

Ecosystem functions of rare arable plants

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Summary

The intensification of agricultural land use led to a strong decline in biodiversity, particularly among arable plants. As primary producers, these plants play an essential role in agroecosystems by supporting various ecosystem functions. Thus far, only few studies investigated the ecosystem functions of rare and threatened arable plant species. Therefore, the present thesis addresses the following ecosystem functions of rare arable plants: their contribution to phytodiversity, their effects on crop and arable plant biomass, soil fertility and nutrient content, their influence on flower-visiting wild bees, and their contribution to biological pest control (biocontrol).

Plots with and without sown rare arable plants were studied on an experimental field and on ten agricultural farms in the *Munich Plain*, southern Bavaria, Germany. There, different crop sowing densities were compared. Data collection was conducted over three vegetation periods (2018–2020) on the experimental field and over two vegetation periods (2018–2019) on the practical farms. The same ecosystem functions were sampled in the experimental field and in the field study.

In **Publication 1**, we analysed the effects of sowing rare arable plants on phytodiversity, their establishment success, biomass production of crops and arable plants, earthworm abundance and biomass as indicators of soil fertility, soil organic matter, and nitrogen content. The results show that rare arable plant established successfully, which led to a considerable increase in phytodiversity. As sowing rare arable plants did not significantly change the production of crop and arable plant biomass, this measure also had no significant effects on the soil parameters earthworm occurrence and soil nutrient content. These results indicate that the conservation of rare and endangered arable plants and food production can be combined, particularly on nutrient-poor soils.

Publication 2 focuses on flower-visiting wild bees on rare arable plants. In this experiment, plots with rare arable plants and without crop sowing were compared with commercial annual and perennial wildflower strips from the *Bavarian Cultural Landscape Program* (Bayerisches Kulturlandschaftsprogramm). Plots exclusively sown with rare arable plants exhibited the same abundance and species richness of flower-visiting wild bees as plots sown with annual and perennial wildflower strips. However, in the second vegetation period, higher abundance and species richness of flower-visiting wild bees were observed on cropped plots sown with rare arable plants in comparison to cropped plots without rare arable plants. Wild bee species with special preferences visited rare arable plants with special flower characteristics: *Andrena bicolor* was found primarily on *Legousia speculum-veneris*, since the second generation of this wild bee species has an affinity for Campanulaceae as food resources. The long-tongued *Bombus hortorum* mainly visited *Consolida regalis*, as the flowers of this species have a very

long spur. These findings illustrate that rare arable plants can positively affect niche diversity and enhance resource availability for wild bees in agricultural landscapes.

Publication 3 compares biocontrol in crops with and without rare arable plants. We sampled the densities of aphids and their predatory antagonists, spiders and carabids. Predators were classified as either active hunting or web-building spiders and as either carnivorous/omnivorous or predominantly granivorous carabids. Cover of rare arable plants and active hunting spiders reduced aphid abundance. However, rare arable plant cover had no direct effects on web-building spider and carabid densities. On already species-rich arable fields, which provide particularly favourable conditions for rare arable plants, the resident arable plant community may already ensure efficient biocontrol, and future studies should investigate interactions between rare and common arable plant densities.

The chapter **further results** complement this thesis with additional results published in the final report of this research project. Here, a count of individuals of rare arable plants in different treatments showed that the establishment success of these plant species depended on several factors, namely crop rotation and crop sowing density. Furthermore, wild bee communities of the different sites were sampled with yellow, white, and blue coloured pan traps. Most of the observed flower-visiting wild bee species were also caught in the colour pan traps in both the experimental field and the field study.

The **general discussion** summarises and combines the results and emphasizes that rare arable plants can provide different ecosystem functions. It also integrates the results of the project into the current scientific discourse on ecosystem functions in agroecosystems. Since agriculture has been shown to provide valuable benefits and ecosystem functions beyond crop yields, agricultural management must make trade-offs between enhancing productivity and meeting the requirements of environmental and biodiversity conservation. Scientists, farmers, and policymakers must therefore strive to develop management techniques that combine food production and biodiversity conservation. This thesis contributes to the understanding of the role of rare arable plants in agroecosystems and highlights the need for their conservation and reintroduction.

Zusammenfassung

Die Intensivierung der Landwirtschaft führte zu einem starken Rückgang der Biodiversität, insbesondere von Ackerwildkräutern. Als Primärproduzenten übernehmen Ackerwildkräuter eine entscheidende Rolle in Agrarökosystemen, da sie verschiedene Ökosystemfunktionen bereitstellen. Bisher gibt es wenige wissenschaftliche Studien, die die Ökosystemfunktionen seltener und gefährdeter Ackerwildkräuter untersuchen. Das Ziel der vorliegenden Dissertation war daher, folgende Ökosystemfunktionen seltener Ackerwildkräuter zu untersuchen: Ihr Beitrag zur Phytodiversität, ihre Auswirkungen auf die Kultur- und Wildkrautbiomasse, die Bodenfruchtbarkeit und Nährstoffverfügbarkeit, ihr Einfluss auf blütenbesuchende Wildbienen und auf die biologische Schädlingsregulierung.

Auf einem Parzellenversuch und auf zehn Praxisbetrieben in der Münchner Schotterebene in Bayern wurden Parzellen mit und ohne Einsaat von zehn seltenen Ackerwildkräutern untersucht. Dabei wurden unterschiedliche Getreideaussaatstärken miteinander verglichen. Der Parzellenversuch wurde über drei (2018–2020), die Praxisbetriebe über zwei Vegetationsperioden (2018–2019) hinweg beprobt. Die gleichen Ökosystemfunktionen wurden auf dem Parzellenversuch und den Praxisbetrieben untersucht.

In der ersten Veröffentlichung (**Publication 1**) wurden die Effekte der Einsaat seltener Ackerwildkräuter auf die Phytodiversität, den Etablierungserfolg der seltenen Ackerwildkrautarten, die Produktion der Kultur- und Wildkrautbiomasse, die Regenwurmabundanz und -biomasse als Indikatoren für die Bodenfruchtbarkeit, die organische Substanz und den Stickstoffgehalt im Boden untersucht. Die Ergebnisse zeigen, dass sich seltene Ackerwildkräuter erfolgreich etablieren konnten, was wiederum zu einer Erhöhung der Phytodiversität geführt hat. Da die Einsaat der seltenen Ackerwildkräuter zu keinen signifikanten Veränderungen bei der Kultur- und Ackerwildkrautbiomasse führte, hatte diese Maßnahme auch keine signifikanten Auswirkungen auf den Regenwurmbesatz und die Nährstoffverfügbarkeit im Boden. Diese Ergebnisse machen deutlich, dass der Schutz seltener und gefährdeter Ackerwildkräuter und die landwirtschaftliche Produktion auf nährstoffarmen Böden erfolgreich kombiniert werden können.

In der zweiten Veröffentlichung (**Publication 2**) wurden die blütenbesuchenden Wildbienen von seltenen Ackerwildkräutern abgefangen. Dabei wurden Parzellen, die ausschließlich mit seltenen Ackerwildkräutern eingesät wurden (ohne Kultureinsaat) mit kommerziellen ein- und mehrjährigen Blümmischungen des bayerischen Kulturlandschaftsprogramms verglichen. Auf Parzellen, die ausschließlich mit seltenen Ackerwildkräutern eingesät waren, wurde eine ähnliche Diversität und Abundanz von Wildbienen festgestellt wie auf ein- und mehrjährigen Blümmischungen. Auf Parzellen mit Getreide und seltenen Ackerwildkräutern wurde im zweiten Versuchsjahr eine höhere Abundanz und Diversität von blütenbesuchenden Wildbienen

beobachtet im Vergleich zu Parzellen mit Getreide und ohne die Einsaat seltener Ackerwildkräuter. In dieser Studie besuchten Wildbienenarten mit speziellen Präferenzen seltene Ackerwildkrautarten mit besonderen Blütenmerkmalen: *Andrena bicolor* wurde hauptsächlich auf *Legousia speculum-veneris* beobachtet, da die zweite Generation dieser Wildbienenart eine Affinität zu Campanulaceae als Nahrungsquelle hat. *Bombus hortorum*, eine Hummel mit sehr langer Zunge, besuchte fast ausschließlich *Consolida regalis*, da die Blüten dieser Art einen langen Sporn haben. Die Ergebnisse verdeutlichen, dass seltene Ackerwildkräuter die Nischenvielfalt erhöhen und die Ressourcenverfügbarkeit für Wildbienen in der Agrarlandschaft verbessern können.

In der dritten Veröffentlichung (**Publication 3**) wurde die biologische Schädlingsregulierung auf Parzellen mit Getreide und mit oder ohne Einsaat seltener Ackerwildkräuter untersucht. Hierfür wurde die Dichte von Blattläusen und deren Prädatoren, Spinnen und Laufkäfer, erfasst. Die Prädatoren wurden in aktiv jagende oder netzbauende Spinnen und in karnivore/omnivore und überwiegend granivore Laufkäfer eingeteilt. Aktiv jagende Spinnen dezimierten die Anzahl der Blattläuse. Die Deckung der seltenen Ackerwildkräuter reduzierte die Blattlausdichte, hatte aber keine direkten Auswirkungen auf die Abundanz von netzbauenden Spinnen und Laufkäfern. Auf bereits artenreichen Äckern, die besonders günstige Bedingungen für seltene Ackerwildkräuter bieten, kann die ansässige Ackerwildkrautgemeinschaft bereits eine effiziente biologische Schädlingsregulierung gewährleisten. Weitere Studien müssen deshalb verschiedene Dichten seltener und häufiger Ackerwildkräuter untersuchen.

Das Kapitel zusätzliche Ergebnisse (**further results**) ergänzt diese Dissertation um weiterführende Daten, die im Abschlussbericht des Forschungsprojekts veröffentlicht wurden. Die Individuen der seltenen Ackerwildkräuter auf den unterschiedlichen Behandlungsvarianten wurden gezählt. Hierbei zeigte sich, dass der Etablierungserfolg der seltenen Ackerwildkräuter von unterschiedlichen Faktoren wie der Fruchtfolge und der Getreideaussaatstärke beeinflusst wird. Des Weiteren wurden die Wildbienengesellschaften an den verschiedenen Standorten mithilfe von gelben, weißen und blauen Farbschalen beprobt. Sowohl auf dem Parzellenversuch, als auch auf den Praxisbetrieben, wurden die meisten der auf den Blüten abgefangenen Wildbienenarten auch in den Farbschalen nachgewiesen.

Die **übergeordnete Diskussion** dieser Dissertation fasst die Ergebnisse der drei Publikationen zusammen und identifiziert den Einfluss seltener Ackerwildkräuter auf Ökosystemfunktionen. Darüber hinaus werden die Erkenntnisse des Forschungsprojektes in die aktuelle wissenschaftliche Debatte über Ökosystemfunktionen in Agrarökosystemen eingebettet. Da die Landwirtschaft nicht nur Ernteerträge, sondern auch wertvolle ökologische, *non-food* Funktionen bereitstellt, muss die landwirtschaftliche Bewirtschaftung einen

Kompromiss zwischen der Nahrungsmittelproduktion und dem Erhalt und Schutz der Umwelt und der biologischen Vielfalt finden. Hierfür müssen sich Wissenschaftler:innen, Landwirt:innen und politische Entscheidungsträger:innen um die Entwicklung von Bewirtschaftungstechniken bemühen, die die Nahrungsmittelproduktion und den Erhalt der biologischen Vielfalt miteinander verbinden. Diese Arbeit trägt zum Verständnis der Rolle seltener Ackerwildkräuter in Agrarökosystemen bei und verdeutlicht die Notwendigkeit ihrer Erhaltung und ihres Schutzes.

INTRODUCTION

Arable plants: origin, development and adaptation mechanisms

With the emergence of agriculture in Central Europe about 7,000 years ago, a new type of ecosystem developed: arable land (Stoate et al., 2001; Willcox, 2012). Arable land is among the most strongly human-influenced ecosystems. It provides valuable and novel habitats not only for crop vegetation, but also for plant species with similar niche requirements that are adapted to open landscapes and soil disturbance (Storkey, 2020; Willcox, 2012). The associated non-crop plants are called *arable plants* or *segetal plants* when named non-judgmentally, or otherwise commonly *weeds*, which implies that the species is considered harmful (Storkey, 2020). Most arable plant species are archaeophytes, meaning they were introduced to Europe before the New World was discovered in 1492 (Meyer, 2020). Like most crop species, the majority of arable plants also originally migrated onto agricultural fields from the Fertile Crescent and the Mediterranean area and evolved under the selective pressure of regular soil disturbance, which lead to a removal of the vegetation and thus favourable living conditions for annual plants (Willcox, 2012).

Plants inhabiting arable fields developed different strategies to adapt to agricultural management. The annual life cycle of most arable plant species and the reproduction by seeds in particular are the most effective adaptation mechanisms to crop production systems. Therefore, most arable plants are generally characterised as R-strategists ('ruderals'), with some also being classified as S-strategists ('stress-tolerators') (Grime, 1974). This means that these opportunistic species produce a high number of rather small seeds and thus are adapted to dispersal, have a short life cycle, and are adjusted to strongly disturbed habitats (Gerowitt et al., 2017; Lososová et al., 2006). Furthermore, most arable plant species produce persistent soil seed banks, allowing them to survive unfavourable phases, sometimes enduring over decades until suitable germination conditions re-occur (Bakker et al., 1996; Lang et al., 2018).

In Central Europe, about 400 plant species are associated with arable land (Meyer, 2020). For Germany, Hofmeister and Garve (2006) listed approximately 350 plant species which are frequently found in arable fields. Generally, arable plant communities reflect the influence of different substrate and crop types and can be classified into five plant sociological associations (Hofmeister and Garve, 2006):

- 1) Winter cereal fields on sandy and clay soils with a low base saturation;
- 2) Root crops and summer cereal fields on nutrient-poor sandy and loamy soils;
- 3) Root crops and summer cereal fields on fresh to moist sandy and loamy soils;

4) Root crops and summer cereal fields on base-rich soils;

5) Winter cereal fields on calcareous soils.

