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# Tillage effects on ground beetles in temperate climates: a review

Phillip Müller<sup>1,2</sup> · Daniel Neuhoff<sup>1</sup> · Moritz Nabel<sup>3</sup> · Katja Schiffrers<sup>1,4</sup> · Thomas F. Döring<sup>1</sup>

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## Abstract

Ground beetles (carabids) constitute an important functional component of biodiversity in agroecosystems, mainly because of their role as predators of pests, but also as consumers of weed seeds and as prey to other organisms. Over the past few decades, there has been a marked and continuous decline of ground beetles in Europe, and many species of this insect family are threatened by intensive agricultural practices. The effect of soil tillage, a standard technique in arable farming, on carabids has been investigated in many experimental studies. However, there is currently no clear and differentiated picture of how ground beetles are affected by tillage operations in direct and indirect ways. In this review, we narrow this gap of knowledge and show that the effects of intensive tillage on ground beetles—especially the use of mouldboard ploughing—are extremely variable. Nonetheless, on balance across multiple studies, greater tillage intensity tends to have a negative effect on abundance, species richness, and diversity. The observed variability may partly be attributed to a change in species-specific food availability or habitat conditions, induced by tillage. Tillage effects on dominant species tend to have a strong impact on total carabid abundance. The high variability of carabid responses to tillage is also a consequence of various modifying factors such as cover cropping, rotations, and variations in weed control associated with tillage. Because different modes of tillage tend to affect different carabid species, the diversification of tillage operations within a farm or region may contribute to the overall diversity of carabid communities.

**Keywords** Ground beetles · Tillage · Conservation · Soil biodiversity · Carabid · Tillage intensity

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✉ Moritz Nabel  
moritz.nabel@bfn.de

<sup>1</sup> Faculty of Agriculture, Agroecology and Organic Farming, University of Bonn, Bonn, Germany

<sup>2</sup> Faculty of Process Engineering, Energy and Mechanical Systems, Technical University Cologne, Gustav-Heinemann-Ufer 54, 50968 Cologne, Germany

<sup>3</sup> BfN, Federal Agency for Nature Conservation, Konstantinstraße 110, 53179 Bonn, Germany

<sup>4</sup> Horticultural Sciences, University of Bonn, Auf dem Hügel 6, 53121 Bonn, Germany

## 1 Introduction

The insect family of ground beetles (Coleoptera, Carabidae) provides a range of important services in agroecosystems such as weed seed predation (Frei et al. 2019; Honek et al. 2013; Kulkarni et al. 2015; Menalled et al. 2007), biological control of slugs and snails (Bohan et al. 2000; El-Danasoury et al. 2017; Oberholzer and Frank 2003), and generalist predation of arthropod pests (Cividanes 2021; Williams et al. 2010; Zaller et al. 2009). Carabids also play an important role as bio-indicators, e.g., for soil attributes (Luff et al. 1989), changes in agroecosystems (Rainio and Niemelä 2003), or agricultural management (Döring and Kromp 2003).

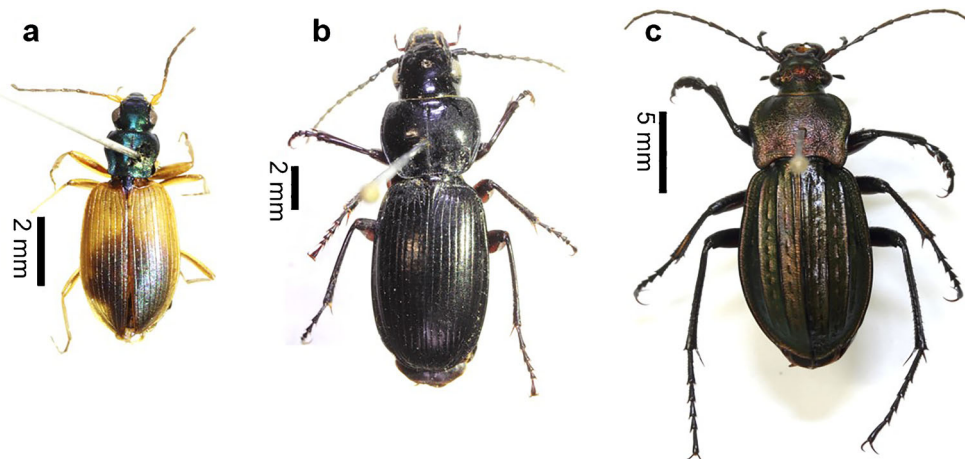
Although not systematically assessed on a larger scale, many studies suggest a decline of carabid abundance and species diversity for arable land in Europe over the past few decades. Brooks et al. (2012) reported a decline in ground beetle biodiversity or abundance in the UK between 1994 and 2008 for about 75% of the existing ground beetle species. In Belgium, Denmark, and the Netherlands, about 46, 31, and 42%, respectively, of the carabid species showed some level of decline over the past 50–100 years, while on average only 20% showed an increase (Kotze and O'Hara 2003). Habitat specialists and large-bodied carabids have declined more than habitat generalists and small-sized species. In the Luneburg Heath, Northern Germany, carabid abundance and species richness declined significantly between 1994 and 2017. However, there was no significant change in total biomass and total number of individuals across all species, indicating a population increase of some dominant species (Homburg et al. 2019). Given the important roles of carabids in agroecosystems, and also from an insect conservation perspective, the trends of declining carabid abundance and species richness, even if only based on limited data, are cause for major concern.

As in other insect groups and contexts (Wagner et al. 2021), the decline of ground beetles in agricultural land can be attributed to various factors. A known major factor is the use of pesticides in agriculture, in particular direct lethal effects of insecticides (Alam and Das 2020; van Toor 2006). Likewise, habitat fragmentation, destruction, or deterioration may lead to a loss of abundance or diversity of ground beetle populations (Keller et al. 2004; Keller and Largiadèr 2003; Massaloux et al. 2020) (Fig. 1).

Arable farming is a main type of land use. The large share and intensive use including regular and diverse tillage operations make arable land a hotspot for changes in biodiversity, in particular for organisms with epigeal or partly hypogean lifestyle such as carabids. The specific effects of soil tillage operations on ground beetles have been investigated in various studies. Tillage may affect ground beetles in a number of ways. First, tillage changes the environmental conditions of carabid habitats, by influencing the physical properties of the soil including structure (Nunes et al. 2020), water balance (Brunel-Saldias et al. 2018), and aeration as well as the distribution of plant residues in the tilled layer (Seitz et al. 2019). Second, there is evidence that tillage has an impact on various organisms living in and on the soil, by altering or destroying the structure of their habitats or by affecting the access to food resources (van Capelle et al. 2012). Third, tillage can also result in physically killing soil organisms (Fadl et al. 1996) or altering their exposition to predators. Overall, tillage may not only affect abundance, but also species composition and relationships between organisms (Kennedy et al. 2013).

While individual studies have collected experimental evidence for the effects of different modes of tillage on ground beetles, the available knowledge has so far not been brought together in a systematic way. The aim of this paper is therefore (1) to quantify and summarize the effects of different tillage

**Fig. 1** Carabid beetles commonly found on arable fields in Central Europe; **a** *Anchomenus dorsalis* (Pontoppidan, 1763); **b** *Pterostichus melanarius* (Illiger, 1798); **c** *Carabus granulatus* (L. 1758). Photo: Isabel Kilian.



systems on ground beetles, with respect to abundance and species composition of communities and diversity; (2) to elucidate the known and putative direct and indirect mechanisms underlying these effects; (3) to give recommendations on how to reconcile agronomic aims of tillage with protection of carabid beetles; and (4) to outline research gaps and directions of future research.

We begin by describing the methodology on which this review is based and then briefly characterize the different tillage systems under comparison. After summarizing key results from the literature, we discuss the general effects of tillage on carabids, focusing on main mechanisms of how tillage affects carabids. We outline important factors that interact with tillage effects on carabids and finally draw conclusions from the current evidence, suggesting directions of future research.

## 2 Methodology

### 2.1 Literature search

A literature search was carried out by means of scientific search engines (Web of Science, Google Scholar, Scopus) with specifically selected search terms relating to groups of organisms and the factor tillage or cultivation system. The search included the keywords (“Carabid\*” OR “ground beetle\*”) AND (“tillage” OR “Plough” OR “no-till”). Further articles were found by searching the reference lists of the papers obtained in previous search rounds. Only peer-reviewed original articles were included in the search (Fig. 2). The latest search was performed

on 25 Feb 2022. Criteria for paper selection included accurate selection and description of contrasting tillage systems allowing a reliable distinction. Decisions on including or excluding the respective studies were made after reading the whole paper or the methods and results section.

