# Selective weed management strategies and their impacts on crop yield and biodiversity

Dissertation

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von

# M.Sc. Marie Luisa Zingsheim

aus

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Referent: Prof. Dr. Thomas F. Döring Korreferentin: Dr. Sabine J. Seidel

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## Publications presented in this thesis

Zingsheim ML, Döring TF 2024. What weeding robots need to know about ecology. Agriculture, Ecosystems & Environment 364, S. 108861. DOI: 10.1016/j.agee.2023.108861

Zingsheim ML, Döring TF 2024. Does weed biodiversity mitigate yield losses? Frontiers in Plant Science 15, S. 1395393. DOI: 10.3389/fpls.2024.1395393.

Zingsheim ML, Döring TF 2023. Video-based monitoring of flower visitors on weed vegetation in organic farming. In:"The future of biodiversity – overcoming barriers of taxa, realms and scales" –  $52^{nd}$  Annual Conference of German Ecological Society. 12 – 16 September 2023. Leipzig, Germany.

## **Further publications**

Massfeller A, Zingsheim ML, Ahmadi A, Storm H. Action- or results-based payments for ecosystem services in the era of smart weeding robots? Biological Conservation. Manuscript under 2<sup>nd</sup> review.

Döring TF, Seidel S, Zingsheim M, Grahmann K, Rascher U. 2023. R2D2 muss viel lernen. Lumbrico 16/23: 37-40

Zingsheim ML, Döring TF 2022. Required input information for sustainable weed management strategies enabled by autonomous in-field intervention technology. In: "Weed Science in a Climate of Change" – The 8th International Weed Science Congress, Abstract Book. 4 - 9 December 2022. Bangkok, Thailand.

# **Summary**

Balancing crop productivity with biodiversity conservation in agricultural systems remains a critical challenge of our time. The emergence of autonomous and AI-driven weeding technologies, such as field robots, offers promising solutions to address this issue. To fully exploit their potential, it is essential to develop targeted weed management strategies that can be effectively implemented within the field.

The aim of this thesis is to investigate on which type of input information (e.g., weed cover, weed species) a weed management strategy must be based on and which level of technological precision for weed removal is needed to reconcile biodiversity and crop production. To assess the effects of various weed management strategies on crop yield and biodiversity parameters, different strategies were modelled using three datasets from organically farmed fields. The results demonstrated that sustaining long-term biodiversity within fields without compromising crop yields necessitates intervention technologies capable of operating at the plant level. Furthermore, these technologies need to be capable of identifying and quantifying weed species and processing this information in real time. In the course of evaluating weed management strategies research gaps regarding species-specific effects of weeds, both competitive and beneficial, were identified.

To address these data gaps, two field experiments were conducted. To evaluate the competitive effects of weeds, different weed species were sown as monocultures and as mixtures beside different crops. The results of the experiment demonstrated that decisions regarding weed management strategies must consider not only the weed species or composition of a weed community but also their current relationships with the crop plant. General assumptions about the occurrence of the competitive effects of a specific weed species or a community are not reliable as long as they are not considered in the specific context.

To investigate the beneficial impacts of different weed species on associated biodiversity, a video-based monitoring system was tested to measure species-specific flower visitation rates on various weed species within organically farmed fields. This method offers significant potential to accelerate data collection on the interactions between weeds and their associated biodiversity. However, for data such as flower visitation rates to serve as effective input for decision-making in weed management, it is essential to define specific objectives – such as

promoting particular ecosystem services – in advance. This is crucial given the complexity and context-dependent nature of interactions between weed species and their associated fauna.

Further interdisciplinary research is needed to advance selective weed management strategies. To anticipate long-term effects, the selection pressure exerted by the implementation of selective weed management strategies on weed populations and their associated species needs to be investigated. The use of multi-sensor systems for data collection, combined with modelling the gathered data across various environments, holds significant potential to accelerate research in this field.

# Zusammenfassung

Eine der größten Herausforderungen unserer Zeit ist es, die Nutzpflanzenproduktion mit dem Erhalt der Biodiversität in Agrarökosystemen in Einklang zu bringen. Die Entwicklung autonomer und KI-gestützter Unkrautbekämpfungstechnologien, wie z. B. Feldroboter, bietet vielversprechende Möglichkeiten, um dieser Herausforderung zu begegnen. Für den Einsatz dieser Technologien müssen angepasste Unkrautmanagementstrategien entwickelt werden, welche im Feld umgesetzt werden können.

dieser Arbeit wird untersucht, welche Art von Input-Informationen (z. B. In Unkrautdeckungsgrad, Unkrautarten) für Unkrautmanagementstrategien benötigt werden und welches Maß an technologischer Präzision bei der Unkrautbeseitigung erforderlich ist, um die Biodiversität im Feld gezielt zu fördern, ohne Erträge zu reduzieren. Um die Auswirkungen verschiedener Unkrautmanagementstrategien auf den und verschiedene Ertrag Biodiversitätsparameter zu bewerten, wurden unterschiedliche Strategien mithilfe von drei Datensätzen aus ökologisch bewirtschafteten Feldern modelliert. Die Ergebnisse zeigten, dass der langfristige Erhalt der Biodiversität innerhalb von Feldern ohne Ertragseinbußen Technologien erfordert, die auf Einzelpflanzenebene operieren können. Diese Technologien müssen zudem in der Lage sein, Unkrautarten zu identifizieren und zu quantifizieren und diese Informationen in Echtzeit zu verarbeiten. Im Rahmen der Evaluierung von Unkrautmanagementstrategien wurden Forschungslücken bezüglich der artspezifischen Effekte von Unkräutern - sowohl in ihrer Konkurrenzfähigkeit als auch in ihrem Nutzen identifiziert.

Zur Schließung dieser Datenlücken wurden zwei Feldexperimente durchgeführt. Um die Konkurrenzwirkungen von Unkräutern zu untersuchen, wurden verschiedene Unkrautarten sowohl in Monokulturen als auch in Mischkulturen neben unterschiedlichen Kulturpflanzen ausgesät. Die Ergebnisse zeigten, dass Entscheidungen in Unkrautmanagementstrategien nicht nur auf der Art oder Zusammensetzung einer Unkrautgemeinschaft basieren sollten, sondern auch auf ihrer aktuellen Beziehung zur Kulturpflanze. Allgemeine Annahmen über Konkurrenzeffekte einer spezifischen Unkrautart oder -gemeinschaft sind unzuverlässig, wenn diese nicht im spezifischen Kontext betrachtet werden.

Um die positiven Auswirkungen verschiedener Unkrautarten auf die assoziierte Biodiversität zu untersuchen, wurde ein videobasiertes Monitoringsystem getestet. Dieses diente dazu, artspezifische Visitationsraten an den Blüten von Unkräutern auf ökologisch bewirtschafteten Feldern zu erfassen. Diese Methode bietet erhebliches Potenzial, die Datenerhebung zu Interaktionen zwischen Unkräutern und der assoziierten Biodiversität zu beschleunigen. Damit Daten wie artspezifische Visitationsraten als effektive Entscheidungsgrundlage für das Unkrautmanagement dienen können, müssen im Vorfeld spezifische Ziele definiert werden – beispielsweise die Förderung bestimmter Ökosystemdienstleistungen. Dies ist entscheidend angesichts der Komplexität und Kontextabhängigkeit der Wechselwirkungen zwischen Unkrautarten und ihrer assoziierten Fauna.

Weitere interdisziplinäre Forschung ist notwendig, um selektive Unkrautmanagementstrategien voranzutreiben. Um langfristige Auswirkungen vorhersehen zu können, ist es notwendig zu erforschen, welchen selektiven Druck die Umsetzung selektiver Unkrautmanagementstrategien auf Unkrautpopulationen und ihre assoziierte Fauna ausübt. Der Einsatz von Multisensorsystemen zur Datenerfassung, kombiniert mit der Modellierung der gesammelten Daten in verschiedenen Umwelten, birgt großes Potenzial, die Forschung in diesem Bereich zu beschleunigen.

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# Abbreviations, acronyms and units

a.s.l.	Above sea level
°C	Degree celsius
CA	Chenopodium album
СКА	Campus Klein Altendorf
cm	Centimetre
DM	Dry mass
e.g.	exempli gratia
et al.	et alii
FB	Faba bean
FBO	Intercrop of faba bean and oat
Fig.	Figure
g	Gram
ha	Hectare
HSD	Honest significant difference
i.e.	id est
K	Potassium
kg	Kilogram
LiDAR	Light Detection and Ranging
LM	Lamium purpureum
m	Metre
Ν	Nitrogen
Р	Phosphorus
R <sup>2</sup>	Coefficient of determination
RGB	Red Green Blue
SM	Stellaria media
Tab.	Table
UAV	Unmanned Aerial Vehicle
UGV	Unmanned Ground Vehicle
VA	Viola arvensis

VH	Vicia hirsuta
VS.	Versus
WG	Wiesengut
z.B.	Zum Beispiel

# 1 General introduction and scientific background

## 1.1 Rise and fall of biodiversity in cultivated land

Throughout the landscape, nature has created its own specific vegetation cover. Even on arable land, which is frequently disturbed by human activity, specific plant communities have developed; these are known as segetal flora, or in agricultural parlance, weeds.

The cultivation of land has inadvertently created a mosaic structure of the landscape with a diverse range of habitats with unoccupied niches, hedgerows, fallow land and field margins, leading to a high diversity of adaption strategies and thus to a high biodiversity of weeds (Grime, 1974). This weed biodiversity in turn, supported a variety of associated organisms, such as arthropods, pollinators, other invertebrates and birds, by providing essential resources like food, shelter, and reproduction sites (Gerowitt et al., 2003). Through this landscape diversification, farmland became of significant value for biodiversity in Europe (Lomba et al., 2014).

Just as old as the establishment of farmland and the emergence of weeds themselves, is weed control. If not managed, weeds can decrease yields of crops by a global average of 34% (Oerke, 2006) as they may compete with the crop plants for resources of water, nutrients and sunlight, threatening food security in the face of a growing global population (United Nations, 2024). While weed control was initially carried out manually and mechanically, it became industrialized in the last decades, as did the entire agricultural systems in western countries (Bauerkämper, 2004). Small-scaled cultivated areas with heterogeneous mosaic-structures were widely transformed into large-scale cultivation of monocultures (Stoate et al., 2001). Biological and ecological differences of weeds were not considered in weed control, but a 'clean field' without any weed left was aimed (**Fig.1a**). Ecological interactions between crop plants and other organisms within agricultural ecosystems were undesired. Intensive fertilization and weed management practices, such as tillage and herbicide application, became dominant and remain widely used today (Clapp, 2021; Heap, 2023). These practices enabled high productivity through a rapid, large-scale weed removal, significantly reducing labour and time costs associated with manual weeding.

However, the reliance of weed control on herbicides and intensive tillage has introduced significant environmental risks. Intensive tillage may cause soil compaction (Orzech et al., 2021), soil erosion (Seitz et al., 2019), decreases in soil quality (Karlen et al., 2013), losses of

organic matter (Koch and Stockfisch, 2006) and nutrient depletion (Gadermaier et al., 2012). The broad application of herbicides has led to the evolution of resistance in weeds to 21 of the 31 known herbicide sites of action and to 168 distinct herbicides. As a result, 273 weed species – comprising 156 dicots and 117 monocots – have developed herbicide resistance (Heap, 2023). These adoptions have led to high competitive species, which are particularly difficult to control (Storkey and Neve, 2018). Furthermore, the intensification and simplification of agricultural systems have significantly reduced the biodiversity of our farmlands (Storkey and Westbury, 2007). Across 29 European countries, 582 plant species depend on arable habitats, with 31% being listed as rare or threatened (Storkey et al., 2012). The decrease in weed diversity also affects higher trophic levels, leading to declines in various animal species dependent on diverse plant communities (Bretagnolle and Gaba, 2015; Marshall et al., 2003; Smith et al., 2020). As a result of these intensive farming practices, agriculture has shifted from being an initial driver of biodiversity to becoming a major contributor to its decline (Wagner et al., 2021). Halting this biodiversity loss has been defined as one of the greatest challenges of our time (IPBES, 2018).

## 1.2 The recognition of beneficial effects of weeds

Beyond the ethical and conservation-driven mandate to prevent species loss (European Union, 2013), the value of biodiversity for food production is increasingly recognized in terms of its importance and beneficial effects of our agroecosystems, i.e. ecosystem services (Bretagnolle and Gaba, 2015; Gerowitt et al., 2003; Storkey and Neve, 2018).

Weeds offer reproduction sites and refuge for a range of associated fauna, including pollinators and natural predators of crop pests in agroecosystems (Balmer et al., 2013; Rebek et al., 2006). For example, effects of floral resources provided by weed plants promote parasitoid wasps (Hymenoptera) and hoverflies (Diptera) and thus naturally reduce pest infestation (Cowgill et al., 1993; Wäckers, 2004). Cereal aphid populations were found to be reduced to approximately one-third of their potential densities across Europe by naturally occurring predators and parasitoids (Thies et al., 2011). Moreover, post-dispersal weed seed predation by granivorous and omnivorous carabid beetles results in substantial natural suppression of weed populations (Kulkarni et al., 2015). Beyond their role in pest regulation, weeds may contribute to soil stability, helping to reduce erosion (Lenka et al., 2017; Liu et al., 2019), and support beneficial mycorrhizal networks, which can enhance soil fertility (Kubota et al., 2015).

These examples represent only a small fraction of the already known functions of weeds in agroecosystems and an even smaller fraction of those yet to be discovered. However, while ecological interactions between crops and other species within agroecosystems were largely unintended in intensive agriculture in past decades, there are now emerging approaches aimed at actively promoting these interactions (Moonen and Bàrberi, 2008). Furthermore, a growing body of research indicates that diversification reduces the dominance of individual weed species and minimizes niche overlap between crops and weeds (Navas, 2012; Storkey and Neve, 2018), thereby fostering high-diverse weed communities that were defined by Esposito et al. (2023) as 'neutral weed communities'. This implies that the preservation of weeds does not necessarily have a negative impact on yields, but with the right management strategies, yield enhancement and biodiversity conservation might be reconciled. The conclusion drawn is that understanding and preserving biodiversity within agroecosystems is crucial for enhancing their functionality and resilience, which is fundamental to ensuring sustainable food production over the long term.

#### **1.3** Approaches towards environmentally sustainable weed management

One approach to reconcile biodiversity conservation with crop productivity is integrated weed management (IWM). The principle of IWM is to manage the farmland habitat with emphasize to the importance of understanding weed biology, environmental factors, and crop-weed interactions (Chauhan, 2021; Swanton et al., 2015). Rather than relying solely on herbicides or tillage, IWM incorporates a diverse set of practices – such as crop rotation, cover cropping, intercropping, reduced fertilization and biological control - to increase environmental heterogeneity and the potential for niche complementarity between crops and weeds (Esposito et al., 2023; Mortensen et al., 2000). Variabilities, as they occur within fields at both macroand micro-scales are taken into account for the application of a site-specific management instead of a homogenized and broad application of weed control interventions over the entire field (Gerhards et al., 2022). For instance, weeds are managed only in areas where infestations exceed specific economic thresholds (Gerhards and Christensen, 2003). In untreated zones, weed communities below these thresholds are allowed to persist (Fig.1b). However, to compete with broad spraying and to be adopted by farmers, the saving of herbicides in site-specific treatment must compensate the economic costs of weed mapping, data processing, decision making and site-specific application technology (Timmermann et al., 2003). Additionally, the adoption of IWM systems remain limited due to their frequent inability to achieve the

performance levels regarding weed control expected by farmers, which hinders their widespread implementation (Young et al., 2017). A more refined approach to site-specific weed management is selective weed management, which is punctual weed control on plant-level (**Fig.1c**). This method allows farmers to reduce herbicide use while achieving greater control over weed infestations compared to site-specific weed management, as no areas remain largely untreated (Esposito et al., 2023). Furthermore, aggressive weed species, which dominate the weed population and therefore impede efforts to establish neutral weed communities can selectively be removed without taking off the surrounding, less competitive species (**Fig.1d**) (Armengot et al., 2017). However, this requires high-resolution weed mapping and technical precision, capable of identifying and treating not only weed patches but individual weed plants. Factors accelerating the development of such new technologies despite their high costs, are the tightened EU regulations on chemical plant protection under the Green Deal and the Farm-to-Fork Strategy, which require a 50% reduction in herbicide usage by 2030 (European Commission, 2020).



**Figure 1**: Schematic representation of different levels of specificity of weed management strategies within a field, with a) non-specific weeding, b) site-specific weeding, c) plant-specific weeding and d) species-specific weeding.

# 1.4 Technological development in modern agriculture and its potential

Current research and development in selective weed management, such as spot spraying, has been rapidly increasing. Multi-sensor systems equipped with RGB-cameras, multispectral cameras, hyperspectral sensors, depth cameras, stereo sensors and light detection and ranging (LiDAR) measure parameters such as plant shape (Lin et al., 2017), colour (Gai et al., 2020), texture (Bakhshipour et al., 2017; Esser et al., 2023), and spectral reflectance (Barrero and Perdomo, 2018; Zisi et al., 2018), enabling differentiation between crops and weeds. Some studies are also exploring technologies to distinguish between individual weed species (Raja et al., 2020). Mounted on unmanned aerial vehicles (UAVs) or ground vehicles (UGVs), such as weeding robots, these systems can collect a wide range of information. Innovations like single nozzle control (Pohl et al., 2020), lasers (Carbon Robotics, 2024; Kaierle et al., 2013), or

mechanical tools (McCool et al., 2018) further allow precise weed removal enabling selective weed management.

These technologies not only offer the potential for removal of individual weed plants but also for the targeted conservation of specific plants to support biodiversity. However, the mentioned innovations have primarily targeted economic benefits through herbicide savings, with reduced environmental impacts promoted as a welcome side effect rather than a primary objective (Christensen et al., 2009; Gerhards and Oebel, 2006; Utstumo et al., 2018). Since 2015, over 40 commercial weeding robots have entered the market, featuring varying levels of automation, effectiveness in distinguishing between crops and weeds, guidance mechanisms, and weeding tools (Zhang et al., 2022). Yet, none of these systems specifically aim to retain certain weeds in the field for biodiversity conservation. Strategies in which individual weed plants are maintained within the field for biodiversity conservation are lacking, which is why the potential of these innovations is currently not used to its full extend. To date, it remains unexplored which type of information (e.g., weed cover, density) and technical precision is required for selective weed management to unlock the ecological potential of these technologies. A shift in perspective, from purely economic motivations to conservation-driven objectives for selective weed management, is crucial to address the challenge of biodiversity loss, much of which is driven by agricultural practices.

# **1.5 Making new technologies relevant form an ecological perspective:** Thesis outline

This thesis aimed to contribute to the targeted development of new weed management strategies for modern weeding technologies, focusing not only on economic advantages but also explicitly on strategies, which maintain a diverse, non-competitive weed flora to support biodiversity and thus ecosystem functionality. It is tested and evaluated, which types of input information are suitable for making decisions about weed removal or retention with this objective in mind.

In a first study, various strategies spanning a gradient of specificity and incorporating different types of input information were modelled using an agronomic dataset, which was collected on organically farmed fields. The impacts of these strategies on various biodiversity parameters and crop yield were then compared by assessing their potential for trade-off reduction between yield maximization and biodiversity conservation. This study is presented in chapter 2 and was published in *Agriculture, Ecosystems & Environment* (Zingsheim and Döring, 2024b) and at the 8th International Weed Science Congress (Zingsheim and Döring, 2022).

