



How does conservation tillage affect redundancy and climate resilience of biological control by carabids?

Lisa Carlstrand

Master thesis in Biology • 30 credits
Swedish University of Agricultural Sciences, SLU
Faculty of Natural Resources and Agricultural Sciences
Department of Ecology
Agriculture Programme - Soil and Plant Sciences
Uppsala 2024



How does conservation tillage affect redundancy and climate resilience of biological control by carabids?

Hur påverkar plöjningsfri jordbearbetning jordlöparsamhällens redundans och klimatreiliens?

Lisa Carlstrand

Supervisor: Cassandra Vogel, SLU, Department of Ecology
Assistant supervisor: Mattias Jonsson, SLU, Department of Ecology
Examiner: Ola Lundin, SLU, Department of Ecology

Credits: 30 credits
Level: Advanced level, A2E
Course title: Independent Project in Biology
Course code: EX0898
Programme: Agriculture Programme - Soil and Plant Sciences
Course coordinating dept: Department of Aquatic Sciences and Assessment
Place of publication: Uppsala
Year of publication: 2024
Cover picture: *P. melanarius* by Fabian Bötzl
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Keywords: biological control, conservation tillage, carabid beetles, Carabidae, climate resilience, functional redundancy, climate niches

Swedish University of Agricultural Sciences
Faculty of Natural Resources and Agricultural Sciences
Department of Ecology

Abstract

Biodiversity plays an important role in sustainable food production, because of its contribution to several important ecosystem services, including biological control of pests by natural enemies. Predatory natural enemies, such as carabid beetles, have the potential to mitigate pest infestations and thereby improve crop yield and quality, as well as reduce the need for pesticides. However, field management, such as tillage, may affect carabid communities negatively, thereby reducing the effectiveness of the biological control. Additionally, anthropogenic climate change will lead to increased temperatures, and how this will affect the carabid communities, pest dynamics and ecosystem services is uncertain. Functional redundancy in the carabid communities can bolster the resilience of the ecosystem service by enhancing the likelihood of functional overlap, thus, ensuring the performance of a specific function, even if some species are lost or reduced. In this study, I assessed how functional redundancy and climate resilience of biological control as well as several carabid community metrics differ between two tilling systems: conservation tillage and ploughing. I also calculated the climate niches for six individual carabid species. Data were collected in 12 conventionally managed fields of winter wheat around Uppsala, Sweden, in June and July 2023. The main results showed that conservation-tilled fields had a higher species evenness and a higher activity density of carnivorous species, while ploughed fields had a higher activity density of omnivorous species, a larger community mean body size and a higher functional redundancy and climate resilience. I suggest that the higher functional redundancy in ploughed fields was partially driven by the increased abundance of large-bodied carabids, which, by consuming more prey due to their higher metabolic requirements, will contribute more to functional redundancy and further improve resilience. However, the dominance of one single large-bodied species will reduce functional redundancy, since it depends on the functional overlap between multiple species. Therefore, there must be additional factors explaining the higher functional redundancy and climate resilience in ploughed fields, beyond the promotion of large body size, which was not determined in this study.

Keywords: biological control, conservation tillage, carabid beetles, Carabidae, climate resilience, functional redundancy, climate niches

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1. Introduction

1.1 Biodiversity and ecosystem services

Biodiversity plays a central role in the functioning of all ecosystems, both natural and managed (Tilman et al. 2014). In agricultural contexts, biodiversity is a hot topic and frequently referred to as key to sustainable food production (Bommarco et al. 2013; Rusch et al. 2016; Dainese et al. 2019). This is because biodiversity contributes to several vital ecosystem functions, some of which can directly benefit humans as ecosystem services. They are beneficial because they contribute to improved crop yield and quality but can also provide an alternative management strategy, thereby reducing the need for agricultural chemicals (Bommarco et al. 2013; Jacobsen et al. 2022). Such biodiversity-driven ecosystem services include pollination and biological control of pests, weeds, and plant diseases (Martin et al. 2019). Insect pests are a problem in agriculture worldwide because they cause damage to crops, which can result in yield losses (Culliney 2014), but several species of arthropods, e.g. carabid beetles and spiders, are known to be predators of insect pests and contribute to biological control of these by being natural enemies (Sunderland et al. 1987; Collins et al. 2002). Unfortunately, research points to a rapid and extensive loss of biodiversity, including natural enemies, in agricultural landscapes due to intense management and landscape simplification, which endangers our global food production (Dainese et al. 2019).

1.2 Climate change

We stand in front of accelerating rates of anthropogenic climate change, and to what extent this will affect predator communities, pests, and ecosystem services in the future remains uncertain (Martin et al. 2019; Lehmann et al. 2020). However, climate change is increasing the mean temperature and is predicted to exceed the global mean warming at higher latitudes, e.g. in Scandinavia (Trenberth 2011; IPCC 2023). At the same time, temperature is the most critical environmental factor shaping arthropod feeding behaviour, survival, and geographic dispersal (Skendžić et al. 2021). This is because arthropods are ectothermic and rely on external heat

sources to regulate their body temperature. Thus, they are directly affected by the ambient temperature (Paaijmans et al. 2013). Furthermore, temperature plays a significant role in regulating their metabolic rate, but also various phenological events in arthropods, including reproduction, development and overwintering (Skendžić et al. 2021). The great impact of temperature on arthropods and the prediction of global mean warming at high latitudes makes Sweden an interesting country to study the potential ecological consequences of climate change on arthropod communities.

Previous studies have pointed out many different scenarios for pests and natural enemies in a future with increasing temperatures. For example, it is predicted that rising temperatures could lead to an expansion of the geographic range of some warm-adapted species and the introduction of new species to ecosystems. Higher temperatures might also contribute to a higher overwinter survival and faster reproduction and development, allowing more generations in one season (Skendžić et al. 2021). However, potential shifts in the timing of phenological events between trophic levels due to different responses to climate change among species may lead to a mismatch between the pest and its predator. For example, the pest could emerge earlier in the season than the predator (Damien & Tougeron 2019). Possible shifts in distribution patterns and phenological events may lead to an absence of natural enemies where the pest is present and vice versa and, hence, a decrease in the effectiveness of biological control (Thomson et al. 2010). It has also been shown that predation activity among carabids is strongly influenced by temperature. Some species become more active at colder temperatures, while others are more active at warmer temperatures (Feit et al. 2021). Further, it is predicted that elevated temperatures will increase the metabolic rates of insect pests, leading to larger populations and higher crop losses (Deutsch et al. 2018). Nevertheless, such kinds of predictive models rarely include the potential influence of natural enemies and underscore the possibilities for further research (Martin et al. 2019).

Another environmental factor affecting arthropods is humidity. As the temperature rises, water evaporation increases, elevating the levels of water vapour in the atmosphere. Although it is predicted that climate change will only have moderate effects on wind patterns, the increased amount of water vapour in the atmosphere can alter the precipitation patterns, potentially leading to more extreme climate events. For example, more intense and long-lasting droughts in usually arid areas and flooding in more wet areas will affect the climate on macro and micro levels (Trenberth 2011; Tabari 2020). As for the temperature, different arthropod species have different preferences regarding humidity; some prefer humid habitats, while others prefer drier ones (Lindroth 1986; Holland 2002). Thus, changes in humidity in habitats could lead to an alteration in species composition (Holland 2002).

Changes in temperature and air humidity due to climate change will most likely have significant impacts on the distribution and activity density of various arthropod species, potentially leading to alterations in entire ecosystems. However, the complexity of the situation makes it difficult to predict how pests and natural enemies will interact in a changing climate. Nevertheless, it is evident that there will be both winners and losers in the context of climate change (Thomson et al. 2010; Deutsch et al. 2018; Skendžić et al. 2021; Outhwaite et al. 2022).

1.3 Resilience of ecosystems

Ever since resilience was introduced as a concept by Holling in 1973, it has been defined extensively in the literature and can be explained as the ability of an ecosystem to resist disturbance by maintaining or regaining its function and stability (Gunderson 2000; Walker et al. 2003; Folke et al. 2010; Oliver et al. 2015). In this case, disturbance can be divided into “press” and “pulse” disturbances. Press is a gradual, long-term change, such as landscape simplification and habitat loss, but also changes in the environmental conditions, potentially resulting in higher mean temperatures and the invasion of new species. Pulse is, on the other hand, a sudden and severe disturbance, that does not persist (Glasby & Underwood 1996; Martin et al. 2019). In agricultural contexts, this could be disturbances connected to crop management, like tillage and pesticide application, but also extreme climate events (Thorbeck & Bilde 2004; Sánchez-Bayo et al. 2011; Donohue et al. 2016; Feit et al. 2019). Hence, an ecosystem with low resilience might not be able to resist disturbances and, therefore, risk passing a tipping point, after which the ecosystem cannot bounce back to its initial state (Folke et al. 2010; Martin et al. 2019). This will further affect the ecosystem services provided by biodiversity in agroecosystems (Biggs et al. 2012).

High biological diversity is thought to increase the resilience of ecosystem services. Different approaches can be used to quantify the biodiversity-induced resilience of ecosystems, including species richness, species evenness, functional diversity, response diversity and functional redundancy, but some approaches are more reliable than others (Martin et al. 2019). Species richness is the number of species found in an ecosystem. It is a simple way to quantify biodiversity but is not, by itself, the most reliable way (Woodcock et al. 2014). Theoretically, a high species richness is associated with an increasing likelihood of diverse species-specific responses to disturbance and, thus, an increased likelihood of ecosystem function maintenance. Especially if the evenness, the relative abundance of species in a community is high and the species are present in relatively same numbers (Alatalo 1981). But, in reality, species-rich ecosystems are not guaranteed to be resilient as their response to disturbance might be similar (Martin et al. 2019). Instead, a more

accurate way to assess resilience is to look into the different functions and responses to disturbance, known as functional diversity and response diversity, within a community (Martin et al. 2019). However, an important factor is also functional redundancy, which refers to the diversity of species performing similar functions (Oliver et al. 2015). Functional redundancy and response diversity are often identified in the literature as key factors in resilience, promoting stability to the ecosystem. It enhances the likelihood of functional overlap, ensuring that there will always be species capable of performing a specific function, even if other species are lost or reduced. In turn, this guarantees the maintenance of the ecosystem services (Feit et al. 2019, 2021; Martin et al. 2019).

1.4 Climate niches

All living organisms have a preferred spectrum of climate conditions, to which they are adapted to thrive, including temperature, precipitation and humidity. For instance, there are species of carabids in agroecosystems that are adapted to cooler temperatures while others are warm-adapted. As for other organisms, there are specialists adapted to a narrow and specific climate niche and generalists adapted to a broader spectrum of conditions (Deutsch et al. 2008). This range of temperature, in which the organism thrives, is referred to as a thermal niche. Carabids often have an optimal temperature where they are most active, foraging and reproducing (Feit et al. 2021).

Further, temperature determines the amount of water vapour that can be present in the air; higher temperature enables a higher amount of water vapour to be held in the air and vice versa (SMHI 2023). However, in practice, in temperate climates, a higher temperature also increases surface warming and evaporation, drying the soil and transporting away the water vapour. Therefore, drier conditions can be expected during hot days in most temperate regions (Henderson-Sellers 1996; Zhang et al. 2020). Humidity and precipitation are important climatic factors and, along with temperature, constitute a species' climate niche. This niche will further determine what types of habitats specific species can be found in (Liu et al. 2020). Despite this, scientific literature rarely highlights the importance of humidity and leaves a knowledge gap that requires further research. Understanding the climate niches of different species will also be an important key to understanding their response to climate change (Liu et al. 2020).