Data with results from the studies were compiled in a database including information on site conditions, duration of the experiment, sampling methods, and statistical significance of results.

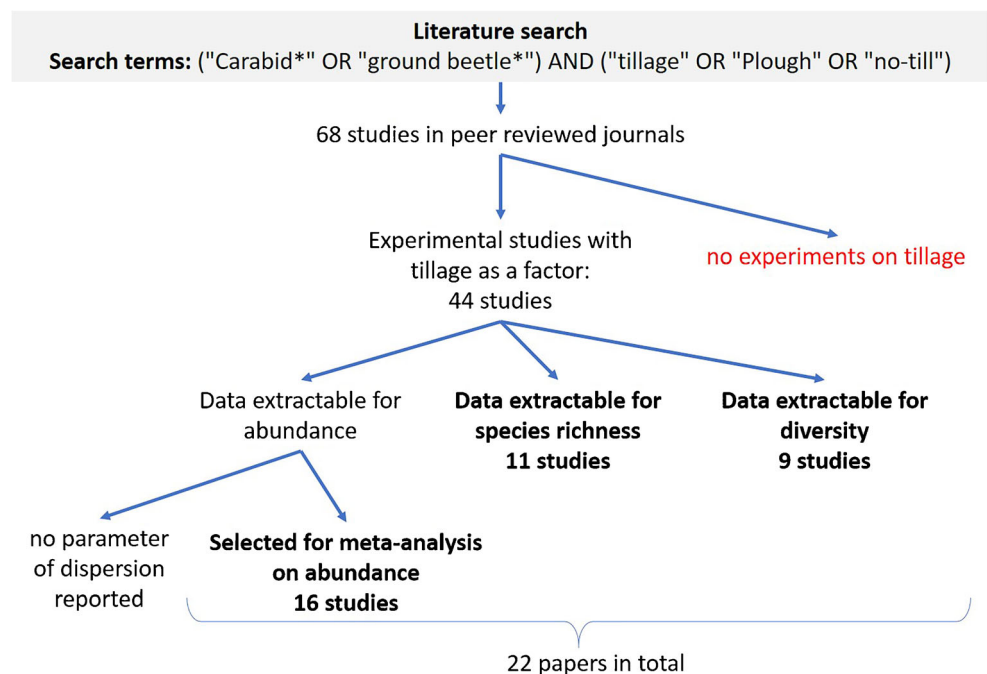
As response parameters, we extracted activity abundance, number of species, and species diversity. For sampling carabids, trapping devices typically used on agricultural land such as pitfall traps do not measure carabid abundance as density (individuals per unit area); instead, numbers of individuals caught depend on both density and activity, e.g., with larger more active species usually having a higher propensity of being caught than smaller species (Spence and Niemelä 1994). Therefore, results from pitfall trapping should be interpreted with caution.

In total, 22 studies were included in the analyses. Of these, five papers covered a research period of 5 years and more, with a median trial duration of 2 years. In 19 papers, the sampling duration was larger than 2 months. In 15 of the 22 papers, more than a total of 500 carabid individuals was caught.

### 2.2 Meta-analysis on carabid activity abundance

To estimate the overall effect of tillage on carabid beetle activity abundances, we pooled effect sizes using a meta-

**Fig. 2** Flow of literature search for selection of papers to be analyzed.



analytic framework. The prerequisites for studies to be included was the availability of information on the average beetle abundances for each treatment group and its standard deviation or standard error. Where this information was presented in figures, we extracted it using the G3Data Graph Analyzer version 1.5.2 (by Jonas Frantz). From the available 44 studies, 16 fulfilled the prerequisites to be included into the analysis. Some of the studies reported on several comparisons of carabid beetle activity abundances, e.g., from different seasons or field crops leading to a total of 33 comparisons. To account for the non-independency of those results, we decided for a three-level meta-analysis (Cheung 2014). The levels refer to (1) the usual averaging of replicates within one comparison, e.g., pooling the differences of several replicate traps, resulting in one effect size per comparison; (2) the pooling of effect sizes of comparisons within studies in case there have been done several comparisons, e.g., for different crops, resulting in one effect size per study; and (3) the pooling of the effect sizes of all 16 studies covered by the analysis, resulting in one overall effect size. To make effect sizes comparable among studies, we standardized the data by dividing the differences in means between treatment groups by the pooled standard deviation. The resulting value expresses the difference between no-/low-tillage and control treatments in units of standard deviations and is known as Cohen's  $d$  (Cohen 1988). We also corrected for small-sample sizes leading to an effect size called Hedges'  $g$ :  $g = \text{Cohen's } d \times (1 - (3/4n - 9))$ , where  $n$  is the total sample size of the study (Hedges 1981). Weights of effect sizes were calculated as the inverse of their variance. As we expected considerable heterogeneity between studies, a random-effects model was used to pool effect sizes. The restricted maximum likelihood estimator (Viechtbauer 2005) was used to calculate the heterogeneity variance and the Knapp-Hartung adjustment (Knapp and Hartung 2003) to estimate the confidence interval around the pooled effect. We also assessed a potential publication bias using Rosenberg's fail-safe number (Rosenberg 2005).

The meta-analysis was conducted using the R statistical software, version 4.1.2 (R Core Team 2021), including the *esc*-package (Lüdecke et al. 2019) and the *metafor*-package (Viechtbauer 2010), following the descriptions by Harrer et al. (2021).

### 2.3 Analysis of carabid species richness and diversity

The parameters' species richness and species diversity were evaluated with another approach due to insufficient data quantity for meta-analysis. For that, results of individual studies were compiled in *comparison pairs*. A comparison pair is a data set consisting of two contrasting tillage systems (e.g., plough vs. no-till) for one measured parameter at one date (e.g., species richness at one date) from a single study. When more than two tillage systems were simultaneously

investigated in a given study, our approach of pairwise comparisons meant that data from a specific tillage system entered the database more than one time, e.g., ploughing was compared to reduced tillage, and separately to a no-till system.

For species richness and species diversity, 11 and 9 studies with 86 and 64 comparison pairs, respectively, were extracted and entered into the database. Differences between tillage systems were classified as significant or non-significant, according to the results reported by the studies. Differences classified by us as non-significant include comparisons from studies only using descriptive but no inferential statistics.

The number of species found in a given area is a general indicator for species richness without specification of relative frequencies. Interpretation of species richness data needs to be done with caution, since sampling effort may strongly influence the absolute number of recorded species (Gardarin and Valantin-Morison 2021), so that the number of species found in a given area with a given sampling effect is only an indicator for actual species richness. Therefore, we restricted the analysis of data to the direction of the difference in species richness between tillage systems, in this case ignoring the size of that difference. Species diversity, often calculated with the Shannon or the Simpson Index, includes information on the abundances (Magurran 2013). For the present evaluation, both parameters for species diversity were pooled by exclusively extracting the direction of difference between tillage systems in a given comparison pair. Comparisons focusing on evenness were not included since the number of available studies reporting evenness ( $n=4$ ) was too low. Based on the number of cases, the directions of tillage effects on carabid species richness and carabid diversity were tested with a non-parametric binomial sign test. Data sets were evaluated using the statistics software R (version 4.0.3) or RStudio (version 1.2.2019).

### 3 Characterization of tillage systems

Farmers pursue several objectives with soil tillage. In addition to seed bed preparation, tillage helps to incorporate crop residues and to control weeds and pests. Tillage, in particular ploughing, has been a paradigm for arable farming systems for millenia (Fussell 1966). Over the last few decades, different forms of reduced (non-inverting) tillage systems have gained increasing importance for reasons of erosion control and cost savings (Gebhardt et al. 1985; Klik and Rosner 2020). Here we only refer to primary tillage, which is the first rough soil agitation of different intensity prior to seed bed preparation.