Chapter 2 identified a research gap concerning the competitive effects of individual weed species, necessitating the use of assumptions to model the impacts of the weeding strategies on crop yield. To fill this research gap and to expand the model with suitable data, a field experiment was conducted aiming to investigate species-specific competitive effects of several weeds sown in monocultures and mixed in communities on crop productivity. As no species-specific competitive effects occurred in this experiment (with one exception) the results were analysed and interpreted with regard to their competitive effects at community level. It was investigated whether weed communities with high biodiversity, especially high evenness, mitigate yield losses compared to weed communities with low evenness. This work has been published in *Frontiers in Plant Science* (Zingsheim and Döring, 2024a).

Considering the beneficial effects of weeds on associated biodiversity, it may be ecologically purposeful to include species-specific advantages in the decision-making process about which weed species should be retained and which one should be removed. In order to incorporate types of information such as species-specific flower-visitation-rates into decision making, methods are needed with which a large amount of such data can be collected. Chapter 4 introduces a video-based monitoring approach for observing flower visitors on various weed species. It further examines the advantages and disadvantages of this method, highlighting its potential applications and limitations. This research was presented in a poster session at the 52<sup>nd</sup>

Annual Conference of German Ecological Society (Zingsheim and Döring, 2023) and was focussed on the assessment and discussion of the methods rather than an interpretation of the data generated through this methods. The integration of this contribution into the broader context of this thesis, particularly regarding its suitability as input information for selective weed management strategies, is addressed comprehensively in the general discussion (chapter 5).

Chapter 5 examines the contributions of the studies conducted in the scope of this thesis to advance the understanding of requirements for the ecologically targeted development of selective weed management strategies. It evaluates the methodological strengths and limitations associated with collecting input data on species-specific competitive and beneficial effects of weeds. Furthermore, the chapter discusses the suitability of the gathered data as input information for decision-making in selective weed management. Finally, it highlights the need for further research and explores the broader implications of these findings for the future of sustainable arable farming.

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# 2 What weeding robots need to know about ecology

## Marie L Zingsheim<sup>1</sup>\*, Thomas F Döring<sup>1</sup>

<sup>1</sup> Institute of Crop Science and Resource Conservation, Department for Agroecology and Organic Farming, Auf dem Hügel 6, 53121, Germany

\*Corresponding author:

Email: marie.zingsheim@uni-bonn.de

## Highlights

- Spatially selective weeding may reduce trade-offs between yield and weed diversity
- However, it requires a high level of input information and technical effort.
- Only conservation of gamma diversity across whole field requires less information.
- Selective robotic weeding may reduce trade-offs even when flora is impoverished.
- There is a research gap regarding competitive effects of individual weed species.

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#### Abstract

In weed control the aims of securing crop productivity and protecting biodiversity are often difficult to reconcile. Currently, the development of autonomous in-field intervention technology, such as field robots, is creating new potential for minimizing trade-offs between these two aims. To exploit this potential, weed management strategies need to adapt. However, it is currently unclear which kind of input information (e.g. weed cover, number of weeds, weed species identity) is required for such a targeted approach, and which impacts the robotic application has on the trade-off between crop yield and biodiversity. Here, we used a dataset from organically farmed fields to assess several weed management strategies, simulating robotsupported weed control. Specifically, we used within-field heterogeneity of several weed and crop productivity variables to model effects of different kinds of input information for a hypothetical, spatially selective robotic weed control system. The results showed that, at a defined yield loss, gamma diversity (number of weed species on the entire investigated area) is maintainable to a large degree, even without information on weed or crop heterogeneity within the field being used to decide where to weed. However, to maintain alpha diversity (average number of weed species per plot), more spatially explicit input information is required, such as on the number of species per plot, weed quantity (weed cover per species), and weed competitiveness. Consequently, a weeding robot would have to be technically capable of distinguishing between individual weed species, measuring weed cover, processing captured information in real time and removing weeds at per-plant level. Further, it could be shown that the success of such a complex weed management strategy is independent of the degree of spatial heterogeneity of crop yield and of the present level of weed species richness.

### **Keywords**

Autonomous in-field intervention, biodiversity conservation, traits, integrated weed control, weed technology

## **2.1 Introduction**

In current agricultural systems, crops are mostly grown in high-input monocultures. Additionally, non-cropped habitats such as field margins have been lost and the size of crop fields has become larger to accommodate increasing size of agricultural machinery. The simplification and intensification of cropping systems have been identified as major contributors to the worldwide biodiversity decline (Meyer et al., 2013), and has resulted in habitat loss and homogenization of plant-animal communities within fields (Stoate et al., 2001). Weed communities have not only suffered declining number of species, but also changed in their species composition (Marshall et al., 2001; Stoate et al., 2001). Further, intensive agriculture has led to herbicide resistances and the emergence of few dominant and highly competitive weed species (Adeux et al., 2019; Foley et al., 2011; Storkey and Neve, 2018). However, while weeds can be harmful to crop production (Oerke, 2006), they can also support agroecosystem services (Gerowitt et al., 2003; Tamburini et al., 2020). They provide reproduction sites and shelter to associated fauna such as pollinators and natural enemies of pests, and they form the food basis for herbivores and thus for higher trophic levels, e.g. farmland birds (Bretagnolle and Gaba, 2015; Marshall et al., 2003; Newton, 2004; Tamburini et al., 2020). Further, weeds also support mycorrhizae, thereby may contribute to increased soil fertility (Kubota et al., 2015). In addition, they may help to reduce soil erosion as well (Lenka et al., 2017; Liu et al., 2019). Adeux et al. (2019) found that diversified weed communities limited the negative effect of competitive and dominant species on crop productivity while potentially promoting ecosystem services provided by subordinate species.

Thus, there is a need to develop weed management strategies that simultaneously maintain crop yield and biodiversity conservation. Here, we approach the development of an optimized weeding strategy (**Fig.2**) by proposing that the potential trade-off between a weed biodiversity and the yield gain effect when weeds are removed – i.e. controlling weeds may lead to a yield gain and simultaneous loss of weed biodiversity – can be reduced by various robotic strategies of spatially differentiating weeding action within the field. We compare this trade-off reduction against a completely proportional trade-off as a theoretical benchmark (black line in **Fig.2**) where each unit of yield gain through weeding would be associated with a proportional loss of weed biodiversity. Notably, we do not claim that such a proportional trade-off function is supported by empirical evidence in farming systems, let alone that this relationship is causal. In fact, when the relationship between yield gain and weed biodiversity is currently inconclusive (Colbach et al., 2020), and

the relationship is indirect and governed largely by farming intensity (Berquer et al., 2023). Armengot et al. (2013) showed that in a conventional farming system with variations in herbicide application levels, cereal yields were high and weed richness low at high herbicide input levels. On the other hand, there are also studies showing that the opposite can be the case, with yield loss being low at high weed diversity levels (Adeux et al., 2019; Storkey and Neve, 2018); also, in the study by Armengot et al. (2013), a trade-off was absent for the investigated organic farming system.

While in a given cropping system, the weed-biodiversity-yield gain function will be highly context dependent (Colbach et al., 2020), we use the linear negative relationship as a theoretical point of reference in a thought experiment.

Various mechanisms have been identified that would lead to deviations from such a linear negative trade-off function. First, below a certain threshold of weed occurrence, there may be no effect of weeding on yield, but on weed biodiversity; therefore, not weeding below the threshold would allow the trade-off to be reduced (also see below). Second, indirect and preventive methods of weed control such as cover cropping and crop rotation can act as compensatory measures for reducing direct weed control intensity, reducing yield losses but maintaining weed diversity. Here, we concentrate on a third mechanism that relates to the heterogeneity within the field.

Due to the heterogeneous distribution of weed species in the field, and also because not all species contribute equally to crop yield loss (Marshall et al., 2003), we expect that in an optimized weed management system the trade-off function would not be linear, but could be represented by a convex trade-off curve (**Fig.2**, green line). Here, gradually increasing weeding intensity would achieve a yield gain that only leads to a relatively small loss in weed biodiversity. The aim to minimize the trade-off between economic damages caused by weeds and the ecological benefits is well established (MacLaren et al., 2020). One approach within the framework of 'Integrated Weed Management' (IWM) (Lewis et al., 1997; Mortensen et al., 2000) is based on the idea that variations in abiotic and biotic conditions are taken into account (Zoschke and Quadranti, 2002). Specifically, since weed infestations are non-uniformly distributed across the field (Borgy et al., 2012), weed control could be limited to the areas within fields where economic damage thresholds are exceeded. Since the application specificity of current IWM systems often fails to meet performance expectations of the farmers, IWM is currently not widely practiced (Young et al., 2017).



**Figure 2**: Potential relationship between biodiversity as a function of the yield gain caused by weeding; a set yield gain of 90% of the maximum (with the maximal potential yield gain being set at removal of all weeds), with associated biodiversity effect, is shown as an example.

An accelerator for the specific application of this approach can be the development of new devices with sensors and hardware for weed control, as it is currently happening in agricultural engineering and technology (Fennimore and Cutulle, 2019; Slaughter et al., 2008; Thorp and Tian, 2004). The use of Unmanned Aerial Vehicles (UAVs) equipped with multiple sensors facilitate the identification of weed patches in the fields (Lottes et al., 2017), whereas innovations such as single nozzle control and direct injection sprayers enable spot spraying (Pohl et al., 2020). Recent research also deals with several technical approaches to distinguish between crops and weeds as well as between single weed species (Raja et al., 2020). Further, with the development of specific algorithms, autonomous robot systems are trained to manage weed removal by herbicide spray or mechanical procedures (Esposito et al., 2021).

Through the potential of autonomous decision making, partly based on artificial intelligence, and spatially highly specific applications of weed control, these new technologies could enable to push the convex curve (**Fig. 2**) closer to the optimum (green arrow), thereby minimizing the trade-offs between biodiversity benefits and yield maximization. So far, studies have focused on the economic potential of weeding robots, but there are no studies on the conditions under which the ecological potential of robotic weeding can be exploited in a targeted manner.

However, it is currently unclear on what kind of input information autonomous decisionmaking should be based in order not only to maximize yield but also to maintain biodiversity. Principally, there are various sectors from which such input information can be generated. For example, decision-making can be based on soil properties such as texture or pH, as this information is easy to generate and can be kept relatively stable through sustainable management practices (Komatsuzaki and Ohta, 2007). In areas within the field where soil properties are comparatively favourable for crop growth, increased weeding intensity could be applied to promote yield, while in areas with less favourable soil properties focus could be on biodiversity conservation (Ritter et al., 2008), so that the trade-off could be reduced. A similar approach would be to base decision-making directly on past yields. This would require yield maps serving as input information for deciding where to weed. Alternatively, spatial weed distribution could be used as input information, including the number of different species per area, the number of weed individuals per area, weed cover, or characteristics and traits of the different species.

To decide which types of input information could lead to a minimization of the trade-off between yield and biodiversity, it is necessary to investigate what effects autonomous decisionmaking based on the different input information would have on yield and biodiversity. Currently, the technologies are not yet developed to the point where real weed management strategies with decision-making based on different input information can be tested and compared in the field simultaneously. Therefore, our aim was to anticipate the imminent developments in weeding technology by simulating decision-making on weeding in nine scenarios. Each scenario is based on a different type of input information and assesses impacts on yield and biodiversity. The main objective of this study is to develop a method to identify type and amount of input information required to reduce trade-offs between crop yield and infield weed biodiversity when applying emergent weeding technology. Specifically, we aim to measure these yield-biodiversity trade-offs in different scenarios to compare the trade-off reduction against the required level of input information and thereby to be able to give recommendations to stakeholders who are concerned with the further development of new technologies, such as weeding robots. We hypothesize that trade-offs may be reduced to a higher degree if more, or more complex input information is used. While we recognize that such scenarios are necessarily based on simplifying assumptions, we believe that our study contributes to a more targeted development of new weeding technologies not only from an economic, but also from an ecological perspective.

Scenarios were based on a set of agronomic and weed data from organically farmed fields. By modelling the scenarios, we investigated (a) what kind of input information would be optimal to minimize trade-offs between biodiversity and crop yield and (b) what impacts the application of autonomous technologies based on different input information would have on the trade-off between crop yield and associated biodiversity in the field. With our scenarios we have developed a concept to quantify trade-offs between yield gain and biodiversity conservation which enables a comparison of different weeding strategies regarding their specific trade-offs. We show that for conserving overall species presence in a field (gamma diversity), input information can be relatively unspecific, while conservation targets that refer to population size of weeds would necessitate higher information specificity.

### 2.2 Methods

Here we first describe the methods for the collection of weed and agronomic data sampled at two organically managed sites in Germany, Wiesengut and Halle. Briefly, at each site, soil, weed and crop data was collected in regular grids to map spatial heterogeneity of these variables within a chosen field. Subsequently, we explain our reasoning and detailed calculation of the nine scenarios.

#### 2.2.1 Experimental Sites

The field experiments were performed on the research station for Organic Farming 'Campus Wiesengut' of the University of Bonn in Hennef, Germany and on an organically farmed field in Halle Westfalen, Germany. Both fields are located in the West of Germany with a distance of approximately 200 km to each other. The Wiesengut farm is located at 50°48' N, 7°17' E with an altitude of 65 m a.s.l. in the lowland of the river Sieg. The site is characterized by a Fluvisol soil with a silty loam texture on gravel layers with soil depth of 0.6 to 2.0 m and fluctuating groundwater level. The particular field was chosen because its soil texture was known to be strongly heterogeneous, with the depth of the gravel layer varying greatly across the field (**Fig. I.A.1, I.A.2**). We expected that this heterogeneity of soil would be reflected in spatial heterogeneity of the weed community composition (Pätzold et al., 2020), which in turn would form the basis of the principle of precision agriculture approaches. The field in Halle is located at 52°02' N and 8°20' E with an altitude of 94 m a.s.l. The site is characterized by the anthropogenic soil type 'Plaggenesch-Pseudogley', which is typical for this region of Germany.

The upper soil layer (0.5 to 0.7 m) contains loamy sand over sandy loam and in the lower layers (to 2 m) sandy clay loam (Geologischer Dienst NRW, 2009). The site Wiesengut was investigated over three years (2018, 2019, and 2020), while data at the site Halle was only collected in 2020. The fields were selected based on heterogeneity as evident from satellite images. For site Wiesengut also soil maps were consulted in order to select heterogeneous areas (**Fig. I.A.1**).

#### 2.2.2 Setup and crop management

The field experiments were performed in a uniform regular grid (12 m distance between grid points), with 6 x 9 grid points, within an area of 72 m x 108 m at the Wiesengut site (**Fig. I.A.2**), and with 4 x 8 grid points (48 m x 96 m) at the Halle site. At each grid point, sampling was done on a plot size of 2 m x 2 m, so that the grid point was the plot centre. Parameters measured at each plot were crop yield, weed cover per species, diaspores and soil properties (see below). At Wiesengut, the grid included 54 plots in 2018 and 2019, but only a subset of 44 plots was sampled in 2020; at site Halle the sampling was done on 32 plots in 2020. Scenarios are based on 44 plots at Wiesengut sampled in 2019 and 2020, and 32 plots at the Halle site. The crops sown at the site Wiesengut were winter wheat in 2018, winter rye in 2019 and a spring-sown mixture of faba bean (cv. Fanfare) and oat (cv. Max) in 2020. At the Halle site in **Table 1**.

#### 2.2.3 Measurement of soil properties

Top soil sampling was conducted by means of a hydraulic cylinder (12 cm diameter, 15 cm sampling depth). In each plot, six samples were taken at a distance of 30 cm. One mixed soil sample was prepared from the six samples per plot and weighed. Soil samples were also taken for the examination of diaspores (see **Appendix I.A.2**). After drying at 105 °C for 10 hours, rolling and sieving (2 mm), soil samples were analysed for pH (10 g samples, VDLUFA method (Thun, 1991)), C/N ratio (20 ml of ground soil, Seal C/N analyser), P and K content (ground soil sample material, VDLUFA method (Thun, 1991)). As a measure of soil texture, the proportion of fine soil fraction was determined as mass of particles < 2 mm relative to total dry matter.
# 2.2.4 Sampling weed vegetation

The vegetation was surveyed on two dates per year to record both early and later germinating species (**Table 1**). Weed species were identified to species level and the respective percentage cover of the different species was visually estimated (Andújar et al., 2010; Lotz et al., 1994; Vitta and Quintanilla, 1996); To facilitate cover estimation, each 4m<sup>2</sup> plot was divided into four parts.

	Wiesengut			Halle
	2018	2019	2020	2020
Crop	winter wheat	winter rye	faba bean - oat - mixture	summer barley
Sowing density	450 seeds m <sup>-2</sup>	300 seeds m <sup>-2</sup>	176 kg ha <sup>-1</sup> faba bean; 20 kg ha <sup>-1</sup> oat	320 seeds m <sup>-2</sup>
Sowing date	Sowing date 2017-11-18 201		2020-03-31	2020-03-15
Harvest date	2018-08-09	2019-07-19	2020-07-23	2020-07-23
Preceding crop	clover-grass (2017)	winter wheat (2018)	winter rye (2019)	corn, spring wheat (2019, 2018)
weed control	none	none	none	harrow
Cover				
1 <sup>st</sup> sampling date		2019-04-16	2020-05-12	2020-05-12
2 <sup>nd</sup> sampling date		2019-05-15	2020-06-08	2020-07-06
Plant height				
1 <sup>st</sup> sampling date		2019-04-16	2020-05-14	2020-05-12
2 <sup>nd</sup> sampling date		2019-05-15	2020-06-08	2020-07-06
Biomass			2020-06-09	

Table 1: Dates of sowing, harvest, and data collection.

### 2.2.5 Crop and weed biomass

The biomass of weeds and crops was measured at Wiesengut on 0.25 m<sup>2</sup> of each plot on June  $6^{\text{th}}$  2020 by cutting off plants just above the soil surface. The plants were separated into faba bean, oat and weed, then fresh and dry mass of the plants were measured. For dry mass, the plants were oven-dried for 12 hours at 60°C and then for 12 hours at 105°C.

### 2.2.6 Determining the yield effect of weeding

Calculating trade-offs between yield effects and biodiversity requires data on weed diversity and on weeding effects on yield. Therefore, in 2020 four 1m<sup>2</sup> plots were kept weed-free throughout the entire growing season. Weeds were removed manually as soon as they emerged to avoid soil movement that would affect plant growth. To calculate yield effects of weeds, each weed-free plot was compared to four immediately surrounding plots. The relative yield ratio of the weed-free plots and the average yield values of their immediate surrounding plots resulted in an average yield gain effect of 14.95% through weeding. Since the weeding-induced yield gain effect is expected to vary due to the heterogeneous weed distribution, this value was adjusted to the weed load of the individual plots in the scenarios (see below, **Eqn. 1**). Since previous research has only quantified yields effect for selected species (e.g. Marshall et al. 2003), we consider this method to be suitable due to the general correlation between cover and competitiveness of plants (Vitta and Fernandez Quintanilla, 1996).

