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Research Article

Tillage regime shapes ground beetle distribution and their potential for weed control under drought conditions

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ABSTRACT

Tillage affects soil invertebrates such as ground beetles (Coleoptera: Carabidae), with potential repercussions on the pest and weed control services they provide. Knowledge about the effects of tillage on weed control through seed predation is particularly important in the context of climate change-induced drought, which may exacerbate weed problems.

In this study, we investigated the effects of tillage (conservation vs. conventional) on the abundance, diversity and in-field distribution of ground beetles in 9 pairs of annual crop fields in Northern Italy. We also tested the effect of tillage, artificially induced drought (-50 % precipitation) and arthropod seed predator exclusion on weed biomass and diversity within the same fields. We expected conservation tillage to increase ground beetle abundance and richness, and seed predator presence to buffer the projected increased weed incidence in conservation tillage and drought conditions.

In conservation tillage fields, ground beetle activity density was overall higher, and decreased from field margin to field center, while in conventional tillage it was lower and had an opposite spatial trend. This pattern, reflected also in the in-field distribution of the dominant species *Pterostichus melas*, is likely caused by differential distribution of habitat and food resources in the two management systems. Conservation tillage also positively affected species richness, further underlying its importance in ground beetle conservation.

Unexpectedly, seed predator exclusion reduced weed biomass in conservation tillage. This may be linked to higher seed density, a situation in which the removal of competing seeds can trigger compensatory mechanisms in the remaining seed bank. As drought also increased weed incidence, strategies such as thick mulching, sowing density manipulation, crop rotations and cover cropping might become increasingly necessary in order to limit weeds to a level at which seed predation can efficiently contribute to weed control in climate change scenarios.

Introduction

Tillage is one of the practices most affecting biodiversity and ecosystem services in agricultural ecosystems globally (Palm et al., 2014; van Capelle et al., 2012). Ground-dwelling invertebrates are especially impacted by this kind of soil disturbance, which can directly kill them by mechanical actions, expose them to predators or adverse conditions, degrade their microhabitat, and reduce their alternative prey (Müller et al., 2022; Rowen et al., 2020). This, in turn, can have repercussions on the ecosystem services provided by such invertebrates, including the biological control of pests and weeds (Lami et al., 2020; Tamburini et al., 2016a). Conservation tillage, broadly defined as including all techniques characterized by non-inversion of soil and permanent vegetation cover, is often proposed as an ecologically sound alternative for soil management, and it was proven to benefit soil quality, biodiversity and a variety of ecosystem services (Chabert & Sarthou, 2020; Jacobsen et al., 2022; Tamburini et al., 2016b). However, conservation tillage also has drawbacks, including a higher susceptibility of fields to weed infestation (Boscutti et al., 2015; Chauhan et al., 2012; Peigné et al., 2007).

The correct management of fields for the protection of biodiversity and the enhancement of services such as biological control is made more complex by the effects of anthropogenic climate change. Rising temperatures, extreme weather events and increasing droughts can directly

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affect crop plants (Marini et al., 2020; Wreford & Neil Adger, 2010), but they are also expected to indirectly impact productivity through effects on weeds, pests and beneficial organisms. Pest insects, for instance, might increase in number according to many climate change scenarios (Cannon, 1998; Skendžić et al., 2021). Perhaps even more importantly, weeds are expected to become an increasingly severe problem, as many weed species possess traits related to efficient water exploitation that will prove advantageous in the face of more frequent and severe drought events (Peters et al., 2014). Weeds are one of the most important biotic factors limiting crop yield worldwide (Oerke, 2006), and given the hefty environmental prices associated with herbicide use (Annett et al., 2014; Délye et al., 2013), biological control by arthropod weed seed predators becomes an attractive alternative, especially for conservation tillage fields (Sarabi, 2019). In climate change scenarios, however, biological control efficiency may be reduced; in the projected increasing weed abundance caused by drought conditions, in fact, seed removal might trigger compensatory mechanisms increasing seed survival and plant growth (Garren & Strauss, 2009; Strauss & Agrawal, 1999). Additionally, drought and other climate-related phenomena might interact with disturbances such as tillage in complex ways (Silva & Lambers, 2021), making it even more difficult to predict their effects on damaging and beneficial organisms.