1.5 Carabids as natural enemies

In agricultural research, carabid beetles (Coleoptera: Carabidae) are extensively studied due to their activity density and diversity in agroecosystems, as well as for their contribution to biological control in a variety of crops (Collins et al. 2002; Holland 2002). Carabids are sensitive to changes in their environment, which, combined with their well-known taxonomy, makes them suitable as bioindicators to monitor changes in the environment (Rainio & Niemelä 2003). Carabid species have diverse dietary preferences, often referred to as feeding guilds; while some are carnivores, actively preying on other invertebrates like aphids, slugs or Lepidoptera larvae, others are granivores, feeding on seeds (Sunderland et al. 1987; Kromp 1999; Wallinger et al. 2015). A combination of these diets, referred to as omnivory, is common among carabids (Schumacher et al. 2020). Carabids in agriculture are often generalists rather than specialists and feed on various pests or seeds, making them attractive in research about biological control (Edwards et al. 1979; Östman et al. 2003). Over the past decades, research has advanced our understanding of carabid behaviour, their functions in agroecosystems and how they are affected by different types of disturbance (Holland & Luff 2000; Holland 2002; Legrand et al. 2011). However, there is a lack of knowledge regarding how functional redundancy and the resilience of biological control in carabid communities are affected by different field management and interventions. Therefore, this study will further assess the role of carabids as biological control agents in agriculture, with a particular focus on how their functional redundancy and resilience are affected by different tilling practices.

1.6 Soil management

Tillage is a fundamental part of agriculture, enabling the mechanical removal of weeds, preparation of the soil prior to sowing, and the incorporation of manure and crop residues for decomposition. There are several methods to use for this, including deep, inverting tillage like ploughing, or reduced tillage which covers a variety of methods often considered less intense than ploughing. Techniques which do not include soil inversion are often referred to as conservation tillage while methods that completely exclude tillage are known as no-till (Stinner & House 1990; Tamburini et al. 2016; Müller et al. 2022). These different methods all have advantages and disadvantages in various respects, including when it comes to how they affect biodiversity in agriculture. Soil tillage, especially ploughing, increases the mortality rate among ground-dwelling arthropods, including carabids, as a direct result of mechanical management practices and the soil inversion (Thorbeck & Bilde 2004). In contrast, carabids are known to be favoured by conservation tillage or no-till (Lalonde et al. 2012; Jacobsen et al. 2022). Additionally, soil

disturbance can affect carabid community traits like body size and shape the community in a certain direction (Kosewska et al. 2014). For example, tillage tends to affect larger-bodied carabids disproportionately, leading to a smaller community body size in more intensively managed fields (Blake et al. 1994). Further, tillage alters the soil physical properties of the soil, such as bulk density and water transportation, as well as the amount of crop residues on the soil surface (Blanco-Canqui & Ruis 2018). These are factors that may affect the carabid communities indirectly by altering the microenvironment and the food supply (Müller et al. 2022).

1.7 IMPRESS

The data used in this thesis is part of a European research project named IMPRESS, which spans over 3 years (2023–2026) and involves four participating countries (Sweden, Germany, Italy and Austria). The primary objective of the IMPRESS project is to increase our understanding of how biodiversity in agriculture can improve the resilience of biological control, both on a local and a landscape scale, and examine how it is affected by factors such as management methods, climate change and the surrounding landscape. Further, the project aims to generate tools and recommendations regarding management strategies to ensure resilient biological control, in order to prepare the European agricultural sector for climate change (SusCrop-ERA-NET 2023).

1.8 Aims and hypotheses

This thesis aims to assess the climate niches of carabid species common in cereal fields in Sweden, to compare the carabid communities between two different tillage treatments (ploughing vs conservation tillage), and further compare the functional redundancy of biological control and climate resilience between the two tillage treatments. Based on these aims, four hypotheses were formulated:

1. Higher activity density, species richness, species evenness and Shannon's diversity index are expected in conservation-tilled fields.
2. A larger community body size of carabids is expected in conservation-tilled fields.
3. Different climate niches are expected for different carabid species.
4. A higher functional redundancy and climate resilience of biological control are expected in conservation-tilled fields.

2. Material and methods

2.1 Study system

The field study was conducted in the summer of 2023. In the study, 12 fields of winter wheat sown during autumn 2022 were selected around Uppsala, Sweden. Winter wheat was selected as the study crop based on the reasons that (1) it is a crop cultivated in all the countries participating in the IMPRESS project (Sweden, Germany, Austria and Italy), (2) it is an economically important crop in the study regions, and (3) it is a crop affected by pests. Many invertebrates can be pests in various agricultural systems. In this study, a winter wheat system was used to test potential pest predation in a general context, not by focusing on a specific pest. Further, six of the fields were ploughed with mouldboard ploughs before sowing, and six were managed without ploughing, using conservation tillage practices, here defined as non-inversion tillage. For the fields where the farmers provided management data, tillage practices in conservation-tilled fields occurred at soil depths of 0–20 cm. This included the use of cultivators and disc ploughs (Table S2). In contrast, tillage practices in ploughed fields, for which the farmers provided management data, ploughing occurred at soil depths of 10–30 cm using a mouldboard plough (Table S2). The fields were arranged into six pairs, with a ploughed field (Figure 2) and a conservation-tilled field (Figure 3) in each pair, with the fields within a pair being directly adjacent or separated by a road. The minimum distance between the pairs was 2 kilometres.

All fields were managed conventionally but could have differed, both within and between pairs, in terms of soil tillage history, such as the duration of conservation tillage practices, pesticide applications or the pre-crop. Nevertheless, the pre-crop was always an annual crop. Detailed information about tillage practices and pesticide applications was provided by the farmers for five of the fields (Table S2–S4). However, the fields within a pair were mostly managed by the same farmer, therefore, the management and the variety of winter wheat planted were likely to be the same or similar.

Field sampling was made in two rounds between mid-June and mid-July. A sampling round was done in 8 days and included the collection of carabids with time-turning traps and dry pitfall traps, as well as recording climate data through temperature and humidity loggers.

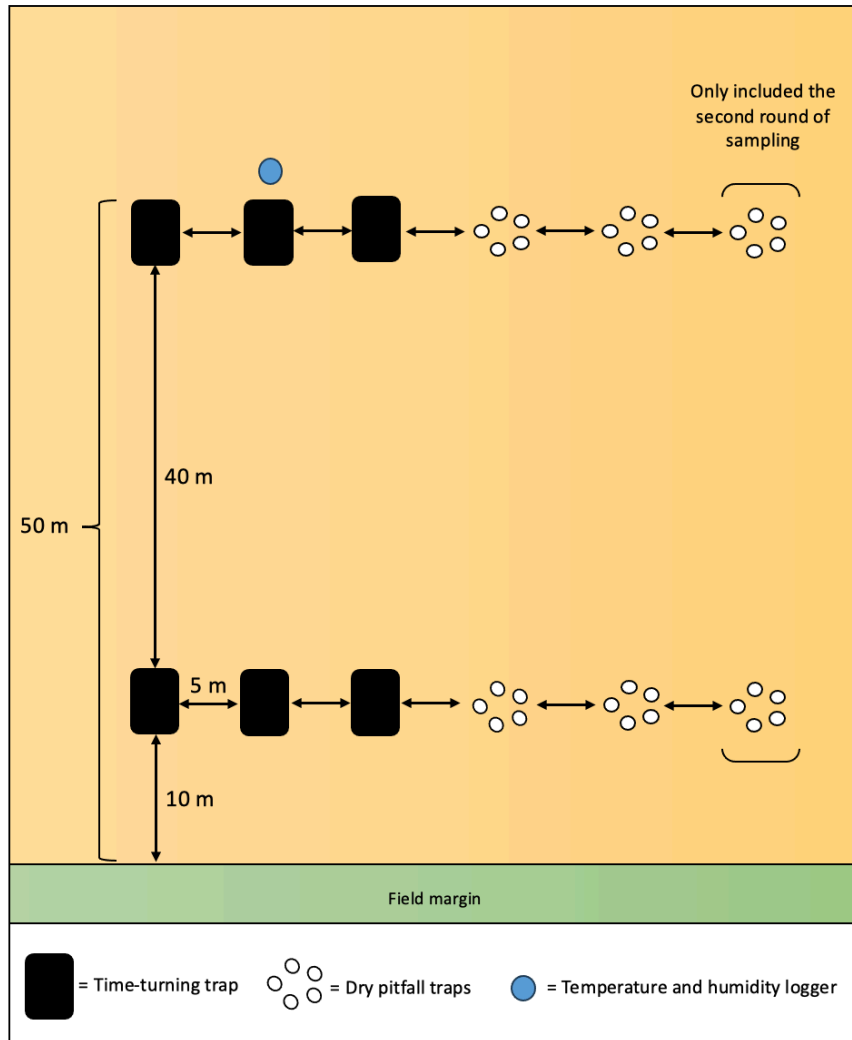


Figure 1. A schematic overview of the study design.



Figure 2. A ploughed field that was part of the field trial. This tillage practice includes soil inversion with a mouldboard plough. The field is located in Forkarby, Uppsala. Photo: Cassandra Vogel



Figure 3. A conservation-tilled field that was part of the field trial, which was tilled using non-inversion practices. The field is located in Forkarby, Uppsala. Photo: Cassandra Vogel

2.2 Sampling of carabids

Six time-turning traps were set up in each field to monitor the activity density and activity window of different carabid species, data which was further used to calculate species-specific climate niches. The trap consisted of a box measuring 27 cm in length, 24 cm in width and 11 cm in height, with an attached funnel (6 cm

height, 8 cm diameter) to serve as the trap entrance. The traps were powered by lithium-ion batteries. Three time-turning traps were placed 10 meters from the field margin, and three were placed at 50 meters, with 5 meters between each trap at the same distance (Figure 4). At least a 50-meter distance was kept between the outermost traps and all the surrounding field margins (Figure 1). The time-turning traps were programmed to turn every 2 hours for 24 hours, collecting ground-dwelling arthropods in vials filled with water and a small amount of dishwashing liquid. Some carabid species are known to be day active, while others are night active (Holland 2002), thus, time-turning traps enable the monitoring of carabid activity both during the day and at night.

In addition to the time-turning traps, dry pitfall traps consisting of plastic cups (11 cm diameter) with wood chips in the bottom (Figure 5) were used to analyse carabid community metrics. The dry pitfall traps were placed in clusters of five at the same distance from the field margin as the time-turning traps and at a distance of 5 meters from the traps at the same distance. During the first round of sampling, 20 dry pitfall traps were used. For the second round, the number of dry pitfall traps was adjusted to 30 due to insufficient captures during the first round. The data across the two rounds from the dry pitfall traps were pooled, therefore, the adjustment does not have any impact on the statistical analysis or the results. The dry pitfall traps were open for 24 hours during the same time as the time-turning traps.



Figure 4. Time-turning traps buried in the soil were used to trap carabids in two-hour intervals to allow interval-based collection and to further determine species-specific climate niches. It consists of a box with a funnel that is dug into the soil with the opening of the funnel in line with the soil surface. Within the box, there is a rotating wheel equipped with vials filled with water and dishwashing liquid. As the carabids fall through the funnel they are caught in the vials, with one vial representing a two-hour interval. Photo: Cassandra Vogel



Figure 5. Dry pitfall traps containing wood chips were used to capture live carabids in the field to further analyse carabid community metrics. Photo: Cassandra Vogel

2.3 Species-specific climate niches

The purpose of determining the species-specific climate niches was to estimate the climatic response diversity within the carabid communities, which in turn contributes to resilience. To do this, an air temperature and humidity logger (Elitech RC-51/51H) was placed in each field at 50 meters from the field margin, close to the time-turning trap in the middle. The logger was placed so that the sensor was approximately one centimetre above the soil surface to make sure that the ambient climate conditions where the carabids live were measured. The air humidity and temperature were measured every one minute for 24 hours. The mean temperature and humidity were calculated for every two-hour interval in which the carabids were captured in the time-turning traps. Then, the species-specific temperature and humidity niches were calculated, following Feit et al. (2021), by translating temperature-dependent activity patterns recorded in the field into a weighted temperature and humidity optimum (mean, μ) and a weighted temperature and humidity niche breadth (standard deviation, σ). For the climate niche calculations, only species where at least 10 individuals were captured in the time-turning traps were used. Thermal niches for six species were calculated from the data provided by this study, but due to insufficient capture of individuals across all species in 2023, 12 data-deficient species were supplemented with thermal niche data

collected in Uppland in 2017 by Feit et al. (2021). Although the thermal niche data covered only 50% of the species found in the study on which this thesis is based, 94% of all individuals in the carabid community detected in the study are covered by the thermal niches included in the resilience calculation.