Main physical effects of primary tillage include loosening of the soil, distribution of organic particles in the soil layer and disruption of the continuous pore system. Furthermore, tillage affects soil aeration and the soil water status (Tebrügge and

Düring 1999). Farmers use a wide range of tilling options, with different agronomic effects, which have been extensively described (Cannell 1985; Tebrügge and Düring 1999; Torabian et al. 2019). In contrast, effects of soil tillage intensity on organisms living in and on the soil have mainly been analyzed for specific groups such as weeds (Chauhan et al. 2006; Chauhan et al. 2012), earthworms (Lumbricidae) (Chan 2001; Pelosi et al. 2009), and regionally for selected soil biota (van Capelle et al. 2012). To quantitatively analyze and evaluate the impact of different tillage implements on carabids, it is important to elucidate the direct and indirect physical effects of soil movement and disturbance. In general, there is a gradient of tillage intensity from ploughing to reduced tillage and no-till.

### 3.1 Conventional tillage (mouldboard plough)

Ploughing with common working depths of 15–30 cm, and occasionally more shallow (10–15 cm) or deeper with >35 cm (Cannell 1985), primarily causes the soil to be lifted and turned by about 140° (Kouwenhoven and Terpstra 1972; Waszkiewicz et al. 2009). Harvest residues and weeds are inverted in the soil, creating a clean seedbed without crop residues. Crop residue distribution along the depth profile is more homogenous compared with other tillage methods. The largest proportion of crop residues can be found at a depth from 15 to 25 cm (Tebrügge and Düring 1999). Loosening, mixing, and turning results in strong aeration and lower density of the topsoil. Soil inversion by ploughing is generally combined with further tillage operations targeted on seed bed preparation (Grant 2003). Relevant effects of soil inversion on carabids include removal of both beetles (mainly pupae and larvae) and plant biomass such as weed seeds from the soil surface.

### 3.2 Reduced tillage

Reducing the intensity of tillage can be done in various ways (Cannell 1985), by reducing the depth or frequency of tillage, but also by non-inversion of the soil. Based on the studies reviewed here, the term reduced tillage only refers to tillage systems with missing soil inversion. A wide range of instruments is used targeted on loosening and mixing the soil for seed bed preparation (Morris et al. 2010). Within non-inversion tillage systems, the soil volume affected by tilling, the depth of tillage, and the number of working passes greatly vary between extensive methods (e.g., strip-till) and intensive tillage such as rotary harrowing. While the intensity of reduced tillage systems varies, they have in common that higher quantities of plant biomass remain on the soil surface and in the upper layer (10 cm), when compared with ploughing (Morris et al. 2010). Instruments with either axial or vertical counter rotating tines can directly affect ground beetles.

Typical instruments used for reduced tillage are straw harrows, rotary or disc harrows, shallow or deep cultivators, deep looseners, chisel ploughs, and various rollers. Tillage heterogeneity results in variable levels of soil loosening and mixing. Special seeding technology (disc or chisel couler) is required to cut through even higher quantities of crop residues and to place the seed optimally (Baker and Saxton 2007; Tebrügge and Düring 1999). Reduced tillage may result in increased weed pressure (Chauhan et al. 2012; Cooper et al. 2016; Moonen and Barberi 2004) if this reduction is not counterbalanced by other weed management methods. Therefore, in non-organic agriculture, reduced tillage is often seen to depend on the effective use of broad spectrum herbicides (Awada et al. 2014; Price et al. 2011).

### 3.3 No-till

No-tillage techniques, sometimes termed zero tillage, or no-till, include soil management systems in which the soil is not tilled at all. Sowing is done without prior disturbance of the soil, using disc or tine coulters with minimal soil disturbance (Baker and Saxton 2007). Loosening, mixing, and turning of the soil is completely absent in no-tillage procedures. As a consequence, long-term no-tillage leads to an accumulation of organic matter, nutrients, and microbial activity at the soil surface (Doran 1980). However, no till systems typically rely on herbicides that help to establish the crop stands without weed competition (Sarangi and Jhala 2018). No-tillage is considered an essential component of conservation agriculture (Rhodes 2012; Sherwood and Uphoff 2000); however, in non-organic practice, it is usually accompanied by the use of non-selective herbicides such as glyphosate.

Advantages and disadvantages of reduced tillage systems also occur in no-tillage, partially to a greater extent. No-tillage provides a high level of protection against silting and erosion, but requires special attention in the management of weeds and pests. A number of management factors are decisive for the success of no-till systems including cover crops, diversified crop rotations, and site-adapted fertilization and plant protection strategies (de Baets et al. 2007; Baker and Saxton 2007; Clark 2008; Derpsch et al. 1986; Hartwig and Ammon 2002; Lal 2020).

## 4 Effects of tillage on ground beetles

The majority of the 23 studies analyzed were carried out in North America while the remaining ones stem from Europe. Data extracted from the studies covered a period from 1983 to 2022. Most studies only included data on carabid activity abundance as affected by tillage.

### 4.1 Activity abundance

In the three-level meta-analytic model, more than half of the comparisons showed a positive effect size indicating that intensive tilling had a negative effect on the carabid beetle abundance (see Fig. 3). The pooled effect was  $r = 0.68$  (95% CI: 0.05–1.32,  $p = 0.035$ ), which is considered a moderate to strong effect according to the conventions by Cohen (1988). Rosenberg’s fail-safe number was assessed to be 143, meaning that at least 143 studies with an effect size of null would have to be added to the analysis to reduce the significance level to  $p \geq 0.05$ . This indicates that our results are very likely not to be influenced by a publication bias.

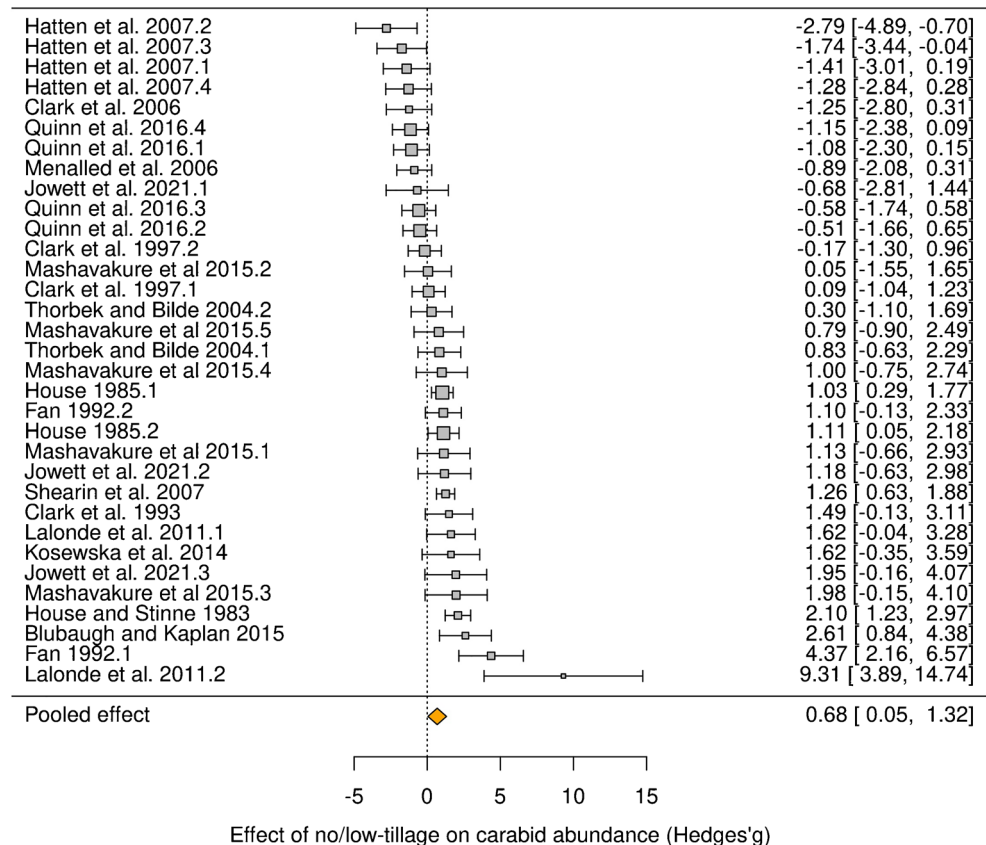
### 4.2 Species richness

The total number of comparison pairs ( $n = 86$ ) reporting number of carabid species was lower than that for abundance and was based on only 11 studies, of which five studies were conducted in the USA; among the comparison pairs, only a single pair was based on quadrat sampling while the other 85 pairs used Barber pitfall traps. Most comparisons were made in maize ( $n = 49$ ), followed by winter cereals ( $n = 22$ ), while the remaining comparisons stemmed from spring crops ( $n =$