However, over the last decades, agricultural intensification led to a dramatic decline of arable plants which are adapted to traditional and extensive farming practices (Albrecht, 1995; Meyer et al., 2013; Storkey et al., 2012).

Degradation and changes of arable flora

Agricultural intensification includes a set of different management techniques that negatively affect biodiversity and other environmental factors. The following factors are considered to be the main drivers of arable plant degradation (e.g. Albrecht et al., 2016; Stoate et al., 2001; Stoate et al., 2009; Storkey et al., 2012). At the field scale, increased application of herbicides in particular decreases the species richness and abundance of arable plants (Gaba et al., 2016). Frequent applications of synthetic fertilisers, slurry and other soil improvement techniques such as liming lead to soil homogenisation and affect arable plant communities, which are adapted to rather nutrient-poor soils. Further management changes are sowing of higher crop densities, the use of competitive crop species and varieties, lower crop diversity, improved seed cleaning techniques, and narrow crop rotation in which fallows and stubbles are omitted. In addition, the agricultural landscape is subject to a constant process of homogenisation. Land consolidation led to a removal of semi-natural and uncropped habitats such as hedges, shrubs, and woody elements, as well as the aggregation of formerly small and mosaic-like arranged fields, which reduced overall field margins (Stoate et al., 2001; Stoate et al., 2009). Finally, land abandonment and the conversion of marginal soils to grasslands or forests reduces habitats for specialised arable plant communities. This development led to a strong increase in crop yields, but it also correlates with the decline of rare, threatened, or recently extinct arable plant species in various European countries (Storkey et al., 2012).

The losses and changes in diverse arable plant communities are documented for many different European countries and regions (e.g. Croatia: Hulina, 2005; Denmark: Andreasen and Streibig, 2011; England: Sutcliffe and Kay, 2000; France: Fried et al., 2009; Fried et al., 2016; Germany: Albrecht, 1989; Baessler and Klotz, 2006; Meyer, 2013; Slovakia: Májeková et al., 2010; Switzerland: Richner et al., 2017; Storkey et al., 2012; Europe: Richner et al., 2015). Meanwhile, even species that used to be very common are becoming less abundant (Fried et al., 2016; Meyer et al., 2013; Walker et al., 2007). In Germany, about 35% of arable plant species which typically inhabit arable fields are threatened (Metzing et al., 2018). Arable plants that are adapted to specific site and management conditions in particular are declining significantly (Meyer et al., 2013; Storkey et al., 2012). The arable plant communities on calcareous soils are most affected (Meyer et al., 2013). In consequence, the arable vegetation of calcareous soils was elected as the “Plant community of the year 2022” (Bergmeier et al., 2021). The loss of typical and specialized arable plant species leads to more generalist communities, which usually include species with wide ecological amplitudes (Fried et al., 2010; Meyer et al., 2013). Furthermore, the share of nitrophilous plant species increased noticeably (Storkey, 2020). This increase includes highly competitive species that can cause significant

yield losses and also outcompete specialised, low-competitive arable plants (Storkey et al., 2010). These specialised species, which are highly threatened and rare, are referred to as “rare arable plants” in this thesis.

Ecosystem functions of arable plants

Phytodiversity

Biodiversity provides many ecosystem functions that also underpin benefits humans derive from ecosystem and thus biodiversity conservation is crucial to human well-being (Cardinale et al., 2012; Tilman et al., 2014). High species richness is required to fulfil various ecosystem functions, because different species provide different functions in different years, different places, and under different environmental scenarios (Isbell et al., 2011). Furthermore, ecosystems are managed to provide not one, but multiple ecosystem functions (Cardinale et al., 2012; Hector and Bagchi, 2007). Generally, high plant diversity has positive bottom-up effects on below- and above-ground multi-trophic levels (Scherber et al., 2010). The review of Tylianakis et al. (2008) underlines that lower species richness of primary producers reduces food web stability and thus the associated fauna.

This implies that arable plants play a key role in agroecosystems (Gaba et al., 2020; Marshall et al., 2003; Petit et al., 2011). Common arable plants are known to provide various ecosystem functions (Blaix et al., 2018; Bretagnolle and Gaba, 2015; Gaba et al., 2020). High arable plant species richness has some additional benefits: Some studies show that diverse arable plant communities compete less with crops and are more resilient to the dominance of strongly competitive weed species (Adeux et al., 2019; Storkey and Neve, 2018). Diverse weed communities are indicators for agronomic and environmental sustainability and arable plant diversity should thus be promoted and conserved (Storkey and Neve, 2018; Storkey and Westbury, 2007). Lastly, beyond their intrinsic value, arable plants are of significant cultural and aesthetic value for humans (Swift et al., 2004).

Biomass production

Arable plants can essentially contribute to plant biomass production and thus have positive effects on carbon sequestration and soil fertility (Blaix et al., 2018). Greater arable plant biomass results in a higher plant cover between the crop rows, which can improve erosion control and water transpiration in the soil. This in turn decreases the probability of drought stress, increases soil quality, and prevents yield losses. As arable plants compete with crops for above- and below-ground resources like water, soil nutrients, light, and space, however, their biomass production may also lead to significant yield losses (Cousens, 1985; Wilson and Wright, 1990). In contrast, some authors argue that arable plants may utilize resources that cannot be used by crops, leading to a win-win situation, which benefits both crops and arable plant species. Thus, overall plant biomass production could be increased on arable fields (Storkey and Westbury, 2007).

Soil fertility and soil nutrient content

Arable plants are part of the nutrient cycle and can increase soil nutrient content and carbon sequestration (Blaix et al., 2018; Power, 2010; Wratten et al., 2012). Arable plants can also enhance various physical properties of the soil such as erosion prevention, water storage, and balance (Blaix et al., 2018; Power, 2010). In addition to abiotic factors, arable plants strongly affect the soil biota, as their biomass serves as food source for earthworms and nematodes (Franke et al., 2009). Earthworms, in turn, are considered *ecosystem engineers* and have a strong influence on soil structure and formation, fertility, and water regulation (Blouin et al., 2013; Marinissen and Rüter, 1993). By decomposing organic matter, earthworms improve nutrient availability and accelerate nitrogen mineralization. Therefore, earthworms are known to not only increase plant biomass production (van Groenigen et al., 2014), but to also affect plant communities through various mechanisms such as modifying seed dispersal and germination or even affecting competitive interactions between plants (Decaëns et al., 2003; Eisenhauer et al., 2009b; Eisenhauer et al., 2009a).

The role of arable plants for flower visitors

Various plant species, including many food plants for humans, depend on pollination by flower visitors (Klein et al., 2007). Wild bees are crucial pollinators (Bommarco et al., 2012; Garibaldi et al., 2013; Holzschuh et al., 2012) whose species richness and abundance declined significantly in recent years (Biesmeijer et al., 2006; Potts et al., 2010; Powney et al., 2019; Zattara and Aizen, 2021). The review of Bretagnolle and Gaba (2015) summarizes the essential role of arable plants for wild bees. They point out that the decrease of arable plants led to reduced numbers of wild bees in agroecosystems, because the decline of flower resources and of wild bee populations is strongly correlated (Biesmeijer et al., 2006). Therefore, Bretagnolle and Gaba (2015) emphasize that arable plants enhance the availability of flower resources over time and space not only for domesticated, but also for wild bees in agricultural landscapes, which otherwise exhibit rather few flower resources. The review of Rollin et al. (2016) even proposed the application of weed-insect pollinator networks as indicators for sustainability on arable land. They point to a strong link between arable plants and different pollinator taxa. Therefore, conservation efforts for wild bee populations require efficient and sustainable arable plant management, a fact that has already been highlighted by various authors (Bretagnolle and Gaba, 2015; Nicholls and Altieri, 2013; Storkey and Westbury, 2007).

The role of arable plants for biocontrol

Biological pest control (biocontrol) is defined as the use of living organisms as a means to reduce or inhibit crop damage by harmful organisms (Stenberg et al., 2021). In cereal fields, aphids belong to the most harmful pests, capable of severely decreasing crop yields (Dedryver et al., 2010). Natural enemies that feed on aphids are considered beneficial insects which can provide efficient biocontrol (Schmidt et al., 2003; Thies et al., 2011). Therefore, efficient biocontrol includes management techniques that support aphid predators (Barbosa et al., 2009; Ben-Issa et al., 2017; Landis et al., 2000). As generalist predators, spiders (Araneae) and predatory carabids (Carabidae) are beneficial insects whose diet includes aphids (Diekötter et al., 2010; Nyffeler and Sunderland, 2003; Symondson et al., 2002).

Arable plants are known to enhance biocontrol (reviewed by Blaix et al., 2018). This review states that arable plants benefit biocontrol through (1) the reduction of pest abundance, (2) an increase in predation or parasitism rates, or (3) an increase in abundance and diversity of natural pest enemies. Most commonly, studies showed that arable plants can provide suitable habitats for natural enemies (Blaix et al., 2018). In summary, a diverse arable plant community can increase vegetation structure, provide more suitable habitats for pest antagonists such as carabids and spiders, and thus improve biocontrol in agroecosystems (Balfour and Rypstra, 1998; Diehl et al., 2013; Gaba et al., 2020; Schirmel et al., 2016; Smith et al., 2020).

Conservation of rare arable plants and ecosystem functions

In general, “land sharing” or “land sparing” can promote nature conservation in agroecosystems. “Land sharing” combines extensive crop production and nature conservation on the same field, whereas “land sparing” separates intensive crop production and nature conservation areas (Phalan et al., 2011). However, the conservation of the arable flora also aims to protect and improve ecosystem functions, as species richness and abundance of arable plants are known to enhance ecosystem functioning (Blaix et al., 2018; Gaba et al., 2020). A variety of management strategies have been developed to maintain arable plant communities and to conserve particularly rare arable plants. The prioritised aim of rare arable plant conservation is to protect and maintain remaining rare arable plant communities (Rotchés-Ribalta et al., 2015b). When seeds are still present in the soil seed bank, reduced farming intensity or changing management can reactivate remaining seeds (Albrecht et al., 2016). Due to the intensification of agricultural management, soil seed banks are frequently impoverished, which makes reintroduction/re-establishment necessary. Seed transfer through targeted sowing of rare arable plant species to favourable sites is an effective and promising method to restore and maintain arable plant diversity (Albrecht et al., 2016; Bischoff and Mahn, 2000; Kohler et al., 2011; Lang et al., 2021; Lang, 2021).

Agri-environmental schemes (AES) are the most important funding instruments in agricultural landscapes. They are subsidized by the Common Agricultural Policy (CAP) of the European Union and generally aim to mitigate or even reverse biodiversity loss in agricultural landscapes (Batáry et al., 2015). AES are often designed to support the conservation and protection of arable plants and thus ecosystem functions on arable land (Batáry et al., 2015).

Land sharing

Organic farming describes the possibility of managing arable land mostly without application of synthetic fertilisers and herbicides. Under organic farming conditions, weed control is thus usually carried out mechanically. As mechanical control is usually less efficient than the application of herbicides, and as other indicators for farming intensity such as stocking rates or nutrient input are also lower in organic systems, environmental conditions for the survival of arable plants on such fields are very favourable (Pinke and Gunton, 2014). Arable plant species richness and abundance benefit from organic farming (e.g. Albrecht et al., 2020; Albrecht and Mattheis, 1998; Berbeć et al., 2020; Tuck et al., 2014, but see Hyvönen, 2007). However, organic farming may also include management techniques that are unfavourable for the conservation of rare arable plants, such as the cultivation of clover grass and intercropping (Albrecht, 2005).

Conservation headlands (cropped field margins in which herbicides, fertilization, and lime application are prohibited and crop sowing rates are reduced) or *management extensification* are important AES that support arable flora conservation (Meyer, 2020; Wietzke et al., 2020). The disadvantages of these AES include their limited duration of no more than five years and the requirement of professional expertise in conservation, as site selection and adapted management are complex.

Arable reserves and *conservation fields* prioritize the preservation of remaining species-rich arable fields over crop production. In Germany, such conservation efforts have been carried out by the project '100 Fields for Biodiversity', for instance, which set up a network of species rich arable fields all over Germany (Meyer and Leuschner, 2015). However, the number of conservation fields is insufficient to conserve arable plant populations on a national scale (Albrecht et al., 2016). Nonetheless, the project explicitly demonstrates the efficiency of low-intensity farming practices for conservation purposes.

Land sparing

Annual or *perennial wildflower strips* are popular, widely applied AES. They were introduced in several European countries to enhance biodiversity, particularly of pollinators (e.g. Aviron et al., 2011; Blaauw and Isaacs, 2014; Grass et al., 2016; Haaland et al., 2011; Scheper et al., 2013; Scheper et al., 2015). However, several disadvantages of wildflower strip sowing are known: Although rare arable plant species are sometimes included in the wildflower strip mixtures, these mixtures often contain highly competitive species, which suppress the resident arable flora, and the sown rare arable species. Furthermore, wildflower strips often include cover crops such as *Onobrychis sativa* Lam., alien plant species such as *Fagopyrum tataricum* (L.) Gaertn. and/or *Phacelia tanacetifolia* Benth, ruderals like *Daucus carota* L. and/or *Hypericum perforatum* L., and grassland species like *Salvia pratensis* L. and/or *Achillea millefolium* L. The seed material is often not regional and can even be of unknown origin. In addition, the species composition of wildflower strip mixtures is frequently rather uniform and mainly supports generalist and common arthropod species, thus offering only limited effects on insect diversity (Dietzel et al., 2019; Haaland et al., 2011; Wood et al., 2015). Ganser et al. (2019) even discuss wildflower strips as ecological traps for arthropods, as they are attractive as overwintering sites, but can be ploughed during wintertime (but see Schmied et al., 2022).