### 2.2.7 Set up of weeding scenarios

The input information on which the nine different scenarios were based are derived from the agronomic and weed data collected at Wiesengut and Halle, as well as from weed traits taken from the literature (see below). All scenarios assume that there is heterogeneity within the field that would allow some plots to be weeded, whereas the remainder of the plots would either be left untreated, or would – in some scenarios – be treated with reduced intensity. Here, weeding intensity refers to frequency of direct weeding operations such as harrowing. The decision whether to treat a plot was based on rules taking different input information into account (Tables 2, 3). The required input information for each scenario (Table 3) included seven different input criteria. (1) Spatial location was used for the *Strip* scenario; this strategy is close to the practice of some arable weed conservation programmes, where strips on the field are left untreated (Critchley et al., 2006). (2) Soil texture was used to feed the Soil scenario; here, the proportion of the fine soil fraction was used as a criterion on which the weeding decision was based, assuming that high proportions of fine soil would be associated with higher crop productivity. (3) Crop yield of the previous season was used in the Yield and the Split Yield scenarios at the Wiesengut site; for Halle, no plot-wise information was available for any of the previous years' yield. (4) Estimated weed cover was used in the Cover scenario, on a per plot basis, i.e. total cover across all species on that plot, while ground cover per species was used in the Threshold and Rare scenarios (details see Table 2). (5) Alpha diversity, i.e. the recorded number of weed species on each plot, was taken for the Alpha and the Split Alpha scenarios. (6) The frequency and rarity of weed species (Klotz et al., 2002) was used in the *Rare* scenario. In particular, weed species that are known to be regionally rare or declining (Table I.B.1) are protected in this scenario by not weeding those plots where these species occur with a predefined minimal cover. (7) Based on the assumption that less competitive weed species may be left to grow, recorded weed species were categorized according to Grime's primary CSR strategies (Grime, 1974; Hunt et al., 2004). Here, a C-coordinate of 1 is associated with competitor type species. Species with a C-coordinate of 0 were left untreated in the Threshold scenario. For the Alpha and the Split Alpha, Rare and Threshold scenarios a robot would be required to recognize individual weed species.

Six of the scenarios assume that when plots are weeded, the entire weed community is removed completely from that plot, whereas weeds on untreated plots are left intact (**Table 3**). We implied that each weed species will be removed by weeding with the same efficacy; for both the scenarios where plot-wise removal would be complete, and for those with intensity-dependent removal (see below), this represents a simplifying deviation from reality of differences in species type and weeding methodology (Cirujeda et al., 2003; Naruhn et al., 2021).

More flexibility is added in three further scenarios. In *Split yield* and *Split alpha*, cover of weeds is reduced proportionally to the defined weeding intensity in each plot; in the *Threshold* scenario, only cover of weeds is removed that exceeds a set cover threshold. In conventional systems, weeding intensity as modelled here in the scenarios would refer to the amount of herbicide sprayed, or the number of treatments or both. In organic agriculture, intensity may refer to the number of passes with the mechanical weeding device (e.g. harrow) or to the aggressiveness of the machine (angle of the tines, depth of harrowing).

To simulate decision-making (treatment or no treatment) within the scenarios, different values were applied for the respective input information. In other words, in all scenarios the quantitative criterion on which the weeding decision is based was varied from a minimal to a maximal value. For example, in scenario *Cover*, the decision rule was to treat plots with weed cover exceeding x %; here x was varied from 0 to 100% in 66 steps. For each value of x we calculated yield effect and biodiversity effect to generate the trade-off curves. We call the variable x the 'sliding criterion'.

In the *Split yield* and *Split alpha* scenarios, the sliding criterion is the weeding intensity, while the number of treated plots remains the same. In the *Split yield* scenario, plots within the field are categorized as high-yield or low yield according to last season's yield, by being above and below a set yield quantile k, respectively (here, k is set to 0.25); weeding intensity is then reduced gradually, first on the low-yield plots from 100 to 0%, while keeping weeding intensity at 100% on the high-yield plots; further reduction of intensity, with low yield plots remaining at 0% intensity is achieved by reducing intensity on the high-yield plots. Similarly, in the *Split alpha* scenario, weeding intensity is first reduced on species rich plots where alpha diversity > 75%-quantile, and further reduction is achieved by gradually reducing intensity on species-poor plots. Additionally, in the *Split yield* and *Split alpha* scenarios it is assumed that weed species with a cover  $c \le$  critical cover  $c_{crit}$  do not survive a set relative weeding intensity  $w \ge$  critical intensity  $w_{crit}$ ; here,  $c_{crit}$  was set to 0.1% and  $w_{crit}$  to 25% of maximal intensity.

#### 2.2.8 Scenario evaluation

For all scenarios and each treated plot, the respective yield gain effect from weeding was calculated assuming that it would be proportional to the removed weed cover, following eqn. (1).

$$y_i = \frac{y_e c_i}{c_e} \qquad \qquad \text{Eqn. (1)}$$

where  $y_i$  is the yield gain in plot i,  $y_e$  is the (constant) percentage yield gain in the weed-free plots (see section 2.6),  $c_i$  is the weed cover in plot i, and  $c_e$  is the weed cover in the immediately surrounding plots of the weed-free plots.

Three main weed diversity variables were chosen to evaluate the effect of each scenario on biodiversity. (1) Weed cover was chosen following the rationale that cover can be seen as an index for the size of the weed population, and that it is associated with the weeds' value for other organisms such as insects and birds (Moorcroft et al., 2002; Moreby, 1999; Newton, 2004); (2) average species richness per plot (alpha diversity); (3) total species richness on the field (i.e. gamma diversity). Note that these evaluators are, for some scenarios identical to the input information, but, crucially, not for all of them. For example, this approach allows us to assess the performance of the *Yield* scenario on the trade-off between yield and cover, or of the *Cover* scenario on the trade-off between yield and alpha diversity. We expected that scenarios would perform well (i.e. would show high values of trade-off reduction) on those evaluators which were identical to their respective input variable.

The sliding criterion within each scenario allowed us to build trade-off curves between productivity (yield gain through weeding) and biodiversity (loss through weeding), as shown schematically in **Fig.2**, as each value of the sliding criterion *x* resulted in a yield gain value and an associated biodiversity value. We chose two ways to represent these trade-off curves. (1) The first one integrated across all values of yield gain within a scenario and we call this the integrated trade-off reduction. We calculated it as the green area between the scenario's trade-off curve and the diagonal (where the diagonal represents the proportional (linear) trade-off), divided by the hatched triangular area between the top right corner (**Fig.2**) and the diagonal. Areas were obtained by summing up individual values of the dependent variable (biodiversity) for each value of the yield effect variable. This operation thus represents the scenario's trade-off reduction relative to maximal trade-off reduction. A value of 0% trade-off reduction would result from the scenario's trade-off curve coinciding with the diagonal. Negative values (i.e. curves below the diagonal) represent exacerbating the trade-off. (2) As an additional way to present the scenarios' results, the value of biodiversity gain at an arbitrarily set value of 10%

foregone yield gain (i.e. 90% yield gain through weeding, **Fig.2**) was determined, by interpolation of the biodiversity values for those yield gain values directly below and above 90%. We call this measure the diversity gain at fixed yield loss.

To test the robustness of the scenarios against variations in the data we designed further variations of the scenarios, in particular varying the standard deviation of input yields, or by removing all currently declining species from the data set (**Fig. I.A.3**).

Scenario name	Rule for decision: weeding in those plots in which criterion is met; else no weeding	Reasoning	Potential limitations
1. Strip	Plots are weeded according to spatial position in a contiguous strip.	No specific information included other than spatial position. A strip of varying size at the edge of the field is left untreated.	Heterogeneity of yield or weed community within the field is not considered.
2. Soil	Plots are weeded when fine soil proportion exceeds threshold of <i>x</i> %.	Where high yields are expected due to favourable soil properties, yield will be protected by removing weeds. Where low yields are expected due to unfavourable soil properties, its loss is accepted to use these areas for weed species conservation.	Soil properties may only be imperfectly correlated with yields.
3. Yield	Plots are weeded when the last season's yield exceeds $x %$ of the maximal yield across all plots in that year.	Where a high yield is expected based on last season's yield data, the yield is protected through weeding. Elsewhere, its loss is accepted to use these areas for weed conservation.	From the last season's yield data, it is not possible to know if poor yield on a plot was caused by unfavourable conditions or increased weed infestation.
4. Split yield	Based on last season's yield, plots are categorized as high or low yield; weeding intensity is reduced first on low-yield plots from 100% to 0%, while keeping intensity at 100% on high yield plots; further reduction is achieved by reducing intensity on high-yield plots. Total weeding intensity ( $x$ %) on the field thus varies from 0% to 100%.	Varying weeding intensity on high-yield plots while maintaining biodiversity on low-yield plots.	Weed species richness or rarity are not considered
5. Cover	Plots are weeded when weed canopy cover of the plot exceeds $x %$ .	Where weed pressure is particularly high, weeds should be removed to reduce competitive weed effects and protect yield. Where weeds cover only small areas, competitive effects are expected to be low, so weeds can be retained for species conservation.	Weed control has to be carried out at an early stage when the weeds are not yet developed enough to cover larger areas.
6. Alpha	Plots are weeded when species richness on that plot is smaller than <i>x</i> .	Where alpha diversity is low weeding is carried out in favour of yield; where alpha diversity is high, the decision is made in favour of species conservation.	Direct yield information from the plot is not considered.
7. Split alpha	Based on plot-wise weed richness, plots are categorized as species rich or poor; weeding intensity is reduced first on species-rich plots from 100% to 0%, while keeping intensity at 100% on species poor plots; further reduction is done by reducing intensity on species-poor plots. Total weeding intensity (x%) on the field thus varies from 0% to 100%.	Weeds are maintained where richness is high and weeds are treated where biodiversity is low.	
8. Rare	Plots are left untreated when cover of declining or rare species exceeds $x$ %.	Rare species are protected by leaving plots untreated where these species show larger populations.	Cover does not guarantee a sufficient number of individuals for population maintenance. Low cover of rare species leads to removal.
9. Threshold	Individual species with C-coordinate >0 (competitors) are treated when their cover exceeds $x $ %; treated species are cut down to a maximal cover of $x$ %.	Weed species with high expected competitiveness are treated, but only if their cover is expected to affect yield, so only the excess cover is removed. Species without expected competitiveness are not treated to maintain biodiversity.	Rarity or other ecologically important traits of species are not considered.

# **Table 2**: Conceptual basis of the weeding scenarios.

threshold removed

				Plot	t-wise informat	ion required	on		
Sce	enario name	Soil properties	Yield	Species richness	Total weed cover	Cover per weed species	Frequency	CSR strategy	Removal of weeds on treated plots
1.	Strip	0	0	0	0	0	0	0	Complete
2.	Soil	1	0	0	0	0	0	0	Complete
3.	Yield	0	1	0	0	0	0	0	Complete
4.	Split yield	0	1	0	0	0	0	0	Intensity dependent
5.	Cover	0	0	0	1	0	0	0	Complete
6.	Alpha	0	0	1	0	0	0	0	Complete
7.	Split alpha	0	0	1	0	0	0	0	Intensity dependent
8.	Rare	0	0	0	0	1	1	0	Complete
9.	Threshold	0	0	0	0	1	1	1	Cover exceeding

**Table 3**: Seven different information requirements and type of weed removal in the nine different weeding scenarios; 0: information not required; 1: information required for decision on weeding.

## 2.2.9 Statistical analysis

The linear correlations between fine soil proportion and alpha diversity, weed cover, biomass and grain yield measured variables in 2020 and 2019 at Wiesengut were calculated by regression analysis with the 'lm' function of the open source program R Studio (R Core Team, 2020).

The scenario analyses were performed with Microsoft Excel and the statistical analysis with R Studio as well. Species accumulation curves were calculated with the package *vegan* (Jari Oksanen et al., 2022) and its function *specaccum*, method='random', with 1000 permutations. In order to examine the results of the scenarios for significant differences, an analysis of variance of the mean values of the respective scenarios of all sites and years (Wiesengut 2019, Wiesengut 2020, Halle 2020) were conducted on the two variables of trade-off reduction (see section on scenario evaluation above). Subsequently, mean comparisons were done with a Tukey HSD test at a significance level of  $\alpha$ =0.05 with the package *rstatix* (Kassambara, 2023).

# **2.3 Results**

### 2.3.1 Characterisation of soil properties, diaspore bank and weed vegetation

At the Wiesengut site, the proportion of fine soil fraction ranged from 26.2% to 92.6% (**Fig. I.A.2**), and its spatial distribution was in accordance with the soil map of the area (**Fig. I.A.1**), e.g. the location of the gravel layer was congruent with lower percentages of fine soil. The proportion of fine soil positively correlated with the soil C:N ratio and its P and K contents (**Table I.B.2**), and with grain yield in both years, but not with weed cover (**Table 4**).

Gamma diversity of weed vegetation (number of weed species on the entire field) was 32, 34 and 33 in Wiesengut 2019, Wiesengut 2020 and Halle 2020, respectively. For these three environments, the observed mean alpha diversity of (average number of weed species per sampling plot) was 18.4, 12.1 and 13.1, respectively. Differences between the environments in alpha and gamma diversity were also in accordance with the species accumulation curves (**Fig. I.B.1**), i.e. the expected number of observed species as a function of sampling effort. The variation in distribution of the different weed species is also shown in heat maps of four key species of the soil diaspore bank at Wiesengut 2018 (**Fig. I.B.2**).

		Fine soil proportion [%]	R <sup>2</sup>
	Number of species	*	0.07
2020	Cover	n.s.	
	Biomass (weeds)	n.s.	
	Biomass (total)	**	0.21
	Grain yield	***	0.36
2019	Number of species	n.s.	
	Cover	n.s.	
	Grain yield	**	0.15

**Table 4**: Linear correlations of the proportion of fine soil fraction and alpha diversity, weedcover, biomass and grain yield measured variables in 2020 and 2019 at Wiesengut.

Significance levels: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

### 2.3.2 Scenarios

The weeding scenarios simulating partial treatment within the field exhibited strongly different shapes of the trade-off-function (**Fig. 3**). With regard to mean weed species richness per plot (alpha diversity), some scenarios that do not consider biodiversity in decision making (*Strip*,

Soil, Yield) showed nearly proportional trade-offs, i.e. were close to the diagonal, meaning that one unit gain in yield would be associated with a corresponding unit loss in biodiversity. Other scenarios which are based on plot-wise weed information (*Cover*, *Alpha*) were more similar to the convex curve described schematically before (**Fig. 2**). The *Rare* scenario showed a tradeoff function below the diagonal, i.e. with the weeding decision leading to a worse than proportional trade-off between yield and weed alpha diversity. A step-wise shape was observed for the *Split yield* and *Split alpha* scenarios. Here, four stepwise gains in biodiversity were seen when gradually reducing weeding intensity down from maximal intensity. For the *Split yield* scenario these steps were associated with (i) moving from maximal intensity to reduced intensity first on the low-yield plots, then (ii) reducing intensity below the threshold (critical intensity  $w_{crit}$ ) at which species with small cover ( $c_{crit}$ ) can survive, then (iii) reducing weeding intensity also on the high-yield plots, and finally (iv) reducing intensity below  $w_{crit}$  on these high-yield plots. In the *Split alpha* scenario, analogous steps were seen when reducing intensity first on the species-rich and then on the species-poor plots.

Regarding gamma diversity, i.e. species richness across the entire field, almost all scenarios show a convex curve, with the exception of the *Split yield* and *Split alpha* scenarios, where again step-wise behaviour was observed (**Fig. 3**). Finally, considering weed cover as the evaluator, all scenarios except the *Threshold* scenario were very close to proportional trade-off. When the trade-off curves are summarized (as area between trade-off curve and diagonal) (**Fig. 6a**) trade-off reduction was generally high (>60 %) for gamma diversity in comparison to the other two evaluators (alpha diversity and cover). Even with the *Strip* scenario, for which no particular information is required (**Table 3**), the trade-off between yield gain and gamma diversity can be reduced by 69 %. In the majority of scenarios, trade-off reduction was higher for alpha-diversity than for weed cover. However, relative trade-off between alpha diversity and yield gain effect was only reduced in three scenarios by >10%. The scenario with the highest values across all three evaluators was the *Threshold* scenario, reaching trade-off reduction between yield and alpha-diversity was also observed in the *Split Alpha* scenario.

In addition, the biodiversity gains for alpha and gamma diversity and cover of the different scenarios are presented for a set yield gain of 90%, i.e. a forgone yield gain of 10% that would be associated with a (partial) reduction in weeding (**Fig. 6b**). Results were similar as when calculated from area between trade-off curve and diagonal. At an estimated forgone yield gain of 10 % the gamma diversity gain was >50 % in all scenarios. In the *Threshold* scenario the

gain was 100 %. The alpha diversity gain was also 100% in this scenario while it was considerably lower in all other scenarios. The biodiversity gain for weed cover ranged from 8.7 % to 14.7 %, except in the *Threshold* scenario where the gain was 77.2 %.

The trade-off behaviour of the scenarios was generally robust against artificially changing yield heterogeneity across the plots (**Fig. I.B.5**), and against artificially reducing the species pool (**Fig. I.B.6**).



**Figure 3**: Biodiversity-productivity trade-off curves for the Wiesengut 2020 dataset, showing alpha diversity (mean number of species per plot across the field) (a, b), gamma diversity (i.e. total number of species on the field) (c, d), and percentage ground cover (e, f) as function of yield gain effect [%] for nine different weeding scenarios, namely the *Strip, Soil, Yield, Split yield*, and *Cover* scenarios (a, c, e) and the *Alpha, Split alpha, Rare* and *Threshold* scenarios (b, d, f).



**Figure 4**: Biodiversity-productivity trade-off curves for the Wiesengut 2019 dataset, showing alpha diversity (mean number of species per plot across the field) (a, b), gamma diversity (i.e. total number of species on the field) (c, d), and percentage ground cover (e, f) as function of yield gain effect [%] for seven different weeding scenarios, namely the *Strip, Soil*, and *Cover* scenarios (a, c, e) and the *Alpha, Split alpha, Rare*, and *Threshold* scenarios (b, d, f).



**Figure 5**: Biodiversity-productivity trade-off curves for the Halle 2020 dataset, showing alpha diversity (mean number of species per plot across the field) (a, b), gamma diversity (i.e. total number of species on the field) (c, d), and percentage ground cover (e, f) as function of yield gain effect [%] for seven different weeding scenarios, namely the *Strip*, *Soil*, and *Cover* scenarios (a, c, e) and the *Alpha*, *Split alpha*, *Rare*, and *Threshold* scenarios (b, d, f).



**Figure 6:** Integrated trade-off reduction (a) and diversity gain at fixed yield loss (b), as defined in section 2.8, for the different scenarios with regard to the variables cover (green), alpha diversity (grey) and gamma diversity (blue), mean (bars) and standard error (error bars) across three environments (Wiesengut 2019, Wiesengut 2020, Halle 2020). For the values of the *Yield* and *Split yield* scenarios, no standard error could be calculated, as historical yield data was available only for one of the three environments (Wiesengut 2020). Letters indicate statistical differences according to Tukeys HSD test.

# **2.4 Discussion**

In the field experiments, heterogeneity was found for soil properties, yield and weed distribution. Thus, we found the collected data particularly suitable for the calculation of our scenarios, as the principle of IWM is based on natural heterogeneity (Lewis et al., 1997; Young et al., 2017). The results of the calculated scenarios differ depending on the biodiversity parameter considered. We hypothesised that with a higher level of input information in the scenario, a stronger reduction of trade-off between biodiversity conservation and yield effect could be achieved. For the biodiversity parameter of gamma diversity, this hypothesis could not be confirmed. The trade-off could already be reduced with a low-level input information as the spatial arrangement of plots (*Strip* scenario) and trade-off reduction was not significantly lower than in scenarios with higher levels of input information.