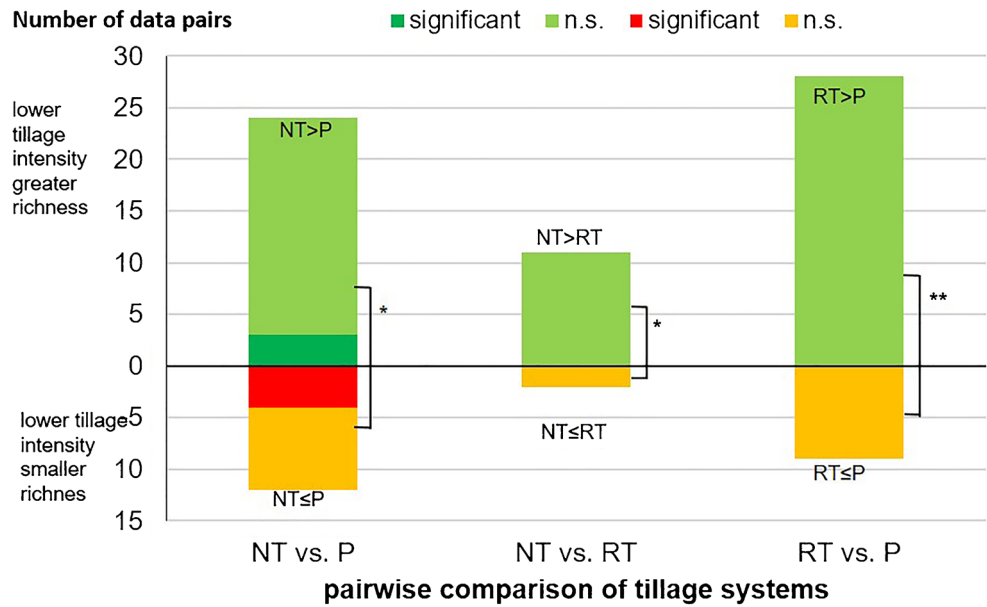
13). None of the studies came from organic cropping systems. The dataset was dominated by a single study (Lalonde et al. 2012) contributing more than a third of the comparison pairs ( $n = 30$ ). Among the studies, the majority of the comparison pairs focused on comparisons versus the plough.

When all comparison pairs were analyzed together, a general trend for higher species numbers after lower than after higher tillage intensity was found (Fig. 4). While 24 comparison pairs indicated a higher number of species under no till compared with plough, the opposite direction was noted in a significantly lower number of 12 cases (sign test:  $p = 0.065$ ). However, the few ( $n=7$ ) comparisons with significant differences were slightly (though not significantly) in favor of a higher carabid species number after ploughing. All other tillage comparisons showed a trend for a higher number of species after reduced versus more intensive soil tillage. When all 86 comparisons were pooled, cases in which lower tillage intensity was associated with higher carabid species richness ( $n = 63$ ) significantly ( $p < 0.001$ ) outnumbered the opposite cases ( $n = 23$ ). To account for potential bias in the dataset, an additional data analysis was conducted after removing the study by Lalonde et al. (2012) from the data; this revealed that also in the remaining subset of data, lower tillage intensity was associated with higher carabid species richness ( $n = 40$  out of 56 cases).

**Fig. 3** Forest plot on the effect of the no/reduced-tillage treatment on carabid abundance in relation to ploughing. The position of the gray boxes represent the observed study effect (Hedges’  $g$ ), with error bars showing the 95% confidence intervals. Sizes of boxes indicate the weight of the studies in the meta-analysis. The orange diamond indicates the pooled effect size with width symbolizing the confidence interval of the pooled result on the  $x$ -axis.



**Fig. 4** Tillage effects on carabid species richness. Number of data pairs indicating higher values for a given system comparison; darker colors indicate number of significant comparisons, lighter colors show non-significant comparisons in the original data; cases with the less intensive tillage system showing a higher carabid species richness than the more intensive system are shown above the horizontal line in green colors, the opposite direction (higher species richness in the more intensive tillage system) is shown below the line, in red and orange. \* $p < 0.05$ ; \*\* $p < 0.01$ , binomial sign test.



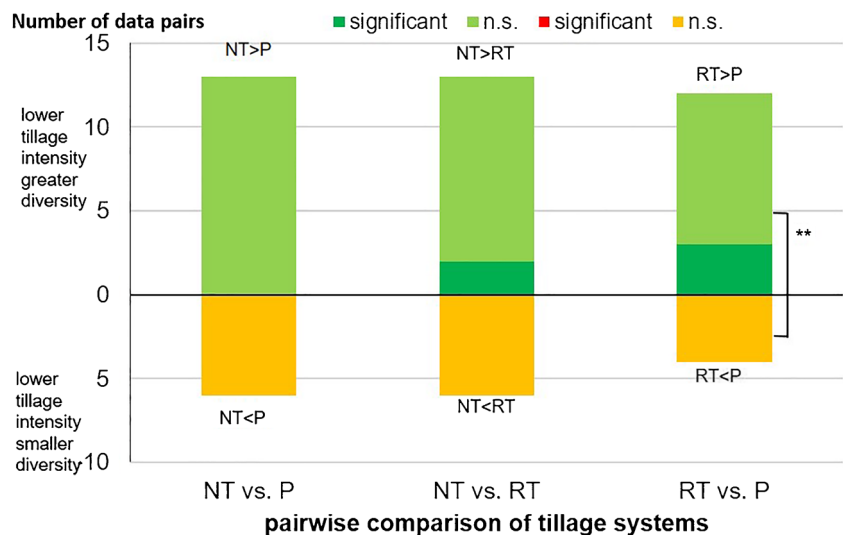
### 4.3 Species diversity

The number of comparison pairs reporting carabid species diversity ( $n = 64$ ) was even lower than those for species richness. Only nine studies dealt with this parameter of biodiversity; these comparison pairs were exclusively based on Barber pitfall traps, and mainly ( $n = 60$ ) reported the Shannon-Wiener index, with the remaining pairs showing the Simpson index. The majority of comparison pairs ( $n = 44$ ) came from observations in maize, and the studies were exclusively conducted in non-organic cropping systems. Again, a large fraction of the comparison pairs stemmed from a single study (Lalonde et al. 2012).

Available studies suggest that reduced intensity of soil tillage favors species diversity (Fig. 5). Although supported by statistical evidence in only a few cases, more than twice the

number of comparison pairs showed a higher species diversity under no till versus ploughing, compared with the opposite case. A comparable trend was noted for the comparison pairs contrasting no till versus reduced tillage. In 13 cases, two of them significant, species diversity was higher after no till, while only six cases were in favor of reduced tillage. Likewise, the comparison between reduced tillage and plough indicated that lower tillage intensity tended to favor carabid species diversity. When all diversity data was pooled, there was an effect of tillage intensity. There were 48 out of 64 cases in which carabid diversity was higher in the system with the lower tillage intensity than in the system with the higher intensity, whereas the opposite was found in only 16 cases; according to a sign test, this effect of tillage intensity on carabid diversity was highly significant ( $p < 0.001$ ). This finding

**Fig. 5** Tillage effect on carabid diversity (measured as Shannon index or Simpson index). Number of data pairs indicating higher values for a given system comparison; darker colors indicate significant differences; cases with the less intensive tillage system showing a higher carabid diversity than the more intensive system are shown above the horizontal line (green), the opposite direction (higher diversity in the more intensive tillage system) is shown below the line (orange and red); \*\* $p < 0.01$ , binomial sign test.





was robust against removing the dataset of the study by Lalonde et al. (2012). Out of 34 remaining comparisons, 30 showed higher carabid diversity in the treatment with the lower tillage intensity.

## 5 Mechanisms underlying tillage effects on ground beetles

### 5.1 Differential effects of tillage operations on different ground beetle species

The present evaluation confirms variable results of tillage effects on ground beetles, in particular with respect to abundance. Inconsistent effects of ploughing versus non-inversion tillage on carabids have already been discussed by Holland and Luff (2000). In a data compilation, they identified from a total of 45 carabid species some 14 species that preferred ploughed soils compared with 15 species favoring minimum tillage. Six species showed no preference for a particular tillage system. One main reason for these ambiguous results are contrasting effects of tillage on those carabid species dominating in a specific field. According to most studies, site-specific carabid assemblages are numerically dominated by few species (Baguette and Hance 1997; Lalonde et al. 2012; Menalled et al. 2007). As a consequence, the overall abundance is mainly affected by the impact of tillage on the dominant species. If a tillage system favors or disfavors a dominating carabid species, the abundance of this species will be positively or negatively affected with possible effects on total abundance.