Following the land sparing strategy, another AES are *fallows/set-aside fields*, where arable fields remain unmanaged for one year. This measure is specifically suitable for low-productive soils (Meyer, 2020; Wietzke et al., 2020). The species composition on fallows depends on different factors like the soil seed bank and species consistence in the surrounding landscape

(Meyer, 2020). In the presence of a sufficient seed bank, this measure can promote arable plant diversity and cover (Wietzke et al., 2020). However, when highly competitive, noxious weeds dominate seed soil banks and/or neighbouring fields, fallows may favour weed infestation (Meyer, 2020).

Current scientific knowledge

Many studies focus on reintroduction, suitable management, or site conditions for the conservation of rare arable plants in different European regions (Kleijn and van der Voort, 1997; Lang et al., 2016; Lang, 2021; Lang et al., 2021; Pinke et al., 2010; Rotchés-Ribalta et al., 2015a; Torra et al., 2018; Torra et al., 2020; Wagner et al., 2017). However, it is known that common arable plants provide various ecosystem functions (Blaix et al., 2018; Bretagnolle and Gaba, 2015; Gaba et al., 2020). Blaix et al. (2018) reviewed 129 studies and showed that arable plants support functions such as biocontrol (improve habitat properties for natural enemies), nutrient content and physical properties of the soil, and pollinator abundance. Maintaining the diversity of arable plants can increase multifunctionality in agroecosystems (Gaba et al., 2020).

However, only few studies make a distinction between common and rare arable plants when investigating their effects on ecosystem functions. Gibson et al. (2006) focused on only three rare arable plant species and only on the ecosystem function pollination. Gaba et al. (2020) analysed various ecosystem functions of abundant and rare arable plants, but their definition was based on the local frequency of species and not their overall threat and rarity. As the abundance of species can significantly vary from field to field, the general validity of this approach may be doubtful. Thus, it still remains unclear how rare and low-competitive arable plants specifically contribute to the ecosystem functions of arable fields. In addition, considering the current trend, it is likely that more and more species will become rare. This in turn increases the need for knowledge about the role of rare species in agroecosystems. Understanding the effects of rare arable plants on the ecosystem as a whole will provide further arguments for their protection that go beyond biodiversity conservation.

OBJECTIVES AND OUTLINE

The objective of this thesis is to explore the ecosystem functions of rare and threatened arable plants (Figure 1) and to compare them with those of annual and perennial wildflower strips. By collecting data not only on an experimental field, but also under practical conditions on ten agricultural farms in the *Munich Plain*, this study includes diverse site properties, which in turn allows the application of the results to a larger context. The following ecosystem functions were investigated at varying crop densities and crop rotations and in different study years: phytodiversity, crop and arable plant biomass production, soil fertility and nutrient content, effects on flower-visitors, and biocontrol potential. **The hypothesis is that increased phytodiversity due to the presence of rare arable plants benefits ecosystem functioning and supports organisms of higher trophic levels such as flower-visiting wild bees and ground-dwelling arthropods.**

The first publication (Twerski et al., 2021a) studies the effects of rare arable plants on plant diversity, productivity, and soil fertility. To address the productivity function, crop and arable plant biomass were analysed. To characterise soil fertility, organic matter, nitrogen concentration, and the biomass and abundance of earthworms were studied. The second publication (Twerski et al., 2022) investigates the effects of rare arable plants on flower-visiting wild bees. The importance of rare arable plants for the wild bee community was studied at varying crop densities and compared with annual and perennial wildflower strips. The third publication (Twerski et al., 2023) examines the effects of rare arable plants sown with crops on biocontrol. To this end, aphid densities and activity densities of active hunting and web-building spiders as well as carnivorous/omnivorous and predominantly granivorous carabids were sampled. A chapter on further results complements this thesis and presents data on the establishment of rare arable plants and the community of flower-visiting wild bees (published in Twerski et al., 2021b).

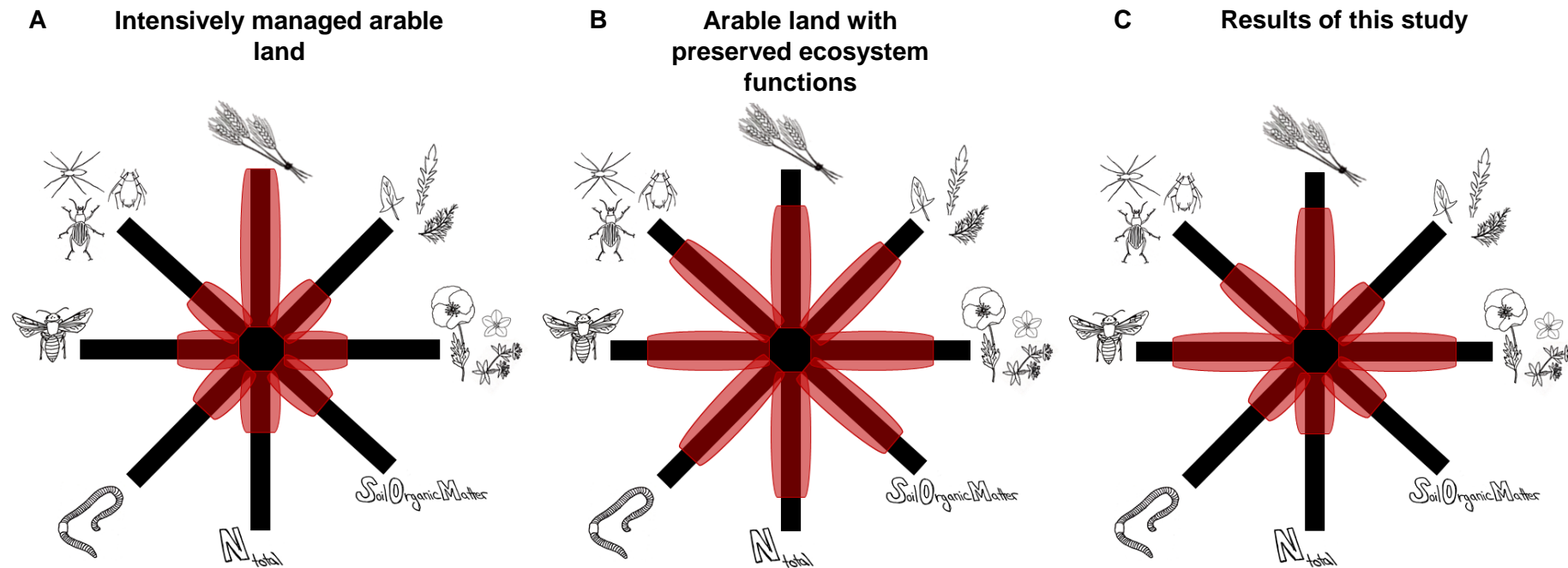


Figure 1: Graphical overview of this thesis with an application of the conceptual framework by Foley et al. (2005) showing hypothesized relationships between ecosystem functions and land-use types (A, B) and a summary of results from publications 1–3 (C). Illustrated are the provision of various ecosystem functions on intensively managed arable land (A) and a desired state on arable land with preserved ecosystem functions (B). The red bands indicate the level at which each ecosystem function is provided. The red bands in (C) indicate whether the provision of ecosystem functions changed after sowing of rare arable plants, with a smaller band indicating that functions did not improve as expected. The following ecosystem functions are illustrated (clockwise and starting from the top): crop biomass production, arable plant biomass production, phytodiversity, soil organic matter content, soil nitrogen concentration, soil fertility (earthworm biomass and abundance), flower-visiting wild bees, and biological pest control (ground-dwelling predators and aphid density). Figure modified after Foley et al. (2005).

MATERIAL AND METHODS

Study region

The study was performed in the *Munich Plain*, located in the federal state of Bavaria, southern Germany (Figure 2). This area covers about 1800 km² and was shaped by the last ice age (Würm ice age). The oligotrophic and shallow soils in this area can be classified as nutrient-poor leptosols with high proportions of calcareous gravel up to the top soil, a low field capacity and high pH-values (Fetzer et al., 1986). The most frequently grown crops are barley, rye, oil seed rape, and potatoes (Bayerisches Landesamt für Statistik, 2016). The average annual temperature is 9.2 °C and the mean annual precipitation is 757 mm per year, with the highest precipitation during the summer (Munich Airport Station ID: 1262; DWD, 1993–2019). The first two study years were characterised by extreme weather events. In 2018, the mean annual temperature was above average at 10.2 °C (DWD, 2018), which caused severe water shortage (DWD, 2019b). On 10th June 2019, a strong hailstorm damaged the vegetation in the study region heavily (DWD, 2019a).

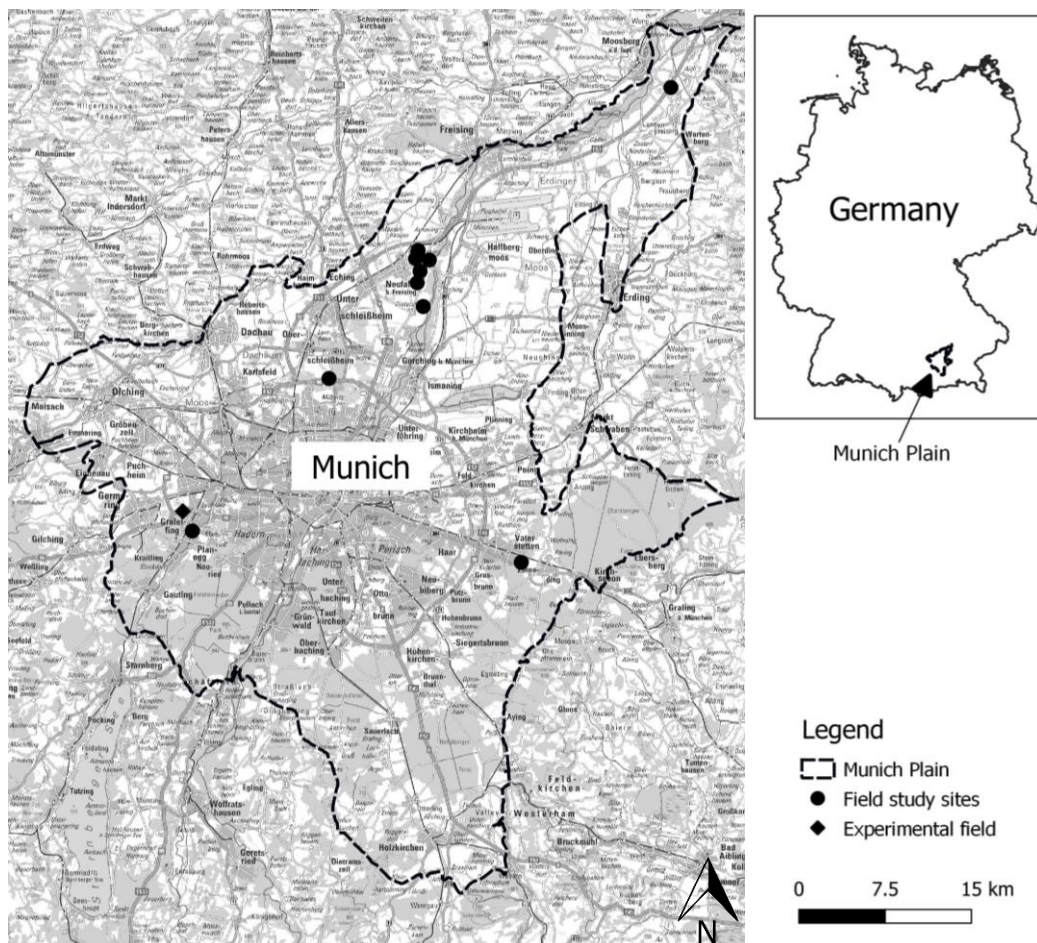


Figure 2: Map of study area in the *Munich Plain*, located in the federal state of Bavaria, Germany (Figure from Twerski et al., 2021a).

Rare arable plants

In this study, a mixture of ten archaeophytic and rare arable plant species were selected (Table 1 and Figure 3). These species have a Red List Status in Germany and/or Bavaria or an infrequent or decreasing abundance in the *Munich Plain* (Metzing et al., 2018; Scheuerer and Ahlmer, 2003) and they show a low- to intermediate competitive capacity (Holzner and Glauning, 2005). In addition, all species belong to different plant families. These study species also covered different germination preferences: three are autumn-germinating, four are spring-germinating and three species are without a seasonal germination preference. Exclusively autochthonous seed material from a local seed supplier was used. Each of the species was sown in varying densities (between 50 and 300 seeds per m²) according to their seed sizes and germinating rates (Table 1) and/or the sowing density recommended by Lang et al. (2016).

Table 1: Species list of rare arable plants with their families (species nomenclature according to The Plant List, 2013); germination preferences (A = autumn-germinating, S = spring-germinating, AS = no seasonal germination preference); Red List status of Germany and Bavaria (Metzing et al., 2018; Scheuerer and Ahlmer, 2003; Red List Status: * = not endangered, V = near threatened, 3 = vulnerable, 2 = endangered); sowing densities and competitive capacity (Holzner and Glauning, 2005; competitive capacity: 1 = very low competitive species; 5 = strongly competitive species) (Table modified after Twerski et al., 2021a).

Species	Family	Germination requirements	Red List Status		Sowing density [seeds m ⁻²]	Competitive capacity
			Germany	Bavaria		
<i>Consolida regalis</i> Gray	Ranunculaceae	A	3	3	150	1–2
<i>Buglossoides arvensis</i> (L.) I.M.Johnst.	Boraginaceae	A	V	3	100	2
<i>Valerianella dentata</i> (L.) Pollich	Caprifoliaceae	A	V	*	150	1
<i>Legousia speculum-veneris</i> (L.) Durande ex Vill.	Campanulaceae	AS	2	3	150	2
<i>Silene noctiflora</i> L.	Caryophyllaceae	AS	3	V	100	2
<i>Papaver rhoeas</i> L.	Papaveraceae	AS	*	*	150	3
<i>Lathyrus tuberosus</i> L.	Fabaceae	S	*	*	50	-
<i>Neslia paniculata</i> (L.) Desv.	Brassicaceae	S	3	3	150	2
<i>Kickxia spuria</i> (L.) Dumort.	Plantaginaceae	S	3	3	300	-
<i>Sherardia arvensis</i> L.	Rubiaceae	S	V	V	100	1



Figure 3: Rare arable plant species: A) *Silene noctiflora*, B) *Consolida regalis*, C) *Kickxia spuria*, D) *Lathyrus tuberosus*, E) *Valerianella dentata*, F) *Papaver rhoeas*, G) *Sherardia arvensis*, H) *Legousia speculum-veneris*, I) *Buglossoides arvensis* and J) *Neslia paniculata* (Figure from Twerski et al., 2021b).