However, with regard to the biodiversity parameter of alpha diversity, our hypothesis was confirmed. The scenario with the highest level of input information (*Threshold*) reduced the trade-offs of alpha diversity and yield effect significantly more than the other scenarios. Since alpha diversity takes into account the distribution and abundance of weeds (in contrast to gamma diversity), we consider this parameter to be more meaningful for the long-term maintenance of in-field biodiversity. As a limiting factor in modelling, we identified a major gap in research regarding competitive effects of individual species in field-level weed communities as well as the response effects of weeds remaining in the field during selective removal.

### 2.4.1 Site heterogeneity

At the landscape scale, trade-offs between crop yield production and biodiversity conservation have long been recognized (Groot et al., 2007) and various strategies to resolve this tension have been suggested (Smith et al., 2012), often with the recommendation to financially compensate farmers for biodiversity friendly measures (Scheper et al., 2023). At a much smaller spatial scale, namely within a field, reducing the trade-off between biodiversity and yield may be achieved by exploiting the underlying natural heterogeneity. Specifically, a requirement for a targeted spot-weeding, as we simulated it in our scenarios, is spatial heterogeneity within the field (Gerhards et al., 2022; Nordmeyer, 2006), thereby enable a 'land sparing' approach (Albrecht et al., 2016) within the field. In fact, spatial heterogeneity has itself be used to explain high species richness (Tilman, 1994). The results of the field experiments showed the presence

of such heterogeneity in different potentially relevant parameters such as soil texture and weed diaspore distribution.

At the Wiesengut site, the proportion of the fine soil fraction varied as expected from the existing soil map. The spatial variability of weed species, both in the soil diaspore bank and the emerged vegetation within the field, were confirmed by the results of the species accumulation curves. Some plots contain high diversity, which is why the curves rise quickly at first. From an ecological perspective, it might be efficient to spare particularly these plots from weeding, also because high weed diversity may mitigate yield losses (Adeux et al., 2019). However, the fact that the curves flatten out but continue slightly increasing shows that with increasing sampling effort, new species are still being added. Thus, to protect the entire diversity with all its species present in the field, a larger number of plots is necessary. Soil diaspore banks contain the accumulated number of species over years. Thus, the number of species is much higher than the actually emerged number of species during a vegetation period, which is why a higher sampling effort is needed for the soil diaspore bank (longer increase of the curve) (Thompson and Grime, 1979). However, it remains to be considered that the results of the species accumulation curve could depend on the spatial scale. In this study, the sites included here are relatively small. On a larger scale as field-scale or landscape-scale species accumulation curve might be altered, as there could potentially be a greater heterogeneity in species localisation across the larger area. Instead of using individual species, an alternative approach that could be included into robotic weeding would be the consideration of the weed's functional traits, targeting the weed community's ecological functions. On the other hand, this might lead to losing sight of the conservation of rare species if their contribution to the community's performance is small.

The heterogeneities of the different parameters were partly correlated (e.g. fine soil proportion and grain yield). These correlations justify the option of a 'short-cut', which would require less technical effort. For example, due to the observed correlation, instead of the number of weed species, the proportion of fine soil could serve as input information, which is easier to measure and constant over time. Such correlations have also been found in previous studies (Pätzold et al., 2020). However, in the current study, species richness could only be explained by 7% by the proportion of fine soil, and neither weed biomass nor weed cover correlated with it. One reason for the lack of such correlations may be carry-over effects, i.e. species are distributed to less favourable areas by machinery during tillage (Benvenuti, 2007). The small-scale heterogeneity of the site Wiesengut might amplify this effect. Another reason may be the complementary reaction of different species to soil properties. For example, the number of *Solanum nigrum* diaspores tended to increase with the proportion of fine soil, whereas the response was the opposite for *Arabidopsis thaliana*.

In summary, in the field experiments heterogeneity was found for soil properties and yields as well as for weed distribution. The approach of IWM is based on natural heterogeneity (Lewis et al., 1997; Young et al., 2017), which is why we found the collected data particularly suitable for calculating the different scenarios, as they are intended to optimise this approach. It remains open, to which degree trade-off reduction between weed diversity and yield gain is (quantitatively) affected by the degree of spatial heterogeneity.

### 2.4.2 Input information required by the scenarios

Exploiting the natural heterogeneity of weed growth within the field can be done with different technologies that vary not only in the way they operate, but also in terms of what kind of input information is processed (Allmendinger et al., 2022; Gerhards et al., 2022). In fact, because weed species classification is computationally expensive, driving speed with such technology is lower, generating a trade-off between the complexity of input information and the area treated per unit time (Allmendinger et al., 2022). The scenarios were based on different types and levels of input information. Depending on this level, the technical effort for the application of the modelled scenarios in the field differs. Some technologies for the implementation already exist while others are not yet developed (Gerhards et al., 2022). The scenario with the lowest level of required input information is the Strip scenario. Here, no site or plot-specific information would be needed, as it simply follows the spatial arrangement of the plots. In fact, as the Strip scenario assumes that a contiguous strip of plots is weeded, it is not only undemanding in terms of input information, but also technically, since the weeding device could be simply be switched off or lifted off the ground on the untreated strip. Thus, this scenario constitutes a benchmark against which more specific, targeted approaches of weeding can be compared. Another scenario requiring relatively low levels of input information is the *Soil* scenario. Here, a georeferenced soil map and a GPS-controlled vehicle that acts based on this map, is needed. The required technologies are already used in practice (Gerhards et al., 2022; Gerhards and Oebel, 2006; Mink et al., 2018). For the Yield and the Split yield scenario, a yield map of the last season would be required; apart from that, the requirements would be the same as for the Soil scenario.

The scenarios mentioned so far are based on information that is generated in advance. Thus, required technologies would not have to be able to do real-time decision-making, which keeps

technical effort for these scenarios relatively low. For the following scenarios, a weeding technology would need to respond to information that is just generated (unless one accepts the extra effort of two crossings, collecting information during the first crossing and intervening during the second). For these scenarios, the actual emerged weed vegetation forms the basis of decision-making. The scenario with lowest level of input information is the Cover scenario. In most cases, a high coverage of a plant means a high level of competitiveness, as the resource of light can be used more effectively, while neighbouring plants are shaded (Goldberg, 2012; Grace, 2012). Using weed cover as a basis for deciding whether or not to remove weeds therefore appears to be a relatively simple and useful way of deciding which plots have high weed pressure and therefore where weeds need to be removed to protect yield. Technically, these requirements can already be met today (Castaldi et al., 2017). A problem with the practical implementation of this strategy may be that weed control has to be carried out at an early stage, when the weeds are not yet developed enough to cover larger areas. The question therefore arises as to whether information on cover at seedling stage is meaningful enough to predict where the competitive effect will start. However, it would be conceivable to use last year's weed maps for this scenario. More problematic might be that typically weed germination and development is drawn out over a long time, so that information collected on weed cover could be extremely short-lived.

By running the Alpha and Split alpha scenarios, the robot would need to be able to differentiate between weed species to determine on which plots the weed diversity is particularly high and where not. In research, there are already algorithms that learn to recognise weed species (Hasan et al., 2021), and the technology begins to be commercialized (Allmendinger et al., 2022). For most studies, however, the distinction is limited to crops vs. weeds in general, (Lottes et al., 2017; Zhang et al., 2022) i.e. the actual identification of different weed species is not implemented. While distinguishing between crops and weeds may allow targeting the competitive effect of the weed community as a whole, this strategy does not provide any information about biodiversity. Thus, the existing biodiversity cannot be considered in the management, which we believe is a major research gap. Current development of new technologies is particularly focused on the economic benefits i.e. maximising yield without specifically promoting biodiversity. In our study, the Alpha and Split alpha scenarios were used to test whether the trade-off between yield and biodiversity could be minimised by considering plot-wise information on weed species richness. When robots are able to distinguish different weed species, it is also possible to feed in known additional information of these species, as we did in the Rare scenario, where regional rarity and population trends were considered.

One of the most central traits of weed species on which a targeted weeding strategy depends is the species' effect on yield. To be able to model the impacts of individual weed removal on yield, it would be necessary to know the respective yield effect of each species. While there are studies in the literature that quantify the competitive effects of individual species (Marshall et al., 2003; Marshall et al., 2001; Wilson et al., 1995), the number of species for which such information is available is currently limited, with major gaps especially for rarer species. In addition, effects will to some degree be context dependent, i.e. interact with site properties (Dieleman et al., 2000), and with the weed community in which the species is present due to niche differentiation, so that transferability to new sites may be questionable. Further, even if these respective effects would be known, it would be difficult to predict how the other present species would behave if a specified target species were removed (Mariotte, 2014; Poggio and Ghersa, 2011), though recently Lang et al. (2021) quantified the response of some rare weed species to the reduction of crop and weed cover. Due to current lack of alternatives, we therefore decided to adjust the average yield effect to the individual weed species by using their respective weed cover. In this gap of information, we identify an important limit to a more targeted use of the new technologies. Even if an autonomous robot was able to identify weed species and remove individual plants, it is currently not possible to predict what impact this selective removal would have on crop yield, or weed biodiversity, without making relatively strong assumptions.

In the *Threshold* scenario, we assumed that weed species are cut down to unharmful cover when they have a known negative effect on yield. In practice, it would also be conceivable to programme a weeding robot to remove only a specific problematic weed species. However, as we could not detect any significant correlations between yield and a specific weed species in our field experiments, we followed a more general approach by linking the established CSR classification, which is available for many weed species, including rare ones (Hunt et al., 2004) to the weeding decision, but in quantifying yield effect assumed that individual yield effects of the treated community would be unaffected by the treatment-induced shift in dominance of the different species.

# 2.4.3 Which scenario is best at reducing trade-offs between biodiversity and productivity?

The main aim of this study was to find out which scenarios are most suitable to reduce tradeoffs between yield effect and the various biodiversity parameters, and compare this performance against the required level of input information. Our hypothesis was that trade-offs may be reduced to a higher degree if more input information is used. In contrast to this expectation, we found that gamma diversity, across all scenarios, is maintainable to a large degree, even with no specific information input as in the *Strip* scenario. This can be explained by the sampling effect, reflected in the species accumulation curves. A few plots already represent a large proportion of the species present in the field, while with every further plot that is sampled (or left untreated), the increase in the cumulative number of species declines. This might be different according to the spatial scale at which these scenarios are operated. Due to a greater heterogeneity in species distribution across a larger area (e.g. on farm-level or landscape-level) the species accumulation curve might be altered.

The fact that the Strip scenario already performed well in terms of trade-off reduction for gamma diversity raises the bar for more targeted (robotic) weed control. Our results showed that for reducing the trade-off between yield and gamma diversity, no scenario was significantly better than the Strip scenario, with the only exception of the Threshold scenario for the biodiversity gain at fixed yield loss. This indicates that gamma diversity at the field level may be protected with relatively little informational or technical input. However, potential edgeeffects near field boundaries, such as higher weed species richness, may alter these relationships, depending on where the strip is placed in relation to the field margin. Also, for maintaining long-term biodiversity in the field, conservation of gamma diversity alone is not sufficient, as for the conservation especially of rare species, population size and spatial fragmentation are also decisive factors (Brütting et al., 2012). However, when other evaluators (mean alpha diversity per plot, or cover) are considered, which would help to ensure longerterm conservation, differences between scenarios become more apparent. The *Rare* scenario was generally weak at trade-off reduction while the Threshold scenario consistently performed best amongst the scenarios, i.e. it was by far the best in terms of maintaining maximal biodiversity at given yield loss and for relative trade-off reduction. This is because there is a threshold above which all species are maintained and non-competitive species can remain in all cases, which is in line with general approach of integrated weed management (MacLaren et al., 2020; Zoschke and Quadranti, 2002). Some scenarios, despite substantial required input information did not perform well in terms of trade-off reduction, e.g. Alpha and Rare. The rule for the Rare scenario was to protect weeds when their cover exceeds a set threshold. Because yield effects were tied to cover (Eqn. 1) this means that the *Rare* scenario had a built-in tradeoff.

Our findings show that to maintain long-term biodiversity within the field, in contrast to the gamma diversity, in a targeted manner, a high level of input information and thus a high technical effort is required. It is not possible to approach the optimum with a 'short-cut' with less information or technical effort. Technical development for the required conditions is progressing rapidly in research (McCool et al., 2018; Redwitz et al., 2022; Slaughter et al., 2008; Thorp and Tian, 2004) while the bigger issue is the described research gap on the quantification of competitive effects of individual weed species. Although new technologies are indeed promising to improve in-field biodiversity (Bajwa et al., 2015) stakeholders involved in their development should be aware of the fact that precise application alone is not satisfactory to reduce trade-offs between yield gain and biodiversity conservation. Rather, new technologies need to be integrated into the context of IWM that specifically considers biodiversity conservation (MacLaren et al., 2020) and do not only pursue a further techno-fixed approach, even if this requires a lot of input information and technical effort, as shown in this study. The biodiversity of weeds also benefits the associated biodiversity as pollinators, birds and other fauna (Kubota et al., 2015; Marshall et al., 2003; Tamburini et al., 2020). These traits can

also be built into the scenarios, but their performance may be dependent on the way in which they enter the model, i.e. either weighted by cover or by richness.

### 2.4.4 Scenario variations

We also tested whether spatially selective weed management is also worthwhile in less heterogeneous crop stands. The *Threshold* scenario was even effective under the condition of 0 yield heterogeneity. Weaker scenarios did not improve regarding trade-off reduction and maintainable biodiversity under a given yield loss, but some parameters as the cover benefit from higher yield heterogeneity.

Since only 9.1% of agricultural land is managed organically (Statistics | Eurostat, 2023), it can be assumed that on most agricultural sites there is less species diversity than measured in this study (Roschewitz et al., 2005). The results of the scenarios were robust against impoverishment of weed flora. If currently declining species are assumed to be missing completely, differences of scenario outcomes in comparison to real data (Wiesengut 2019) are only small. Robotic weeding and complex weed management strategies could therefore be beneficial not only for sites with high weed species diversity, but also for sites that are already impoverished in terms of biodiversity. However, it remains difficult to foresee how specific

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these findings might be to the particular weed communities present, or at different spatial scales. Further research is needed to clarify this uncertainty.

# **2.5 Conclusions**

For weeding robots to be able to reduce the trade-off between yield maximisation and biodiversity conservation through autonomous in-field decision-making, a high level of input information and technical devices are necessary. While we show that no specific information may be required to maintain gamma diversity (total number of species in the entire field) to a large degree, this is not sufficient for population maintenance and thus the long-term conservation of biodiversity. To maintain also alpha diversity (number of species per plot), information on (i) the number of species per area, (ii) weed quantity (weed cover per species), (iii) C-component according to Hunt et al. (2004) and (iv) the application of certain thresholds are required. Consequently, a robot would have to be technically capable not only of distinguishing between crops and weeds, but also of distinguishing between individual weed species, measuring weed cover, processing this information in real time and removing weeds at a per-plant level. Due to the high functionality of weed in the agro-ecosystem (support of pollinators or birds), it may be promising to integrate the associated biodiversity into decision-making.

As a limiting factor in modelling, we identified a major gap in research regarding competitive effects of individual species in field-level weed communities as well as the response effects of weeds remaining in the field during selective removal. Without valid data on these effects, predictions about the impacts of weed management on yield will inevitably remain based on simplifying assumptions (as e.g. expressed in Eqn 1). In addition, the question of how such robotic weeding affects the soil diaspore bank and what selective pressure will exert on weed population in the long term, currently remains unclear. Further research is needed in these areas to assess the ecological potential and of robotic weeding.

A recent review on the trade-off between weed diversity and yield found high complexity and inconsistent results due to heterogeneous methodology (Colbach et al., 2020); in particular, the question of yield effects of herbicide reduction critically depends on the condition whether or not other compensatory methods of weed control are introduced when reducing weeding intensity (e.g. by reducing herbicide application frequency). Here we have concentrated on variations in the spatial distribution and intensity of direct measures of weed control. This method that exploits heterogeneity within the field and compensatory measures of indirect weed

control can therefore be seen as complementary approaches that may both help to reduce tradeoffs between maintaining weed diversity and protecting crop yield.

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**Data availability** The dataset generated during the current study is available as electronic supplementary material.

# **Conflict of interest**

The authors declare no conflict of interest.

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# **3** Does weed diversity mitigate yield losses?

# Marie L Zingsheim<sup>1\*</sup>, Thomas F Döring<sup>1</sup>

<sup>1</sup>Institute of Crop Science and Resource Conservation, Department for Agroecology and

Resource conservation, Bonn, Germany

# \* Correspondence:

Corresponding Author

marie.zingsheim@uni-bonn.de

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### Abstract

While intensive control of weed populations plays a central role in current agriculture, numerous studies highlight the multifaceted contribution of weeds to the functionality and resilience of agroecosystems. Recent research indicates that increased evenness within weed communities may mitigate yield losses in contrast to communities characterized by lower diversity, since weed species that strongly affect crop yields, also dominate weed communities, with a concurrent reduction of evenness. If confirmed, this observation would suggest a paradigm shift in weed management towards promoting higher community diversity. To validate whether the evenness of weed communities is indeed linked to higher crop productivity, we conducted two field experiments: one analyzing the effects of a natural weed community in an intercrop of faba bean and oat, and the other analyzing the effects of artificially created weed communities, together with the individual sown weed species, in faba bean, oats and an intercrop of both crops. The evenness of the weed communities ranged from 0.2 to 0.9 in the natural weed community, from 0.2 to 0.7 in faba bean, from 0 to 0.8 in the intercrop and from 0.3 to 0.9 in oats. Neither the natural nor the artificial weed community showed significant effects of evenness on crop grain yield or crop biomass. The results of this study do not validate a positive relationship of crop productivity and weed evenness, possibly due to low weed pressure and the absence of competitive effects but suggest that also less diverse weed communities may be maintained without suffering yield losses. This is expected to have far reaching implications, since not only diverse weed communities, but also higher abundances of few weed species may contribute to ecosystem functions and may support faunal diversity associated with weeds.