Ground beetles (Coleoptera: Carabidae) are among the most important and well-known ground-dwelling arthropods (Lövei & Sunderland, 1996). In many environmental contexts, they are considered useful ecological or biodiversity indicators (Corcos et al., 2021; Lami et al., 2023). More importantly, ground beetles have a variety of feeding preferences, including omnivorous, predatory and granivorous species (Talarico et al., 2016). Predatory species feed on other invertebrates, including many pests, while granivorous species feed mostly on weed seeds. Ground beetles are thus considered important biological control agents of both invertebrate pests and weeds (Charalabidis et al., 2025; de Heij & Willenborg, 2020). While vertebrates such as birds and rodents also act as postdispersal weed seed consumers (Sarabi, 2019), ground beetles are in fact the most abundant and important weed seed predators in many European agroecosystems (Honek et al., 2003; Lundgren, 2009), although other ground-dwelling arthropods such as ants and crickets also play a role (Baraibar et al., 2011; Lami et al., 2020). Ground beetle roles as biological control agents vary not only based on their general food item preferences, but also on other aspects of their functional diversity, defined as the distribution of ecological and morphological trait values in a community (Tilman, 2001). Body size, specifically, can affect ground beetle voracity and prey choice, influencing not only the biological control efficacy of individual species, but also of entire communities depending on their functional composition (Kulkarni et al., 2015; Lami et al., 2020; Perez-Alvarez et al., 2021). There is thus great interest in the conservation of ground beetle communities in ways which can enhance their ability to perform biological control. These efforts should be rooted in a deep understanding of both ground beetle responses to agricultural practices and their spatial distribution. Ground beetles, in fact, often have inhomogeneous or aggregated distributions within fields (Jowett et al., 2019), also depending on practices such as tillage regime (Boscutti et al., 2015; Trichard et al., 2014), resulting in different levels of biological control in different field areas (González et al., 2020; Lami et al., 2020).

In this study, we tested the effects of tillage regime on ground beetle communities and their potential for weed biological control in annual crop agroecosystems (i.e. soybean and wheat), as well as the interaction of tillage with other environmental factors. In the first part of the research, we investigated ground beetle community features (including taxonomic and functional diversity in terms of body size and feeding type) and their distribution in both conservation and conventional tillage fields. In the second part, we tested the effect of tillage, artificially induced drought conditions and arthropod seed predator exclusion (through mechanical barriers) on weed communities. We hypothesized that i) conservation tillage would have a positive impact on ground beetle communities due to reduced soil disturbance, and ii) conservation tillage and drought conditions would be associated with higher weed problems due to the notorious affinity of weeds for such conditions, but seed predator access would be able to mitigate these problems due to increased weed seed mortality. Our results could inform the management of ground beetle diversity and the associated ecosystem services in both present day and future climate change scenarios.

Materials and methods

Study area and experimental design

Experimental activity was carried out between 2018 and 2019 across 9 field pairs in the lowland area of the Friuli Venezia Giulia Region (NE Italy), within an agricultural landscape (c. 615 km^2) characterized by temperate climate (mean annual precipitation of c. 1300 mm; mean annual temperature of 13 °C). Each field pair included one conventional tillage field and one conservation tillage field, with conservation tillage fields being managed by non-inversion of soil for at least 8 to a maximum of 18 years. The distance between fields in a pair was <300 m, except for one pair in which it was 900 m (Table A.1). In all fields, soybean was sown in May 2018 and harvested in October 2018, while wheat was sown in November 2019 and harvested in June 2019.

Ground beetle sampling, identification and characterization

We carried out two rounds of sampling, respectively in June and August 2018, using pitfall traps (Lami et al., 2020). Traps consisted of 500 ml plastic cups (10 cm in diameter) activated with 200 ml of ethylene glycol 40 %. In each field, we sampled three transects 4 m apart from each other. Each transect included four traps placed at different distances from the margin between the crop field and natural vegetation (1 m, 3 m, 8 m and 20 m), for a total of 12 traps per field. Distance from field margin (in meters) was transformed with natural logarithm (ln) when used for statistical analysis (see Chapter 2.5). During each sampling round, traps were activated for three days, a timespan that we judged adequate given the very high activity density of ground beetles in the area known from previous samplings and from literature (Lami et al., 2021; Tamburini et al., 2016c).

Collected ground beetles were stored in ethanol 70 % and identified to species or, in some cases, morphospecies level by morphological traits. For each species, information on body size (i.e. average body length) and feeding type (i.e. predominantly granivorous vs. predominantly predatory species) was retrieved from literature (Honek et al., 2003; Tamburini et al., 2016b, c). For each trap, we calculated a community-weighted mean (CWM) (Lavorel et al., 2008) of both body size and feeding type. For feeding type, we assigned the values of 0 and 1 to the two feeding types, resulting in CWM values ranging from 0 (only granivorous species) to 1 (only predatory species) (Rusch et al., 2016). We excluded three individuals from the CWM calculations due to insufficient level of detail of their taxonomic identification, and thus the impossibility of retrieving reliable trait information.

Drought treatment

Weed control potential was assessed in the context of a parallel experiment focusing on the effect of soil management and drought on multiple ecosystem services (Lami et al., 2025). In each field, we defined a 20 × 60 m strip in contact with the margin in which the crop was sown but agrochemicals (including fertilizers) were not used. Roughly at the center of this strip, we selected a 4 × 4 m drought treatment plot and an equally sized control plot. The treatment and the control plot were placed at around 1 m from each other, to ensure homogeneity of conditions. Half of the area of each treatment and control plot was normally sown with the crop, while the other half was left unsown.

