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Landscape- and time-dependent effects of wildflower areas on the
non-target group of ground-dwelling arthropods

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vorgelegt von M.Sc. Hannes Hoffmann
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Dekan: Prof. Dr. Karl H. Mühling

1. Berichterstatter: Prof. Dr. Tim Diekötter

2. Berichterstatter: Prof. Dr. Volkmar Wolters

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“The truth is: the natural world is changing. And we are totally dependent on that world. It provides our food, water and air. It is the most precious thing we have and we need to defend it.”

SIR DAVID ATTENBOROUGH

SUMMARY

Agri-environmental schemes (AES), such as wildflower areas, aim at halting the loss of species and their associated ecosystem services by compensating the ongoing decline of semi-natural habitats in agro-ecosystems. However, recent assessments of their efficacy imply that European AES are not always fulfilling their goals. Inconsistent benefits may be owed to neglecting the landscape context in their establishment and of temporal dynamics in their evaluation. Positive effects frequently have been shown during the vegetation period and for pollinators. It is less known, whether wildflower areas may enfold benefits also for the non-target group of ground-dwelling arthropods in and outside the vegetation period. Here, I studied the role of wildflower areas as overwintering habitats as well as landscape- and time-dependent effects of wildflower areas on the ground-dwelling arthropods across three consecutive years to contribute to the improvement of future AES in multifunctional agro-ecosystems.

To quantify the structural complexity of agro-ecosystems that may affect the efficacy of wildflower areas, I innovatively distinguished between permanent semi-natural habitats (e.g. hedges) and transient wildflower areas and selected ten landscapes, which encompass independent gradients of these two resource-rich habitat types. Within these landscapes, I sampled rove beetles, carabid beetles and spiders in wildflower areas and adjacent crop fields, since these natural enemies are the main groups of ground-dwelling arthropods and contribute to ecosystem services such as natural pest control. I studied ground-dwelling arthropods overwintering in wildflower areas and adjacent crop fields by two emergence traps, each, from January till April, to advance our understanding of the benefits of wildflower areas beyond the vegetation period. In order to better understand landscape- and time-dependent benefits of wildflower areas, I studied abundance, species richness and community composition as well as the change of selected traits (body size, diet, flight ability) and the functional diversity of ground-dwelling arthropods by pitfall traps from May till July over a period of three consecutive years. Additionally, I was interested how landscape context, i.e. additive and interactive effects of proportions of permanent semi-natural habitats and transient wildflower areas, alters benefits of wildflower areas.

I found more rove beetles and spiders to overwinter in wildflower areas as compared to adjacent crop fields. Local characteristics such as vegetation density as well as the landscape context affected in particular the overwintering of rove and carabid beetles. While outside the vegetation period positive biodiversity relationships with the proportions of permanent semi-

natural habitats and transient wildflower areas were hump-shaped, during the vegetation period beetles responded to permanent semi-natural habitats also in a hump-shaped manner, whereas transient wildflower areas seemed to drive linear responses. In addition to these additive effects, I found that both habitat types had an interactive effect on species richness of rove beetles in wildflower areas, on the functional diversity of carabid beetles in wildflower areas and the diet of carabid beetles in crop fields. Although abundance and species richness of ground-dwelling arthropods did not change substantially across my three-year study, their community composition became more similar between wildflower areas and crop fields due to bidirectional cross-habitat spillover. Yet, going beyond the traditional abundance and species richness measures of biodiversity, I was able to show that the functional diversity of rove beetles in wildflower areas and of carabid beetles in crop fields increased across the three years. At the same time, these natural enemies may have transported their ecosystem services from the wildflower areas into the adjacent fields.

My results show that wildflower areas provide a suitable habitat for ground-dwelling arthropods in agro-ecosystems throughout the entire year and increased their functional diversity. These cross-seasonal benefits highlight the potential of wildflower areas to support diversity also beyond abundance and species richness. At the same time, however, I show that the efficacy of wildflower areas is crucially shaped by landscape context. Both, permanent semi-natural habitats and transient wildflower areas, seem to complement each other and considered in concert, maximized benefits of wildflower areas to ground-dwelling arthropods at intermediate landscape complexity. Since the results of my study are in line with the general claim to secure 10-15% of semi-natural habitats in agroecosystems, the future challenge is to effectively protect remaining permanent semi-natural habitats as well as to target specific landscape situations when establishing new wildflower areas in order reach this threshold. To conclude, my results indicate that future AES should ensure a more continuous provisioning of wildflower areas and support the potential of wildflower areas to promote biodiversity and contribute to multifunctional agro-ecosystems, if implemented landscape-specific.

ZUSAMMENFASSUNG

Die Anlage von Blühflächen im Rahmen von Agrarumweltmaßnahmen zielt darauf ab, den Rückgang der Arten und ihrer Ökosystemdienstleistungen zu stoppen, indem der anhaltende Verlust an naturnahen Landschaftsstrukturen in Agrarlandschaften ausgeglichen wird. Aktuelle Studien zu ihrer Wirksamkeit zeigen jedoch, dass europäische Agrarumweltmaßnahmen ihre Ziele nicht immer erreichen. Uneinheitliche Ergebnisse bei der Bewertung der Wirksamkeit von Blühflächen scheinen der Vernachlässigung der Einbeziehung der Landschaftskomplexität und der Bewertung der zeitlichen Dynamik geschuldet zu sein. Positive Effekte konnten bislang vielfach während der Vegetationsperiode und für Bestäuber festgestellt werden, wohingegen Blühflächen auch für Nichtzielarten wie bodenbewohnende Arthropoden während und außerhalb der Vegetationsperiode eine wichtige Rolle spielen könnten. Vor diesem Hintergrund habe ich die Funktion von Blühflächen als Überwinterungshabitat sowie die landschafts- und zeitabhängigen Einflüsse von Blühflächen auf bodenbewohnende Arthropoden in drei aufeinanderfolgenden Jahren untersucht, um zur Verbesserung von künftigen Agrarumweltmaßnahmen in multifunktionalen Agrarlandschaften beizutragen.

Als Maß für die Landschaftskomplexität, die die Wirksamkeit von Blühflächen beeinflussen könnte, habe ich erstmalig zwischen permanenten (z.B. Hecken) und transienten Landschaftsstrukturen (z.B. Blühflächen) unterschieden und zehn Landschaften ausgewählt, die unabhängige Gradienten dieser beiden ressourcenreichen Landschaftsstrukturen umfassen. In diesen Landschaften habe ich Kurzflügelkäfer, Laufkäfer und Spinnen in Blühflächen und angrenzenden Getreidefeldern beprobt, da sie die häufigsten bodenbewohnenden Arthropoden darstellen und zu Ökosystemdienstleistungen wie der natürlichen Schädlingsbekämpfung beitragen. Zunächst erfasste ich bodenbewohnende Arthropoden, die in Blühflächen und Getreidefeldern überwintert haben, von Januar bis April mit jeweils zwei Eklektoren je Blühfläche und Getreidefeld, um das Verständnis der Wirksamkeit von Blühflächen über die Vegetationsperiode hinaus zu verbessern. Um die landschafts- und zeitabhängigen Einflüsse von Blühflächen besser zu verstehen, habe ich die Häufigkeit, den Artenreichtum und die Gemeinschaftszusammensetzung, sowie die Veränderung ausgewählter Merkmale (Körpergröße, Ernährungsweise, Flugfähigkeit) und die funktionelle Diversität bodenbewohnender Arthropoden jeweils von Mai bis Juli über einen Zeitraum von drei aufeinanderfolgenden Jahren mit Bodenfallen untersucht. Darüber hinaus war ich daran interessiert, wie die Landschaftskomplexität, also zusätzliche und interaktive Effekte von

Anteilen permanenter und transienter Landschaftsstrukturen, die Wirksamkeit von Blühflächen beeinflusst.

Ich konnte mehr überwinternde Kurzflügelkäfer und Spinnen in Blühflächen als in angrenzenden Getreidefeldern nachweisen. Lokale Parameter wie die Vegetationsdichte sowie die Landschaftskomplexität beeinflussten insbesondere die Überwinterung von Kurzflügel- und Laufkäfern. Sie zeigten einen unimodalen Zusammenhang mit den Anteilen permanenter und transienter Landschaftsstrukturen. Im Gegensatz dazu zeigten die Käfer während der Vegetationsperiode zwar auch einen unimodalen Zusammenhang mit den Anteilen permanenter Landschaftsstrukturen, aber einen linearen Zusammenhang mit den Anteilen transienter Blühflächen. Des Weiteren stellte ich interaktive Effekte dieser beiden Landschaftsstrukturen auf den Artenreichtum von Kurzflügelkäfern in Blühflächen, auf die funktionelle Diversität von Laufkäfern in Blühflächen und auf die Ernährungsweise von Laufkäfern in Getreidefeldern fest. Obwohl sich die Häufigkeit und der Artenreichtum bodenbewohnender Arthropoden in meiner dreijährigen Studie nicht wesentlich verändert haben, wurde die Zusammensetzung ihrer Gemeinschaften durch einen bidirektionalen Austausch zwischen Blühflächen und Getreidefeldern immer ähnlicher. Über die traditionellen Maße für Häufigkeit und Artenreichtum der biologischen Vielfalt konnte ich darüber hinaus sogar zeigen, dass die funktionelle Diversität von Kurzflügelkäfern in Blühflächen und von Laufkäfern in Getreidefeldern über die drei Jahre zunahm. Dabei konnten sie womöglich gleichzeitig ihre Ökosystemdienstleistungen von den Blühflächen in die angrenzenden Felder transportieren.

Meine Ergebnisse zeigen, dass Blühflächen über das ganze Jahr hinweg einen geeigneten Lebensraum für bodenbewohnende Arthropoden in Agrarlandschaften bieten und die funktionelle Diversität erhöhen können. Diese saisonübergreifenden Vorteile unterstreichen das Potenzial von Blühflächen, die Diversität über die Häufigkeit und Artenreichtum hinaus zu fördern. Gleichzeitig jedoch zeigte sich, dass die Wirksamkeit entscheidend von der Landschaftskomplexität beeinflusst wird. Permanente und transiente naturnahe Landschaftsstrukturen scheinen sich dabei zu ergänzen und können gemeinsam betrachtet die positiven Effekte von Blühflächen auf die Diversität in einfach strukturierten Landschaften mit mittleren Anteilen permanenter und transienter Landschaftsstrukturen maximieren. Da die Ergebnisse meiner Untersuchungen mit der allgemeinen Forderung übereinstimmen, 10-15% naturnaher Landschaftsstrukturen in Agrarlandschaften zu erhalten, ist die künftige Herausforderung, verbleibende permanente Strukturen effektiv zu schützen, sowie bei der

Anlage neuer Blühflächen auf bestimmte Landschaftsgegebenheiten abzielen, um diesen Schwellenwert zu erreichen. Darüber hinaus deuten meine Ergebnisse darauf hin, dass künftige Agrarumweltmaßnahmen eine kontinuierlichere Etablierung von Blühflächen in diesen Landschaften gewährleisten sollten. Zusammenfassend unterstützen die hier vorgestellten Ergebnisse das Potenzial von Blühflächen, die biologische Vielfalt zu fördern und zu multifunktionellen Agrarökosystemen beizutragen, sofern ihre Anlage landschaftsspezifisch umgesetzt wird.

“It is not the strongest of the species that survives, not the most intelligent that survives. It is the one that is the most adaptable to change.”

CHARLES DARWIN

GENERAL INTRODUCTION

Sown wildflower areas constitute a popular agri-environment scheme (AES), aiming to counteract the ongoing loss of species and their associated ecosystem services in modern agro-ecosystems (Haaland et al., 2011). Yet, benefits of wildflower areas to biodiversity were not unequivocal when evaluated and often showed only modest increases in abundance and richness of common species (Batáry et al., 2015; Ekroos et al., 2014). In order to advance our understanding of the conservation benefits of sown wildflower areas beyond the vegetation period, the current knowledge on the landscape-dependencies of these benefits and beyond abundance and species richness, I studied the value of wildflower areas as overwintering habitats for, the effects of permanent and transient semi-natural habitats on and the functional diversity of the community of ground-dwelling arthropods. Since these natural enemies are known to spillover between different habitat types in agro-ecosystems in search for food or shelter, I simultaneously studied the community of ground-dwelling arthropods in a crop field adjacent to each wildflower area. As benefits of wildflower areas, however, may need time to establish and previous studies mainly focused on annual snap-shots, I studied the abovementioned effects of newly established wildflower areas on ground-dwelling arthropods over a period of three consecutive years.

Anthropogenic land-use change has resulted in an enormous loss of species diversity, i.e. a decrease in abundance and species richness of plants (e.g. Kleijn et al., 2009), birds (e.g. Gayer et al., 2019), butterflies (van Strien et al., 2019), pollinators (Potts et al., 2010) and other arthropods (Lichtenberg et al., 2017). In temperate regions, for instance, nearly 40% of insects such as butterflies, hymenopterans, dipterans and beetles are classified as threatened to some degree (Sánchez-Bayo & Wyckhuys, 2019). Hallmann et al. (2017) reported a decline of 76% of the insect biomass over a 27-year period in German protected areas and 55% of common butterflies declined in abundance and distribution from 1992-2007 in the Netherlands (van Dyck et al., 2009). Similarly, carabid beetles declined in both abundance (-60%) and species richness (-32%) over the last 23 years on an unmanaged xerophytic grassland in Southern Germany (Skarbek et al., 2021) and Nyffeler & Bonte (2020) recorded a dramatic population density decline of a once very common spider in the Swiss midland. Thus, circumstances of e.g. pollinator and ground-dwelling arthropod groups seem to have changed dramatically due to anthropogenic changes in agro-ecosystems (Wagner et al., 2021).

Indeed, agro-ecosystems have been shaped substantially throughout the last decades towards a large-scale homogeneous agriculture, i.e. characterised by larger management units, an increased use of fertilizers and pesticides, elimination of weeds, removal of hedgerows and filling of ditches (Raven & Wagner, 2020). In Great Britain, for instance, 50% of all hedges and further linear landscape elements, particularly crucial for dispersing species, have been destroyed (Krewenka et al., 2011; Robinson & Sutherland, 2002). Herbicides, moreover, have been shown to reduce plant-related resources and concomitantly with insecticides caused a reduction in fitness of e.g. bees and negatively affected their populations (Rundlöf et al., 2015). Consequently, land-use change (habitat fragmentation) and pollution (fertilizer, pesticides) have become the main drivers for the declines of ground-dwelling arthropods in agro-ecosystems (Sánchez-Bayo & Wyckhuys, 2019).

From a biodiversity perspective, the loss and isolation of semi-natural habitats such as field margins and hedgerows act as ecological filter, which is known to be a major mechanism in structuring communities (Birkhofer et al., 2017; Cadotte & Tucker, 2017). The ecological filter is reflected by response traits, i.e. body size is effected by resource availability and wing morphology may be a proxy for dispersal ability (Rusch et al., 2015, Gallé et al., 2020). The intensification of agro-ecosystems has diminished the species pool of ground-dwelling arthropods (Duflot et al., 2015), since the loss of semi-natural habitats seem to have less affected e.g. more rapidly developing and mobile species in contrast to specialists, whose combination of traits does not allow shifts to alternative habitats (Habel et al., 2019). In addition, a smaller species pool and thus, more homogenous assemblages with a reduced functional diversity have been shown to reduce ecosystem services (Albrecht et al., 2020; Loreau & de Mazancourt, 2013). Hence, linking functional traits such as body size or food preference to land-use change may be a better predictor of e.g. pest control in agro-ecosystems than species identity (Gagic et al., 2015). Trait-based multi-taxa studies may be used as a proxy for ecosystem services (Gallé & Batáry, 2019), but this has rarely been studied (but see e.g. Gallé et al., 2020; Gayer et al., 2019).

Rove beetles, carabid beetles and spiders are among the most important ground-dwelling arthropods in agro-ecosystems and provide those services such as natural pest control (conservation biological control). Rove beetles, for instance, have been shown to prey on aphids and posed a mortality risk to their colonies (Balog et al., 2013). Carabid beetles contributed to the natural control of slug populations in wheat fields (Fusser et al., 2017) and spiders are known to highly respond to agricultural practices (Campbell et al., 2020).

However, habitat preferences of ground-dwelling arthropods are driven by distinct environmental conditions and their dispersal abilities between different types of habitats (Rega et al., 2018), but agro-ecosystems are characterised by highly disturbed habitats due to common management practices such as tillage, harvest and crop rotation. The vegetation structure and potential resources may change abruptly which may directly led to a mortality of agrobiont arthropods (Raven & Wagner, 2021). To avoid those negative consequences, ground-dwelling arthropods need to spillover from arable to adjacent and remaining semi-natural habitats (Blitzer et al., 2012; Boetzi et al., 2018).

Originally being targeted to decrease management intensity and thus, to mitigate the impact of agriculture on biodiversity, AES nowadays aim to compensate for the abovementioned lacks of semi-natural habitats, to enhance their connectivity and thus, to complement resource provisioning and counteract the loss of agro-biodiversity and associated ecosystem services (Haaland et al., 2011). AES constitute semi-natural and low managed habitat patches on formerly arable fields within temperate agricultural landscapes and with a total budget of 362.8 billion Euro for 2014–2020, e.g. the Common Agricultural Policy of the European Union highly subsidized AES (Pe'er et al., 2014.). A common measure within these schemes are sown, temporary wildflower strips and fields which are in particular tailored to support farmland birds or pollinators (Haaland et al., 2011). Indeed, wildflower areas have been shown to enhance abundance, species richness and pollination potential of e.g. wild bees (Scheper et al., 2013), bumble bees (Carvell et al., 2007), butterflies (Aviron et al., 2011) and syrphids (Warzecha et al., 2018). Unfortunately, effects of wildflower areas on non-target organisms such as ground-dwelling arthropods have rarely been addressed and it is unclear whether wildflower areas extend their shown benefits beyond the vegetation period.

To survive outside the vegetation period in agro-ecosystem, ground-dwelling arthropods have to colonize alternative habitats, in particular after crop harvest in late summer. In contrast to arable fields, wildflower areas may provide suitable overwintering habitats as their soils stay relatively undisturbed why they may benefit arthropods overwintering in the soils (Ganser et al., 2019). Moreover, the quality as overwintering habitat depends on the plant species richness and density which have been shown to result in a positive linear relationship between the age of wildflower areas and overwintering of arthropods (Frank & Reichhart, 2004). However, wildflower areas can also act as ecological traps when they are ploughed during the overwintering period (Ganser et al., 2019). Although these effects have rarely been assessed, studies found that wildflower areas provided valuable overwintering habitats for ground-

dwelling arthropods (Frank & Reichhart, 2004; Ganser et al., 2019; Mestre et al., 2018) as well as for parasitoid wasps or flower bugs (Sarhou et al., 2014).

At one point, wildflower areas may compensate the lack of semi-natural habitats and provide valuable habitats and sufficient resources throughout the entire year, they may also play a major role for the long-term persistence of populations of ground-dwelling arthropods in agro-ecosystems. Due to the transient character of many cultures, ground-dwelling arthropods are used to frequently move and colonize alternative habitats, but ongoing changes in landscape structure and connectivity may increasingly hamper these processes. Concomitantly, the establishment of wildflower areas may again change the landscape and benefits may be altered by landscape context (Scheper et al., 2013). It was hypothesized that AES may show highest benefits if established in simple landscapes with 1-20% of permanent semi-natural habitats (Tscharntke et al., 2012). Indeed, this hump-shaped pattern was described for e.g. bees and grasshoppers (Scheper et al., 2013; Tscharntke et al., 2012) since here, the species pool is large enough to promote dispersal and thus, the long-term persistence of well-connected meta-populations as compared to cleared or complex landscapes (Tscharntke et al., 2012).

In contrast to shown benefits of wildflower areas, recent assessments found that overall, European AES are not fulfilling their goals (Pe'er et al., 2014). Studies found positive effects only in 50% of the cases (Kleijn et al., 2006), often with rather modest increases in abundance or species richness of common species (Batáry et al., 2015). As one reason, studies frequently neglected the landscape context and temporal dynamics when evaluating the efficacy of AES (Ekroos et al., 2014). Temporal continuity, however, plays an important role for biodiversity patterns in agro-ecosystems in general (e.g. Wamser et al., 2011) and in wildflower areas in particular (e.g. Blaauw & Isaacs, 2014), since newly established transient habitats like sown wildflower areas need to be colonized. Although wildflower areas may differ in their temporal continuity as compared to permanent semi-natural habitats such as hedges, both resource-rich habitat types have the potential to alter meta-population dynamics in agro-ecosystems.

In order to contribute to the future improvement of the establishment of wildflower areas in agro-ecosystems, I studied ground-dwelling arthropods in landscapes that varied in their proportions of semi-natural habitats, while I specifically distinguished between permanent (e.g. hedgerows, ditches) and transient (e.g. wildflower areas) semi-natural habitats to examine benefits of wildflower areas for ground-dwelling arthropods across three consecutive years during and outside the vegetation period.

CHAPTER 1: Ground-dwelling arthropods in agro-ecosystems have to colonize alternative habitats for overwintering in particular after disturbances due to crop harvest in late summer. Wildflower areas have been shown to provide those habitats but their efficacy mainly depends on local characteristics such as vegetation structure. Unexpectedly, landscape context did not seem to affect arthropod overwintering, but effects merely may have been overlooked due to a lack of differentiation between permanent semi-natural habitats and transient wildflower areas. Hence, to advance our understanding of the conservation benefits of wildflower areas beyond the vegetation period and as a function of landscape context, I studied, in a novel approach, the additive and interactive effects of landscape proportions of permanent semi-natural habitats (e.g. hedgerows, ditches) and transient wildflower areas on ground-dwelling arthropods overwintering in wildflower areas and crop fields.

CHAPTER 2: If wildflower areas may compensate the lack of semi-natural habitats by e.g. providing suitable overwintering habitats, these transient elements may also enhance bidirectional cross-habitat spillover effects and thus, contribute to the long-term persistence of ground-dwelling arthropod populations in agro-ecosystems. However, wildflower areas need to be colonized first, but this colonization and effects for adjacent crop fields due to spillover processes may show a time lag. Yet, recent studies focused on annual snapshots and neglected temporal shifts in biodiversity benefits of wildflower areas beyond their initial year. Hence, in order to better understand time-dependent benefits of sown wildflower areas, I studied the abundance, species richness and community composition of ground-dwelling arthropods in pairs of wildflower areas and crop fields over a period of three consecutive years. Additionally, I was interested how landscape context, i.e. additive and interactive effects of proportions of permanent semi-natural habitats and transient wildflower areas, alters benefits of wildflower areas for agro-biodiversity.

CHAPTER 3: Land-use change has been shown to act as environmental filter by effecting certain traits. So far, studies mainly focused on taxonomic diversity (abundance, species richness) rather than functional diversity. However, trait-based approaches may reveal new findings and can be used as a proxy for ecosystem services such as natural pest control. Hence, in this study, I compared the change of the functional diversity of ground-dwelling arthropods in wildflower areas and adjacent crop fields between the first and the third year after the establishment of wildflower areas. To understand how landscape context shapes the benefits of sown wildflower areas and to hopefully enhance their efficacy, I simultaneously distinguished between permanent semi-natural habitats and transient wildflower areas.

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CHAPTER 1

Benefits of wildflower areas as overwintering habitats for ground-dwelling arthropods depend on landscape structural complexity

Hoffmann H | Peter F | Hermann JD | Donath TW | Diekötter T

ABSTRACT

Wildflower areas are a popular agri-environment scheme to counteract the biodiversity loss in agro-ecosystems. While benefits for flower-visiting and predatory insects during the vegetation period were frequently shown, few studies addressed the suitability of wildflower areas as overwintering habitats. Here, we studied the significance of wildflower areas as overwintering habitats and whether their benefits vary with landscape context, i.e. the proportions of permanent semi-natural habitats such as hedges.

We selected ten landscapes that encompassed independent gradients of proportions of permanent semi-natural habitats (e.g. hedgerows, ditches) and transient wildflower areas. The centres of the landscapes were pairs of wildflower areas and arable fields on which we sampled overwintering ground-dwelling arthropods by emergence traps.

In total, we recorded 2,838 overwintering individuals from 115 species of rove and carabid beetles as well as spiders. Abundance of rove beetle larvae, as well as species richness of adult rove beetles and spiders was significantly higher in wildflower areas than in arable fields. With respect to landscape context, abundance and species richness of adult rove beetles showed a hump-shaped relationship with the proportion of permanent semi-natural habitats. The abundance of adult carabid beetles showed a hump-shaped relationship with the proportion of transient wildflower areas, while the abundance of carabid beetle larvae showed a hump-shaped pattern with permanent semi-natural habitats.

For the first time we showed that, similar to the vegetation period, benefits of wildflower areas as overwintering habitats for ground-dwelling arthropods depend on both local habitat characteristics as well as landscape context. Benefits of wildflower areas for overwintering were highest in simple landscapes with an intermediate proportion of either permanent semi-natural habitats or transient wildflower areas. Our results suggest that in order to sustainably maintain the functional guild of ground-dwelling arthropods, agricultural landscapes should provide both sown wildflower areas and permanent semi-natural habitats. Our results also support the general claim that semi-natural habitats should at least contribute 10-15% to agricultural landscapes in order to maintain the characteristic biodiversity in modern agro-ecosystems.

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INTRODUCTION

In modern agro-ecosystems, sown wildflower areas constitute a popular agri-environment scheme aiming to mitigate the loss of resources formerly provided by permanent semi-natural habitats and thus, to counteract the associated decline of agro-biodiversity (Haaland et al., 2011). A final evaluation of the benefits of wildflower areas, however, is difficult as previous studies largely neglected the significance of landscape context and mainly focused on obvious target species such as flower-visiting insects during the vegetation period (e.g. Ekroos et al., 2014; Kleijn et al., 2006). Hence, with this study we aimed to advance our understanding of the conservation benefits of sown wildflower areas as overwintering habitats for ground-dwelling arthropods as a function of landscape context.

Semi-natural habitats such as hedgerows, extensive permanent grasslands, or fallows are available throughout the year and provide food or shelter (Vickery et al., 2004) as well as nesting (Sardiñas & Kremen, 2014) or overwintering sites for various species (Geiger et al., 2009; Pywell et al., 2005). During the last decades, however, agricultural intensification has resulted in the overall loss and increased fragmentation of semi-natural habitats (Duflot et al., 2015), which has repeatedly been shown to drive species loss, alter trophic interactions and thus, threaten ecosystem services in agro-ecosystems (Benton et al., 2003). Hence, to compensate for the lack of semi-natural habitats, to complement resource provisioning and thus, to hopefully counteract this loss of agro-biodiversity, wildflower areas have frequently been established within temperate agricultural landscapes (Haaland et al., 2011).

Overall, findings of previous studies largely confirm the aspired benefits of wildflower areas for agro-biodiversity (Ekroos et al., 2014; Haaland et al., 2011; but see e.g. Wood et al., 2015). However, it has also been shown that these benefits may be altered by landscape context (Scheper et al., 2013). In general, benefits of wildflower areas may be shaped through a bidirectional dependency with landscape context, predominantly via the availability of alternative resources or source populations (Batáry et al., 2011; Holland et al., 2016). In fact, more recent findings indicate that benefits of wildflower areas for biodiversity may be linearly related to the surrounding proportion of semi-natural habitats in general (e.g. Aviron et al., 2018) or grassland in particular (e.g. Hoffmann et al., 2020). Other studies revealed that benefits of wildflower areas to e.g. birds, bees and crickets were highest in simple landscapes with intermediate structural complexity compared to cleared or complex landscapes (Concepción et al., 2008; Scheper et al., 2013; Tschardt et al., 2012). This hump-shaped

pattern indicates that the sole presence of wildflower areas in cleared resource-poor agro-ecosystems may not suffice to promote biodiversity while their contribution to habitat diversity in complex, resource-rich landscapes and thus, their benefits to biodiversity may be negligible (Kleijn et al., 2011; Tscharntke et al., 2012). Thus, wildflower areas may deliver greatest benefits in landscapes with intermediate complexity, where additional resource provisioning may complement the existing network of semi-natural habitats and significantly promote agro-biodiversity (Marja et al., 2019; Martin et al., 2019).

Besides the potential significance of landscape context, knowledge gaps particularly concern benefits of wildflower areas for species other than the obvious target groups such as flower-visiting insects. Moreover, it is unclear whether shown benefits of wildflower areas extend beyond the vegetation period where the ecological contrast in floral resources is highest (Ganser et al., 2019; Scheper et al., 2013). Only recently, Ganser et al. (2019) found that wildflower areas may provide valuable overwintering habitats for ground-dwelling arthropods, which would increase their significance and thus, confirm the potential of wildflower areas to compensate for the lack of permanent semi-natural habitats. However, similar to its importance during the vegetation period, landscape context may alter arthropod overwintering in wildflower areas indirectly, via species' colonisation during the preceding vegetation period (Blitzer et al., 2012) and a subsequent utilization of the colonised field as an overwintering habitat. In addition, landscape context may alter the benefits of wildflower areas directly, through systematic colonisation as a result of active search for overwintering habitats later in the season.

So far, only few studies assessed the significance of wildflower areas as overwintering habitats and incorporated differences in landscape context, e.g. for rove and carabid beetles or spiders (but see e.g. Frank & Reichhart, 2004; Ganser et al., 2019; Thomas and Marshall, 1999) as well as parasitoid wasps or flower bugs (Sarhou et al., 2014). In these studies, overwintering of arthropods was driven by local habitat characteristics of the wildflower areas, such as plant species richness, bare ground cover or management practices like ploughing. Unexpectedly, landscape context, i.e. the proportions of semi-natural habitats or crops, did not affect overwintering patterns of arthropods. While those findings imply a low significance of landscape context for arthropod overwintering, we suggest that effects merely may have been overlooked due to a lack of discrimination between permanent semi-natural habitats such as hedges and transient wildflower areas. Yet, assuming equal significance of both habitat types, despite the strong seasonal character of wildflower areas and their potential of source habitats, newly established transient wildflower areas may affect connectivity

between existing habitats and may enhance dispersal of e.g. predators by simultaneously transporting their functions into adjacent agricultural fields (Blitzer et al., 2012).

Therefore, to advance our understanding of the conservation benefits of wildflower areas beyond the vegetation period and as a function of landscape context, we studied the additive and interactive effects of landscape proportions of permanent semi-natural habitats (e.g. hedgerows, ditches) and transient wildflower areas on ground-dwelling arthropods overwintering in wildflower areas and arable field. Specifically, we addressed the following questions: (1) Do wildflower areas provide more valuable overwintering habitats for ground-dwelling arthropods, here rove beetles, carabid beetles and spiders, than arable fields? (2) Do local habitat characteristics of wildflower areas affect the abundance and species richness of overwintering arthropods? (3) Do landscape proportions of permanent semi-natural habitats and transient wildflower areas additively or interactively affect the benefits of wildflower areas as overwintering habitats for ground-dwelling arthropods?

MATERIAL & METHODS

STUDY REGION

The study took place in the federal state of Schleswig-Holstein, northern Germany, a region dominated by agricultural land-use (70%) and forests (11%). Under a regional agri-environment scheme for the promotion of the Grey Partridge (*Perdix perdix*), approximately 85 wildflower areas with a total area of 150 ha were sown on arable land. The scheme does not allow any agricultural management but requires resowing of fields twice within the contracted five-year period (2016-2021) between 1st April and 15th May with a mixture of 27 regional plant species, dominated by *Linum usitatissimum* (20%), *Medicago lupulina* (13%), *Petroselinum sativum* (11%) and *Trifolium repens* (6%). We selected ten landscapes along independent gradients (Pearson correlation: estimate = -0.02, $p = 0.963$) in the proportions of permanent semi-natural habitats and transient wildflower areas in the surrounding landscape (Appendix A). We quantified habitat proportions for a landscape extent with a 750 m radius around the centres of the focal wildflower areas. We chose this spatial scale as a large set of previous studies identified it as highly appropriate with respect to inter-patch dispersal of ground-dwelling arthropods (Grab et al., 2018; Martin et al., 2019). We defined permanent semi-natural habitats as hedgerows, single trees, tree rows, forest patches smaller than 2000 m², field margins, drainage ditches, ponds, kettle holes and further wetlands larger than 2000 m² and near-natural stonewalls. These landscape elements are effectively used by arthropods

or provide edge habitats (ecotones) which may increase habitat availability and connectivity (Brandmayr et al., 1998). Similar to the assessment of a recent study (Rega et al., 2018), proportions of permanent semi-natural habitats and transient wildflower areas ranged from 0% to 7% ($4\% \pm 2\%$, mean \pm SD, hereafter; Table 1, appendix B) and from 0% to 14% ($5\% \pm 5\%$; Table 1, Appendix B), respectively. While we used the proportions of permanent semi-natural habitats and transient wildflower areas as continuous predictors for our regression analyses, we decided to apply the concept of intermediate landscape-complexity (Tschamtker et al., 2012) for the interpretation and discussion of our results in context with previous studies. We defined cleared, simple and complex landscapes but intentionally differentiated between permanent semi-natural habitats and transient wildflower areas which leads to a range shift in proportions for the three categories. Hence, simple landscapes were characterized by intermediate proportions of permanent semi-natural habitats ($\geq 2\% - \leq 5\%$) and transient wildflower areas ($\geq 4\% - \leq 10\%$), while cleared and complex landscapes covered proportions below (for permanent habitats $\geq 0.1\%$ and for transient ones $\geq 0.4\%$) and above the aforementioned ranges (for permanent habitats $\leq 7\%$ and for transient ones $\leq 14.2\%$).

To compare the suitability of wildflower areas and arable fields for the overwintering of ground-dwelling arthropods, we selected a wildflower area and an arable field per landscape that ideally were adjacent to each other. However, site selection based on both independent landscape gradients and adjacent pairs of wildflower areas and arable fields was not feasible across all study sites. Hence, if pairs of the habitat types were not adjacent to each other, we ensured similar landscape composition surrounding the wildflower areas and arable fields (distance: 0 m – 785 m, $180\text{ m} \pm 272\text{ m}$, Table 1). To do so, we tested differences in landscape characteristics with either the wildflower areas or arable fields in the centre ('T.TEST' from the 'STATS' package) and found no significant differences (for permanent semi-natural habitats: estimate = -0.08, $p = 0.506$, for transient wildflower areas: estimate = 0.17, $p = 0.466$, Table 1).

As site selection comprised the consideration of both the landscape context and appropriate pairs of wildflower areas and arable fields, it was not always feasible to choose the same crop type throughout the study. For three landscapes no winter wheat fields were available and instead, we selected one maize and two winter greening fields. The maize field was harvested during October 2017 and stayed fallow until April with stubbles up to 50 cm. All other arable fields (winter greening and winter wheat fields) were cultivated by winter wheat before, were ploughed during autumn 2017 and either established as winter greening or winter wheat again

and stayed unmanaged until the end of the study period. Hence, independent of the crop type or crop rotation, arable fields received neither fertilizers or pesticides, nor any mechanical treatment such as tilling, during overwintering and emergence of the arthropods.

Table 1. Characteristics of wildflower areas and arable fields for each study site. Proportions of permanent semi-natural habitats (Perma) and transient wildflower areas (Trans) were quantified with a radius of 750 m around the field centres. Temperature represents the mean daily ground temperature during our study period based on five different weather station in close proximity to our study sites. Age represents time since last resowing of the wildflower area. Temperature, vegetation density and soil density are presented as mean \pm standard error.

Study sites			Wildflower areas					Arable fields		
Perma [%]	Trans [%]	Temperature [°C]	Plant species richness	Vegetation density [%]	Soil density [psi]	Patch size [ha]	age [yrs]	Perma [%]	Trans [%]	Type of cultivation
5.2	3.9	1.6 \pm 3.1	17	12.9 \pm 4.2	210 \pm 89.4	4.2	1	5.8	3.9	winter wheat
4.4	6.8	1.3 \pm 3.5	30	5.6 \pm 2.5	60 \pm 22.4	7.9	1	4.7	7.7	winter greening
7.0	14.2	1.6 \pm 3.1	28	44.7 \pm 8.9	210 \pm 65.2	3.2	1	6.8	13.9	winter wheat
0.3	13.5	1.3 \pm 3.1	28	49.2 \pm 29.8	160 \pm 41.8	1.0	1	0.1	11.6	winter wheat
2.1	0.6	1.3 \pm 3.7	15	2.1 \pm 1.3	125 \pm 55.9	0.5	2	2.2	0.6	maize
1.2	0.4	1.4 \pm 3.2	21	41.4 \pm 33.9	225 \pm 25.0	0.6	1	1.1	0.4	winter greening
5.3	0.7	1.7 \pm 3.3	15	7.6 \pm 2.8	240 \pm 96.2	1.3	2	4.8	0.7	winter wheat
3.2	6.6	1.6 \pm 3.1	20	17.0 \pm 11.8	220 \pm 27.4	5.0	1	3.4	6.6	winter wheat
6.9	0.4	1.7 \pm 3.3	12	1.6 \pm 1.3	260 \pm 82.2	0.2	2	6.8	0.4	winter wheat
1.6	4.6	1.3 \pm 3.1	28	46.5 \pm 33.6	50 \pm 7.1	7.9	1	2.3	4.1	winter wheat
										Distance to the wildflower area [m]
										20
										265
										20
										785
										0
										190
										0
										0
										515

Nevertheless, we statistically tested for differences in the abundance and species of the studied arthropod groups among the crop types using linear mixed-effects models and found no significant results (for all models $p > 0.085$, $t < -0.95$). Furthermore, the different crop types were randomly distributed across chosen landscapes and thus, did not show a pattern with any of the remaining predictor variables such as the proportion of permanent semi-natural habitats and transient wildflower areas. Spatial distances between pairs of wildflower areas and arable fields ranged from 2 km to 155 km ($74 \text{ km} \pm 44 \text{ km}$) and study sites were thus, independent from each other. Site selection aimed to prevent spatial autocorrelation and at the same time, even at large spatial distances, ensured comparable seasonality during our study.

The whole study region is characterized by warm temperate climate (Kottek et al., 2006) with annual mean temperatures of 8.4°C and annual mean precipitation of 770 mm (Fick & Hijmans, 2017). Across our study sites, mean daily temperature ranged from $1.27^\circ\text{C} - 1.72^\circ\text{C}$ and averaged $1.44^\circ\text{C} \pm 3.32^\circ\text{C}$ (mean \pm SD) during our study period from January to April 2018 based on five weather stations in close proximity of our study sites (Deutscher Wetterdienst, 2021).

Landscape analyses were performed in ArcGIS 10 (ESRI, CA, USA).

ARTHROPOD SAMPLING

Ground-dwelling arthropods were sampled from 10th/11th January until 5th/6th April 2018 with two emergence traps per wildflower area and arable field, respectively (Appendix C + D). The period from January until April was chosen to avoid conflicts between arthropod sampling and management activities on wildflower areas (e.g. ploughing) and arable fields (e.g. fertilizer application) that started mid-April. Emergence traps had a basal area of $1 \text{ m} \times 1 \text{ m}$ and a height of 50 cm. The emergence traps were fully closed except for the basal area to allow the collection of emerging arthropods from the ground. To prevent individuals from getting in or out along the sides, the emergence traps were sunk 10 cm into the ground. We placed the emergence traps at 10 m parallel from one of the field borders (e.g. Birkhofer et al., 2014; Boetzel et al., 2018) and at 20 m from each other. Within emergence traps, we placed three pitfall traps diagonal (two in opposite corners and one in the centre), consisting of 500 ml plastic cups filled with 150 ml water, 50 ml ethylene-glycol and a drop of detergent solution. Wire nets (mesh size: 31 mm) in the cups prevented unintended by-catch, i.e. of small vertebrates. Pitfall traps were emptied three times (every four weeks) and individuals were stored in 70% ethanol before species identification following Besuchet (1974) and

Assing & Schülke (2012) for Staphylinidae (within subfamily Aleocharinae only the genera *Aleochara*, *Autalia* and *Callicerus*), Müller-Motzfeld (2004) for Carabidae and Roberts (1996, 1987), Almquist (2006, 2005) and Nentwig et al. (2018) for spiders. Beetle larvae were identified to family level (Klausnitzer, 2011). Finally, we merged the data of the three pitfall traps per emergence trap over the three sampling rounds by summing the abundances and accumulating species richness of rove beetles, carabid beetles and spiders per habitat type and study site resulting in two observations per habitat type and study site.