# **3.1 Introduction**

With the establishment of farmland, humans created agroecosystems that differ from natural ecosystems by high disturbance frequencies and high resource availabilities through tillage and fertilization (Wet and Harlan, 1975). The resulting niches of agroecosystems are occupied by a wide variety of weeds species (O'Brien and Laland, 2012). Weeds compete with crops for light, water and nutrients, and infestation of weeds has a global potential yield loss of 34% (for wheat, rice, maize, potatoes, soybeans, and cotton) (Oerke, 2006). Therefore, weeds are controlled by several direct actions such as mechanical and chemical intervention, or indirect control measures including use of diverse crop rotations and breeding highly competitive crops (Gianessi, 2013; Liebman and Dyck, 1993; Naruhn et al., 2021; Wolfe et al., 2008). To keep economic costs of management interventions low, agricultural systems have tended to develop towards monocultures on which herbicides and fertilizers can be applied quickly over large areas. While efficient weed management does have its justification for ensuring food production in sufficient quantity and quality, weeds are not only detrimental but provide resilience and functionality of agroecosystems (Gerowitt et al., 2003; Ilic, 2023; Storkey and Neve, 2018). The different plant parts of weeds form the food basis for herbivores (Gaba et al., 2019) and thus for higher trophic levels e.g. birds (Siriwardena et al., 1998; Wilson et al., 1997). In addition, weeds provide reproduction sites and shelter to associated fauna including pollinators and natural predators of crop pests (Holzschuh et al., 2013; Rebek et al., 2006) and contribute to the reduction of soil erosion (Lenka et al., 2017; Mendez and Buschiazzo, 2015). This longterm functionality of agroecosystems is at risk. The intensification of agricultural systems has been recognized as a significant factor contributing to the global decline in biodiversity (Hallmann et al., 2017; Wagner et al., 2021) as it largely destroyed the diverse supply of niches, has led to herbicide resistances and the emergence of few dominant and highly competitive weed species (Foley et al., 2011; Storkey and Neve, 2018). Thus, there is a need to take actions in agriculture, to secure the functionality of agro-ecosystems either within or outside fields (e.g. flower strips). The ongoing debate on land sparing vs. land sharing has highlighted the advantages and disadvantages of biodiversity-promoting actions within versus outside production fields. Both approaches do have their justification (Grass et al., 2021). One landsharing action that has the potential to contribute securing functionality is the development of weed management strategies that consider both food supply and biodiversity conservation in the field. These two objectives are not necessarily incompatible and recent research has shown that not all weed species and communities are detrimental to crop production although these findings are context dependent and many species can be harmful under specific conditions (Boström et al., 2003; Esposito et al., 2023). Nevertheless, it is evident that diverse weed communities implicate a high diversity of traits, which limits the intensive niche overlap with crop plants compared to communities dominated by highly competitive and strongly adapted species to a specific cropping system (Navas, 2012; Smith et al., 2010). In particular, Navas (2012) suggested that "high [trait] divergence inducing complementarity in resource use by weeds and crop across time or space, in relation to niche differentiation, should result in a reduced impact of weeds on crops". In accordance with this, Adeux et al. (2019) found that with increasing evenness within a weed community, weed biomass decreased by 83% and crop productivity increased by 23%. Similarly, already (Cierjacks et al., 2016) found positive correlations between weed evenness and banana and coconut yields. These findings are thus also in line with theoretical expectations that weed traits conferring high competitiveness against crops, especially under nutrient-rich conditions, would also tend to suppress other weed species, thereby reducing community evenness. In practical terms, these findings might offer an in-field trade-off reduction by managing weeds towards a diverse weed community without suffering yield losses; we therefore see these results as potentially promising for future research on integrated weed management. On the other hand, in a comprehensive study on the effects of weeds on multifunctionality in agroecosystems, Gaba et al. (2020) reported that "weed diversity had no significant effects on [...] oilseed rape fruiting success", as a measure of crop productivity. Further, correlations between weed species richness and crop yield were found to be non-significant so far (Adeux et al., 2019; Cierjacks et al., 2016; Gaba et al., 2020; Stefan et al., 2021). Finally, only a few studies have so far tested relationships between weed diversity and crop yield, and, despite some significant results, these are characterized by large variance (Adeux et al., 2019; Cierjacks et al., 2016). Thus, the conclusions of these studies remain somewhat uncertain so far. Therefore, further research is needed to consolidate the picture of how weed diversity and crop productivity are related. In particular, without a comprehensive research base, the willingness of farmers to maintain weeds on their fields will remain low due to concerns about yield losses caused by weed infestation.

The aim of this study was to validate the relationship between diversity of the weed community, especially the evenness, and crop productivity by conducting two field experiments. In one experiment the natural appearing weed community was investigated, whereas in another experiment, an artificial weed community was established and studied. This enabled the measurement of both species-specific effects and the effects of weed communities varying in evenness on the crops' productivity.
## **3.2 Materials and Methods**

To investigate the effects of weed evenness on crop yield, both natural and artificial weed communities were investigated in separate, complementary field experiments at different locations. The experiment in a natural weed community enables the investigation of effects between weed species and crops as they occur naturally. However, the natural heterogeneous distribution of weeds restricts the separation of the evenness effects from species-composition effects as these compositions vary among the investigated plots. The second experiment with an artificial community enabled this separation as species-composition remains (almost) constant and only the evenness differs between plots. The range of contexts in which the experiments were conducted was increased by including two different experimental locations and three different cropping systems in this study.

#### 3.2.1 Natural weed community

#### 3.2.1.1 Experimental field site

Both experiments were located in west Germany with a distance of approximately 50 km to each other. The investigation of the natural weed community was conducted on the research station for Organic Farming 'Campus Wiesengut' of the University of Bonn in Hennef, Germany. The local climatic conditions are characterized by a mean annual temperature of 10.3°C and a mean annual precipitation of 840 mm. The Wiesengut farm is located at 50°48' N, 7°17' E with an altitude of 65 m a.s.l. in the lowland of the river Sieg. The site is characterized by a 'Fluvisol' soil with a silty loam texture on gravel layers with soil depth of 0.6 to 2.0 m and fluctuating groundwater level. The particular field was chosen because its soil texture was known to be strongly heterogeneous, with the depth of the gravel layer varying greatly across the field. Previous field experiments have shown a spatial heterogeneity of the weed community composition as well (Zingsheim and Döring, 2024), which in turn was expected to form the basis of a high variation in evenness.

#### 3.2.1.2 Setup

The experiment was performed in a uniform regular grid (12 m distance between grid points), with 44 grid points, within an area of 72 m x 108 m in spring-sown intercrop of faba bean (cv. Fanfare) and oat (cv. Max). The previous crops sown at the site were winter wheat in 2018 and

winter rye in 2019. The seedbed was prepared with a rotary harrow; no fertilization, irrigation or direct weed control was carried out.

## **3.2.1.3 Data acquisition**

The vegetation was surveyed on two dates (**Tab.6**) at each grid point to record both early and later germinating species. At each grid point, sampling was performed on a plot size of 2 m x 2 m, so that the grid point was the plot centre (Zingsheim and Döring, 2024). The frequency of present species is presented in the supplementary material (**Fig.II.A3**). Crop emergence (i.e. crop density) was counted in two rows for two meters and computed on plants per square meter. The biomass of crops and weeds was measured on 0.25 m<sup>2</sup> at each grid point on June 9th 2020 by cutting off plants just above the soil surface. Crops and weed plants were in flowering stage at this time. The plants were separated into faba bean, oat and weed, then fresh and dry mass of the plants were measured. For determining dry mass, the plants were oven-dried for 12 hours at 60°C and then for 12 hours at 105°C. Furthermore, the species-specific cover of weed plants was estimated on to dates (**Tab.6**).

## 3.2.2 Artificial community

#### **3.2.2.1 Experimental field sites**

The field experiment for the artificial weed community was conducted at the experimental and research station Campus Klein Altendorf, located in vicinity of Bonn, Germany (50°37' N, 6°59' E). A mean annual temperature of 9.6°C and a mean annual precipitation of 625 mm characterize the local climatic conditions. The soil type prevalent at the location is a Haplic Luvisol, which is derived from loess deposits. The homogeneous soil conditions ensured better control of the artificially created weed communities, which is why this site was chosen.

## 3.2.2.2 Selection of target weed species

The selection of target weed species for the artificial communities was based on various criteria. Target species were common species in central Europe and abundant in the natural weed community at Wiesengut, ensuring their native status and adaptation to faba bean, oat, and intercrop cultivation. Further, the species of the artificial community represent different taxonomic families and ecological strategy types (Grime, 1977). Finally, sufficient availability of high-quality seeds was required, as some species are not available from seed traders.

Based on these criteria, the five following species were selected: *Chenopodium album* L. (abbreviated as CA), *Lamium purpureum* L. (LP), *Stellaria media* (L.) Vill. (SM), *Vicia hirsuta* (L.) Gray (VH) and *Viola arvensis* Murray (VA). Ecological traits of the respective species are listed in **Tab. 5**.

**Table 5**: Primary strategy (Grime, 1977) (CR: competitor/ruderal; R: ruderal); competitive index (Marshall et al., 2003) with higher values indicating lower competitiveness; value for invertebrates and for seed-eating birds (Marshall et al., 2003) with number of starts corresponding to importance; indicator values (Ellenberg et al., 2001) with L: light, T: temperature, K: continentality, F: soil moisture, R: reaction, N: nitrogen (all ranging from 1 to 9), and S: soil salinity, with 0 = intolerant to salinity; X: indifferent; NA: not available.

	Primary	Primary Competitive V		Importance for	Ellenberg indicator						
	strategy	index	invertebrates	seed-eating birds	values						
					L	Т	Κ	F	R	Ν	S
Chenopodium album	CR	25	***	***	Х	Х	Х	4	Х	7	0
Lamium purpureum	R	62.5	**	-	7	5	3	5	7	7	0
Stellaria media	R	25	***	***	6	Х	Х	Х	7	8	0
Vicia hirsuta	R	NA	NA	NA	7	6	5	4	Х	4	0
Viola arvensis	R	250	-	**	6	5	Х	Х	Х	Х	0

#### 3.2.2.3 Setup

The experiment was conducted in three different spring crops (faba bean (FB), oat, intercrop of faba bean and oat (FBO)). As in the experiment with natural weeds, faba bean variety was 'Fanfare' and the oat variety was 'Max'. The crops were sown with a Hege machine in three separate blocks (i.e. the crops were not randomized across the experiment). Each block comprised 48 plots á 1.5 m width x 2.0 m length, with 6 rows of crops and 10 rows of weeds (respectively two weed rows in between two crop rows). The coulters of the sowing machine were set 2 cm above the soil surface so that the weed seeds were deposited in a strip of respectively 3 cm. As a certain minimum volume of seeds is required to ensure an even distribution of the seed over the distribution cone to the downpipes, the weed seed was enriched with 50 g of wheat grit. This method was based on a study by Wilson et al. (1995), who conducted a field experiment in which weed seed was mixed with grit to ensure even

distribution of seeds. Directly after sowing, nets were used to cover the plots until germination to protect the experiment from birds.

Each of the three separate blocks comprised two experimental factors with four replicates. Factor 1 comprised six levels consisting of the five individual weed species sown as single species ("monocultures"), and in addition, as the sixth level, as an equiproportional substitutive mixture composed of all five species, with proportions based on density. Factor 2 varied weed density with three levels (each of the five species with a proportion of 0.2). Each variant (sole weed species or mixture) was sown in a high and a low density (Swanton et al., 2015), and a negative control (no sown weeds) was added as well. The high-density variant targeted 300 weed individuals per m<sup>2</sup> while the low-density variant targeted 150 individuals per m<sup>2</sup>, with the required amount of seeds determined following germination tests. Within each of the three experimental blocks the variants (combination of the two experimental factors) were completely randomized.

Crop and weed seedlings were counted on the central square meter of each plot and all excess seedlings, as well as seedlings of other non-target species germinated from natural soil storage, were removed by hand. During the vegetation period, plots were checked and cleared of non-target weed species once a week.

## 3.2.2.4 Data acquisition

Plant density of crops and weeds was counted in each central square meter of a plot. Plant height and biomass of crop and weed plants were determined 5 times (date 1 - date 5) (**Tab.6**). Biomass samples were taken outside the central square meter to minimize disturbance of the area in which final crop yield was sampled. Four crop plants (or 2 plants of FB) and 4 weed plants (or 2 per species in mixtures) were collected per plot at each time point. Fresh weight and dry weight of the plants were determined and upscaled to g m<sup>-2</sup> by multiplying mean weights per plant by plant density (Suppl. Material A2). On June 2<sup>nd</sup>, weed cover of each species and crop was visually estimated (Lotz et al., 1994; Vitta and Quintanilla, 1996).

On August 16<sup>th</sup> the central square meter of each plot was harvested and the yield parameters including fresh biomass, dry biomass, ears or pods per m<sup>2</sup>, grains per ear or pod and grains per m<sup>2</sup> were determined.

	Natural community	Artificial Community				
	2020		2021			
Crop	FBO	FB	Oat	FBO		
Sowing density	36 seeds m <sup>-2</sup> faba bean 136 seeds m <sup>-2</sup> oat	54 seeds m <sup>-2</sup>	408 seeds m <sup>-2</sup>	36 seeds m <sup>-2</sup> faba bean 136 seeds m <sup>-2</sup> oat		
Sowing date	2020-03-31	2021-03-31				
Harvest date	2020-07-23	2021-08-16				
Preceding crop	winter rye (2019)	soybean				
weed control	none	selective				
Plant height						
1 <sup>st</sup> sampling date	2020-05-14 2021-05-14			4		
2 <sup>nd</sup> sampling date	2020-06-08	2020-06-08 2021-05-28				
3rd sampling date			2021-06-0	8		
4th sampling date			2021-06-3	0		
5 <sup>th</sup> sampling date			2021-07-1	5		
Biomass						
1st sampling date	2020-06-09		2021-05-2	7		
2 <sup>nd</sup> sampling date			2021-06-0	7		
3rd sampling date			2021-06-2	1		
4th sampling date			2021-07-0	5		
5 <sup>th</sup> sampling date			2021-07-2	0		

Table 6: Experimental details with sowing density, sowing and harvest date, and sampling dates.

## 3.2.3 Data analysis

#### 3.2.3.1 Statistical analysis

To test whether the loss of crop biomass decreases with increasing evenness of a weed community, several linear regression models were performed. The independent variables weed evenness and weed biomass were analyzed with and without taking interactions into account while the different sampling dates were considered as random factor with the *lme*–function of the package 'lme4' (Bates et al., 2015). Also crop density was included into the model as covariate, but no significant effects were found with any of the terms including crop density. Similar analyses were performed for crop grain yield and weed evenness. In addition, regression analyses were conducted for all dates separately as a strategy to determine if significance effects at individual dates might be hidden behind overall non-significant results. To test whether the effects of weed biomass and weed evenness can be disentangled in our study, regression analyses were also conducted for weed biomass as function of weed evenness.

The setup of the experiment with artificial weed community allowed investigating the competitive effects of the different weed species on crop yield separately as well. Therefore, the mean yield value of the control was subtracted from the yield values of the different variants with the different weed species (**Appendix II.A1**). The data was then analyzed applying a two-factorial ANOVA with weed species and weed density (high, low, control) as factors.

All statistical analyses were conducted with the open source program R Studio (R Core Team, 2020).

#### **3.2.3.2 Weed diversity measures**

The diversity of the natural communities and the artificial weed communities in Mix treatments were characterized through the Shannon diversity index H' (Eqn. 2) and Pielou's evenness index (Eqn. 1). In the artificial communities these indices were computed on both weed density and weed biomass. As the biomass samples in the natural communities was only separated between the three most abundant species and remaining weeds, the diversity indices for that experiment were computed based on the species-specific weed cover.

Evenness = 
$$\frac{H'}{H_{max}}$$
;  $H_{max} = ln(S)$  Eqn. 1

$$H' = -\sum_{i=1}^{S} p_i \ ln(p_i); p_i = \frac{N_i}{N}$$
 Eqn. 2

Where *S* is the overall number of species,  $H_{max}$  is the maximum diversity, *N* is the number of individuals,  $N_i$  is the number of individuals of species *i* and  $p_i$  is the relative ratio of species *i* between 0 and 1.

#### 3.2.3.3 Mixing effects

Because we sowed weeds as individual species as well as in mixture, an alternative way to test the effect of weed diversity on crop yield is to analyze absolute mixture effects of the weed communities in comparison to the average of the individual weed species. In particular, if evenness of the weed community is related to crop yield, we would expect the effect of individual weed species (i.e. evenness of 0) on crops yield to be more detrimental, on average, than of a mixed community. To analyze mixing effects of the weeds on crop yield in the artificial weed community experiments, the average of the crop yield values of the five speciesspecific plots (single weed species) were subtracted from the yield value of the respective spatially closest plots with mixed weed communities. This means that the crop yield values of the single weed species plots were calculated with a respective proportion of 0.2, which corresponds to the proportion of the sowing in the mixed variants. Subsequently, the mean values of these yield-differences (absolute mixture effects) were calculated for each experiment (FB, oat, FBO) and ANOVAs were performed to test the absolute mixture effects against zero.

## **3.3 Results**

The results of the regression analyses and mixing effects are presented below, while results of the analyses of the separate competitive effects of the different weed species are described in the supplementary material (**Appendix II.A1**).

#### 3.3.1 Evenness

In the experiment with natural weed community weed evenness based on biomass ranged from 0.2 to 0.9 (**Fig.7**). Neither the regression analysis of crop biomass and weed evenness nor between grain yield and weed evenness showed any significant effects. Only a very slightly significant, positive relationship was found for faba bean grains (separated from the intercrop) with a p-value of 0.053 and  $R^2$  of 0.086 but only with the evenness recorded on date 2. No significant relationships occurred for total grain yield of the intercrop of oat and faba bean and evenness at any date.



**Figure 7**: Crop biomass as function of evenness (based on weed cover) of natural weed community at Wiesengut in 2020 in a faba bean oats intercrop, with evenness measured on two different dates (2020-05-14, 2020-06-08) and ns = non-significant.

In the experiment with artificial weed communities, the regression analyses did not show any significant relationships between crop biomass (or grain yield) and weed evenness either. For

none of the terms in the over-all model, i.e. when date was a random factor, the calculation of the linear regressions was significant in any of the three field trials (FB, oat, FBO). Although in individual cases, significant correlations were found for the relationship between crop biomass and the both variables of weed evenness and weed biomass, these were not consistent. E.g. in FB this relationship was negative with a p-value of 0.02, but only for date 5 and in FBO it was positive in the model with date as random factor with a p-value 0.09 but was not consistent in the models of the respective dates. Weed evenness ranged from 0.2 to 0.7 in FB, 0 to 0.8 in FBO and 0.3 to 0.9 in oat (**Fig.8**). For the relationship between crop grain yield and weed evenness, no significant effects were found.

Regression analyses were also calculated with weed evenness based on weed density. However, no significant effects were detected with this analysis either. Regression analysis with weed biomass and weed evenness showed no significant correlations for either the natural or the artificial weed communities.



**Figure 8**: Crop biomass (dry matter, DM, in g per m<sup>2</sup>) as a function of evenness (based on weed biomass) of the artificial weed mixture at the five different sampling dates in three different crops, namely faba bean (a), the faba bean oats intercrop (b) and oats (c).

#### 3.3.2 Mixing effects

We did not detect any significant absolute mixture effects on crop yield when comparing mixed weed communities with the average of the single weed species (**Fig.9**). The absolute mixture effects were also not consistent across experiments and densities. In the faba bean crop, the average yield was lower in treatments with weed mixtures than with relative proportion of the single sown weeds in both density variants. In FBO and oat the yields of the species-specific variants in low density were just above those of the mix variants, while those in high density also showed a tendency for lower yields.



**Figure 9**: Difference between yield in weed mixture and yield in separately sown single weed species (CA, LP, SM, VA, VH) in high and low density variants the three crops (faba bean sole crop (FB), the intercrop of faba bean and oats (FBO), and the oats sole crop).

## **3.4 Discussion**

Recent research in the field of integrated weed management suggests to support more diverse weed communities. Most prominent in this context might be the results of Adeux et al. (2019) who found in a comprehensive study that crop yield losses are mitigated through weed diversity. These findings are promising as they unite both objectives of high crop productivity on the one hand and biodiversity conservation on the other. Furthermore, the results indicate that the possibility of limited or even no intervention in a field depends on the present diversity and considering more precisely, on high weed evenness of the weed community.

The aim of this study was to investigate the relationship between crop biomass production and weed evenness and to test whether a positive relationship between both variables can be shown, as previously reported by some studies (Adeux et al., 2019; Cierjacks et al., 2016). However, neither the results of the experiments with natural nor those with artificial weed communities validated a higher crop biomass production when weed evenness was high. Since no crop yield losses occurred in any of the weed communities in our study, it was also not possible for mitigation of yield losses to occur, either due to evenness of the weed community or any other reasons. This raises the question why the various weed communities did not cause any yield losses. One reason might have been the low biomass production of the weeds in relation to the total biomass (crops and weeds). Weed biomass as a proportion of total biomass ranged between 1 and 27% at CKA (median of 4% across all values) and between 2 and 36% in WG (median of 8%). In comparison, in a study by Hyvönen and Salonen (2005) on weeds in different cereal cropping systems, values ranged between 4 and 11%, and a similar range (4 to 15%) was observed in an intercropping study by Corre-Hellou et al. (2011). In a further study (Szumigalski and van Acker, 2005) the range was larger (1 to 88%), with a median of 14.5%. While these comparisons show that our values are broadly comparable with values found in other investigations, the weed biomass found in our study might still not have been high enough to cause any yield losses.