Annual and perennial wildflower strips

To compare ecosystem functions of rare arable plants with those provided by wildflower strips, annual and perennial wildflower strips from the *Bavarian Cultural Landscape Program* were sown. These wildflower strips were designed to provide not only nectar and pollen for flower-visiting insects, but also to serve as habitats and food resources for wildlife (Bayerische Landesanstalt für Landwirtschaft, 2020). We used the mixtures B47 “Annual flowering mixture” and the perennial B48 “Living fields for dry sites” (Bayerische Landesanstalt für Landwirtschaft, 2020) and excluded the species *Cyanus segetum* Hill from both, because this species has a high weed infestation potential on organically managed fields. The annual wildflower strip included 16 species (14 cultural and two wild species) and the perennial 43 species (nine cultural, 33 wild dicots and one grass species) (Table A2 in the supplementary material in Twerski et al., 2022).

Experimental setup

The study was conducted under controlled conditions on an experimental field located in the southwest of Munich and under practical conditions on ten agricultural fields (field study) in the *Munich Plain*. On the experimental field, data was collected during three years (2018–2020), on the field study for two years (2018–2019). Rare arable plants as well as annual and perennial wildflower strips were sown in broadcast and at the same time with the respective crop at the beginning of the experiment in March and April 2018. Therefore, the second and third years' analyses strongly dependent on the successful establishment of rare arable plants and perennial wildflower strips at the beginning of the experiment. After the first vegetation period (autumn 2018), the annual wildflower strip terminated and was worked into the soil. Afterwards, the regular crop rotation continued and data sampling proceeded, which allowed us to conclude about the impact of annual wildflower strips after the program terminates.

Experimental field

To analyse the ecosystem functions of rare arable plants under controlled conditions, a field experiment (48°07'42"N, 11°24'58"E) was set up on the farm of the Seidlhof foundation in Gräfelfing. This fields had been under organic farming since 1974. Over three study years (2018–2020), we tested 12 different treatments with combinations of the following management options (Figure 5):

- Crop sowing density: regular (Crop 100%) vs. reduced (half of the regular density; Crop 50%) vs. uncropped (Crop 0%)
- Rare arable plants: with (+RAP) and without sowing (-RAP)
- Sowing of annual (a WFS) or perennial wildflower strips (p WFS)
- Different crop rotations: clover grass seeding after annual crop cultivation vs. perennial crop cultivation

Each treatment was replicated five times with a plot size of 2.3 m × 6.0 m. The plots had a distances of at least 1.2 m from each other. The treatments at the “with/without rare arable plants” field were arranged in a randomised block design, i.e. each treatment was repeated once in a block. The blocks were 10 m apart from each other. To avoid a “dilution effect” (flower-visitors can be strongly attracted by the flower-rich wildflower strips; Kovács-Hostyánszki et al., 2013), the annual and perennial wildflower strips were established separately from the field trial where rare arable plants were sown. The wildflower strips were located at least 150 m away on another field (Figure 5) (Gathmann and Tschardt, 2002).



Figure 4: Experimental field near Gräfelfing, southwest of Munich, Germany. The experiment was conducted on one field “with/without rare arable plants” with randomized blocks and on a second field “wildflower strips” (BayernAtlas, 2019; Figures from Twerski et al., 2021b).

The space between the crop rows was either 11 cm (regular density) or 22 cm (reduced density). In March 2018 and April 2020, the hulless oat breed 'Saul' (regular seed rate: 140 kg ha⁻¹; reduced: 70 kg ha⁻¹) was cultivated. Afterwards, the spelt breed 'Oberkulmer Rotkorn' (regular seed rate: 190 kg ha⁻¹; reduced: 95 kg ha⁻¹) was sown in September 2018. Between crop sowing, ploughless and shallow tillage (10 cm depth) with a rotary cultivator was performed. No chemical or mechanical weed control were applied during the whole study. In the treatments with clover grass sowing after an annual crop cultivation (Figure 5), the clover grass mixture was sown in August 2018 at a sowing rate of 30 kg ha⁻¹. The mixture consisted of 10% *Festuca pratensis* Huds., 34% *Lolium multiflorum* Lam., 15% *Lolium perenne* L., 34% *Trifolium pratense* L. and 7% *Trifolium repens* L.. It was mulched once in July 2019.

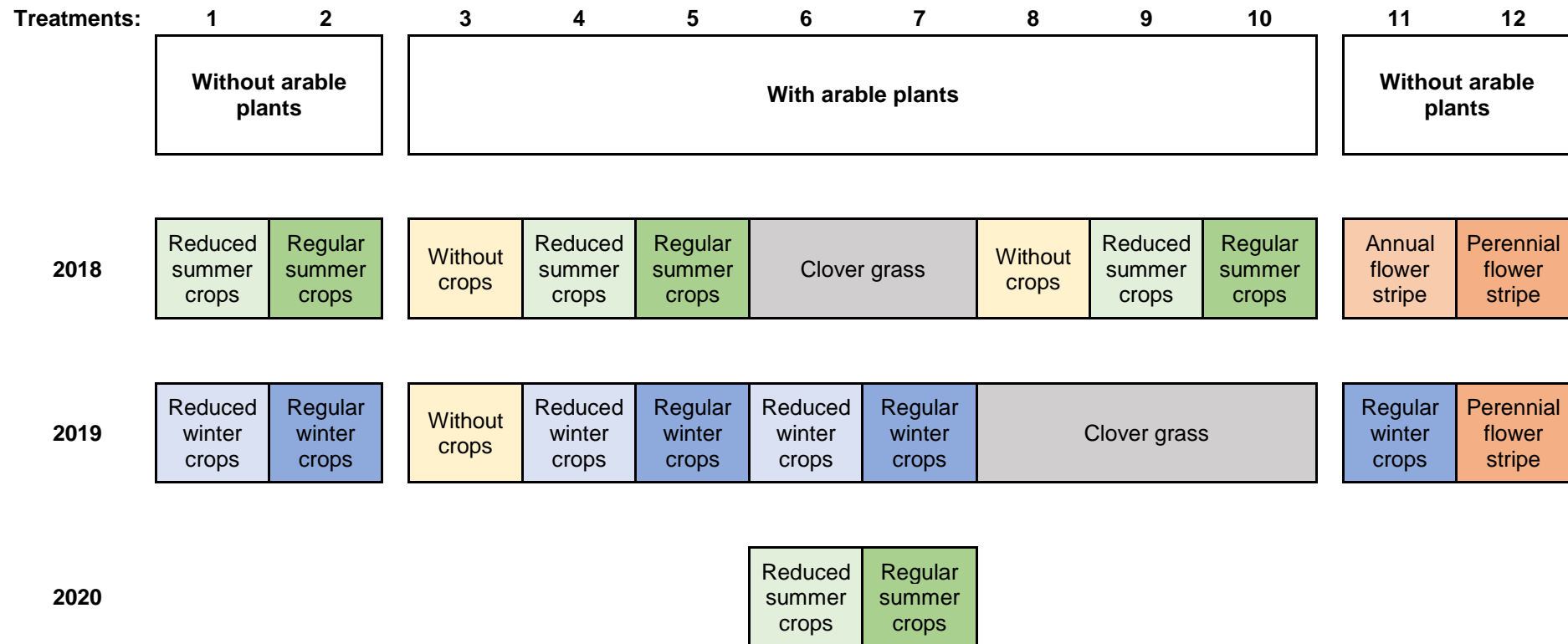


Figure 5: Structural design of the experimental field near Gräfelfing, southwest of Munich, Germany. Twelve treatments were divided into three major groups: Without and with sowing of rare arable plants and annual or perennial wildflower strips. The experiment was conducted on two fields (see Figure 4). Further varying parameters: crop sowing density (regular, reduced by 50%, and uncropped), study years (2018–2020), and crop rotations (Figure from Twerski et al., 2021b).

Field study

To analyse the ecosystem functions of rare arable plants under different site and management conditions, we set up a field study on ten practical farms in the *Munich Plain*, around Munich (Figure 2). On the practical farms, crops were sown in two sowing densities: reduced (half of the regular density; Crop 50%) vs. uncropped (Crop 0%). The following five treatments were established in five plots on each of the farms:

- Reduced crop density without rare arable plant sowing (Crop 50% - RAP)
- Without crops, but with rare arable plant sowing (Crop 0% + RAP)
- Reduced crop density with rare arable plant sowing (Crop 50% + RAP)
- Annual wildflower strip (a WFS)
- Perennial wildflower strip (p WFS)

The plots with/without rare arable plant sowing had a distance of 10 m to each other. The wildflower strips were located on another field, at least 250 m apart from the plots with and without the rare arable plants (Gathmann and Tschardt, 2002). Annual and perennial wildflower strips had a minimum distance of 100 m to each other. The field study lasted two years (2018–2019) with spring cereals in the first vegetation period and winter cereals in the second season. The plot size, row distance, cereal species and variety, and crop sowing rates varied between the agricultural farms (see supplemental material Twerski et al., 2021a). Eight fields were under organic, two under conventional management. Again, shallow tillage (max. 10 cm depth) was performed between the two vegetation periods and no weed control was conducted during the study.

Data sampling

Phytodiversity, establishment success and flower cover

In all plots, vegetation surveys were conducted in July of each study year (Figure 6A). Therefore, plant species were identified and the cover per plant species and the crop's cover were estimated visually. Each plant species was assigned to one of the following groups: sown rare arable plants, spontaneously occurring arable plants and volunteer crops (species that re-emerge after cultivation from previous years).

The establishment success of rare arable plants was measured only in plots where rare arable plants were sown. In July of each study year, shortly before the crop's harvest, all rare arable plant individuals were counted in four randomly placed 0.5 m × 0.5 m sampling squares per plot.

The flower cover (excluding wind-pollinated Poaceae, *Plantago*, and *Rumex* spp.) sampling was performed in two subplots per plot. Each subplot had a size of 0.58 m × 1.0 m. These subplots were located in parts of the plots that had the highest flower density and diversity of rare arable plants or sown wildflower strips species. The subplots were sampled twice per year (during each flower-visitor sampling round in June and July). The location of the subplots within the plots was maintained over the two sampling rounds. For each flowering species, the number of individuals and flowers per individuals were counted (for Asteraceae and Apiaceae: flower heads). Species that showed a high abundance per subplot (>15 individuals per 0.58 m × 1.0 m) were counted on only one quarter per subplot and the number of individuals was extrapolated afterwards. This was also applied for plant species with a high number of flowers per individual. To estimate the attractiveness of flowers, the size of the flower heads was measured on ten randomly selected individuals per species. For species with zygomorphic flowers, flower length and width were measured. Afterwards, the frontal view was scanned, loaded into Vectorworks (2019) and the flower surface was calculated. For radial flowers, we measured the diameter of the flower and calculated the surface area afterwards ($A = \pi * r^2$). Finally, the flower cover was summed for the two sampling rounds and subplots per plot and extrapolated to [cover mm²].

Biomass production

To analyse the effects of rare arable plants sowing on the systems productivity, we sampled crop (Figure 6B) and arable plant biomass production. The arable plant biomass (rare arable plants + volunteer crops + spontaneous arable plants) was harvested in July and August 2018 and 2019 in three 0.5 m × 0.5 m sampling squares, which were randomly placed in each plot.

Afterwards, the arable plant biomass was dried at 65 °C for 48 hours, weighed, and projected as [g m⁻²]. For the crop biomass, three randomly selected rows per plot were cut. Afterwards, crop biomass was dried, weighed and also projected as [g m⁻²].

Soil fertility and nutrient content

As an indicator for soil fertility, we sampled earthworm abundance and biomass in spring and autumn in the study years 2018 and 2019. Earthworms sampling was performed by chemical expulsion with allyl isothiocyanate (AITC; non-toxic for earthworms) (Figure 6C) and additionally, by hand-sorting of the remaining individuals (Pelosi et al., 2009). The sampling squares were located in the corner of the plot and changed the corners with each sampling round. For the chemical expulsion, a sampling square of 30 cm × 30 cm was flooded with 2 l of 100 mg l⁻¹ AITC solution (Zaborski, 2003). After 5 min, all to the soil surface emerging earthworms were collected and the sampling was repeated for another 5 min. Sampling quadrats were then excavated to a depth of 20 cm and the remaining earthworms were hand-sorted for 30 min (Pelosi et al., 2009). All collected earthworms were rinsed with water, dried, counted, weighed, and released afterwards. As the results of the two sampling methods were significantly correlated (earthworm biomass: $r_s = 0.24$, $p = 0.006$, $n = 154$, and abundance: $r_s = 0.31$, $p < 0.001$, $n = 154$; Spearman's rank correlation) and due to the fact that hand-sorting is a very time consuming method, it was only performed on the experimental field and not in the field study. The earthworm's biomass and abundance were summed up per year and extrapolated to [g m⁻²] and [individuals m⁻²].

To analyse the effects of rare arable plants on the soil nutrient concentration, we took soil samples at the beginning and the end of the experiment. In the centre of each plot, a soil sample was taken from a depth of 20 cm using a 90 mm wide borer. Afterwards, the samples were analysed by the AGROLAB Group (Landshut, Germany) for soil organic matter [%] and nitrogen concentration [%] (DIN EN 15936; 2012 and DIN EN 16168; 2012-11).