In general, species abundance and mobility have been suggested to affect the observed species richness which in turn, may differ from true species richness, particularly in landscapes with increasing heterogeneity (Brose and Martinez, 2004; Chao and Chiu, 2016). For our data, abundance and observed species richness were correlated (Pearson correlation: $p = 0.002$; correlation estimate > 0.5). Hence, to account for potential under-sampling, we calculated the non-parametric abundance-based species richness estimator Chao1 ('ESTIMATER' from the 'VEGAN' package (Oksanen et al., 2019)), which has been suggested to be less dependent on equal detection probability, especially compared to less accurate incidence-based species richness estimators (Chao & Chiu, 2016). Observed species richness and Chao1 were strongly correlated (Pearson correlation: $p < 0.001$; correlation estimate > 0.7). As the results of further analyses for observed species richness and Chao1 were highly similar, we decided to retain the results for effects on observed species richness.

LOCAL HABITAT CHARACTERISTICS OF THE WILDFLOWER AREAS

For each focal wildflower area, we recorded plant species richness in one randomly chosen 10 m x 10 m plot in August 2017 during the end of the main flowering period as during this time effects on colonization could have been expected. Based on Jäger (2011), we identified 97 different plant species from 22 families (Appendix E). Plant species richness per study site ranged from 12 to 30 and averaged of 21 ± 7 plant species (Table 1). Vegetation density was quantified as the percentage of incoming light by measuring light availability at five randomly chosen locations above the vegetation and at ground level within the vegetation using a light sensor (Licor 1500G Light Sensor Logger with GPS). Vegetation density ranged from 2% to 49% and averaged $23\% \pm 20\%$ (Table 1). At the same five locations, we measured soil density with a penetrometer, which ranged from 50 psi to 260 psi and averaged of $176 \text{ psi} \pm 75 \text{ psi}$ (Table 1). Since vegetation characteristics may be correlated with the age of the wildflower area, we tested correlations between age and plant species richness (Pearson correlation: $p < 0.001$, estimate = -0.77) and vegetation density (Pearson correlation: $p =$

0.002, estimate = -0.66), respectively, and decided to retain the vegetation parameters for further statistical analyses. Local habitat characteristics were not correlated with landscape characteristics, except a significant correlation between plant species richness and the proportion of transient wildflower areas (Pearson correlation: $p = 0.013$, correlation estimate = 0.75).

STATISTICAL ANALYSES

To study the effects of habitat type, local characteristics of the wildflower areas and landscape context on overwintering patterns of ground-dwelling arthropods, we used generalized linear mixed-effect models (GLMM; ‘GLMMPQL’ from the ‘MASS’ package (Wood, 2019)). We used separate regression models to test: (1) the effect of the habitat type, here wildflower area or arable field, (2) the effects of local habitat characteristics, being patch size, plant species richness, vegetation density and soil density of the focal wildflower area and (3) the additive and interactive effects of the proportions of permanent semi-natural habitats and transient wildflower areas on the abundance and species richness of overwintering arthropods. Since model 1 supported our hypothesis that abundance and species richness of overwintering arthropods differ between wildflower areas and arable fields, models 2 and 3 exclusively utilize data of wildflower areas in order to further evaluate whether the benefits of wildflower areas for arthropod overwintering depend on local habitat characteristics (model 2) and landscape context (model 3), respectively ($n = 10$, with 20 observations from two emergence traps across ten study sites). As we had two observations per habitat type and study site, we defined study site (models 1, 2 and 3) and the interaction of study site and habitat type (model 1) as the respective random effects. Residuals were assumed to follow a Poisson error distribution. To account for the hypothesized non-linear, hump-shaped relationship between abundance and species richness of arthropods, respectively, and landscape context in model 3, we fitted arthropod abundance and species richness both as a linear and as a quadratic function of the proportions of permanent semi-natural habitats and transient wildflower areas (Bolker, 2008). For model 2 and 3, we performed manual stepwise backwards elimination of non-significant predictors in order to find the most appropriate, final model. Finally, if both the linear and quadratic term of the same variable were significant, we did model selection between a full model (containing both the linear and the quadratic term) and a reduced model (containing the linear term only) based on the AICc (Quinn and Keogh, 2002). If the full model performed relatively better than the reduced model, we subsequently focused on the presentation and discussion of the effect of the quadratic term as it implicitly covers the linear

effect (Quinn and Keogh, 2002). For all models, we calculated the marginal and conditional R^2 including both fixed and random effects ('R.SQUAREDGLMM' from the 'MUMIN' package (Barton, 2020)).

Statistical analyses were performed in R 3.5.3 (R Development Core Team, 2019).

RESULTS

In total, we captured 2,838 ground-dwelling arthropods from 115 species (Appendix F). Altogether, arthropods were largely dominated by rove beetles (54%, 41 species), followed by carabid beetles (29%, 34 species) and spiders (17%, 40 species). The most abundant rove beetles were *Anthobium unicolor* (35%), *Olophrum piceum* (20%) and *Lesteva longoelytrata* (12%). The most abundant carabid beetles were *Bembidion tetracolum* (30%), *B. aeneum* (18%) and *Trechus quadristriatus* (16%), and the most abundant spiders were *Bathyphantes gracilis* (16%), *Centromerita bicolor* (13%) and *Erigone atra* (11%). Furthermore, we captured 304 larvae, mainly of rove beetles (72%) and to a smaller extent of carabid beetles (28%).

LOCAL EFFECTS ON OVERWINTERING PATTERNS IN ARABLE AND WILDFLOWER AREAS

The average abundance of adult rove and carabid beetles as well as spiders did not differ significantly between wildflower areas and arable fields. While the average abundance of rove beetle larvae was 2.1 times higher in wildflower areas than in arable fields, average abundance of carabid beetle larvae did not differ significantly between wildflower areas and arable fields (Table 2, Fig. 1A). The average species richness of rove beetles and spiders, respectively, was about 1.7 and 1.4 times higher in wildflower areas than in arable fields (Table 2, Fig. 1B). In contrast, the average species richness of carabid beetles did not differ significantly between wildflower areas and arable fields.

Considering local habitat characteristics of the wildflower areas, the abundance of rove beetles in wildflower areas significantly increased with plant species richness and vegetation density whereas patch size and soil density had no effect (Table 3, Appendix G). In contrast to rove beetles, the abundance of carabid beetles significantly increased with increasing patch size of the focal wildflower areas (Table 3), whereas plant species richness, vegetation density and soil density had no significant effect. The abundance of spiders was unaffected by local wildflower area characteristics. Similar to adult rove beetles, the abundance of rove beetle larvae significantly increased with plant species richness and vegetation density (Table 3),

whereas neither patch size nor soil density had an effect. In contrast, none of the local habitat characteristics of the wildflower areas affected the abundance of carabid beetle larvae.

None of the local characteristics of the wildflower areas significantly affected species richness of rove beetles, carabid beetles or spiders.

Table 2. Effect of habitat type, here arable fields (AF) and wildflower areas (WF) on the abundance and species richness of adult and juvenile rove and carabid beetles as well as spiders (model 1). Degrees of freedom (DF), *t*-value (T), *P*-value (P) and the marginal and conditional R^2 (R^2_m and R^2_c) are given for the most parsimonious model. Detailed statistics for non-significant (n.s.) effects are provided within the appendix.

Response	DF	T	P	R^2_m	R^2_c
Rove beetle abundance			n.s.		
Rove beetle species richness					
Habitat (AF~WF)	2	-2.34	0.044	0.09	0.63
Carabid beetle abundance			n.s.		
Carabid beetle species richness			n.s.		
Spider abundance			n.s.		
Spider species richness					
Habitat (AF~WF)	2	-2.87	0.019	0.09	0.40
Rove beetle larvae abundance					
Habitat (AF~WF)	2	-2.72	0.024	0.15	0.81
Carabid beetle larvae abundance			n.s.		

LANDSCAPE EFFECTS ON OVERWINTERING PATTERNS IN WILDFLOWER AREAS

Overall, proportions of permanent semi-natural habitats and transient wildflower areas solely had additive but no interactive effects on abundance and species richness of arthropods.

The abundance of rove beetles showed a significant hump-shaped relationship with the proportion of permanent semi-natural habitats (Table 3), whereas the proportion of transient wildflower areas did not have an effect. The hump-shaped pattern implies that abundances of rove beetles were highest for wildflower areas in simple landscapes with an intermediate amount of 3-4% of permanent semi-natural habitats (Fig. 2A). In contrast, the abundance of carabid beetles showed a significant hump-shaped relationship with the proportion of transient wildflower areas (Table 3), whereas permanent semi-natural habitats had no effect on carabid beetle abundance. Abundances of carabid beetles in wildflower areas were highest in simple landscapes with an intermediate amount of 6-7% of transient wildflower areas (Fig. 2B). The abundance of spiders was unaffected by landscape characteristics.

Table 3. Effects of local habitat characteristics (model 2) of the focal wildflower areas and landscape characteristics (model 3), i.e. proportions of permanent semi-natural habitats (Perma) and transient wildflower areas (Trans) on the abundance and species richness of adult and juvenile rove beetles, adult and juvenile carabid beetles as well as spiders. Note that we solely focused on the observations for the wildflower areas in order to further evaluate the benefits of wildflower areas for arthropod overwintering. Degrees of freedoms (DF), *t*-value (T), *P*-value (P) and the marginal and conditional R^2 (R^2m and R^2c) are given for the most parsimonious model. AICc-values were calculated for reduced and full models, if the linear (*x*) and quadratic term (x^2) of the same variable was significant. Detailed statistics for non-significant (n.s.) effects are provided within the appendix.

Response	model	DF	T	P	R ² m	R ² c	AICc	
Rove beetle abundance								
Plant species richness	2	7	4.24	0.004	0.90	0.99	226.18	
Vegetation density	2	7	-6.46	< 0.001				
Perma (x)	3	7	2.74	0.029	0.61	0.99		
Perma (x ²)	3	7	-2.58	0.036				
Rove beetle species richness								
Perma (x)	3	7	2.70	0.031	0.40	0.60	111.38	
Perma (x ²)	3	7	-2.71	0.030			108.29	
Carabid beetle abundance								
Patch size	2	8	2.83	0.022	0.76	0.76	190.29	
Trans (x)	3	7	3.20	0.015	0.81	0.81		
Trans (x ²)	3	7	-3.22	0.015				187.95
Carabid beetle species richness				n.s.				
Spider abundance				n.s.				
Spider species richness				n.s.				
Rove beetle larvae abundance								
Plant species richness	2	7	2.40	0.047	0.79	0.79	92.84	
Vegetation density	2	7	-3.07	0.018				
Carabid beetle larvae abundance								
Perma (x)	3	5	3.23	0.023	0.81	0.81		79.58
Perma (x ²)	3	5	-3.22	0.024				90.30
Trans (x)	3	5	-3.22	0.023			79.58	
Trans (x ²)	3	5	3.16	0.025				

While the abundance of rove beetle larvae was unaffected by either landscape characteristics, the abundance of carabid beetle larvae was highest for wildflower areas in simple landscapes with an intermediate amount of 3-4% of permanent semi-natural habitats (Table 3, Fig. 2C). Furthermore, the abundance of carabid beetle larvae showed a hump-shaped distribution with higher values in low and high proportions of transient wildflower areas (Table 3, Fig 2D).

Similar to the abundance of rove beetles, species richness of rove beetles showed a significant hump-shaped relationship with the proportion of permanent semi-natural habitats (Table 3), being highest in simple landscapes with an intermediate amount of 3-4% of semi-natural habitats (Fig. 2E). Neither species richness of carabid beetles nor spiders were significantly affected by landscape characteristics.

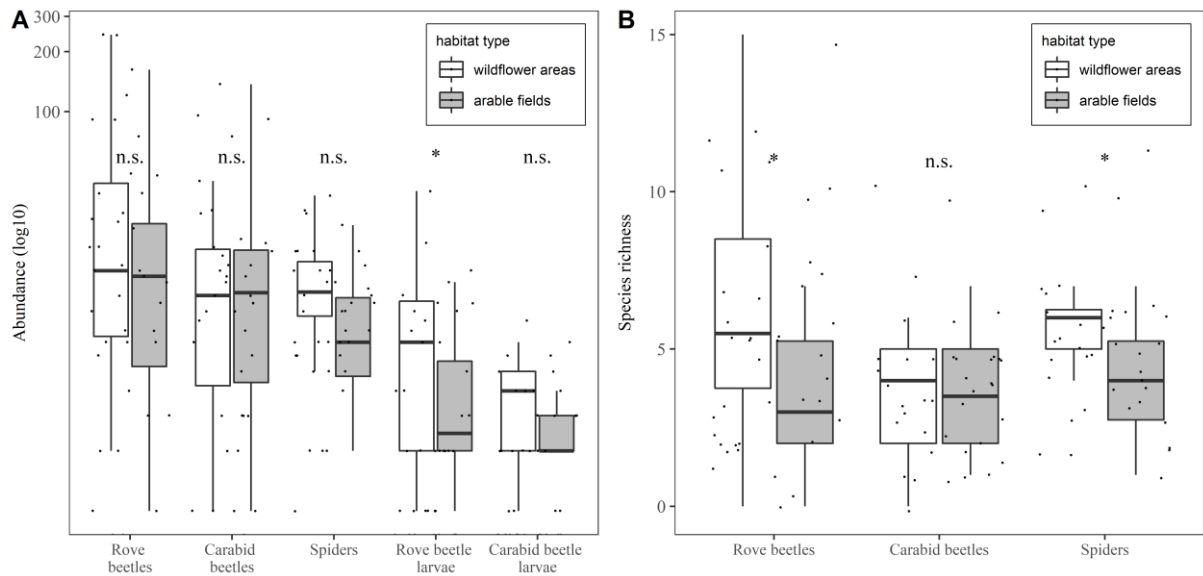


Figure 1. Effect of habitat type, here wildflower area (white) and arable field (grey), on the abundance (A) and species richness (B) of rove and carabid beetles as well as spiders. Boxplots show raw data and stars indicate significance levels: n.s. ≥ 0.05 ; $0.05 > * > 0.01$; $0.01 < ** > 0.001$; $*** < 0.001$.

DISCUSSION

For the first time, we show that the benefits of wildflower areas as overwintering habitats depend on both local characteristics of the wildflower area as well as the surrounding landscape. Similar to studies addressing the vegetation period, wildflower areas seem to promote the overwintering of ground-dwelling arthropods particularly in simple landscapes with intermediate proportion of permanent semi-natural habitats and transient wildflower areas, respectively. Interestingly, adult rove and carabid beetles only responded to either transient or permanent resource-rich habitat type. Finally, despite additive effects of the two resource-rich habitat types, we did not find any interactive effects on arthropod abundance or species richness.

LOCAL EFFECTS ON OVERWINTERING PATTERNS IN ARABLE AND WILDFLOWER AREAS

Our study confirms the recently reported significant role of wildflower areas as overwintering habitats for ground-dwelling arthropods in agricultural landscapes (Ganser et al., 2019; Sarthou et al., 2014). Significantly higher abundances of juvenile rove beetles and spiders, as well as species richness of adult rove beetles and spiders in wildflower areas than in arable fields during winter imply that this agri-environment scheme supports biodiversity in agro-ecosystems throughout the whole year.

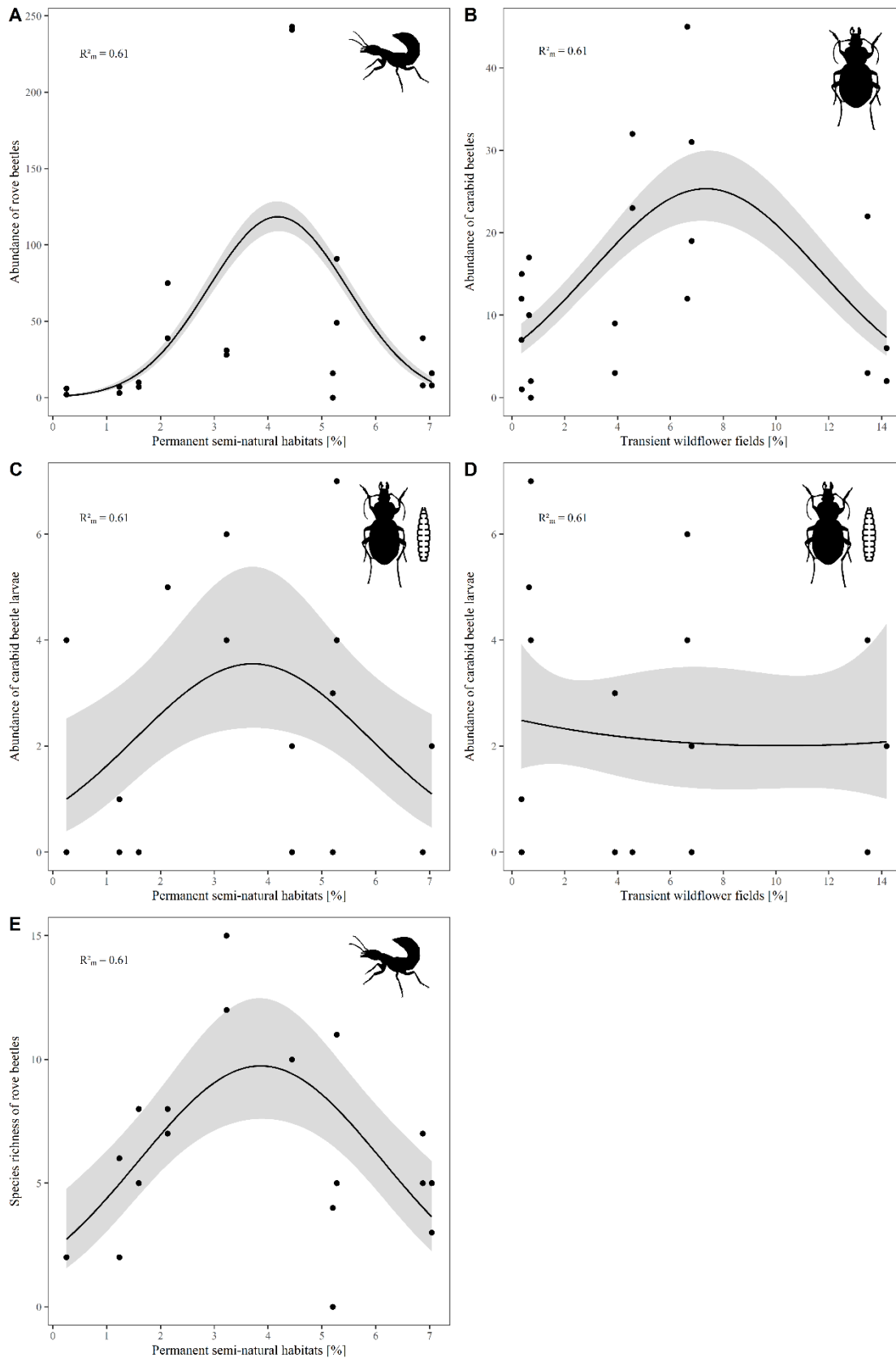


Figure 2. Effect of the proportions of permanent semi-natural habitats (*perma*) and transient wildflower areas (*trans*) on ground-dwelling arthropods: (A) abundance of adult rove beetles ~ *perma* (B) abundance of adult carabid beetles ~ *trans* (C) abundance of carabid beetle larvae ~ *perma* (D) abundance of carabid beetle larvae ~ *trans* (E) species richness of adult rove beetles ~ *perma*. Points represent raw data; the solid line and shaded area represent the model fit and 95% confidence intervals, respectively.

Rove beetles like *Tachyporus* spp. are beneficial predators of agricultural pests (i.e. of cereal aphids) and therefore, show high foraging activity within arable fields (Balog et al., 2013). However, for reproduction and overwintering, agrobiont rove beetles are known to shift their habitat preference from arable fields to habitats with high vegetation density and sufficient leaf litter where decaying plant material provides microhabitats and shelter against predators (Bohác, 1999; Magura et al., 2013). Similarly, in our study rove beetles were significantly more abundant in wildflower areas compared to arable fields. Moreover, differences in rove beetle abundances across the wildflower areas were explained by plant species richness and vegetation density particularly supporting suggested preferences for high vegetation density. Promoted rove beetle overwintering in wildflower areas, particularly at high vegetation complexity, may be explained by initial benefits from increased quantity and quality of prey and thus, trophic bottom-up effects during the vegetation period which subsequently, may carry over to the overwintering period (Clough et al., 2007).

Similar to rove beetles, spiders are known to prefer dry shelter within vegetation or litter for overwintering, which renders arable fields with high management intensity and uncovered soil unsuitable for overwintering (Booij et al., 1996). The shown preference in our study, that spiders seemed to prefer to overwinter in wildflower areas rather than in arable fields, supports previous studies which identified dense perennial vegetation as the key feature of overwintering habitats for spiders (Jögar et al., 2004; Schmidt & Tschardt, 2005). The absence of an effect of plant species richness on spider abundance and richness together with the significant role of successional age of perennial habitats shown previously (Campbell et al., 2020), indicates that vegetation structure rather than plant species richness affects the habitat preference of spiders (Blake et al., 2013). In addition, the absence of any management activities like ploughing and the use of pesticides may have promoted the overwintering of rove beetles and spiders in wildflower areas as well (Clough et al., 2007; Ganser et al., 2019).

In contrast to rove beetles and spiders, abundance and species richness of overwintering carabid beetles did not differ between arable fields and wildflower areas. This pattern contradicts our expectations and previous findings (Frank and Reichhart, 2004; Ganser et al., 2019). While habitat type had no significant overall effect, we found rather high abundances of carabid beetles on the arable, here winter crop, compared to wildflower areas for two out of the ten study sites. This may largely be owed to the aggregation of two species, *Bembidion aeneum* and *B. tetracolum*, that strongly dominated the beetle community. Such aggregations were previously shown for areas with a well-developed sod layer (Desender, 1982), which may correspond to the extensive management of the respective arable fields in both study

sites in our study (Fusser et al., 2018). Hence, although we could not detect an overall effect of habitat type on the abundance of carabid beetles, our results support the assumption, that agrobiont *Bembidion* spp. prefer arable land and disappear once arable fields have been transformed to wildflower areas (Baulechner et al., 2019; Knapp & Saska, 2012). In contrast to *Bembidion* spp., other carabid beetle species and further natural enemies have been shown to directly benefit from larger wildflower areas at least during the vegetation period (Blaauw & Isaacs, 2012; Bommarco, 1998). This is in accordance with increasing carabid beetle abundance with increasing patch size of the focal wildflower area in our study and with the theory of island biogeography (MacArthur & Wilson, 1967).

Although the arable fields did not have the same crop type across all study sites, rove beetles and spiders still seemed to prefer wildflower areas over arable fields. Consequently, we assumed that differences in crop type and thus, potential variance in vegetation structure or management practices of the chosen arable fields did not affect the colonization of ground-dwelling arthropods during the vegetation period and thus, did not diminish the overall preference for wildflower areas. This is in line with previous studies where ground-dwelling arthropods did not seem to show e.g. a preference for either winter wheat or maize fields, whereas higher vegetation density of oilseed rape fields may cause higher species richness (Duelli et al., 1990; Frank, 1997).

LANDSCAPE EFFECTS ON OVERWINTERING PATTERNS IN WILDFLOWER AREAS

Overwintering patterns found for ground-dwelling arthropods in wildflower areas are in line with theoretical considerations such as the intermediate landscape-complexity hypothesis (Martin et al., 2019; Tscharncke et al., 2012) and support empirical studies that showed that wildflower areas strongly benefit birds, bees, butterflies and crickets during the vegetation period in simple landscapes as compared to cleared or complex landscapes (Concepción et al., 2008; Scheper et al., 2013; Tscharncke et al., 2012; Wix et al., 2019).

By distinguishing between permanent and transient semi-natural habitats when quantifying the structural complexity of agricultural landscapes, for the first time, we were able to show the importance of the landscape context for the benefits of wildflower areas as overwintering habitats. We found abundance and species richness of adult rove beetles and abundance of juvenile carabid beetles to be highest in wildflower areas surrounded by simple landscapes with intermediate amounts of 3-4% of permanent semi-natural habitats. This is in line with studies that found increased species richness of agrobiont rove beetles with increasing

proportions of non-crop areas, which may constitute refuges for source populations and thus, promote colonization (Bohác, 1999; Clough et al., 2007).

In contrast to rove beetles, we found highest abundances of adult carabid beetles in simple landscapes with 6-8% of transient wildflower areas, whereas permanent semi-natural habitats had no effect. Similar to permanent semi-natural habitats, transient wildflower areas may improve the qualitative and quantitative food availability, which benefits fitness and reproductive rates of carabid beetles (Bommarco, 1998; Diekötter et al., 2016). Moreover, particularly intermediate proportions of wildflower areas may provide corridors or stepping stones and thus, increase the connectivity between annual and perennial habitats in agricultural landscapes (Bommarco, 1998; Holland, 2002). In contrast, if sown wildflower areas are embedded in simple or complex landscapes, the created contrast in resources may be rather low and thus, may not significantly promote agro-biodiversity (Holzschuh et al., 2010; Tscharncke et al., 2012).

The abundance and species richness of spiders was independent of landscape complexity in our study. This finding contradicts our expectation based on previous studies that found spider diversity to increase with non-crop habitats in the surrounding landscape (Clough et al., 2005; Schmidt et al., 2008) due to higher structural diversity as well as the provisioning of more predictable and diverse food resources of permanent semi-natural habitats (Diehl et al., 2013). However, other studies also found habitat characteristics at the local rather than the landscape scale important for habitat choice of spiders (Ganser et al., 2019; Sarthou et al., 2014), which is in line with our finding that spiders preferred wildflower areas over arable fields.

While the benefits for ground-dwelling arthropods were highest in simple landscapes, rove and carabid beetles in our study positively responded to either permanent semi-natural habitats or transient wildflower areas. This indicates that these two resource-rich habitat types may serve different purposes and that the promotion of the completely functional guild of ground-dwelling arthropods requires the simultaneous availability of both habitat types in the appropriate shares at the landscape scale.

CONCLUSIONS AND FUTURE PERSPECTIVES

Due to limited financial resources and the land-use competition between agriculture and nature conservation, it is crucial to optimize currently applied agri-environment schemes in order to maximize their conservation benefits. Findings of our study indicate that ground-dwelling arthropods prefer overwintering in wildflower areas compared to arable fields. In addition, our study is among the first to provide empirical evidence that wildflower areas may

benefit non-target species, such as ground-dwelling arthropods, outside the vegetation period but that these benefits were highest in simple landscapes with intermediate proportions of permanent semi-natural habitats and transient wildflower areas. However, to corroborate our findings, future studies should include other crop types, different management regimes in these crops and extend the sampling period in order to assess whether annual resowing of wildflower areas may create ecological traps for late emerging ground-dwelling arthropods. Based on the existing knowledge we conclude that wildflower areas not only provide important resources during the vegetation but also the winter period. In order to sustainably maintain the functional guild of ground-dwelling arthropods, agricultural landscapes should encompass both sown wildflower areas and permanent semi-natural habitats. In conclusion, the joint proportions of wildflower areas and permanent semi-natural habitats, found to maximise the diversity of rove and carabid beetles in our study, support the general claim of a safe minimum standard of 10-15% of semi-natural habitats to conserve the characteristic biodiversity in modern agro-ecosystems.

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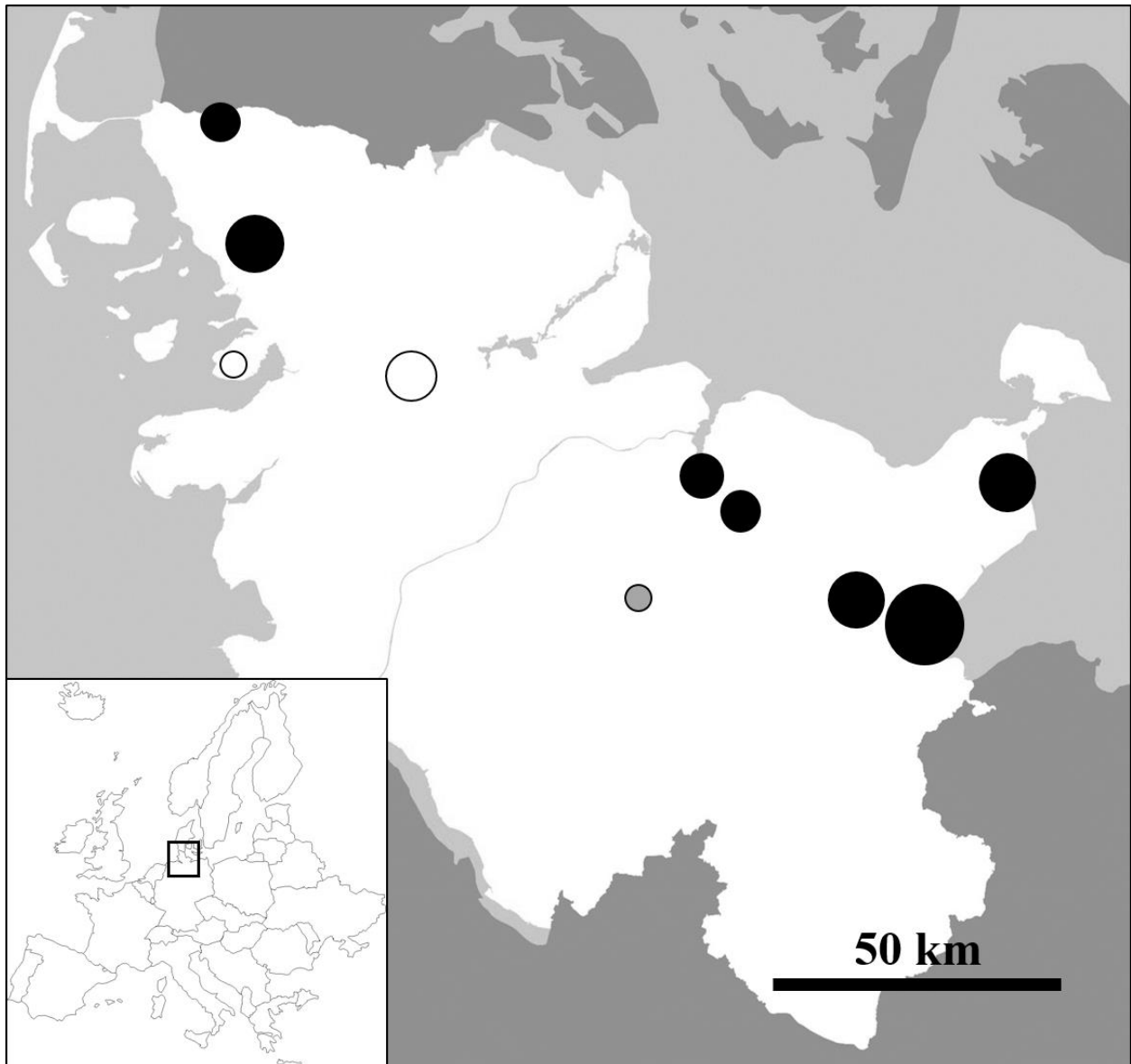
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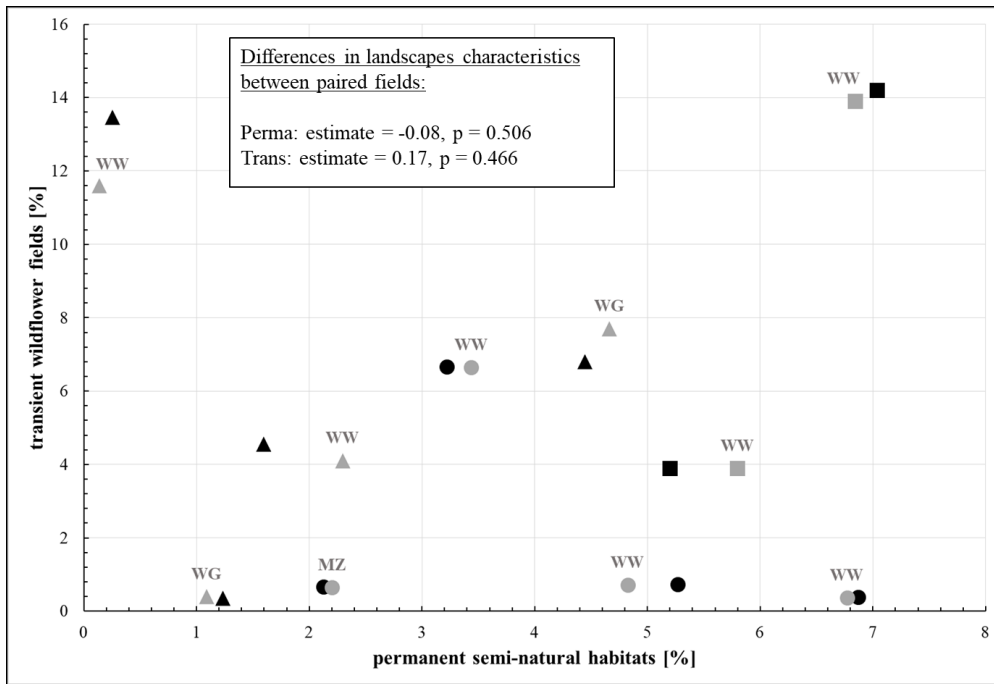
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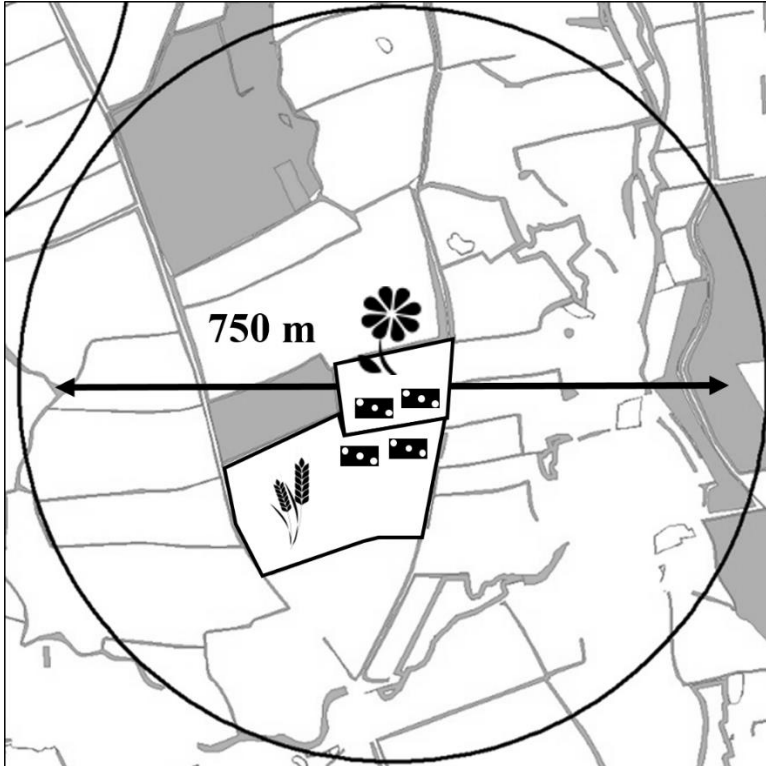
APPENDIX



Appendix A. Supporting Information B. Map showing the ten study sites as pairs of wildflower areas and crop fields in Schleswig-Holstein, Northern Germany. Size of circles represents proportions of semi-natural habitats as the sum of permanent semi-natural habitats and transient wildflower areas (Table 1).



Appendix B. Distribution of selected wildflower areas (black) and arable (grey) fields within the ten studied landscapes. We highlighted different types of crops (winter wheat: WW, winter greening: WG, maize: MZ) as well as paired fields which were either adjacent (circles) or showed higher distances to each other (squares: distance > 0 - < 100 m, triangles: distance > 100 m). Differences in landscape characteristics, i.e. permanent semi-natural habitats (Perma) and transient wildflower areas (Trans) between paired fields were tested using 'T.TEST' from 'STATS' package in R.



Appendix C. Map showing our study design exemplary for one study site. We selected one arable field and wildflower area per study site and sampled ground-dwelling arthropods using two emergence traps (black rectangles) with three pitfall traps (white circle) per habitat type and study site. For statistical analyses, we pooled the data and calculated abundance and species richness per emergence trap and habitat type and study site, totalling 40 observations (10 sites * 2 habitat types * 2 emergence traps).



Appendix D. Examples of emergence traps on a winter wheat field (A), on a winter greening mixture (B) and on a maize field (C) at the beginning of the sampling period from January until April 2018.

Appendix E. List of all recorded plant species. Plant species contained in the wildflower seed mixture are given in bold.

Plant species	Plant family
<i>Achillea millefolium</i>	Asteraceae
<i>Agrostis capillaris</i>	Poaceae
<i>Agrostis gigantea</i>	Poaceae
<i>Alopecurus myosuroides</i>	Poaceae
<i>Alopecurus pratensis</i>	Poaceae
<i>Anethum graveolens</i>	Apiaceae
<i>Anthoxanthum odoratum</i>	Poaceae
<i>Arabidopsis thaliana</i>	Brassicaceae
<i>Arctium lappa</i>	Asteraceae
<i>Artemisia vulgaris</i>	Asteraceae
<i>Avena strigosa</i>	Poaceae
<i>Borago officinalis</i>	Boraginaceae
<i>Brassica napus</i>	Brassicaceae
<i>Brassica oleracea</i>	Brassicaceae
<i>Capsella bursa-pastoris</i>	Brassicaceae
<i>Centaurea jacea</i>	Asteraceae
<i>Circaea lutetiana</i>	Onagraceae
<i>Cirsium arvense</i>	Asteraceae
<i>Cirsium vulgare</i>	Asteraceae
<i>Conyza canadensis</i>	Asteraceae
<i>Coriandrum sativum</i>	Apiaceae
<i>Cyanus segetum</i>	Asteraceae
<i>Dactylis glomerata</i>	Poaceae
<i>Daucus carota</i>	Apiaceae
<i>Echinochloa muricata</i>	Poaceae
<i>Echium vulgare</i>	Boraginaceae
<i>Elymus repens</i>	Poaceae
<i>Epilobium hirsutum</i>	Onagraceae
<i>Epilobium parviflorum</i>	Onagraceae
<i>Erodium cicutarium</i>	Geraniaceae
<i>Fagopyrum esculentum</i>	Polygonaceae
<i>Fallopia japonica</i>	Polygonaceae
<i>Festuca pratensis</i>	Poaceae
<i>Fraxinus excelsior</i>	Oleaceae
<i>Galium album</i>	Rubiaceae
<i>Galium</i> sp.	Rubiaceae
<i>Geranium dissectum</i>	Geraniaceae
<i>Geranium pusillum</i>	Geraniaceae
<i>Helianthus annuus</i>	Asteraceae
<i>Holcus lanatus</i>	Poaceae
<i>Hypochaeris radicata</i>	Asteraceae
<i>Juncus effusus</i>	Juncaceae
<i>Lamium</i> sp.	Lamiaceae
<i>Lapsana communis</i>	Asteraceae
<i>Leucanthemum ircutianum</i>	Asteraceae
<i>Linum usitatissimum</i>	Linaceae
<i>Lolium perenne</i>	Poaceae
<i>Lotus corniculatus</i>	Fabaceae
<i>Lycopsis arvensis</i>	Boraginaceae
<i>Malva sylvestris</i>	Malvaceae
<i>Matricaria chamomilla</i>	Asteraceae
<i>Medicago lupulina</i>	Fabaceae
<i>Medicago varia</i>	Fabaceae
<i>Myosotis scorpioides</i>	Boraginaceae
<i>Myosotis</i> sp.	Boraginaceae
<i>Ornithopus sativus</i>	Fabaceae
<i>Persicaria lapathifolia</i>	Polygonaceae

<i>Persicaria maculosa</i>	Polygonaceae
<i>Petroselinum crispum</i>	Apiaceae
<i>Phacelia tanacetifolia</i>	Boraginaceae
<i>Phleum pratense</i>	Poaceae
<i>Plantago lanceolata</i>	Plantaginaceae
<i>Plantago major</i>	Plantaginaceae
<i>Poa annua</i>	Poaceae
<i>Poa pratensis</i>	Poaceae
<i>Poa trivialis</i>	Poaceae
<i>Polygonum aviculare</i>	Polygonaceae
<i>Prunella vulgaris</i>	Lamiaceae
<i>Ranunculus acris</i>	Ranunculaceae
<i>Ranunculus repens</i>	Ranunculaceae
<i>Raphanus sativus</i>	Brassicaceae
<i>Rumex crispus</i>	Polygonaceae
<i>Rumex obtusifolius</i>	Polygonaceae
<i>Rumex</i> sp.	Polygonaceae
<i>Salix</i> sp.	Salicaceae
<i>Scleranthus annuus</i>	Caryophyllaceae
<i>Silene latifolia</i>	Caryophyllaceae
<i>Silene vulgaris</i>	Caryophyllaceae
<i>Silphium perfoliatum</i>	Asteraceae
<i>Sinapis arvensis</i>	Brassicaceae
<i>Sisymbrium officinale</i>	Brassicaceae
<i>Solanum villosum</i>	Solanaceae
<i>Sonchus asper</i>	Asteraceae
<i>Stellaria aquatica</i>	Caryophyllaceae
<i>Stellaria graminea</i>	Caryophyllaceae
<i>Taraxacum officinale</i> agg.	Asteraceae
<i>Thlaspi arvense</i>	Brassicaceae
<i>Trifolium arvense</i>	Fabaceae
<i>Trifolium campestre</i>	Fabaceae
<i>Trifolium pratense</i>	Fabaceae
<i>Trifolium repens</i>	Fabaceae
<i>Trifolium striatum</i>	Fabaceae
<i>Urtica dioica</i>	Urticaceae
<i>Veronica chamaedrys</i>	Plantaginaceae
<i>Veronica montana</i>	Plantaginaceae
<i>Vicia sativa</i>	Fabaceae
<i>Viola arvensis</i>	Violaceae

Appendix F. Total number across all study sites as well as mean and standard deviation (mean \pm SD) per wildflower area (WF) and arable field (AF) for all recorded ground-dwelling arthropod species.