Another possible explanation could be that other influencing factors may have superimposed or compensated the occurrence of competitive effects, e. g., the effects of extreme weather conditions, but as we argue below, this explanation is unlikely to be valid.

In 2021, the amount of precipitation was relatively high with 487 mm from January to July (long-term average: 345 mm), which might have reduced competition between weeds and crops for water resources and enabled high crop biomass production although weeds were present

(Kaur et al., 2018). In contrast to 2021, in 2020 there was a relatively low amount of precipitation with 354 mm (long-term average: 455 mm), so water was presumably a limiting growth factor (Iqbal and Wright, 1998). Nevertheless, no competitive effects between crops and weeds occurred in 2020, as both might have suffered from drought. Whether competitive effects actually occur in the vegetation does not only depend on the availability or deficiency of a resource but also on the capability of plants to use it (Patterson, 1995). If neither the crop plants nor the weed plants are able to absorb the resources in sufficient quantities, the coexistence is not dominated by one of the two. However, as our study was performed in two years with contrasting weather conditions, we think that this is unlikely to be the decisive reason for the lack of a significant relationship between crop biomass production and weed evenness.

Higher crop biomass productivity with lower weed evenness, i.e. an effect opposite to the one which would be expected due to niche complementarity, may also occur under favorable conditions with a sufficient supply of potentially growth-limiting resources as water (see above), nutrients and light (Craine and Dybzinski, 2013). Under these conditions, crop plants can build high biomass although weeds are present as there is no need to compete for resources. Independently of the lacking competitive effects between the crops and the weed community, different weed species within that community might still compete for resources. If conditions are favorable for crops, weed species that occupy a similar niche to the crop plant might find favorable conditions as well (Borgy et al., 2012; Neve et al., 2009; Storkey and Neve, 2018). This may then result in a weed community dominated by these adapted species and decrease the evenness of the weed community (Blackshaw and Brandt, 2008; Kordbacheh et al., 2023) while crop biomass remains high. This hypothesis is partly validated by the results of our field experiment in 2021 as the accompanying weed community of faba bean was highly dominated by Chenopodium album a species adapted to spring sown crops (Aper et al., 2012; Bajwa et al., 2019a; Eslami and Ward, 2021); indeed, C. album produced 80% of the average weed biomass of the entire weed community.

Competitiveness not only depends on weed density, height and biomass but also on when these are established in relation to crop height and biomass (Valizadeh and Mirshekari, 2011). In a study of Boström et al. (2003) in which weed species were ranked according their association with the extend of yield loss, *Chenopodium album* and *Viola arvensis* did not, as assumed, emerge as important for predicting yield loss despite being abundant in the experiments. They explain this phenomenon with the fact that small-seeded species, like *C. album*, may take longer before they begin to interfere with the crop and, in the case of drought later in the spring, may

already have ceased growing before any crop interference. However, in our experimental year 2021 there was no drought in spring so that this is unlikely to be the explanation in this case. However, crops can gain a decisive growth advantage at an early stage, with the potential to suppress the competition effects of the weeds. With such an advantage of the crop plants, the effect of high or low weed evenness might be of secondary importance for competitiveness on crop production. A comparison of the average height of crops and weeds in the artificial community experiment showed a large difference even at the first sampling date in all crops (14 cm vs. 2 cm in FBO; 9 cm vs. 2 cm in FB; 18 cm vs. 2 cm in oat). In this case weed evenness might indeed have been of secondary importance regarding the competitive ability of the weed community.

For the artificial weed community, the question arises if the target weed species generally hold too little competitive power for mitigation to occur in crop yield losses through weed diversity. However, the competitive indices defined by Marshall et al. (2003) for Chenopodium album and Stellaria media were exceeded in our experiment. Furthermore, Chenopodium album is listed as one of the ten most widely distributed and problematic weed species for several crops (Bajwa et al., 2019b) which is why competitive effects would have generally been expected in our case as well. The lack of competitive effects, despite the weeds exceeding the thresholds, supports the assumption that competition effects were overlaid or compensated by other effects (Ingle et al., 1997; Lutman et al., 2000). Competition and compensation effects are strongly context dependent. We see a large gap in research on weed damage thresholds at a community level instead of at species level to predict in which weed community a certain weed species is detrimental and in which community this species is restricted in its competitive power and can be retained without crop yield losses. However, these effects are complex (Esposito et al., 2023) and it remains questionable whether this research gap can be closed satisfactorily at all. Just as essential ecological effects explain the emergence of competitive effects between crop yield and weeds, they explain the absence of these effects with high diversity of the weed community through niche complementarity, but they also explain the absence of these effects independent of a high diversity as found in this study.

Another hypothetical argument for our results may be that the variability of evenness found was just too low to show a positive relationship between crop biomass production and weed evenness. However, this was not the case. While in the study of Adeux et al. (2019), weed evenness varied from 0 to 1 with a mean value of 0.6, in our study evenness ranged from 0.2 to

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0.9 in the natural weed community, from 0.2 to 0.7 in FB, from 0 to 0.8 in FBO and from 0.3 to 0.9 in oats; thus, in all cases, evenness varied substantially.

A limitation of our results might have been the methodological differences in the calculation of evenness between both field experiments, i.e. the natural and the artificial weed communities. As for the natural weed community no species-specific biomass values were available (except for the three most abundant species), weed evenness was calculated by using weed cover instead. Although the cover might be a less precise estimate of species abundance than the biomass due to subjectivity in data acquisition (Andújar et al., 2010), Chiarucci et al. (1999) showed a highly significant positive correlation between evenness values based on weed biomass and evenness values based on weed cover. Evenness based on weed cover was also used in further research, e.g. in a study by Chamorro et al. (2016) on organic farming effects on biodiversity in Northeast Spain. Furthermore, a regression analysis between estimated weed cover and weed biomass of the three most abundant weed species in the natural weed community at Wiesengut showed significantly positive relationships between both variables (**Tab.II.A7**). This is similar to the results found by Andújar et al. (2010), where estimated weed cover and weed biomass were positively correlated. Despite these correlations, our results based on cover-based evenness need to be interpretated with caution.

In summary, we have investigated two environments with different soil properties in two years with contrasting weather conditions and with different management practices (organic, conventional) while variability of evenness was similar to the one found in the reference study (Adeux et al., 2019). In the different locations, we examined natural and artificial weed communities which included species with a high competitive potential as Chenopodium album and in which the number of individuals at least partially exceeded the competitive indices described by Marshall et al. (2003). Despite this variety of conditions, we did not find any significant relationships between crop biomass production and weed evenness or, in fact, any detrimental effect of the weeds on the crop plants. We conclude that, while even a diverse weed community might indeed have the potential to strongly reduce yield losses (Esposito et al., 2023; Navas, 2012), there are numerous conditions and compensatory effects under which this may not be observed. Possibly, the absence of competitive effects of weeds on crop biomass production is more likely when weed diversity is high. However, currently it is unclear under which (environmental) conditions this effect reliably occurs; it therefore may become of less relevance for the weed management at an individual farm. Furthermore, for farmers it is crucial whether the (potential) positive relationship between crop biomass production and weed evenness is also reflected in crop grain yield. However, neither such a positive relationship between crop grain yield and weed evenness could be shown in our study, nor was it reported in the study of Adeux et al. (2019).

In terms of methodology, we chose two complementary approaches, namely monitoring effects in naturally occurring weed communities across a heterogeneous field on the one hand, and sowing single weed species and a defined artificial community of carefully selected, locally typical weed species, on the other. A further potential method would be to manipulate real weed communities to make them more even, by removing the dominant species; this has the advantage of maintaining species and genotypes adapted to site and management, and, while possibly labour intensity, is a possible avenue to explore the relationships between crop productivity and weed diversity in future research.

Although we investigated crop mixtures (faba bean plus oats) along with their respective monocultures in our study, the design of our experiment does unfortunately not allow us to make a direct comparison between the crop mixture and its components. In a way, our investigation is complementary to a study conducted in Switzerland and Spain by Stefan et al. (2021) where various crop mixtures were compared to their respective component sole crops with regard to their effects on weed communities, but where the composition of weed communities was not experimentally manipulated. There, intercropping was shown to reduce weed biomass and diversity in one country but not in the other. If both experimental approaches are combined to independently vary the diversity of both the weed community and the crops, it is currently difficult to predict outcomes of this complex and dynamic interplay between multiple partners. Using crop-weed models could help to form hypotheses in this case before embarking on empirical studies in the field.

In this study we showed that there are also weed communities of relatively low diversity, which do not have detrimental effects on crop productivity. With the calculation of the mixing effects of the weeds, we showed that even weeds in 'monoculture' did not cause significant yield losses compared to the weed community. This might indicate that at least in some contexts, non-intervention is not only possible with highly diverse weed communities but also with lower diversity and evenness. This is of particular importance since even low-diversity weed communities may make significant contributions to ecosystem functioning. For soil erosion control it may be of greater importance whether there is a sufficient soil cover than the occurrence of many different species or a high community evenness (Gyssels et al., 2005; Lenka et al., 2017; Panagos et al., 2015). Also, as resource for the associated biodiversity, mass

flowering or a sufficient biomass of certain weed species can be beneficial or even decisive for the population development of associated species (Holzschuh et al., 2013), e.g. many phytophagous insects feed on just one or two plant families (Ward and Spalding, 1993). Therefore, the aim of weed management should be to preserve not only diverse communities, but in fact all non-competitive weed communities in the field as they are likely to contribute to ecosystem functions.

## **3.5 Conclusions**

This study was based on the assumption that an in-field trade-off reduction between crop productivity and biodiversity conservation can be achieved by managing weeds towards a diverse community, which is supported by current literature in weed research. The results of this study do not underpin these findings, possibly due to low weed pressure and the absence of competitive effects but rather indicate that also little diverse weed communities may be maintained without suffering yield losses in some cases. While the results based on weed cover as in the natural weed community need to be interpreted with caution, we consider our findings important as not only diverse weed communities contribute to ecosystem functions, but also higher abundances of few individual species, especially when considering not only weed diversity but also the associated diversity, which uses specific weed species as main food source or shelter and depend on minimum abundances of these species.

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## **Conflict of interest**

The authors declare no conflict of interest.

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# 4 Video-based monitoring of flower visitors on weed vegetation in organic farming

# Marie L. Zingsheim<sup>1</sup>, Thomas F. Döring<sup>1</sup>

<sup>1</sup>The University of Bonn, Department for Agroecology and Organic Farming; E-mail:

marie.zingsheim@uni-bonn.de.

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#### Abstract

The challenge of implementing biodiversity conservation in agriculture is becoming increasingly relevant as it is recognised as the basis for functionality and resilience of agricultural systems. Current research seeks to address this challenge through the development of highly precise and AI-supported technologies such as weeding robots. However, these technologies may fail to achieve their ecological potential without coordinated focus on the interactions between different weed species and their associated biodiversity. In this study, different weed species were investigated in terms of their associated biodiversity in form of flower visitation rates. Since visual insect observations in the field are labour-intensive, we tested a camera supported method that (a) enables a single person to take multiple observation videos simultaneously and (b) generates suitable video material for subsequent analysis. The tested method successfully generated data that allowed manual post-hoc analysis and determination of flower visitation rates, while an automated video analysis is still pending. In total, 105 hours of video material were generated at four different organically farmed sites in North Rhine-Westphalia, Germany. 182 flower visitors were recorded. With 0.67 visitations per 15 minutes, the weed species Matricaria chamomilla showed the highest visitation rate per individual. However, a larger sample size would have been required to detect significant differences in visitation rates between weed species. Further research is needed to address the lack of knowledge regarding associated biodiversity of weeds to exploit species-specific differences in decision-making by weeding robots to either remove or retain certain weeds in the field.

# **4.1 Introduction**

The importance of biodiversity conservation in agriculture is increasingly recognized as essential for maintaining the functionality and resilience of farming systems (MacLaren et al., 2020; Storkey and Neve, 2018). To reduce the impact of agriculture on the environment, current research focuses on developing advanced AI-driven technologies, such as precision weeding robots (Gerhards et al., 2022). However, these innovations may not fully realize their ecological benefits unless they integrate a deeper understanding of the interactions between various weed species and the biodiversity they support. Therefore, there is a strong need for research into the relationships between weed species and insects within agricultural ecosystems, which have so far been largely underexplored (Marshall et al., 2003).

Traditional methods of observing insects in the field to study weed interactions with associated biodiversity are highly labour-intensive and demand specialized skills in insect identification and trapping. Studies on visitation rates of flower visitors on weeds are rare and when they exist, they are often not conducted in the field, but in flower strip mixtures (Kuppler et al., 2023), in artificially planted patches (Morrison et al., 2021) or in other semi-natural or natural habitats (Sutter et al., 2017). To collect the extensive data necessary for studying plant-insect interactions, there is currently rapid development of new technologies that could facilitate such research in the future (Pegoraro et al., 2020). However, the application of such technologies has not been tested for their suitability in the arable field for studying weed flower visitors.

In this study, we tested a camera supported method that (a) enables not-trained persons in insect identification to capture multiple observation videos simultaneously and (b) generates suitable video material for later analysis, i.e. the determination of visitation rates of the different weed species.

Our work contributes to the growing body of literature on the use of video technology in ecological monitoring, offering insights into both the potential and the limitations of these systems when applied to complex, organic farming landscapes. It aims to lay the groundwork for more comprehensive studies that can translate these methodological advancements into practical applications for enhancing biodiversity and ecosystem services in agriculture.

## 4.2 Methods

#### 4.2.1 Experimental sites

To identify suitable experimental fields, the vegetation was systematically assessed across eight different sites. Four organically managed sites were finally selected for the experiment, where different weed species frequently grew in proximity, enabling a direct comparison of their specific visitation rates. All sites are located within a 25 km radius in Northrhine-Westphalia, Germany. The first site is located in the village of Birlinghoven at 50°74' N, 007°21' E, with an elevation of 106 m above sea level, and was cultivated with oats during the sampling year 2022. The second site, Villiprott, is located at 50°65' N, 007°09' E, at an elevation of 177 m above sea level, and was also sown with oats. The remaining two sites are part of the Research Station for Organic Farming 'Campus Wiesengut,' affiliated with the University of Bonn, in Hennef, Germany. The Wiesengut farm is positioned at 50°48' N, 7°17' E, at an altitude of 65 m above sea level, within the lowlands of the Sieg River. One of the Wiesengut sites was cultivated with oats, while the other was sown with an oat and faba bean intercrop.

#### **4.2.2 Data acquisition**

The sites were regularly visited after crop sowing to monitor the onset of weed flowering. When the flowering phase was reached, video sampling was started. For the video recordings, the offthe-shelf camera model Ricoh WG 80 was used. At each site, eight plots á 4 m<sup>2</sup> were marked (four at the edge and four in the centre of the field). The recordings were conducted on warm days under windless conditions and without precipitation. Before the recording was started, temperature, wind speed and cloud cover were determined with a portable thermometer and anemometer. The cameras were set up on a spike with a distance of 50 cm to 100 cm to the weed. The image frame was selected to ensure that one or more open flowers were recorded in sufficient detail to allow for the most precise possible identification of the flower visitor. Within the plots, five weed species were recorded simultaneously for at least 15 minutes by one camera respectively. In plots in which less than five different weed species were present, several individuals of the same species were recorded to utilize all camera capacities. As a total of ten cameras was available for the recordings, one plot at the field edge and one plot in the centre were recorded simultaneously. Following the completion of the first recordings, the cameras were repositioned to the next two plots, which were selected randomly and so on. Afterwards, all videos were viewed, number of visits and number of visible flowers were counted. For certain species, such as Matricaria chamomilla and Chenopodium album, the number of open flowers could not be reliably determined under field conditions. Therefore, for *M. chamomilla*, the entire inflorescence was used as a proxy, while for *C. album*, the entire individual plant was considered. Flower contact was defined as visit.

Additionally, one square meter within each video-plot served as sampling area for vegetation surveys. This survey included the determination of the number of open flowers per weed individual and number of individuals per square meter. For the determination of open flowers per species and square metre, the mean number of open flowers of five individuals was counted and extrapolated on the total number of individuals within this square metre. This data was collected to enable the extrapolation from a visitation rate per open flower to a visitation rate per individual and finally a visitation rate per area.



Figure 10: Two Ricoh WG 80 cameras adjusted for recording weeds in intercrop at the Wiesengut site.

To ensure high-quality imagery for visitor identification, the videos recorded only a portion of the open flowers provided by the respective plant. As the number of open flowers per individual can vary markedly among weed species, the parameter of open flowers per individual of the respective weed species needs to be taken into account to compare species-specific visitation rates. Accordingly, the visitation rate was determined by multiplying the number of recorded flower visitations by the average number of open flowers per individual over all vegetation plots and sites for each weed species.

# 4.3 Results

In this study, the primary aim was to test and critically evaluate the methods used, identifying a range of challenges that may complicate the subsequent processing and interpretation of the data. Rather than focusing on a detailed analysis of the collected data, the emphasis here is placed on a reflective and critical assessment of the methodologies applied. Nevertheless, some of the data collected by this video-based monitoring method is presented to give an impression of the quality of the data generated.

## 4.3.1 Weather conditions

The temperature ranged from 22°C to 30°C, with an overall average of 27°C across all sites and sampling dates. The average wind speed was 0.8 m s<sup>-2</sup>, ranging between 0.6 and 1.2 m s<sup>-2</sup>. The cloud cover varied from 0% to 100%, with a mean value of 41%.

## 4.3.2 Video recordings

In total 378 videos were recorded with 105 hours 10 minutes and 11 seconds video material in which 182 flower visitations were captured. 55% of the video material was sharp, while in 45% of the videos, the focus was either not successfully adjusted on the target flower, shifted during the recording, the flower was overexposed or leaves were pushed in front of the lens by wind (**Fig.11**). The handling of the cameras in combination with the ground spikes was very practical in the field, but the cameras occasionally overheated in the intensive sunlight. They had to be cooled down in the shade for about 5 minutes and the battery often had to be replaced afterwards.



**Figure 11**: Technical errors due to incorrectly adjusted autofocus (a), overexposure of the flower (b), leaves pushed in front of the lens by wind (c).

Over all sites and sampling dates, 20 different weed species were recorded. Some species appeared only on one site or were found in less than 10 plots over all sampling sites. Only for species which appeared at least at two experimental sites and which were recorded at least 10 times, the visitation rate was determined and presented (**Tab.7**).

	sites				Total
	Bi	Vi	Wi11	Wi5	
Capsella bursa-pastoris		4	17		21
Chenopodium album	7	12	9	17	45
Lamium purpureum		12	29	11	52
Matricaria chamomilla	2	2	4	7	15
Myosotis arvensis	3		6	4	13
Stellaria media		2	11		13
Veronica spec.	17	10	20	7	54
Vicia hirsuta	25		4	15	44
Viola arvensis		21	29	4	54
Total	54	63	129	65	311

**Table 7**: Number of recordings of the weed species at the four different sites; Biringhofen (Bi), Villiprott (Bi), Wiesengut 11 (WG11) and Wiesengut 5 (WG5).