Flower visitor sampling

Flower-visiting wild bees were observed in two subplots per plot and in two sampling rounds (same subplots and sampling rounds as the flower cover measurements; see above) (Figure 6D). In each sampling round, a morning (9:00–13:00) and an afternoon shift (14:00–18:00) were sampled. In each shift, flower-vising (contact with an open flower, regardless of the plant species) wild bees were collected for 5 min. In total, 40 min were observed per plot and study year: 2 subplots * 2 sampling rounds * 2 shifts * 5 min. Observations were conducted under

suitable sampling conditions: min. 17 °C, low wind, no precipitation, and dry vegetation (Westphal et al., 2008). *Apis mellifera*, *Bombus lapidarius*, and *B. pascuorum* were identified in the field and released after collection; all other wild bees were transferred into 70% ethanol. The observed wild bees were summed for the two subplots, the two sampling rounds, and the two shifts for each plot.

After each sampling round (twice per year), the entire flower visitor community was sampled with colour pan traps (Figure 6E). The pans were painted with UV-active paints in blue, white and yellow (Sparvar Leuchtfarbe from Spray-Color GmbH). On the experimental field, three colour pan traps per replicate were set up in 2018, four in 2019 and two in 2020. Additionally, five colour pan traps were installed at the wildflower strips. In the field study, four colour pan traps per agricultural farm were deployed (in both study years): one in each wildflower strip plot and two in the plots with/without rare arable plant sowing. Each colour pan trap consisted of three (yellow, white and blue) pans, which were filled with approximately 300 ml of water and a drop of odour- and colourless dishwashing liquid and activated for 48 hours. The captured flower visitors were transferred into 70% ethanol.

All wild bees were identified to species level as far as possible. Rare and questionable species were identified by the taxonomic expert Dr. Klaus Mandery (Institut für Biodiversitätsinformation e.V.). The females of *Halictus simplex*, *H. eurygnathus*, and *H. langobardicus* were aggregated to *H. simplex* agg.

Aphid and ground-dwelling arthropod sampling

In each plot in which crops were sown, aphids, aphids mummies and vegetation-dwelling predators (hoverflies and green lacewings larvae and larvae and imagos of ladybugs) were counted on 100 shoots on two crop rows (50 shoots per crop row) (Figure 6G). We measured aphid density twice per year, once during crop flowering (BBCH 61; beginning of aphid population growth) and once during crop milk ripening stage (BBCH 75).

Pitfall traps with a volume of 500 ml and a diameter of 90 mm were used to sample the ground-dwelling predators (namely Araneae and Carabidae) (Figure 6F) (Lange et al., 2011). Predator sampling was performed after each round of aphid counting. We dug the traps at ground level in the middle of each plot, filled them with ca 120 ml mixture of water and ethylene glycol (1:1) and left them active for seven days per round. We covered the traps with plastic roofs and a metal grid (15 mm × 15 mm) to avoid overflowing by rain and to exclude mice and lizards. All collected arthropods were transferred into 70% ethanol and spiders and carabids were identified at species level according to Hurka (1996) and Nentwig et al. (2019) by the taxonomic experts Róbert Gallé and Péter Császár. Spiders were classified according to their hunting

strategy as either active hunting or web-building spiders (Cardoso et al., 2011). Carabids were classified according to their feeding behaviour as either carnivorous/omnivorous or predominantly granivorous (Homburg et al., 2014).

For data analysis, aphid density and the numbers of spiders and carabids were summed up for the two sampling rounds per plot. Due to a hailstorm that severely damaged the experimental field's vegetation and strongly impacted aphid and predator sampling, the 2019 experimental field data was excluded from statistical analysis. Furthermore, the abundances of aphid mummies and vegetation-dwelling predators were too low for statistical analyses.



Figure 6: Study methods: A) Uncropped plot sown with rare arable plants, B) Crop biomass sampling, C) Earthworm sampling, D) *Bombus* spec. on *Consolida regalis* (photo: Simon Dietzel), E) Colour pan trap for sampling of flower visitor community (photo: Michaela Moosner), F) Pitfall trap for sampling of ground-dwelling arthropods (photo: Fabian Sauter), G) Aphid's mummy (Figure, except D) from Twerski et al., 2021b).

Statistical analyses

Statistical analyses were conducted with R versions 3.5.3. and 4.0.3. (R Core Team, 2020).. We used linear mixed-effect models (*lme*; library *nlme* versions 3.1-145 and 3.1-150, Pinheiro et al., 2020) to analyse the effects of different treatments on the response variables species richness of rare arable plants, volunteer crops, spontaneous arable plants; crop and rare arable plant cover; crop and arable plant biomass; earthworm biomass and abundance; the percentage of soil organic matter and soil nitrogen concentration (**Publication 1**); wild bee abundance and species richness (**Publication 2**); aphid density and activity density of active hunting and web-building spiders and carnivorous/omnivorous and predominantly granivorous carabids (**Publication 3**). The following applies to the analyses of all three publications: Data from the experimental field and the field study were analysed separately. As random factors, we use “block” (n = 5) for the experimental field and “agricultural farm” (n = 10) for the field study to account for spatial and temporal autocorrelation. The two study years were analysed together. To avoid heteroscedasticity, we applied variance functions (“year”, “rare arable plant sowing”, “wildflower strip sowing”, and “crop sowing”, *varIdent* and/or *varComb*) and selected models with the lowest AIC value (Akaike Information Criterion; Zuur et al., 2009). For model simplification, automatic backward stepwise procedure based on smallest AIC was performed (*stepAIC*; library *MASS* version 7.3-53, Venables and Ripley, 2002). To analyse the differences between the treatments, Sidak post hoc tests were performed (*clt*; library *emmeans* version 1.5.2-1, Lenth et al., 2020). Whenever necessary, the response variables were log-, log+1 or square root transformed. In the thesis, arithmetic means \pm SD are given (*ddply*; library *plyr* version 1.8.6, Wickham, 2011).

In **Publication 1** we also analysed the effects of crop and arable plant biomass production on the response variables earthworm biomass and abundance using linear mixed-effect models (*lme*; library *nlme* versions 3.1-145 and 3.1-150, Pinheiro et al., 2020). Furthermore, In **Publication 2** we analysed the effects of rare arable plant, wildflower strip, and spontaneous arable plant cover on the response variables wild bee abundance and species richness using linear mixed-effect models (*lme*; library *nlme* versions 3.1-145 and 3.1-150, Pinheiro et al., 2020). The two study years were analysed separately for the response variables earthworm biomass and abundance, as well as soil organic matter and nitrogen concentration in **Publication 1**, because we expected these parameters to react with a time-lag after rare arable plant sowing. In **Publication 3**, “year” was included as a fixed effect in the analyses of the field study. For the analyses of the experimental field data in **Publication 2**, we also included “field” (n = 2) as random factor, because the wildflower strips plots were located on a different field.

In **Publication 2**, we used plant-pollinator networks to analyse if rare arable plants support different wild bees than wildflower strips or spontaneous arable plants (*bipartite* version 2.15 Dormann et al., 2009; Dormann, C. F., Gruber, B., & Fründ, J., 2008). To account for the fact that some plant species were more abundant than others, we divided all interactions by the number of plots in which the plant species occurred. Afterwards, we calculated the following indices (*specieslevel*; library *bipartite* version 2.15, Dormann, 2011): *species strength* (Bascompte et al., 2006), *effective number of partner species* (Bersier et al., 2002), and d' (Brütting et al., 2012). Afterwards, we applied Kruskal-Wallis tests to analyse the differences between the indices of the plant groups (1) rare arable plants, (2) wildflower strips, and (3) spontaneous arable plants.

In **Publication 3**, we additionally used structural equation models (SEM) to study the impact of rare arable plants and crop cover on food web interactions between aphids and ground-dwelling arthropods (*psem*; library *piecewiseSEM* version 2.1.0, Lefcheck, 2016). The model was based on the following hypothesized relationships from Twerski et al. (2023): (1) vegetation structure (rare arable plant and crop cover) affects aphid abundance and activity densities of ground-dwelling predators (Diehl et al., 2013; Honěk and Jarošík, 2000; Langellotto and Denno, 2004; Schirmel et al., 2016); (2) active hunting spiders and carnivorous/omnivorous carabids reduce aphid abundance (Diehl et al., 2013; Schmidt et al., 2003; Thies et al., 2011); and (3) there are interactions between activity densities of carnivorous/omnivorous carabids, active hunting spiders, and predominantly granivorous carabids (De Heij and Willenborg, 2020; Rusch et al., 2016; Straub et al., 2008). The individual models that were included in the SEM followed the same principles as the *lmes*: separate analyses of experimental field and field study, variable transformations and random factors were the same as described previously. For the field study, “year” was included as a fixed effect in the SEM. The model simplification was conducted manually: we removed the variables with the lowest significance ($p > 0.05$) until the minimal SEM with the lowest AIC was reached.

SUMMARY OF PUBLICATIONS

Publication 1: Effects of rare arable plants on plant diversity, productivity and soil fertility in agricultural fields

Twerski, A., Fischer, C., & Albrecht, H. (2021). Effects of rare arable plants on plant diversity, productivity and soil fertility in agricultural fields. *Agriculture, Ecosystems & Environment*, 307, doi: 10.1016/j.agee.2020.107237

Author contribution

CF (Christina Fischer) and HA (Harald Albrecht) designed the experiment; **AT** (Alina Twerski) and HA conducted the fieldwork; **AT** and CF analysed the data; **AT** wrote the manuscript; all authors revised the final version of the manuscript.

Summary

Today, agro-biodiversity is significantly declining due to agricultural intensification in European agricultural landscapes. Particularly the primary producers of agroecosystems, arable plants, suffered from this development. Little is known about the ecosystem functions of rare and threatened arable plants, but better knowledge of their ecosystem functions could provide both strong arguments for their conservation as well as improved recommendations for agro-biodiversity management. The objective of this study was to analyse the effects of rare arable plants on phytodiversity, crop and arable plant biomass production, soil organic matter and nitrogen concentration, as well as the biomass and abundance of earthworms (Figure 7). The study was performed on an experimental field and on ten practical farms distributed in the *Munich Plain* in southern Germany, an area with nutrient-poor soils. A mixture of ten rare arable plant species was sown with varying crop densities (uncropped, reduced and regular crop sowing density) and compared to plots without rare arable plants. The cover of rare arable plants did not differ between reduced and regular crop sowing densities, but was highest when no crops were sown. In this study, rare arable plant sowing did not reduce crop biomass. Furthermore, rare arable plants did not affect indicators for soil fertility (Figure 7). However, on the experimental field, soil organic matter and earthworm occurrence decreased during the study period, probably due to pre-crops (clover grass was cultivated before the experiment started) and summer droughts. To investigate the effects of rare arable plants on long-term developing processes, such as soil organic matter content and earthworm occurrence, further perennial experiments are needed. However, our study demonstrates that rare arable plant

sowing can be a suitable tool for plant diversity conservation and simultaneous crop production on nutrient-poor sites.

Graphical abstract

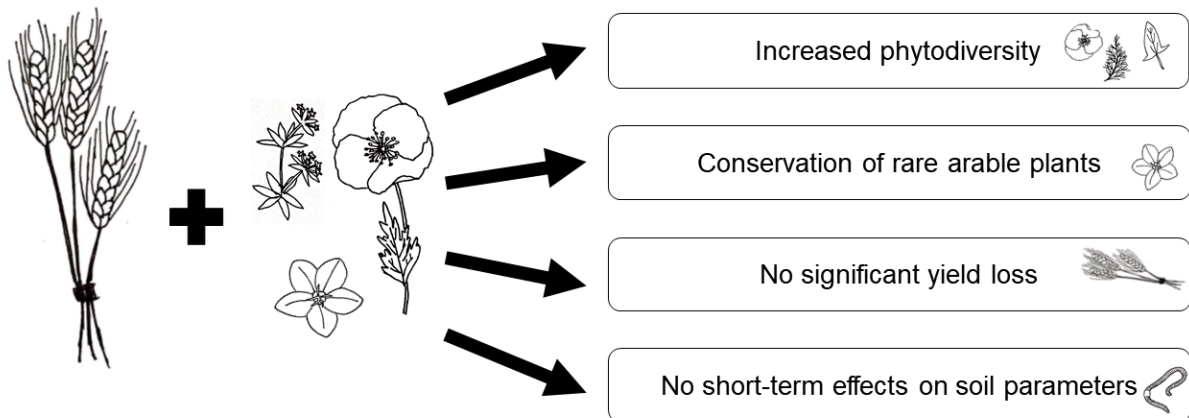


Figure 7: Graphical abstract of Publication 1 presenting the effects of sowing rare arable plants with crops. The study was performed on an experimental field and on ten agricultural farms around Munich. The following parameters were recorded on plots with and without rare arable plant sowing: Number of plant species, number of rare arable plant species, crop and arable plant biomass production, earthworm abundance and biomass, and soil organic matter and nitrogen content. The sowing of rare arable plants increased phytodiversity, which in turn supported the species conservation. Furthermore, rare arable plant sowing did not affect soil parameters and crop biomass production.

Publication 2: Effects of rare arable plants on flower-visiting wild bees in agricultural fields

Twerski, A., Albrecht, H., Fründ, J., Moosner, M., & Fischer, C. (2022). Effects of rare arable plants on flower-visiting wild bees in agricultural fields. *Agriculture, Ecosystems & Environment*, 323, doi: 10.1016/j.agee.2021.107685

Author contribution

CF (Christina Fischer) and HA (Harald Albrecht) designed the experiment; **AT** (Alina Twerski), MM (Michaela Moosner) and HA conducted the fieldwork; **AT**, JF (Jochen Fründ) and CF analysed the data; **AT** wrote the manuscript; all authors revised the final version of the manuscript.