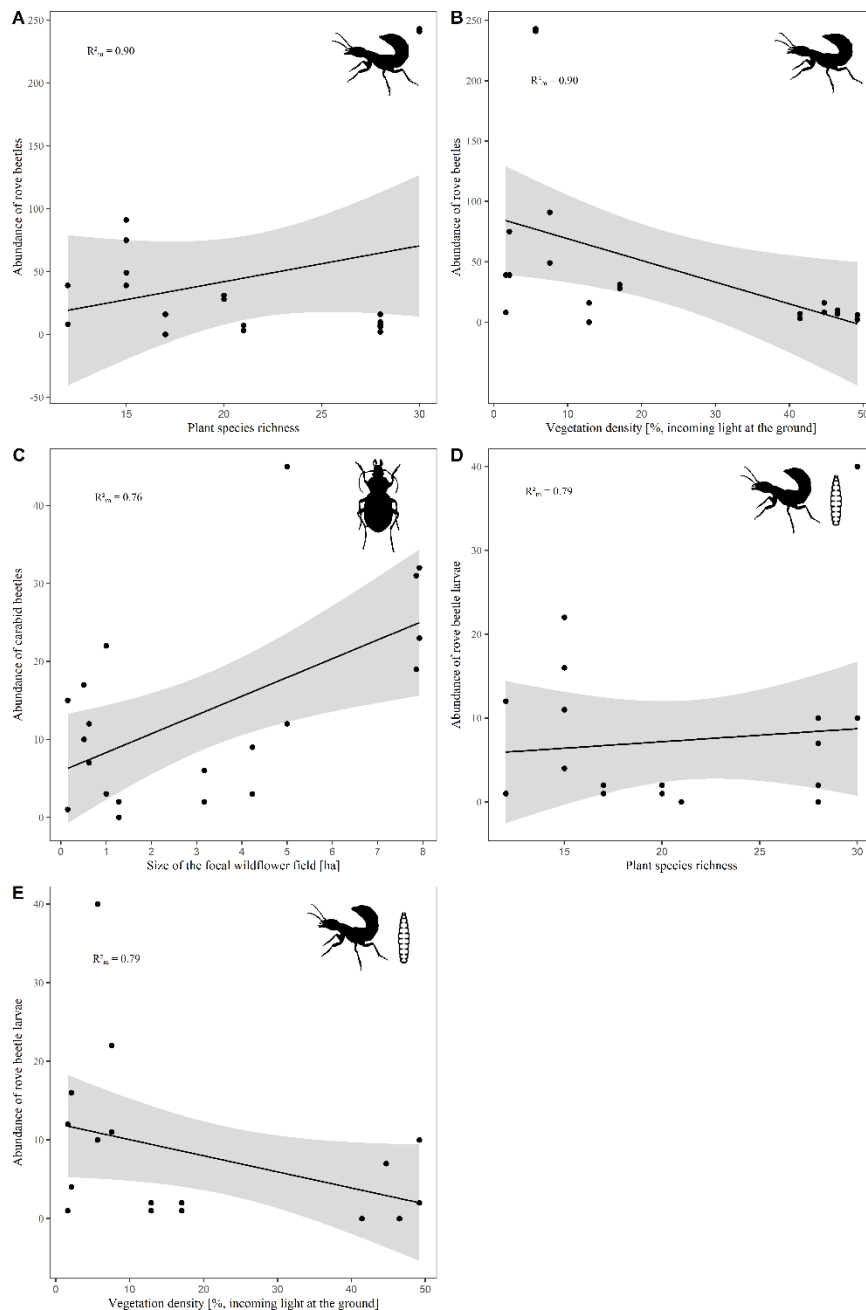
Arthropod species	Total numbers	Mean \pm SD for WF	Mean \pm SD for AF
Rove beetles			
<i>Aleochara lanuginosa</i> Grav., 1802	2	0.1 \pm 0.1	0.1 \pm 0.1
<i>Anotylus rugosus</i> (F., 1775)	41	1.1 \pm 0.3	1.0 \pm 0.4
<i>Anotylus sculpturatus</i> (Grav., 1806)	36	1.4 \pm 0.8	0.4 \pm 0.3
<i>Anthobium unicolor</i> (Marsh., 1802)	531	17.4 \pm 7.0	9.2 \pm 5.1
<i>Autalia impressa</i> (Ol., 1795)	1	0.1 \pm 0.1	0.0 \pm 0.0
<i>Bledius gallicus</i> (Grav., 1806)	2	0.1 \pm 0.1	0.0 \pm 0.0
<i>Brachygluta fossulata</i> (Reichb., 1816)	1	0.1 \pm 0.1	0.0 \pm 0.0
<i>Callicerus obscurus</i> Grav., 1802	2	0.1 \pm 0.1	0.1 \pm 0.1
<i>Carpelimus corticinus</i> (Grav., 1806)	1	0.0 \pm 0.0	0.1 \pm 0.1
<i>Coprophilus striatulus</i> (F., 1793)	2	0.1 \pm 0.1	0.1 \pm 0.1
<i>Euaesthetus bipunctatus</i> (Ljungh, 1804)	2	0.1 \pm 0.1	0.0 \pm 0.0
<i>Gabrieus appendiculatus</i> Sharp, 1910	11	0.4 \pm 0.2	0.2 \pm 0.2
<i>Gyrophypus angustatus</i> Steph., 1833	4	0.2 \pm 0.1	0.0 \pm 0.0
<i>Heterothops dissimilis</i> (Grav., 1802)	1	0.1 \pm 0.1	0.0 \pm 0.0
<i>Ischnosoma splendidum</i> (Grav., 1806)	1	0.1 \pm 0.1	0.0 \pm 0.0
<i>Lathrobium brunnipes</i> (F., 1792)	3	0.0 \pm 0.0	0.2 \pm 0.1
<i>Lathrobium fulvipenne</i> (Grav., 1806)	14	0.3 \pm 0.2	0.5 \pm 0.3
<i>Lathrobium longulum</i> Grav., 1802	7	0.1 \pm 0.1	0.3 \pm 0.2
<i>Lesteva longoelytrata</i> (Goeze, 1777)	181	0.1 \pm 0.1	9.0 \pm 4.7
<i>Olophrum assimile</i> (Payk., 1800)	25	1.3 \pm 0.7	0.0 \pm 0.0
<i>Olophrum piceum</i> (Gyll., 1810)	306	13.4 \pm 6.8	2.0 \pm 1.1
<i>Omalius excavatum</i> Steph., 1834	3	0.1 \pm 0.1	0.1 \pm 0.1
<i>Omalius rivulare</i> (Payk., 1789)	83	0.1 \pm 0.1	4.1 \pm 3.1
<i>Othius punctulatus</i> (Goeze, 1777)	1	0.1 \pm 0.1	0.0 \pm 0.0
<i>Philonthus carbonarius</i> (Grav., 1802)	1	0.1 \pm 0.1	0.0 \pm 0.0
<i>Proteinus brachypterus</i> (F., 1792)	10	0.3 \pm 0.2	0.2 \pm 0.2
<i>Quedius fuliginosus</i> (Grav., 1802)	2	0.0 \pm 0.0	0.1 \pm 0.1
<i>Quedius longicornis</i> Kr., 1857	1	0.1 \pm 0.1	0.0 \pm 0.0
<i>Quedius maurus</i> (Sahlb., 1830)	1	0.0 \pm 0.0	0.1 \pm 0.1
<i>Stenus cicindeloides</i> (Schall., 1783)	1	0.1 \pm 0.1	0.0 \pm 0.0
<i>Stenus clavicornis</i> (Scop., 1763)	2	0.1 \pm 0.1	0.0 \pm 0.0
<i>Tachinus corticinus</i> Grav., 1802	92	4.0 \pm 1.8	0.6 \pm 0.3
<i>Tachinus fimetarius</i> Grav., 1802	7	0.0 \pm 0.0	0.4 \pm 0.2
<i>Tachinus marginellus</i> (F., 1781)	46	1.2 \pm 0.5	0.4 \pm 0.2
<i>Tachinus rufipes</i> (L., 1758)	3	1.8 \pm 0.6	0.6 \pm 0.3
<i>Tachinus subterraneus</i> (L., 1758)	35	0.1 \pm 0.1	0.2 \pm 0.1
<i>Tachyporus hypnorum</i> (F., 1775)	30	0.1 \pm 0.1	0.1 \pm 0.1
<i>Tachyporus pusillus</i> Grav., 1806	4	1.0 \pm 1.0	0.8 \pm 0.4
<i>Xantholinus dvoraki</i> Coiff., 1956	5	0.3 \pm 0.2	0.0 \pm 0.0
<i>Xantholinus linearis</i> (Ol., 1795)	1	0.1 \pm 0.1	0.0 \pm 0.0
<i>Xantholinus longiventris</i> Heer, 1839	23	0.9 \pm 0.3	0.3 \pm 0.1
Carabid beetles			
<i>Acupalpus meridianus</i> (L., 1761)	1	0.1 \pm 0.1	0.0 \pm 0.0
<i>Agonum muelleri</i> (Hbst., 1784)	1	0.1 \pm 0.1	0.0 \pm 0.0
<i>Amara aenea</i> (Geer, 1774)	1	0.0 \pm 0.0	0.1 \pm 0.1
<i>Amara apricaria</i> (Payk., 1790)	3	0.2 \pm 0.1	0.0 \pm 0.0
<i>Amara familiaris</i> (Duft., 1812)	2	0.1 \pm 0.1	0.0 \pm 0.0
<i>Amara ingenua</i> (Duft., 1812)	2	0.1 \pm 0.1	0.0 \pm 0.0
<i>Amara plebeja</i> (Gyll., 1810)	2	0.1 \pm 0.1	0.0 \pm 0.0
<i>Amara similata</i> (Gyll., 1810)	1	0.1 \pm 0.1	0.0 \pm 0.0

<i>Anchomenus dorsalis</i> (Pont., 1763)	2	0.1 ± 0.1	0.1 ± 0.1
<i>Asaphidion curtum</i> Heyd., 1870	1	0.0 ± 0.0	0.1 ± 0.1
<i>Bembidion aeneum</i> Germ., 1824	149	1.0 ± 0.5	6.5 ± 4.3
<i>Bembidion biguttatum</i> (F., 1779)	18	0.7 ± 0.4	0.2 ± 0.1
<i>Bembidion femoratum</i> Sturm, 1825	2	0.0 ± 0.0	0.1 ± 0.1
<i>Bembidion lampros</i> (Hbst., 1784)	13	0.7 ± 0.3	0.0 ± 0.0
<i>Bembidion mannerheimii</i> Sahlb., 1827	5	0.2 ± 0.1	0.1 ± 0.1
<i>Bembidion obtusum</i> Serv., 1821	63	0.5 ± 0.2	2.7 ± 1.0
<i>Bembidion properans</i> (Steph., 1828)	2	0.1 ± 0.1	0.0 ± 0.0
<i>Bembidion quadrimaculatum</i> (L., 1761)	4	0.0 ± 0.0	0.2 ± 0.2
<i>Bembidion tetracolum</i> Say, 1823	248	0.4 ± 0.4	12 ± 6.9
<i>Bradycellus harpalinus</i> (Serv., 1821)	49	2.4 ± 1.3	0.1 ± 0.1
<i>Calathus fuscipes</i> (Goeze, 1777)	2	0.1 ± 0.1	0.0 ± 0.0
<i>Calathus melanocephalus</i> (L., 1758)	2	0.1 ± 0.1	0.0 ± 0.0
<i>Clivina fossor</i> (L., 1758)	7	0.2 ± 0.1	0.2 ± 0.1
<i>Demetrias atricapillus</i> (L., 1758)	1	0.0 ± 0.0	0.1 ± 0.1
<i>Dicheirotichus placidus</i> (Gyl., 1827)	7	0.1 ± 0.1	0.3 ± 0.2
<i>Harpalus affinis</i> (Schrk., 1781)	4	0.2 ± 0.1	0.0 ± 0.0
<i>Notiophilus biguttatus</i> (F., 1779)	1	0.0 ± 0.0	0.1 ± 0.1
<i>Philorhizus melanocephalus</i> Dej., 1825	1	0.0 ± 0.0	0.1 ± 0.1
<i>Poecilus cupreus</i> (L., 1758)	2	0.1 ± 0.1	0.0 ± 0.0
<i>Pterostichus melanarius</i> (Ill., 1798)	4	0.2 ± 0.1	0.1 ± 0.1
<i>Pterostichus strenuus</i> (Panz., 1797)	96	1.8 ± 0.6	3.1 ± 1.1
<i>Pterostichus vernalis</i> (Panz., 1796)	1	0.1 ± 0.1	0.0 ± 0.0
<i>Trechoblemus micros</i> (Hbst., 1784)	1	0.0 ± 0.0	0.1 ± 0.1
<i>Trechus quadristriatus</i> (Schrk., 1781)	130	4.3 ± 1.3	2.2 ± 0.7

Spiders

<i>Agyneta rurestris</i> (Koch, 1836)	2	0.0 ± 0.0	0.1 ± 0.1
<i>Anguliphantes angulipalpis</i> (Westr., 1851)	2	0.1 ± 0.1	0.1 ± 0.1
<i>Araeoncus humilis</i> (Blackw., 1841)	3	0.1 ± 0.1	0.1 ± 0.1
<i>Bathyphantes gracilis</i> (Blackw., 1841)	75	2.4 ± 0.6	1.4 ± 0.3
<i>Bathyphantes parvulus</i> (Westr., 1851)	1	0.0 ± 0.0	0.1 ± 0.1
<i>Centromerita bicolor</i> (Blackw., 1833)	63	2.4 ± 1.3	0.8 ± 0.4
<i>Centromerus prudens</i> (Cambr., 1873)	2	0.1 ± 0.1	0.0 ± 0.0
<i>Centromerus sylvaticus</i> (Blackw., 1841)	7	0.3 ± 0.2	0.1 ± 0.1
<i>Cicurina cicur</i> (F., 1793)	2	0.1 ± 0.1	0.1 ± 0.1
<i>Collinsia inerrans</i> (Cambr., 1885)	1	0.1 ± 0.1	0.0 ± 0.0
<i>Dicymbium nigrum</i> (Blackw., 1834)	2	0.1 ± 0.1	0.1 ± 0.1
<i>Dicymbium tibiale</i> (Blackw., 1836)	2	0.1 ± 0.1	0.0 ± 0.0
<i>Diplostyla concolor</i> (Wider, 1834)	42	2.0 ± 1.4	0.2 ± 0.1
<i>Erigone atra</i> Blackw., 1833	55	0.0 ± 0.0	0.1 ± 0.1
<i>Erigone dentipalpis</i> (Wider, 1834)	41	1.5 ± 0.7	1.3 ± 0.5
<i>Erigone arctica maritima</i> (Kulczy., 1902)	1	0.7 ± 0.3	1.4 ± 0.4
<i>Erigone longipalpis</i> (Sundev., 1830)	2	0.1 ± 0.1	0.1 ± 0.1
<i>Ero cambridgei</i> Kulczy., 1911	1	0.1 ± 0.1	0.0 ± 0.0
<i>Leptorhoptrum robustum</i> (Westr., 1851)	4	0.1 ± 0.1	0.2 ± 0.1
<i>Mermessus trilobatus</i> (Emerton, 1882)	1	0.0 ± 0.0	0.1 ± 0.1
<i>Microneta viaria</i> (Blackw., 1841)	2	0.1 ± 0.1	0.1 ± 0.1
<i>Nerienne clathrata</i> (Sundev., 1830)	6	0.1 ± 0.1	0.3 ± 0.2
<i>Oedothorax apicatus</i> (Blackw., 1850)	2	0.1 ± 0.1	0.0 ± 0.0
<i>Oedothorax retusus</i> (Westr., 1851)	1	0.1 ± 0.1	0.0 ± 0.0
<i>Pachygnatha clercki</i> Sundev., 1823	25	0.7 ± 0.2	0.6 ± 0.2
<i>Pachygnatha degeeri</i> Sundev., 1830	10	0.5 ± 0.2	0.0 ± 0.0
<i>Palliduphantes ericaeus</i> (Blackw., 1853)	1	0.1 ± 0.1	0.0 ± 0.0
<i>Palliduphantes insignis</i> (Cambr., 1913)	1	0.1 ± 0.1	0.0 ± 0.0
<i>Palliduphantes pallidus</i> (Cambr., 1871)	3	0.1 ± 0.1	0.1 ± 0.1
<i>Porrhomma microphthalmum</i> (Cambr., 1871)	39	0.7 ± 0.2	1.3 ± 0.6
<i>Porrhomma oblitum</i> (Cambr., 1871)	1	0.0 ± 0.0	0.1 ± 0.1

<i>Robertus lividus</i> (Blackw., 1836)	3	0.2 ± 0.1	0.0 ± 0.0
<i>Savignya frontata</i> Blackw., 1833	10	0.3 ± 0.2	0.2 ± 0.2
<i>Stemonyphantes lineatus</i> (L., 1758)	16	0.6 ± 0.4	0.2 ± 0.1
<i>Tallusia experta</i> (Cambr., 1871)	24	0.8 ± 0.3	0.4 ± 0.2
<i>Tegenaria silvestris</i> (Koch, 1872)	7	0.3 ± 0.2	0.1 ± 0.1
<i>Tenuiphantes tenuis</i> (Blackw., 1852)	7	0.2 ± 0.1	0.2 ± 0.1
<i>Trochosa ruricola</i> (De Geer, 1778)	4	0.2 ± 0.1	0.1 ± 0.1
<i>Walckenaeria acuminata</i> Blackw., 1833	4	0.1 ± 0.1	0.1 ± 0.1
<i>Walckenaeria nudipalpis</i> (Westr., 1851)	10	0.5 ± 0.2	0.0 ± 0.0



Appendix G. Effect of plant species richness (A) and vegetation density (B) on the abundance of adult rove beetles, the effect of wildflower patch size (C) on the abundance of adult carabid beetles, as well as the effect of plant species richness (D) and vegetation density (E) on the abundance of juvenile rove beetles in wildflower areas. Points represent raw data; solid line and shaded area represent the model fit and 95% confidence intervals, respectively.



CHAPTER 2

Time- and landscape-dependent benefits of wildflower areas on ground-dwelling arthropods

Hoffmann H | Peter F | Donath TW | Diekötter T

ABSTRACT

Sown wildflower areas are a popular agri-environment scheme to counteract agro-biodiversity loss. Yet, their benefits are still controversially discussed. Since inconsistent benefits may be owed to temporal dynamics and landscape context, we studied the time-dependent effects of two distinct habitats on ground-dwelling arthropods in wildflower areas and adjacent crop fields.

We selected ten study sites, each consisting of a paired wildflower area and a crop field, that encompassed independent gradients of proportions of permanent semi-natural habitats and transient wildflower areas. Across three consecutive years, we studied abundance, species richness and community composition of rove and carabid beetles and spiders in both habitat types.

Arthropod responses to the proportions of permanent semi-natural habitats seemed hump-shaped, whereas transient wildflower areas seemed to drive linear responses. Moreover, an interactive effect on species richness of rove beetles in wildflower areas implies, that benefits were highest either at intermediate proportions of permanent semi-natural habitats (5%) or at lower proportions (3%), but with additional availability of transient wildflower areas. At the same time, in landscapes with low proportions of permanent semi-natural habitats, wildflower areas enfolded maximum benefits when present at highest proportions (14%).

Our results suggest that both habitats differ in how they affect biodiversity, possibly due to different temporal continuity and resource diversity. Benefits of permanent semi-natural habitats seemed highest at an equilibrium between an increasing resource-related species pool and an increasing diversity dilution, whereas benefits of transient wildflower areas seemed to increase with resource complementarity and connectivity at the landscape scale. Nevertheless, both habitats seem to complement each other and considered in concert, seem to be most effective in promoting benefits of wildflower areas to ground-dwelling arthropods at intermediate landscape complexity. Together with the variation in diversity patterns among years with weather extremes, optimising benefits of wildflower areas requires further investigation across multiple years.

Basic and Applied Ecology (submitted)

INTRODUCTION

Among agri-environment schemes, wildflower areas have widely been applied to counteract species loss in agricultural landscapes (Cardinale et al., 2012). Despite a considerable number of studies, however, there is no consensus on the benefits of wildflower areas for agrobiodiversity (Ekroos et al., 2014), possibly due to different temporal scales and landscape context covered in these studies (Batáry et al., 2020). Hence, over a period of three consecutive years, we compared patterns in the community composition of ground-dwelling arthropods between sown wildflower areas and adjacent crop fields along independent gradients of the proportions of resource-rich habitats in the surrounding landscape, here permanent semi-natural habitats and transient wildflower areas.

Sown wildflower areas, originally targeting flower-visiting insects, have been shown to benefit wild bees (Scheper et al., 2013), butterflies (Aviron et al., 2011) and other, non-prominent flower visitors (Grass et al., 2016) in temperate ecosystems worldwide. Despite these findings, studies evaluating the benefits of wildflower areas for biodiversity found positive effects in only 50% of the cases (Kleijn et al., 2006), often with rather modest increases in abundance or species richness of mainly common species (Batáry et al., 2015). Moreover, studies on benefits of wildflower areas have rarely addressed non-target organisms like ground-dwelling arthropods, which precludes conclusions on benefits for overall agrobiodiversity and thus, on the multifunctionality of wildflower areas. In addition, previous studies may have neglected the role of temporal dynamics as well as landscape context in shaping biodiversity responses to wildflower areas, which may have hampered consensus regarding the benefits of this popular agri-environment scheme (Ekroos et al., 2014; Kleijn et al., 2006).

Temporal dynamics play an important role for biodiversity patterns in agro-ecosystems in general (e.g. Wamser et al., 2011) and in wildflower areas in particular (e.g. Rusch et al., 2013). To be a successful measure within agricultural landscapes, newly established transient habitats like sown wildflower areas need to be colonized in the first place. This colonization may show a time lag and, depending on the floristic development, may be followed by a successive change in its faunal community composition. For example, studies showed that the abundance of spiders overwintering in wildflower areas increased across four years after sowing (Ganser et al., 2019), possibly due to the long-term absence of management practice (Mestre et al., 2018). Moreover, through changes in vegetation structure, carabid beetle communities shifted from small carnivorous towards larger proportions of medium-sized

herbivorous species within one year after the conversion from arable to wildflower areas (Baulechner et al., 2019).

Apart from successional changes within the wildflower area regarding the structure or resources, the composition of communities utilizing wildflower areas may depend on source populations within the surrounding landscape and thus, other semi-natural habitats such as hedgerows. A dependency of the benefits of wildflower areas on the overall availability of semi-natural habitats within the wider landscape has been shown for e.g. bees (Scheper et al., 2013) that benefited most in simple landscapes with intermediate structural complexity as compared to cleared or complex landscapes (Tscharntke et al., 2012). This hump-shaped pattern indicates that simple landscapes, with proportions of 2% to 20% of semi-natural habitats, comprise sufficient source habitats and populations, respectively, to promote the colonization and persistence of species within newly established wildflower areas (Tscharntke et al., 2012). In contrast, the surplus created by wildflower areas in complex landscapes characterized by well-connected habitats and meta-populations may only have limited ecological impact due to the prevalence of resources already existing in these landscapes (Kleijn et al., 2006). On the other hand, in cleared landscapes, the species pool may be small and species dynamics in wildflower areas may strongly rely on continuous unidirectional colonization flows from surrounding species-rich habitat remnants.

Apart from initial colonization of newly created structures such as wildflower areas, species persistence in intensively managed and very dynamic landscapes such as agro-ecosystems often depends on repeated bidirectional spillover between different types of semi-natural habitats as well as across the crop-non-crop interface (Blitzer et al., 2012). Hedgerows, for instance, increased abundances of beneficial syrphids and promoted their spillover to adjacent crop fields, especially when they were connected to forests (Haenke et al., 2014). Similarly, wildflower areas have been shown to increase the proportion of predatory carabid beetle species and simultaneously decrease the proportion of herbivorous species in adjacent oilseed rape fields (Boetzel et al., 2019). Thus, semi-natural habitats and wildflower areas both have the potential to alter meta-population dynamics, while their benefits for agro-biodiversity may differ due to the obvious difference in their temporal continuance within the landscape.

In order to better understand time-dependent benefits of sown wildflower areas, we studied the abundance, species richness and community composition of rove beetles, carabid beetles and spiders in pairs of wildflower areas and crop fields over a period of three consecutive years. Additionally, we were interested how landscape context, in terms of proportions of

permanent semi-natural habitats and transient wildflower areas, alters benefits of wildflower areas for agro-biodiversity.

MATERIAL & METHODS

STUDY REGION

We studied benefits of sown wildflower areas from 2017 to 2019 in the federal state of Schleswig-Holstein, Northern Germany, a region dominated by intensive agriculture. Under a regional agri-environment scheme to promote the Grey Partridge (*Perdix perdix*), wildflower areas were established on arable land by sowing a special weed mix (Appendix A). The scheme did not allow any agricultural management (e.g. use of insecticides and pesticides), but required resowing of fields twice within the contracted five-year period (2016-2021) between 1st April and 15th May.

We selected ten wildflower areas along independent gradients in the proportions of permanent semi-natural habitats and transient wildflower areas in the surrounding landscape (Pearson correlation = -0.02, $p = 0.963$, Appendix B). We quantified habitat proportions at a radius of 750 m around the centres of the focal wildflower areas, since this spatial scale has previously been identified as highly relevant for inter-patch dispersal of ground-dwelling arthropods (Martin et al., 2019). We defined permanent semi-natural habitats as hedgerows, single trees, tree rows, forest patches smaller than 2000 m², field margins, drainage ditches, ponds, kettle holes and further wetlands larger than 2000 m² and near-natural stonewalls. These landscape elements are effectively used by arthropods or provide edge habitats (ecotones) which may increase habitat availability and connectivity (Brandmayr et al., 1998).

Proportions of permanent semi-natural habitats ranged from 0% to 7% ($4\% \pm 2\%$, mean \pm SD, hereafter; Table 1) while proportions of transient wildflower areas ranged from 0% to 14% ($5\% \pm 5\%$; Table 1; cf. Rega et al., 2018). While we used the proportions of permanent semi-natural habitats and transient wildflower areas as continuous predictors for our regression analyses, we decided to apply the concept of intermediate landscape-complexity (Tscharntke et al., 2012) for the interpretation and discussion of our results in context with previous studies. We defined cleared, simple and complex landscapes but intentionally differentiated between permanent semi-natural habitats and transient wildflower areas, which leads to a range shift in proportions for the three categories. Hence, cleared, simple and complex landscapes were characterized by comparably low, intermediate and high proportions of permanent semi-natural habitats ($> 0.1\%$; $2\% - 5\%$; $< 7\%$) and transient

wildflower areas ($> 0.4\%$; $4\% - 10\%$; $< 14.2\%$). Landscape analyses were done using ArcGIS 10 (ESRI, CA, USA).

In addition to each wildflower area, we selected a winter crop field to assess differences in biodiversity patterns between these two habitat types and capture habitat-specific shifts across three consecutive years. Winter crop fields were selected as close as possible to the focal wildflower areas ($0\text{ m} - 795\text{ m}$, $124\text{ m} \pm 175\text{ m}$; Table 1). Due to crop rotation on the selected winter crop fields, we had to switch to another winter crop field during the study period in order to maintain the comparison with winter crop management and to minimize the distance within each pair of wildflower area and winter crop field. Winter crop fields constitute one of the main crops in Northern Germany and are characterized by homogeneous management and vegetation structure.

Table 1. Proportions of permanent semi-natural habitats (*Perma*) and transient wildflower areas (*Trans*), patch size of the focal wildflower areas (*WA*) as well as the distance to the closest crop fields of the ten study sites in Northern Germany.

Site ID	Perma [%]	Trans [%]	Patch size of WA [ha]	Distance to crop fields [m]		
				2017	2018	2019
Barkau	5.2	3.9	4.2	10	20	10
Gross Rheide	4.4	6.8	7.9	285	285	335
Kesdorf	7.0	14.2	3.2	20	20	20
Langenhorn	0.3	13.5	1.0	305	795	250
Neumuenster	2.1	0.6	0.5	0	0	0
Nordstrand	1.2	0.4	0.6	195	220	10
Pohnsdorf	5.3	0.7	1.3	0	0	0
Riepsdorf	3.2	6.6	5.0	20	20	20
Roenne	6.9	0.4	0.2	220	0	170
Suederluegum	1.6	4.6	7.9	150	320	10

ARTHROPOD SAMPLING

We used pitfall traps to sample ground-dwelling arthropods in 2017, 2018 and 2019. Each year at the end of May (latest possibility of resowing of the wildflower areas by landowners), three pitfall traps each were installed at the wildflower areas and the crop fields, at a distance of 10 m to the field border and 10 m between traps (e.g. Boetzel et al., 2019). Pitfall traps were 500 ml plastic cups filled with 150 ml water, 50 ml ethylene-glycol and a drop of detergent solution. To prevent unintended by-catch, i.e. of small vertebrates, traps were fitted with wire nets (mesh size: 31 mm x 31 mm). To protect the traps from rain and litter we attached a transparent plastic roof (30 cm x 30 cm) 10 cm aboveground. Pitfall traps were emptied biweekly until the harvest of winter crop fields in mid-July, totalling four collections per study site and thus, 720 samples ($3\text{ traps} * 2\text{ habitat types} * 4\text{ collections} * 10\text{ study sites} * 3$

years). All arthropods were stored in 70% ethanol until identification to species-level of rove beetles (Assing & Schülke, 2012; Besuchet, 1974; within subfamily Aleocharinae only the genera *Aleochara*, *Cordalia*, *Drusilla*, *Falagrioma*, *Ilyobates* and *Oligota*), carabid beetles (Müller-Motzfeld, 2004) and spiders (Almquist, 2005, 2006; Nentwig et al., 2018).

Abundance and species richness of rove beetles, carabid beetles and spiders were calculated by combining the four arthropod samples per pitfall trap and year resulting in a nested design of three observations per habitat type and study site, and a total of 180 observations (3 traps * 2 habitat types * 10 study sites * 3 years). In general, species abundance has been suggested to affect the observed species richness, which in turn, may differ from true species richness, particularly in landscapes with increasing heterogeneity (Brose & Martinez, 2004; Chao & Chiu, 2016). Based on a linear mixed-effects model ('LME4' package (Bates et al., 2014)), that accounts for the nested structure of our data, we found abundance and observed species richness to be significantly correlated for each arthropod group (p-value < 0.001; estimate > 0.01). Hence, to account for potential under-sampling, we calculated the non-parametric abundance-based species richness estimator Chao1 ('VEGAN' package (Oksanen et al., 2019)), which has been suggested to be less dependent on equal detection probability, especially compared to less accurate incidence-based species richness estimators (Chao & Chiu, 2016).

STATISTICAL ANALYSES

To test effects of time and landscape context on ground-dwelling arthropods, we ran generalized linear mixed-effects models ('MASS package (Wood, 2019)). First, we studied whether abundance and estimated species richness (species richness, hereafter) of ground-dwelling arthropods changed across the three consecutive years and if patterns differed between wildflower areas and crop fields. To evaluate significant differences among the three years, we ran an analysis of variance ('CAR' package (Fox & Weisberg, 2019)), followed by Tukey's multiple contrast tests ('MULTCOMP' package (Hothorn et al., 2008)).

Secondly, we studied additive and interactive effects of the proportions of permanent semi-natural habitats and transient wildflower areas on the abundance and species richness of ground-dwelling arthropods. Here, we used separate regression models for each habitat type and year. As fixed factors, we included both a linear and a quadratic function to account for the hypothesized non-linear, hump-shaped relationship between abundance and species richness of arthropods, respectively, with landscape context (Bolker, 2008). Moreover, to account for synergistic effects of the two habitat types, we included an interaction term in

addition to the additive effects of the two habitat types. Throughout all models, we defined study site as the random factor to account for the non-independence of multiple observations per study site (temporal and spatial pseudoreplication). The residuals were assumed to follow a Poisson error distribution. Based on the full models, we performed a manual stepwise backwards elimination of non-significant predictors ($\alpha = 0.05$) in order to find the most parsimonious model. Finally, if both the linear and the quadratic term of the predictor variable were significant, we did model selection between a full model (containing both the linear and the quadratic term) and a reduced model (containing the linear term only) based on the corrected Akaike information criterion (AICc) appropriate for small sample sizes (Quinn & Keogh, 2002). If the full model performed relatively better than the reduced model, we subsequently focused on the presentation and discussion of the effect of the quadratic term as it implicitly covers the linear effect (Quinn & Keogh, 2002). Based on the final models, we calculated the marginal and conditional R^2 including both fixed and random effects ('MUMIN' package (Barton, 2020)).

To assess the inter-annual changes of the arthropod communities in wildflower areas and crop fields over three consecutive years, we first pooled data into a single sample per study site for each habitat and year and compared arthropod communities using non-metric multidimensional scaling based on Bray Curtis distances ('VEGAN' package (Oksanen et al., 2019)). This type of ordination performs well with zero-inflated data, making it particularly useful for community data sets in ecology. We tested for the effects of habitat type and year and for differences among obtained clusters in NMDS ordinations using a PERMANOVA ('VEGAN' package (Oksanen et al., 2019)).

All statistical analyses were performed in R 4.0 (R Development Core Team, 2019).

RESULTS

In total, we captured 86,445 ground-dwelling arthropods from 334 different species (Appendix C). Altogether, arthropods were largely dominated by carabid beetles (67%, 101 species), followed by spiders (18%, 122 species) and rove beetles (15%, 111 species). The most abundant rove beetles were *Tachinus rufipes* (25%), *Aleochara brevipennis* (13%) and *Philonthus cognatus* (11%). The most abundant carabid beetles were *Pterostichus melanarius* (25%), *Poecilus cupreus* (18%) and *Anchomenus dorsalis* (16%), and the most abundant spiders were *Erigone atra* (26%), *Oedothorax apicatus* (13%) and *Pardosa agrestis* (9%).

TEMPORAL DYNAMICS

Habitat-specific abundance and species richness of rove beetles did not show an overall trend across the three years, except for a significant drop in abundance for the second year and rove beetle abundances in crop fields being significantly lower in the third as compared to the first year (Table 2, Fig. 1 A + D).

Similarly, habitat-specific abundance and species richness of carabid beetles did not show an overall trend across the study period, the only exception being a significant decrease in carabid beetle abundance in crop fields from the first to the second and third year, respectively (Table 2, Fig. 1 B + E).

In contrast, spider abundance significantly increased from the first and second to the third year for both habitat types (Table 2, Fig. 1 C). Moreover, species richness of spiders in crop fields significantly increased from the first to the third year (Table 2, Fig. 1 F).

Table 2. Significant differences of the abundance and estimated species richness of rove beetles, carabid beetles as well as spiders between the three years for wildflower areas (WA) and crop fields (CF), respectively. Degrees of freedom (DF), *t*-value (T), *P*-value (P) and the marginal (R^2_m) and conditional R^2 (R^2_c) are given for the most parsimonious model.

Taxa	Dependent	Habitat	Explanatory	DF	T	P	R^2_m	R^2_c
Rove beetles	Abundance	WA	year (2018 2017)	2	-3.32	0.006	0.47	0.98
			year (2019 2018)	2	4.34	<0.001		
		CF	year (2018 2017)	2	-7.58	<0.001		
			year (2019 2017)	2	-4.23	<0.001		
			year (2019 2018)	2	4.62	<0.001		
			year (2019 2018)	2	4.62	<0.001		
	Species richness	WA	year (2019 2018)	2	3.38	0.005	0.22	0.66
			year (2019 2018)	2	2.83	0.029		
Carabid beetles	Abundance	CF	year (2018 2017)	2	-2.9	0.023	0.09	0.99
			year (2019 2017)	2	-4.97	<0.001		
Spiders	Abundance	WA	year (2019 2017)	2	6.1	<0.001	0.54	0.95
			year (2019 2018)	2	4.84	<0.001		
		CF	year (2019 2017)	2	5.29	<0.001		
			year (2019 2018)	2	2.74	0.036		
	Species richness	CF	year (2019 2017)	2	3.05	0.015	0.17	0.56
			year (2019 2017)	2	3.05	0.015		

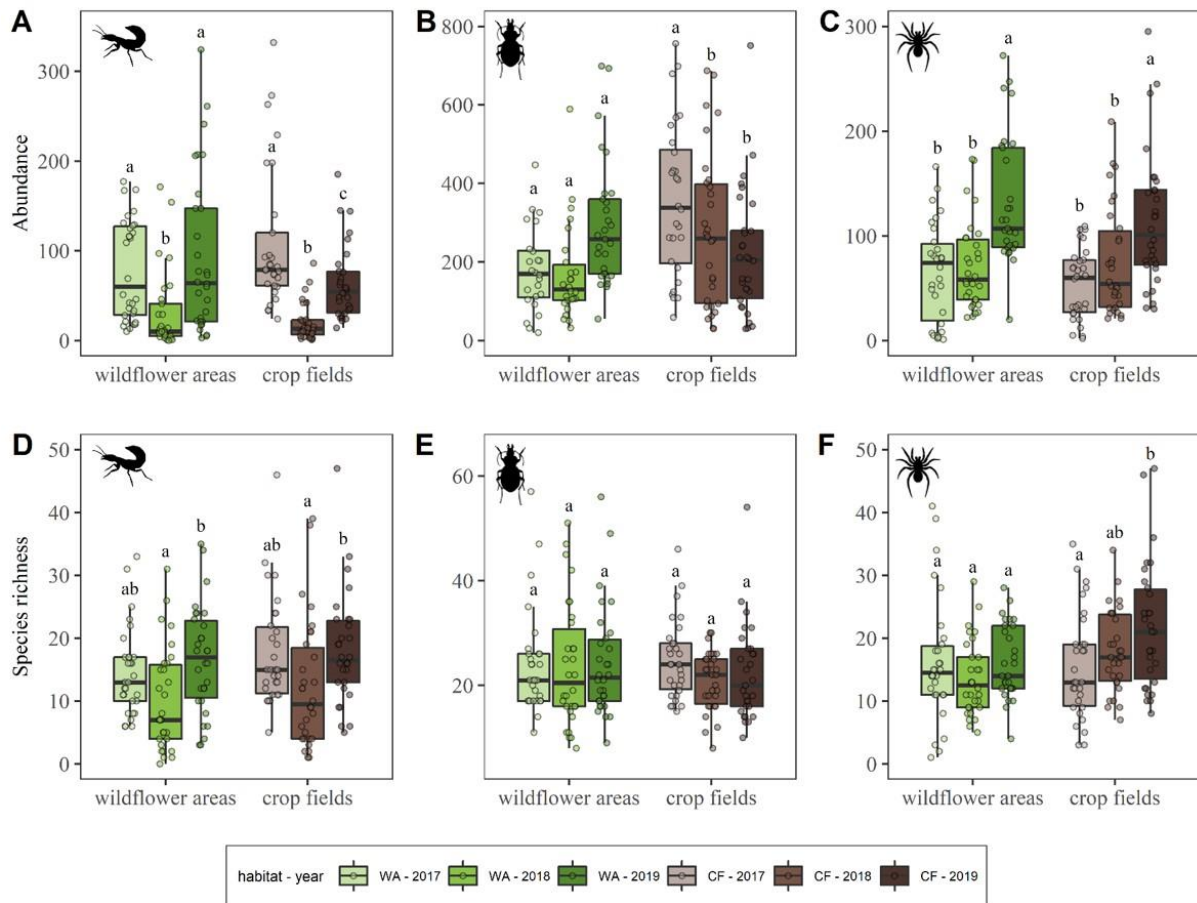


Figure 1. Differences between years separately per habitat type (wildflower areas = WA, crop fields = CF) on the abundance and estimated species richness of rove beetles (A + D), carabid beetles (B + E) and spiders (C + F). Boxplots show raw data and letters indicate significant difference between years per habitat type.