In a Canadian study, carabid abundance was strongly affected after 18 years of different soil tillage. About 60% of all carabid individuals were collected in no-till plots, while only 20% in either chisel or moldboard ploughed plots. From a total of 19 carabid species, only four accounted for 97% of the abundance, where *Harpalus rufipes* dominated with 71% of activity abundance. The dominance of this omnivorous species in no-till plots could partly be attributed to predatory feeding (Lalonde et al. 2012), possibly because slugs (Kennedy et al. 2013) and earthworms (Pelosi et al. 2009) tend to be more abundant in no-till compared with ploughed fields.

In contrast, total carabid activity density was two times higher in ploughed compared with no-till plots in field experiments in the Midwest, USA. Likewise, only three out of 33 species were dominating (82.5%) of overall 1609 trapped carabids. The authors explained the dominance of the native spring breeder *Poecilus chalcites* with the tolerance of this species to intensive soil disturbance (Menalled et al. 2007). However, in the same study, the abundance of seed predated carabids was three times higher in no-till compared with ploughed plots indicating a change of food availability induced by tillage. Even one dominating species can be decisive for overall carabid abundance. In another Canadian study, for

instance, total carabid abundance in ploughed plots ( $n = 1480$ ) was clearly higher compared with reduced tillage ( $n = 835$ ). When excluding the by far dominating species *Agonum placidum* with 608 more individuals in ploughed plots, carabid abundance tended to be equal in both tillage systems (Cárcamo 1995).

Moreover, interactions between tillage and crop type still complicate a clear view. In a recent study in Pennsylvania, USA, the abundance of *Agonum muelleri* was significantly higher after full versus reduced tillage, but only in rye and not in timothy/clover. The authors assume that cereals created a more suitable habitat for the carnivorous medium-sized species also providing more prey (Pisani Gareau et al. 2020).

In an Irish study, the aggregate number of carabids captured did not differ between intensive and minimum tillage (Kennedy et al. 2013). However, species-specific responses to tillage were noted. The abundance of the larger species *Pterostichus melanarius* was significantly higher after reduced tillage, while the smaller *Bembidion* spp. were more abundant after intensive tillage. The abundance of *P. melanarius* was correlated with increased slug abundance in plots with minimum tillage (Kennedy et al. 2013). Higher *P. melanarius* and slug abundances after non-inversion tillage were also noted in an earlier study, where 84% of the beetles contained slug remains. The authors concluded that *P. melanarius* tend to have a preferential feeding upon slugs in areas with high slug biomass (Symondson et al. 1996).

Further, it is obvious that timing is a major factor explaining tillage effects on different carabid species (Holland and Luff 2000; Roger-Estrade et al. 2010; Wardle 1995). Carabid abundance reducing effects of tillage operations can mainly be expected when carried out at vulnerable growth stages of tillage-sensitive species. Indirectly, ground beetle species whose larvae develop in spring benefit from the higher amount of crop residues on the soil surface in no-tillage systems, since crop and cover crop residues can serve as habitat during winter (Lalonde et al. 2012; Larochelle and Larivière 2003; Thiele 2012). Accordingly, species with autumn oviposition, such as *Harpalus rufipes* and *Pterostichus melanarius*, tend to have a higher abundance in permanent no-tillage areas. Lalonde et al. (2012) argue that the larvae of these species hibernate at soil depths that make them vulnerable in autumn or winter tillage, especially ploughing—which is why these species prefer no-till over tilled fields (Lalonde et al. 2012). In a Belgian study by Baguette and Hance (1997), biological properties of carabid species could be linked to tillage regimes. Here, in contrast to the study by Lalonde et al. (2012), autumn breeders were more abundant in ploughed plots; in addition, small carabid species were more abundant in plots with a low ploughing intensity (Baguette and Hance 1997).

A comprehensive assessment of tillage effects on carabid diversity also requires the inclusion of data on species

richness. The present evaluation of 40 studies showed that carabid diversity tends to be favored by lowering tillage intensity (Fig. 2), but not in an entirely conclusive way.

For a deeper understanding of soil tillage impacts on carabid populations, it is necessary to link direct and indirect effects of tillage to the biological profile of individual carabid species including data on reproduction biology such as egg laying depth and vertical distribution of larvae. Tillage influences soil organisms directly through mechanical intervention on the one hand, and indirectly through a change in habitat structures on the other (Wardle 1995). Unfavorable environmental conditions induced by tillage include interruption of access to food, destruction of habitats, and drying out of the soil (House and Del Alzugaray 1989). The extent of injury depends on the specific vulnerability of a carabid species including the flexibility to adapt to changing environmental conditions induced by tillage. Hence, tillage may lead to a shift in species composition. Most evident are tillage effects on food access for carabids.

## 5.2 Ground beetles in the food web

Soil tillage may result in a removal or concentration of biomass, thereby changing access and availability of food sources. The strength of the tillage effect depends of the site-specific carabid species composition and their individual feeding behavior. Tillage not only has a direct effect on arthropods and physical soil parameters, but also indirectly affects the entire food web in the soil including lower trophic levels. Ploughing, for example, influences the species composition of soil organisms within the soil food web in terms of body size, nutrition, generation time, and dispersal rate (Andrén and Lagerlöf 1983; Hendrix et al. 1986). Therefore, not only phytophagous, saprophagous, and granivorous species are affected by tillage, but also representatives of higher trophic levels, i.e., predators (Wardle 1995). In general, larger organisms of the mega fauna (organisms > 2 mm, earthworms and large invertebrates) tend to react more strongly to intensive tillage than smaller organisms of the meso- and microfauna and microflora (Ball and Robertson 1994; Barnes and Ellis 1979; Black and Okwakol 1997; Chan 2001; Folgarait 1998). This may also be a reason for a shift in the ground beetle population due to a change in the tillage regime, as the prey of some species of ground beetles appears more or less frequently after tillage. Physical interference with the soil, in particular by ploughing, results in larger organisms of higher trophic levels being disadvantaged, while small organisms of lower trophic levels are less affected or even benefit to a small extent (Wardle 1995).

Ploughing also causes fragmented crop residues in the soil to be broken down mainly by bacteria, while the coarse plant residues on the soil surface are broken down more by fungi in no-tillage. Ground beetle species which feed on fungivores

such as Collembola (McNabb et al. 2001) could thus indirectly benefit from zero tillage. Due to the wide range of food sources for ground beetles, it can therefore be assumed that a tillage-induced interference in the soil food web has an influence on the species composition and abundance of ground beetle populations in a field.

However, the dietary requirements of many ground beetle species are not yet fully understood (Da Matta et al. 2017; Kulkarni et al. 2015). Most carabids are polyphagous with feeding habits ranging from herbivory or carnivory to omnivory (Hengeveld 1979). Plant-consuming carabids are either feeding on seeds or feeding on green plants. Molecular studies have shown that some carabid species considered to be highly carnivorous were also feeding on weed seeds (Lundgren et al. 2013). While the large majority of ground beetles is not noxious to plants, species in some genera, e.g., *Zabrus*, *Harpalus* and *Pterostichus*, may also be noxious to some crop species (Larochelle 1990; Lövei and Sunderland 1996).

Direct effects of tillage become evident when looking at weed seed-consuming ground beetle species. Each type of tillage, but in particular soil inversion by ploughing, removes seeds from the soil surface. In addition to the mechanical intervention in the soil by tillage implements and the intensity of tillage (primary effect), the longer-term control of weeds by tillage (secondary effect) thus also plays an important role, since weeds and their seeds serve as a food source for some species of ground beetles (Andersen 1999, 2003). Seed-feeding ground beetles, e.g., in the genus *Harpalus*, tend to occur more frequently with higher weed pressure often induced by reduced tillage (Andersen 2003). Seed-feeding carabid species generally prefer fields with no mechanical disturbance (Hatten et al. 2007; Trichard et al. 2013), because of higher food availability in those systems.