2.4 Carabid identification and carabid traits

All carabids collected in the field were identified to species in the lab. To estimate the body length of each species, the median of the minimum and maximum body length stated for each species in Lindroth (1986) was calculated. Using information on the feeding guilds of carabid species or genera as described in Lindroth (1986), the carabid species were divided into three groups: granivores, carnivores and omnivores (Table S1).

2.5 Functional redundancy of biological control

Functional redundancy was defined as similarities in dietary preference among the carabids. Based on the feeding guild of the carabid species, the probability of a carabid with a certain feeding guild eating an insect pest was estimated. The probability was set to 0.9 for carnivores, 0.5 for omnivores and 0.1 for granivores, modified from Daouti et al. (2022). This means that the probability of eating an insect pest is high for carnivores, intermediate for omnivores, and low for granivores. By using a method similar to Feit et al. (2019), the feeding rate of different carabid species was estimated as a function of the species-specific metabolic rate. The metabolic rate scales as a function of body mass. The dry body mass of individual carabids M_i was estimated as a function of body length, following Jarošik (1989):

$$M_i = 0.03069 \times BL_i^{2.64}$$

where BL is the average body length for the given species i (Lindroth 1986). Next, the metabolic rate I of the given species i was estimated as a measure of their feeding rate:

$$I_i = 0.544 \times M_i^{3/4}$$

where 0.544 is a taxon-specific normalisation constant for carabids (Ehnes et al. 2011) and M is the average dry body mass of the carabid species i . Then, the estimated risk of pest predation R by the given carabid species i was calculated based on the probability of biological control based on feeding guilds p , activity density from the dry pitfall traps A and metabolic rate I :

$$R_i = p_i \times A_i \times I_i$$

Last, the functional redundancy of biological control of pests was calculated as the exponential of Shannon's diversity index $\Sigma(R_i \times \ln(R_i))$:

$$e^{H'b} = \exp(-\Sigma R_i \times \ln(R_i))$$

The calculation uses the risk of pest predation of a given species R_i instead of species activity density, which is commonly used for Shannon's diversity index (Stirling & Wilsey 2001; Hill et al. 2003). However, activity density was included in the calculations of R_i . Further, this approach follows a linear distribution with a doubling property. This will make it possible to directly compare functional redundancy between communities. For example, a community with an $e^{H'}$ value of 2 is considered to have a double functional redundancy compared to a community with a $e^{H'}$ value of 1. In dissimilar communities, the value of $e^{H'}$ is approaching zero and equals the total number of species in those communities which entirely consist of functional identical species occupying the same niche. Consequently, $e^{H'}$ penalises the carabid communities with a lower species richness. This means that if two communities show an identical niche overlap among individuals, but community A consists of twice as many species as community B, the $e^{H'}$ of community A is twice as much as of community B (Feit et al. 2019). Essentially, functional redundancy is here defined as the diversity of predation risk R_i provided by a specific carabid community. In this calculation, the functional overlap between species providing pest control contributes to a higher functional redundancy of pest control.

2.6 Climate resilience of biological control

Using the method from Feit et al. (2021), the risk of pest predation P by a given carabid species i at ambient temperature T , was calculated. The calculation was adjusted based on an approximation of metabolic rates and temperature-dependent probability of predator activity:

$$P_{T,i} = p_i \times A_i \times 0.544 \times M_i^{3/4} \times \exp\left(\frac{-(T - \mu_i)^2}{(2 \times \sigma_i^2)}\right)$$

Where p is the probability of a given carabid species i feeding on insect pests (0.9 for carnivores, 0.5 for omnivores and 0.1 for granivores), A is the activity density (from the dry pitfall traps) of carabids belonging to species i , 0.544 is the taxon-specific normalization constant (Ehnes et al. 2011), M is the average body weight

of species i , μ is the temperature activity optimum and σ is the thermal niche breadth of species i .

Further, the functional redundancy F of carabid community i at a given temperature T was calculated, and expressed as the exponential of the Shannon index (Feit et al. 2019, 2021):

$$F_{T,i} = \exp\left(-\sum_{i=1}^{\max(i)} P_{T,i} \times \ln P_{T,i}\right)$$

Finally, the climate resilience of biological control of pests R was calculated within the predator community i as the integral of functional redundancy along the temperature gradient:

$$R_i = \int_{T=6^{\circ}\text{C}}^{44^{\circ}\text{C}} F_{T,i}$$

2.7 Statistical analysis

All statistical analyses were performed in R Statistical Software (version 4.3.2; R Core Team 2023). Generalised mixed models (GLMMs) were used for all comparisons between ploughed and conservation-tilled fields, using the function ‘glmmTMB’ from the ‘glmmTMB’ package (Brooks et al. 2017). In these models, tillage treatment (ploughed vs conservation tillage) was used as a fixed factor and pair as a random factor. Pair was used as a random factor because the fields were arranged in pairs in the landscape and the paired fields could not be considered as independent replicates. Fixed and random factors were the same across all models. Since the catches from the time-turning traps were not sufficient enough to use for analyses, only carabids captured in the dry pitfall traps were used to compare the carabid communities between ploughed and conservation-tilled fields. However, the data from the time-turning traps was used to calculate temperature and humidity niches.

2.7.1 Carabid community metrics

To compare the carabid communities between ploughed and conservation-tilled fields, the following was calculated for each field on both of the sampling rounds: the activity density (i.e. the sum of individuals across all traps) and species richness (i.e. cumulative species richness across all traps). Additionally, by using the ‘diversity’ function of the package ‘vegan’, Shannon’s diversity index ($H = -\sum(p_i \times$

$\ln(p_i)$), where p is the proportion of species i in the community) and the species evenness ($E=H/\ln(S)$, where H is Shannon's diversity index and S is the species richness) were calculated (version 2.6-4; Oksanen et al. 2022). Shannon's diversity is a commonly used index that includes both the richness and evenness of the species within a community, based on the relative activity density of each species (Hill et al. 2003).

The activity density and species richness were count data, and therefore, the negative binomial and Poisson distribution were used for these models respectively. For activity density, the negative binomial distribution was used because the residuals were overdispersed. For Shannon's diversity index and species evenness, a Gaussian distribution was used.

To compare the proportional representation of the six most abundant carabid species (*Pterostichus melanarius*, *Poecilus cupreus*, *Trechus quadristriatus*, *Harpalus rufipes*, *Bembidion lampros* and *Epaphius secalis*) in the community, a binomial distribution was used. In these models, the captured number of individuals representing a specific species compared to the number of individuals not representing that species was tested. Additionally, the proportional representation of each feeding guild (granivore, carnivore and omnivore) was tested to examine if they differed between tillage treatments. This was done by using a binomial distribution, where the number of individuals in a certain feeding guild was compared to the number of individuals outside that feeding guild in each field. The proportional representation of individual species and feeding guilds were tested to find potential explanations and drivers for the results of functional redundancy and resilience.

To investigate if there was any difference in carabid community body size between the tilling treatments, the community weighted mean of carabid body size was calculated for each field. To calculate the community weighted mean of carabid body size, the function 'cwm' from the 'BAT' package was used (Cardoso et al. 2024). A Gaussian distribution was used to test for differences between tillage treatments.

2.7.2 Functional redundancy of biological control

To compare the functional redundancy of biological control between ploughed and conservation-tilled fields, the predation risk of pests by carabids was estimated based on the feeding guilds, body mass and metabolic rate of carabids, as described in section 2.5. For models assessing the difference in functional redundancy between the two tillage treatments, a Gaussian distribution was used.

2.7.3 Climate resilience of biological control

To compare the climate resilience of biological control between ploughed and conservation-tilled fields, the sum of the functional redundancy of biological control in a carabid community was calculated along a gradient of ambient temperature, as described in section 2.7. For models assessing the difference in climate resilience between the two tillage treatments, a Gaussian distribution was used.

All models were tested for the assumptions of normality, over- and under-dispersion, distributions (of residuals) and heteroscedasticity using the package ‘DHARMA’ (version 0.4.6; Hartig & Lohse 2022). For data visualisation, the packages ‘ggplot2’ and ‘gghalves’ were used (Wickman 2016; Tiedemann 2024).

3. Results

In the time-turning traps, 332 individuals from 23 species were captured (Table S1). For six of the species, 10 or more individuals were captured, and those were further used for species-specific calculations of climate niches. Those species were *Pterostichus melanarius* (n=126), *Poecilus cupreus* (n=62), *Trechus quadristriatus* (n=35), *Harpalus rufipes* (n=36), *Bembidion lampros* (n=17) and *Epaphius secalis* (n=24).

In addition, 1728 individuals of 36 different species were captured in the dry pitfall traps, and those were further used to analyse community metrics. The six most abundant species in the dry pitfall traps were similarly *Pterostichus melanarius* (n=655), *Poecilus cupreus* (n=258), *Trechus quadristriatus* (n=449), *Harpalus rufipes* (n=175), *Bembidion lampros* (n=77) and *Epaphius secalis* (n=112). The activity density data from the dry pitfall traps were added to the data from the time-turning traps to further calculate the carabid community metrics.

Across all catches, 29% of the species were carnivorous, 4% granivorous, and 67% omnivorous.

3.1 Carabid community metrics

The species evenness was higher in conservation-tilled fields compared to ploughed fields ($p=0.004$; Figure 6a; Table 1). However, the species richness ($p=0.135$; Figure 6b; Table 1) and the total activity density of carabids ($p=0.270$; Figure 6c; Table 1) did not differ between tillage treatments. Shannon's diversity index was marginally significant towards a higher diversity in conservation-tilled fields ($p=0.089$; Figure 6d; Table 1).

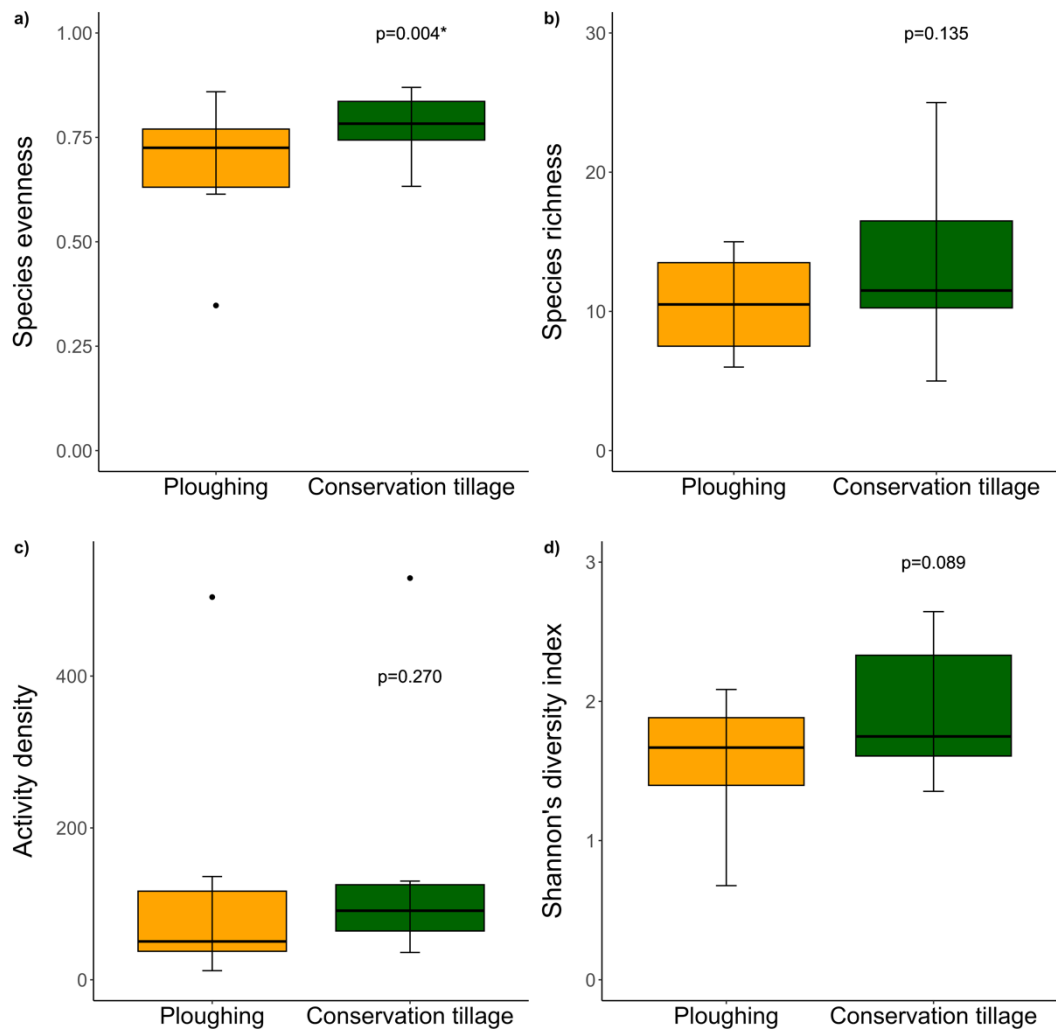


Figure 6. Species evenness (a), species richness (b), activity density (c) and Shannon's diversity index (d) of the carabid communities in ploughed and conservation-tilled fields. Boxplots represent the median (black line), 1st and 3rd quantiles, and the minimum and maximum of the data. * indicate significance level (* = $p < 0.050$, ** = $p < 0.01$, *** = $p < 0.001$). Dots indicate outliers.