Summary

Flower-visiting wild bees are suffering from increased flower and habitat losses in agricultural landscapes. It is currently unclear how rare arable plants can contribute to wild bee communities in rather homogeneous agricultural landscapes with few flowers. We investigated the effects of sowing ten rare arable plant species on flower-visiting wild bees on the same sites and plots as described in Publication 1. Furthermore, sowing of rare arable plants on uncropped plots was compared with annual and perennial wildflower strips. Our results show that rare arable plants on uncropped plots can attract as many flower-visiting wild bees as wildflower strips (Figure 8). Especially winter annual rare arable plants increased the species richness and abundance of wild bees in plots sown with crops. Interaction networks pointed out that rare arable plants with diverse flower traits, which nowadays are often missing in intensively managed arable fields, tended to be visited by wild bee species with particular preferences. The flowers of *Consolida regalis* have long spurs and attracted the long-tongued bumblebee *Bombus hortorum*. Furthermore, the wild bee *Andrena bicolor* was strongly attracted by *Legousia speculum-veneris*, because its second generation has an affinity for plant species of the Campanulaceae family. Overall, our results were consistent on the experimental field and the ten arable farms, demonstrating the validation under practical conditions. In conclusion, rare arable plant sowing can increase niche diversity and resource availability for flower-visiting wild bees and also conserve rare and threatened arable plants (Figure 8). Therefore, promoting rare arable plant sowing on nutrient-poor sites may become an important tool for pollinator-friendly management in agricultural landscapes.

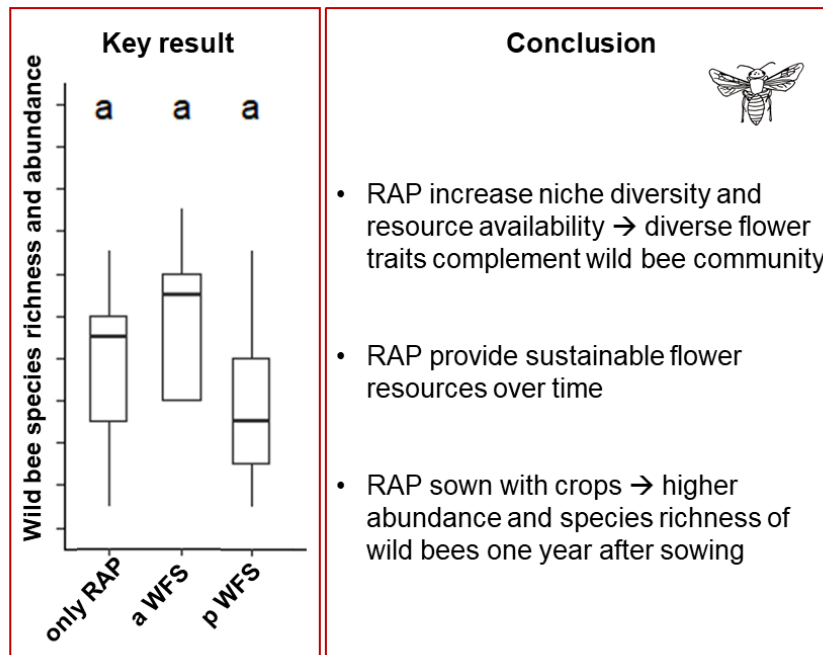
Graphical abstract

Figure 8: Graphical abstract of Publication 2 presenting the effects of rare arable plants (RAP) on flower-visiting wild bees. The study was performed on an experimental field and on ten agricultural farms around Munich, southern Germany. Number and species richness of flower-visiting wild bees were recorded on uncropped plots sown with rare arable plants and on annual (a WFS) and perennial wildflower strips (p WFS). Letters indicate significant differences ($p < 0.05$) between the treatments. RAP on uncropped plots can attract as many flower-visiting wild bees as wildflower strips. Furthermore, RAP sowing increased flower resource availability and niche diversity for wild bees, which is more sustainable over years than the flower resources supplied by WFS. (Figure modified after Twerski et al., 2021b).

Publication 3: Can rare arable plants benefit biological pest control potential of cereal aphids in croplands?

Twerski, A., Albrecht, H., Gallé, R., Sauter, F., Császár, P., Fischer, C. (2023): Can rare arable plants benefit biological pest control potential of cereal aphids in croplands? *Basic and Applied Ecology* 66, doi: 10.1016/j.baae.2022.12.003

Author contribution

CF (Christina Fischer) and HA (Harald Albrecht) designed the experiment; **AT** (Alina Twerski), FS (Fabian Sauter) and HA conducted the fieldwork; RG (Róbert Gallé) and PC (Péter Császár) identified spiders and carabids; **AT**, FS and CF analysed the data; **AT** wrote the manuscript; all authors revised the final version of the manuscript.

Summary

Biological pest control (biocontrol) is a complex and important ecological process, which is negatively affected by agricultural intensification. Arable plants are primary producers and can provide suitable habitats for carabids and spiders, resulting in improved biocontrol in agroecosystems. However, while much is known about the ecosystem functions of common arable plants, it remains unclear how rare and threatened arable plants can influence biocontrol in cereal fields. This study therefore aimed to examine how rare arable plants influence aphid density and activity densities of generalist predators, namely active hunting and web-building spiders and carnivorous/omnivorous carabids. The study was performed on the same sites and plots as described in Publication 1. In each plot, we counted the number of aphids on 100 cereal shoots and set up pitfall traps twice a year in 2018 and 2019. We analysed the effects of rare arable plant occurrence using mixed-effect models. Furthermore, effects of rare arable plant and crop cover on direct and indirect food web interactions were analysed using structural equation models. The structural equation models showed that rare arable plant cover can reduce aphid density and that active hunting spiders, but not web-building spiders and carnivorous/omnivorous carabids, reduced aphid densities (Figure 9). There were no indirect effects of rare arable plant cover via the aphids' predators in the structural equation models. The mechanisms that underlie the network of interactions between rare arable plants, aphids, and their predators are complex and still unclear. However, in this study, we did not identify a sufficiently strong impact of rare arable plants on spiders and carabids, which may suggest that rare arable plants in species-rich plant communities have a weak impact on taxa of higher trophic levels. Further research should evaluate the effect of different rare and common arable plant densities.

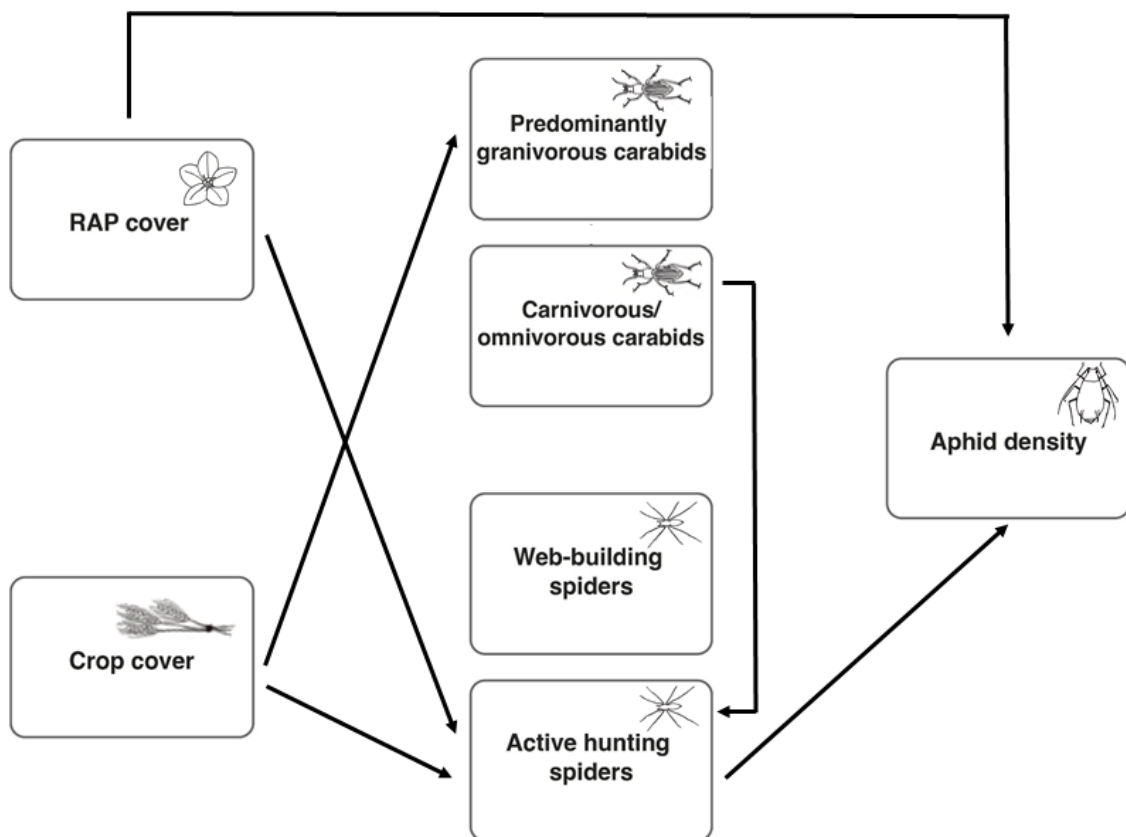
Graphical abstract

Figure 9: Graphical abstract of Publication 3 presenting the effects of rare arable plants (RAP) and crop cover on direct and indirect food web interactions between aphids and their predators, spiders and carabids. The study was performed on an experimental field and on ten agricultural farms around Munich. The following parameters were recorded on plots with and without sowing of rare arable plants: RAP and crop cover, activity densities of active hunting and web-building spiders, and carnivorous/omnivorous and predominantly granivorous carabids and aphid densities. The arrows show significant effects either on the experimental field and/or in the field study. Besides the effect of carnivorous/omnivorous carabids on active hunting spiders, the detected significant interactions were negative. Not significant interactions were removed from this figure. RAP cover and active hunting spiders reduced aphid density. Surprisingly, RAP cover did not enhance activity densities of aphids' natural predators (Figure modified after Twerski et al., 2023).

Further results of the study

To present a comprehensive picture of the ecosystem functions of rare arable plants, additional results are included in this thesis. They show the establishment of the rare arable plants, because better establishment of rare arable plants should improve the ecosystem functions they provide. Additionally, we sampled the wild bee communities at the study sites. These results were published in the final report for the project funder:

Twerski, A., Fischer, C., Meyer, S., Schertler, K., Bühler, A., Stieglitz, A., Albrecht, H. (2021): *Verwendung seltener Ackerwildpflanzen zur Erhöhung der funktionalen Diversität von Agrarlandschaften*. Abschlussbericht DBU-Projekt (AZ: 34029/01), Technische Universität München, Weihenstephan.

Author contribution

CF (Christina Fischer) and HA (Harald Albrecht) designed the experiment; Alina Twerski (**AT**), and HA conducted the fieldwork; **AT** and CF analysed the data; **AT** wrote the report; CF, HA and **AT** revised the related report chapters; SM (Stefan Meyer), KS (Katharina Schertler), AB (Anna Bühler), and AS (Aline Stieglitz) contributed chapters to the report that are not relevant for the results presented here

Rare arable plant establishment

In this study, rare arable plant successfully established in both the experimental field and in the field study (Figure 10). On the experimental field, the mean number of individuals was higher in the autumn-sown crops (228.8 ± 81.2 individuals m^{-2}) than in the spring-sown crops (96.8 ± 41.6 individuals m^{-2}). Contrary, in the field study the mean number of individuals was slightly higher in the spring-sown crops (92.2 ± 43.1 individuals m^{-2}) than in the autumn-sown crops (83.9 ± 70.4 individuals m^{-2}). The reduced crop density positively affected the mean number of individuals. In uncropped plots, rare arable plant establishment was more successful than in plots with crops sown, except in spring-sown crops on the experimental field.

Treatment	Experimental field								Field study	
	3	4	5	6	7	8	9	10		
2018	Without crops	Reduced summer crops	Regular summer crops	Clover grass	Clover grass	Without crops	Reduced summer crops	Regular summer crops	Without crops	Reduced summer crops
	56.2 ± 18.9	88.4 ± 31.1	64.4 ± 19.2			100.0 ± 16.6	113.2 ± 30.6	101.0 ± 16.1	93.9 ± 43.7	90.5 ± 44.9
2019	Without crops	Reduced winter crops	Regular winter crops	Reduced winter crops	Regular winter crops	Clover grass	Clover grass	Clover grass	Without crops	Reduced winter crops
	169.0 ± 53.0	110.8 ± 33.9	68.6 ± 17.2	184.4 ± 53.7	167.4 ± 27.5	25.4 ± 6.9	31.8 ± 11.5	21.2 ± 6.1	104.7 ± 83.0	63.1 ± 51.2
2020				Reduced summer crops	Regular summer crops					
				306.6 ± 74.6	256.8 ± 79.8					

Figure 10: Number of rare arable plant individuals on the experimental field and in the field study. The varying parameters were crop sowing density (regular, reduced by 50%, and uncropped), study years (2018–2020), and crop rotations. Shown are mean number of individuals [m⁻²] ± SD in different treatments (n = 5) and study years (from Twerski et al., 2021b).

Wild bee community

A total of 18 wild bee species were found during flower observations and in the colour pan traps in both, the experimental field and the field study (for complete species list see supplementary material in Table 11 in Twerski et al., 2021b). Within the three study years, 630 wild bees from 51 species were caught in the colour pan traps on the experimental field (Figure 11A). 26 of these species were also observed on flowers. In contrast, 15 wild bee species were sampled only during flower observations and 25 species only in the colour pan traps. The following Red List (either Red List of Germany and/or Bavaria; Westrich et al., 2011; Mandery et al., 2004) species were only detected in the colour pan traps on the experimental field: *Bombus jonellus*, *B. ruderarius*, *Halictus eurygnathus*, *Hylaeus pectoralis*, *Lasioglossum aeratum*, *Megachile ligniseca*, and *M. pilidens*.