The species *Matricaria chamomilla* showed the highest visitation-rate with an average visitation rate of 0.67 visitations per 15 minutes per individual over all experimental sites (**Fig.12**). The standard deviation was large and no significant differences between the visitation rates over all sites and locations (centre and margin) (**Fig.12**) or between centre and margin were found (**Fig.13**). As mentioned above, the focus of this contribution is on the methodological criticism and not on the detailed data analysis, which is why no further statistical analysis was carried out at this point.



**Figure 12**: Average visitation rate per 15 minutes and per individual over all sampling dates and experimental sites and locations (centre and edge).



Figure 13: Average visitation rate per 15 minutes and per open flower over all sampling dates and experimental sites.

## **4.4 Discussion**

The presented method of video-based insect monitoring of flower visitors allowed a single person, who is neither trained in species identification nor in insect trapping, to observe several species simultaneously in the field. Notably, no living beings had to be captured or sacrificed for the analysis. However, during the conduction of the field experiment several challenges and obstacles were identified, which in some instances constrained the evaluation and interpretation of the data collected. These issues are outlined and critically assessed in the following paragraphs.

In the conducted field experiments, only 55% of the recorded videos maintained sharp focus throughout the entire recording, enabling an identification of at least genus-level of the visitors. In the remaining 45% of the video material, the species identification of the visitors was not possible due to a shift of the focus, overexposure or coverage of the flower by another plant. To prevent these technical errors and to achieve a better quota in sharpness of the videos, different measures might improve the tested method. For example, shading or diffusing the shooting area could prevent overexposure of the flower and at the same time provide a better view on the display of the camera, which would facilitate adjusting the focus to the right spot. This measure might also prevent overheating of the cameras in intensive sunlight. However, it needs to be considered that shading could influence the visitation activities of insects (Arnold and Chittka, 2012; McKinney and Goodell, 2010). An alternative approach could be to utilize cameras equipped with a viewfinder, enabling users to accurately check focus and exposure settings even under bright sunlight conditions

Another challenge encountered was the high standard deviation in visitation rates of the respective weed species, despite being recorded in the same crop (except one of the two sites at Campus Wiesengut at which oat was sown as intercrop with faba bean), the sampling sites being geographically close and managed under similar (organic) farming practices. This calls into question whether the number of four sites and, at least, ten replicates over all sites, was sufficient to compare the weeds regarding their species-specific visitation rates. An increase of environments and sampling size might reduce the standard deviation. However, during the assessment of potential experimental fields, the identification of areas where different weed species coexisted in a small area (at the plot level within 4 m<sup>2</sup>) appeared to be a significant challenge. A solution for this issue might be an artificial planting of the target weed species into the field (Balmer et al., 2013; Haro et al., 2018). The same species composition in the respective sampling plots could be adjusted, enabling a direct comparison of predefined target weed

species. Planting the target species would also save the time required to assess and search for suitable plots with the natural weed composition and allow for an increase in the number of replicates within the field and across sites. For this method, it might be important to ensure that the introduced weed species naturally occur within the experimental field, as this suggests the potential presence of associated flower visitors (Durka et al., 2019).

An alternative solution to the challenge of finding plots with several weed species coexisting in spatial proximity would be to record the different species in separate plots instead of requiring them to coexist within a single plot. Given that weeds occur in patches rather than in a uniform distribution (Borgy et al., 2012), the plots could be selected to ensure that a target species is more frequently present. This might even enable recording more flowers of a species in one video frame, increasing the sampling size regarding the number of recorded flowers. However, abandoning the requirement for close spatial proximity when recording different target weed species would overlook the substantial environmental variability between plots, such as differences in microclimate and distance from the field margin and thus prevent standardized conditions. This variation could obscure direct comparisons of weed species in terms of their visitation rates, complicating the analysis. Morrison et al. (2021) attempted to address this issue by sowing weed species both as monoculture and in mixtures in separated plots using a randomized block design. Through this method, weed species might be evaluated and compared for their attractiveness to flower visitors; however, it does not accurately represent natural field conditions, especially as weeds were grown with absence of any crops. Furthermore, the artificially elevated flower density through sowing may have influenced visitation rates (Blaauw and Isaacs, 2014). Consequently, this method does not provide a realistic assessment of the ecological benefits of maintaining natural weed vegetation in the field.

Instead of increasing the number of recorded flowers, recording time may be increased to increase the sampling size. However, observing multiple flowers enhances the representativeness of the sample by capturing the natural variation among individuals (Essenberg, 2021). This broader sampling may reduce the influence of outliers and provides a more accurate and comprehensive measure of species-level attractiveness.

The sample size necessary to accurately identify relationships between plant species, especially weed species in natural communities, and associated biodiversity underscores the importance of implementing time-efficient, automated monitoring systems that facilitate large-scale data collection. Although taking videos instead of manual observations reduces time and resources in the field, the manually examination of all the footage is, nevertheless, making the method

very time consuming. All the video material needs to be viewed, which is a tedious and monotonous task. We do not recommend increasing the watching-speed above twice as fast, as above this speed visits can be completely missed. There are several devices and software which might speed up the video analysis significantly as automated move detection systems, which only record when activity occurs (Barlow et al., 2017) or software for automated motion-detection in the post-processing of the videos (Weinstein, 2015). A potential challenge for such a recording trigger or automated video analysis might be the presence of significant movement in the recorded videos that is not caused by flower visitors but by insects in the background or wind-induced motion. Furthermore, small insects might be overseen as they cause relatively small pixel movement. However, a test of the videos recorded in this study with freely accessible software such as MotionMeerkat (Weinstein, 2015) is still pending.

# **4.5** Conclusion

The method tested in this study successfully generated data suitable for manual post-hoc analysis of flower visitation rates, despite the identification of certain challenges. To mitigate technical errors, it is recommended to explore shading or diffusing the target flower as a means to reduce the risk of overexposure and camera overheating under intense sunlight. Additionally, incorporating a manual viewfinder alongside the camera display could enhance the ability to adjust focus and exposure in bright light conditions.

A key challenge in comparing and evaluating visitation rates across different weed species was the identification of areas where multiple weed species co-occurred in sufficient abundance and replication to enable a robust statistical analysis. Instead of studying naturally occurring species, an alternative approach is planting the target plants together in the field. However, this might reduce the representativeness of the results as it is not the actually natural occurring vegetation.

Given the time-intensive nature of manual post-hoc video analysis, efficiency could be substantially improved through the use of automated video analysis software. However, current software may struggle with accurately detecting small-sized visitors, as well as with differentiating motion caused by wind or insects in the background. The feasibility of automated post-hoc analysis for this video material remains to be tested.

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# 5 General Discussion

# **5.1** Collecting, integrating and assessing input information for selective weed management

In this thesis, it was investigated what would be required to exploit the potential of new weeding technologies, such as field robots, for the development of selective weed management strategies from an ecological perspective (chapter 1). Additionally, it was examined how input information for a decision support system for selective weeding may be gathered (chapter 3 & 4).

In chapter 2, it was shown that to maintain long-term biodiversity within a field without compromising yield, the weeding technology must be technically capable to distinguish between individual weed species, measure weed quantity and processes the captured information in real time. A management approach with less spatial and species-specific precision may preserve weed diversity at the field level but cannot guarantee long-term biodiversity conservation within the field. Thus, this requires a high level of technical precision for weed removal on a plant-level. Moreover, the findings demonstrate that the efficacy of such a complex weed management strategy remains robust independent of the spatial heterogeneity in crop yield and weed species richness. These findings support the need for the development of smart and precise technology not only from an economic, but also from an ecological perspective. However, these findings are based on simplified assumptions concerning species-specific mutualistic and antagonistic effects of weeds on crop yield. Furthermore, the weed effects on biodiversity parameters not only considering weed biodiversity but also biodiversity of the associated fauna could not be assessed.

For this reason, the species-specific competitive effects of weeds were analyzed (chapter 3) as well as the beneficial effects of different weed species (chapter 4) by conducting two field experiments. The following section provides a critical discussion of the methodological limitations and perspectives of both field experiments and evaluates the suitability of the resulting data as input information for decision-making in selective weeding, as it was indicated in chapter 2.

#### **5.2** Challenges in investigating competitive effects of weeds

Despite expected species-specific or community-specific competitive effects of weeds on the field trials, almost no competitive effects occurred. These results prevented a comparison and assessment of the weeds for their species-specific competitive potential and restricted adding the competitive effects as another factor in the model (chapter 2), as it was originally planned. The challenges in assessing species-specific competitive effects led to an analysis of competitiveness on a community-level instead (chapter 3). This analysis was based on the concept that if weed competitiveness decreases with increasing biodiversity, particularly increasing evenness, a selective weed management strategy might aim to establish a community that is as diverse and even as possible (Adeux et al., 2019; Storkey and Neve, 2018). However, also at the community level, no significant effects on yield in either the artificial community or the natural community occurred. The absence of these competitive effects at community level has already been discussed in detail in chapter 3. For the lack of competitive effects observed in the field experiment on the artificial monoculture-sown weed species and community, a methodological factor might have limited the detection of any significant yield reductions. Overall, the sampling size of the biomass of crops and weeds may have been insufficient. Biomass was collected from four weed plants in treatments where weed species were sown individually and from two plants in mixed-species weed treatments, leading to high standard deviations. Similarly, crop biomass sampling was limited to four plants in faba bean and oat monocultures, and two plants in intercrop settings. Due to the substantial workload involved in selective, manual weeding, counting individuals, frequent sampling and the number of experimental replicates, it was not feasible to increase the plot sizes within the scope of this study, which would have allowed for a larger sample size. This small sampling size may have biased the results by failing to capture representative biomass measurements for the respective variants. In addition to the relatively small plot size, another factor limited the sampling size for biomass. The initial experimental design aimed for a sowing density of 150 weed individuals per square meter for the low-density treatment and 300 individuals per square meter for the high-density treatment. Such a density of individuals would have enabled the collection of more plants for the biomass survey. Despite pre-experimental germination tests, these target densities were only achieved for Stellaria media. For Lamium purpureum, even in the high-density treatment, only 45, 58, and 59 seedlings per square meter emerged in intercrop, faba bean and oat, respectively. This low density limited the ability to collect more than two plants from a plot (1.5 m x 2 m) while ensuring that the central square meter remained undisturbed for final measurements of crop biomass and yield. This observation brings into question why seed germination did not occur in the field as anticipated from the results of germination tests. When comparing our germination rates in the field with those reported in the literature, varying results can be found. Olsen et al. (2006) conducted experiments over two different years, in which they sowed weeds and, deviating from the methodology used here, rolled the soil after sowing. In addition, irrigation was applied 7, 9, and 11 days after sowing in the first year, and immediately after sowing in the second year. Their study reported germination rates of 13% and 18.4% for Chenopodium album, and 14.7% and 23.1% for Stellaria media in the respective years. In contrast, our field experiment showed a germination rate of 6.1% for Chenopodium album and a rate exceeding 26% for Stellaria media, while Lamium purpureum exhibited the lowest germination rates, at 2.6%. These findings suggest that soil rolling and irrigation after sowing may promote weed germination in field experiments. These interventions may artificially alter the environment and potentially bias experimental outcomes, as irrigation may shift crop-weed competition in favour of the crop (Kaur et al., 2018; Swanton et al., 2015). However, it could be argued that the act of sowing itself introduces an artificial element to the environment and that applying uniform irrigation across all treatments may be preferable to maintaining natural conditions, which carries the risk of inadequate germination of the target weeds.

An alternative method for the investigation of species-specific competitive effects on yield production might be a selective weeding of the naturally occurring segetal flora, which would only maintain one weed species per plot. However, finding sites where multiple species coexist at densities high enough to allow for direct comparisons of their individual competitive effects is relatively rare, as also experienced and reported in chapter 4. Weeds typically grow in clustered patches across broader areas (Borgy et al., 2012) which complicates randomization. Such clustering could result in comparisons that are confounded by varying environmental conditions, including differences in soil quality, water availability, nutrient levels, and topography, which should be carefully avoided in studies investigating competitive effects (Swanton et al., 2015).

However, the absence of competitive effects across all three variants – natural communities, artificial communities, and artificial monocultures – illustrates how context-dependent the actual occurrence of competitive effects is. It is well-established that unmanaged weed communities can lead to significant yield losses (Kristensen et al., 2008; Oerke, 2006) and our results should not be interpreted as suggesting that weed management is generally unnecessary. Rather, it highlights that generalized statements about the competitive effects of either a single weed species or an entire community, in terms of biodiversity (evenness), cannot be made.

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Thus, to integrate information on competitive effects into decision-making in selective weed management, it is crucial to connect specific environmental conditions and competition indicators, such as weed cover and height, to their relationship with the associated crop plants in the field. This, in turn, requires a technology capable of identifying weed species and crops, measuring parameters such as cover or height, and additionally being able to relate these parameters to one another.

#### **5.3** Challenges in investigating beneficial effects of weeds

Chapter 2 emphasized that, beyond considering the competitive potential of weeds, their beneficial effects on associated biodiversity can also be incorporated into a decision-support system for selective weed management. For example, weed species with higher flower visitation rates, and therefore greater attractiveness to flower visitors, could be prioritized for conservation over other, less attractive weed species. As a research gap for data on species-specific visitation rates of weeds was identified, in chapter 4 a method of a video-based monitoring was introduced and evaluated that might significantly accelerate the study of interactions between weed species and their associated flower visitors. Indeed, the method enabled a person not trained in taxonomy and insect trapping to generate large amounts of video material suitable for a post-hoc analysis. The method can therefore be evaluated as time and resource efficient in terms of fieldwork. However, several technical challenges were identified, resulting in reduced image quality in 45% of the video material and thereby hindering or entirely preventing post-hoc analysis for species identification of flower visitors in the affected videos. Nevertheless, these challenges do not warrant abandoning the method; rather, they could be addressed through relatively simple measures, as discussed in chapter 4.

A statistical analysis of the flower visitation rates is still pending; however, due to the high standard deviation, significant results are not anticipated. Nevertheless, it should still be noted here that flower visitation rates in the field appeared to be relatively low to us. Unfortunately, there is a lack of comparable studies conducted on natural weed vegetation in the field, which limits the contextualization of our data within the existing literature. In other studies, examining for example, artificially sown weeds (Morrison et al., 2021) or flower strips (Kuppler et al., 2023), absolute sample sizes – such as the number of observed flowers and observation duration – are often not reported. Instead, these studies typically present results ranking plant species to show which one provided the greatest benefit to pollinators. This lack of comparable

quantitative data makes it difficult to determine whether the visitation rates we observed on naturally occurring weeds within the field are high or low relative to those in, for instance, flower strips. This information would be especially valuable in the context of the land-sharing vs. land-sparing debate (Grass et al., 2021), as it would provide insight into the relative benefits of scattered weed flowers across the field compared to a spatially concentrated flower strip. However, further research on weed-pollinator interactions within natural weed communities in the field is necessary to enable such comparisons.

The presented video-based monitoring and other methods currently being developed for automated monitoring and video analysis hold considerable promise for future research on the ecological networks of weeds and their associated fauna (Pegoraro et al., 2020). The more critical challenge in the presented method was identifying suitable sites for data collection, necessary for comparing species-specific visitation rates of weeds and achieving a sample size sufficient for statistical analysis. This large sample size is required due to the high context dependency between plants and their associated fauna. In a study by Kuppler et al. (2023) with a sample size of more than 100,000 visitations of wild bees recorded in southwest Germany (Baden-Württemberg with a focus around Stuttgart, the Upper-Rhine and Heilbronn), 34 plant species were classified as having 'high visitor richness', 56 species as having 'low visitor richness', and 93 species as having 'medium visitor richness' that did not significantly differ from visits by chance. However, comparisons between regions and with other studies reveal discrepancies in the categorization of species attractiveness. Species identified as key species for the promotion of wild bees in studies of Sutter et al. (2017) in central Switzerland, Nichols et al. (2019) in one location near Bath, UK, and Warzecha et al. (2018) in one location near Gießen, Germany, were classified as having only 'medium visitor richness' in the study of Kuppler et al. (2023). Moreover, focusing solely on wild bees provides a limited perspective on flower visitors as different plant species can enhance visitor richness and interaction frequency for wild bees (Kuppler et al., 2023) compared to hoverflies (Scheper et al., 2021). The integration of other associated groups than flower visitors makes it even more complex as a weed species that is unattractive to pollinators may still play a crucial role for other organisms, such as herbivore arthropods, seed eating avifauna (Marshall et al., 2003) or beneficial microorganisms in the soil (Ilic, 2023). This underscores the complexities involved in evaluating individual weed species based on their attractiveness to flower visitors and raises questions about how such differing and species-depending beneficial effects might be integrated into decision-making for selective weeding. Prioritizing the benefits of a specific weed species for one ecological group can inadvertently disadvantage other species or groups

and achieving a balance between the resulting trade-offs may prove to be an unrealistic goal. Two conclusions can be drawn from this: (1) Evaluations of the beneficial effects of weed species might be considered region-specific, which present challenges for their integration into a universally and automatically applied decision support system and (2) integrating such input information is only useful if a specific biodiversity goal is defined in advance. This could involve, for example, the targeted promotion of functional providing specific ecosystem services or the conservation of an endangered species (Moonen and Bàrberi, 2008).

## 5.4 Bringing it together: Outlook for further research

In chapter 2 it was indicated that technologies need to be able to identify weeds and to remove them on plant level to reduce trade-offs between crop production and biodiversity conservation within the field. Therefore, accurate weed identification represents a major challenge, as the phenotype of individuals of the same weed species can frequently appear different. In chapter 1, various approaches were described that can already correctly identify certain weed species with a high success rate (Buddha et al., 2019; Lottes et al., 2017; Olsen et al., 2019). However, reliably identifying all species, or at least a substantial portion of them under field conditions is not yet feasible and requires further research. Since the focus of this thesis is not on technological development but rather on the impacts and environmental context associated with the application of such technologies, further research in the field of technological development is not elaborated upon here. However, this research can be effectively combined with the second identified research need: the investigation of competitive effects of weeds in different environments.

In chapter 3 the challenges in studying competitive effects of weeds in several spatiotemporal environments have been described. These challenges can be mitigated by developing management strategies based on models that incorporate numerous influencing factors, such as soil properties, soil moisture, weather conditions, and inter- and intraspecific interactions (Colbach et al., 2021). In the modelling of impacts on yield and biodiversity presented in chapter 2, no weed plant parameters have yet been tested in relation to the crop plant. Parameters such as the cover and height ratio (McDonald et al., 2010) or the distance of the weed plant from the crop plant (Redwitz et al., 2024) may serve as effective, context-sensitive input information and should be tested accordingly. However, developing smart models that achieve an acceptable level of uncertainty will be highly dependent on the quality of the dataset

used to boost the generalization ability of the model. Such an "acceptable" level of uncertainty is determined by weighing the costs – such as labour and financial resources required for field experiments – against the potential benefits for improved decision-making. As technological advancements in data collection (e.g. autonomous sensors or video-based monitoring) and computational power progress, models may eventually reach a stage where additional field experiments provide diminishing returns. Until that point, fieldwork remains indispensable for validating and refining models and for addressing knowledge gaps related to novel contexts or emerging challenges. Simultaneously, the collected data can be used as training data for algorithms aimed at developing automated weed identification systems. Weed research and the development of weed identification sensor systems can thus be conducted within the same field experiments, mutually supporting each other.