In contrast to this, however, a Canadian study found that weed seed predation was high in both no-till and ploughed, but lower in non-inversion tillage systems using a chisel plough (Cromar et al. 1999). Cardina et al. (2002) investigated the effect of long-term no-tillage compared to conservation tillage and ploughing on the abundance and biodiversity of weed seeds in the soil. At both sites, the no-tillage plots in the soil layer 0 to 5 cm showed the highest number of viable weed seeds and the highest number of arthropod species. In particular, granivorous animal species are therefore expected to benefit from no-tillage procedures. In a field trial in the Midwest, USA, higher weed seed consumption was found on long-term no-tillage areas. Seed predators, in particular *Anisodactylus ruficus*, made up 32% of the total individuals captured in no-till, while it constituted only 4% of individuals in the ploughed plots (Menalled et al. 2007). Ploughing compared with undisturbed plots or chisel ploughing reduced activity of weed seed predators *H. rufipes*, *Agonum muelleri*, *Anisodactylus merula*, and *Amara cupreolata* on two sites in

Maine, USA, by about 50%, probably as a result of seed burial. In contrast, abundance of arthropod predator *Pterostichus melanarius* was clearly reduced after all types of tillage indicating a higher vulnerability of this species (Shearin et al. 2007).

Tillage effects on activity abundance of carnivorous carabids tend to be less clear and more complex than for seed-feeding carabids. In general, the abundance of carabid species feeding on pests is associated with pest incidence. Pests favoring specific tillage systems may therefore lead to a higher carabid abundance (Andersen 1999). Compared to high-disturbance tillage systems, a suite of invertebrate pest species tends to be more problematic in fields managed with reduced-tillage practices (Douglas and Tooker 2012; Stinner and House 1990). For example, slugs tend to be more abundant in no-till systems and can be overwhelming when conditions are cool and rainy during the planting season, at times causing damage severe enough to require replanting (Douglas and Tooker 2012). Thus, larger ground beetle species (e.g., from the genus *Carabus*), which feed on earthworms, slugs, and snails, may benefit from increased prey populations with reduced tillage (Kennedy et al. 2013). However, in a Polish study, no significant differences between ploughing and non-inversion tillage in terms of numbers of large carnivorous carabids were noted (Kosewska et al. 2014).

The issue of indirect tillage effects on carabids through the food web is complicated further by intraguild predation (Heij and Willenborg 2020), as tillage may shift the balance of predation among carabids, e.g., by smaller carabid species falling prey to larger generalist carabids.

Apart from the complex effects of tillage on food webs, and the role of carabids in them, specific habitat requirements of individual species are a further factor explaining tillage-induced changes of carabid species assemblages.

### 5.3 Tillage-induced habitat changes

Soil tillage leads to a variation in crop habitat. No-tillage, for instance, a system with minimized mechanical intervention in the soil leads to a clearly separated stratification due to the accumulation of organic matter at the soil surface. In addition to higher soil moisture due to reduced evaporation and buffering of temperature extremes, more food is provided for litter inhabitants and decomposers (House and All 1981; House and Parmelee 1985). Larger quantities of plant biomass on the soil surface, however, serve soil organisms not only as a food source but also as a habitat. Likewise, weeds and crop residues typical for reduced-tillage systems can provide refugia, buffer temperature, and moisture fluctuations and improve habitat for insect and slug pests. As a result, the arthropod community on no-tillage areas is less mobile, but more resilient (House and Stinner 1983). Modifications of the microclimate at soil surface through different tillage systems also need to be seen

in relationship with the ecological preferences of carabids with respect to temperature and moisture; as microclimatic preferences among carabid species vary (Thiele 1977, 2012), this mechanism is a likely explanation for shifts in community composition between tillage systems.

In addition, the residues lead to the soil drying out less quickly and freezing later in winter, which can benefit arthropods, among others (Sapkota et al. 2012). Higher arthropod abundance and diversity in no-till versus ploughed plots in Georgia, USA, was partly explained with the clear buffering capacity of no-till against drought due to an increased soil moisture retention (Blumberg and Crossley 1983). Soil moisture, substrate porosity, and altitude were the main factors determining ground beetle composition in North East England (Luff et al. 1989). Tillage-induced changes in soil moisture may hence favor hygrophilic and disfavor xerophilic species. However, dominating factors on soil humidity are site-specific precipitation and soil type, while tillage effects remain comparatively weak. Temperature, in theory, may also play an indirect role, as thermophilic species may respond to faster warming of ploughed than of no-till soils in spring.

### 5.4 Direct lethal effects of tillage on ground beetles including larvae

Inversive tillage is the most energy intense form of soil cultivation in agriculture. It is therefore not surprising that the related forces do also have a direct impact on ground beetles. Thorbek and Bilde (2004) found that tillage accounted for a direct mortality of 27% of ground beetles within the observed area. However, in most studies, the direct lethal effect of tillage remained difficult to quantify. Studies showed two main aspects of direct lethal effects, first, effects related to the physical effects of tillage and second related to the exposure of ground beetles and their larvae after tillage.

The physical effects refer to injuring, killing, or burying of ground beetles (Kladivko 2001). The heavy machinery for ploughing is associated with strong forces that can physically kill ground beetles (Fadl et al. 1996). Kladivko (2001) showed that larger beetles are more affected than smaller ones as they have a greater surface and are less likely pushed aside. Beetle larvae as well are physically injured or killed by tillage (Thorbek and Bilde 2004), most likely due to their soft-bodied larval instar (Fadl et al. 1996).

The exposure effects relate to predation and climate conditions. The inversion of the soil by tillage moves the soft bodied larval instars of ground beetles to the surface where they are without any cover an easy prey for birds or other predators (Fadl et al. 1996). As tillage leaves the soil blank without any cover of plants or litter, also full-grown ground beetles are very exposed and thus more likely captured by natural predators, especially on large arable areas. Reduced ground cover also makes the soil and the associated ground beetle

populations more vulnerable to weather and climate conditions. During the cold season, tillage may move larvae from a soil depth of 15 to 20 cm to the soil surface, where they are exposed to frost and thus can freeze to death (Larochelle and Larivière 2003). In dry periods, desiccation can have lethal effects on ground beetles as the lack of soil coverage by plants or litter does not provide any refuges and reduces the humidity of the microclimate at the soil surface (Shearin et al. 2014).

Studies clearly indicate direct lethal effects on ground beetles, but according to Thorbek and Bilde (2004) these effects remain relatively partial and accounted for 25–60% of the total population declines related to tillage. This is mainly because direct effects depend on the specific point of time, while otherwise indirect effects on ground beetle populations extend over the time span until the succeeding soil cultivation. Further, Neave and Fox (1998) argued that under favorable conditions, a sufficient period without tillage can help to increase or stabilize the population density of soil-dwelling organisms after tillage during the growing season.

### 5.5 A critical look at methodology: the effects of trapping devices

Extensification of tillage and, in extreme cases, no-tillage lead to an accumulation of organic material at the soil surface (Dick et al. 1986; Huggins and Reganold 2008). The mobility of the ground beetles may be restricted by plant material. As the radius of action and the dispersal speed depend on the habitat, differences in abundance between conservation tillage, ploughing, and no-tillage can also be attributed to the physical habitat structure. According to the concept of spatial resistance (Heydemann 1957), carabid activity may be recorded as low if there are large amounts of (plant) material on the ground that physically hinder or slow down direct movement. Following this concept, a higher activity abundance after intensive soil tillage, e.g., determined with pitfall traps, can be attributed to the lower amount of organic matter. The ground beetles may reach the pitfall traps more easily than on a no-tillage area with a significantly higher amount of plant residues on the soil surface (Crist and Wiens 1995). Thus, insects are more mobile on ploughed fields than on no-tillage areas. Furthermore, insects from surrounding habitats, such as hedges or overgrown or weedy arable land, can migrate more easily to freshly ploughed and sown fields (House and Stinner 1983). For sampling carabids, trapping devices typically used on agricultural land such as pitfall traps do not measure carabid abundance as density (individuals per unit area); instead, numbers of individuals caught depend on both density and activity, e.g., with larger more active species usually having a higher propensity of being caught than smaller species (Spence and Niemelä 1994). Therefore, results from pitfall trapping should be interpreted with caution.

Furthermore, the type of pitfall trap, depending on the ground beetle species and size, influences the number of captured individuals (Greenslade 1964; Spence and Niemelä 1994). The population size and the activity of the individual species and individuals also affect the abundance determined by pitfall traps (Greenslade 1964). Lange et al. (2011) found that a larger diameter of pitfall traps in combination with a funnel led to a higher abundance of ground beetles, while the number of species remained almost constant regardless of the trap size.