Within the two study years, 1,520 wild bees from 61 species were caught in the colour pan traps in the field study. 40 of these species were also observed on flowers. In contrast, 15 wild bee species were sampled only during flower observations and 25 species only in the colour pan traps (Figure 11B). Following Red List (either Red List of Germany and/or Bavaria; Westrich et al., 2011; Mandery et al., 2004) species were only detected in the colour pan traps in the field study: *Halictus sexcinctus*, *Lasioglossum minutulum*, *Lasioglossum sabulosum*, and *Megachile centuncularis*.

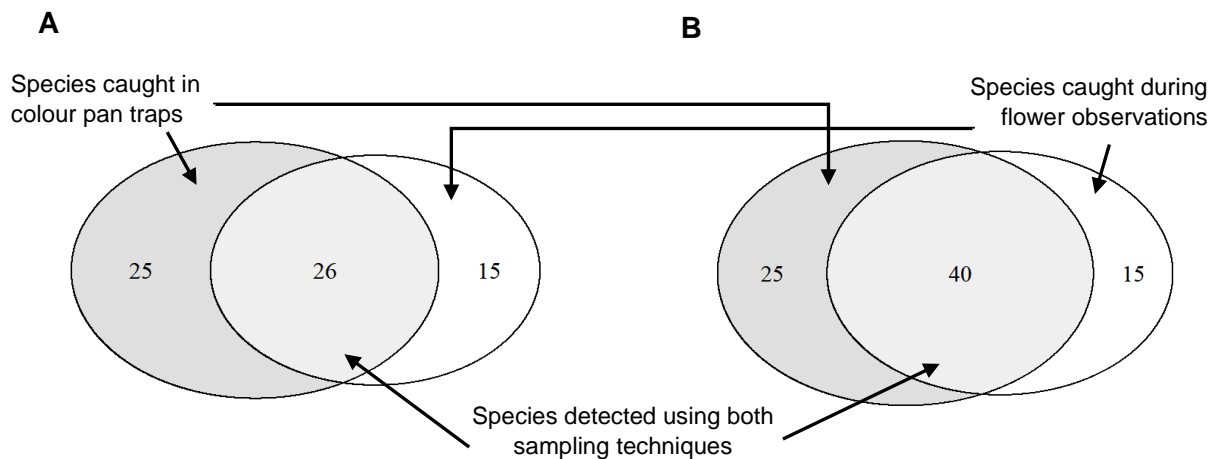


Figure 11: The number of wild bee species collected on A) the experimental field and B) in the field study. Wild bee were sampled either with colour pan traps (dark grey circle) or collected from flowers (white circle). The light grey area shows the number of species detected trough both sampling techniques.

DISCUSSION

Agricultural intensification had a strong negative impact on agrobiodiversity (Stoate et al., 2001). Especially the primary producers of agroecosystems, the spontaneously occurring arable plants, decline in abundance and species richness in many European countries (Richner et al., 2015). There have been strong efforts to mitigate the effects of intensive food production on the arable flora, for example different agri-environmental schemes (AES). However, only few AES focused on the conservation and reintroduction of particularly rare, threatened and low-competitive arable plants. Understanding the role of rare arable plants in agroecosystems is essential to provide multifunctional agroecosystems. According to the mass ratio hypothesis (Grime, 1998), ecosystem functions are driven primarily by the characteristics of the dominant plant species and rare species do not play an important role. However, some studies contradict the mass ratio hypothesis and state that rare species can contribute disproportionately to ecosystem functions (Dee et al., 2019; Leitão et al., 2016; Lyons et al., 2005). In addition, different species provide different ecosystem functions in different years, different places, and under different environmental scenarios, such that it is difficult to say in all cases which species are the most important for functioning (Isbell et al., 2011).

The objective of this thesis was to fill a gap in ecological knowledge of rare arable plants that have not received much attention in ecology. Improving the understanding of ecosystem functions provided by rare arable plants is a key component in counteracting this lack of knowledge. Thus, a better understanding of their contribution to ecosystem functions could help to target conservation management measures, provide an even better justification for their conservation, and create multifunctional arable ecosystems that do not only focus on crop yields. For this purpose, we investigated the effects of sowing rare arable plants on the ecosystem functions phytodiversity, crop and arable plant biomass, soil fertility and nutrient content, flower-visiting wild bees, and biocontrol. The main findings are summarised in Figure 12.

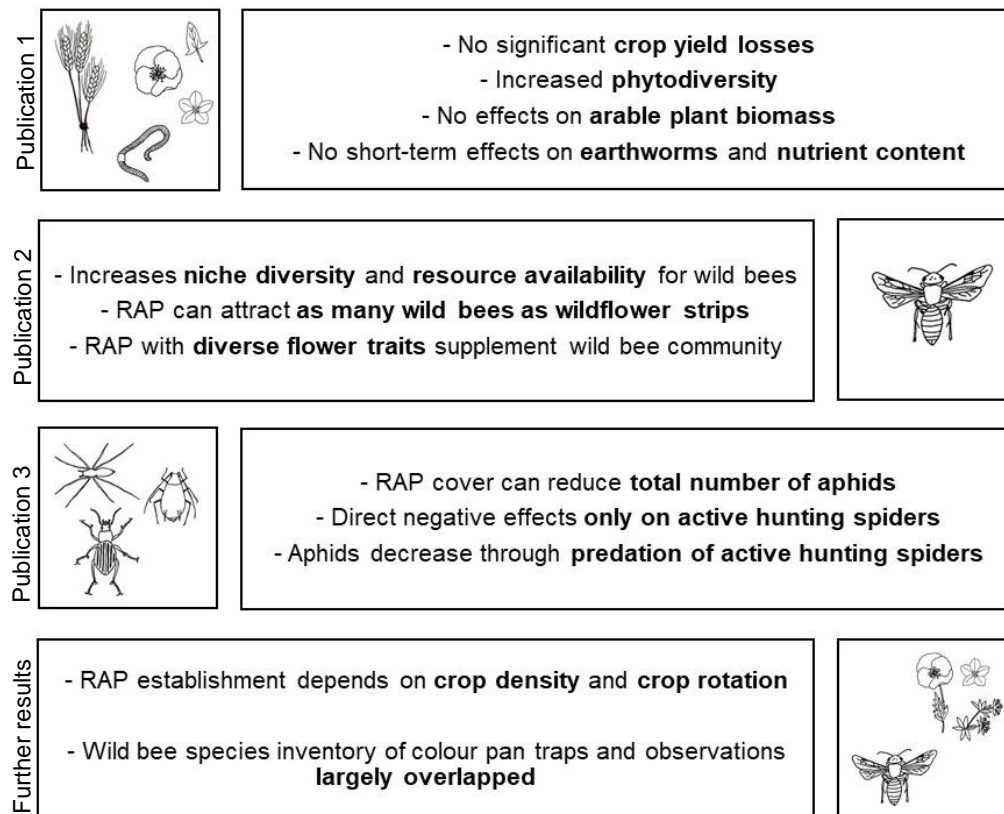


Figure 12: Main findings of this thesis including Publication 1 (Twerski et al., 2021a), 2 (Twerski et al., 2022), 3 (Twerski et al., 2023), and further results (Twerski et al., 2021b). The effects of sowing rare arable plants (RAP) on following ecosystem function were analysed: crop biomass production, arable plant biomass production, phytodiversity, soil organic matter content, soil nitrogen concentration, soil fertility (earthworm biomass and abundance; Publication 1), flower-visiting wild bees (Publication 2), and biological pest control (ground-dwelling predators and aphid density; Publication 3).

Rare arable plants provide ecosystem functions

In this study, establishment of rare arable plants was species-specific, but overall successful, and therefore sowing of rare arable plant increased phytodiversity (Publication 1 and further results). The method of sowing selected species has been widely demonstrated as a successful tool for the reintroduction and conservation of rare arable plant species (Albrecht et al., 2016; Lang et al., 2016; Lang et al., 2018; Lang et al., 2021; Wagner et al., 2017). Such measures could therefore effectively counteract the ongoing loss of rare arable plant species richness and abundance in agricultural landscapes and thus generally increase farmland diversity (Bretagnolle and Gaba, 2015; Marshall et al., 2003). The sowing of rare arable plants is a sustainable measure, because most arable plant species form persistent soil seed banks (Bakker et al., 1996; Lang et al., 2018), so re-sowing after successful establishment becomes unnecessary.

Reduced crop sowing densities facilitated the establishment of rare arable plants (Publication 1 and further results). This result is in line with other studies (Lang et al., 2021; Rotchés-Ribalta et al., 2020; Wagner et al., 2017) and should be adopted in conservation and reintroduction practice. Though, it should also be noted that reduced crop sowing densities may lower crop yields. However, since reintroduction of rare arable plants is recommended on nutrient-poor soils without major weed infestation (Lang et al., 2018; Lang et al., 2021), yield losses are relative low (Epperlein et al., 2014; Lang et al., 2016). If these recommendations on reintroduction are ignored on nutrient-rich soils, reduced crop sowing densities may not only increase weed infestation in the future, but also minimise the establishment of rare arable plants. However, in this study, sowing of rare arable plants did not result in crop biomass losses (Publication 1), suggesting that rare arable plant species with low competitive ability have little impact on crop production (Holzner and Glauning, 2005). Storkey and Westbury (2007) showed that arable plants may use resources unavailable for crops, resulting in an overall increase in the total productivity of the system. Nevertheless, as noted above, this does not apply for all sites, as e.g. rare arable plants will be outcompeted by harmful weeds with higher competitive ability. Therefore, site selection and adaptive management is crucial for effective conservation of rare arable plants (Lang, 2021).

Regarding the wild bee communities, the species inventory caught in the colour pan traps and in the observations of flower visitors largely overlapped (further results). Most of the observed flower-visiting wild bee species were also captured in the colour pan traps in both the experimental field and the field study. Furthermore, on plots where rare arable plants were sown with crops, higher abundance and species richness of flower-visiting wild bees was observed only one year after sowing (Publication 2). Rare arable plant flower cover positively affected wild bee abundance and species richness (Publication 2). The additional flower

resources improved the habitat quality for wild bees, which colonized the flower resources fast (Exeler et al., 2009). Rare arable plant sowing also enhanced niche diversity for flower-visiting wild bees (Publication 2). As also in the study by Gibson et al. (2006), most rare arable plant species shared their flower visitors with common plant species. However, there were two exceptions in our study: The two rare arable plant species *Legousia speculum-veneris* and *Consolida regalis* were mainly visited by wild bee species with special preferences. The long-tongued bumblebee *Bombus hortorum* visited mainly *Consolida regalis*, because this plant species has a long spur. Moreover, the wild bee species *Andrena bicolor* was almost exclusively observed on *Legousia speculum-veneris*, as its second generation has an affinity for Campanulaceae (Schmid-Egger and Scheuchl, 1997). These results confirm that the diversification of flower traits such as flower colour, size, shape, and flowering time increases flower resource heterogeneity and therefore pollinator species richness (Ebeling et al., 2008).

The occurrence of rare arable plants in addition to the unendangered species can also contribute to a wider temporal spectrum of flower availability. Thus, species like *Buglossoides arvensis* or *Veronica triphyllos* L. already flower in April, while others like *Kickxia spuria*, *Sherardia arvensis* or *Stachys annua* (L.) L. flower in the cereal stubble once the removal of the crop competition by harvesting operations has improved light availability (Pinke et al., 2021; Pinke and Pál, 2009). Moreover, arable plants show a high phenotypic plasticity i.e. the capacity of a single genotype to exhibit variable phenotypes in response to environmental conditions (West-Eberhard, 1989). Arable plants are also able to re-sprout or gradually form new flowers after the crop harvest. Therefore, these species can provide temporal continuity of flower resources in fields and thus stabilize food supply for wild bee communities (Neumüller et al., 2021; Scheper et al., 2015; Williams et al., 2015). This is important for wild bees, as they do not store pollen or nectar to survive unfavourable times. In agricultural landscapes, wild bee conservation concepts should include high floristic diversity (Nichols et al., 2019; Schubert et al., 2022; Wood et al., 2017). The sowing of rare arable plants can substantially support the resident arable plant community due to the introduction of additional flower traits and therefore increase floristic diversity.

When rare arable plants were sown without crops, they attracted the same species richness and abundance of wild bees as annual and perennial wildflower strips (Publication 2). Compared to rare arable plant sowing, wildflower strips show some disadvantages. Thus, plant species included in wildflower strips usually have transient soil seed banks. Therefore, these species disappear when the agri-environmental programs end and the farmer revert to their farming practices. In this study, wild bees almost completely disappeared after the annual wildflower strip plots returned to the regular crop rotation (Publication 2). In contrast, formation of persistent soil seed banks in arable plants (Bakker et al., 1996) renders re-sowing

superfluous. Such sustainable provision of flower resources over years can also compensate for the relatively high costs of the seed material of rare arable plants (Geisbauer and Hampicke, 2012). On the other hand, perennial wildflower strips provide overwintering habitats for arthropods (Ganser et al., 2019), which is not the case for sowing rare arable plants without crops and annual wildflowers strips. To ensure continuity and diversity of flower resources for wild bees in agricultural landscapes, both rare arable plants and perennial wildflower strips should be sown. However, it is important to consider site conditions for the different measures, as rare arable plants are not competitive on productive sites with high weed diversities and should preferably be sown on nutrient-poor soils without major weed infestation (Lang et al., 2018; Lang et al., 2021). In contrast, wildflower strips should only be sown on nutrient-rich soils, which would reduce competition for land with the conservation of rare arable plants.