LANDSCAPE EFFECTS

While landscape effects on abundance and species richness of rove beetles, carabid beetles and spiders were rather heterogeneous across the three years and the two habitat types (Table 3, Fig. 2) two patterns seemed to emerge: First, landscape effects on the abundance of ground-dwelling arthropods became apparent in wildflower areas first, followed by the crop fields. While this was also true for species richness of spiders, landscape effects on species richness of rove and carabid beetles in crop fields were already apparent in the first year. Second, responses of arthropods to proportions of permanent semi-natural habitats largely seemed to follow a hump-shaped pattern, where abundance or species richness was highest in simple landscapes with intermediate proportions of permanent semi-natural habitats. In contrast, responses of arthropods to proportions of transient wildflower areas mainly seemed to show a linear increase.

Table 3. Significant effects of proportions of permanent semi-natural habitats (Perma) and transient wildflower areas (Trans) on the abundance and estimated species richness of rove beetles, carabid beetles as well as spiders in wildflower areas (WA) and crop fields (CF), respectively. Degrees of freedom (DF), *t*-value (T), *P*-value (P) and the marginal (R^2_m) and conditional R^2 (R^2_c) are given for the most parsimonious model.

	dependent	habitat	year	Explanatory	Df	T	P	AICc	R ² _m	R ² _c	
Rove beetles	Abundance	WF	2017	Perma (x)	6	7.96	< 0.001	309.93	0.94	0.98	
				Perma (x ²)	6	-6.98	< 0.001	295.89			
				Trans (x)	6	5.96	0.010				
		CF	2018	Perma (x)	6	4.06	0.007	261.60	0.74	0.94	
				Perma (x ²)	6	-3.97	0.007	254.39			
				Trans (x)	6	2.57	0.043				
	Species richness	WF	2017	Trans (x)	7	4.37	0.003	158.92	0.38	0.48	
				Trans (x ²)	7	-4.05	0.005	151.72			
			2018	Perma (x)	7	1.71	0.049	172.82	0.36	0.71	
				Perma (x ²)	7	-2.39	0.048	170.90			
			2019	Perma (x)	5	3.95	0.011	175.44	0.63	0.80	
				Perma (x ²)	5	-3.57	0.016	169.36			
		CF	2017	Trans (x)	5	3.25	0.023				
				Perma:Trans	5	-3.74	0.013				
			2018	Perma (x)	6	7.66	< 0.001	165.88	0.50	0.50	
				Perma (x ²)	6	-7.43	< 0.001	151.53			
				Trans (x)	6	5.94	< 0.001				
Carabid beetles	Abundance	CF	2018	Trans (x ²)	8	-3.62	0.007		0.73	0.99	
	Species richness	CF	2017	Perma (x ²)	8	2.77	0.024		0.21	0.41	
			2018	Perma (x)	7	4.65	0.002	168.35	0.34	0.40	
				Perma (x ²)	7	-4.40	0.003	160.60			
	Spiders	Abundance	WF	2017	Trans (x)	7	4.08	0.005	327.81	0.74	0.99
					Trans (x ²)	7	-3.39	0.012	322.74		
2018				Perma (x)	7	4.94	0.002	449.13	0.95	0.95	
				Perma (x ²)	7	-5.34	0.001	435.39			
2019			Trans (x ²)	8	3.15	0.012		0.58	0.96		
Species richness		CF	2018	Trans (x)	7	3.04	0.019	361.04	0.57	0.96	
				Trans (x ²)	7	-3.23	0.015	356.41			
		WF	2017	Perma (x)	5	-3.94	0.011		0.73	0.75	
				Trans (x)	5	2.99	0.031	161.34			
				Trans (x ²)	5	-3.08	0.027	156.98			
2018			Perma:Trans	5	4.10	0.009					
2019			Perma (x)	6	2.66	0.037		0.43	0.50		
			Trans (x)	6	4.93	0.003	159.22				
			Trans (x ²)	6	-5.10	0.002	148.52				
CF	2018	Perma (x)	8	4.33	0.003		0.36	0.39			
	2019	Perma (x)	6	3.18	0.019	163.78	0.23	0.23			
		Perma (x ²)	6	-2.89	0.028	161.05					
		Trans (x ²)	6	2.50	0.047						

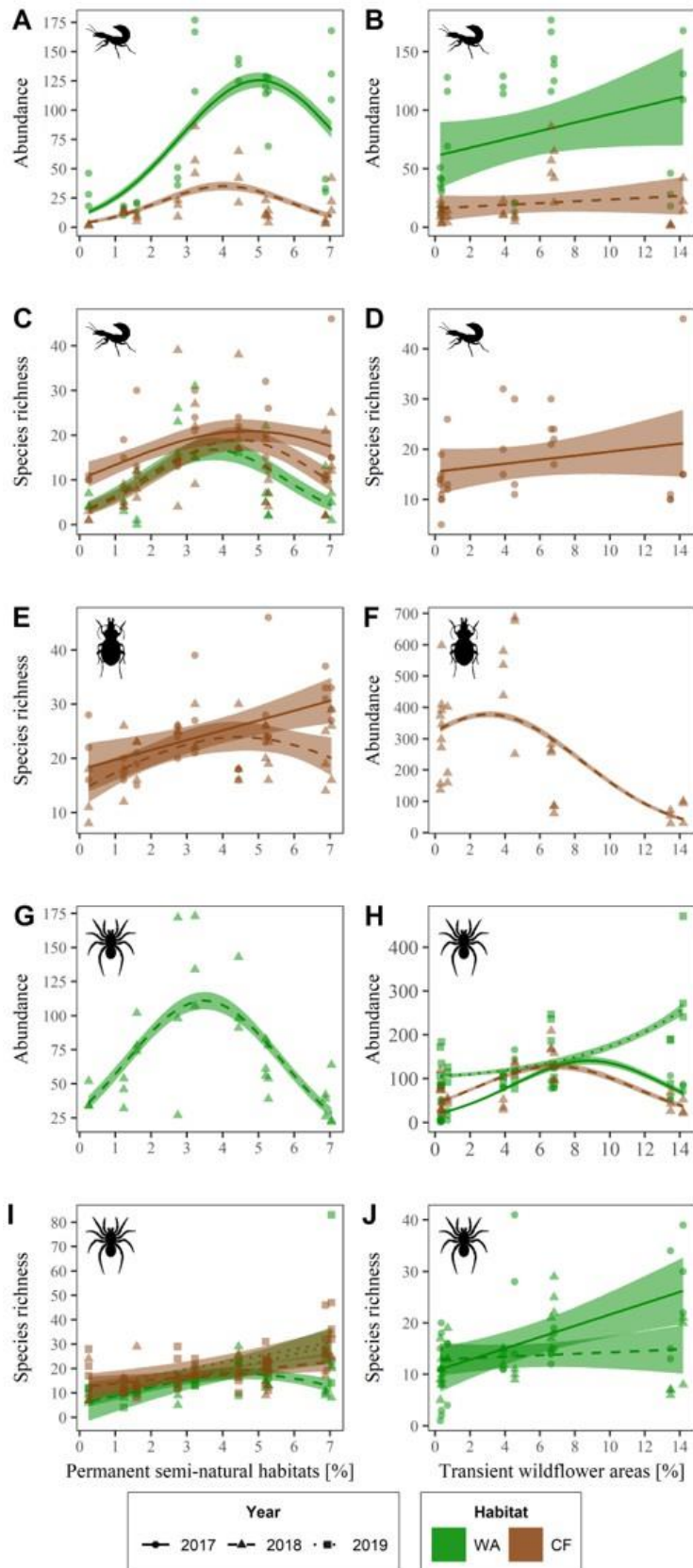


Figure 2. Effects of the proportions of permanent semi-natural habitats (left column) and transient wildflower areas (right column) on the abundance and estimated species richness of rove beetles (A – D), carabid beetles (E – F) and spiders (G – J) separately for wildflower areas (WA) and crop fields (CF). Points represent raw data, lines and shaded areas represent the model fit and 95% confidence intervals, respectively.

In addition to these main effects, proportions of permanent semi-natural habitats and transient wildflower areas had a significant interactive effect on species richness of rove beetles in wildflower areas in the third year (Table 3, Fig. 3). The hump-shaped pattern of species richness of rove beetles was shifted to the left when proportions of wildflower areas were high, indicating higher species richness at lower levels of permanent semi-natural habitats when levels of transient wildflower areas were comparably high. At the same time, species richness of rove beetles increased linearly with proportions of transient wildflower areas when proportions of permanent semi-natural habitats were low, but showed the opposite pattern when proportions of permanent semi-natural habitats were high.

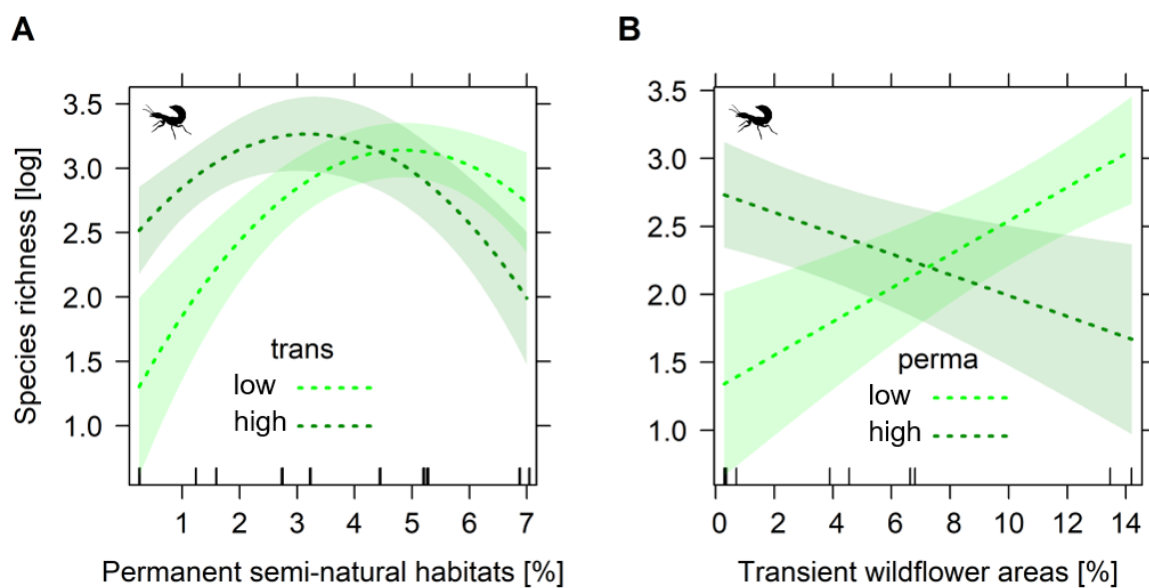


Figure. 3. Interactive effects of the proportions of permanent semi-natural habitats (perma; A) and transient wildflower areas (trans; B) on the estimated species richness of rove beetles in 2019 in wildflower areas. Points represent raw data, lines and shaded areas represent the model fit and 95% confidence intervals, respectively.

COMMUNITY COMPOSITION

Community composition of rove beetles, carabid beetles and spiders significantly differed between wildflower areas and crop fields and substantially changed over the three years (Table 4). For rove and carabid beetles, similarity between wildflower areas and crop fields increased over time (Fig 4 A + B), whereas similarity of spider communities decreased across the three years (Fig. 4 C).

Table 4. PERMANOVA analyses of species assemblages in relation to habitat type and year. Degrees of freedom (DF), F-value (F), significant P-values (P) and the R² are given for the most parsimonious model.

Taxa	Explanatory	Df	F	P	R ²
Rove beetles	habitat	1	3.60	0.001	0.06
	year	2	2.75	0.001	0.08
Carabid beetles	habitat	1	1.87	0.042	0.03
Spiders	habitat	1	3.58	0.001	0.06
	year	2	2.14	0.004	0.07

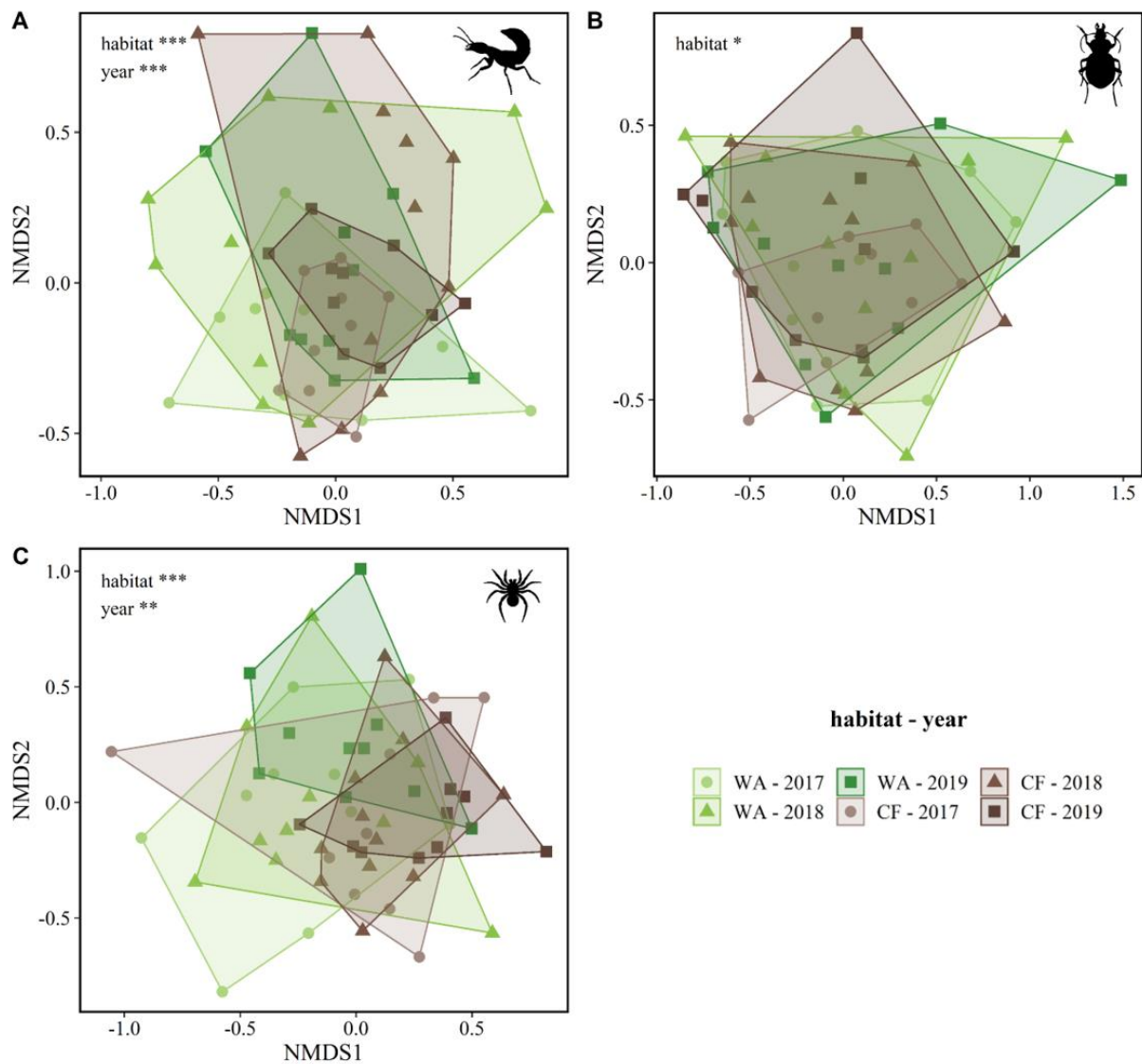


Figure 4. Nonmetric multidimensional scaling (NMDS) ordination of communities of rove beetles (A), carabid beetles (B) and spiders (C) separately per year and habitat (WA = wildflower areas, CF = crop fields). Polygons represent 2-D convex hulls for each habitat type per year. Significant factors in PERMANOVA tests indicated in the corners of the respective panels (* indicates $p < 0.05$, ** indicates $p < 0.01$, *** indicates $p < 0.001$). Statistics see Table 4.

DISCUSSION

In our study, arthropod responses became apparent in wildflower areas earlier than in crop fields. Moreover, arthropod responses to permanent semi-natural habitats largely seemed to follow a hump-shaped pattern but showed a linear increase with the proportion of transient wildflower areas. In part, both source habitats seemed to act in concert: Benefits were highest at intermediate proportions of permanent semi-natural habitats, while lower proportions seemed to be complemented by additional availability of transient wildflower areas. At the same time, wildflower areas enfolded maximum benefits in cleared landscapes when present at highest proportions. Finally, rove and carabid beetle communities in wildflower areas and adjacent crop fields became more similar across the three-year study period, whereas spider communities showed the opposite pattern.

TEMPORAL DYNAMICS

Overall, we observed no clear trends of arthropod abundance or species richness over the three years. Rove beetle abundance and species richness in both habitat types showed a drop in the second year while carabid beetle abundance in crop fields showed an overall decrease from the first towards the second and third year, respectively. While these patterns contradict our expectation of an increase towards the third year (Haaland et al., 2011), they may largely be owed to weather extremes during the second year of our study. In our study region, Schleswig-Holstein (Northern Germany), particularly May to July 2018 were the warmest months on record with unusually high temperatures (17 °C daily mean temperature) and comparatively low precipitation (25 l/m² in total; Deutscher Wetterdienst, 2021). These weather extremes may have affected species phenology, body sizes, species-specific interactions and as a consequence, reduced abundances and species richness (cf. Scheffers et al., 2016).

In contrast to rove and carabid beetles, spider abundance increased from the second to the third year, which may partly be explained by competitive release as a result of lower abundances of predatory beetles (Schmidt et al., 2008). However, at the same time, weather extremes during the second year or an overall lag-time in spider responses may have delayed the increase in abundances and species richness of spiders.

LANDSCAPE EFFECTS

Despite varying responses of ground-dwelling arthropods in wildflower areas and adjacent crop fields to landscape context in our three-year study, two patterns seemed to emerge: First,

arthropod responses to landscape structure became apparent in wildflower areas first, followed by the crop fields. These delayed effects observed for crop fields suggest that wildflower areas may be colonized first and cross-habitat spillover from the wildflower areas to adjacent crop fields may only occur after successful establishment, reproduction and overwintering of these species in the wildflower areas (Boetzel et al., 2019; Hoffmann et al., submitted).

Second, our findings imply that landscape effects may not solely spill over from wildflower areas to the adjacent crop field with a time lag, but may also differ with respect to the potential source habitat. Species responses to proportions of permanent semi-natural habitats mainly seemed to follow a hump-shaped pattern, whereas proportions of transient wildflower areas rather seemed to drive linear arthropod responses. Hence, benefits of permanent semi-natural habitats seemed to be highest at an equilibrium between an increasing resource-related species pool and a dilution effect (Tscharntke et al., 2012), whereas benefits of transient wildflower areas seem to increase with resource complementarity and connectivity at the landscape scale (Warzecha et al., submitted). These diverging patterns for permanent semi-natural habitats and transient wildflower areas imply that both habitat types strongly differ in their capacities to foster biodiversity benefits of newly established wildflower areas (Hoffmann et al., submitted).

Predominantly, permanent semi-natural habitats and transient wildflower areas differ in their configuration and temporal continuity. Particularly hedgerows constitute a well-connected, structurally rich and diverse habitat network that facilitates species dispersal in agricultural landscapes (Duflot et al., 2015) and meets species-specific resource requirements across a wide range of arthropod species (Sutter et al., 2018). In comparison, sown wildflower areas often are isolated elements within the agricultural matrix and thus, may only be colonized slowly despite diverse and abundant food resources for many species (Frank et al., 2007; Hoffmann et al., 2020). Additionally, due to the young age and disturbances through prescribed management activities, populations on wildflower areas are often below the carrying capacity (Ganser et al., 2019; Winqvist et al., 2011). Hence, benefits of these newly established and transient resource-rich habitats may only become apparent at higher levels of landscape proportions, which in turn, increases inter-patch connectivity and facilitates dispersal and persistence at the landscape level (Aviron et al., 2011; Fahrig, 2003).

Beyond those additive effects, permanent semi-natural habitats and transient wildflower areas had an interactive effect on species richness of rove beetles in the wildflower areas in the third year. Here, maximum benefits were realized at low levels of permanent semi-natural

habitats when levels of transient wildflower areas were comparatively high. This pattern supports the importance of source habitats that may even be enhanced in their beneficial effects when plenty of foraging resources are provided by transient wildflower areas at the landscape level (Blitzer et al., 2012). Wildflower areas may reduce e.g. the distance of foraging trips (Hoffmann et al., 2020) resulting in higher abundances due to higher survival and hatching rates (Frank et al., 2007; Ganser et al., 2020).

However, the interactive effect found in our study also suggests that species richness of rove beetles only increased with proportions of transient wildflower areas when proportions of permanent semi-natural habitats were low. This is in line with a study that found an increase in flower visits of pollinators in oilseed rape fields with increasing proportions of permanent semi-natural habitats when adjacent wildflower areas were small, but the opposite when they were large (Krimmer et al. 2019). Hence, despite differences between flower-visiting insects and ground-dwelling arthropods, the quantitative availability of high-quality habitats in the landscape may alter benefits of a focal habitat. In turn, high proportions of permanent semi-natural habitats in our study may have diminished the potential of the wildflower areas to attract and sustain high populations of ground-dwelling arthropods, and vice versa.

Altogether, our results suggest that the underlying mechanisms responsible for benefits of permanent semi-natural habitats and transient wildflower areas may differ. Nevertheless, benefits seemed to be highest at intermediate proportions considering both source habitats in concert: Benefits of permanent semi-natural habitats were highest either at intermediate proportions (5%) or at lower proportions (3%) when proportions of transient wildflower areas were high. In contrast, maximum benefits of transient wildflower areas were met at highest proportions (14%) but only when proportions of permanent semi-natural habitats were low. This finding is in line with the intermediate landscape complexity hypothesis (Tscharntke et al., 2012), which predicts highest benefits in simple landscapes with intermediate proportions of semi-natural habitats compared to cleared or complex landscapes. Hence, our findings contradict previous assumptions (Scheper et al., 2013; Tscharntke et al., 2012), since they imply that wildflower areas can also enfold benefits to agro-biodiversity in cleared landscapes but only if implemented at high proportions (Hoffmann et al., submitted; Warzecha et al., submitted).

COMMUNITY COMPOSITION

Altogether, the community composition significantly differed between wildflower areas and adjacent crop fields and changed substantially during the three-year study period. Similarity of rove and carabid beetle communities in wildflower areas and the adjacent crop fields increased towards the third year. An increase in the similarity between the two habitat types supports our assumption that wildflower areas may be colonized first, followed by a subsequent cross-habitat spillover from the wildflower areas to the surrounding crop fields (Albrecht et al., 2020; Boetzl et al., 2019).

Regarding species-specific responses, particularly herbivorous carabid beetles such as *Harpalus* spp. became more abundant during our study period in both habitat types. This finding is in line with previous studies that showed an overall shift from small carnivorous towards large herbivorous beetles with time after sowing of the wildflower areas (Baulechner et al., 2019; Gayer et al., 2019). Higher abundances of herbivorous carabid beetles may be due to increased resource availability provided by the wildflower areas (Gallé et al., 2020; Labruyere et al., 2016). Apart from herbivorous carabid beetles, abundances of aphidophagous rove beetles such as *Tachyporus hypnorum* showed a 2-fold increase in the crop fields, possibly because this effective aphid predator is negatively correlated with canopy cover and prefers open habitats (Irmeler & Gürlich, 2007). Hence, increasing similarity between communities of wildflower areas and adjacent crop fields over time may predominantly result from increased abundances of certain rove and carabid beetle species that are known to annually spillover from overwintering places such as wildflower areas into adjacent crop fields (Lipkow, 1966).

In contrast to rove and carabid beetles, similarity in the community composition of spiders between wildflower areas and crop fields decreased across the three years. In our study, spider communities were dominated by Linyphiids (55%) and Lycosids (19%) that primarily disperse by ballooning (Blandenier, 2009), which therefore, may have resulted in less directed dispersal from wildflower areas into adjacent crop fields as found for beetles (Bishop & Riechert, 1990; van Huizen, 1977). Besides the dispersal strategy, differences in the predominant hunting strategy of spider communities in the wildflower areas and the crop fields may have contributed to distinct species communities. For example, more than 80% of all *Xysticus* spp. crab spiders (Thomisidae) in our study were found in wildflower areas, which may largely be explained by the availability of floral resources and thus, prey availability (Bell et al., 2001). Similarly, the proportion of web-building species on wildflower areas nearly doubled from the first towards the third year, possibly as a result of a

denser vegetation structure in wildflower areas, which at the same time, may be unfavourable for some active hunting spiders (Campbell et al., 2020).

CONCLUSION

Our results support that wildflower areas provide suitable habitats for ground-dwelling arthropods in agro-ecosystems. Yet, these benefits seem to be time- and landscape-dependent. Inconsistent arthropod responses during our study period may be driven by species-specific responses of the arthropod communities, which may partly be owed to the weather extremes during the second year. As climatic extremes such as dry and hot summers are expected to occur more frequently in the future, our findings indicate the necessity to consider interactive effects of land-use and climate change when designing agri-environment schemes. Moreover, by differentiating between permanent and transient semi-natural habitats, we showed that the intermediate landscape-complexity hypothesis may particularly apply for permanent semi-natural habitats when complemented by other resource-rich habitats, i.e. sown wildflower areas. In contrast, transient wildflower areas seemed to drive linear responses and when implemented in high proportions this measure can enfold benefits to agro-biodiversity even in cleared landscapes, i.e. with low proportions of permanent semi-natural habitats. Hence, both source habitats seem to complement each other and in order to maximise benefits for agro-biodiversity, wildflower areas should be implemented at a landscape-dependent minimum proportion and maintained over multiple years.

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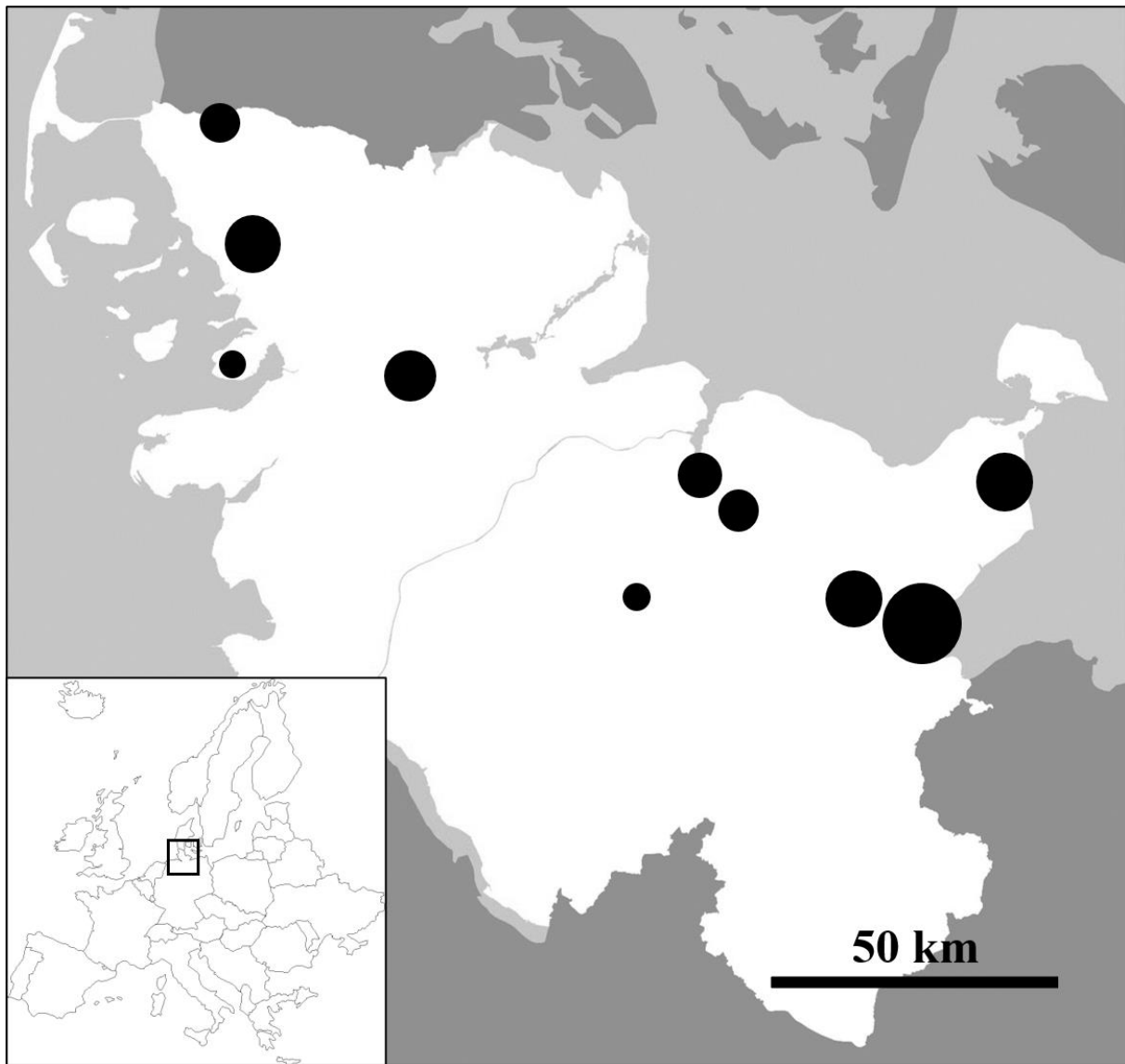
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APPENDIX

Appendix A. List and proportions of all plant species of the regional seed mix

Plant species	Proportion [%]
<i>Linum usitatissimum</i>	20
<i>Medicago lupulina</i>	12.5
<i>Petroselinum sativum</i>	11
<i>Trifolium repens</i>	6
<i>Galium album</i>	5
<i>Leucanthemum ircutianum</i>	5
<i>Lotus corniculatus</i>	5
<i>Ornithopus sativus</i>	5
<i>Trifolium subterraneum</i>	5
<i>Vicia sativa</i>	5
<i>Trifolium pratense</i>	3
<i>Lotus pedunculatus</i>	2
<i>Plantago lanceolata</i>	2
<i>Silene vulgaris</i>	2
<i>Coriandrum sativum</i>	2
<i>Phacelia tanacetifolia</i>	2
<i>Prunella vulgaris</i>	1.5
<i>Achillea millefolium</i>	1
<i>Trifolium dubium</i>	1
<i>Centaurea jacea</i>	0.5
<i>Daucus carota</i>	0.5
<i>Echium vulgare</i>	0.5
<i>Hypochoeris radicata</i>	0.5
<i>Lychnis-flos-cuculi</i>	0.5
<i>Ranunculus acris</i>	0.5
<i>Rumex acetosa</i>	0.5
<i>Stellaria graminea</i>	0.5



Appendix B. Supporting Information B. Map showing the ten study sites as pairs of wildflower areas and crop fields in Schleswig-Holstein, Northern Germany. Size of circles represents proportions of semi-natural habitats as the sum of permanent semi-natural habitats and transient wildflower areas (Table 1).

Appendix C. List, total number and mean \pm SD for wildflower areas (WA) and crop fields (CF) per year of all recorded ground-dwelling arthropod species.

Arthropod species	Total numbers	Mean ± SD for 2017		Mean ± SD for 2018		Mean ± SD for 2019	
		WA	CF	WA	CF	WA	CF
Staphylinidae							
<i>Aleochara bilineata</i> Gyll., 1810	205	6.3 ± 13.8	0.1 ± 0.3	0.3 ± 0.7	0.1 ± 0.3	3.8 ± 5.1	9.9 ± 28.9
<i>Aleochara bipustulata</i> (L., 1760)	1239	45.5 ± 66.9	1.6 ± 1.8	21.1 ± 45.5	4.7 ± 12.8	42.6 ± 40.9	8.4 ± 13.4
<i>Aleochara brevipennis</i> Grav., 1806	1680	26.2 ± 52	9.6 ± 12.8	36.9 ± 80.4	4.6 ± 9.4	73.8 ± 127.5	16.9 ± 19.6
<i>Aleochara curtula</i> (Goeze, 1777)	9	0.1 ± 0.3		0.1 ± 0.3	0.2 ± 0.6		0.5 ± 0.8
<i>Aleochara lanuginosa</i> Grav., 1802	1		0.1 ± 0.3				
<i>Aleochara ruficornis</i> Grav., 1802	2					0.2 ± 0.6	
<i>Anotylus inustus</i> (Grav., 1806)	1		0.1 ± 0.3				
<i>Anotylus nitidulus</i> (Grav., 1802)	105	9.1 ± 24.6	0.1 ± 0.3	0.3 ± 0.7	0.2 ± 0.6	0.6 ± 0.8	0.2 ± 0.6
<i>Anotylus rugosus</i> (F., 1775)	938	22.1 ± 19.7	11.2 ± 12.5	26.6 ± 60.1	1.6 ± 1.4	27.9 ± 37.7	4.4 ± 3.7
<i>Anotylus sculpturatus</i> (Grav., 1806)	26	0.2 ± 0.4	0.6 ± 1.6	1.6 ± 4.4		0.1 ± 0.3	0.1 ± 0.3
<i>Anotylus tetracarinatus</i> (Block, 1799)	33	0.5 ± 1.6	0.2 ± 0.6	0.2 ± 0.4		2.2 ± 3.8	0.2 ± 0.4
<i>Anthobium unicolor</i> (Marsh., 1802)	12	0.1 ± 0.3		0.6 ± 1.9		0.4 ± 1.3	0.1 ± 0.3
<i>Bisnius nitidulus</i> (Grav., 1802)	1					0.1 ± 0.3	
<i>Bisnius sordidus</i> (Grav., 1802)	1				0.1 ± 0.3		
<i>Bisnius spermophili</i> (Ganglb., 1897)	3					0.3 ± 0.9	
<i>Bledius gallicus</i> (Grav., 1806)	2				0.1 ± 0.3	0.1 ± 0.3	
<i>Bolitobius castaneus boreomontanicus</i> Schülke, 2010	1			0.1 ± 0.3			
<i>Bolitobius cingulatus</i> Mannerh., 1830	1						0.1 ± 0.3
<i>Brachygluta fossulata</i> (Reichb., 1816)	1	0.1 ± 0.3					
<i>Carpelimus bilineatus</i> Steph., 1834	1	0.1 ± 0.3					
<i>Carpelimus corticinus</i> (Grav., 1806)	9	0.5 ± 1.1				0.3 ± 0.9	0.1 ± 0.3
<i>Carpelimus gracilis</i> (Mannerh., 1830)	1	0.1 ± 0.3					
<i>Cordalia obscura</i> (Grav., 1802)	1	0.1 ± 0.3					
<i>Drusilla canaliculata</i> (F., 1787)	506	2.8 ± 5.2	22.5 ± 40.1	2.1 ± 5.6	1.3 ± 2.8	8.4 ± 24.5	13.5 ± 27.6
<i>Euaesthetus bipunctatus</i> (Ljungh, 1804)	15	0.1 ± 0.3	0.8 ± 2.2	0.2 ± 0.4		0.2 ± 0.6	0.2 ± 0.6
<i>Falagrioma thoracica</i> (Steph., 1832)	54	0.4 ± 1.3	2.7 ± 8.5	1.8 ± 5.3	0.2 ± 0.6	0.1 ± 0.3	0.2 ± 0.6
<i>Gabrius appendiculatus</i> Sharp, 1910	60	2.3 ± 5.9	0.5 ± 1.6	1.5 ± 3	0.8 ± 1	0.6 ± 1.3	0.3 ± 0.9
<i>Gabrius austriacus</i> Scheerp., 1947	4		0.1 ± 0.3		0.2 ± 0.6	0.1 ± 0.3	
<i>Gabrius breviventer</i> (Sperk, 1835)	100	1.3 ± 1.8	1 ± 1.3	1.1 ± 2.1	0.2 ± 0.4	3.9 ± 6.4	2.5 ± 3.7
<i>Gabrius osseticus</i> (Kolen., 1846)	2	0.1 ± 0.3	0.1 ± 0.3				
<i>Gyrophypnus angustatus</i> Steph., 1833	146	3 ± 4.6	3.3 ± 4.5	2.9 ± 5.6	1.5 ± 2.5	1.9 ± 2.4	2 ± 2.3
<i>Gyrophypnus punctulatus</i> (Payk., 1789)	1			0.1 ± 0.3			
<i>Heterothops dissimilis</i> (Grav., 1802)	17		0.3 ± 0.7	0.3 ± 0.7	0.6 ± 1.9	0.4 ± 1	0.1 ± 0.3
<i>Ilyobates bennetti</i> Donisth., 1914	52	0.8 ± 1.5	1 ± 1.2	0.2 ± 0.4	0.3 ± 0.5	0.8 ± 1.2	2.1 ± 3.7
<i>Ilyobates nigricollis</i> (Payk., 1800)	1						0.1 ± 0.3
<i>Ischnosoma splendidum</i> (Grav., 1806)	97	1.5 ± 3.2	0.8 ± 2.5			3.9 ± 10.9	3.5 ± 6.6
<i>Lathrobium brunnipes</i> (F., 1792)	7	0.1 ± 0.3				0.6 ± 1.6	
<i>Lathrobium elongatum</i> (L., 1767)	1			0.1 ± 0.3			
<i>Lathrobium fulvipenne</i> (Grav., 1806)	110	0.5 ± 0.7	1.7 ± 2.3	0.3 ± 0.7	2.8 ± 6.5	1.2 ± 1.3	4.5 ± 3.8
<i>Lathrobium impressum</i> Heer, 1841	1					0.1 ± 0.3	
<i>Lesteva longoelytrata</i> (Goeze, 1777)	518	0.7 ± 1.3	30.5 ± 69.8			0.1 ± 0.3	20.5 ± 42.8
<i>Megalinus glabratus</i> (Grav., 1802)	1			0.1 ± 0.3			
<i>Megarthrus prosseni</i> Schatzm., 1904	1	0.1 ± 0.3					
<i>Metopsia similis</i> Zerche, 1998	1						0.1 ± 0.3
<i>Mycetoporus bimaculatus</i> Lacord., 1835	2				0.2 ± 0.6		
<i>Mycetoporus lepidus</i> (Grav., 1806)	4			0.2 ± 0.6		0.2 ± 0.6	
<i>Mycetoporus longulus</i> Mannerh., 1830	2						0.2 ± 0.6