Although most of the studies examined used pitfall traps, there are other methods for catching ground beetles. When comparing pitfall traps with manual samples from light towers, neither of the two methods was able to identify all species present at the site. Pitfall traps were able to detect a significantly higher carabid species number, while the number of captured individuals and thus the sample size was larger in manual sampling at light towers (Liu et al. 2007).

Pitfall traps on the soil surface do not capture larvae in relevant amounts. Recently, it has been suggested to use subterranean pitfall traps to monitor carabid assemblages. These traps are delineated by a mesh tube (1.2-cm grid) through which soil organisms fall (Jowett et al. 2021). In field experiments with contrasting soil tillage and different crops using both trapping types, significant species-specific differences in catches between traps were noted. Trap type accounted for the most variance observed in carabid community composition, followed by crop. Reduced activity abundance at the species level after tillage versus no-till was only apparent for three of eight species (Jowett et al. 2021).

The comparison of tillage systems with regard to possible effects on abundance, species numbers, and diversity of ground beetle populations is impaired by methodological differences between the studies. Besides the method used to catch the ground beetles, the distances between the traps, the position, the sampling date, and the number of sampling dates may also play a role. Further, the experimental design also influences the results: apart from the location, there were also differences between the studies with regard to the plant species selected, the management (e.g., fertilization, plant protection), and the farming history. This, together with interactions between tillage and crop species, makes it difficult to draw any clear-cut conclusions on the effects of tillage on carabids unless the methodological issues mentioned above are resolved.

### 5.6 Experimental and sampling duration

In many cases, field experiments on tillage are run as static long-term trials. The duration of field experiment is an important factor that may influence the observations made in individual studies. In long-term experiments, cumulative effects over many years may be expected in contrast to shorter term

experiments where effects may be weaker overall. However, there are unfortunately currently not enough long-term trials testing tillage effects on carabids to quantify any cumulative effect over time. On the other hand, the total duration of sampling carabids within the experiment may have an effect on the observations of carabid abundance, species richness, and diversity. In the analyzed literature, the sampling duration was often much shorter than the total length of the experiment (e.g., Lalonde et al. 2012); most studies analyzed only present results of 1 or 2 years of sampling.

## 6 Factors interacting with soil tillage effects

The effects of the intensity of tillage on soil-dwelling organisms such as ground beetles should not be considered in isolation, since carabids are sensitive to a range of cultivation practices, and tillage practices are associated with specific crop management such as cover cropping.

Various factors play an important role by modifying and partly compensating for the effects of tillage on soil-inhabiting organisms in general, and ground beetles in particular. External factors include the climatic conditions and the agricultural landscape context; management factors include the system (conventional, organic), and especially weed control and crop rotation. In particular, the negative effects of intensive tillage on soil life can be partially offset by other biodiversity-promoting measures.

In the factorial studies in which interactions between tillage and other management measures on soil flora and fauna were investigated (e.g., Baird and Bernard 1984; Murphy et al. 2006; Zhang et al. 2012), often no statistically significant interactions were found. Nevertheless, the consideration of these further measures in the context of tillage may offer the opportunity to identify management systems that have a positive impact on soil biodiversity.

### 6.1 Site and climate

Ground beetles, as well as their prey and their predators, are highly dependent on the location. Soil type is known to affect ground beetle communities. Already Thiele (1977) observed that more ground beetle species and higher abundances are typically found on loamy than on sandy soils. In addition to soil type and its associated physical properties, in particular soil water balance, but also pH and soil organic matter content, has a significant impact on soil biodiversity. An example of this is the location dependence of the arable weed vegetation. At the same time, however, the site factors also determine which system of soil cultivation is chosen in practice at the respective location. Thus, under comparatively low precipitation conditions, the favorable effects of reduced tillage on the soil water balance, in particular the reduction of evaporation

(Mitchell et al. 2012), become more relevant. Furthermore, van Capelle et al. (2012) noted interactions between tillage and soil texture on the soil fauna. Earthworm abundances on sandy and clay soils were not significantly influenced by tillage, whereas on clayey and silty soils their data analysis showed strongly increased earthworm abundances after no-till compared to the conventional tillage.

### 6.2 Landscape context

Biodiversity on agricultural land is strongly affected by landscape structure. Species numbers and abundances often increase with diversity and the proportion of non-agricultural land such as hedges, field margins, or fallow land (Clough et al. 2005; Devictor and Jiguet 2007; Thomas and Marshall 1999). The abundance, number of species, and species diversity of arthropods in an agricultural landscape are further influenced by the size of the area, the geometry of the area, and the perimeter-to-area ratio. If the perimeter is relatively large in relation to the area, ground beetles, for example, benefit from marginal structures that serve as habitat and can provide food (Zangger et al. 1994). Edge structures can also favor the overwintering of individual species (Petersen et al. 1996).

The landscape context is of indirect importance for tillage, in that risk of soil erosion can be increased by a pronounced relief, large field sizes, or a small proportion of structural elements in the landscape; thus, the use of the plough can become more problematic. In this context, it is interesting to note that the negative effects of landscape homogenization on the regulation of pests are partly compensated by the use of reduced tillage (Tamburini et al. 2016a). The negative effects of urbanization on ground beetle populations could also be mitigated by reduced tillage (Tamburini et al. 2016b). Conversely, it can be assumed that negative effects of intensive tillage on soil biodiversity in small-scale landscapes may be partially compensated.

### 6.3 Conventional vs. organic management

Due to its integrated approach, organic farming has some systemic advantages in terms of promoting biodiversity in agroecosystems, which have repeatedly been described (Bengtsson et al. 2005; Hole et al. 2005; Petersen 2002; Tuck et al. 2014). Ecological land management can lead to a higher abundance of plants, insects, and birds, among others (Tuck et al. 2014). A distinction can be made between direct effects of the management system, e.g., through the use of insecticides in conventional agriculture, and indirect effects such as a more diverse and richer food base on organically farmed land through the non-use of herbicides. For example, chemical weed control may result in the absence of preferred food plants and their seeds on conventional land and certain

insect species that feed on these seeds may be disadvantaged compared with organic farming (Östman et al. 2001).

On the other hand, however, it tends to be agronomically more difficult in organic than in conventional farming to reduce the intensity of tillage (Cooper et al. 2016). This is partly due to yield losses when ploughing is abandoned, a consequence of reduced nitrogen mineralization and increased weed pressure (Salonen and Ketoja 2020) under reduced tillage. However, organic farming has a package of compensatory measures to promote soil biodiversity. On average, both reduced tillage and organic farming tend to have a positive effect on (soil) biodiversity, but in practice, the combination of reduced tillage and organic farming faces several obstacles for the reasons mentioned above.

#### 6.4 Weed control

Weed control measures, especially the use of herbicides, can have significant direct and indirect effects on soil biodiversity. The weed flora in particular is directly affected as the target of the regulatory measures. Since herbicides reduce the abundance and diversity of weeds, the habitat structure also changes. Depending on the weed abundance and biomass, the microclimate including temperature and humidity in the crop stand may change. Weeds may also provide protection against predators and influence the mobility of individual species in the stand. Herbicide-induced reduction of weed biomass and weed seed abundance may also decrease food supply for herbivorous and granivorous arthropods, respectively (Holland and Luff 2000).

In addition to chemical tillage, mechanical weed control, e.g., weeding or hoeing, analogous to tillage, can also negatively influence the diversity of soil organisms. In particular, hoeing can lead to destruction of the arable weed flora, as a result of which it is no longer available as a food source. Especially in the case of wide row spacing in hoeing and row crops, mechanical tillage may cause a reduction of plant biomass at the soil surface and thus a change in habitat.

In the context of tillage, a central question is how systems with reduced or no tillage at all affect soil biodiversity when non-selective herbicides are applied, especially because carabids may be more affected by herbicide than by the tillage operation (Svobodová et al. 2018). In conventional agricultural practice, the reduction of tillage intensity is often accompanied by the use of such herbicides, especially glyphosate. Negative effects of glyphosate on soil micro-organisms (Druille et al. 2016), on mycorrhizal fungi (Helander et al. 2018), and on earthworms (Lazurick et al. 2017; Stellan et al. 2018) have been documented. With regard to carabids, several studies have shown negative impact of glyphosate use on the abundance of various species (e.g., Svobodová et al. (2018)), though one study also showed that carabid species richness was higher under glyphosate than under a

conventional herbicide regime (García-Ruiz et al. 2018). The decisive factor determining carabid response seems to be sufficient weed cover (García-Ruiz et al. 2018; Svobodová et al. 2018).