To investigate the effects of sowing rare arable plants on higher trophic taxa, not only flower-visiting wild bees, but also biocontrol was studied. Rare arable plant cover directly reduced the density of phytophagous aphids (Publication 3), supporting the associated resistance-hypothesis (Barbosa et al., 2009). This hypothesis implies that neighbouring plant species can strengthen the associated resistance of crops against pests through e.g. camouflaging the crop (Perrin and Phillips, 1978), which in turn reduces the infestation of crops with aphids (Ben-Issa et al., 2017). Surprisingly, the increased phytodiversity through sowing of rare arable plants did not enhance activity densities of aphids' natural predators, active hunting and web building spiders and carnivorous/omnivorous carabids (Publication 3), which contradicts the literature (Blaix et al., 2018; Gaba et al., 2020; Langellotto and Denno, 2004; Letourneau et al., 2011). In this study, plant species richness was already high in most of the sampled arable fields, such that they do not necessarily represent the average situation on arable fields. With a species rich and abundant resident flora, the presence of rare arable plants does not additionally affect higher trophic levels. The lack of a significant influence obtained in this study would probably become noticeable in floristically poorer areas with a less diverse residential arable flora. Therefore, the additional effect of rather small and low competitive rare arable plant sowing may have been marginal under these study conditions. Furthermore, the effect that the relationship curve of plant and predator diversity can come to a saturation point observed in a grassland experiment (Scherber et al., 2010), may also apply for our situation on arable land. On species-rich and extensively managed arable fields, which provide particularly favourable conditions for rare arable plants, the resident arable plant community may already ensure efficient biocontrol. To create an all-encompassing functional network, further analyses must include interactions between rare and common arable plant densities.

Trade-offs between ecosystem functions

During recent centuries, agricultural land use has created new ecosystems and thus also agrobiodiversity (Stoate et al., 2001; Willcox, 2012). Until now, agricultural management has mainly focused on increasing productivity and achieving high crop yields (Power, 2010). Moreover, besides yields, agriculture also generates essential non-food functions such as nutrient cycling, pollination, decomposition, etc., that are not provided by other economic sectors (Dobbs and Pretty, 2004). The modern agricultural land use significantly has increased crop yields, but on the other hand, it has also caused persistent losses of multiple ecosystem functions that in turn are essential for securing food supply (Foley et al., 2005). The management of agroecosystem faces the trade-off between enforcing the productivity vs. meeting the requirements of environmental and biodiversity protection and conservation.

The conceptual framework of Foley et al. (2005) compares different types of land use and trade-offs of ecosystem functions. They conclude that a small reduction in yields could lead to a noticeable improvement in agroecosystem functioning. Actually, there are increasing indications that aiming for multifunctionality does not necessarily lead to crop yield losses: In organic food production the crop yields of different crops can even be as high as in conventional agriculture (Badgley et al., 2007, but see Ponti et al., 2012; Wittwer et al., 2021). On arable land, a neutral relationship was found between crop yields and ecosystem multifunctionality (Gaba et al., 2020). The results of this dissertation underline previous findings that sowing of rare arable plants did not result in measurable crop yield losses, while other functions such as phytodiversity and abundance of wild bees increased. However, since sowing of rare arable plants is recommended on rather nutrient-poor sites (Lang et al., 2018; Lang et al., 2021), crop yields on these sites are already lower compared to more fertile soils. Therefore, nutrient-poor sites are especially suitable for the 'land sharing' strategy, because the trade-off between biodiversity conservation and food production can be overcome. In the tradition of Foley et al. (2005), broader implications and improvements must be met for agroecosystems to provide not only crop yields, but also non-food functions:

1. Because farmers have so far been focusing mainly on food production, they sometimes lack the necessary knowledge for the production of non-food ecosystem functions. Therefore, farmers need a reasonable degree of continuing education (Gerowitt et al., 2017), which also expands their knowledge of how to manage different arable plant species.
2. Organic and ecological farming methods already exist, usually combining crop yields with non-food production. However, these practices need to be integrated into current cropping systems, which in turn would promote the arable flora (MacLaren et al., 2020). In addition, the scientific community has to allocate resources for further research to

develop new management techniques and options that optimise agriculture to perform multiple functions (Badgley et al., 2007; Neve et al., 2018).

3. Solving the dilemma of what and how to produce in agroecosystems requires a holistic approach. Unfortunately, scientists who study agroecosystems are divided into agronomists, who focus on the productivity of agroecosystems, and ecologists or environmental researchers who concentrate on the environmental impact of agriculture and the conservation or restoration of agroecosystems (Wittwer et al., 2021). This is also the case for arable plants that are either seen as noxious weeds, or as an important part of the agro-biodiversity (Storkey and Neve, 2018). The man-made division of a system or even a selected group of species into two research areas impacts the gain of knowledge which is possible by joint research efforts. Therefore, the scientific debate should be more structured, and inter- and transdisciplinary research is needed (Fusco, 2021; Mupepele et al., 2021; Neve et al., 2018).
4. To mitigate biodiversity loss in agricultural landscapes, the CAP introduced the voluntary funding instruments AES (Batáry et al., 2015) and the in some cases obligatory greening measures (Zinngrebe et al., 2017). However, the measures are not sufficient to maintain biodiversity and especially rare arable plant conservation (Kleijn et al., 2001; Kleijn and Sutherland, 2003; Pe'er et al., 2017, but see Walker et al., 2007). Furthermore, agri-environmental schemes do not provide effective incentives for farmers (Zinngrebe et al., 2017). Policymakers must create support and subsidy mechanisms that enable biodiversity conservation and multifunctionality of agroecosystems. Thus, several authors suggest improvements to increase the effectiveness of funding instruments to conserve biodiversity (Lakner et al., 2017; Mupepele et al., 2021; Pe'er et al., 2017; Pe'er et al., 2020).
5. Finally, the recently published study by Tschardt et al. (2021) shows that the successful promotion of biodiversity does not primarily depend on the management of individual fields, but on the landscape level. They conclude that a mosaic of natural habitat patches and diversified small fields are key elements for large-scale biodiversity promotion. The conservation of rare arable plants should be one of many measures to diversify arable fields.

However, to balance the trade-offs between the different ecosystem functions, it is important to assess the ecosystem functions provided by arable land. Since this is a complex process, an indicator that evaluates the different ecosystem functions could help to address this need.

Indicator of multifunctionality

Our study supports the indispensable role of arable plants for various ecosystem functions and extends the knowledge of the effects of particularly rare arable plants. However, ecosystem functions should not only be considered individually, but should be integrated into a combined metric that provides an indicator of multifunctionality (Hölting et al., 2019). Generally, indicators help to evaluate conditions or changes or to set up environmental goals (Heink and Kowarik, 2010). The ecosystem functions examined here individually could unfortunately not be combined into a multifunctionality indicator within the scope of this study. Gaba et al. (2020) studied the effects of arable plant diversity on ecosystem multifunctionality. They showed that arable plant diversity contributed to ecosystem multifunctionality. However, Gaba et al. (2020) distinguished between common and rare arable plants, but their definition referred to the local abundance of species in their study area and not to their threatened status or general rarity. In their study, the most frequently occurring species among the rare arable plant species were *Medicago lupulina* L., *Galium aparine* L. and *Vicia sativa* L. None of these three species are threatened or protected at national or larger regional levels. *Galium aparine* is even considered as a noxious weed in arable fields and therefore its classification as rare arable plants does not correspond to our definition. Further research on conservation of rare arable plants should combine the individual ecosystem functions into a multifunctionality indicator, which would help to evaluate the changes over time or to set up goals in rare arable plant conservation and reintroduction. Interestingly, the effects of arable plant diversity for most functions in Gaba et al. (2020) were weaker when considered individually rather than combined into a multifunctional indicator. Therefore, it is likely that this studies results will show stronger implications when the individual ecosystem functions of rare arable plants are combined in an indicator of multifunctionality.

Perspectives for arable plant conservation

In this study, the presence of rare arable plants diversified plant communities and increased phytodiversity. Furthermore, our study shows that rare arable plants affect higher trophic levels and therefore increase ecosystem functioning. Besides benefitting biodiversity, some highly competitive arable plants can also cause ecosystem dis-services through severe losses of crop yields (Gerowitt et al., 2017). Therefore, arable plants are mainly seen as either noxious, yield-reducing weeds which need sufficient weed control, or as an important part of the agrobiodiversity, which need to be managed from a conservation point of view (Storkey and Neve, 2018). This ambivalent relationship to arable plants recently led to the “Paradox of arable weeds” (Fagúndez, 2015). It implies that on the one hand, weed control is nowadays used as much as never before, and on the other hand, various AES have been established to restore and to conserve the arable flora in agricultural fields. Therefore, Storkey and Westbury (2007) suggest distinguishing between beneficial and noxious arable plants species, with the latter requiring efficient weed control. Thereby, beneficial arable plant species need to be separated from the problematic species. In this study, we exclusively selected species that show a low- to intermediate competitive capacity (Holzner and Glauning, 2005) and are threatened or have an infrequent or decreasing abundance in the study area. Storkey and Westbury (2007) defined beneficial species, referred to as ‘good weeds’, as species that are also relatively poor competitors for crops, but have additional potential value to higher trophic taxa in agroecosystems. They categorised arable plant species based on their value to associated invertebrates and birds and also their competitive index, and defined groups of beneficial arable plants (Storkey, 2006; Storkey and Westbury, 2007). Contrary to the low competitive species investigated in our study, some of the species in at least one of the ‘good weeds’ groups are considered as noxious weeds with high to very high competitive capacity (e.g. *Chenopodium album* L., *Sinapis arvensis* L., *Fallopia convolvulus* (L.) Á.Löve, Holzner and Glauning, 2005). This in turn means that farmer’s acceptance to tolerate these species in their fields could become quite low. In addition, to reduce the ongoing loss of phytodiversity and to conserve already threatened plants, the species rarity and conservation value must be factored into ‘good weeds’ considerations. In winter wheat fields, Storkey et al. (2010) found a ‘rare weed trait syndrome’ of short stature, large seeds and late flowering species. However, for rare arable plant species, knowledge of their role in agroecosystems and for the associated higher trophic taxa is scarce. This study contributes to fill this gap; therefore, further research is essential.

CONCLUSION

This study analysed the effects of rare, low-competitive arable plants on different ecosystem functions in agroecosystems. Rare arable plant sowing increased phytodiversity without reducing crop biomass production on nutrient-poor soils (**Publication 1**). Furthermore, rare arable plant sowing increased flower resource availability and niche diversity for flower-visiting wild bees. The flower resources provided by rare arable plants are more sustainable over years than those supplied by wildflower strips (**Publication 2**). Moreover, rare arable plant cover directly reduced the density of phytophagous aphids, but had no positive effects on the abundance of aphids' natural predators (**Publication 3**). These results underline that conservation of rare arable plants, food production and the provision of different non-food ecosystem functions can occur simultaneously on nutrient-poor agricultural fields.

The findings of this dissertation support the premise that crop productivity and environmental and biodiversity protection need not be mutually exclusive. Comprehensive provision of ecosystem functions is becoming increasingly important in a world experiencing major global change pressures. Because the long-term changes to agroecosystems are nearly irreversible, farmers, scientists, and policy makers must strive to transform the agricultural sector, which includes a rethinking of the role of arable plants in agroecosystems. The thesis contributes to the understanding of the role of rare and threatened arable plants in agroecosystems and highlights the need for their conservation and reintroduction as they support various ecosystem functions. Moreover, two to three years is too short a time to study soil-forming processes, so further long-term studies are needed. Finally, it is important to point out that for a holistic understanding of rare arable plants and their role in agroecosystems, their functions would next need to be analysed not only separately but also combined into a multifunctionality indicator.

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Appendix

A1 Publication list

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Peer reviewed journal publications

Twerski, A., Albrecht, H., Gallé, R., Sauter, F., Császár, P., Fischer, C. (2023). Can rare arable plants benefit biological pest control potential of cereal aphids in croplands? *Basic and Applied Ecology* 66, 40–49.

Twerski, A., Albrecht, H., Fründ, J., Moosner, M. & Fischer, C. (2022). Effects of rare arable plants on flower-visiting wild bees in agricultural fields. *Agriculture, Ecosystems & Environment*, 323, 107685.

Twerski, A., Fischer, C., & Albrecht, H. (2021). Effects of rare arable plants on plant diversity, productivity and soil fertility in agricultural fields. *Agriculture, Ecosystems & Environment*, 307, 107237.

Eibes, P. M., Oldeland, J., Irl, S. D. H., **Twerski, A.**, Kühne, N., & Schmiedel, U. (2021). Partitioned beta diversity patterns of plants across sharp and distinct boundaries of quartz habitat islands. *Journal of Vegetation Science*, 32(3), e13036.

Damasceno-Junior, G. A., Oldeland, J., de Andrade Amador, G., Casagrande, J. C., & **Twerski, A.** (2021). Environmental drivers of three neighbouring monodominant stands in Pantanal wetland. *Journal of Vegetation Science*, 32(3), e13023.

Schmiedel, U., Kühne, N., **Twerski, A.**, & Oldeland, J. (2015). Small-scale soil patterns drive sharp boundaries between succulent “dwarf” biomes (or habitats) in the arid Succulent Karoo, South Africa. *South African Journal of Botany*, 101, 129-138.

Other publications

Twerski, A., Fischer, C., Meyer, S., Schertler, K., Bühler, A., Stieglitz, A., Albrecht, H. (2021). Verwendung seltener Ackerwildpflanzen zur Erhöhung der funktionalen Diversität von Agrarlandschaften. Abschlussbericht DBU-Projekt (AZ: 34029/01), Technische Universität München, Weihenstephan

Talks and poster contributions at international conferences

Twerski, A., Fischer, F., Albrecht, H. (2021). Ecosystem functions of rare arable plants. *50th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland*, Online. (talk)

Twerski, A., Fischer, F., Albrecht, H. (2019). The use of rare arable plants to enhance ecosystem functions of agro-ecosystems. *7th meeting of the EWRS working group “Weeds and biodiversity”*, Universität Hohenheim, Germany. (talk)

Twerski, A., Fischer, F., Kollmann, J., Albrecht, H. (2018). The use of rare arable plants to enhance ecosystem functions of agroecosystems. *48th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland*, Vienna, Austria. (poster)

Schmiedel, U., Kühne, N., **Twerski, A.**, Oldeland J. (2015). Small-scale soil patterns drive sharp boundaries between habitats in the arid Succulent Karoo, South Africa. *45th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland*, Göttingen, Germany. (poster)