<i>Ocypus brunnipes</i> (F., 1781)	15		1.1 ± 3.1	0.2 ± 0.6	0.1 ± 0.3	0.1 ± 0.3	
<i>Oligota pumilio</i> Kiesw., 1858	42	0.2 ± 0.6	0.9 ± 1.4		0.4 ± 1	1.5 ± 3.7	1.2 ± 2.6
<i>Olophrum assimile</i> (Payk., 1800)	1	0.1 ± 0.3					
<i>Olophrum piceum</i> (Gyll., 1810)	3			0.1 ± 0.3		0.2 ± 0.6	
<i>Omalium caesum</i> Grav., 1806	1						0.1 ± 0.3
<i>Omalium excavatum</i> Steph., 1834	1						0.1 ± 0.3
<i>Omalium rivulare</i> (Payk., 1789)	3		0.2 ± 0.4	0.1 ± 0.3			
<i>Omalium rugatum</i> Muls. & Rey, 1880	1	0.1 ± 0.3					
<i>Oxyporus rufus</i> (L., 1758)	1		0.1 ± 0.3				
<i>Oxytelus laqueatus</i> (Marsh., 1802)	1					0.1 ± 0.3	
<i>Oxytelus sculptus</i> Grav., 1806	1					0.1 ± 0.3	
<i>Philonthus addendus</i> Sharp, 1867	3			0.2 ± 0.4			0.1 ± 0.3
<i>Philonthus atratus</i> (Grav., 1802)	44	1.7 ± 3.5		0.3 ± 0.9	0.1 ± 0.3	2.2 ± 5.2	0.1 ± 0.3
<i>Philonthus carbonarius</i> (Grav., 1802)	114	5.5 ± 6.4	1.8 ± 2.1	0.7 ± 1.6	1.4 ± 3.4	1.5 ± 1.6	0.5 ± 0.7
<i>Philonthus cognatus</i> Steph., 1832	1330	41.8 ± 71.4	32 ± 39.2	8 ± 16.3	7.1 ± 14.5	36.8 ± 48.2	7.3 ± 9.8
<i>Philonthus concinnus</i> (Grav., 1802)	5	0.4 ± 1.3	0.1 ± 0.3				
<i>Philonthus corruscus</i> (Grav., 1802)	2					0.2 ± 0.4	
<i>Philonthus decorus</i> (Grav., 1802)	16	0.3 ± 0.5	0.8 ± 1.3	0.5 ± 1			
<i>Philonthus fumarius</i> (Grav., 1806)	4			0.4 ± 0.8			
<i>Philonthus laminatus</i> (Creutzer, 1799)	74	1.9 ± 3.8	1.9 ± 3.6	1 ± 2.5	0.4 ± 0.8	1.3 ± 2.3	0.9 ± 2.8
<i>Philonthus marginatus</i> (Müll., 1764)	1				0.1 ± 0.3		
<i>Philonthus micans</i> (Grav., 1802)	2	0.2 ± 0.6					
<i>Philonthus rotundicollis</i> (Ménétr., 1832)	15		0.3 ± 0.9	0.1 ± 0.3	0.3 ± 0.7	0.5 ± 1.1	0.3 ± 0.7
<i>Philonthus varians</i> (Payk., 1789)	1			0.1 ± 0.3			
<i>Platystethus arenarius</i> (Geoffr., 1785)	1						0.1 ± 0.3
<i>Quedius boops</i> (Grav., 1802)	4			0.1 ± 0.3	0.1 ± 0.3		0.2 ± 0.6
<i>Quedius fuliginosus</i> (Grav., 1802)	12	0.7 ± 1.9	0.1 ± 0.3			0.2 ± 0.4	0.2 ± 0.4
<i>Quedius longicornis</i> Kr., 1857	1					0.1 ± 0.3	
<i>Quedius maurorufus</i> (Grav., 1806)	2				0.1 ± 0.3		0.1 ± 0.3
<i>Quedius molochinus</i> (Grav., 1806)	1					0.1 ± 0.3	
<i>Rugilus erichsonii</i> (Fauvel, 1867)	1				0.1 ± 0.3		
<i>Rugilus rufipes</i> (Germar, 1836)	6		0.2 ± 0.6			0.3 ± 0.9	0.1 ± 0.3
<i>Scydmaenus tarsatus</i> Müll.&Kunz., 1822	1						0.1 ± 0.3
<i>Sepedophilus marshami</i> (Steph., 1832)	169		10.5 ± 21.1	0.3 ± 0.9	1.3 ± 2.5	0.1 ± 0.3	4.7 ± 7.9
<i>Sepedophilus pedicularius</i> (Grav., 1802)	5	0.2 ± 0.4	0.2 ± 0.4				0.1 ± 0.3
<i>Stenichnus collaris</i> (Müll. & Kunz., 1822)	2	0.2 ± 0.4					
<i>Stenus atratulus</i> Er., 1839	5	0.1 ± 0.3	0.4 ± 1				
<i>Stenus biguttatus</i> (L., 1758)	9		0.1 ± 0.3		0.1 ± 0.3	0.1 ± 0.3	0.6 ± 1.9
<i>Stenus bimaculatus</i> Gyll., 1810	5	0.1 ± 0.3		0.1 ± 0.3	0.2 ± 0.6		0.1 ± 0.3
<i>Stenus brunnipes</i> Steph., 1833	1				0.1 ± 0.3		
<i>Stenus canaliculatus</i> Gyll., 1827	18		0.3 ± 0.5	0.1 ± 0.3	1 ± 1.7		0.4 ± 0.8
<i>Stenus clavicornis</i> (Scop., 1763)	69	0.5 ± 1	1.3 ± 1.7	1.1 ± 2.1	0.8 ± 1.5	0.2 ± 0.4	3 ± 2.8
<i>Stenus junco</i> (Payk., 1789)	7		0.5 ± 1.3		0.2 ± 0.4		
<i>Stenus pallipes</i> Grav., 1802	14	0.1 ± 0.3		0.7 ± 1.6	0.1 ± 0.3	0.4 ± 0.7	0.1 ± 0.3
<i>Stenus pusillus</i> Steph., 1833	2			0.1 ± 0.3	0.1 ± 0.3		
<i>Stenus similis</i> (Herbst, 1784)	1				0.1 ± 0.3		
<i>Sunius bicolor</i> (Ol., 1795)	3				0.1 ± 0.3	0.2 ± 0.6	
<i>Tachinus corticinus</i> Grav., 1802	212	1.6 ± 3.8	1.4 ± 2.7	3.6 ± 5.5		12.1 ± 27.6	2.5 ± 5.8
<i>Tachinus fimetarius</i> (Grav., 1802)	69	0.1 ± 0.3	1.3 ± 1.6		0.5 ± 1.3	0.1 ± 0.3	4.9 ± 12.6
<i>Tachinus laticollis</i> Grav., 1802	1				0.1 ± 0.3		
<i>Tachinus marginellus</i> (F., 1781)	21	0.7 ± 1.5	0.5 ± 1.3			0.9 ± 1.3	
<i>Tachinus rufipes</i> (L., 1758)	3192	43.1 ± 71	194.1 ± 253.6	4.3 ± 5.3	10.7 ± 27	22.6 ± 50.9	44.4 ± 51.3
<i>Tachyporus chrysomelinus</i> (L., 1758)	61	0.9 ± 2.5	1.8 ± 1.8	0.6 ± 1.6	1.1 ± 2.1	0.8 ± 1.1	0.9 ± 0.9
<i>Tachyporus dispar</i> (Payk., 1789)	86	1.4 ± 3.2		0.1 ± 0.3	0.2 ± 0.4	0.3 ± 0.7	6.6 ±

							19.1
<i>Tachyporus hypnorum</i> (F., 1775)	348	3 ± 3.7	7.5 ± 4.1	1.2 ± 2	5.8 ± 5.8	6.9 ± 7.5	10.4 ± 9.7
<i>Tachyporus nitidulus</i> (F., 1781)	47					4.3 ± 9.1	0.4 ± 0.7
<i>Tachyporus obtusus</i> (L., 1767)	153	3.7 ± 7.6	3.3 ± 3.1	1.5 ± 3.8	3 ± 4.1	2.4 ± 3.9	1.4 ± 2.5
<i>Tachyporus pusillus</i> Grav., 1806	19	0.9 ± 2.8	0.4 ± 1	0.1 ± 0.3	0.5 ± 0.7		
<i>Tachyporus solutus</i> Er., 1839	1						0.1 ± 0.3
<i>Tachyporus transversalis</i> Grav., 1806	1		0.1 ± 0.3				
<i>Tychus niger</i> (Payk., 1800)	15	0.6 ± 1.3	0.1 ± 0.3			0.2 ± 0.4	0.6 ± 1.1
<i>Xantholinus dvoraki</i> Coiff., 1956	1						0.1 ± 0.3
<i>Xantholinus linearis</i> (Ol., 1795)	1					0.1 ± 0.3	
<i>Xantholinus longiventris</i> Heer, 1839	305	2.7 ± 2.1	3.8 ± 2.3	3.6 ± 4.5	3.9 ± 2.8	9 ± 10.4	7.5 ± 6
Carabidae							
<i>Abax parallelepipedus</i> (Pill. & Mitt., 1783)	15		0.1 ± 0.3	1.1 ± 3.1		0.1 ± 0.3	0.2 ± 0.6
<i>Acupalpus exiguus</i> (Dejean, 1829)	35	1.5 ± 3.4	0.2 ± 0.4		0.1 ± 0.3	1.2 ± 3.1	0.5 ± 0.8
<i>Acupalpus meridianus</i> (L., 1761)	41	1.8 ± 3.6	0.3 ± 0.9			1.5 ± 2.4	0.5 ± 1.3
<i>Agonum emarginatum</i> (Gyll., 1827)	40	2 ± 4.2	0.7 ± 1.9	1.1 ± 2.8	0.1 ± 0.3	0.1 ± 0.3	
<i>Agonum fuliginosum</i> (Panzer, 1809)	6	0.1 ± 0.3	0.5 ± 1.3				
<i>Agonum marginatum</i> (L., 1758)	1	0.1 ± 0.3					
<i>Agonum muelleri</i> (Herbst, 1784)	1429	45 ± 66.6	63.7 ± 104	10 ± 16.4	7.4 ± 11.4	11.8 ± 15.9	5 ± 10.1
<i>Agonum sexpunctatum</i> (L., 1758)	19		1 ± 2.8		0.7 ± 1.9	0.1 ± 0.3	0.1 ± 0.3
<i>Amara aenea</i> (De Geer, 1774)	148	3.2 ± 6.6	0.3 ± 0.5	2.8 ± 5.7	0.3 ± 0.7	8.1 ± 25.3	0.1 ± 0.3
<i>Amara apricaria</i> (Payk., 1790)	85	0.7 ± 1.3		1.2 ± 2	2.8 ± 8.9	3.5 ± 9.4	0.3 ± 0.7
<i>Amara aulica</i> (Panzer, 1796)	28	0.1 ± 0.3	0.2 ± 0.4	1.2 ± 2.2	0.2 ± 0.4	1 ± 2.8	0.1 ± 0.3
<i>Amara bifrons</i> (Gyll., 1810)	58	0.6 ± 1.9	0.1 ± 0.3	4.9 ± 13.2		0.2 ± 0.4	
<i>Amara familiaris</i> (Duft., 1812)	14			0.5 ± 1.1	0.2 ± 0.4	0.2 ± 0.4	0.5 ± 1.6
<i>Amara fulva</i> (Müller, 1776)	15	0.1 ± 0.3	0.6 ± 1.3	0.1 ± 0.3	0.5 ± 1.6	0.1 ± 0.3	0.1 ± 0.3
<i>Amara lunicollis</i> Schiodte, 1837	40	0.6 ± 1.6	2.1 ± 4	0.4 ± 1	0.3 ± 0.7	0.2 ± 0.6	0.4 ± 0.8
<i>Amara ovata</i> (F., 1792)	119	0.1 ± 0.3	1.1 ± 2.6	0.2 ± 0.6		10.3 ± 24	0.2 ± 0.4
<i>Amara plebeja</i> (Gyll., 1810)	351	10.4 ± 27.7	2 ± 3.2	7.4 ± 14.4	8.3 ± 23.1	1.3 ± 2.2	5.7 ± 12.9
<i>Amara similata</i> (Gyll., 1810)	42	0.2 ± 0.6	0.2 ± 0.4	1 ± 2.2	0.5 ± 1.3	2 ± 5.7	0.3 ± 0.5
<i>Amara spreta</i> Dejean, 1831	131	3.1 ± 6.5	0.4 ± 1	4.9 ± 13.8	1 ± 3.2	1 ± 2.3	2.7 ± 8.5
<i>Amara tibialis</i> (Payk., 1798)	2			0.2 ± 0.6			
<i>Anchomenus dorsalis</i> (Pont., 1763)	9234	84.1 ± 97.1	451.9 ± 687	85 ± 126.9	131.5 ± 116.5	64.4 ± 103.6	106.5 ± 136.3
<i>Anisodactylus binotatus</i> (F., 1787)	89	1.6 ± 3.3	0.6 ± 1	0.3 ± 0.9	4.4 ± 11.4	1 ± 1.9	1 ± 1.9
<i>Anisodactylus signatus</i> (Panzer, 1797)	2	0.1 ± 0.3		0.1 ± 0.3			
<i>Asaphidion curtum</i> (Heyden, 1870)	3		0.3 ± 0.7				
<i>Badister bullatus</i> (Schränk, 1798)	22	0.2 ± 0.4	0.6 ± 0.7	0.1 ± 0.3	0.1 ± 0.3		1.2 ± 1.9
<i>Badister dilatatus</i> Chaud., 1837	1		0.1 ± 0.3				
<i>Bembidion aeneum</i> Germar, 1824	1028	11.6 ± 22.2	34.7 ± 69.6	8.5 ± 17.9	17.1 ± 38.6	12.1 ± 19.7	18.8 ± 30.5
<i>Bembidion biguttatum</i> (F., 1779)	418	4.1 ± 7.9	2.9 ± 6.6	0.4 ± 1	5.3 ± 12.6	26.3 ± 58.2	2.8 ± 5.2
<i>Bembidion femoratum</i> Sturm, 1825	7				0.7 ± 2.2		
<i>Bembidion gilvipes</i> Sturm, 1825	17				0.8 ± 2.5		0.9 ± 2.8
<i>Bembidion lampros</i> (Herbst, 1784)	2616	109.3 ± 149.1	33.9 ± 48.5	39.5 ± 68.3	10.1 ± 11.4	47.7 ± 69.1	21.1 ± 28.8
<i>Bembidion mannerheimii</i> Sahlb., 1827	275	0.1 ± 0.3	3.6 ± 4.4	1.5 ± 2	1.6 ± 2.5	3.7 ± 7.4	17 ± 33.6
<i>Bembidion obtusum</i> Aud.-Serv., 1821	123	1.3 ± 2.1	1.3 ± 2.1	0.2 ± 0.6	0.6 ± 1.1	1.8 ± 2.9	7.1 ± 12.3
<i>Bembidion properans</i> (Steph., 1828)	334	24.2 ± 40.4	2.7 ± 4.2	2 ± 2.7	1.3 ± 1.6	2 ± 2.1	1.2 ± 1.5
<i>Bembidion quadrimaculatum</i> (L., 1761)	154	4.8 ± 7.8	0.4 ± 0.7	1.7 ± 3.4	4.9 ± 6.6	3.5 ± 5.2	0.1 ± 0.3
<i>Bembidion tetracolum</i> Say, 1823	3404	16.7 ± 24.8	52.2 ± 59.1	37.4 ± 49	107 ± 128.3	65.3 ± 86.9	61.8 ± 88.4
<i>Blemus discus</i> (F., 1792)	57	0.1 ± 0.3	1.1 ± 2	0.7 ± 1.6	3.6 ± 7.3	0.2 ± 0.6	
<i>Bradycellus harpalinus</i> (Aud.-Serv.,	5					0.4 ± 1	0.1 ± 0.3

1821)							
<i>Bradycellus verbasci</i> (Duft., 1812)	4	0.1 ± 0.3		0.1 ± 0.3		0.2 ± 0.6	
<i>Calathus cinctus</i> (Motsch., 1850)	47	0.6 ± 1.9	0.4 ± 1	0.8 ± 1.6	1.9 ± 5.7	0.3 ± 0.7	0.7 ± 1.6
<i>Calathus erratus</i> (Sahlb., 1827)	5					0.4 ± 1.3	0.1 ± 0.3
<i>Calathus fuscipes</i> (Goeze, 1777)	307	10.3 ± 28.2	1.9 ± 3	7.2 ± 19.1	1.2 ± 2.1	8.9 ± 24.8	1.2 ± 2.8
<i>Calathus melanocephalus</i> (L., 1758)	29	0.8 ± 1.6	0.6 ± 1.6	0.9 ± 2	0.2 ± 0.4	0.2 ± 0.6	0.2 ± 0.4
<i>Calosoma maderae</i> (F., 1775)	1						0.1 ± 0.3
<i>Carabus auratus</i> L., 1761	267	2.9 ± 9.2	16.6 ± 52.5	2.4 ± 7.2	1.9 ± 4.2	1.8 ± 5.7	1.1 ± 3.5
<i>Carabus convexus</i> F., 1775	4	0.1 ± 0.3	0.1 ± 0.3		0.1 ± 0.3		0.1 ± 0.3
<i>Carabus coriaceus</i> L., 1758	20			0.6 ± 1.6	0.8 ± 1.1	0.1 ± 0.3	0.5 ± 0.7
<i>Carabus granulatus</i> L., 1758	1364	19.1 ± 23.1	29.2 ± 42.9	23.1 ± 27	20.5 ± 42.9	23 ± 63.7	21.5 ± 43.8
<i>Carabus hortensis</i> L., 1758	2			0.1 ± 0.3		0.1 ± 0.3	
<i>Carabus nemoralis</i> Müller, 1764	26	0.4 ± 0.8	0.9 ± 1.7	0.6 ± 1.9		0.3 ± 0.9	0.4 ± 1.3
<i>Carabus violaceus</i> L., 1758	15	0.1 ± 0.3	0.1 ± 0.3	0.9 ± 2.5		0.3 ± 0.9	0.1 ± 0.3
<i>Chlaenius nigricornis</i> (F., 1787)	10	0.2 ± 0.4		0.4 ± 1.3		0.4 ± 1.3	
<i>Cicindela campestris</i> L., 1758	1					0.1 ± 0.3	
<i>Clivina fossor</i> (L., 1758)	510	5.2 ± 5.2	11.7 ± 13.5	3.7 ± 4.6	3.8 ± 5.6	11.9 ± 13.2	14.7 ± 14.2
<i>Cychrus caraboides</i> (L., 1758)	1				0.1 ± 0.3		
<i>Demetrias atricapillus</i> (L., 1758)	43	0.2 ± 0.4	0.8 ± 1		1.3 ± 2.4	0.2 ± 0.6	1.8 ± 4
<i>Dromius quadrimaculatus</i> (L., 1758)	1		0.1 ± 0.3				
<i>Dyschirius globosus</i> (Herbst, 1784)	115	0.2 ± 0.6	10.7 ± 32.8	0.4 ± 1.3		0.2 ± 0.4	
<i>Harpalus affinis</i> (Schränk, 1781)	988	27.1 ± 55.1	7.2 ± 11.6	16.4 ± 21.7	10.4 ± 12.2	35.4 ± 80.8	2.3 ± 5.2
<i>Harpalus distinguendus</i> (Duft., 1812)	1					0.1 ± 0.3	
<i>Harpalus griseus</i> (Panzer, 1796)	8			0.4 ± 1.3		0.4 ± 1.3	
<i>Harpalus latus</i> (L., 1758)	29	0.7 ± 1.9	0.2 ± 0.4	0.3 ± 0.7	0.7 ± 1.9	0.6 ± 0.8	0.4 ± 0.8
<i>Harpalus rubripes</i> (Duft., 1812)	54	1.3 ± 4.1		1.2 ± 2.8		2.9 ± 8.5	
<i>Harpalus rufipes</i> (De Geer, 1774)	2342	33.6 ± 80	16 ± 33.2	90.7 ± 88.4	27.5 ± 21.5	60.6 ± 100.4	5.8 ± 11.3
<i>Harpalus signaticornis</i> (Duft., 1812)	3		0.2 ± 0.6			0.1 ± 0.3	
<i>Harpalus smaragdinus</i> (Duft., 1812)	5			0.1 ± 0.3		0.4 ± 1.3	
<i>Harpalus tardus</i> (Panzer, 1796)	582	4.6 ± 13.2	4.2 ± 12.6	7.4 ± 22.4	0.6 ± 1.6	34.3 ± 107.4	7.1 ± 22.5
<i>Leistus ferrugineus</i> (L., 1758)	15		0.1 ± 0.3	0.2 ± 0.6	0.2 ± 0.4		1 ± 2.2
<i>Leistus fulvibarbis</i> Dejean, 1826	1						0.1 ± 0.3
<i>Leistus rufomarginatus</i> (Duft., 1812)	1	0.1 ± 0.3					
<i>Limodromus assimilis</i> (Payk., 1790)	233	1.1 ± 3.1	7.4 ± 14.8	0.3 ± 0.7	2.4 ± 6.6	0.8 ± 2.2	11.3 ± 32.3
<i>Loricera pilicornis</i> (F., 1775)	223	1.2 ± 2.3	8 ± 6.7	1.6 ± 3.5	3.2 ± 3	0.2 ± 0.6	8.1 ± 11.5
<i>Microlestes minutulus</i> (Goeze, 1777)	4				0.1 ± 0.3	0.3 ± 0.7	
<i>Nebria brevicollis</i> (F., 1792)	564	20.6 ± 39.9	8 ± 12.7	1.2 ± 2.3	9.6 ± 26.9	12.7 ± 34.1	4.3 ± 9
<i>Nebria salina</i> Fairm. & Lab., 1854	227	3.7 ± 8	0.1 ± 0.3	0.2 ± 0.4	7.7 ± 22.3	6.2 ± 9.5	4.8 ± 8.3
<i>Notiophilus biguttatus</i> (F., 1779)	101	1.8 ± 2.9	3.5 ± 4.3	1 ± 1.4	1.8 ± 2.7	0.4 ± 1	1.6 ± 2.1
<i>Notiophilus palustris</i> (Duft., 1812)	11		0.3 ± 0.7	0.3 ± 0.9	0.3 ± 0.9		0.2 ± 0.6
<i>Oodes helopioides</i> (F., 1792)	2	0.1 ± 0.3	0.1 ± 0.3				
<i>Ophonus laticollis</i> (Mannerh., 1825)	2			0.2 ± 0.6			
<i>Ophonus rufibarbis</i> (F., 1792)	8		0.1 ± 0.3	0.2 ± 0.4		0.2 ± 0.4	0.3 ± 0.5
<i>Oxypselaphus obscurus</i> (Herbst, 1784)	9		0.5 ± 1.6		0.1 ± 0.3		0.3 ± 0.5
<i>Panagaeus cruxmajor</i> (L., 1758)	4	0.1 ± 0.3		0.2 ± 0.6			0.1 ± 0.3
<i>Paradromius linearis</i> (Ol., 1795)	3			0.2 ± 0.6		0.1 ± 0.3	
<i>Patrobus atrorufus</i> (Ström, 1768)	9	0.6 ± 1.3	0.2 ± 0.4				0.1 ± 0.3
<i>Philorhizus melanocephalus</i> Dejean, 1825	1						0.1 ± 0.3
<i>Poecilus cupreus</i> (L., 1758)	10459	320.5 ± 655.1	155.5 ± 369.2	60.2 ± 127	164.4 ± 445.3	197.8 ± 237.5	147.5 ± 284.7
<i>Poecilus lepidus</i> (Leske, 1785)	1		0.1 ± 0.3				
<i>Poecilus versicolor</i> (Sturm, 1824)	959	18.1 ± 25.8	25.9 ± 38.8	9.9 ± 17	5.9 ± 12.4	20.6 ± 29.7	15.5 ± 28.2

<i>Pterostichus melanarius</i> (Ill., 1798)	14601	296.5 ± 759.5	201.2 ± 332.2	492 ± 1036.8	172.9 ± 258.6	181.9 ± 345.5	115.6 ± 219.8
<i>Pterostichus minor</i> (Gyll., 1827)	4		0.2 ± 0.4			0.2 ± 0.4	
<i>Pterostichus niger</i> (Schaller, 1783)	2026	20.8 ± 42	27.3 ± 44.4	45 ± 79	69.1 ± 143.4	29.9 ± 40.4	10.5 ± 9.5
<i>Pterostichus nigrita</i> (Payk., 1790)	85	1.2 ± 2.3		0.6 ± 0.7	0.1 ± 0.3	5.9 ± 15.6	0.7 ± 1.3
<i>Pterostichus strenuus</i> (Panzer, 1796)	561	5.9 ± 5.6	17.3 ± 16.5	2.4 ± 2.8	4.4 ± 7.7	9.9 ± 14.2	16.2 ± 13.7
<i>Pterostichus vernalis</i> (Panzer, 1796)	217	4.4 ± 6	3.3 ± 4.2	2.3 ± 2.3	2 ± 2.9	7 ± 14.3	2.7 ± 1.1
<i>Stomis pumicatus</i> (Panzer, 1796)	17	0.2 ± 0.4	0.3 ± 0.5	0.4 ± 1.3	0.4 ± 0.5	0.1 ± 0.3	0.3 ± 0.9
<i>Syntomus foveatus</i> (Geoffr., 1785)	306	11 ± 28.5	1.5 ± 3.4	5.4 ± 12.3	1.8 ± 3.8	9.6 ± 20.3	1.3 ± 3.8
<i>Syntomus truncatellus</i> (L., 1761)	10		0.2 ± 0.6	0.1 ± 0.3		0.2 ± 0.6	0.5 ± 1.6
<i>Synuchus vivalis</i> (Ill., 1798)	42	0.4 ± 0.5	0.1 ± 0.3	3.3 ± 6.9	0.2 ± 0.6	0.2 ± 0.6	
<i>Trechoblemus micros</i> (Herbst, 1784)	16	0.4 ± 1.3	0.4 ± 0.7		0.7 ± 1.9		0.1 ± 0.3
<i>Trechus quadristriatus</i> (Schränk, 1781)	280	1.4 ± 2.8	17.5 ± 41.3	1.6 ± 2.3	1.8 ± 2.7	1.1 ± 1.4	4.6 ± 8.9
<i>Trechus secalis</i> (Payk., 1790)	16		1.2 ± 3.8		0.4 ± 0.8		
Araneae							
<i>Agyneta cauta</i> (Cambr., 1902)	3					0.3 ± 0.7	
<i>Agyneta conigera</i> (Cambr., 1863)	10				0.1 ± 0.3	0.8 ± 2.5	0.1 ± 0.3
<i>Agyneta rurestris</i> (Koch, 1836)	76	0.6 ± 0.8	0.1 ± 0.3	0.3 ± 0.7	1 ± 1.2	2.4 ± 2.5	3.2 ± 3.5
<i>Agyneta saxatilis</i> (Blackw., 1844)	2				0.1 ± 0.3		0.1 ± 0.3
<i>Alopecosa pulverulenta</i> (Clerck, 1757)	11	0.3 ± 0.7	0.3 ± 0.5	0.4 ± 1		0.1 ± 0.3	
<i>Araeoncus humilis</i> (Blackw., 1841)	168	1.7 ± 4.7	1 ± 1.1	1.1 ± 2.2	2.2 ± 2.9	4.2 ± 6.6	6.6 ± 5.5
<i>Argenna subnigra</i> (Cambr., 1861)	1	0.1 ± 0.3					
<i>Bathyphantes approximatus</i> (Cambr., 1871)	10		0.4 ± 1	0.1 ± 0.3	0.2 ± 0.4		0.3 ± 0.5
<i>Bathyphantes gracilis</i> (Blackw., 1841)	928	10.2 ± 11.5	25 ± 25.4	9.8 ± 10	21.3 ± 26.1	1.8 ± 3.4	24.7 ± 25.3
<i>Bathyphantes nigrinus</i> (Westr., 1851)	4		0.1 ± 0.3			0.3 ± 0.7	
<i>Bathyphantes parvulus</i> (Westr., 1851)	43		0.1 ± 0.3		1 ± 2.5	1.1 ± 1.8	2.1 ± 6
<i>Centromerus dilutus</i> (Cambr., 1875)	4					0.4 ± 1.3	
<i>Centromerus sylvaticus</i> (Blackw., 1841)	1		0.1 ± 0.3				
<i>Clubiona lutescens</i> Westr., 1851	7		0.2 ± 0.6	0.1 ± 0.3	0.3 ± 0.7		0.1 ± 0.3
<i>Clubiona pallidula</i> (Clerck, 1757)	1				0.1 ± 0.3		
<i>Clubiona phragmitis</i> Koch, 1843	2				0.2 ± 0.6		
<i>Clubiona reclusa</i> Cambr., 1863	8		0.1 ± 0.3	0.2 ± 0.6	0.1 ± 0.3		0.4 ± 0.7
<i>Collinsia inerrans</i> (Cambr., 1885)	3			0.1 ± 0.3		0.1 ± 0.3	0.1 ± 0.3
<i>Cryptachaea riparia</i> (Blackw., 1834)	1			0.1 ± 0.3			
<i>Dicambium nigrum</i> (Blackw., 1834)	12	0.4 ± 0.5	0.3 ± 0.7	0.2 ± 0.4	0.3 ± 0.5		
<i>Dicymbium tibiale</i> (Blackw., 1836)	7	0.2 ± 0.4			0.3 ± 0.7		0.2 ± 0.4
<i>Diplocephalus cristatus</i> (Blackw., 1833)	1				0.1 ± 0.3		
<i>Diplocephalus picinus</i> (Blackw., 1841)	6	0.1 ± 0.3	0.3 ± 0.7		0.1 ± 0.3		0.1 ± 0.3
<i>Diplostyla concolor</i> (Wider, 1834)	176	0.1 ± 0.3	1.3 ± 1.2	1 ± 1.3	3.3 ± 6	1.8 ± 2.4	10.1 ± 12.3
<i>Dismodicus bifrons</i> (Blackw., 1841)	5	0.1 ± 0.3	0.2 ± 0.6	0.1 ± 0.3			0.1 ± 0.3
<i>Drassylus praeficus</i> (Koch, 1866)	1					0.1 ± 0.3	
<i>Drassylus pusillus</i> (Koch, 1833)	14	0.5 ± 1.3	0.1 ± 0.3	0.2 ± 0.6	0.2 ± 0.4		0.4 ± 0.5
<i>Enoplognatha thoracica</i> (Hahn, 1833)	3	0.2 ± 0.6	0.1 ± 0.3				
<i>Erigone arctica</i> (White, 1852)	37	0.8 ± 1.6	0.2 ± 0.6	0.2 ± 0.6	0.5 ± 1.6		2 ± 6
<i>Erigone atra</i> (Blackw., 1833)	4075	33.4 ± 47.1	41.9 ± 28.5	57.2 ± 75.5	71 ± 94.5	71.6 ± 74.4	132.4 ± 106.1
<i>Erigone dentipalpis</i> (Wider, 1834)	1201	15.4 ± 25.9	12.3 ± 16.1	16.5 ± 25.3	12.3 ± 19	36.9 ± 38.7	26.7 ± 40.8
<i>Erigonella hiemalis</i> (Blackw., 1841)	1		0.1 ± 0.3				
<i>Ero furcata</i> (Villers, 1789)	1			0.1 ± 0.3			
<i>Euophrys frontalis</i> (Walck., 1802)	2		0.1 ± 0.3				0.1 ± 0.3
<i>Gnathonarium dentatum</i> (Wider, 1834)	4	0.1 ± 0.3	0.2 ± 0.6				0.1 ± 0.3
<i>Gongylidiellum vivum</i> (Cambr., 1875)	2		0.1 ± 0.3				0.1 ± 0.3
<i>Gongylidium rufipes</i> (L., 1758)	1						0.1 ± 0.3

<i>Hahnia pusilla</i> (Koch, 1841)	1		0.1 ± 0.3				
<i>Hypomma bituberculatum</i> (Wider, 1834)	1					0.1 ± 0.3	
<i>Hypomma cornutum</i> (Blackw., 1833)	1				0.1 ± 0.3		
<i>Kaestneria dorsalis</i> (Wider, 1834)	2					0.2 ± 0.4	
<i>Leptorhoptrum robustum</i> (Westr., 1851)	13	0.2 ± 0.4	0.3 ± 0.7	0.1 ± 0.3	0.2 ± 0.4	0.3 ± 0.9	0.2 ± 0.6
<i>Linyphia hortensis</i> Sundev., 1830	4	0.1 ± 0.3		0.1 ± 0.3		0.2 ± 0.6	
<i>Lophomma punctatum</i> (Blackw., 1841)	1		0.1 ± 0.3				
<i>Maso sundevalli</i> (Westr., 1851)	6	0.1 ± 0.3		0.1 ± 0.3		0.3 ± 0.9	0.1 ± 0.3
<i>Mermessus trilobatus</i> (Emerton, 1882)	7			0.1 ± 0.3	0.3 ± 0.7		0.3 ± 0.5
<i>Micaria pulicaria</i> (Sundev., 1832)	25	0.5 ± 1	0.1 ± 0.3	0.3 ± 0.7	0.8 ± 1.3	0.7 ± 1.6	0.1 ± 0.3
<i>Micaria silesiaca</i> Koch, 1875	2					0.2 ± 0.6	
<i>Micaria subopaca</i> Westr., 1862	20		0.4 ± 0.5		0.6 ± 0.8	0.1 ± 0.3	0.9 ± 2
<i>Micrargus herbigradus</i> (Blackw., 1854)	14	0.1 ± 0.3			0.4 ± 0.7	0.3 ± 0.5	0.6 ± 1.3
<i>Microlinyphia pusilla</i> (Sundev., 1830)	2	0.1 ± 0.3		0.1 ± 0.3			
<i>Microneta viaria</i> (Blackw., 1841)	2		0.1 ± 0.3		0.1 ± 0.3		
<i>Neottiura bimaculatum</i> (L., 1767)	1					0.1 ± 0.3	
<i>Neriere clathrata</i> (Sundev., 1830)	2		0.1 ± 0.3				0.1 ± 0.3
<i>Oedothorax agrestis</i> (Blackw., 1853)	2					0.2 ± 0.6	
<i>Oedothorax apicatus</i> (Blackw., 1850)	2105	17.2 ± 24.6	23.6 ± 34.1	30.9 ± 55.2	34.7 ± 33	74.2 ± 95.6	29.9 ± 27.9
<i>Oedothorax fuscus</i> (Blackw., 1854)	367	6 ± 12.8	2.1 ± 2.8	5.6 ± 5.4	8.4 ± 12.3	9.2 ± 5.3	5.4 ± 5.9
<i>Oedothorax gibbosus</i> (Blackw., 1841)	6		0.2 ± 0.6			0.2 ± 0.4	0.2 ± 0.6
<i>Oedothorax retusus</i> (Westr., 1841)	182	1.8 ± 2.4	1.2 ± 1.3	3.7 ± 6.3	2.5 ± 6.2	7.5 ± 20.6	1.5 ± 1.7
<i>Ostearius melanopygius</i> (Cambr., 1879)	2		0.1 ± 0.3		0.1 ± 0.3		
<i>Ozyptila praticola</i> (Koch, 1837)	9		0.3 ± 0.7		0.1 ± 0.3		0.5 ± 1.1
<i>Ozyptila trux</i> (Blackw., 1846)	8	0.1 ± 0.3	0.1 ± 0.3				0.6 ± 1.3
<i>Pachygnatha clercki</i> Sundev., 1823	109	0.4 ± 0.7	2.2 ± 2.5	3.2 ± 7.8	3.2 ± 5.7		1.9 ± 3.6
<i>Pachygnatha degeeri</i> Sundev., 1830	241	4.3 ± 4.1	8 ± 13.9	2.9 ± 4.1	4.1 ± 4.5	1.6 ± 1.8	3.2 ± 6.7
<i>Paidiscura pallens</i> (Blackw., 1834)	1	0.1 ± 0.3					
<i>Palliduphantes ericaeus</i> (Blackw., 1853)	1						0.1 ± 0.3
<i>Palliduphantes pallidus</i> (Cambr., 1871)	12	0.1 ± 0.3	0.3 ± 0.7	0.2 ± 0.4			0.6 ± 1.1
<i>Pardosa agrestis</i> (Westr., 1862)	1444	51.9 ± 95	3.6 ± 10	18.4 ± 33	21.8 ± 55	40.4 ± 56.7	8.3 ± 21.5
<i>Pardosa agricola</i> (Thorell, 1856)	24					2.4 ± 5.3	
<i>Pardosa amentata</i> (Clerck, 1757)	702	10 ± 12.6	2.7 ± 1.9	24.5 ± 29.6	5 ± 4.6	25.4 ± 35	2.6 ± 2.8
<i>Pardosa lugubris</i> (Walck., 1802)	34		0.9 ± 2	0.3 ± 0.7	0.2 ± 0.4	0.1 ± 0.3	1.9 ± 6
<i>Pardosa monticola</i> (Clerck, 1757)	39					3.9 ± 7.7	
<i>Pardosa nigriceps</i> (Thorell, 1856)	2			0.2 ± 0.6			
<i>Pardosa palustris</i> (L., 1758)	688	10.5 ± 16.5	2.6 ± 5.2	3.3 ± 4	6.3 ± 7.9	33.2 ± 48.7	12.9 ± 29
<i>Pardosa prativaga</i> (Koch, 1870)	830	4.2 ± 6.8	4.1 ± 3.2	11.4 ± 15.6	7.5 ± 4.8	28.9 ± 28.9	26.9 ± 30.9
<i>Pardosa pullata</i> (Clerck, 1757)	63	0.3 ± 0.7		2.1 ± 6	0.1 ± 0.3	3.5 ± 4	0.3 ± 0.5
<i>Pardosa saltans</i> Toep-Hofm., 2000	13	0.1 ± 0.3	0.6 ± 1.1	0.3 ± 0.9	0.3 ± 0.9		
<i>Pelecopsis parallela</i> (Wider, 1834)	25		1 ± 2.5		0.2 ± 0.6		1.3 ± 2.8
<i>Pelecopsis radicularis</i> (Koch, 1872)	10	0.1 ± 0.3	0.4 ± 0.7				0.5 ± 1.6
<i>Philodromus dispar</i> Walck., 1826	1				0.1 ± 0.3		
<i>Phrurolithus festivus</i> (Koch, 1835)	1						0.1 ± 0.3
<i>Phylloneta impressa</i> (Koch, 1881)	1	0.1 ± 0.3					
<i>Pirata hygrophilus</i> Thorell, 1872	12	0.2 ± 0.4				0.2 ± 0.6	0.8 ± 2.2
<i>Pirata piraticus</i> (Clerck, 1757)	14	0.4 ± 0.8		0.1 ± 0.3	0.3 ± 0.7	0.2 ± 0.6	0.4 ± 0.7
<i>Pirata piscatorius</i> (Clerck, 1757)	1	0.1 ± 0.3					
<i>Pisaura mirabilis</i> (Clerck, 1757)	6			0.1 ± 0.3	0.2 ± 0.4		0.3 ± 0.5
<i>Pocadicnemis juncea</i> Lock. & Mill., 1953	11	0.2 ± 0.4	0.1 ± 0.3		0.4 ± 0.7		0.4 ± 0.7
<i>Pocadicnemis pumila</i> (Blackw., 1841)	12		0.1 ± 0.3	0.1 ± 0.3	0.2 ± 0.4		0.8 ± 2.2
<i>Porrhomma microptalmum</i> (Cambr., 1871)	163	4.8 ± 9.5	1.5 ± 2.3	1.3 ± 3.5	0.9 ± 1.3	2.7 ± 3.7	5.1 ± 6
<i>Porrhomma pygmaeum</i> (Blackw., 1834)	2	0.2 ± 0.6					
<i>Robertus lividus</i> (Blackw., 1836)	6	0.1 ± 0.3		0.1 ± 0.3	0.1 ± 0.3	0.3 ± 0.5	

<i>Saariotoa abnormis</i> (Blackw., 1841)	1			0.1 ± 0.3			
<i>Savignya frontata</i> (Blackw., 1833)	34		0.7 ± 1.6	0.1 ± 0.3	0.6 ± 1.9	0.4 ± 1	1.6 ± 3.1
<i>Segestria senoculata</i> (L., 1758)	2			0.1 ± 0.3	0.1 ± 0.3		
<i>Silometopus elegans</i> (Cambr., 1872)	1					0.1 ± 0.3	
<i>Stemonyphantes lineatus</i> (L., 1758)	3				0.2 ± 0.6		0.1 ± 0.3
<i>Tallusia experta</i> (Cambr., 1871)	1	0.1 ± 0.3					
<i>Tapinocyba pallens</i> (Cambr., 1873)	2					0.2 ± 0.4	
<i>Tegenaria silvestris</i> Koch, 1872	2				0.2 ± 0.6		
<i>Tenuiphantes tenuis</i> (Blackw., 1852)	458	6.3 ± 6.5	12.2 ± 16.6	2.1 ± 3.2	5.8 ± 4.7	3 ± 2.6	16.4 ± 7.8
<i>Tenuiphantes zimmermanni</i> (Bertkau, 1890)	1						0.1 ± 0.3
<i>Tetragnatha montana</i> Simon, 1874	1					0.1 ± 0.3	
<i>Tiso vagans</i> (Blackw., 1834)	13	0.2 ± 0.4	0.2 ± 0.4	0.3 ± 0.9		0.2 ± 0.4	0.4 ± 0.7
<i>Trochosa robusta</i> (Simon, 1876)	20					2 ± 2.8	
<i>Trochosa ruficola</i> (De Geer, 1778)	260	5.2 ± 6.3	2.7 ± 2.3	7.6 ± 9.9	4.8 ± 2.6	3.7 ± 4.6	2 ± 2.6
<i>Trochosa terricola</i> Thorell, 1856	31	0.3 ± 0.5	0.5 ± 0.8	0.7 ± 1.9	0.3 ± 0.7	1.3 ± 0.9	
<i>Troxochrus scabriculus</i> (Westr., 1851)	14	0.1 ± 0.3	1.2 ± 2.5				0.1 ± 0.3
<i>Walckenaeria acuminata</i> Blackw., 1833	1				0.1 ± 0.3		
<i>Walckenaeria atrotibialis</i> (Cambr., 1878)	16	0.1 ± 0.3	0.5 ± 1.1	0.2 ± 0.6	0.1 ± 0.3		0.7 ± 1.3
<i>Walckenaeria corniculans</i> (Cambr., 1875)	2						0.2 ± 0.6
<i>Walckenaeria dysderoides</i> (Wider, 1834)	3		0.1 ± 0.3				0.2 ± 0.4
<i>Walckenaeria nudipalpis</i> (Westr., 1851)	5		0.2 ± 0.6	0.1 ± 0.3			0.2 ± 0.4
<i>Walckenaeria unicornis</i> (Cambr., 1861)	3	0.1 ± 0.3	0.1 ± 0.3				0.1 ± 0.3
<i>Xerolycosa miniata</i> (Koch, 1834)	676	2.7 ± 8.5		4.5 ± 14.2	0.2 ± 0.6	60.2 ± 189.3	
<i>Xysticus cristatus</i> (Clerck, 1757)	20	1 ± 1.4		0.5 ± 0.7	0.1 ± 0.3	0.3 ± 0.5	0.1 ± 0.3
<i>Xysticus kochi</i> Thorell, 1872	34	1.7 ± 4.4	0.1 ± 0.3	0.1 ± 0.3	0.5 ± 1.3	0.8 ± 1.3	0.2 ± 0.4
<i>Xysticus ulmi</i> (Hahn, 1831)	2	0.1 ± 0.3				0.1 ± 0.3	
<i>Zelotes latreillei</i> (Simon, 1878)	1	0.1 ± 0.3					
<i>Zelotes longipes</i> (Koch, 1866)	3					0.3 ± 0.7	
<i>Zelotes petrensis</i> (Koch, 1839)	1					0.1 ± 0.3	
<i>Zelotes subterraneus</i> (Koch, 1833)	5				0.2 ± 0.4	0.3 ± 0.7	
<i>Zora spinimana</i> (Sundev., 1833)	5						0.5 ± 0.8

“Alles wissenschaftliche Arbeiten ist nichts
anderes als immer neuen Stoff in
allgemeine Gesetze zu bringen.”