#### 6.5 Crop rotation

Crop rotations have a significant impact on soil biodiversity and are, at the same time, intricately linked with the tillage system. Rotations affect carabids as the species composition and abundance of ground beetles depend on the crop cultivated. In field trials, spring-sown crops showed lower abundance and species numbers and lower diversity than autumn-sown crops; the differences between autumn-sown and spring-sown crops were greater than the differences between crop species within a group (Booij 1994; Booij and Noorlander 1992). This can be explained by the time of tillage and the influence of the microclimate in the stand, since the microclimate in cereal stands is warmer and drier than that in root crops (Holland and Luff 2000). Since the activity of ground beetles increases with temperature, a higher abundance in cereals can be explained by the microclimate (Baars 1979; Jones 1976). In addition, ground beetles prefer crops that cover the soil quickly. Especially in root crops with wide row spacing, such as maize or sugar beet, row or stand closure is achieved much later than in cereal stands (Booij 1994).

#### 6.6 Cover crops

Cover crops are an important component for maintaining soil fertility in arable farming systems, especially in those with reduced tillage intensity. Due to their ability to suppress weeds, cover crops are used in particular in reduced or no-tillage farming systems, inter alia to regulate weeds, which otherwise occur through tillage. In a study conducted in the Northern Great Plains, cover crops were found to be beneficial for carabids (DuPre et al. 2021). More indirectly, plant residues of cover crops serve as food for several soil organisms. In a field trial, for example, the cultivation of mustard (*Brassica juncea*) or hairy vetch (*Vicia villosa*) as cover crops led to a higher number of microarthropod species than in a cultivation system without catch crop, probably by serving as food source for some carabids. When comparing different cover crop systems with fallow, a higher activity density of the carabid *Harpalus rufipes* in cover crop systems could be observed. However, the effect varied depending on cover crop mixtures and tillage date (Shearin et al. 2008).

### 7 Conclusions

The species composition and abundance of carabid communities on arable fields is a consequence of heterogeneous

environments, which is influenced by a variety of tillage practices. Ground beetles tend to generally benefit from a reduction of tillage intensity. However, proof of this effect is often not possible due to the complexity of underlying ecological mechanisms and other compensatory factors, especially crop rotation, cover cropping, and crop protection measures. Part of this complexity is formed by the food webs on arable fields, of which carabids constitute an important component. Tillage affects the food of carabids; e.g., weeds and earthworms generally benefit from a reduction in tillage intensity. Generally, the advantages of reduced tillage and no-tillage for carabids and other soil-dwelling organisms may mainly be seen as a consequence of the accumulation of biomass and organic matter at the soil surface and the permanent or temporary lack of disturbance of the soil.

This review has shown that (a) high tillage intensity, on average, negatively affects ground beetle abundance, richness, and diversity in agroecosystems, but that (b) these effects of tillage are highly variable and dependent on a complex set of environmental and management factors. These insights implicate recommendations for both agricultural practice and research.

In particular, for agricultural practice to promote and protect carabids in arable land, the following measures can be deduced. (1) On average, carabid beetles are likely to benefit from reduced tillage intensity; replacing the plough with less intensive tillage systems or even moving to no-till will therefore often help to protect this insect group. (2) However, based on the current evidence, we conclude that no particular tillage system may be given a general preference with regard to the support of carabids. The principle “diversity creates diversity” applies in particular when considering a larger landscape area, in which a variety of tillage systems will create a higher overall diversity (gamma diversity) as different carabid species benefit from different tillage systems. Nevertheless, specific effects on the diversity of carabids can also be associated with certain tillage practices. (3) Further, tillage may be adapted in time (e.g., through timing of tillage to avoid vulnerable larval stages), and space (e.g., through strip tillage). (4) Where a reduction of tillage intensity is agronomically difficult, other measures may help to compensate the negative effects of tillage on carabids, thereby helping to reconcile agronomic aims of tillage with protection of carabid beetles; these include (a) spatial and temporal diversification on all levels of arable crop production including diversified crop rotations and the use of cover crops; (b) reduced use of pesticide, in particular of insecticides; (c) less vigorous weed control to help promote carabids feeding on weed seeds; (d) conversion to organic farming as a combination of different extensification measures; (e) provision of perennial refuge habitats such as grass margins or beetle banks.

In addition, our review has also highlighted the many methodological difficulties in research on the response of ground

beetles to tillage. Based on these findings, there are several recommendations for future research:

- (1) The assessment of tillage disturbance on assemblages of ground beetles is complex. Understanding realistic effects of tillage on ground beetles therefore needs to take account several other management measures and the environmental conditions shaping this management. The present study shows, also due to partly contradictory statements on the influence of tillage on ground beetles, a need for further research, in particular on the interaction of the major factors that can have a compensatory effect. While researchers may set up experiments to separate tillage effects from those of other influences, farming practice always requires tillage to be part of a package that is designed to be compatible with this multiplicity of factors.
- (2) With a view to the goal of promoting soil biodiversity, and carabid beetles in particular, there is a need for research to develop and evaluate practical methods of reduced tillage in organic farming (e.g., Krauss et al. 2020), or other alternative systems that combine a reduction in tillage with a non-use of herbicides.
- (3) Many studies could not be integrated in the meta-analysis because some basic requirements were not met; in particular, dispersion parameters (such as standard deviation) were not given in all cases. Future research should always provide this information to facilitate meta-research that is likely to make it easier to reveal any more general patterns in the response of carabids to tillage. More generally, open data policies are likely to enable secondary use and cross-regional studies.
- (4) To more deeply understand carabid responses to tillage, it will be necessary to study parameters that have not yet been sufficiently included in previous research, such as the resilience of species communities after various tillage measures. In this context, resilience refers to the ability of the community to recover after a defined stress event. The resilience could be measured via the time course of the abundance, diversity, or richness of the community following a specific tillage operation.
- (5) In order to quantify the effects of various factors, including tillage, on ground beetles, a profound knowledge of the habitat requirements of the respective species is required. In view of the large number of potential species to be studied, and the faunistic differences in species communities across geographic areas, we recommend two complementary approaches. The first approach is the identification of key species that may serve as reliable indicators of biodiversity. Suitable for this purpose would be species whose biology is sufficiently known, which occupy a specific place in the food web, which respond sensitively to changing environmental

conditions and for which a reliable recording method is available in the field. In the medium term, this would make it possible to develop the foundations for a systematic assessment framework for the carabid diversity in response to tillage systems. Alternatively, a more trait-based approach would use data from all carabid species at a site, but would more strongly rely on species-specific information about their morphological, phenological, and ecological properties. This would make it possible to draw conclusions about the response of functional groups rather than individual species to tillage practices. Such a functional approach would not only potentially help to reveal mechanisms that underlie these responses, but also to quantitatively bring studies together from different geographic regions, where taxonomic identities are different but ecological properties are similar.

For the overall evaluation of tillage effects on carabids, it is clear that, particularly from a practical farming point of view, other criteria are of primary importance when farmers choose a tillage system. First and foremost, these are production-related and economic criteria, as well as abiotic resource protection, especially against soil erosion. In order to enhance biodiversity of carabids—and to manipulate carabid assemblages—a reduction in the intensity of tillage alone is not sufficient. Permanent or at least temporary no-tillage in combination with an adapted, diverse crop rotation, cultivation of cover crops, reduction of insecticide and fungicide use, and increase of diversity within the cultural landscape, e.g., through field margins or hedges may be suitable for promoting carabids.

**Author contribution** All authors contributed to the review conception and design. Literature collection and analysis were performed by PM, DN, and TFD. Meta-analysis was carried out by KS. The first draft of the manuscript was written by PM, DN, MN, and TFD and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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**Data availability** All data used for the analyses in this study are extracted from scientific publications and available and can be found following the respective literature references.

**Code availability** All used R-packages are clearly referenced in the “Materials and methods” section.

## Declarations

**Ethics declarations** Not applicable

**Consent to participate** Not applicable

**Consent for publication** Not applicable

**Conflict of interest** The authors declare no competing interests.

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