Furthermore, in such interdisciplinary field experiments, the effects of selectively removing certain weed species on the remaining weed vegetation need to be studied. For instance, it is important to investigate whether the removal of a dominant weed species leads to a long-term reduction of competitive effects on the crops as another remaining species might fill the niche and develop dominance, potentially compromising the effectiveness of the intervention. Studies on the response of selective plant removal are available for grassland and meadow (Li et al., 2015; McLaren and Turkington, 2010) but are lacking for weed communities within cropped fields.

Further investigation to unravel the complex interactions between weeds and associated fauna in agricultural landscapes is needed, enabling more focused conservation efforts (Bàrberi et al., 2010). Automated monitoring systems could play a key role in advancing research on these interactions by speeding up data collection, although further developments in software for species identification and quantification are necessary for efficient post-hoc analysis (Pegoraro et al., 2020; Weinstein, 2015). A high amount of data enables comparisons of results across different environments and can feed AI based modelling (Pashanejad et al., 2023). However, generalized models can provide valuable guidance for local decisions, though primarily as a baseline. For specific decisions at a particular site, adjusting or calibrating the model with site-specific data is recommended to maximize the relevance and accuracy of predictions. Local experts as farmers themselves and conservation authorities might be involved to enable the adaption of selection and ratio of plant species to local conditions promoting local communities. To facilitate the integration of species-specific associated fauna information into a decision support system, it may be beneficial to define specific objectives. This could involve, for

example, promoting particular functional groups which provide a specific ecosystem service. However, such defined aims would not necessarily promote overall biodiversity but rather shift species community to promote crop production, which Moonen and Bàrberi (2008) defined as 'biodiversity for agriculture' instead of 'agriculture for biodiversity'. Following this approach, long-term effects need to be investigated, as applying the respective weeding strategies might create a strong selective filter on both target and non-target species (MacLaren et al., 2020).

Weed control practices inherently create a selection pressure that influences weed adaptation, with the emergence of herbicide resistance serving as a prominent example of how quickly weeds can adapt in response to intense selection pressures (Neve and Powles, 2005). However, adaptations in response to weed management extend beyond just herbicide resistance. Research has shown that repeated mowing or grazing can lead to changes in weed morphology, and phenological adaptations, such as adjustments in germination and flowering times, have also been observed (Fried et al., 2012; McKinney and Fowler, 1991). The development of new weed management technologies introduces additional selection pressures, which are likely to drive further adaptations within weed populations. Coleman et al. (2023), for example, explored the potential of image-based algorithms for weed recognition to promote crop mimicry among weeds. For this research field, an interplay of action and monitoring over several vegetation periods is needed to gain valid predictions of long-term impacts and selective pressure on biodiversity while assessing selective weeding strategies. This also extends to the development and accumulation of diaspores in the soil seed bank. Maintaining a certain level of weed vegetation increases seed dispersal, thereby expanding the soil diaspore bank. As a result, this may lead to an elevated weed pressure in subsequent years or even several years later, due to the long-term viability of weed seeds.

To bring the findings of the different studies within this thesis together, a schematic representation of a selective weeding process and its impacts on the agroecosystem was created (**Fig.14**). The figure shows the required input information, decision-making process, the required precision of intervention and the aimed impacts of a selective weed management strategy. Furthermore, remaining uncertainties which might limit or prevent the success of the applied strategy are integrated, representing further needs for research.



**Figure 14**: Schematic representation of a selective weeding process and its impacts on the agroecosystem, based on the findings of this thesis. The dashed yellow rectangle represents the type of input information both, gathered in the field by multi-sensor-systems and form a data base; the dashed blue rectangle represents the processing of the data for decision-making; the red rectangle represents the intervention; the dashed green rectangle represents the aimed effects of the applied selective weeding; the grey rectangles represent uncertainties which are not explored yet and which might limit or even prevent the success of the selective weeding.

# **5.3** Selective weeding strategies and findings relevant for future arable farming

The relevance of implementing selective weeding strategies is dependent on the environmental context and the prevailing cropping system. In industrialized countries, where landscapes are heavily anthropogenically influenced and crops are cultivated extensively as monocultures, maintaining certain weeds in the field provides a significantly larger and relatively more important contribution to biodiversity conservation than in countries where agriculture is practiced on a smaller, subsistence-based scale and is embedded within natural habitats (Tuck et al., 2014). In areas, where natural habitats have been extensively replaced by cropland, it often becomes a surrogate habitat for biodiversity (Lomba et al., 2014). Strategies like selective weeding can create ecological niches within agricultural fields, contributing to overall biodiversity (Esposito et al., 2023). Furthermore, economic factors also play a critical role, including the high acquisition costs of selective weeding technologies, global disparities in labour costs, and the need for skilled personnel to operate and maintain modern technologies.

In industrialized countries, the unresolved research questions discussed previously hinder currently the practical application of sophisticated selective weeding strategies. However, the proposed concept for strategy development is promising and could enable farmers to increase biodiversity under controlled conditions without risking yield losses from weed infestations. This approach is likely to significantly enhance farmers' willingness to adopt biodiversityfriendly strategies, particularly when specific ecosystem services are targeted. Economically, such new technologies might be particularly profitable in cash crops, such as vegetables with wide row spacing, whose cultivation is labour- and cost-intensive. Within the wide row spacing of the crops, the establishment of a controlled weed flora between the rows can function as a natural cover crop without causing costs for seed or sowing technology. Such a weed flora can provide several ecosystem services as preventing soil erosion and drying, as well as mitigating nutrient leaching (Kubota et al., 2015). Furthermore, selective weeding technologies hold potential for integration into broader precision farming systems, where data-driven approaches optimize various agricultural processes. By coupling weed detection data with systems for precision irrigation, fertilization, and pest control, farmers could manage resources more efficiently while minimizing environmental impact (AI.Land, 2024).

Given that the long-term effects of selective weeding strategies are still unknown, future research should focus on developing flexible, adaptive tools that integrate selective weeding

with other sustainable farming practices, such as crop rotation, cover cropping, and no-tillage systems (MacLaren et al., 2020).

Biodiversity is fundamentally important to civilization, contributing significantly through its roles in food production, livestock, medicine, and numerous industrial products (Ehrlich, 1992). Protecting biodiversity preserves future options and potential for new discoveries, while a loss in species diversity constrains these options and reduces flexibility in utilizing new resources. Regardless of the strategy applied in selective weed management – whether aimed at promoting general biodiversity, supporting specific ecosystem services, or conserving certain species – it is crucial to retain non-target plants as alternative resources. It is impossible to predict which species will become particularly valuable to society in the future (Díaz et al., 2018). Therefore, any intervention in the ecosystem, such as weed management, should consider that maintaining this diversity of alternatives provides an important buffer against future challenges.

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# **Appendix I: Supplementary material from article "What weeding robots need to know about ecology"**

# I.A. Supplementary methods

## I.A.1 Site description and soil properties



	Boundaries ground units
• 0 • • • • • • • • • • • • • • • • • •	Increased gravel and sand
$\leq$	Changing water conditions

Fig. I.A.1 Soil map of the Wiesengut site. The red-line rectangle contains the sampled part of the field.



Figure I.A.2 Fine soil fractions of the respective plots at the Wiesengut site

#### I.A.2 Sampling of the soil diaspore bank

Following recommendations about timing of sampling the diaspore bank (Poschlod, 1991; Thompson and Grime, 1979), samples were taken at the end of winter, on February 27<sup>th</sup>, March 2<sup>nd</sup> and March 5<sup>th</sup> in 2018, then stored outside during frost and after the end of frost stored at 6°C in the refrigerator until further processing. Sampling was conducted with a hydraulic cylinder of 12 cm diameter to sampling depth of 15 cm. Each plot sample consisted of six sub-samples taken at a distance of 30 cm. For analysing soil diaspore the emergence method was chosen in which soil samples are crumbled and vegetative plant parts are removed before they are cultivated under controlled conditions. The emerged seedlings are determined and counted (Poschlod, 1991). After pooling subsamples per plot and weighing the samples, larger soil aggregates were destroyed and large stones were removed and washed. The washing water was

later used to pour the respective planter box to reduce the risk of losing diaspores. Three planter boxes were filled with sample material from each plot. The planter boxes (30 x 40 x 6 cm) were filled with 1500 g of growing medium, standard soil type ED 73. This substrate was spread out evenly, so that the sample material could be applied evenly over in a thin layer on top. In addition, five blank samples were added to detect possible contamination of the growing medium. Contamination was found in one of the blank samples with two individuals of *Cornus saunguinea*. Since only two individuals were found in one sample, the growing medium was considered to be largely free of contamination.

Exposure in the greenhouse took place over approx. 3 months form March 15<sup>th</sup> to June 11<sup>th</sup>, 2018. Initially the planter boxes were placed in a completely closed greenhouse. On April 17<sup>th</sup>17.04.2018, the experiment was relocated to another greenhouse, as its open construction was closer to outdoor conditions than the previous one. To prevent diaspores from entering from the outside, the entire experiment was surrounded by a tightly woven gauze.

The greenhouses were not illuminated. The day-night rhythm was based on the natural conditions. The average air temperature, recorded hourly by a data logger placed between the planter boxes, was 21.9°C. The minimum and maximum daily air temperature averages were 5.9°C and 31.2°C. The average relative humidity of the daily means was 59.2 %. The minimum and maximum daily averages of the relative humidity were 43.8 % and 85.5 %.

Seedlings were recorded when new individuals emerged. Emerging seedlings were quantified, their species determined and removed from the planter boxes. The determination was done with the help of (Hanf, 1984). Non-identifiable seedlings were pricked out and determined in the flowering state with the help of (Jäger, 2017).

#### I.A.3 Variations of scenarios

To test the robustness of the scenarios against variations in the assumptions and the data, two additional approaches were pursued. First, we tested the performance of all scenarios for the Wiesengut 2019 data set with increased or decreased yield heterogeneity within the field. Specifically, while keeping everything else the same, including the mean yield across all plots, the individual yields on the plots within a field were linearly transformed to vary the standard deviation (SD) between 0 and the maximally possibly SD (**Fig. I.B.5.**).

Second, we assessed the scenarios against general impoverishment of the species pool, by artificially (*in silico*) removing all species that are recorded to be currently declining.

As an alternative way to quantify the yield effect was also tested. This assumed that the yield effect would not only be proportional to the weed cover in a plot, but also would also be proportional to the cover-weighted C-coordinate (Hunt et al. 2004) of all weed species (**Eqn.I.A.1**).

$$y_i = \frac{y_e c_i Z_i}{c_e Z_e}$$
 Eqn.I.A.1

where  $y_i$ ,  $y_e$  ci and  $c_e$  are defined as for Eqn 1, and  $Z_i$  and  $Z_e$  are the cover-weighted C-coordinate for plot i and for the experimental weeding, respectively.

# I.B. Supplementary results

## I.B.1 Weed distribution



Figure I.B.1 Species accumulation curves for each year and site

a)						b)						c)						d)					
269	225	146	140	123	228	30	20	60	44	64	34	48	37	26	33	59	38	55	112	65	35	79	75
456	108	45	103	94	124	30	32	33	28	34	40	49	44	48	36	65	45	53	45	12	55	36	50
191	74	23	38	54	379	58	88	52	108	86	29	74	63	36	39	22	43	55	48	23	54	28	44
161	26	12	30	46	78	53	58	70	113	53	85	32	39	20	19	49	59	50	34	66	21	46	31
86	50	52	39	33	181	58	33	137	119	115	101	22	13	4	30	38	37	21	13	23	59	42	52
124	75	89	87	111	80	80	41	56	64	23	85	14	58	23	6	25	12	50	29	13	16	17	16
54	52	59	37	44	28	54	40	23	60	52	43	36	12	13	37	65	51	14	11	12	18	29	30
88	151	62	55	38	25	57	31	44	39	68	23	43	25	16	37	62	53	13	21	35	7	8	10
134	85	38	48	73	42	37	38	10	16	38	53	43	6	19	33	45	56	22	23	8	9	7	10

**Figure I.B.2** Heat-maps showing diaspores in the soil per plot at Wiesengut 2018 of a) *Matricaria chamomilla*, b) *Arabidopsis thaliana*, c) *Lamium purpureum* and d) *Veronica arvensis*.

#### I.B.2 Rare and declining species

Sito

	bite				
WG19	19 WG20 Halle20		scientific name	trend index <sup>a</sup>	regional rarity index <sup>b</sup>
		х	Anchusa arvensis	2	1
х	х		Apera spica-venti	1	0
х			Aphanes arvensis	2	1
х			Arabidopsis thaliana	0	1
	х		Arenaria serpyllifolia	0	1
х		х	Centaurea cyanus	3	1
	Х	Х	Chenopodium polyspermum	0	1
х	х		Fumaria officinalis	0	1
х	х		Geranium dissectum	1	1
х	Х		Geranium molle	0	2
х	х		Matricaria chamomilla	2	0
		Х	Matricaria recutita	2	0
х	х		Papaver rhoeas	2	1
х			Ranunculus sardous	3	2
	х		Raphanus raphanistrum	1	0
	х		Solanum nigrum	1	1
		Х	Spergula arvensis	1	0
х			Veronica agrestis	3	2
11	10	5			

Table I.B.1 Recorded rare and declining weed species

<sup>a</sup> 0: stable or increasing; 1: slightly decreasing; 2: decreasing

<sup>b</sup> 0: very frequent; 1: less frequent; 2: rare

#### I.B.3 Diaspore bank at Wiesengut

During cultivation of diaspores from Wiesengut, 22,658 individuals of 68 species emerged. More than half of the 68 species germinated in less than 20% of all planter boxes. *Matricaria chamomilla* was the most frequent species with a total number of 5293 individuals and a proportion of the total number of individuals of 23% (**Fig. I.B.3**). Further dominant species in the diaspore bank included *Arabidopsis thaliana* (**Fig. I.B.4**), *Lamium purpureum*, *Veronica arvensis* and *Papaver rhoeas*.

The emergence of the soil diaspore bank was a species-rich plant community adapted to the floodplain site Wiesengut, which confirms the expectations. Nevertheless, it can be seen that the plateau of the curves of emerged weed vegetation is reached much faster than the plateau of the curve of the diaspores. This can be explained by the significantly higher total number of species, which was found in the soil diaspore bank, as this factor has an influence on the slope of the function. We do not consider soil diaspore banks to be suitable as input information, as

the effort involved in obtaining this data is extremely high and cannot be done autonomously by a field robot. However, the heterogeneous distribution of the diaspores indicates that parameters of the weed community may be suitable for exploiting natural heterogeneity in weed management and thus be suitable as input information.



Figure I.B.3 Proportion of total number of individuals of diaspores on the Wiesengut site, for the ten most dominant species.



Figure I.B.4 Example of response patterns of different weed species to proportion of fine soil (soil diaspore bank 2018, Wiesengut).

	fine-soil	pН	CN-	Р	K
	ratio		ratio		
Fine-soil ratio		0.21	0.66	0.71	0.56
pH	ns		0.09	0.14	0.13
CN-ratio	***	ns		0.49	0.28
Р	***	ns	***		0.65
Κ	***	ns	***	***	

**Table I.B.2** Correlation between different parameters of the investigation of diaspores at Wiesengut 2018; Above the diagonal: correlation coefficients; below the diagonal: significance levels: ns: not significant, (\*). p<0.1, \* p<0.05, \*\* p<0.01, \*\*\* p<0.001.

#### **I.B.4** Variations of scenarios and evaluators

It turned out that the results are mostly robust against differences in yield heterogeneity. The *Threshold* scenario remains best by far and is even effective at an assumed value of zero yield heterogeneity. Gamma diversity under these conditions is maintainable to large degree with all scenarios as well. Weak scenarios did not become any better by reducing yield heterogeneity. Weed cover benefit from higher yield heterogeneity in terms of trade-off reduction and maintainable biodiversity. In addition, it was calculated to what extent trade-off reduction and biodiversity conservation could be implemented on less species-rich areas. The results are robust against impoverishment of weed flora. If currently declining species are assumed to be missing completely, differences of scenario outcomes in comparison to real data (2019) are only small.



**Figure I.B.5** Relative trade-offs of scenarios regarding alpha diversity (a), gamma diversity (b) and ground cover (c), as function of varied standard deviation (SD) of yield between SD=0 and maximally possibly SD for the Wiesengut 2019 data set for the different scenarios, namely the *Strip Soil, Yield, Split yield, Cover, Alpha, Split alpha, Rare* and *Gamma* scenarios.



**Figure I.B.6** Relative trade-offs of scenarios regarding alpha diversity (a), gamma diversity (b) and ground cover (c)of the different scenarios between real data and impoverished data (declining species removed in dataset) for the Wiesengut 2019 data.

# Appendix II: Supplementary material from article "Does weed diversity mitigate yield losses?"

# **II.A Results**

## Precipitation

The long-term average precipitation was calculated with data of the last 30 years for Wiesengut and with the last 60 years for Campus Klein Altendorf.



**Figure II.A1** Average monthly and long-term average precipitation in 2020 at Wiesengut (a) and in 2021 at Campus Klein Altendorf (b)

### Species-specific yield effects

CA at high density (CA high) caused significantly lower yields than LP at high density and VA at low density (**Fig. II.A2a**). The yield in CA high was lower than all other treatments as well, but no significances were found. The yield in CA high was significantly lower than in the control about 27.7%. In order to explain the significant effects in FB, linear regression analyses between the yield differences and several weed parameters were calculated. The results showed high significant negative correlations between yield and biomass (p-value = 0.00006; df = 46;  $R^2 = 0.3$ ) and yield and weed height (p-value = 0.0001; df = 46;  $R^2 = 0.28$ ), whereas weed density and weed cover did not show any significances.

In FBO and oat, no treatment caused significant yield losses compared to the yield of the control. Differences between the treatments were not significant as well.



**Figure II.A2** Differences in Yield between the different species in high (red) and low (green) density in FB (a), oat (b) and FBO (c). Letters indicate statistical differences between treatmens according to Tukey HSD test. Significance levels: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 '' 1.



## Species frequency of natural weed community at Wiesengut

**Figure II.A3** Relative species frequency (n=44) of the natural weed community at Wiesengut in %.

## Soil properties at experimental sites

Table II.A4 Chemical soil properties at Wiesengut 2020 and Campus Klein Altendorf 2021.

	Wiesengut	Campus Klein Altendorf					
	Intercrop	Faba bean	Oat	Intercrop			
P (mg/100g soil)	10.8	2.3	2.7	2.2			
K (mg/100g soil)	7.9	53.9	15.9	34.7			
C/N ratio	9.3	9.6	9.6	9.3			
pH (CaCl <sub>2</sub> )	5.9	6.9	6.9	6.9			



#### Weed biomass as function of weed evenness

**Figure II.A5.1** Weed biomass as functions of weed evenness (based on biomass) at Campus Klein Altendorf in the different crops and to the five different dates (note the different ranges of the axes).



**Figure II.A5.2** Weed biomass as functions of weed evenness (based on biomass) at Wiesengut to the two different dates.



### **Biomass of crops and weeds**

**Figure II.A6** Biomass (DM) of crops and weeds (on sampling date 5) at Campus Klein Altendorf (CKA) in the different crops and at Wiesengut (WG) in intercrop.

## Relationship between weed cover and weed biomass

**Table II.A7** Results of the regression analysis in the natural weed community at Wiesengut. Significance levels: \*\*\*: <0.001'. Estimate refers to the value of the slope for the regression of biomass against cover. Cover1 and Cover2 in the model refer to the percentage cover at date 1 and 2, respectively.

Date	Model	Estimate	P-value	Significance
Date 1	Biomass ~ Cover1 + species	1.142	2.73E-08	***
Date 2	Biomass ~ Cover2 + species	0.448	6.58E-09	***