ALEXANDER VON HUMBOLDT



CHAPTER 3

Sown wildflower areas increase the functional diversity of ground-dwelling arthropods in simple and complex landscapes across three years after their establishment

Hoffmann H | Diekötter T | Peter F

ABSTRACT

Agri-environmental schemes such as wildflower areas are aimed to support ecological intensification of agro-ecosystems through provisioning of ecosystem services, but their benefits are still controversially discussed. Studying functional traits, related to ecosystem services, instead of abundance and specie richness, may result in novel findings and help to improve the management and establishment of future wildflower areas.

To do so, we selected ten landscapes with paired wildflower areas and crop fields that encompassed independent gradients of proportions of permanent semi-natural habitats and transient wildflower areas and compared traits (body size, diet, flight ability) and the functional diversity of rove beetles, carabid beetles and spiders between the third and the first years after the establishment of wildflower areas in both habitats.

Rove beetles became smaller and showed a higher functional diversity in wildflower areas after three years. In contrast, carabid beetles in wildflower areas became larger and showed a higher proportion of herbivorous ones, whereas spiders showed a higher proportion of active hunters after three years. The change of traits to landscape context largely seemed to have affected ground-dwelling arthropods in wildflower areas and show a hump-shaped pattern in relation to permanent semi-natural habitats and a linear response in relation to transient wildflower areas. Moreover, the diet in crop fields and the functional diversity in wildflower areas of carabid beetles were interactively affected by these two habitat types and traits of spiders in crop fields were unaffected by landscape context.

Although responses of arthropods differed between taxa and landscape context, the establishment of wildflower areas in simple landscapes seem to be most beneficial to increase their functional diversity. The sum of at least 4-6% of both transient wildflower areas and permanent semi-natural habitats may provide ample resources for a wide range of arthropods and enhance spillover effects due to a better connectivity. In addition, interactive effects of both source habitats indicate that wildflower areas can also increase the functional diversity in cleared landscapes, but only if implemented at high proportions.

To conclude, transient wildflower areas and permanent semi-natural habitats seem to complement each other. Hence, the protection of remaining semi-natural habitats as well as to target specific landscape situations when establishing new wildflower areas in order reach the 10-15% threshold of semi-natural habitats in agro-ecosystems, should be given the highest priority to enhance the agro-biodiversity and their associated ecosystem services.

Manuscript in preparation

INTRODUCTION

Agri-environmental schemes (AES) aim at mitigating the negative impacts of agricultural intensification. Yet, their benefits are still controversially discussed (Haaland et al., 2011). In contrast to many other studies, here we focus on functional traits rather than solely considering abundance and species richness, in order to advance our understanding of the mechanisms underlying the efficacy of AES. Particularly, we studied the change of functional traits of ground-dwelling arthropods across three years after the establishment of wildflower areas along independent gradients of transient and permanent semi-natural habitats in the surrounding landscape.

Land-use change has resulted in an enormous loss not only of abundance and species richness but also the functional diversity of e.g. of pollinators and insect-pollinated plants (Biesmeijer et al., 2006) or arthropods in general (Lichtenberg et al., 2017). Along with this loss may go a reduced agricultural productivity through lower ecosystem services provisioning by e.g. pollinators and natural enemies (Foley et al., 2005). AES are thought to counteract this biodiversity loss (Haaland et al., 2011). Yet, their implementation, such as the sowing of wildflower areas, resulted in inconsistent effects on biodiversity or only affected specific components of biodiversity. Because functional diversity has recently been shown to describe the contribution to ecosystem services better than species richness (Gallé & Batáry, 2019) and also to sensibly respond to land-use change (Gallé et al., 2020), its study may lead to new insights that help to improve the efficacy of future AES.

The functional diversity of communities expresses its composition of traits (Petchey & Gaston, 2006). Traits are attributes of individuals or species that are linked to their short-term performance or their long-term fitness and include morphological, ecological, physiological or life-history characteristics (Violle et al., 2007). In response to environmental change, particular traits may be lost from a local community ('response traits', Lavorel & Garnier, 2002). This loss, in turn, may then affect ecosystem functions ('effect traits', Lavorel & Garnier, 2002). In wildflower areas, for example, carabid beetle communities shifted from small carnivorous in newly established areas towards larger proportions of medium-sized herbivorous species within the first year of their existence through changes in vegetation structure (Baulechner et al., 2019). The body size distribution in arthropod communities in agricultural landscapes has also been shown to strongly depend on landscape structure (Schweiger et al., 2005) as has the body size distribution in single taxa. *Harpalus affinis*, for instance, increased in body size when crop fields were surrounded by high proportions of

organically managed land (Diekötter et al., 2016). Since predator body size, in turn, is among the best predictors of predation rates (Rusch et al., 2015), also the ecosystem service of conservation biological may change with landscape structure.

The efficacy of AES, such as wildflower areas, in benefitting biodiversity has been shown to be highest in simple landscapes with intermediate structural complexity as compared to cleared or complex landscapes (Scheper et al., 2013; Tschardt et al., 2012). Very recent studies suggest, however, that this landscape dependency of the functioning of wildflower areas might be even more complex as different types of semi-natural habitats seem to affect their benefits differently (Hoffmann et al., submitted). While permanent semi-natural habitats showed a hump-shaped relationship with abundance and species richness, these diversity components were linearly related to transient semi-natural habitats. Accordingly, wildflower areas may enfold benefits for biodiversity even in cleared landscapes, but only if established in high proportions (Boetzel et al., 2021; Hoffmann et al., submitted).

As newly established wildflower areas may alter ground-dwelling arthropods and their trait composition in dependence of the landscape context, also land-use types adjacent to wildflowers areas may be affected by these changes. Large carabid beetles, for instance, are more mobile than small ones and may disperse further into the crop fields from adjacent habitats where they exert a controlling effect on weed and insect pest species (Boetzel et al., 2018; Gallé et al., 2019). Moreover, spider body size decreased, ballooning ability increased and hunting strategy changed from active hunters to more web-builders from the field edges towards crop field centres (Gallé et al., 2020). This may affect ecological functioning as active hunting spiders have been shown to utilize less mobile prey, while web-building spiders were more effective in capturing mobile prey (Michalko et al., 2019). While spillover from natural to agricultural habitats has frequently been studied with regard to abundance, richness or potential impact of insect natural enemies (e.g. Boetzel et al., 2018), trait-based multi-taxa studies across several years are still scarce.

Here, we compared selected traits and the functional diversity of ground-dwelling arthropod communities in wildflower areas and adjacent crop fields between the first and the third year after the establishment of wildflower areas in dependence of the landscape proportions of permanent semi-natural habitats (e.g. hedgerows, ditches) and transient wildflower areas. As the studied taxa of rove beetles, carabid beetles and spiders are essential for conservation biological control, e.g. of aphids (Balog et al., 2013) or slugs (Fusser et al., 2017), new insights into the landscape dependency of wildflower areas in affecting the trait

diversity of ground-dwelling arthropods are thought to improve the future contribution of this AES to multifunctional agroecosystems.

MATERIAL & METHODS

STUDY AREA

We studied benefits of sown wildflower areas in 2017 and 2019 in the federal state of Schleswig-Holstein, Northern Germany. The whole study region is characterised by intensive agriculture and warm temperate climate (Kottek et al., 2006) with annual mean temperatures of 8.4 °C and annual mean precipitation of 770 mm (Fick & Hijmans, 2017). Under a regional agri-environment scheme to promote the Grey Partridge (*Perdix perdix*), wildflower areas were established on arable land by sowing a regional weed mix (Appendix A). The scheme did not allow any agricultural management (e.g. use of insecticides and pesticides), but required resowing of fields twice within the contracted five-year period (2016-2021) between 1st April and 15th May.

We selected ten wildflower areas along independent gradients in the proportions of permanent semi-natural habitats and transient wildflower areas in the surrounding landscape (Pearson correlation = -0.02, $p = 0.963$, Appendix B). We quantified habitat proportions at a radius of 750 m around the centres of the focal wildflower areas, since this spatial scale has previously been identified as highly relevant for inter-patch dispersal of ground-dwelling arthropods (Martin et al., 2019). We defined permanent semi-natural habitats as hedgerows, single trees, tree rows, forest patches smaller than 2000 m², field margins, drainage ditches, ponds, kettle holes and further wetlands larger than 2000 m² and near-natural stonewalls. These landscape elements are effectively used by arthropods or provide edge habitats (ecotones) which may increase habitat availability and connectivity (Brandmayr et al., 1998).

Proportions of permanent semi-natural habitats ranged from 0% to 7% ($4\% \pm 2\%$, mean \pm SD, hereafter; Table 1) while proportions of transient wildflower areas ranged from 0% to 14% ($5\% \pm 5\%$; Table 1; cf. Rega et al., 2018). While we used the proportions of permanent semi-natural habitats and transient wildflower areas as continuous predictors for our regression analyses, we decided to apply the concept of intermediate landscape-complexity (Tschamntke et al., 2012) for the interpretation and discussion of our results in context with previous studies. We defined cleared, simple and complex landscapes but intentionally differentiated between permanent semi-natural habitats and transient wildflower areas, which leads to a range shift in proportions for the three categories. Hence, cleared, simple and complex landscapes were characterized by comparably low, intermediate and high

proportions of permanent semi-natural habitats ($> 0.1\%$; $2\% - 5\%$; $< 7\%$) and transient wildflower areas ($> 0.4\%$; $4\% - 10\%$; $< 14.2\%$). In addition to each wildflower area, we selected a winter crop field to assess differences in biodiversity patterns between these two habitat types and capture habitat-specific shifts across three consecutive years. Winter crop fields were selected as close as possible to the focal wildflower areas ($0\text{ m} - 335\text{ m}$, $102\text{ m} \pm 122\text{ m}$; Table 1). Due to crop rotation on the selected winter crop fields, we had to switch to another winter crop field during the study period in order to maintain the comparison with winter crop management and to minimize the distance within each pair of wildflower area and winter crop field. Winter crop fields constitute one of the main crops in Northern Germany and are characterized by homogeneous management and vegetation structure.

Landscape analyses were done using ArcGIS 10 (ESRI, CA, USA).

Table 1. Proportions of permanent semi-natural habitats (*Perma*) and transient wildflower areas (*Trans*), patch size of the focal wildflower areas (*WA*) as well as the distance to the closest crop fields of the ten study sites in Northern Germany.

Site ID	Perma [%]	Trans [%]	Patch size of WA [ha]	Distance to crop fields [m]	
				2017	2019
Barkau	5.2	3.9	4.2	10	10
Gross Rheide	4.4	6.8	7.9	285	335
Kesdorf	7.0	14.2	3.2	20	20
Langenhorn	0.3	13.5	1.0	305	250
Neumuenster	2.1	0.6	0.5	0	0
Nordstrand	1.2	0.4	0.6	195	10
Pohnsdorf	5.3	0.7	1.3	0	0
Riepsdorf	3.2	6.6	5.0	20	20
Roenne	6.9	0.4	0.2	220	170
Suederluegum	1.6	4.6	7.9	150	10

SAMPLING OF GROUND-DWELLING ARTHROPODS

Ground-dwelling arthropods were sampled with pitfall traps in 2017 and 2019 by starting one week after 15th May (latest possibility of resowing of the wildflower areas by landowners) in the selected wildflower areas and crop fields, respectively. Three traps were placed at 10 m distance and parallel from one of the field borders (e.g. Boetzel et al., 2019) and with an inter-trap distance of 10 m. We emptied traps biweekly four times until middle of July concomitant before the harvest of winter crop fields (resulting in 480 pitfall capture dates in total). Every trap consisted of a 500 ml plastic cup filled with 150 ml water, 50 ml ethylene-glycol and a drop of detergent solution. Wire nets (mesh size: 31 mm) in the cups prevented unintended by-catch, i.e. of small vertebrates and transparent plastic roofs above the traps protected them from rain and litter.

All arthropods were stored in 70% ethanol before species identification following Besuchet (1974) and Assing and Schülke (2012) for rove beetles (within subfamily Aleocharinae only the genera *Aleochara*, *Cordalia*, *Drusilla*, *Falagrioma*, *Ilyobates* and *Oligota*), Müller-Motzfeld (2004) for carabid beetles and Roberts (1987, 1996), Almquist (2005, 2006) and Nentwig et al. (2018) for spiders. Abundance and species richness of rove beetles, carabid beetles or spiders were calculated by adding up all samples per pitfall trap across the four sampling rounds per year resulting in a nested design of three observations per habitat type, study site and year ($n = 30$).

ECOLOGICAL TRAITS OF GROUND-DWELLING ARTHROPODS

We selected two ecological traits for each ground-dwelling arthropod group (body size and diet) and used flight ability as additional trait for carabid beetles, respectively. We defined body size as the mean body size of each species based on Homburg et al. (2014) resulting in a continuous variable. Diet was coded as follows: (i) rove beetles: 0 = herbivore (including fungivore and detritivore), 1 = carnivore; (ii) carabid beetles: 0 = herbivore, 0.5 = omnivore, 1 = carnivore; (iii) spiders: 0 = web-builder, 1 = active hunter. Flight ability of carabid beetles was coded as follows: 0 = short-winged/wingless, 0.5 = dimorphic, 1 = winged. We derived the trait classification for rove beetles on information from Assing and Schülke (2012), Freude et al. (1974) and Koch (1989), for carabid species on Homburg et al. (2014) and for spiders on Nentwig et al. (2018).

For each trait, we calculated a community weighted mean value (CWM) per habitat type and study site. CWMs represent the average of a trait's value weighted by the relative abundances of each species. Furthermore, we calculated functional dispersion (FDis; 'FDisp' from the 'FD' package (Laliberté & Shipley, 2010)), which is a metric of functional structure, which considers species relative abundances by estimating their dispersion in a multidimensional trait space and may be interpreted as functional diversity per se (Laliberté & Legendre, 2010).

STATISTICAL ANALYSES

First, in order to evaluate differences of CWMs and FDis of arthropod communities between the two studied years (2017 and 2019) per habitat (wildflower area or crop field), we used generalized mixed-effects models (GLMM; 'GLMMPQL' from the 'MASS' package (Wood, 2019)). The site and the habitat were regarded as a random factor. The residuals were assumed to follow a Poisson distribution. Based on these models, an analysis of variances

(‘ANOVA’ type III from the ‘CAR’ package (Fox & Weisberg, 2019)) was conducted, followed by multiple contrast tests (‘GLHT’ from the ‘MULTCOMP’ package (Hothorn et al., 2008)).

Secondly, to study the additive and interactive effects of proportions of permanent semi-natural habitats and transient wildflower areas on the change of traits between the first and the third year, we calculated the ratios of CWM and the FDis by dividing the values from 2019 by 2017. To do so, we used generalized mixed-effects models, separately for the two habitat types. Study site was regarded as a random factor. The residuals were assumed to follow a Gamma distribution. To account for the hypothesized non-linear, hump-shaped relationship between arthropods and landscape context, the model defines a quadratic relation of the y-values depending on the covariates (Bolker, 2008). Additionally, we included a linear interaction term for both covariates. Afterwards, we performed a manual stepwise backwards elimination of non-significant predictors in order to find the most appropriate final model. Finally, if both the linear and quadratic term of the same variable were significant, we focused on the presentation and discussion of the effect with the lowest p-value. Based on all final models, we calculated the marginal and conditional R^2 including both fixed and random effects (‘RSQUARED’ from the ‘PIECEWISESEM’ package (Lefcheck, 2016)).

We did all statistical analyses using R 4.0 for Windows (R Development Core Team, 2019).

RESULTS

In total, we captured 61,833 ground-dwelling arthropods from 304 species (Appendix C), with individuals largely being dominated by carabid beetles (65%, 97 species), followed by spiders (18%, 110 species) and rove beetles (17%, 97 species).

Overall, changes of the CWM of traits and the FDis of ground-dwelling arthropods differed between the three groups and were in particular affected in wildflower areas. Here, responses to proportions of permanent semi-natural habitats seemed to follow an inverse hump-shape pattern with lowest values in simple landscapes with intermediate proportions of permanent semi-natural habitats, whereas proportions of transient wildflower areas mainly seemed to follow a linear increase.

ROVE BEETLES

Across all samples, body size of rove beetles ranged from 1.2 mm to 14.0 mm ($5.1 \text{ mm} \pm 2.8 \text{ mm}$) and 64% were carnivorous. From the first to the third year, average body size of rove beetles decreased by 0.7 mm and 1.0 mm in wildflower areas and crop fields, respectively,

(Table 2, Fig. 1 A). The proportions of herbivorous rove beetles in crop fields increased by 1.2 times from the first to the third year, as did the functional diversity of rove beetles in wildflower areas (Table 2, Fig. 1 B-C).

Body size of rove beetles in wildflower areas only increased in intermediate and complex landscapes with at least 6% of permanent semi-natural habitats or 7% of transient wildflower areas (Table 3, Fig. 2 A+B). The proportions of carnivorous rove beetles in wildflower areas increased in landscapes with more than 4% of permanent or transient semi-natural habitats over time, whereas in landscapes below these proportions of semi-natural habitats herbivorous rove beetles increased (Table 3, Fig. 2 C+D). Traits of rove beetles in crop fields were unaffected by landscape context, except a marginal response to transient wildflower areas with increasing proportions of herbivorous rove beetles in complex landscapes (Table 3, Fig. 2 D).

Table 2. Differences of the community weighted mean values (CWM) of the selected traits and the functional diversity (FDis) of rove beetles, carabid beetles and spiders between the two studied years (2019 ~ 2017) for wildflower areas (WA) and crop fields (CF). Degrees of freedom (DF), *t*-value (T), *P*-value (P) and the marginal (R^2_m) and conditional R^2 (R^2_c) are given for the most parsimonious model. Significant results are given in bold.

Taxa	Trait	Habitat	DF	T	P	R^2_m	R^2_c
Rove beetles	Size	WA	1	-3.26	0.003	0.14	0.50
		CF	1	-4.66	<0.001		
	Diet	WA	1	-2.18	0.063	0.15	0.38
		CF	1	-2.36	0.040		
	FDis	WA	1	2.40	0.036	0.05	0.33
		CF	1	1.41	0.295		
Carabid beetles	Size	WA	1	2.53	0.026	0.05	0.63
		CF	1	-0.69	0.739		
	Diet	WA	1	-2.91	0.009	0.18	0.68
		CF	1	-1.56	0.229		
	Flight ability	WA	1	-1.23	0.393	0.05	0.56
		CF	1	-3.01	0.007		
	FDis	WA	1	1.79	0.146	0.21	0.43
		CF	1	4.23	<0.001		
Spiders	Size	WA	1	-2.00	0.094	0.27	0.56
		CF	1	0.20	0.975		
	Diet	WA	1	-1.99	0.096	0.28	0.68
		CF	1	2.76	0.014		
	FDis	WA	1	0.72	0.722	0.07	0.33
		CF	1	1.61	0.210		

CARABID BEETLES

Body size of carabid beetle species ranged from 2.0 mm to 37.0 mm ($8.7 \text{ mm} \pm 6.2 \text{ mm}$), 71% of carabid beetle species were carnivorous and 55% belonged to winged species. Carabid beetles in wildflower areas were on average 0.8 mm larger and showed a 1.1 times higher proportion of herbivorous species in the third as compared to the first year (Table 2, Fig. 1 D-E). In crop fields, the proportion of wingless species increased by 1.1 and functional diversity by 1.3 times from the first to the third year (Table 2, Fig. 1 F-G).

The ratio of CWM of flight ability of carabid beetles in wildflower areas showed a hump-shaped pattern with the proportions of permanent semi-natural habitats and a linear response to transient ones. In complex landscapes, the proportions of winged carabid beetles increased over the three years, whereas in cleared and simple landscapes wingless ones increased (Table 3, Fig. 2 E). High proportions of transient wildflower areas led to an increase in winged carabid beetles over time, while in landscapes with proportions of transient wildflower areas of 7% and less, wingless ones increased (Table 3, Fig. 2 F). From the first to the third year, the FDis of carabid beetles in crop fields increased and was positively related with the proportions of transient wildflower areas and increased twice as much in complex than in cleared landscapes (Table 3, Fig. 2 G). Changes in the trophic group assemblage of carabid beetle communities in crop fields was interactively affected by the proportions of permanent semi-natural habitats and transient wildflower areas as were changes from year one to year three in the FDis of carabid beetles in wildflower areas (Table 3, Fig. 3). More precisely, the proportions of carnivorous carabid beetles in crop fields decreased over time in landscapes with intermediate proportions of permanent semi-natural landscapes whereas it increased in cleared or complex landscapes with low proportions of transient wildflower areas and even more so in complex landscapes with high proportions of transient wildflower areas (Fig. 3 A). In contrast, proportions of carnivorous carabid beetles increased in simple landscapes with regard to transient wildflower areas. This increase was stronger in landscapes with high proportions of permanent semi-natural habitats. In landscapes with proportions of transient wildflower areas higher than 9%, communities shifted towards herbivorous species over time when proportions of permanent semi-natural habitats were low (Fig. 3 B). The FDis of carabid communities in wildflower areas increased with permanent semi-natural habitats over time only when proportions of transient wildflower areas were low (Fig. 3 C). When permanent semi-natural habitats were low, the FDis in carabid communities in wildflower areas increased with increasing proportions of transient wildflower areas over time, whereas it decreased when semi-natural habitats were high (Fig. 3 D).

SPIDERS

Body size of spiders ranged from 1.4 mm to 13.5 mm ($3.9 \text{ mm} \pm 2.4 \text{ mm}$) and 35% of spider species were active hunters. While body sizes of spiders did not change over time in wildflower areas or crop fields (Fig. 1 H), spiders in crop fields showed a 1.6 times higher proportion of web-building species after three years, but did not change in their community composition with regard to hunting mode in wildflower areas (Table 2, Fig. 1 I). The FDis in spider communities did not change over time in wildflower areas or crop fields (Fig. 1 J).

Over time, spider communities in wildflower areas showed higher proportions of small species in cleared and simple landscapes, whereas larger species became more dominant in landscapes with 7 or more percent of transient wildflower areas (Table 3, Fig. 2 H). Spider communities of wildflower areas in simple and complex landscapes with intermediate and high proportions of transient wildflower areas showed higher proportions of active hunters over time, while in landscapes with lower proportions of transient wildflower areas web-building species became more dominant (Table 3, Fig. 2 I). Body size and diet increased only in landscapes with at least 6% (for body size) and 3% (for diet) of transient wildflower areas (Fig. 2 H+I), respectively. The ratio of the FDis showed a hump-shaped pattern with the proportions of transient wildflower areas, i.e. the FDis increased over time in simple landscapes but by trend decreased in cleared landscapes and largely stayed the same in complex landscapes (Fig. 2 J). In crop fields, the ratio of traits and the FDis of spiders were unaffected by landscape context across the three years.

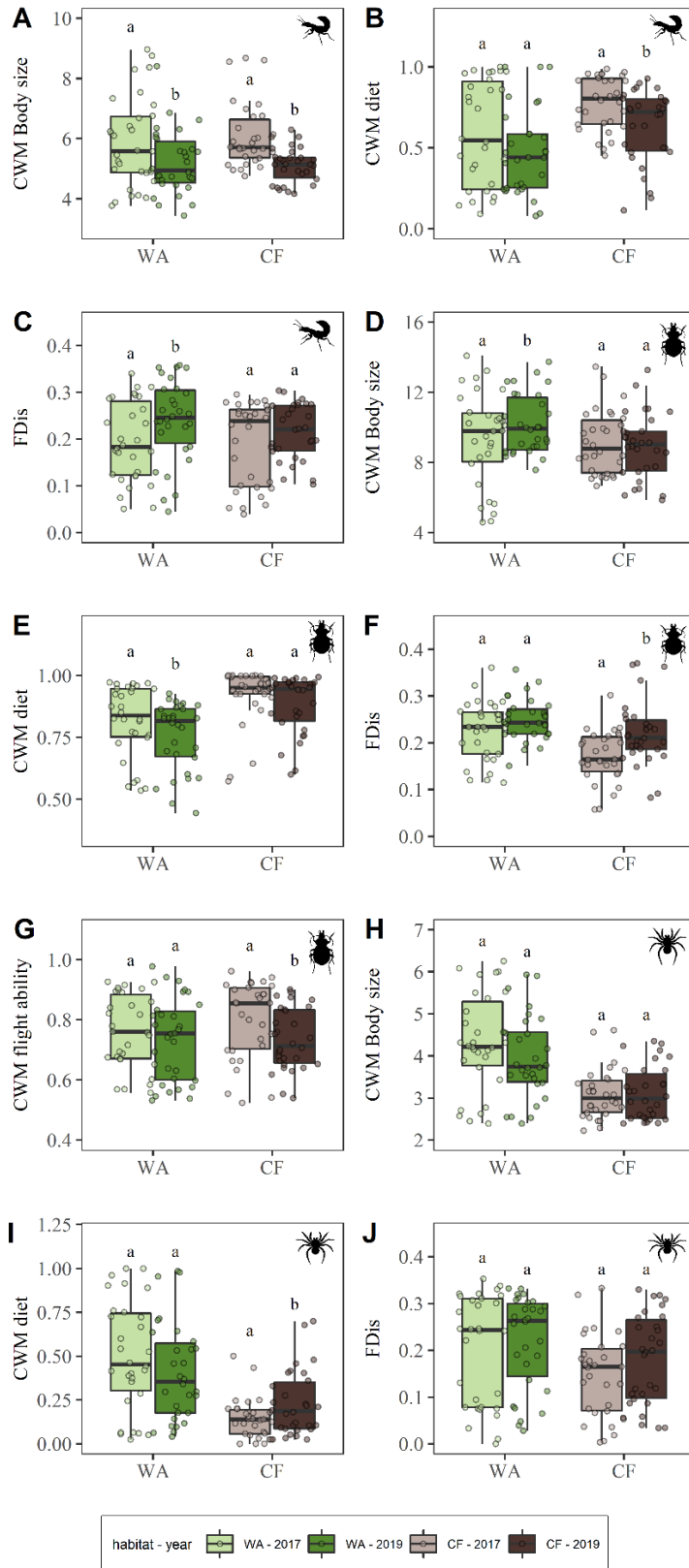


Figure 1. Differences between the two studied years (2019 ~ 2017) per habitat type (wildflower area = WA, crop field = CF) on the community weighted mean values (CWM) of body size, diet (0 = herbivore/web-builder, 0.5 = omnivore, 1 = carnivore/active hunter) and flight ability (0 = short-winged/wingless, 0.5 = dimorphic, 1 = winged) as well as the functional diversity (FDIs) of rove beetles (A-D), carabid beetles (E-F) and spiders (G-H). Boxplots show raw data and letters indicate significant differences between years per habitat type.

Table 3. Effects of proportions of permanent semi-natural habitats (Perma) and transient wildflower areas (Trans) on the ratio of the community weighted mean values (CWM) of the selected traits and the functional diversity (FDis) between the two studied years (2019 ~ 2017) of rove beetles, carabid beetles and spiders, separately for wildflower areas (WA) and crop fields (CF). Degrees of freedom (DF), t-value (T), P-value (P), and the marginal (R^2_m) and conditional R^2 (R^2_c) are given for the most parsimonious model. Significant results are given in bold.

Taxa	Trait	Habitat	Explanatory	DF	T	P	R^2_m	R^2_c
Rove beetles	Size	WA	Perma [x^2]	7	4.19	0.004	0.64	0.69
			Trans [x]	7	4.09	0.005		
		CF	Perma [x]	8	-1.68	0.132	0.18	0.65
	Diet	WA	Perma [x^2]	6	5.97	0.001	0.86	0.92
			Trans [x]	6	4.56	0.004		
			Trans [x^2]	6	-2.90	0.027		
		CF	Trans [x^2]	8	-3.50	0.008	0.31	0.31
		WA	Trans [x]	8	-1.76	0.117	0.21	0.72
		CF	Perma [x^2]	8	2.24	0.055	0.27	0.64
Carabid beetles	Size	WA	Trans [x^2]	8	1.97	0.084	0.24	0.68
		CF	Trans [x]	8	0.81	0.441	0.06	0.73
	Diet	WA	Perma [x]	8	-1.39	0.203	0.16	0.85
			Perma [x]	4	-3.37	0.020		
			Perma [x^2]	4	4.01	0.016		
		CF	Trans [x]	4	3.85	0.018	0.81	0.81
			Trans [x^2]	4	-6.15	0.004		
			Perma:Trans	4	5.05	0.007		
	Flight ability	WA	Perma [x^2]	7	4.07	0.005	0.77	0.80
			Trans [x]	7	6.66	<0.001		
		CF	Perma [x]	8	-0.90	0.394	0.08	0.93
	FDis	WA	Perma [x]	5	4.47	0.007	0.55	0.55
			Perma [x^2]	5	-3.54	0.017		
			Trans [x]	5	3.09	0.027		
			Perma:Trans	5	-3.92	0.011		
		CF	Trans [x]	8	2.43	0.041	0.35	0.82
Spiders	Size	WA	Trans [x]	8	4.33	0.003	0.61	0.85
		CF	Perma [x]	8	-1.16	0.280	0.09	0.56
	Diet	WA	Trans [x]	7	3.57	0.009	0.65	0.85
			Trans [x^2]	7	-2.56	0.038		
	FDis	CF	Perma [x]	8	-0.50	0.631	0.02	0.67
		WA	Trans [x^2]	8	-2.35	0.047	0.17	0.17
		CF	Trans [x]	8	-1.80	0.109	0.11	0.11

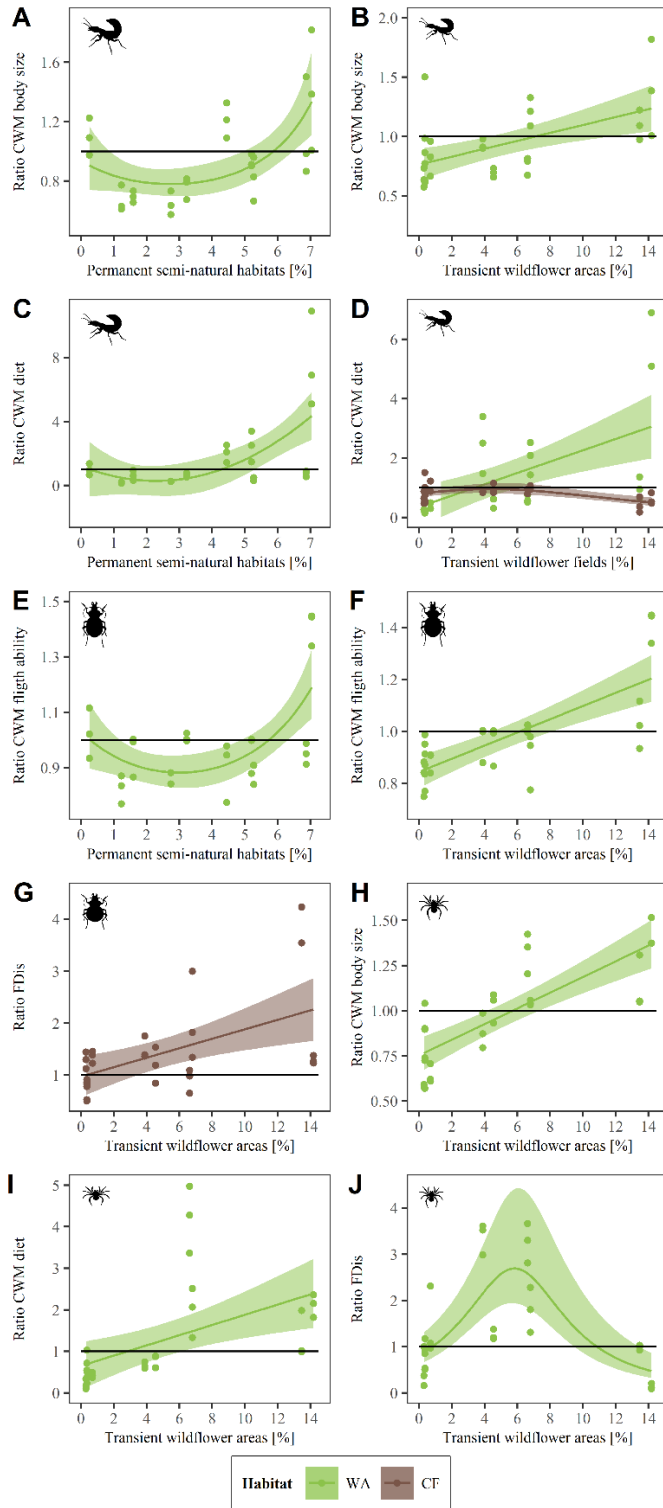


Figure 2. Effects of the proportions of permanent semi-natural habitats and transient wildflower areas on the ratio of the community weighted mean values (CWM) of body size, diet and flight ability as well as the functional diversity (FDis) of rove beetles (A-D), carabid beetles (E-G) and spiders (H-J) between the two studied years (2019 ~ 2017), separately for wildflower areas (WA) and crop fields (CF). Points represent raw data, coloured lines and shaded areas represent the model fit and 95% confidence intervals, respectively. The black lines represent the border between an increase (larger, more carnivore/active hunting and winged arthropods) and a decrease (smaller, more herbivore/web-building and wingless arthropods) of traits and FDis over three years, respectively.

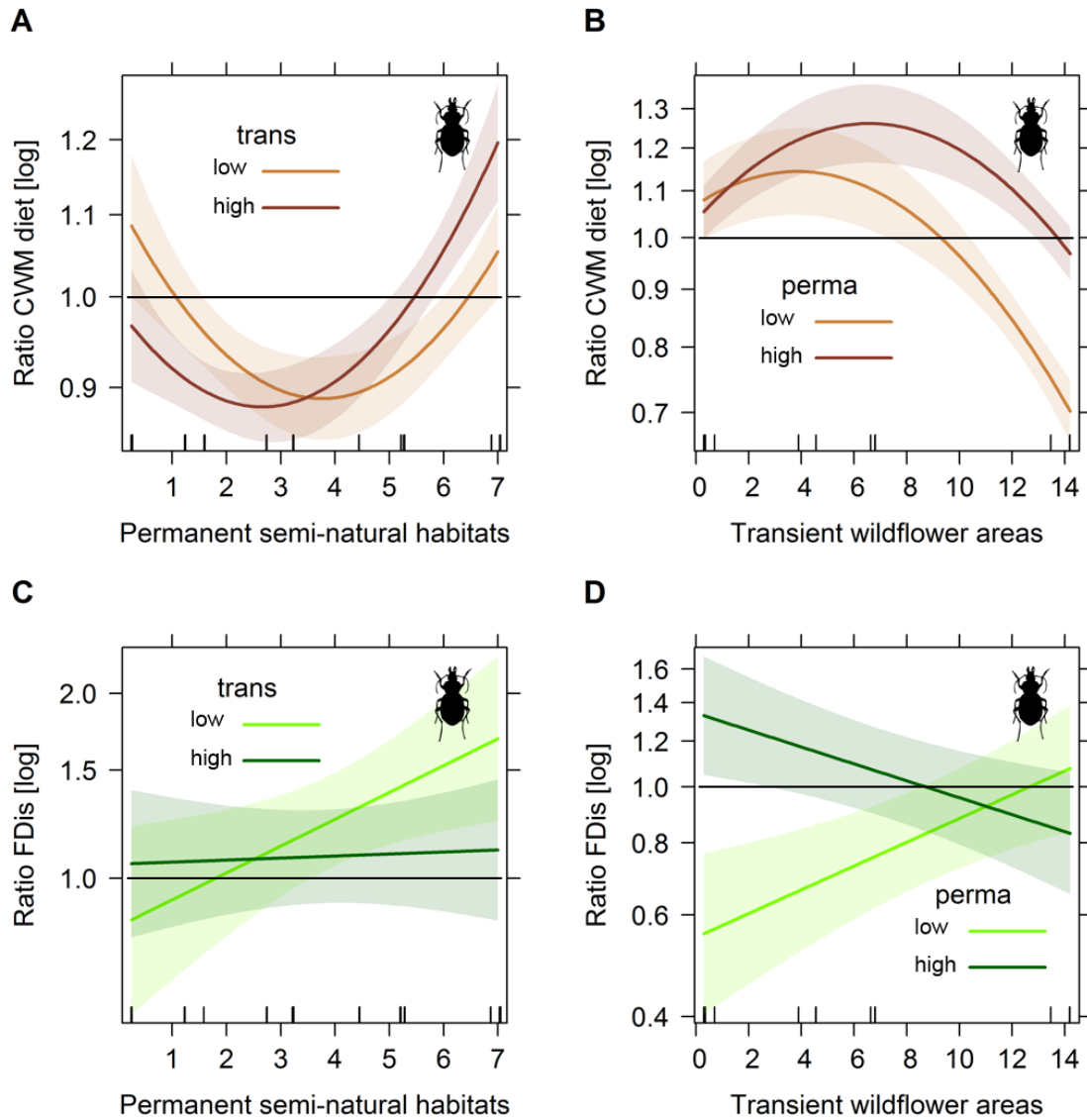


Figure 3. Interactive effects of the proportions of permanent semi-natural habitats (Perma) and transient wildflower areas (Trans) on the ratio of the community weighted mean values (CWM) of the diet of carabid beetles in crop fields (A-B) as well as the functional diversity (FDis) of carabid beetles in wildflower areas (C-D). Points represent raw data, lines and shaded areas represent the model fit and 95% confidence intervals, respectively. The black lines represent the border between increase (more carnivorous carabid beetles) and a decrease (more herbivorous carabid beetles) of the diet and FDis over three years, respectively.