Out of the six most abundant species, *E. secalis* ($p < 0.001$; Table 1; Figure S2a), *P. cupreus* ($p < 0.001$; Table 1; Figure S2b) and *T. quadristriatus* ($p < 0.001$; Table 1; Figure S2e) had a higher proportional activity density in conservation-tilled fields. In contrast, *P. melanarius* ($p < 0.001$; Table 1, Figure S2c) showed a higher proportional activity density in ploughed fields. The activity density of *B. lampros* ($p = 0.194$; Table 1; Figure S2f) and *H. rufipes* ($p = 0.352$; Table 1; Figure S2d) was not affected by the tilling system.

Further, the results showed that omnivorous carabids had a higher activity density in ploughed fields ($p < 0.001$; Figure 7c; Table 1) while carnivorous carabids had a higher activity density in conservation-tilled fields ($p < 0.001$; Figure 7a; Table 1). For granivores, there were no differences between tillage treatments ($p = 0.254$; Figure 7b; Table 1). In addition, the evenness of omnivorous species was higher in conservation-tilled fields ($p = 0.019$; Figure S3; Table 1)

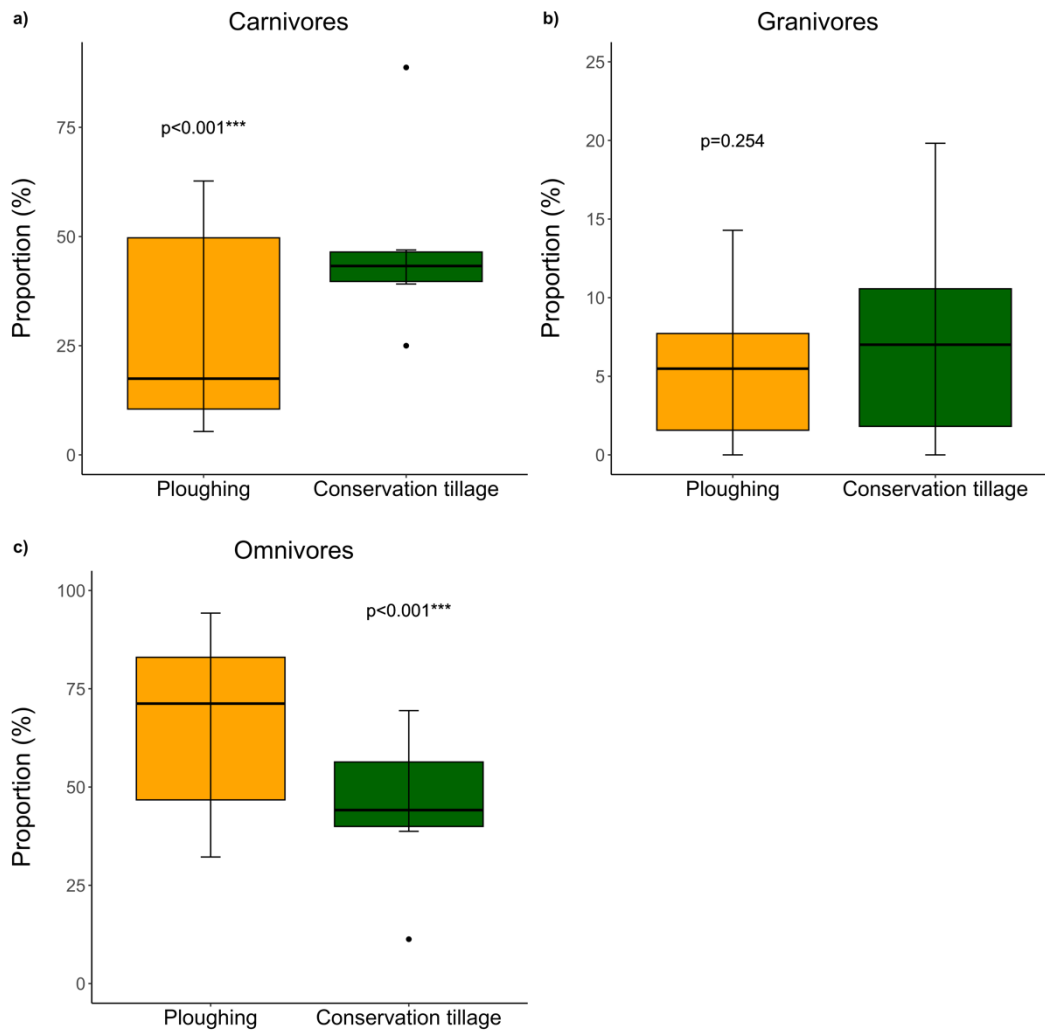


Figure 7. The proportions of carnivores (a), granivores (b) and omnivores (c) in ploughed and conservation-tilled fields. Boxplots represent the median (black line), 1st and 3rd quantiles, and the minimum and maximum of the data. * indicate significance level ($* = p < 0.050$, $** = p < 0.01$, $*** = p < 0.001$). Dots indicate outliers.

The community weighted mean of carabid body size was higher in ploughed fields compared to conservation-tilled fields ($p=0.003$; Figure 8; Table 1)

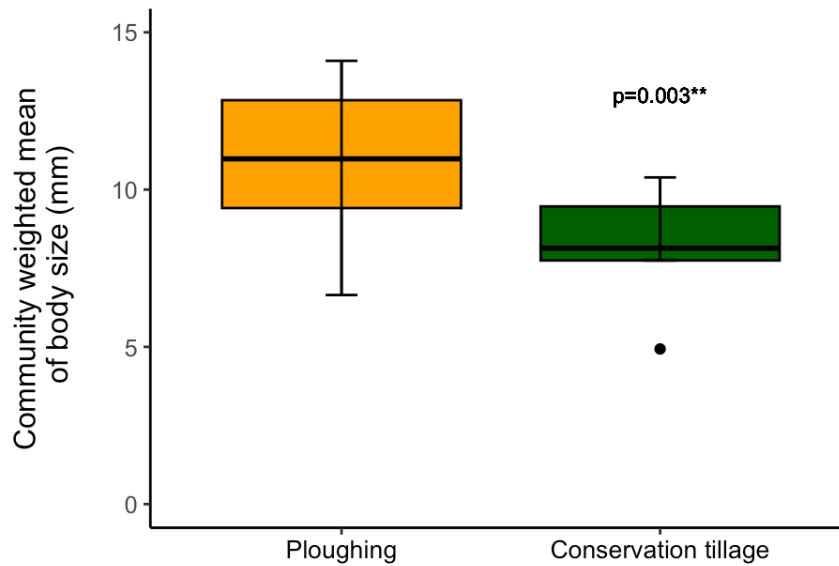


Figure 8. The community weighted mean of carabid body size in ploughed and conservation-tilled fields. Boxplots represent the median (black line), 1st and 3rd quantiles, and the minimum and maximum of the data. * indicate significance level (* = $p<0.050$, ** = $p<0.01$, *** = $p<0.001$). Dots indicate outliers.

3.2 Species-specific climate niches

The climate niches were calculated for six carabid species (Figure 9). The temperature optimum (mean, μ) for the different species ranged between 19.38°C and 32.41°C, with a mean optimum of 23.58°C. The thermal niche breadth ranged (standard deviation, σ) from 2.42°C to 8.73°C, with a mean breadth of 6.77°C. *P. cupreus* showed a higher activity density at warmer temperatures. *T. quadristriatus* had the most narrow thermal niche breadth, while *P. cupreus* had the broadest.

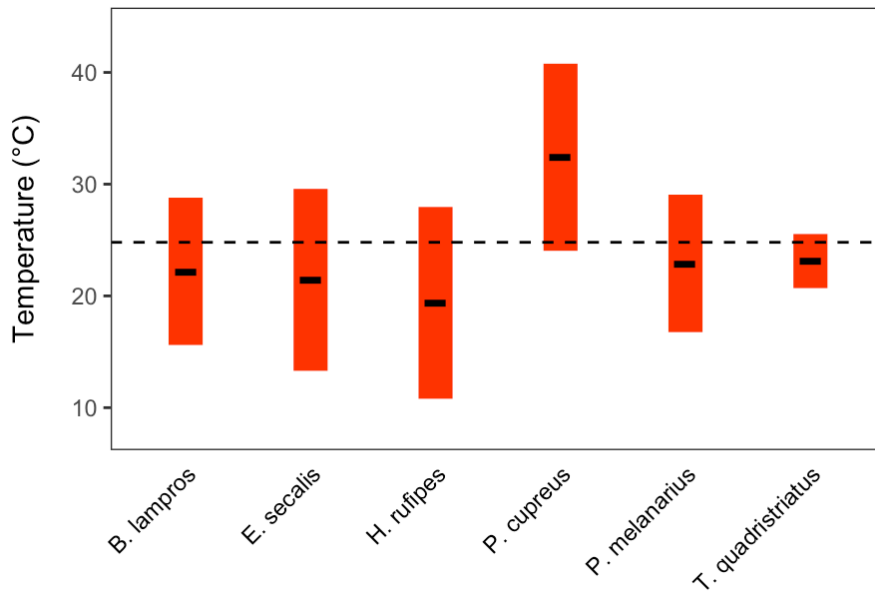


Figure 9. The species-specific thermal niches of the six most abundant carabid species in the field trial. The temperature optimum (mean, μ ; black lines) and the thermal niche breadth (standard deviation, σ ; red bars) are shown. The dashed line shows the mean ambient temperature (24.80°C) during the field trial.

The calculations of the humidity niches showed that the air humidity optimum (mean, μ) ranged from 51.14% to 76.63% for the six different species, with a mean optimum of 66.11% (Figure 10). The humidity niche breadth ranged from 4.55% to 22.35%, with a mean breadth of 16.97%.

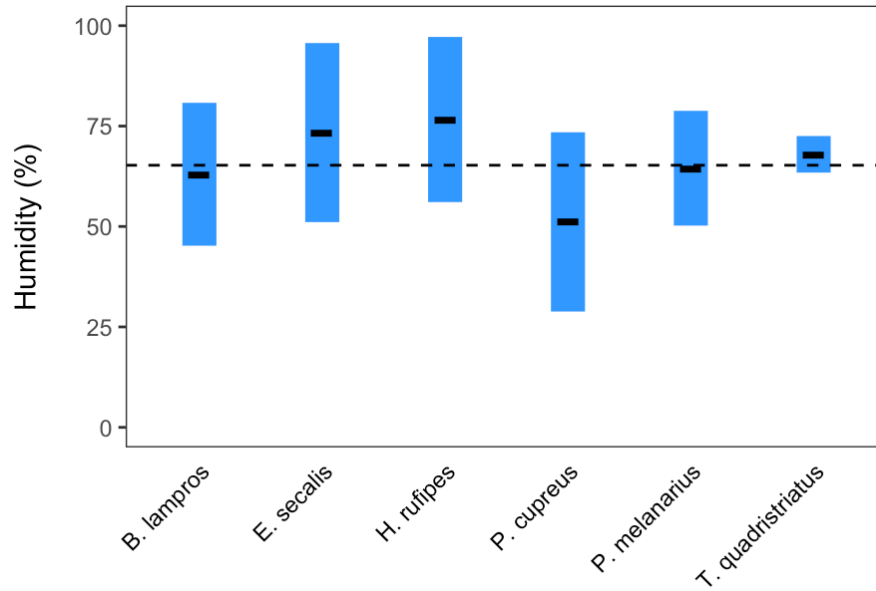


Figure 10. The species-specific humidity niches of the six most abundant carabid species in the field trial. The humidity optimum (mean, μ ; black lines) and the humidity niche breadth (standard deviation, σ ; blue bars) are shown. The dashed line shows the mean air humidity (65.25%) during the field trial.

