegenden Prinzipien der Bereitstellung von Ökosystemdienstleistungen durch Biodiversität, nämlich Nischenergänzung („niche complementarity“) und Stichprobeneffekt („sampling effect“), auf den Anbau von Zwischenfrüchten übertragen. Das Ziel dabei war, Artenmischungen und Zwischenfrüchte in Reinsaat auf die Wirksamkeit und Zuverlässigkeit der Unkrautunterdrückung zu testen. Zu diesem Zweck wurden sechs Zwischenfruchtarten, nämlich *Anethum graveolens*, *Raphanus sativus* var *oleiformis*, *Avena strigosa*, *Carthamus tinctorius*, *Vicia sativa* und *Phacelia tanacetifolia*, einzeln und als Mischungen in einem Feldversuch ausgesät und in der Herbstsaison untersucht. Die Mischungen enthielten drei oder sechs der Arten zu unterschiedlichen Anteilen. Behandlungen mit guter Etablierung der Zwischenfrüchte und überdurchschnittlicher Biomasseproduktion wiesen überwiegend die geringsten Unkrauttrockenmassen und -dichten auf. *A. strigosa* und *R. sativus* zeigten die höchste Wirksamkeit bei der Unkrautbekämpfung im Jahr 2017 von jeweils 72% bzw. 83%. Im Gegensatz dazu schnitten die Mischungen im Allgemeinen schlechter ab und erreichten in Bezug auf Bodenbedeckung, oberirdische Trockensubstanz und Unkrautbekämpfung Durchschnittswerte von ca. 57%. Nichtsdestoweniger verhielten sich die Mischungen, in Bezug auf die gemessenen Parameter, wesentlich einheitlicher als die Zwischenfrüchte in Reinsaat. Diese beobachtete Widerstandsfähigkeit gegen ungünstige Wetterbedingungen ermöglicht dem Landwirt eine zuverlässigere Unkrautbekämpfung über einen langfristigen Zeitraum. Obwohl bestimmte Zwischenfrüchte in Reinsaat effektiver bei der

Unkrautbekämpfung waren, deuten die Ergebnisse darauf hin, dass Mischungen unter wechselnden Bedingungen zuverlässiger sind. Darüber hinaus scheint die Zusammensetzung von Zwischenfruchtmischungen wichtiger zu sein als die Anzahl der enthaltenen Arten. Eine Änderung der Artenzusammensetzung der Zwischenfruchtmischungen durch Auswahl von sich ergänzenden Pflanzeneigenschaften könnte deren Wirksamkeit in der Unkrautbekämpfung weiter verbessern.

Die Ergebnisse der vorliegenden Dissertation veranschaulichen die Bedeutung der pflanzlichen Biodiversität für die Bereitstellung und Zuverlässigkeit von Ökosystemdienstleistungen mit Unkrautbekämpfungscharakter. Diese werden dabei entweder durch Unkräuter selbst oder durch speziell entwickelte Zwischenfruchtmischungen bereitgestellt. Diese Arbeit hatte zum Ziel, die Wechselwirkungen zwischen landwirtschaftlicher Praxis, Artenvielfalt der Pflanzen und Ökosystemdienstleistungen zu untersuchen und das gewonnene Wissen zur Optimierung von Naturschutzbemühungen und zur Entwicklung (ökologisch inspirierter) biologischer Unkrautbekämpfungsstrategien zu nutzen. Die Weiterentwicklung von Precision Farming Technologien und das zunehmende Wissen über die Multifunktionalität der biologischen Vielfalt bieten die Chance, in Zukunft nachhaltigere und wirtschaftlich sinnvollere, aber trotzdem vielfältige Bewirtschaftungssysteme zu schaffen.

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Bless the LORD, O my soul, and all that is within me, bless his holy name.
Bless the LORD, O my soul, and forget not all his benefits.

(Ps. 103, 1-2)

9. Affidavit

Declaration in lieu of an oath on independent work

according to Sec. 18(3) sentence 5 of the University of Hohenheim's Doctoral Regulations for the Faculties of Agricultural Sciences, Natural Sciences, and Business, Economics and Social Sciences

1. The dissertation submitted on the topic

Interactions of farming and plant biodiversity in weed control related ecosystem service provision and weed conservation

is work done independently by me.

2. I only used the sources and aids listed and did not make use of any impermissible assistance from third parties. In particular, I marked all content taken word-for-word or paraphrased from other works.