DISCUSSION

Our results show that the establishment of wildflower areas significantly affected selected traits and the functional diversity of ground-dwelling arthropods across three years in wildflower areas and adjacent crop fields. Rove beetles became smaller and showed a higher functional diversity in wildflower areas after three years. Carabid beetles in wildflower areas became larger and showed a higher proportion of herbivorous ones and the functional diversity in crop fields was higher in the third year, whereas spiders showed a higher proportion of active hunters after three years. Changes of traits to landscape context largely

seemed to effect ground-dwelling arthropods in wildflower areas and a hump-shaped pattern in relation to permanent semi-natural habitats and a linear response in relation to transient wildflower areas. Moreover, the diet in crop fields and the functional diversity in wildflower areas of carabid beetles were interactively affected by these two habitat types.

ROVE BEETLES

Rove beetles in wildflower areas and crop fields in our study were smaller after three compared to the first year. Since the majority of rove beetles is small in size, i.e. in our study only one third of rove beetle species were larger than the mean size of 5.1 mm, smaller rove beetles may be correlated by overall higher species richness of rove beetles after three years (cf. Hoffmann et al., submitted). Although we found smaller rove beetles after three years, body size of rove beetles in wildflower areas was increasing, but only in simple and complex landscapes with at least 6% of both the proportions of permanent semi-natural habitats and transient wildflower areas. Similarly, the proportion of carnivorous rove beetles in wildflower areas only increased in simple and complex landscapes with at least 4% of both the proportions of permanent semi-natural habitats and transient wildflower areas. Since the majority of large rove beetles in our study, such as *Philonthus* spp. and *Quedius* spp., was simultaneously carnivorous, this may indicate that the establishment of wildflower areas benefit large and carnivorous rove beetles, but only in simple and complex landscapes. Those species seem to need a minimum of available habitats and therefore, prey resources in agro-ecosystems (Bohác, 1999), which may have been provided in our study by the sum of 8-10% of resource-rich habitats. This hypothesis is supported by an increased species richness of agrobiont rove beetles with increasing proportions of non-crop areas which may constitute refuges for source populations and thus, promote colonization (Bohác, 1999; Clough et al., 2007).

In contrast to increasing carnivorous rove beetles in wildflower areas, we found a higher proportion of herbivorous (including fungivore and detritivore) rove beetles in crop fields in the third year. This is in line with a previous study which found more detritivorous rove beetles and a higher activity-density in organic compared to conventional fields in terms of a higher resource quality (Clough et al., 2007). Initially, wildflower areas have provided a higher plant species richness and a denser vegetation structure as compared to adjacent crop fields which may have resulted in a higher availability of decaying plant material and fungal development through increased humidity levels, important for fungivore and detritivore rove beetles. Since herbivorous rove beetles were nearly absent in crop fields during the first year

in our study, crop fields may have benefited through continuous spillover across the three years. Indeed, rove beetles are known to be highly mobile e.g. by moving and flying along the field borders (Coombes & Sotherton, 1986) and to annually spillover from overwintering places such as wildflower areas into adjacent crop fields (Lipkow, 1966).

Unfortunately, rove beetles have not been the subject of species-level research nearly as often as other arthropod groups (Hole et al., 2005), although they are feeding on aphids, collembolans, algae, fungi and decaying organic matter and are therefore good indicators of changes in agricultural techniques and may contribute to ecosystem services such a natural pest control (Betz et al., 2018; Bohác, 1999). A higher functional diversity of rove beetles in wildflower areas after three years in our study supports this hypothesis, since a higher functional diversity may enhance ecosystem services (Albrecht et al., 2020), here possibly achieved by more feeding preferences as shown above.

CARABID BEETLES

In contrast to smaller rove beetles, carabid beetles in wildflower areas were larger after three years in our study. Larger carabid beetles are more mobile (Homburg et al., 2014) and may colonize new habitats faster than small ones (Boetzl et al., 2018). Concomitantly, large carabid beetles such as *Carabus* spp. are in general simultaneously wingless ones, which may explain higher proportions of wingless carabid beetles in crop fields after three years in our study. Regarding the landscape context, the proportion of winged carabid beetles in wildflower areas increased only in simple and complex landscapes with at least 6% of both permanent semi-natural habitats and transient wildflower areas, respectively. Similarly, carabid beetles in hedgerows were smaller than in grassy field margins in diverse landscapes, but were larger in hedgerows than in grassy field margins in simple landscapes (Gallé et al., 2018). This is also in line with a study which found more mobile carabid beetles in 2003 compared to the 1980s (Rusch et al., 2013), since species with poor dispersal abilities showed a restricted occurrence in highly fragmented landscapes or disturbed habitats (Henle et al., 2004). Thus, especially large and wingless species may benefit from the establishment of wildflower areas due to an improved connectivity and resource availability between wildflower areas and crop fields. Concomitantly, carabid beetles capable to fly may spillover to adjacent fields more quickly and larger predators may feed on more and larger prey (Gallé et al., 2020; Rusch et al., 2015), thus may exert a more effective pest control of insect pest species (Albrecht et al., 2020).

The proportion of herbivorous carabid beetles in wildflower areas were higher after the third year. Similar results showed an increase of medium-sized herbivorous species and a decrease in small carnivorous species after the conversion from arable to flowering areas (Baulechner et al., 2019). Wildflower areas provide suitable and stable conditions concomitantly with an increasing structural heterogeneity due to more field edges and have probably increased the availability of arable plant material for herbivorous species (Alignier et al., 2020) that have become less abundant in impoverished agricultural landscapes (Gallé et al., 2020; Rusch et al., 2013). Thus, more herbivorous carabid beetles such as *Harpalus* spp. in our study may contribute to seed predation since they are strongly specialized in feeding weeds (Baulechner et al., 2020; Diekötter et al., 2016).

Interestingly, permanent semi-natural habitats and transient wildflower areas had an interactive effect on the change of the diet in crop fields. The proportion of herbivorous carabid beetles increased either with at least 9% of transient wildflower areas in cleared landscapes or with 14% of transient wildflower areas in complex landscapes. High proportions of permanent semi-natural habitats in our study may have diminished the potential of the wildflower areas to attract and sustain high populations of herbivorous carabid beetles in adjacent crop fields (Tscharntke et al., 2012). Similarly, the functional diversity in wildflower areas was interactively affected by the proportions of permanent semi-natural habitats and transient wildflower areas. Here, an increase of the functional diversity was achieved only if a minimum of permanent semi-natural habitats (2%) is available and when transient wildflower areas were implemented in high proportions. This pattern supports the importance of source habitats provided by transient wildflower areas at the landscape level (Blitzer et al., 2012) due to e.g. a reduction in the distance of foraging trips (Hoffmann et al., 2020). In contrast, the functional diversity of carabid beetles in crop fields was higher in the third compared to the first year and increased with higher proportions of transient wildflower areas. This supports recent studies that even the establishment of relatively small wildflower areas promote multi-taxa diversity as well as ecosystem services and that three years were sufficient to colonize adjacent crop fields (Boetzel et al., 2021; Hoffmann et al., submitted).

SPIDERS

The diet of spiders in crop fields changed towards more active hunters in our study and may be explained by denser vegetation within wildflower areas compared to crop fields which is unfavourable for some spiders such as active hunters (Gallé et al., 2020). Moreover, we showed at least a tendency towards smaller spiders after three years in wildflower areas which

is in line with a decrease of body size of spiders towards older successional stages of heathlands (Schirmel et al., 2012).

Regarding the landscape context, body size, active hunters and functional diversity of spiders were affected by the proportions of transient wildflower areas only in wildflower areas and showed highest increases in simple and complex landscapes. Sown wildflower areas may benefit hunting/web-building guilds within agro-ecosystems probably due to an increased prey abundance (Campbell et al., 2020; Schmidt-Entling & Döbeli, 2009). Less obvious effects of landscapes context on spiders in crop fields as found in further studies (Ganser et al., 2019; Růžicková et al., 2020) may be explained by their colonization behaviour as they primarily arrive by ballooning which occurs randomly by air condition (Bishop & Riechert, 1990). Thus, spider assemblages in cleared landscapes surrounded by agricultural fields may simply be dependent on the nearby spider assemblages for colonization (Campbell et al., 2020) which seemed to be favoured in simple and complex landscapes in our study. However, previous studies found that spider diversity increased with non-crop habitats in the surrounding landscape (Clough et al., 2005; Gallé et al., 2018; Schmidt et al., 2008) due to higher structural diversity as well as the provisioning of more predictable and diverse food resources of permanent semi-natural habitats (Diehl et al., 2013).

CONCLUSION

Studying the change of functional traits of ground-dwelling arthropods across three years revealed new findings and benefits of wildflower areas differed substantially between studied taxa, landscape context and were in particular detectable in wildflower areas. Less obviously effects in crop fields may be due to shifts in selected crop fields induced through common crop rotations. Although selected crop fields were as close as possible to the focal wildflower areas each year, varying fields may be characterized by different field margins which may have affected colonization processes of ground-dwelling arthropods. However, a higher functional diversity of rove beetles in wildflower areas and carabid beetles in crop fields after three years imply that wildflower areas may provide ample resources for a wide range of arthropods and enhanced spillover effects due to a better connectivity in agro-ecosystems.

Regarding the landscape context, simple landscapes with at least 4-6% of both transient wildflower areas and permanent semi-natural habitats increased, for instance, the proportion of large and carnivorous rove beetles, winged carabid beetles as well as the functional diversity of spiders. In addition, interactive effects of both source habitats indicate that wildflower areas can also enfold benefits to agro-biodiversity in cleared landscapes but only if

implemented at high proportions. Thus, we conclude that both source habitats seem to complement each other and in order to maximise benefits for agro-biodiversity, the future establishment of wildflower areas should be implemented at a landscape-dependent minimum proportion and maintained over multiple years. Since a higher functional diversity contributes to the stability of ecosystem functioning, our results also indicate that a more directed establishment of wildflower areas in a landscape context may benefit natural enemies and concomitantly their ecosystem services such as pest control and finally the agricultural production.

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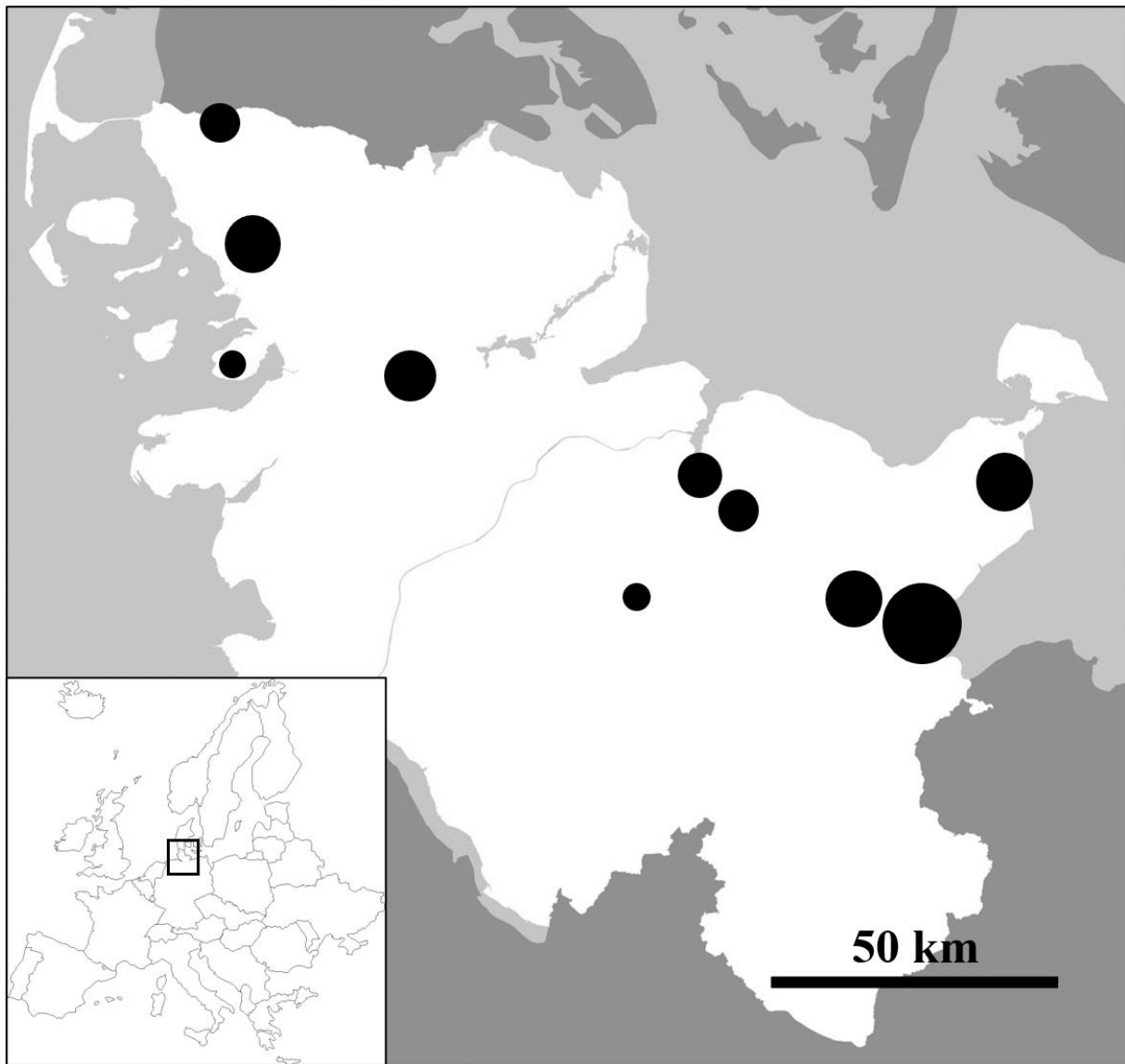
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APPENDIX

Appendix A. List and proportions of all plant species of the regional seed mix

Plant species	Proportion [%]
<i>Linum usitatissimum</i>	20
<i>Medicago lupulina</i>	12.5
<i>Petroselinum sativum</i>	11
<i>Trifolium repens</i>	6
<i>Galium album</i>	5
<i>Leucanthemum ircutianum</i>	5
<i>Lotus corniculatus</i>	5
<i>Ornithopus sativus</i>	5
<i>Trifolium subterraneum</i>	5
<i>Vicia sativa</i>	5
<i>Trifolium pratense</i>	3
<i>Lotus pedunculatus</i>	2
<i>Plantago lanceolata</i>	2
<i>Silene vulgaris</i>	2
<i>Coriandrum sativum</i>	2
<i>Phacelia tanacetifolia</i>	2
<i>Prunella vulgaris</i>	1.5
<i>Achillea millefolium</i>	1
<i>Trifolium dubium</i>	1
<i>Centaurea jacea</i>	0.5
<i>Daucus carota</i>	0.5
<i>Echium vulgare</i>	0.5
<i>Hypochoeris radicata</i>	0.5
<i>Lychnis-flos-cuculi</i>	0.5
<i>Ranunculus acris</i>	0.5
<i>Rumex acetosa</i>	0.5
<i>Stellaria graminea</i>	0.5



Appendix B. Supporting Information B. Map showing the ten study sites as pairs of wildflower areas and crop fields in Schleswig-Holstein, Northern Germany. Size of circles represents proportions of semi-natural habitats as the sum of permanent semi-natural habitats and transient wildflower areas (Table 1).

Appendix C. List, traits, mean \pm SD and total numbers for wildflower areas (WA) and crop fields (CF) per year of all recorded ground-dwelling arthropod species. (diet/hunting method: 0 = herbivore, 0.5 = omnivore, 1 = carnivore; flight ability: 0 = short-winged/wingless, 0.5 = dimorphic, 1 = winged)

Arthropod species	Mean size [mm]	Diet/hunting method	Flight ability	Mean \pm SD in 2017		Mean \pm SD in 2019		Total numbers
				WA	CF	WA	CF	
Staphylinidae								
<i>Aleochara bilineata</i> Gyll., 1810	4	0	NA	6.3 \pm 13.8	0.1 \pm 0.3	3.8 \pm 5.1	9.9 \pm 28.9	205
<i>Aleochara bipustulata</i> (L., 1760)	3.25	0	NA	45.5 \pm 66.9	1.6 \pm 1.8	42.6 \pm 40.9	8.4 \pm 13.4	1239
<i>Aleochara brevipennis</i> Grav., 1806	4.5	0	NA	26.2 \pm 52.0	9.6 \pm 12.8	73.8 \pm 127.5	16.9 \pm 19.6	1680
<i>Aleochara curtula</i> (Goeze, 1777)	6	0	NA	0.1 \pm 0.3	0 \pm 0	0 \pm 0	0.5 \pm 0.8	9
<i>Aleochara lanuginosa</i> Grav., 1802	4.25	0	NA	0 \pm 0	0.1 \pm 0.3	0 \pm 0	0 \pm 0	1
<i>Aleochara ruficornis</i> Grav., 1802	5.75	0	NA	0 \pm 0	0 \pm 0	0.2 \pm 0.6	0 \pm 0	2
<i>Anotylus inustus</i> (Grav., 1806)	3.7	0	NA	0 \pm 0	0.1 \pm 0.3	0 \pm 0	0 \pm 0	1
<i>Anotylus nitidulus</i> (Grav., 1802)	2.45	0	NA	9.1 \pm 24.6	0.1 \pm 0.3	0.6 \pm 0.8	0.2 \pm 0.6	105
<i>Anotylus rugosus</i> (F., 1775)	4.7	0	NA	22.1 \pm 19.7	11.2 \pm 12.5	27.9 \pm 37.7	4.4 \pm 3.7	938
<i>Anotylus sculpturatus</i> (Grav., 1806)	3.9	0	NA	0.2 \pm 0.4	0.6 \pm 1.6	0.1 \pm 0.3	0.1 \pm 0.3	26
<i>Anotylus tetracarinatus</i> (Block, 1799)	2.2	0	NA	0.5 \pm 1.6	0.2 \pm 0.6	2.2 \pm 3.8	0.2 \pm 0.4	33
<i>Anthobium unicolor</i> (Marsh., 1802)	3.25	0	NA	0.1 \pm 0.3	0 \pm 0	0.4 \pm 1.3	0.1 \pm 0.3	12
<i>Bisnius nitidulus</i> (Grav., 1802)	4.25	1	NA	0 \pm 0	0 \pm 0	0.1 \pm 0.3	0 \pm 0	1
<i>Bisnius spermophili</i> (Ganglb., 1897)	6	1	NA	0 \pm 0	0 \pm 0	0.3 \pm 0.9	0 \pm 0	3
<i>Bledius gallicus</i> (Grav., 1806)	4.25	0	NA	0 \pm 0	0 \pm 0	0.1 \pm 0.3	0 \pm 0	2
<i>Bolitobius cingulatus</i> Mannerh., 1830	8.25	1	NA	0 \pm 0	0 \pm 0	0 \pm 0	0.1 \pm 0.3	1
<i>Brachygluta fossulata</i> (Reichb., 1816)	1.8	1	NA	0.1 \pm 0.3	0 \pm 0	0 \pm 0	0 \pm 0	1
<i>Carpelimus bilineatus</i> Steph., 1834	3.1	0	NA	0.1 \pm 0.3	0 \pm 0	0 \pm 0	0 \pm 0	1
<i>Carpelimus corticinus</i> (Grav., 1806)	2.15	0	NA	0.5 \pm 1.1	0 \pm 0	0.3 \pm 0.9	0.1 \pm 0.3	9
<i>Carpelimus gracilis</i> (Mannerh., 1830)	1.55	0	NA	0.1 \pm 0.3	0 \pm 0	0 \pm 0	0 \pm 0	1
<i>Cordalia obscura</i> (Grav., 1802)	2.4	1	NA	0.1 \pm 0.3	0 \pm 0	0 \pm 0	0 \pm 0	1
<i>Drusilla canaliculata</i> (F., 1787)	4.4	1	NA	2.8 \pm 5.2	22.5 \pm 40.1	8.4 \pm 24.5	13.5 \pm 27.6	506
<i>Euaesthetus bipunctatus</i> (Ljungh, 1804)	1.75	1	NA	0.1 \pm 0.3	0.8 \pm 2.2	0.2 \pm 0.6	0.2 \pm 0.6	15
<i>Falagrioma thoracica</i> (Steph., 1832)	2.7	1	NA	0.4 \pm 1.3	2.7 \pm 8.5	0.1 \pm 0.3	0.2 \pm 0.6	54
<i>Gabrius appendiculatus</i> Sharp, 1910	4	1	NA	2.3 \pm 5.9	0.5 \pm 1.6	0.6 \pm 1.3	0.3 \pm 0.9	60
<i>Gabrius austriacus</i> Scheerp., 1947	4.25	1	NA	0 \pm 0	0.1 \pm 0.3	0.1 \pm 0.3	0 \pm 0	4
<i>Gabrius breviventer</i> (Sperk, 1835)	4	1	NA	1.3 \pm 1.8	1.0 \pm 1.3	3.9 \pm 6.4	2.5 \pm 3.7	100
<i>Gabrius osseticus</i> (Kolen., 1846)	6.75	1	NA	0.1 \pm 0.3	0.1 \pm 0.3	0 \pm 0	0 \pm 0	2
<i>Gyrophypnus angustatus</i> Steph., 1833	7.25	1	NA	3.0 \pm 4.6	3.3 \pm 4.5	1.9 \pm 2.4	2.0 \pm 2.3	146
<i>Heterothops dissimilis</i> (Grav., 1802)	4.15	1	NA	0 \pm 0	0.3 \pm 0.7	0.4 \pm 1	0.1 \pm 0.3	17
<i>Ilyobates bennetti</i> Donisth., 1914	4.25	1	NA	0.8 \pm 1.5	1.0 \pm 1.2	0.8 \pm 1.2	2.1 \pm 3.7	52
<i>Ilyobates nigricollis</i> (Payk., 1800)	5.75	1	NA	0 \pm 0	0 \pm 0	0 \pm 0	0.1 \pm	1

							0.3	
<i>Ischnosoma splendidum</i> (Grav., 1806)	4.25	0	NA	1.5 ± 3.2	0.8 ± 2.5	3.9 ± 10.9	3.5 ± 6.6	97
<i>Lathrobium brunnipes</i> (F., 1792)	9.5	1	NA	0.1 ± 0.3	0 ± 0	0.6 ± 1.6	0 ± 0	7
<i>Lathrobium fulvipenne</i> (Grav., 1806)	9	1	NA	0.5 ± 0.7	1.7 ± 2.3	1.2 ± 1.3	4.5 ± 3.8	110
<i>Lathrobium impressum</i> Heer, 1841	6.7	1	NA	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	1
<i>Lesteva longoelytrata</i> (Goeze, 1777)	4	0	NA	0.7 ± 1.3	30.5 ± 69.8	0.1 ± 0.3	20.5 ± 42.8	518
<i>Megarthus prosseni</i> Schatzm., 1904	2.45	0	NA	0.1 ± 0.3	0 ± 0	0 ± 0	0 ± 0	1
<i>Metopsia similis</i> Zerche, 1998	2.6	0	NA	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	1
<i>Mycetoporus lepidus</i> (Grav., 1806)	4.75	0	NA	0 ± 0	0 ± 0	0.2 ± 0.6	0 ± 0	4
<i>Mycetoporus longulus</i> Mannerh., 1830	4.85	0	NA	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.6	2
<i>Ocypus brunnipes</i> (F., 1781)	14	1	NA	0 ± 0	1.1 ± 3.1	0.1 ± 0.3	0 ± 0	15
<i>Oligota pumilio</i> Kiesw., 1858	1.15	0	NA	0.2 ± 0.6	0.9 ± 1.4	1.5 ± 3.7	1.2 ± 2.6	42
<i>Olophrum assimile</i> (Payk., 1800)	4.25	0	NA	0.1 ± 0.3	0 ± 0	0 ± 0	0 ± 0	1
<i>Olophrum piceum</i> (Gyll., 1810)	5.05	0	NA	0 ± 0	0 ± 0	0.2 ± 0.6	0 ± 0	3
<i>Omalium caesum</i> Grav., 1806	3	0	NA	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	1
<i>Omalium excavatum</i> Steph., 1834	3.5	0	NA	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	1
<i>Omalium rivulare</i> (Payk., 1789)	3.5	0	NA	0 ± 0	0.2 ± 0.4	0 ± 0	0 ± 0	3
<i>Omalium rugatum</i> Muls. & Rey, 1880	3	0	NA	0.1 ± 0.3	0 ± 0	0 ± 0	0 ± 0	1
<i>Oxyporus rufus</i> (L., 1758)	9.5	0	NA	0 ± 0	0.1 ± 0.3	0 ± 0	0 ± 0	1
<i>Oxytelus laqueatus</i> (Marsh., 1802)	4.4	0	NA	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	1
<i>Oxytelus sculptus</i> Grav., 1806	4	0	NA	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	1
<i>Philonthus addendus</i> Sharp, 1867	10.5	1	NA	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	3
<i>Philonthus atratus</i> (Grav., 1802)	9.25	1	NA	1.7 ± 3.5	0 ± 0	2.2 ± 5.2	0.1 ± 0.3	44
<i>Philonthus carbonarius</i> (Grav., 1802)	7	1	NA	5.5 ± 6.4	1.8 ± 2.1	1.5 ± 1.6	0.5 ± 0.7	114
<i>Philonthus cognatus</i> Steph., 1832	11.25	1	NA	41.8 ± 71.4	32 ± 39.2	36.8 ± 48.2	7.3 ± 9.8	1330
<i>Philonthus concinnus</i> (Grav., 1802)	6.75	1	NA	0.4 ± 1.3	0.1 ± 0.3	0 ± 0	0 ± 0	5
<i>Philonthus corruscus</i> (Grav., 1802)	7.5	1	NA	0 ± 0	0 ± 0	0.2 ± 0.4	0 ± 0	2
<i>Philonthus decorus</i> (Grav., 1802)	13.5	1	NA	0.3 ± 0.5	0.8 ± 1.3	0 ± 0	0 ± 0	16
<i>Philonthus laminatus</i> (Creutzer, 1799)	11.25	1	NA	1.9 ± 3.8	1.9 ± 3.6	1.3 ± 2.3	0.9 ± 2.8	74
<i>Philonthus micans</i> (Grav., 1802)	6.5	1	NA	0.2 ± 0.6	0 ± 0	0 ± 0	0 ± 0	2
<i>Philonthus rotundicollis</i> (Ménétr., 1832)	11.5	1	NA	0 ± 0	0.3 ± 0.9	0.5 ± 1.1	0.3 ± 0.7	15
<i>Platystethus arenarius</i> (Geoffr., 1785)	3.05	0	NA	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	1
<i>Quedius boops</i> (Grav., 1802)	5	1	NA	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.6	4
<i>Quedius fuliginosus</i> (Grav., 1802)	12.5	1	NA	0.7 ± 1.9	0.1 ± 0.3	0.2 ± 0.4	0.2 ± 0.4	12
<i>Quedius longicornis</i> Kr., 1857	9.5	1	NA	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	1
<i>Quedius maurorufus</i> (Grav., 1806)	6.5	1	NA	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	2
<i>Quedius molochinus</i> (Grav., 1806)	11.25	1	NA	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	1
<i>Rugilus rufipes</i> (Germar, 1836)	6.5	1	NA	0 ± 0	0.2 ±	0.3 ±	0.1 ±	6

					0.6	0.9	0.3	
<i>Scydmaenus tarsatus</i> Müll.&Kunz., 1822	2.05	1	NA	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	1
<i>Sepedophilus marshami</i> (Steph., 1832)	4.5	0	NA	0 ± 0	10.5 ± 21.1	0.1 ± 0.3	4.7 ± 7.9	169
<i>Sepedophilus pedicularius</i> (Grav., 1802)	2.9	0	NA	0.2 ± 0.4	0.2 ± 0.4	0 ± 0	0.1 ± 0.3	5
<i>Stenichnus collaris</i> (Müll. & Kunz., 1822)	1.45	1	NA	0.2 ± 0.4	0 ± 0	0 ± 0	0 ± 0	2
<i>Stenus atratulus</i> Er., 1839	2.7	1	NA	0.1 ± 0.3	0.4 ± 1	0 ± 0	0 ± 0	5
<i>Stenus biguttatus</i> (L., 1758)	4.8	1	NA	0 ± 0	0.1 ± 0.3	0.1 ± 0.3	0.6 ± 1.9	9
<i>Stenus bimaculatus</i> Gyll., 1810	4.3	1	NA	0.1 ± 0.3	0 ± 0	0 ± 0	0.1 ± 0.3	5
<i>Stenus canaliculatus</i> Gyll., 1827	3.35	1	NA	0 ± 0	0.3 ± 0.5	0 ± 0	0.4 ± 0.8	18
<i>Stenus clavicornis</i> (Scop., 1763)	4.75	1	NA	0.5 ± 1	1.3 ± 1.7	0.2 ± 0.4	3 ± 2.8	69
<i>Stenus juno</i> (Payk., 1789)	5.5	1	NA	0 ± 0	0.5 ± 1.3	0 ± 0	0 ± 0	7
<i>Stenus pallipes</i> Grav., 1802	2.7	1	NA	0.1 ± 0.3	0 ± 0	0.4 ± 0.7	0.1 ± 0.3	14
<i>Sunius bicolor</i> (Ol., 1795)	3.75	1	NA	0 ± 0	0 ± 0	0.2 ± 0.6	0 ± 0	3
<i>Tachinus corticinus</i> Grav., 1802	3.65	1	NA	1.6 ± 3.8	1.4 ± 2.7	12.1 ± 27.6	2.5 ± 5.8	212
<i>Tachinus fimetarius</i> (Grav., 1802)	4.85	1	NA	0.1 ± 0.3	1.3 ± 1.6	0.1 ± 0.3	4.9 ± 12.6	69
<i>Tachinus marginellus</i> (F., 1781)	4.1	1	NA	0.7 ± 1.5	0.5 ± 1.3	0.9 ± 1.3	0 ± 0	21
<i>Tachinus rufipes</i> (L., 1758)	5.75	1	NA	43.1 ± 71	194.1 ± 253.6	22.6 ± 50.9	44.4 ± 51.3	3192
<i>Tachyporus chrysomelinus</i> (L., 1758)	3.6	1	NA	0.9 ± 2.5	1.8 ± 1.8	0.8 ± 1.1	0.9 ± 0.9	61
<i>Tachyporus dispar</i> (Payk., 1789)	3.6	1	NA	1.4 ± 3.2	0 ± 0	0.3 ± 0.7	6.6 ± 19.1	86
<i>Tachyporus hypnorum</i> (F., 1775)	3.55	1	NA	3 ± 3.7	7.5 ± 4.1	6.9 ± 7.5	10.4 ± 9.7	348
<i>Tachyporus nitidulus</i> (F., 1781)	2.7	1	NA	0 ± 0	0 ± 0	4.3 ± 9.1	0.4 ± 0.7	47
<i>Tachyporus obtusus</i> (L., 1767)	4.1	1	NA	3.7 ± 7.6	3.3 ± 3.1	2.4 ± 3.9	1.4 ± 2.5	153
<i>Tachyporus pusillus</i> Grav., 1806	3.25	1	NA	0.9 ± 2.8	0.4 ± 1	0 ± 0	0 ± 0	19
<i>Tachyporus solutus</i> Er., 1839	3.4	1	NA	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	1
<i>Tachyporus transversalis</i> Grav., 1806	3	1	NA	0 ± 0	0.1 ± 0.3	0 ± 0	0 ± 0	1
<i>Tychus niger</i> (Payk., 1800)	1.55	1	NA	0.6 ± 1.3	0.1 ± 0.3	0.2 ± 0.4	0.6 ± 1.1	15
<i>Xantholinus dvoraki</i> Coiff., 1956	8.25	1	NA	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	1
<i>Xantholinus linearis</i> (Ol., 1795)	7.5	1	NA	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	1
<i>Xantholinus longiventris</i> Heer, 1839	8.25	1	NA	2.7 ± 2.1	3.8 ± 2.3	9 ± 10.4	7.5 ± 6	305
Carabidae								
<i>Abax parallelepipedus</i> (Pill. & Mitt., 1783)	19	1	0	0 ± 0	0.1 ± 0.3	0.1 ± 0.3	0.2 ± 0.6	15
<i>Acupalpus exiguus</i> (Dejean, 1829)	2	0.5	1	1.5 ± 3.4	0.2 ± 0.4	1.2 ± 3.1	0.5 ± 0.8	35
<i>Acupalpus meridianus</i> (L., 1761)	3.5	0.5	1	1.8 ± 3.6	0.3 ± 0.9	1.5 ± 2.4	0.5 ± 1.3	41
<i>Agonum emarginatum</i> (Gyll., 1827)	8	1	0.5	2 ± 4.2	0.7 ± 1.9	0.1 ± 0.3	0 ± 0	40
<i>Agonum fuliginosum</i> (Panzer, 1809)	6	1	0.5	0.1 ± 0.3	0.5 ± 1.3	0 ± 0	0 ± 0	6
<i>Agonum marginatum</i> (L., 1758)	9	1	1	0.1 ± 0.3	0 ± 0	0 ± 0	0 ± 0	1
<i>Agonum muelleri</i> (Herbst, 1784)	7.5	1	1	45 ± 66.6	63.7 ± 104	11.8 ± 15.9	5 ± 10.1	1429

<i>Agonum sexpunctatum</i> (L., 1758)	7.5	1	1	0 ± 0	1 ± 2.8	0.1 ± 0.3	0.1 ± 0.3	19
<i>Amara aenea</i> (De Geer, 1774)	7	0	1	3.2 ± 6.6	0.3 ± 0.5	8.1 ± 25.3	0.1 ± 0.3	148
<i>Amara apricaria</i> (Payk., 1790)	7.5	0	1	0.7 ± 1.3	0 ± 0	3.5 ± 9.4	0.3 ± 0.7	85
<i>Amara aulica</i> (Panzer, 1796)	12.5	0	1	0.1 ± 0.3	0.2 ± 0.4	1 ± 2.8	0.1 ± 0.3	28
<i>Amara bifrons</i> (Gyll., 1810)	6	0	1	0.6 ± 1.9	0.1 ± 0.3	0.2 ± 0.4	0 ± 0	58
<i>Amara familiaris</i> (Duft., 1812)	7	0	1	0 ± 0	0 ± 0	0.2 ± 0.4	0.5 ± 1.6	14
<i>Amara fulva</i> (Müller, 1776)	9	0	1	0.1 ± 0.3	0.6 ± 1.3	0.1 ± 0.3	0.1 ± 0.3	15
<i>Amara lunicollis</i> Schiodte, 1837	7.5	0	1	0.6 ± 1.6	2.1 ± 4	0.2 ± 0.6	0.4 ± 0.8	40
<i>Amara ovata</i> (F., 1792)	8.5	0	1	0.1 ± 0.3	1.1 ± 2.6	10.3 ± 24	0.2 ± 0.4	119
<i>Amara plebeja</i> (Gyll., 1810)	7	0	1	10.4 ± 27.7	2 ± 3.2	1.3 ± 2.2	5.7 ± 12.9	351
<i>Amara similata</i> (Gyll., 1810)	8.5	0	1	0.2 ± 0.6	0.2 ± 0.4	2 ± 5.7	0.3 ± 0.5	42
<i>Amara sprete</i> Dejean, 1831	8	0	1	3.1 ± 6.5	0.4 ± 1	1 ± 2.3	2.7 ± 8.5	131
<i>Anchomenus dorsalis</i> (Pont., 1763)	6.5	1	1	84.1 ± 97.1	451.9 ± 687	64.4 ± 103.6	106.5 ± 136.3	9234
<i>Anisodactylus binotatus</i> (F., 1787)	10.5	0	1	1.6 ± 3.3	0.6 ± 1	1 ± 1.9	1 ± 1.9	89
<i>Anisodactylus signatus</i> (Panzer, 1797)	12	0.5	1	0.1 ± 0.3	0 ± 0	0 ± 0	0 ± 0	2
<i>Asaphidion curtum</i> (Heyden, 1870)	3.5	1	1	0 ± 0	0.3 ± 0.7	0 ± 0	0 ± 0	3
<i>Badister bullatus</i> (Schrank, 1798)	5	1	1	0.2 ± 0.4	0.6 ± 0.7	0 ± 0	1.2 ± 1.9	22
<i>Badister dilatatus</i> Chaud., 1837	5	1	1	0 ± 0	0.1 ± 0.3	0 ± 0	0 ± 0	1
<i>Bembidion aeneum</i> Germar, 1824	3.5	1	0.5	11.6 ± 22.2	34.7 ± 69.6	12.1 ± 19.7	18.8 ± 30.5	1028
<i>Bembidion biguttatum</i> (F., 1779)	3.5	1	1	4.1 ± 7.9	2.9 ± 6.6	26.3 ± 58.2	2.8 ± 5.2	418
<i>Bembidion gilvipes</i> Sturm, 1825	2	1	0.5	0 ± 0	0 ± 0	0 ± 0	0.9 ± 2.8	17
<i>Bembidion lampros</i> (Herbst, 1784)	3	1	0.5	109.3 ± 149.1	33.9 ± 48.5	47.7 ± 69.1	21.1 ± 28.8	2616
<i>Bembidion mannerheimii</i> Sahlb., 1827	2.5	1	0.5	0.1 ± 0.3	3.6 ± 4.4	3.7 ± 7.4	17 ± 33.6	275
<i>Bembidion obtusum</i> Aud.-Serv., 1821	2.5	1	0.5	1.3 ± 2.1	1.3 ± 2.1	1.8 ± 2.9	7.1 ± 12.3	123
<i>Bembidion properans</i> (Steph., 1828)	3.5	1	0.5	24.2 ± 40.4	2.7 ± 4.2	2 ± 2.1	1.2 ± 1.5	334
<i>Bembidion quadrimaculatum</i> (L., 1761)	2.5	1	1	4.8 ± 7.8	0.4 ± 0.7	3.5 ± 5.2	0.1 ± 0.3	154
<i>Bembidion tetracolum</i> Say, 1823	5	1	0.5	16.7 ± 24.8	52.2 ± 59.1	65.3 ± 86.9	61.8 ± 88.4	3404
<i>Blemus discus</i> (F., 1792)	4.5	1	1	0.1 ± 0.3	1.1 ± 2	0.2 ± 0.6	0 ± 0	57
<i>Bradycellus harpalinus</i> (Aud.-Serv., 1821)	4	0.5	1	0 ± 0	0 ± 0	0.4 ± 1	0.1 ± 0.3	5
<i>Bradycellus verbasci</i> (Duft., 1812)	4.5	0.5	1	0.1 ± 0.3	0 ± 0	0.2 ± 0.6	0 ± 0	4
<i>Calathus cinctus</i> (Motsch., 1850)	7.5	1	0.5	0.6 ± 1.9	0.4 ± 1	0.3 ± 0.7	0.7 ± 1.6	47
<i>Calathus erratus</i> (Sahlb., 1827)	10	1	0.5	0 ± 0	0 ± 0	0.4 ± 1.3	0.1 ± 0.3	5
<i>Calathus fuscipes</i> (Goeze, 1777)	12	1	0.5	10.3 ± 28.2	1.9 ± 3	8.9 ± 24.8	1.2 ± 2.8	307
<i>Calathus melanocephalus</i> (L., 1758)	7.5	1	0.5	0.8 ± 1.6	0.6 ± 1.6	0.2 ± 0.6	0.2 ± 0.4	29
<i>Calosoma maderae</i> (F., 1775)	24	1	1	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	1
<i>Carabus auratus</i> L., 1761	23.5	1	0	2.9 ± 9.2	16.6 ± 52.5	1.8 ± 5.7	1.1 ± 3.5	267
<i>Carabus convexus</i> F., 1775	17	1	0	0.1 ± 0.3	0.1 ± 0.3	0 ± 0	0.1 ± 0.3	4