3.3 Functional redundancy of biological control

Functional redundancy of biological control was higher in ploughed fields compared to conservation-tilled fields ($p=0.044$; Figure 11; Table 1).

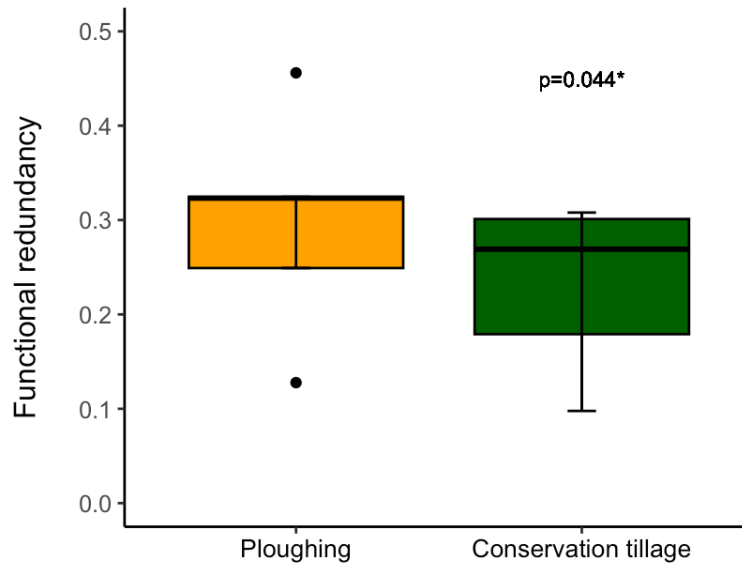


Figure 11. Functional redundancy of the carabid communities in ploughed and conservation-tilled fields. Boxplots represent the median (black line), 1st and 3rd quantiles, and the minimum and maximum of the data. * indicate significance level (* = $p < 0.050$, ** = $p < 0.01$, *** = $p < 0.001$). Dots indicate outliers. Functional redundancy is unitless, but it scales linearly.

3.4 Climate resilience of biological control

The climate resilience was higher in ploughed fields compared to conservation-tilled fields ($p=0.011$; Figure 12; Table 1).

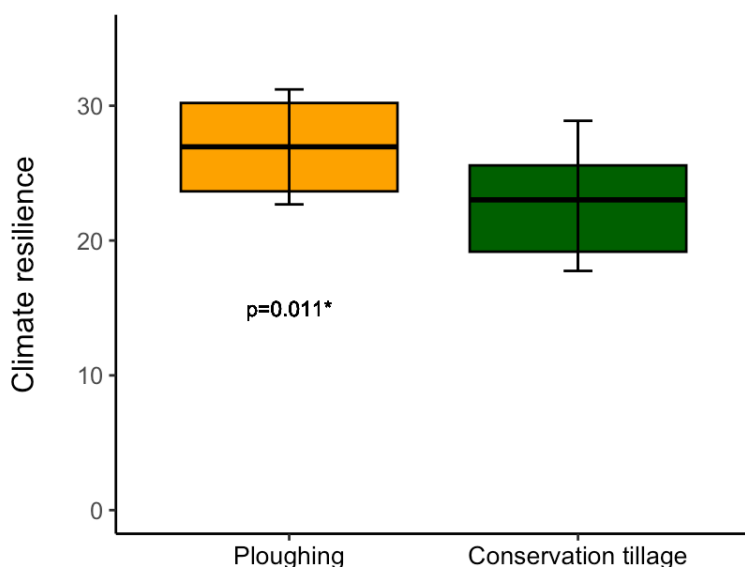


Figure 12. The climate resilience of the carabid communities in ploughed and conservation-tilled fields. Boxplots represent the median (black line), 1st and 3rd quantiles, and the minimum and maximum of the data. * indicate significance level (* = $p < 0.050$, ** = $p < 0.01$, *** = $p < 0.001$). Dots indicate outliers. Climate resilience is unitless, but it scales linearly.

Table 1. The results of the models used for assessing the responses of the carabid communities. df_{num} = numerator degrees of freedom; df_{den} = denominator degrees of freedom; R^2_m = marginal R^2 ; R^2_C = conditional R^2 . * indicate significance level (* = $p < 0.050$, ** = $p < 0.01$, *** = $p < 0.001$).

Response	Model type	Chi ²	p-value	df_{num}/df_{den}	R^2_m/R^2_C
Total activity density	GLMM with a negative binomial distribution	1.22	0.270	1/8	0.05/0.67
Species richness	GLMM with a Poisson distribution	2.24	0.135	1/9	0.09/0.58
Species evenness	LMM with a Gaussian distribution	4.07	0.044 *	1/8	0.14/0.61

Shannon's diversity index	LMM with a Gaussian distribution	2.89	0.089	1/8	0.14/0.45
Proportion of <i>E. secalis</i>	GLMM with a binomial distribution	25.3	<0.001***	1/9	0.40/0.99
Proportion of <i>B. lampros</i>	GLMM with a binomial distribution	1.69	0.194	1/9	0.02/0.99
Proportion of <i>H. rufipes</i>	GLMM with a binomial distribution	0.87	0.352	1/9	0.01/0.98
Proportion of <i>P. cupreus</i>	GLMM with a binomial distribution	14.6	<0.001***	1/9	0.04/0.99
Proportion of <i>P. melanarius</i>	GLMM with a binomial distribution	260	<0.001***	1/9	0.16/1
Proportion of <i>T. quadristriatus</i>	GLMM with a binomial distribution	260	<0.001***	1/9	0.58/0.99
Proportion of carnivores	GLMM with a binomial distribution	133	<0.001***	1/9	0.44/0.98
Proportion of granivores	GLMM with a binomial distribution	1.30	0.254	1/9	0.01/0.99
Proportion of omnivores	GLMM with a binomial distribution	140	<0.001***	1/9	0.47/0.98
Community weighted mean of carabid body size	LMM with a Gaussian distribution	8.55	0.003**	1/8	0.29/0.63

Evenness of omnivorous species	LMM with a Gaussian distribution	5.53	0.019*	1/6	0.25/0.59
Functional redundancy	LMM with a Gaussian distribution	4.06	0.044 *	1/8	0.19/0.48
Climate resilience	LMM with a Gaussian distribution	6.40	0.011*	1/8	0.25/0.58

4. Discussion

In line with my expectations (H1), ploughing significantly reduced the species evenness of carabids. However, no differences were observed for the total activity density, species richness, or Shannon's diversity index. Additionally, the community weighted mean of carabid body size was higher in ploughed fields, indicating a higher activity density of larger carabids in those fields, which contradicts my hypothesis (H2). I also determined different climate niches for six individual species (H3). Unexpectedly, ploughing increased the functional redundancy and the climate resilience of biological control, contrary to my expectations (H4). The results showed that the six individually tested species were affected by tillage treatment in various ways; some were favoured in ploughed fields, others in conservation-tilled fields or not affected at all. Several studies have discussed the complexity of the linkage between biodiversity and tillage treatment, showing various impacts on carabid beetles. However, while most studies conclude that minimum tillage benefits the carabid communities the most (Lalonde et al. 2012; Kosewska et al. 2014; Müller et al. 2022), my study shows ambiguous results. Thus, in summary, ploughing modified the structure of carabid communities and, surprisingly, improved functional redundancy and climate resilience of biological control.

4.1 Carabid community metrics

No differences in activity density were observed between tilling treatments in my study, contradictory to my hypothesis (H1). Although they are few, there are existing studies that support my findings (Müller et al. 2022; Heinen 2023). For example, Heinen (2023) measured the activity density of carabids before and after tillage. The study found that the effects of ploughing on carabid activity density were only evident immediately after the ploughing event in September. However, no effects were detectable when measured during June and July of the following year. Additionally, the same study revealed that no-till and conservation tillage practices had no impact on the carabid communities at all, neither immediately after tillage in September nor in June and July the following year, when compared to the sampling of the communities before the tilling event. These results align with my study, which sampled during June and July, showing no effects from either

ploughing or conservation tillage during those months. This suggests that tillage primarily affects the carabid communities during a short period after the tilling event, with quick recovery over time.

In contrast to my results, most studies report higher activity densities in conservation-tilled fields. For example, Kosewska et al. (2014) found that the overall activity density of carabids was higher in conservation-tilled fields. Similarly, Lalonde et al. (2012) reported a higher affinity for no-till among carabids due to improved food resources and refuges. Occasionally, these contrasting results can be explained by the dominance of one single species in the community. Activity density then becomes dependent on how this particular species is affected by tillage (Baguette & Hance 1997; Müller et al. 2022). For instance, Hatten et al. (2007) showed that excluding the dominant species from the analysis changed the results from indicating a higher total activity density in no-tilled fields to showing no differences between no-till and ploughing.

Out of the six individually tested species, *E. secalis*, *P. cupreus*, and *T. quadristriatus* had a higher proportional activity density in conservation-tilled fields. One factor considered to be the main reason why carabids prefer conservation tillage is that the crop residues are left on the surface, leaving the soil covered to a larger extent (Kladivko 2001). This provides the carabids with improved food resources in terms of alternative prey and weed seeds (Holland 2004), which could be inaccessible if the soil is ploughed and the crop residues buried. Surface crop residues also provide shelter from predators and shade during hot days (Lalonde et al. 2012). Moreover, the reduction of ground cover due to ploughing increases the soil surface temperature and causes the soil to dry up faster (Holland 2004). *P. cupreus* has previously been observed to prefer habitats with minimum tillage, while, in contrast to my results, *T. quadristriatus* has been associated with ploughed fields (Holland & Luff 2000). To my knowledge, the existing literature on *E. secalis* is more limited than that of the other species in my study. However, according to Wallin (1989), *E. secalis* is often found in uncultivated habitats adjacent to fields, and this preference for less disturbed environments is due to its forest origin. This could also explain why this species has a higher activity density in conservation-tilled fields in my study.

Some interesting observations were made by Sacco-Martret de Preville et al. (2022) regarding *P. cupreus* and *T. quadristriatus* and their occurrence in conservation-tilled and ploughed fields. The study compared the activity densities of carabids that emerged in the field to those of carabids that were circulating in the fields. The emerging community included carabid that had overwintered within the fields and that was captured in emergence tents. In contrast, the circulating community included carabids that were present and active within the field, but had not

necessarily emerged from them; these were caught in pitfall traps. Their findings showed that emerging carabids had a higher activity density in conservation-tilled fields, indicating a higher overwinter survival. Further, *T. quadristriatus* was the most abundant species in the emergence traps and almost 2.5 times more abundant in conservation-tilled fields. A reason for this could be that *T. quadristriatus* overwinters within the field as both adult and larvae and that the mortality rate among larvae is higher when the soil is ploughed (Thorbek & Bilde 2004; Sacco-Martret de Preville et al. 2022). Moreover, *P. cupreus* was mainly associated with the circulating carabid community, rather than the emerging one, and showed no preference for ploughing or conservation tillage (Sacco-Martret de Preville et al. 2022), in contrast to my results.

P. melanarius was the only species in my study which showed a higher proportional activity density in ploughed fields. Similar findings were reported by Baguette and Hance (1997). *P. melanarius* is an autumn breeder which often overwinters within the field, and by the time of ploughing prior to winter wheat, the eggs and early larval stage are already at a safe depth in the soil and, therefore, are less disturbed by ploughing compared to individuals present as adults at the time (Baguette & Hance 1997; Holland & Luff 2000; Larochelle & Larivière 2003). On the contrary, Shearin et al. (2007) showed that the activity density of *P. melanarius* declined for both ploughing and conservation tillage, further suggesting that this species is particularly vulnerable to soil disturbance. This is an interesting conclusion since the complete opposite was shown for *P. melanarius* in my study and the study of Baguette and Hance (1997), where it rather exhibited a preference for ploughed fields. However, the implementations between the different studies vary, which could be the cause of the contradictory results. Shearin et al. (2007) measured the effects of direct mortality directly after tillage but did not take overwintering individuals into account. The data collection in my study, as well as in Baguette and Hance (1997), was made in June and from April to harvest, i.e., at least 8 months after tillage. In other words, the carabid communities have had time for recovery and recolonization.