3. I did not use the assistance of a commercial doctoral placement or advising agency.

4. I am aware of the importance of the declaration in lieu of oath and the criminal consequences of false or incomplete declarations in lieu of oath.

I confirm that the declaration above is correct. I declare in lieu of oath that I have declared only the truth to the best of my knowledge and have not omitted anything.

Stuttgart-Hohenheim, 24.09.2019

Place, Date

Signature

10. Curriculum Vitae

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University Education

Since 09/2016	Doctoral candidate in the Department of Weed Science, University of Hohenheim Doctoral thesis: *Interactions of farming and plant biodiversity in weed control related ecosystem service provision and weed conservation*
10/2011-03/2014	Master of Crop Sciences, University of Hohenheim Major: Crop Protection Master thesis: *Influence of elevated temperature and changed precipitation patterns on biomass allocation and yield quality of barley*
10/2008-10/2011	Bachelor in Agricultural Biology, University of Hohenheim Bachelor thesis: *Verbreitung von seltenen Ackerwildkräutern in der Gemarkung Mehrstetten 2011 im Vergleich zu den vegetationskundlichen Erhebungen von 1948/1949 und 1975-1978*

Peer-reviewed journal articles

Gerhards, R., Dieterich, M., Schumacher, M., 2013. Rückgang von Ackerunkräutern in Baden-Württemberg – ein Vergleich von vegetationskundlichen Erhebungen in den Jahren 1948/49, 1975–1978 und 2011 im Raum Mehrstetten – Empfehlungen für Landwirtschaft und Naturschutz. *Gesunde Pflanzen* **65**, 151–160.

Blaix, C., Moonen, A.C., Dostatny, D.F., Izquierdo, J., Le Corff, J., Morrison, J., Von Redwitz, C., Schumacher, M., Westerman, P.R., 2018. Quantification of regulating ecosystem services provided by weeds in annual cropping systems using a systematic map approach. *Weed Research* **58**, 151–164.

Schumacher, M., Hahn, A.-K., Gerhards, R., 2018. The influence of farming on weed flora in the Gäu region of Southwestern Germany with an emphasis on rare arable weed species. Presented at the 28. Deutsche Arbeitsbesprechung über Fragen der Unkrautbiologie und –bekämpfung, Julius-Kühn-Archiv, Braunschweig, Germany, pp. 30–34.

Schumacher, M., Ohnmacht, S., Rosenstein, R., Gerhards, R., 2018. How Management Factors Influence Weed Communities of Cereals, Their Diversity and Endangered Weed Species in Central Europe. *Agriculture* **8**, 172.

Schappert, A., Schumacher, M., Gerhards, R., 2019. Weed Control Ability of Single Sown Cover Crops Compared to Species Mixtures. *Agronomy* **9**, 294.

Scientific presentations

„Decline of arable weed species in Southern Germany – a comparison of vegetation recordings from the last 60 years“

5th workshop of the EWRS Working Group Weeds and Biodiversity

17. – 19. November 2014 in Pisa, Italy

„Veränderung der Unkrautartengesellschaft in der Gemarkung Mehrstetten (Schwäbische Alb) – Ein Vergleich zwischen 1950, 1980 und 2011“

29. Jahrestagung des DPG-Arbeitskreises Herbologie

February 2015 in Bingen am Rhein

„The influence of farming and weed biodiversity on seed predation“

7th International Weed Science Conference

19. – 25. June 2016 in Prag, Czech Republic

„Fördern Untersaaten und Zwischenfrüchte die Samenprädation von Unkräutern?“ (Poster)

30. Jahrestagung des DPG-Arbeitskreises Herbologie

February 2017 in Bingen am Rhein

„The influence of farming on weed flora in the Gäu region of Southwestern Germany with an emphasis on rare arable weed species“

28. Deutsche Arbeitsbesprechung über Fragen der Unkrautbiologie und –bekämpfung

27. February – 01. March 2018 in Braunschweig

„Living mulch and cover crops enhance weed seed predation after crop harvest“

18. European Weed Research Society Symposium

17. – 21. June 2018 in Ljubljana, Slovenia

„Wie Bewirtschaftungsparameter die Unkrautbiodiversität und seltene Arten beeinflußen“

31. Jahrestagung des DPG-Arbeitskreises Herbologie

February 2019 in Bingen am Rhein

Matthias Schumacher
Filderstadt, den 26.03.2020