<i>Carabus coriaceus</i> L., 1758	37	1	0	0 ± 0	0 ± 0	0.1 ± 0.3	0.5 ± 0.7	20
<i>Carabus granulatus</i> L., 1758	21.5	1	0.5	19.1 ± 23.1	29.2 ± 42.9	23 ± 63.7	21.5 ± 43.8	1364
<i>Carabus hortensis</i> L., 1758	26	1	0	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	2
<i>Carabus nemoralis</i> Müller, 1764	23	1	0	0.4 ± 0.8	0.9 ± 1.7	0.3 ± 0.9	0.4 ± 1.3	26
<i>Carabus violaceus</i> L., 1758	30	1	0	0.1 ± 0.3	0.1 ± 0.3	0.3 ± 0.9	0.1 ± 0.3	15
<i>Chlaenius nigricornis</i> (F., 1787)	11	1	1	0.2 ± 0.4	0 ± 0	0.4 ± 1.3	0 ± 0	10
<i>Cicindela campestris</i> L., 1758	12	1	1	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	1
<i>Clivina fossor</i> (L., 1758)	6	1	0.5	5.2 ± 5.2	11.7 ± 13.5	11.9 ± 13.2	14.7 ± 14.2	510
<i>Demetrias atricapillus</i> (L., 1758)	5	1	1	0.2 ± 0.4	0.8 ± 1	0.2 ± 0.6	1.8 ± 4	43
<i>Dromius quadrimaculatus</i> (L., 1758)	5	1	1	0 ± 0	0.1 ± 0.3	0 ± 0	0 ± 0	1
<i>Dyschirius globosus</i> (Herbst, 1784)	2.5	1	0.5	0.2 ± 0.6	10.7 ± 32.8	0.2 ± 0.4	0 ± 0	115
<i>Harpalus affinis</i> (Schrank, 1781)	10	0	1	27.1 ± 55.1	7.2 ± 11.6	35.4 ± 80.8	2.3 ± 5.2	988
<i>Harpalus distinguendus</i> (Duft., 1812)	9	0	1	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	1
<i>Harpalus griseus</i> (Panzer, 1796)	10	0.5	1	0 ± 0	0 ± 0	0.4 ± 1.3	0 ± 0	8
<i>Harpalus latus</i> (L., 1758)	9.5	0	1	0.7 ± 1.9	0.2 ± 0.4	0.6 ± 0.8	0.4 ± 0.8	29
<i>Harpalus rubripes</i> (Duft., 1812)	10	0	1	1.3 ± 4.1	0 ± 0	2.9 ± 8.5	0 ± 0	54
<i>Harpalus rufipes</i> (De Geer, 1774)	13.5	0	0.5	33.6 ± 80	16 ± 33.2	60.6 ± 100.4	5.8 ± 11.3	2342
<i>Harpalus signaticornis</i> (Duft., 1812)	6.5	0	1	0 ± 0	0.2 ± 0.6	0.1 ± 0.3	0 ± 0	3
<i>Harpalus smaragdinus</i> (Duft., 1812)	9.5	0	1	0 ± 0	0 ± 0	0.4 ± 1.3	0 ± 0	5
<i>Harpalus tardus</i> (Panzer, 1796)	9	1	1	4.6 ± 13.2	4.2 ± 12.6	34.3 ± 107.4	7.1 ± 22.5	582
<i>Leistus ferrugineus</i> (L., 1758)	6.5	1	1	0 ± 0	0.1 ± 0.3	0 ± 0	1 ± 2.2	15
<i>Leistus fulvibarbis</i> Dejean, 1826	7.5	1	1	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	1
<i>Leistus rufomarginatus</i> (Duft., 1812)	8	1	0.5	0.1 ± 0.3	0 ± 0	0 ± 0	0 ± 0	1
<i>Limodromus assimilis</i> (Payk., 1790)	11.5	1	1	1.1 ± 3.1	7.4 ± 14.8	0.8 ± 2.2	11.3 ± 32.3	233
<i>Loricera pilicornis</i> (F., 1775)	7	1	1	1.2 ± 2.3	8 ± 6.7	0.2 ± 0.6	8.1 ± 11.5	223
<i>Microlestes minutulus</i> (Goeze, 1777)	2.5	1	1	0 ± 0	0 ± 0	0.3 ± 0.7	0 ± 0	4
<i>Nebria brevicollis</i> (F., 1792)	11.5	1	1	20.6 ± 39.9	8 ± 12.7	12.7 ± 34.1	4.3 ± 9	564
<i>Nebria salina</i> Fairm. & Lab., 1854	11	1	1	3.7 ± 8	0.1 ± 0.3	6.2 ± 9.5	4.8 ± 8.3	227
<i>Notiophilus biguttatus</i> (F., 1779)	4.5	1	0.5	1.8 ± 2.9	3.5 ± 4.3	0.4 ± 1	1.6 ± 2.1	101
<i>Notiophilus palustris</i> (Duft., 1812)	5	1	0.5	0 ± 0	0.3 ± 0.7	0 ± 0	0.2 ± 0.6	11
<i>Oodes helopioides</i> (F., 1792)	8	1	1	0.1 ± 0.3	0.1 ± 0.3	0 ± 0	0 ± 0	2
<i>Ophonus rufibarbis</i> (F., 1792)	7.5	0	1	0 ± 0	0.1 ± 0.3	0.2 ± 0.4	0.3 ± 0.5	8
<i>Oxypselaphus obscurus</i> (Herbst, 1784)	5	1	0.5	0 ± 0	0.5 ± 1.6	0 ± 0	0.3 ± 0.5	9
<i>Panagaeus cruxmajor</i> (L., 1758)	8	0	1	0.1 ± 0.3	0 ± 0	0 ± 0	0.1 ± 0.3	4
<i>Paradromius linearis</i> (Ol., 1795)	4.5	1	0.5	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	3
<i>Patrobus atrorufus</i> (Ström, 1768)	8.5	1	0.5	0.6 ± 1.3	0.2 ± 0.4	0 ± 0	0.1 ± 0.3	9
<i>Philorhizus melanocephalus</i> Dejean, 1825	2.5	1	0.5	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	1

<i>Poecilus cupreus</i> (L., 1758)	11	0.5	1	320.5 ± 655.1	155.5 ± 369.2	197.8 ± 237.5	147.5 ± 284.7	10459
<i>Poecilus lepidus</i> (Leske, 1785)	12	1	0.5	0 ± 0	0.1 ± 0.3	0 ± 0	0 ± 0	1
<i>Poecilus versicolor</i> (Sturm, 1824)	10	1	1	18.1 ± 25.8	25.9 ± 38.8	20.6 ± 29.7	15.5 ± 28.2	959
<i>Pterostichus melanarius</i> (Ill., 1798)	15	1	0.5	296.5 ± 759.5	201.2 ± 332.2	181.9 ± 345.5	115.6 ± 219.8	14601
<i>Pterostichus minor</i> (Gyll., 1827)	7	1	0.5	0 ± 0	0.2 ± 0.4	0.2 ± 0.4	0 ± 0	4
<i>Pterostichus niger</i> (Schaller, 1783)	18.5	1	0.5	20.8 ± 42	27.3 ± 44.4	29.9 ± 40.4	10.5 ± 9.5	2026
<i>Pterostichus nigritya</i> (Payk., 1790)	10	1	0.5	1.2 ± 2.3	0 ± 0	5.9 ± 15.6	0.7 ± 1.3	85
<i>Pterostichus strenuus</i> (Panzer, 1796)	6	1	0.5	5.9 ± 5.6	17.3 ± 16.5	9.9 ± 14.2	16.2 ± 13.7	561
<i>Pterostichus vernalis</i> (Panzer, 1796)	6.5	1	0.5	4.4 ± 6	3.3 ± 4.2	7 ± 14.3	2.7 ± 1.1	217
<i>Stomis pumicatus</i> (Panzer, 1796)	7	1	0.5	0.2 ± 0.4	0.3 ± 0.5	0.1 ± 0.3	0.3 ± 0.9	17
<i>Syntomus foveatus</i> (Geoffr., 1785)	2.5	1	0.5	11 ± 28.5	1.5 ± 3.4	9.6 ± 20.3	1.3 ± 3.8	306
<i>Syntomus truncatellus</i> (L., 1761)	2.5	1	0.5	0 ± 0	0.2 ± 0.6	0.2 ± 0.6	0.5 ± 1.6	10
<i>Synuchus vivalis</i> (Ill., 1798)	7	1	0.5	0.4 ± 0.5	0.1 ± 0.3	0.2 ± 0.6	0 ± 0	42
<i>Trechoblemus micros</i> (Herbst, 1784)	4.5	1	1	0.4 ± 1.3	0.4 ± 0.7	0 ± 0	0.1 ± 0.3	16
<i>Trechus quadristriatus</i> (Schrank, 1781)	3.5	1	0.5	1.4 ± 2.8	17.5 ± 41.3	1.1 ± 1.4	4.6 ± 8.9	280
<i>Trechus secalis</i> (Payk., 1790)	3.5	1	0	0 ± 0	1.2 ± 3.8	0 ± 0	0 ± 0	16
Araneae								
<i>Agyneta cauta</i> (Cambr., 1902)	2.5	0	NA	0 ± 0	0 ± 0	0.3 ± 0.7	0 ± 0	3
<i>Agyneta conigera</i> (Cambr., 1863)	2.05	0	NA	0 ± 0	0 ± 0	0.8 ± 2.5	0.1 ± 0.3	10
<i>Agyneta rurestris</i> (Koch, 1836)	2.3	0	NA	0.6 ± 0.8	0.1 ± 0.3	2.4 ± 2.5	3.2 ± 3.5	76
<i>Agyneta saxatilis</i> (Blackw., 1844)	2.15	0	NA	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	2
<i>Alopecosa pulverulenta</i> (Clerck, 1757)	9	1	NA	0.3 ± 0.7	0.3 ± 0.5	0.1 ± 0.3	0 ± 0	11
<i>Araeoncus humilis</i> (Blackw., 1841)	1.7	0	NA	1.7 ± 4.7	1 ± 1.1	4.2 ± 6.6	6.6 ± 5.5	168
<i>Argenna subnigra</i> (Cambr., 1861)	3.25	0	NA	0.1 ± 0.3	0 ± 0	0 ± 0	0 ± 0	1
<i>Bathypantes approximatus</i> (Cambr., 1871)	2.75	0	NA	0 ± 0	0.4 ± 1	0 ± 0	0.3 ± 0.5	10
<i>Bathypantes gracilis</i> (Blackw., 1841)	2	0	NA	10.2 ± 11.5	25 ± 25.4	1.8 ± 3.4	24.7 ± 25.3	928
<i>Bathypantes nigrinus</i> (Westr., 1851)	2.75	0	NA	0 ± 0	0.1 ± 0.3	0.3 ± 0.7	0 ± 0	4
<i>Bathypantes parvulus</i> (Westr., 1851)	2.15	0	NA	0 ± 0	0.1 ± 0.3	1.1 ± 1.8	2.1 ± 6	43
<i>Centromerus dilutus</i> (Cambr., 1875)	1.5	0	NA	0 ± 0	0 ± 0	0.4 ± 1.3	0 ± 0	4
<i>Centromerus sylvaticus</i> (Blackw., 1841)	3.1	0	NA	0 ± 0	0.1 ± 0.3	0 ± 0	0 ± 0	1
<i>Clubiona lutescens</i> Westr., 1851	6.5	1	NA	0 ± 0	0.2 ± 0.6	0 ± 0	0.1 ± 0.3	7
<i>Clubiona reclusa</i> Cambr., 1863	6.5	1	NA	0 ± 0	0.1 ± 0.3	0 ± 0	0.4 ± 0.7	8
<i>Collinsia inerrans</i> (Cambr., 1885)	2.25	0	NA	0 ± 0	0 ± 0	0.1 ± 0.3	0.1 ± 0.3	3
<i>Dicambium nigrum</i> (Blackw., 1834)	2.15	0	NA	0.4 ± 0.5	0.3 ± 0.7	0 ± 0	0 ± 0	12
<i>Dicymbium tibiale</i> (Blackw., 1836)	2.3	0	NA	0.2 ± 0.4	0 ± 0	0 ± 0	0.2 ± 0.4	7
<i>Diplocephalus picinus</i> (Blackw., 1841)	1.9	0	NA	0.1 ± 0.3	0.3 ± 0.7	0 ± 0	0.1 ± 0.3	6
<i>Diplostyla concolor</i> (Wider, 1834)	2.75	1	NA	0.1 ±	1.3 ±	1.8 ±	10.1 ±	176

				0.3	1.2	2.4	12.3	
<i>Dismodicus bifrons</i> (Blackw., 1841)	2.175	0	NA	0.1 ± 0.3	0.2 ± 0.6	0 ± 0	0.1 ± 0.3	5
<i>Drassylus praeficus</i> (Koch, 1866)	6.5	1	NA	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	1
<i>Drassylus pusillus</i> (Koch, 1833)	4.5	1	NA	0.5 ± 1.3	0.1 ± 0.3	0 ± 0	0.4 ± 0.5	14
<i>Enoplognatha thoracica</i> (Hahn, 1833)	4.25	0	NA	0.2 ± 0.6	0.1 ± 0.3	0 ± 0	0 ± 0	3
<i>Erigone arctica</i> (White, 1852)	3.05	0	NA	0.8 ± 1.6	0.2 ± 0.6	0 ± 0	2 ± 6	37
<i>Erigone atra</i> (Blackw., 1833)	2.3	0	NA	33.4 ± 47.1	41.9 ± 28.5	71.6 ± 74.4	132.4 ± 106.1	4075
<i>Erigone dentipalpis</i> (Wider, 1834)	2.3	0	NA	15.4 ± 25.9	12.3 ± 16.1	36.9 ± 38.7	26.7 ± 40.8	1201
<i>Erigonella hiemalis</i> (Blackw., 1841)	1.725	0	NA	0 ± 0	0.1 ± 0.3	0 ± 0	0 ± 0	1
<i>Euophrys frontalis</i> (Walck., 1802)	3.565	1	NA	0 ± 0	0.1 ± 0.3	0 ± 0	0.1 ± 0.3	2
<i>Gnathonarium dentatum</i> (Wider, 1834)	2.6	0	NA	0.1 ± 0.3	0.2 ± 0.6	0 ± 0	0.1 ± 0.3	4
<i>Gongylidiellum vivum</i> (Cambr., 1875)	1.6	0	NA	0 ± 0	0.1 ± 0.3	0 ± 0	0.1 ± 0.3	2
<i>Gongylidium rufipes</i> (L., 1758)	3.15	0	NA	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	1
<i>Hahnia pusilla</i> (Koch, 1841)	1.4	0	NA	0 ± 0	0.1 ± 0.3	0 ± 0	0 ± 0	1
<i>Hypomma bituberculatum</i> (Wider, 1834)	2.6	0	NA	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	1
<i>Kaestneria dorsalis</i> (Wider, 1834)	2.75	0	NA	0 ± 0	0 ± 0	0.2 ± 0.4	0 ± 0	2
<i>Leptorhoptrum robustum</i> (Westr., 1851)	3.9	0	NA	0.2 ± 0.4	0.3 ± 0.7	0.3 ± 0.9	0.2 ± 0.6	13
<i>Linyphia hortensis</i> Sundev., 1830	5.05	0	NA	0.1 ± 0.3	0 ± 0	0.2 ± 0.6	0 ± 0	4
<i>Lophomma punctatum</i> (Blackw., 1841)	2.3	0	NA	0 ± 0	0.1 ± 0.3	0 ± 0	0 ± 0	1
<i>Maso sundevalli</i> (Westr., 1851)	1.65	0	NA	0.1 ± 0.3	0 ± 0	0.3 ± 0.9	0.1 ± 0.3	6
<i>Mermessus trilobatus</i> (Emerton, 1882)	1.85	0	NA	0 ± 0	0 ± 0	0 ± 0	0.3 ± 0.5	7
<i>Micaria pulicaria</i> (Sundev., 1832)	3.6	1	NA	0.5 ± 1	0.1 ± 0.3	0.7 ± 1.6	0.1 ± 0.3	25
<i>Micaria silesiaca</i> Koch, 1875	3.75	1	NA	0 ± 0	0 ± 0	0.2 ± 0.6	0 ± 0	2
<i>Micaria subopaca</i> Westr., 1862	2.55	1	NA	0 ± 0	0.4 ± 0.5	0.1 ± 0.3	0.9 ± 2	20
<i>Micrargus herbigradus</i> (Blackw., 1854)	2.15	0	NA	0.1 ± 0.3	0 ± 0	0.3 ± 0.5	0.6 ± 1.3	14
<i>Microlinyphia pusilla</i> (Sundev., 1830)	4.25	0	NA	0.1 ± 0.3	0 ± 0	0 ± 0	0 ± 0	2
<i>Microneta viaria</i> (Blackw., 1841)	2.25	0	NA	0 ± 0	0.1 ± 0.3	0 ± 0	0 ± 0	2
<i>Neottiura bimaculatum</i> (L., 1767)	2.6	0	NA	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	1
<i>Neriene clathrata</i> (Sundev., 1830)	4.25	0	NA	0 ± 0	0.1 ± 0.3	0 ± 0	0.1 ± 0.3	2
<i>Oedothorax agrestis</i> (Blackw., 1853)	2.6	0	NA	0 ± 0	0 ± 0	0.2 ± 0.6	0 ± 0	2
<i>Oedothorax apicatus</i> (Blackw., 1850)	2.75	0	NA	17.2 ± 24.6	23.6 ± 34.1	74.2 ± 95.6	29.9 ± 27.9	2105
<i>Oedothorax fuscus</i> (Blackw., 1854)	2.5	0	NA	6 ± 12.8	2.1 ± 2.8	9.2 ± 5.3	5.4 ± 5.9	367
<i>Oedothorax gibbosus</i> (Blackw., 1841)	2.6	0	NA	0 ± 0	0.2 ± 0.6	0.2 ± 0.4	0.2 ± 0.6	6
<i>Oedothorax retusus</i> (Westr., 1841)	2.6	0	NA	1.8 ± 2.4	1.2 ± 1.3	7.5 ± 20.6	1.5 ± 1.7	182
<i>Ostearius melanopygius</i> (Cambr., 1879)	2.2	0	NA	0 ± 0	0.1 ± 0.3	0 ± 0	0 ± 0	2
<i>Ozyptila praticola</i> (Koch, 1837)	3.9	1	NA	0 ± 0	0.3 ± 0.7	0 ± 0	0.5 ± 1.1	9
<i>Ozyptila trux</i> (Blackw., 1846)	4.2	1	NA	0.1 ± 0.3	0.1 ± 0.3	0 ± 0	0.6 ± 1.3	8
<i>Pachygnatha clercki</i> Sundev., 1823	5.25	0	NA	0.4 ±	2.2 ±	0 ± 0	1.9 ±	109

				0.7	2.5		3.6	
<i>Pachygnatha degeeri</i> Sundev., 1830	3.6	0	NA	4.3 ± 4.1	8 ± 13.9	1.6 ± 1.8	3.2 ± 6.7	241
<i>Paidiscura pallens</i> (Blackw., 1834)	1.6	0	NA	0.1 ± 0.3	0 ± 0	0 ± 0	0 ± 0	1
<i>Palliduphantes ericaeus</i> (Blackw., 1853)	1.85	0	NA	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	1
<i>Palliduphantes pallidus</i> (Cambr., 1871)	1.95	0	NA	0.1 ± 0.3	0.3 ± 0.7	0 ± 0	0.6 ± 1.1	12
<i>Pardosa agrestis</i> (Westr., 1862)	4.75	1	NA	51.9 ± 95	3.6 ± 10	40.4 ± 56.7	8.3 ± 21.5	1444
<i>Pardosa agricola</i> (Thorell, 1856)	6.75	1	NA	0 ± 0	0 ± 0	2.4 ± 5.3	0 ± 0	24
<i>Pardosa amentata</i> (Clerck, 1757)	6.5	1	NA	10 ± 12.6	2.7 ± 1.9	25.4 ± 35	2.6 ± 2.8	702
<i>Pardosa lugubris</i> (Walck., 1802)	6.3	1	NA	0 ± 0	0.9 ± 2	0.1 ± 0.3	1.9 ± 6	34
<i>Pardosa monticola</i> (Clerck, 1757)	5.5	1	NA	0 ± 0	0 ± 0	3.9 ± 7.7	0 ± 0	39
<i>Pardosa palustris</i> (L., 1758)	6	1	NA	10.5 ± 16.5	2.6 ± 5.2	33.2 ± 48.7	12.9 ± 29	688
<i>Pardosa prativaga</i> (Koch, 1870)	6.35	1	NA	4.2 ± 6.8	4.1 ± 3.2	28.9 ± 28.9	26.9 ± 30.9	830
<i>Pardosa pullata</i> (Clerck, 1757)	5	1	NA	0.3 ± 0.7	0 ± 0	3.5 ± 4	0.3 ± 0.5	63
<i>Pardosa saltans</i> Toep-Hofm., 2000	5.8	1	NA	0.1 ± 0.3	0.6 ± 1.1	0 ± 0	0 ± 0	13
<i>Pelecopsis parallela</i> (Wider, 1834)	1.4	0	NA	0 ± 0	1 ± 2.5	0 ± 0	1.3 ± 2.8	25
<i>Pelecopsis radicola</i> (Koch, 1872)	1.5	0	NA	0.1 ± 0.3	0.4 ± 0.7	0 ± 0	0.5 ± 1.6	10
<i>Phrurolithus festivus</i> (Koch, 1835)	2.7	1	NA	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	1
<i>Pirata hygrophilus</i> Thorell, 1872	5.1	1	NA	0.2 ± 0.4	0 ± 0	0.2 ± 0.6	0.8 ± 2.2	12
<i>Pirata piraticus</i> (Clerck, 1757)	6.5	1	NA	0.4 ± 0.8	0 ± 0	0.2 ± 0.6	0.4 ± 0.7	14
<i>Pirata piscatorius</i> (Clerck, 1757)	8.85	1	NA	0.1 ± 0.3	0 ± 0	0 ± 0	0 ± 0	1
<i>Pisaura mirabilis</i> (Clerck, 1757)	12.5	1	NA	0 ± 0	0 ± 0	0 ± 0	0.3 ± 0.5	6
<i>Pocadicnemis juncea</i> Lock. & Mill., 1953	1.85	0	NA	0.2 ± 0.4	0.1 ± 0.3	0 ± 0	0.4 ± 0.7	11
<i>Pocadicnemis pumila</i> (Blackw., 1841)	2.05	0	NA	0 ± 0	0.1 ± 0.3	0 ± 0	0.8 ± 2.2	12
<i>Porrhomma microphthalmum</i> (Cambr., 1871)	1.85	0	NA	4.8 ± 9.5	1.5 ± 2.3	2.7 ± 3.7	5.1 ± 6	163
<i>Porrhomma pygmaeum</i> (Blackw., 1834)	2.45	0	NA	0.2 ± 0.6	0 ± 0	0 ± 0	0 ± 0	2
<i>Robertus lividus</i> (Blackw., 1836)	3.5	0	NA	0.1 ± 0.3	0 ± 0	0.3 ± 0.5	0 ± 0	6
<i>Savignya frontata</i> (Blackw., 1833)	1.75	0	NA	0 ± 0	0.7 ± 1.6	0.4 ± 1	1.6 ± 3.1	34
<i>Silometopus elegans</i> (Cambr., 1872)	1.5	0	NA	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	1
<i>Stemonyphantes lineatus</i> (L., 1758)	5.75	0	NA	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	3
<i>Tallusia experta</i> (Cambr., 1871)	3.25	0	NA	0.1 ± 0.3	0 ± 0	0 ± 0	0 ± 0	1
<i>Tapinocyba pallens</i> (Cambr., 1873)	1.6	0	NA	0 ± 0	0 ± 0	0.2 ± 0.4	0 ± 0	2
<i>Tenuiphantes tenuis</i> (Blackw., 1852)	3.15	0	NA	6.3 ± 6.5	12.2 ± 16.6	3 ± 2.6	16.4 ± 7.8	458
<i>Tenuiphantes zimmermanni</i> (Bertkau, 1890)	2.6	0	NA	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	1
<i>Tetragnatha montana</i> Simon, 1874	9.5	0	NA	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	1
<i>Tiso vagans</i> (Blackw., 1834)	2.1	0	NA	0.2 ± 0.4	0.2 ± 0.4	0.2 ± 0.4	0.4 ± 0.7	13
<i>Trochosa robusta</i> (Simon, 1876)	13.5	1	NA	0 ± 0	0 ± 0	2 ± 2.8	0 ± 0	20
<i>Trochosa rucicola</i> (De Geer, 1778)	10.5	1	NA	5.2 ± 6.3	2.7 ± 2.3	3.7 ± 4.6	2 ± 2.6	260
<i>Trochosa terricola</i> Thorell, 1856	10.5	1	NA	0.3 ± 0.5	0.5 ± 0.8	1.3 ± 0.9	0 ± 0	31

<i>Troxochrus scabriculus</i> (Westr., 1851)	1.85	0	NA	0.1 ± 0.3	1.2 ± 2.5	0 ± 0	0.1 ± 0.3	14
<i>Walckenaeria atrotibialis</i> (Cambr., 1878)	2.5	0	NA	0.1 ± 0.3	0.5 ± 1.1	0 ± 0	0.7 ± 1.3	16
<i>Walckenaeria corniculans</i> (Cambr., 1875)	2.75	0	NA	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.6	2
<i>Walckenaeria dysderoides</i> (Wider, 1834)	2	0	NA	0 ± 0	0.1 ± 0.3	0 ± 0	0.2 ± 0.4	3
<i>Walckenaeria nudipalpis</i> (Westr., 1851)	3.15	0	NA	0 ± 0	0.2 ± 0.6	0 ± 0	0.2 ± 0.4	5
<i>Walckenaeria unicornis</i> (Cambr., 1861)	2.1	0	NA	0.1 ± 0.3	0.1 ± 0.3	0 ± 0	0.1 ± 0.3	3
<i>Xerolycosa miniata</i> (Koch, 1834)	6.15	1	NA	2.7 ± 8.5	0 ± 0	60.2 ± 189.3	0 ± 0	676
<i>Xysticus cristatus</i> (Clerck, 1757)	5.75	1	NA	1 ± 1.4	0 ± 0	0.3 ± 0.5	0.1 ± 0.3	20
<i>Xysticus kochi</i> Thorell, 1872	7.4	1	NA	1.7 ± 4.4	0.1 ± 0.3	0.8 ± 1.3	0.2 ± 0.4	34
<i>Xysticus ulmi</i> (Hahn, 1831)	5.65	1	NA	0.1 ± 0.3	0 ± 0	0.1 ± 0.3	0 ± 0	2
<i>Zelotes latreillei</i> (Simon, 1878)	7	1	NA	0.1 ± 0.3	0 ± 0	0 ± 0	0 ± 0	1
<i>Zelotes longipes</i> (Koch, 1866)	6.35	1	NA	0 ± 0	0 ± 0	0.3 ± 0.7	0 ± 0	3
<i>Zelotes petrensis</i> (Koch, 1839)	6	1	NA	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	1
<i>Zelotes subterraneus</i> (Koch, 1833)	6.5	1	NA	0 ± 0	0 ± 0	0.3 ± 0.7	0 ± 0	5
<i>Zora spinimana</i> (Sundev., 1833)	6.1	1	NA	0 ± 0	0 ± 0	0 ± 0	0.5 ± 0.8	5

GENERAL DISCUSSION

My study highlights that wildflower areas provide a suitable habitat during the vegetation period but also for the overwintering of ground-dwelling arthropods. As overwintering habitat, benefits were highest in simple landscapes with intermediate proportions of permanent semi-natural habitats and transient wildflower areas. During the vegetation period, ground-dwelling arthropod responses to permanent semi-natural habitats largely seemed to follow a hump-shaped pattern but showed a linear increase with the proportions of transient wildflower areas. Moreover, both types of semi-natural source habitats showed additive and interactive effects with generally highest benefits in simple landscapes. At the same time, wildflower areas enfolded positive effects in cleared landscapes, but only if established in high proportions. Although overall abundance and species richness of ground-dwelling arthropods did not increase across the three-year study period, an increased functional diversity of rove beetles in wildflower areas as well as of carabid beetles in crop fields show the enhancement of natural enemies and possibly their associated ecosystems services through the establishment of wildflower areas.

Since ground-dwelling arthropods vary in how they utilize different types of habitats in agro-ecosystems, i.e. partly for foraging during the vegetation period or solely as overwintering habitats, newly established wildflower areas may affect these cross-habitat spillover effects. By comparing wildflower areas and crop fields as overwintering habitats for ground-dwelling arthropods, I revealed that at least rove beetles and spiders seemed to prefer wildflower areas over crop fields, which is in line with previous studies (e.g. Frank & Reichhardt 1999; Ganser et al., 2019). Wildflower areas provide more stable overwintering habitats as compared to crop fields through abandoned management, which resulted in more undisturbed soils and a denser vegetation structure. Indeed, vegetation cover and density seemed to be most beneficial for rove beetle and spider overwintering as shown for wildflower areas and further semi-natural habitats such as hedgerows (Ganser et al., 2019, Mestre et al., 2018). The absence of management practices and pesticides as well as a high vegetation density in wildflower areas have also favored e.g. fitness and reproduction rates of carabid beetles and wild bees during the vegetation period (e.g. Diekötter et al., 2016; Ganser et al., 2020). A denser vegetation structure, for instance, may result in an increased quality and quantity of prey (e.g. Hoffmann et al., 2020) as well as may favour insulation to survive the overwintering period (Thomas et al., 1991). Hence, wildflower areas benefit ground-dwelling arthropods in agro-ecosystems during the entire year by providing suitable overwintering

habitats as well as ample resources during the vegetation period for a wide range of arthropods. However, since annual wildflower areas, which are ploughed during the overwintering period, have been shown to be poor overwintering habitats and may act as ecological traps (Ganser et al., 2019), future management of wildflower areas should be abandoned during the overwintering period, like realised in my study.

At this point, if wildflower areas benefit ground-dwelling arthropods during the entire year, these natural enemies should be able to stabilize or even increase their populations over time. My results show, however, that three years after the establishment of wildflower areas were not enough to overall increase abundance and species richness of ground-dwelling arthropods. The summer of the second year in my study was the warmest one on record with extremely high temperatures and low precipitations, which especially may have affected species phenology, body sizes, species-specific interactions and as a consequence, reduced abundance and species richness of rove and carabid beetles (cf. Scheffers et al., 2016). On the one hand, it seems surprising, that although abundance of rove and carabid beetles did not change substantially, wildflower areas have positively affected adjacent crop fields in my study. The community composition of beetles was initially distinct in wildflower areas and crop fields, but over time, it became more and more similar between these two habitat types. This may be the result of continuous spillover effects which are bidirectional between managed areas and semi-natural habitats (Boetzl et al., 2018). On the other hand, however, it is known that these spillover effects depend on selected traits of arthropods, i.e. larger carabid beetles are more mobile (Homburg et al., 2014) and may colonize new habitats faster than small ones (Boetzl et al., 2018). Hence, wildflower areas seem not to promote the entirety of ground-dwelling arthropods, but species with selected traits. In my study, this led to smaller and higher proportions of herbivorous rove beetles in crop fields, larger and higher proportions of herbivorous carabid beetles in wildflower areas and to more active hunting spiders in crop fields. Simultaneously with these spillover effects, ground-dwelling arthropods, as natural enemies, may bring their services into the adjacent crop fields and may increase the potential to control e.g. undesired arable weed seeds or to regulate pest species such as aphids (Diekötter et al., 2016, Rusch et al. 2015). This hypothesis is supported by an increased functional diversity of rove beetles in wildflower areas and of carabid beetles in crop fields in my study, which may also contribute to the overall stability of ecosystem functioning (Loreau & de Mazancourt, 2013).

The abovementioned, delayed effects observed for crop fields suggest that wildflower areas provide required corridors or stepping stones to increase the connectivity between annual and perennial habitats in agro-ecosystems (Bommarco, 1998). Spillover effects, however, depend on the landscape context and in particular on remaining permanent semi-natural habitats and recent findings showed that wildflower areas maximized benefits to arthropods such as bees and grasshoppers in simple landscapes as compared to cleared or complex landscapes (e.g. Concepción et al., 2008; Scheper et al., 2013). My results support these findings and additionally, show that this is also true for the benefits of wildflower areas as overwintering habitats. Throughout the entire year, abundance and species richness of ground-dwelling arthropods were in general highest in simple landscapes with intermediate proportions of 3-5% of permanent semi-natural habitats and increased linearly with higher proportions of transient wildflower areas. Apart from abundance and species richness, also selected traits and the functional diversity showed similar responses to the landscape context. Beyond those additive effects, permanent semi-natural habitats and transient wildflower areas had an interactive effect on ground-dwelling arthropods. Here, maximum benefits were realized at low proportions of permanent semi-natural habitats when proportions of transient wildflower areas were comparatively high. These diverging patterns for permanent semi-natural habitats and transient wildflower areas imply that, due to configurational and temporal differences, both habitat types differ in their completion to foster biodiversity benefits of newly established wildflower areas (Hoffmann et al., submitted). Benefits of permanent semi-natural habitats seemed to be highest at an equilibrium between an increasing resource-related species pool and a dilution effect (Tscharntke et al., 2012), whereas benefits of transient wildflower areas seem to increase with resource complementarity and connectivity at the landscape scale (Warzecha et al., submitted). In contrast to previous assumptions (Scheper et al., 2013; Tscharntke et al., 2012), my results imply that wildflower areas can also enfold benefits to agro-biodiversity in cleared landscapes but only if established at high proportions (Boetzel et al., 2021).

Beside overall positive effects of wildflower areas found in my study, AES have to gain credence as they are highly subsidized and conservationists and landowners thus, expect crucial conservation benefits. Due to limited financial resources and the land-use competition between agriculture and nature conservation, it is therefore, a key challenge to optimize currently applied AES. My results are among the first that highlight that wildflower areas also enhance non-target species such as ground-dwelling arthropods throughout the entire year and

thus, seem to counteract the lack of semi-natural habitats in agro-ecosystems by providing ample resources as well as suitable habitats e.g. for overwintering. Benefits, however, were crucially shaped by landscape context and temporal continuity. Inconsistent temporal arthropod responses across my study period may be driven by species-specific responses, which may partly be owed to the weather extremes. As climatic extremes such as dry and hot summers are expected to occur more frequently in the future, my findings indicate that it is important to establish wildflower areas that persist multiple years in order to ensure their aspired benefits. Moreover, further investigations should consider interactive effects of land-use and climate change beyond the three years in my study.

In order to sustainably maintain the functional guild of ground-dwelling arthropods and thus, their ecosystem services, conservation measures in agro-ecosystems should aim to protect remaining permanent semi-natural habitat as well as to establish additional sown wildflower areas, as both source habitats seem to complement each other. When resources are limited and priorities have to be set in intensively managed agro-ecosystems like in Northern Germany, sown wildflower areas should be established primarily in simple landscapes with intermediate proportions of already 3-5% of permanent semi-natural habitats. Here, transient wildflower areas should encompass at least 6-8% of the landscape and be maintained over multiple years. Also in cleared landscapes with less than 2% of permanent semi-natural habitats, wildflower areas can enfold benefits to agro-biodiversity, but only if established at high proportions with more than 10%. Thus, the joint proportions of permanent semi-natural habitats and transient wildflower areas in my study support the general claim of a safe minimum standard of 10-15% of semi-natural habitats to conserve the characteristic biodiversity in modern agro-ecosystems. Policymakers should compile future AES based on the landscape context to achieve the required proportions of semi-natural habitats in agro-ecosystems and thus, to ensuring their success.

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CURRICULUM VITAE**Personal Data**

Name	Hannes Hoffmann
Date of birth	17.11.1989
Place of birth	Neubrandenburg, Germany
Nationality	German

Education

Since 2020	Public employee at the Ministry for Environment, Climate, Energy and Agriculture Hamburg, Germany
2016 – 2020	PhD candidate at the Institute for Natural Resource Conservation in Kiel, Germany <i>Landscape- and time-dependent effects of wildflower areas on the non-target group of ground-dwelling arthropods</i>
2014 – 2016	Master of Science, Ernst-Moritz-Arndt-University Greifswald, Germany <i>Röntgen-mikroskopische Analyse von fossilen Laufkäfern (Coleoptera: Carabidae) im Baltischen Bernstein</i>
2010 – 2013	Bachelor of Science, Ernst-Moritz-Arndt-University Greifswald, Germany <i>Einfluss der Paludikultur auf die Staphylinidenfauna (Coleoptera: Staphylinidae) im Peenetal bei Anklam</i>
2006 – 2008	High school, Fritz-Greve-Gymnasium Malchin, Germany

LIST OF PUBLICATIONS

- ❖ **Hoffmann H**, Peter F, Diekötter T (in preparation) Sown wildflower areas increase the functional diversity of ground-dwelling arthropods in simple and complex landscapes across three years after their establishment.
- ❖ **Hoffmann H**, Peter F, Donath TW, Diekötter T (submitted) Time-dependent effects of permanent and transient semi-natural habitats on ground-dwelling arthropods in sown wildflower areas and adjacent crops. *Basic and Applied Ecology*.
- ❖ **Hoffmann H** (in press) Erstnachweis von *Anisodactylus signatus* (Panzer, 1797) (Coleoptera: Carabidae) in Schleswig-Holstein. *Faunistisch-ökologische Mitteilungen*.
- ❖ **Hoffmann H** (in press) Faunistisch bemerkenswerte Käfernachweise von Blühflächen in Schleswig-Holstein. *Faunistisch-ökologische Mitteilungen*.
- ❖ **Hoffmann H**, Peter F, Hermann JD, Donath TW, Diekötter T (2021) Benefits of wildflower areas as overwintering habitats for ground-dwelling arthropods depend on landscape structural complexity. *Agriculture, Ecosystems & Environment* 314: 107421.
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DECLARATION OF CO-AUTHORSHIP

If a dissertation is based on already published or submitted co-authored articles, a declaration from each of the authors regarding the part of the work done by the doctoral candidate must be enclosed when submitting the dissertation.

1. Doctoral candidate

Name: Hannes Hoffmann

2. This co-author declaration applies to the following article:





Benefits of wildflower areas as overwintering habitats for ground-dwelling arthropods depend on landscape structural complexity

The extent of the doctoral candidate's contribution to the article is assessed on the following scale:

- A. Has contributed to the work (0-33%)
- B. Has made a substantial contribution (34-66%)
- C. Did the majority of the work independently (67-100%)

3. Declaration on the individual phases of the scientific work (A,B,C)	Extent
Concept: Formulation of the basic scientific problem based on theoretical questions which require clarification, including a summary of the general questions which, it is assumed, will be answerable via analyses or concrete experiments/investigations	B
Planning: Planning of experiments/analyses and formulation of investigative methodology, including choice of method and independent methodological development, in such a way that the scientific questions asked can be expected to be answered	C
Execution: Involvement in the analysis or the concrete experiments/investigation	C
Manuscript preparation: Presentation, interpretation and discussion of the results obtained in article form	C

4. Signature of all co-authors

Date	Name	Signature
15.04.2021	John Herrmann	
15.04.2021	Tobias Donath	
14.04.2021	Franziska Peter	
14.04.2021	Tim Diekötter	

5. Signature of doctoral candidate

Date	Name	Signature
	Hannes Hoffmann	

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If a dissertation is based on already published or submitted co-authored articles, a declaration from each of the authors regarding the part of the work done by the doctoral candidate must be enclosed when submitting the dissertation.

1. Doctoral candidate

Name: Hannes Hoffmann

2. This co-author declaration applies to the following article:

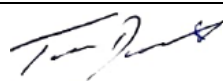


Time-dependent effects of permanent and transient semi-natural habitats on ground-dwelling arthropods in sown wildflower areas and adjacent crops

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- C. Did the majority of the work independently (67-100%)

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Manuscript preparation: Presentation, interpretation and discussion of the results obtained in article form	C

4. Signature of all co-authors

Date	Name	Signature
15.04.2021	Tobias Donath	
14.04.2021	Franziska Peter	
14.04.2021	Tim Diekötter	

5. Signature of doctoral candidate

Date	Name	Signature
	Hannes Hoffmann	