Tillage did not affect the proportional activity densities of *B. lampros* and *H. rufipes*. This is supported by previous observations indicating that they have no preference for ploughed and minimum tillage (Holland & Luff 2000). This suggests that they are adapted to different tillage practices and can thrive in various agricultural environments.

Carnivorous carabids had a higher proportional activity density in conservation-tilled fields, while omnivores had a higher proportional activity density in ploughed fields. For granivores, no differences between tillage treatments were observed. Looking at the activity density of the different feeding guilds between the tillage

treatments, it is evidently connected to the activity density of the most dominant species and their feeding guild. For instance, the carnivorous species *E. secalis* and *T. quadristriatus* had a preference for conservation tillage in my study. Similarly, omnivorous carabids in ploughed fields are reflected by *P. melanarius*'s preference for ploughing. Among the six most abundant species, there were no granivores present, and the activity density of granivores was overall low (4% across all catches). Their low number does not, however, explain why no effect of tillage was detected. Comparing the tillage treatments in terms of weed abundance is challenging due to the lack of information on potential herbicide applications. However, since no effect was detected, it is suggested that both treatments provide equal food resources in terms of weed seeds, or that other factors may influence their activity density.

A higher species evenness was observed in conservation-tilled fields in my study, aligning with my hypothesis (H1). I suggest that could be due to a selection towards a more specialized carabid community in ploughed fields, favouring certain types of species that tolerate ploughing and the environment it creates afterwards. Further, conservation-tilled fields could potentially favour a broader range of species equally, resulting in a more generalised carabid community further increasing the species' evenness. However, limited research exists on species evenness as a community metric regarding carabids in different tilling systems. In the limited literature available there are reports of a greater species evenness in conservation-tilled spring crops such as spring wheat, pea, and barley but no difference between tillage treatments in winter wheat (Hatten et al. 2007), which is the crop in my study, thereby, providing contradicting results.

No increase in species richness or Shannon's diversity index was seen in conservation tillage, contradicting my hypothesis (H1). However, there was a trend towards a higher Shannon's diversity in conservation-tilled fields, although it was marginally significant. Shannon's diversity index combines species richness and species evenness (Hill et al. 2003), and in cases where species richness remains stable while species evenness increases, a higher Shannon's diversity is expected. This was evident in my study, where species richness was unaffected by tillage practices, while species evenness was significantly higher in conservation-tilled fields. This explains the trend towards a higher Shannon's diversity under conservation tillage. Looking at previous research, Kosewska et al. (2014) found no effect of conservation tillage or ploughing on the average species richness over the season, but noted slight differences in the seasonal distribution of species between the tilling treatments, with a higher richness in ploughed fields at some points during the season, and vice versa. However, the majority of the existing studies report both a greater species richness and higher Shannon's diversity index

under conservation tillage or no-till conditions (Baguette & Hance 1997; Müller et al. 2022).

Finally, ploughed fields benefitted carabid species with larger body sizes, contradicting my hypothesis (H2). In my study, the most abundant species was *P. melanarius* which is considered a large species (Jacobsen et al. 2022) and is favoured by ploughing, therefore, it is reasonable to suggest that this dominating species explains the result. Body size is frequently brought up as a functional trait affected by habitat disturbance (Blake et al. 1994; Kladivko 2001; Jacobsen et al. 2022). Generally, large-bodied organisms have a greater dispersal ability (Jenkins et al. 2007), thus, a greater capacity to escape unfavourable conditions as well as quickly recolonize when the conditions are favourable again (Wardle 1995). The high activity density of large-bodied carabids in ploughed fields could therefore be due to a quick recolonization from adjacent habitats. However, there are differences in the flying capacity among carabid species, and this should be taken into account when considering their dispersal and recolonization patterns (Venn 2016). In addition, there could be possible differences in overwintering strategies between species, causing more or less harm during the tillage event. For instance, this could involve whether they are active and can escape the disturbance or if they are in hibernation stage in the soil, and in that case on what depth, when tillage occurs. Individuals overwintering on a shallow depth are therefore more vulnerable to tillage than those who are active or on an overwintering depth below the tillage zone (Holland & Luff 2000). However, some contradictory studies show a decline in the activity density of large-bodied carabids with increasing management intensity (Blake et al. 1994; Kladivko 2001), potentially due to unfavourable shifts in the food web or a higher mortality risk among larger individuals (Wardle 1995; Kladivko 2001).

4.2 Species-specific climate niches

The species-specific temperature and humidity niches in my study evidently reflect each other, which is due to the strong negative correlation between temperature and humidity (Figure S1). Because of this, a broad thermal niche is associated with a broad humidity niche, and a high thermal optimum is associated with a low humidity optimum. For instance, the results show that *T. quadristriatus* had the narrowest thermal and humidity niches, while *H. rufipes* and *P. cupreus* had the broadest. These results confirm my hypothesis regarding different climate niches for different carabid species (H3), thus, it demonstrates the diversity in the climate response within the carabid communities. However, given this strong correlation between temperature and humidity in my study, an essential question arises: what is the limiting niche for carabids under field conditions? Based on the fact that

carabids are ectothermic and temperature regulates their metabolism and various phenological events (Paaijmans et al. 2013; Skendžić et al. 2021), it is likely that temperature is the driving factor in determining a species climate niche. Additionally, the impact of temperature on the biological control of pests is supported by experiments demonstrating an increase in carabids' attack rates when the ambient temperature falls within their thermal niche (Feit et al. 2021).

P. cupreus was the most warm-adapted species in my study with an optimum of 32°C and the majority of the niche above the mean ambient temperature of 24.8°C. Interestingly, this was the only species in my study that had an optimum above the mean ambient temperature. Similar observations regarding *P. cupreus* were made by Feit et al. (2021), who determined an optimum of 30.2°C under a mean ambient temperature of 24.1°C. *P. cupreus* is a commonly occurring species in agroecosystems across our latitudes in Sweden, but its range and abundance extend to southern Europe (Boetzl et al. 2023). These findings together indicate that *P. cupreus* is highly adaptive and tolerates warmer temperatures than is expected around Uppsala, Sweden. Therefore, it might be more dominant in the future when a warmer climate is expected, making it an interesting species for studying the impacts of climate change on biological control.

4.3 Functional redundancy of biological control

In contrast with my expectations (H4), ploughing significantly increased the functional redundancy of biological control, hence, indicating a higher degree of functional overlap in fields where the soil is inverted. Functional redundancy of predator communities in agroecosystems has been a subject of investigation in numerous studies up until today. However, the focus has been assessing the overall functional redundancy on a community level, not by looking at a specific ecosystem service such as biological control (Rusch et al. 2014; Woodcock et al. 2014; Roubinet et al. 2018). Feit et al. (2019) developed “a method to quantify the level of functional redundancy for individual ecosystem processes within functional groups”, which is also the method on which the calculations for my study are based. However, according to my knowledge, no existing studies have compared the functional redundancy of carabid communities between different tilling systems, such as ploughing and conservation tillage. Instead, the existing studies rather focused on how functional redundancy is affected by farming systems such as organic versus conventional farming (Rusch et al. 2014; Woodcock et al. 2014; Roubinet et al. 2018; Feit et al. 2019), while I focused on an individual intervention.

Another factor frequently analyzed in studies assessing functional redundancy is the complexity of a landscape, characterized by the diversity and distribution of

different habitats (Rusch et al. 2016; Dainese et al. 2019; Feit et al. 2019, 2021). A more complex landscape contains a higher proportion of diverse natural or semi-natural habitats in relation to arable land, making the landscape more heterogeneous (Tamburini et al. 2016). The availability of natural or semi-natural habitats such as field margins, forest patches, pastures, beetle banks and non-crop habitat islands is known to benefit carabids and other natural enemies, by providing shelter, sites for overwintering and alternative food resources (Landis et al. 2000; Collins et al. 2002; Holland et al. 2017). Feit et al. (2019) found that the functional redundancy of biological control was positively affected by this type of heterogeneous landscape. This shows that the complexity of the surrounding landscape is an important driver in understanding the dynamics of functional redundancy of biological control within ecosystems. Therefore, I suggest that landscape complexity should be included in future research assessing how functional redundancy of biological control is affected by a particular field management.

The analysis of functional redundancy in my study was based on variables such as Shannon's diversity index, total activity density, feeding guilds and body size. The only effect of tillage on community metrics was species evenness, community body size and feeding guild, whereas feeding guilds can be considered a result of species evenness. Therefore, I suggest that the differences in functional redundancy between ploughed and conservation-tilled fields are partially driven by ploughing benefitting large-bodied carabids. Larger species have a higher metabolic rate and consume more prey; thus, they potentially also have a greater impact on functional redundancy than small species. The large species, most of which are generalist species, in my study might also occupy a similar ecological niche, and therefore they might be redundant. However, this is not a complete explanation. The presence of one single large-bodied species does not increase functional redundancy; on the contrary, it reduces it. Even though highly abundant species are assumed to contribute the most to ecosystem services (Gaston 2010; Winfree et al. 2015), functional redundancy is dependent on the degree of functional overlap between several species, and therefore a certain richness of evenly distributed species is required. Thus, there must be an additional factor explaining the higher functional redundancy in ploughed fields, other than the promotion of a large body size.

Furthermore, it is relevant to investigate if different tilling methods contribute to trade-offs between different ecosystem services, such as biological control of pests and biological control of weed seeds. For instance, while certain tillage practices might enhance the biological control of pests, the same practice might affect the biological control of seed weeds, or other ecosystem services, negatively. Tillage practices can also affect different taxa differently (Thorbeck & Bilde 2004; Heinen 2023), therefore, it is important to investigate the effects on natural enemies other than carabids. Additionally, it is essential to repeat the study in other cropping

systems, to see if the findings are consistent. This would give us a broader understanding of how tillage practices impact natural enemies and their functional redundancy across various agricultural contexts.

4.4 Climate resilience of biological control

Similar to the functional redundancy, the climate resilience was higher in ploughed fields, contradictory to my hypothesis (H4). It was expected to see the results of climate resilience reflecting those of functional redundancy. In my study, I assessed the climate resilience of biological control, defined as the sum of functional redundancy within carabid communities, along a gradient of ambient temperature (Feit et al. 2021). Consequently, climate resilience in my study depends on the level of functional redundancy in combination with the response diversity in the carabid communities.

Resilience is a widely used concept in ecological contexts (Folke et al. 2010; Biggs et al. 2012; Kühnel & Blüthgen 2015; Oliver et al. 2015), but it is difficult to measure it in complex agroecosystems (Cabell & Oelofse 2012). However, other variables are commonly used to estimate resilience, and the approaches often vary between studies. For example, as seen in my study, functional redundancy is known to be one predictor of resilience, but a high redundancy does not solely guarantee high resilience. If the species contributing to similar functions in a community respond similarly to environmental changes, it still might lead to the extinction of a specific function (Mori et al. 2013). In other words, functional redundancy only contributes to a resilient ecosystem if there is a high response diversity in the community, meaning the individual species respond differently to disturbance (Elmqvist et al. 2003). In my study, the species-specific response to temperature was investigated and I concluded that the responses were different between species. It was also possible to see that species were affected differently by tillage due to the different species-specific activity densities, thus, there was a certain degree of response diversity in the communities. However, it is difficult to draw any conclusions regarding the responses to tillage since the mechanisms behind the response are unknown. It could have been caused by the direct effect of mechanical disturbance, changes in food availability or other changes in the environment.

My approach to estimating resilience was based on functional redundancy, but other approaches can also be used. For example, functional diversity is considered an indicator of ecosystem service resilience according to several authors (Woodcock et al. 2014; Martin et al. 2019; Jacobsen et al. 2022). This is because a high functional diversity potentially allows the carabid communities to effectively perform a given function in a wider range of crops with different traits and

management, thus, increasing the resilience of the particular ecosystem service (Martin et al. 2019). Functional diversity in carabid communities has been compared between tillage treatments in a recent study by Jacobsen et al. (2022). In this case, functional diversity was assessed based on one single functional trait, namely body size, which is known to be strongly associated with several other traits, for example, dispersal, habitat selection, diet and metabolic rate (Kotze & O'Hara 2003; Woodcock et al. 2014; Daouti et al. 2022), which in turn are traits that affect the biological control. Jacobsen et al. (2022) found that conservation tillage promoted a greater variation of body sizes compared to ploughing and reduced tillage, thus, a higher functional diversity, further suggesting a higher resilience in those communities. Additionally, functional diversity was positively affected by higher availability of semi-natural habitats (Jacobsen et al. 2022), confirming that the surrounding landscape influences the resilience (Tamburini et al. 2016; Feit et al. 2021). Despite different approaches, making it difficult to compare the results of Jacobsen et al. (2022) to my results, this points out that resilience can be assessed and interpreted in various ways.

Although research on climate resilience of biological control is limited, one study examined the thermal resilience of another ecosystem service: pollination. This was performed by Kühnel & Blüthgen (2015), who determined the thermal resilience of pollination along a gradient of land use intensity in grasslands, ranging from semi-natural grasslands to intensively managed grasslands. It was shown that the species in intensively managed grasslands had a broader thermal niche and were more generalist species, indicating a pollinator community with high thermal tolerance. In addition, the species-specific thermal optima were more variable within intensively managed grassland, resulting in a higher response diversity in those ecosystems and, hence, a higher thermal resilience (Kühnel & Blüthgen 2015). However, functional redundancy of pollination at different temperatures was not calculated in the study by Kühnel & Blüthgen (2015). It could, therefore, be considered a limiting factor, since resilience is both dependent on functional redundancy and response diversity (Elmqvist et al. 2003). Nevertheless, these findings imply that agroecosystems with intense management have promising potential to withstand future temperature changes caused by climate change. This is by promoting generalists with broad niches and high tolerance resulting in a higher resilience, and thereby ensuring the provision of essential ecosystem services. In contrast, it is reasonable to expect a decline for specialized species (Kotze & O'Hara 2003), which may, due to their narrow niche breadth, be more vulnerable to climate change and landscape simplification.

4.5 Limitations of the study

The field study was conducted at privately owned fields around Uppsala, and the management of those during the cropping season was carried out without taking the field trial into account. For instance, insecticides were applied once in two fields during the study (on the dates 26.06.2023 and 23.06.2023; Table S3), and also fungicides and herbicides were applied in some of the fields (Table S3–S4). This type of detailed information was only provided by the farmers for five of the 12 fields in the study. However, these are interventions that possibly could have affected the results. Pesticides can potentially harm non-target organisms like carabids (Geiger et al. 2010), and an application close to the carabid sampling events may have resulted in a lower activity density in those fields. However, the recorded applications were similar within each pair and should therefore even out the differences within each pair. Additionally, previous crops cultivated in the field may also impact the carabid communities. Perennial ley crops, for instance, are considered a more favourable habitat due to the minimal disturbance compared to annual crops (Bommarco 1999; Heinen et al. 2023), and this could affect the carabid community in the following years. Different crops also leave different amounts and quality of crop residues in the field, which could affect the food webs and the microenvironments (Kladivko 2001; Holland 2004; Lalonde et al. 2012). Further, conservation tillage was defined as non-inversion tillage in this study, thus, it does not imply a complete exclusion of soil disturbance. The level of soil disturbance within the conservation tillage method may also vary; it may be relatively deep whereas ploughing might be shallow. This could potentially even out the differences between the carabid communities in conservation-tilled and ploughed fields.

Possible limitations could also have occurred due to the trapping method. While time-turning traps are theoretically efficient tools enabling the capture of ground-dwelling arthropods in a short time frame with minimum work effort, regular pitfall traps require manual emptying, thus, a greater work effort if captures are to be accomplished in a short time frame. The time-turning traps consist of a box with a funnel that is dug into the soil with the opening of the funnel in line with the soil surface. However, as the box was buried in the soil, a significant area of the soil surface surrounding the funnel entrance was disturbed by the digging. This area was differently aggregated, contained cracks and lacked vegetation (see Figure 4). This difference could potentially have been sensed and avoided by the carabids, which could have resulted in the overall low captures in the time-turning traps. Regular pitfall traps are a more common capture technique in field research which does not disturb the surrounding soil surface to the same extent as time-turning traps (see Figure 5), although they tend to be biased towards the capture of larger-sized carabids (Spence & Niemelä 1994). Additionally, the carabid community metrics

in my study were calculated based on the data from the dry pitfall traps with six replicates in each treatment. Having such relatively few replicates makes the result sensitive to outliers.

Further, to assess functional redundancy and resilience of biological control, I divided the carabids into three broad feeding guilds (granivores, carnivores and omnivores). Omnivores were the most abundant feeding guild in my study, but even within the guild, species might still vary a lot in their preference of prey and their feeding rate on cereal pests. An alternative method would be to utilize data provided from gut content analyses, enabling a more detailed insight into species-specific diets.

Finally, my study lacks a measure of pest feeding rates, which could be obtained by using aphid cards or assessing pest density within the field. Thus, it is impossible to fully ascertain that the high resilience and functional redundancy in ploughed fields contribute to better biological pest control. This is an aspect that could be considered in future research, to contribute to the knowledge regarding how carabids and their biological control are affected by tillage.

4.6 Conclusions

In this study, I assessed the climate niches of six individual carabid species and compared how several carabid community metrics were affected by tillage, namely conservation-tillage and ploughing. Further, I assessed how functional redundancy and climate resilience of biological control by carabids were affected by tillage. By doing this, I presented a novel approach that looks into the redundancy and resilience of a particular ecosystem service and compares those metrics between two tilling systems. Understanding these dynamics is important to predict how carabid communities and their biological control are affected by agricultural management, particularly in the context of climate change. Furthermore, this knowledge is essential for maintaining ecosystem functioning and the provision of ecosystem services. Based on the findings of the study I can conclude that ploughing significantly reduced species evenness, but, surprisingly, it enhanced functional redundancy and resilience of biological control, partially by promoting carabid species with a larger body size. Large species have, due to their higher metabolic rate, a larger impact on functional redundancy, which in turn also affects resilience. However, there must be another factor, besides body size, behind this result, since the dominance of one single large-bodied species would decrease the resilience rather than increase it. What this additional factor was, was not possible to determine in this study.

Nevertheless, it is important to keep in mind that ploughing can be disadvantageous compared to conservation tillage in other aspects. For example, ploughing negatively affects soil biodiversity including soil bacteria and fungi, as well as soil fauna such as earthworms (Briones & Schmidt 2017; Sun et al. 2020). Further, it requires greater fuel consumption, reduces soil carbon sequestration and may lead to greater soil carbon emissions which have negative environmental impacts (West & Marland 2002; Sarauskis et al. 2012). These are all things that farmers have to consider when making decisions regarding soil management.

Overall, my findings emphasise that carabid communities in agricultural ecosystems are highly adapted to disturbed environments, thus, they have a promising capacity to maintain their ecosystem service even under intense soil disturbance or climate change. Nevertheless, increased disturbance from multiple sources risks pushing the communities past a tipping point. At this point, the disturbance is too great for the community and will affect the species in a way where recovery is implausible, thus, causing persistent damage to the provision of the ecosystem service. Therefore, I recommend carefully monitoring the response of carabid communities to management disturbance and climate change and to further use this knowledge when advising farmers. Adapting the management with this in mind is important to maintain functional redundancy and resilience of biological control by carabids under future conditions.

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Populärvetenskaplig sammanfattning

Biologisk mångfald spelar en viktig roll i ekosystemens funktion och för de ekosystemtjänster vi kan dra nytta av inom jordbruket. Ett exempel på en sådan ekosystemtjänst är kontroll av skadedjur. Denna ekosystemtjänst utförs av olika rovlevande nyttodjur, bland annat jordlöpare som en är familj inom skalbaggar. Jordlöpare, och andra nyttodjur, kan dock påverkas negativt av olika åtgärder som görs i fältet, såsom jordbearbetning och användning av bekämpningsmedel. Dessutom står vi inför klimatförändringar och ökande medeltemperaturer som kommer ändra förhållandena i fälten. Vi vet inte säkert hur detta kommer påverka jordlöpare och om de kommer kunna fortsätta leverera viktiga ekosystemtjänster när klimatet förändras. För att bibehålla ekosystemtjänster under störningar som jordbearbetning och temperaturhöjningar behövs en motståndskraft, så kallad resiliens, i jordlöparsamhället, vilket kan uppnås genom en hög grad av funktionell redundans. Funktionell redundans betyder att det finns ett överlapp gällande olika arters funktion i ekosystemet, till exempel att flera arter äter samma skadedjur. På så sätt kan några arter försvinna eller minska i antal, men ekosystemtjänsten bibehållas.

I denna studie undersökte jag hur funktionell redundans och klimatreiliens hos jordlöparens biologisk kontroll av skadedjur påverkas av två typer av jordbearbetningsmetoder: plöjning och plöjningsfri bearbetning. Jag undersökte även hur olika populationsfaktorer såsom artrikedom och jämnhet påverkades, samt beräknade klimatnicherna för sex olika arter av jordlöpare. Data samlades in från 12 höstvetefält runt Uppsala i juni och juli 2023. De huvudsakliga resultaten visade att plöjningsfria fält hade en högre artjämnhet, medan plöjda fält hade en högre grad av funktionell redundans och resiliens, samt en högre förekomst av stora jordlöpararter. Den högre graden av funktionella redundans och resiliens i plöjda fält kan delvis, i detta fall, bero på att plöjning gynnade stora jordlöpare. Dessa har i sin tur högre metaboliska krav än små arter och bidrar därför till den funktionella redundansen i en högre utsträckning. Detta tros dock inte vara den enda bakomliggande faktorn till detta resultat. Ett ökat antal av en enda stor art skulle inte öka den funktionella redundansen, utan snarare minska den, eftersom den beror på graden av funktionellt överlapp mellan flera arter. Andra eventuella bakomliggande faktorer har inte fastställts i denna studie.

Acknowledgements

A special thanks to my supervisor Cassandra Vogel for all her consistent support and guidance during the project. Her assistance and availability have been so valuable and I am very grateful. I would also like to thank my assistant supervisor Mattias Jonsson for the great inputs that have improved my thesis.

Many thanks to Professor Cory Straub, Katelyn Jenkins, Katrina Folmer, and Benjamin Feit for their assistance in the field during data collection. Thanks to Fabian Bötzl for identifying the carabids, and for sharing the great picture of *P. melanarius* for my front page.

Thanks should also go to all the farmers who have generously allowed us to use their fields for data collection. This study would not been possible without them.

Finally, I want to send a big thanks to my family, who always love and support me unconditionally.

Supplementary data

Table S1. The carabid species found during the study period were listed by their average body size, feeding guild, temperature optimum, and standard deviation (SD) (Lindroth 1986; Feit et al. 2021).

Genus	Species	Body size (mm)	Feeding guild	Temperature optimum (°C)	Temperature SD (°C)
Amara	<i>Amara aena</i>	7.50	Granivore	26.70	3.40
	<i>Amara aulica</i>	12.65	Granivore		
	<i>Amara communis</i>	6.30	Granivore		
	<i>Amara eurynota</i>	11.50	Granivore		
	<i>Amara familiaris</i>	6.40	Granivore		
	<i>Amara lunicollis</i>	8.15	Granivore		
	<i>Amara similata</i>	8.90	Granivore	24.50	3.10
Anchomenus	<i>Anchomenus dorsalis</i>	7.10	Carnivore		
Bembidion	<i>Bembidion gilvipes</i>	2.75	Carnivore		
	<i>Bembidion guttula</i>	3.15	Carnivore	21.10	9.20
	<i>Bembidion lampros</i>	3.70	Carnivore	22.20	6.60
	<i>Bembidion obtusum</i>	3.15	Carnivore	20.70	8.70
	<i>Bembidion quadrimaculatum</i>	3.15	Carnivore	25.20	9.70
Calathus	<i>Calathus fuscipes</i>	12.20	Carnivore		
	<i>Calathus melanocephalus</i>	7.40	Carnivore		
Clivina	<i>Clivina fossor</i>	6.00	Omnivore	24.60	7.10

Epaphius	<i>Epaphius secalis</i>	3.75	Carnivore	21.40	8.14
Harpalus	<i>Harpalus affinis</i>	10.25	Granivore	24.20	2.30
	<i>Harpalus distinguendus</i>	10.00	Granivore		
	<i>Harpalus latus</i>	9.60	Omnivore		
	<i>Harpalus rufipes</i>	13.35	Omnivore	19.40	8.60
Loricera	<i>Loricera pilicornis</i>	7.25	Carnivore	17.70	7.70
Microlestus	<i>Microlestus minutulus</i>	3.20	Carnivore	24.50	4.00
Nebria	<i>Nebria bevicollis</i>	12.00	Carnivore	40.00	5.40
Notiophilus	<i>Notiophilus aquaticus</i>	5.25	Carnivore		
	<i>Notiophilus palustris</i>	5.50	Carnivore		
Ophonus	<i>Ophonus rufibarbis</i>	7.85	Omnivore		
Patrobus	<i>Patrobus atrorufus</i>	8.70	Carnivore		
Poecilus	<i>Poecilus cupreus</i>	12.20	Omnivore	32.42	8.73
Pterostichus	<i>Pterostichus melanarius</i>	15.00	Omnivore	22.90	6.20
	<i>Pterostichus niger</i>	17.75	Carnivore	18.00	11.20
	<i>Pterostichus vernalis</i>	6.75	Carnivore	31.00	7.20
Stomis	<i>Stomis pumicatus</i>	7.55	Carnivore		
Synuchus	<i>Synuchus vivalis</i>	7.25	Omnivore		
Trechus	<i>Trechus obtusus</i>	3.85	Carnivore		
	<i>Trechus quadristriatus</i>	3.75	Carnivore	18.40	8.30

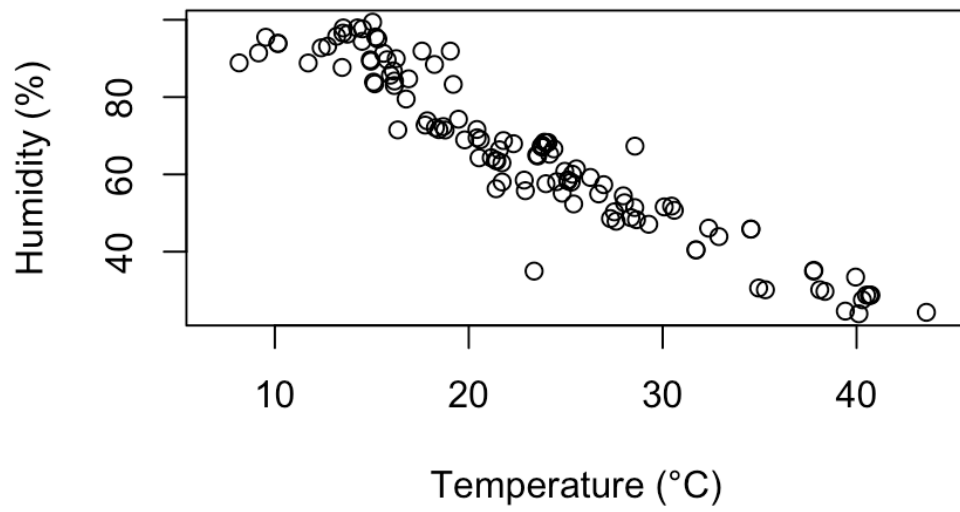


Figure S1. The correlation between temperature and humidity during the field study, from mid-June to mid-July of 2023. The correlation is strongly negative.

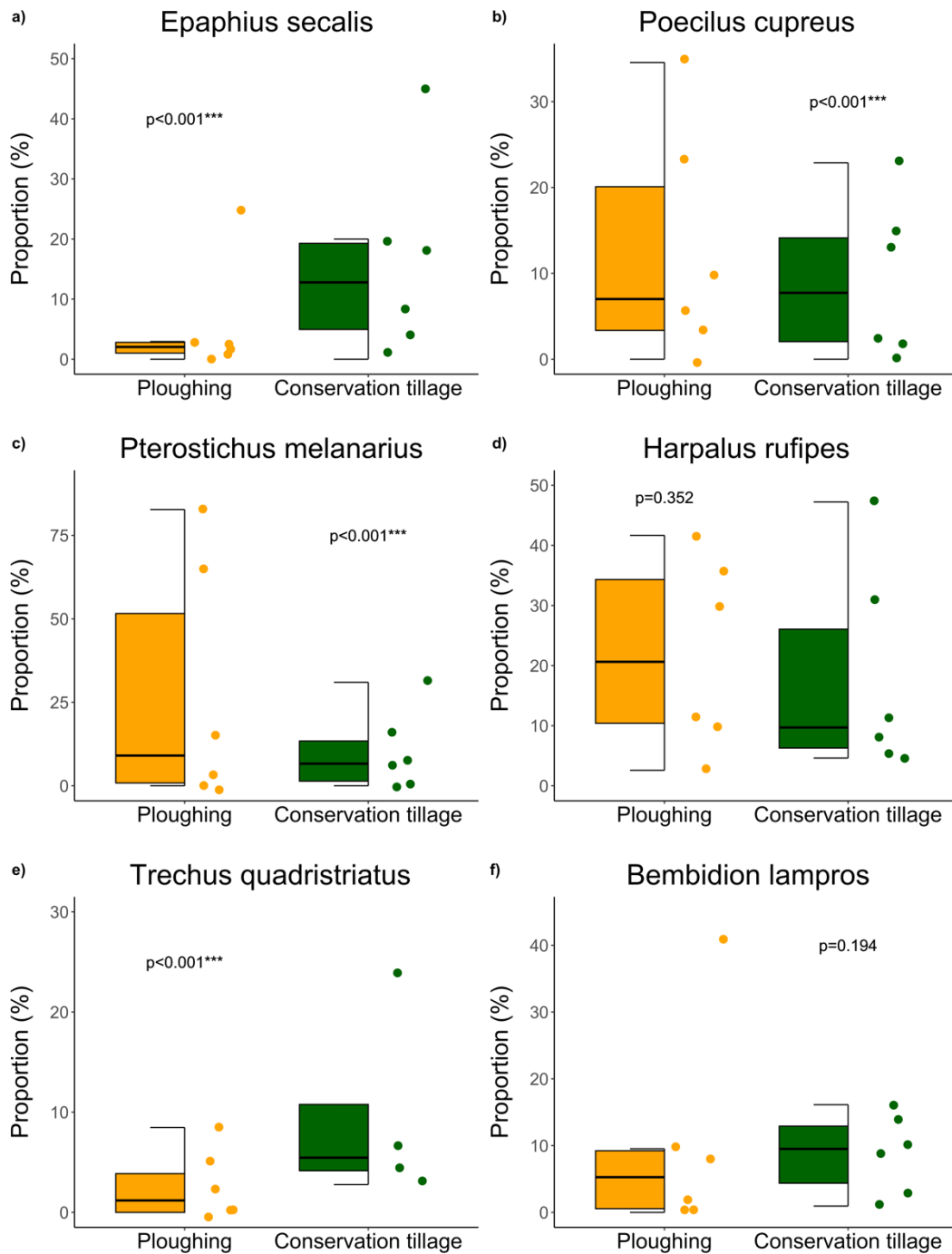


Figure S2. The proportional representation of six individual species in ploughed and conservation-tilled fields; *E. secalis* (a), *P. cupreus* (b), *P. melanarius* (c), *H. rufipes* (d), *T. quadristriatus* (e) and *B. lampros* (f). Boxplots represent the median (black bar), 1st and 3rd quantiles, and the minimum and maximum of the data. * indicate significance level (* = $p < 0.050$, ** = $p < 0.01$, *** = $p < 0.001$). Dots show data from the six replicates.

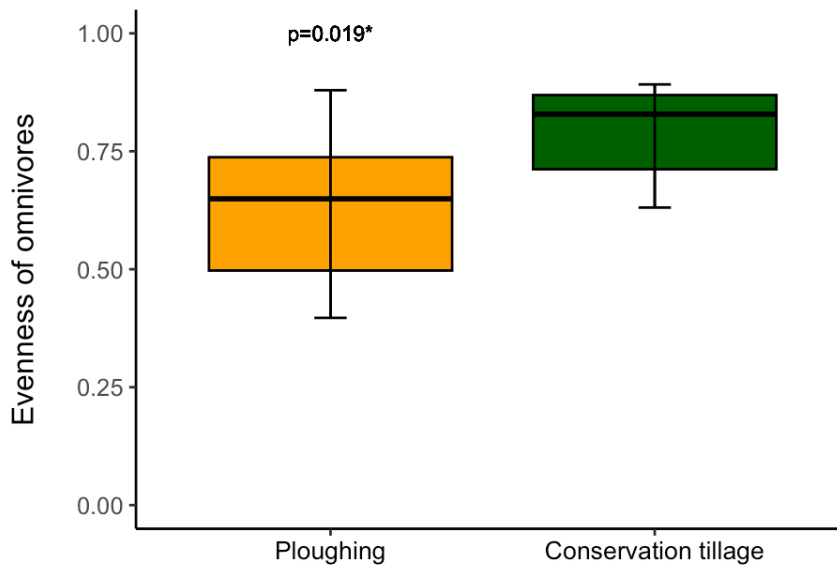


Figure S3. The evenness of omnivorous carabid species in ploughed and conservation-tilled fields. Boxplots represent the median (black bar), 1st and 3rd quantiles, and the minimum and maximum of the data. * indicate significance level (* = $p < 0.050$, ** = $p < 0.01$, *** = $p < 0.001$).

Table S2. A compilation of the management of the fields included in the field trial. Tillage type refers to the tilling method which was done during autumn 2022 prior to sowing of winter wheat. Detailed information was only obtained from the farmers of fields 10-14.

Field number	Pair	Tillage type	Implement	Depth (cm)	Last ploughed
1	A	CT	NA	NA	NA
2	A	Ploughing	NA	NA	NA
3	B	Ploughing	NA	NA	NA
4	B	CT	NA	NA	NA
7	C	Ploughing	NA	NA	NA
8	C	CT	NA	NA	NA
9	D	Ploughing	NA	NA	NA
10	D	CT (deep tillage)	Disk plough	10 to 20 cm	2000
11	E	Ploughing	Moldboard plough	20 to 30 cm	2022
12	E	CT (shallow tillage)	Disk plough Cultivator + Disk	0 to 5 cm	2018
13	F	CT (shallow tillage)	plough	5 to 10 cm	2021
14	F	Ploughing	moldboard plough	10 to 20 cm	2022

Table S3. A compilation of the insecticide and herbicide applications of the fields included in the field trial. Detailed information was only obtained from the farmers of fields 10-14.

Field number	Pair	Insecticide applications	Type	Application date	Herbicide applications	Type	Application date
1	A	NA		NA	NA	NA	NA
2	A	NA		NA	NA	NA	NA
3	B	NA		NA	NA	NA	NA
4	B	NA		NA	NA	NA	NA
7	C	NA		NA	NA	NA	NA
8	C	NA		NA	NA	NA	NA
9	D	NA		NA	NA	NA	NA
10	D	0		-	0	-	-
11	E	0		-	1	Sempre	2022.10.19
12	E	0		-	1	Sempre	2022.10.19
13	F	1	Carnadine	2023.06.26	2	Atlantis OD + Harub	2023.05.13
14	F	1	Carnadine	2023.06.23	2	Atlantis OD + Harub	2023.05.13

Table S4. A compilation of the fungicide applications of the fields included in the field trial. Detailed information was only obtained from the farmers of fields 10-14.

Field number	Pair	Fungicide applications	Type	Application date
1	A	NA	NA	NA
2	A	NA	NA	NA
3	B	NA	NA	NA
4	B	NA	NA	NA
7	C	NA	NA	NA
8	C	NA	NA	NA
9	D	NA	NA	NA
10	D	0	-	-
11	E	1	Elatus	2023.06.20
12	E	1	Elatus plus	2023.06.20
13	F	0	-	-
14	F	0	-	-

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