Rainout shelters (4 × 4 m) were employed to simulate drought conditions (Kundel et al., 2018). The shelters were covered with 18 polycarbonate gutters (11 cm wide, 400 cm long and 3 cm deep) excluding about 50 % of the precipitations. Shelters were 170 cm high on one side and 150 cm high on the other, and water was collected in a gutter at the back of the shelter and then released on field at about 5 m from the plot through a plastic tube. Shelters were placed on field one week after soybean sowing and temporarily removed in between soybean harvesting and wheat sowing.

The efficiency of the rainout shelters in simulating drought conditions was verified using ECH_2O EC-5 soil humidity probes and ICT Em5b data loggers in three of the field pairs from May to October 2018 (during the soybean period) (Lami et al., 2025).

Seed predator exclusion: weed diversity and biomass

We set up an experiment aimed at evaluating the effect of arthropod seed predators in general on weed diversity and biomass, under the assumption that the highest contribution to weed seed predation would come from ground beetles, given their prevalence in European seed predator communities (Honek et al., 2003; Lundgren, 2009). In early June 2018 we installed in the unsown half of each plot two 1 × 1 m invertebrate exclusion subplots. Subplots were placed at the distance of at least 70 cm from the border of the shelter/control plot. Each of these subplots was fenced with a 30 cm high plastic barrier interred for roughly 5 cm. Two pitfall traps were installed at opposite corners inside each exclusion fence, consisting of 500 ml plastic cups (10 cm in diameter) buried flush with soil surface and pierced at the bottom for rainwater drainage. Pitfall traps ensured continuous removal of seed predators that potentially managed to pass over the barrier and enter the exclusion subplot.

Weed diversity was evaluated in the two exclusion subplots as well as in two 1 × 1 m control subplots in each treated and control plot. Surveys were carried out in February and April of 2019, after shelters had been in place exerting their action throughout all of the soybean period, but before the sowing of wheat. We took high-res pictures of each subplot, and weed species richness was measured based on them. At the time of wheat harvest in June 2019, all weed biomass was gathered from the subplots, dried for 48 h at 65 °C and then weighed. In one of the drought control plots of conservation tillage, weed biomass could not be gathered due to external interference. The long duration of the exclusion experiment ensured that it encompassed multiple peaks of seed predation activity, as this ecosystem service is known to vary seasonally with repeated peaks depending on the species involved and the environmental conditions (Heggenstaller et al., 2006; Honek et al., 2006).

Statistical analysis

Sampling completeness was evaluated by calculating sample coverage in the conservation and conventional tillage fields separately (Chao et al., 2014; Chao & Jost, 2012).

We used generalized linear mixed effect models (GLMMs) to test the effects of tillage treatment and distance from field margin (ln-transformed) and their interaction on trap-level ground beetle abundance, species richness, mean body size and feeding type composition, as well as on the abundance of the dominant predatory and granivorous species (Models 1–6). Specifically, we used GLMMs with Gaussian distribution for the continuous variables (body size and feeding type composition), while GLMMs with Poisson distribution were our first choice for discrete count variables (abundance and species richness). However, we ended up using a Poisson GLMM only for species richness, while for overall ground beetle abundance and abundance of the dominant species we used GLMMs with negative binomial distribution, based on improved residual diagnostic plots (qq-plots, residuals v. predicted values) when employing the latter. Given that traps were placed in the same positions in both sampling rounds, for Models 1–6 we used field pair ID, field ID, transect ID and trap position ID (in this order from outermost to innermost) as nested random factors to account for spatial autocorrelation. If interactions between explanatory variables were not significant ($P > 0.05$), we removed them and re-ran the model to avoid overfitting and correctly interpret the main effects. The complete list of tested fixed effects and interactions for Models 1–6 can be found in Table 1.

To check the effects of tillage treatment and distance from margin on ground beetle community composition, we used a Nonmetric MultiDimensional Scaling (NMDS) plot (Minchin, 1987), and also performed an analysis of similarities (ANOSIM) (Clarke, 1993), in both cases using Bray-Curtis distance (Bray & Curtis, 1957).

Finally, we used GLMMs with Gaussian distribution to test the effects of tillage treatment, drought treatment, seed predator exclusion and their interactions on weed biomass and species richness (Models 7–8). Our first choice for species richness (a discrete count variable) would have been a Poisson GLMM, but we changed to Gaussian due to improved diagnostic residual plots. Biomass was square-root transformed to meet model assumptions. To account for spatial autocorrelation, field pair ID, field ID and plot ID were used as nested random factors (in this order from outermost to innermost), with subplot ID also being included (nested within plot ID) for the species richness model, given that there were two surveys of weed species richness per subplot. Non-significant interactions were removed from the models. In case of significant interactions, we conducted a post-hoc test by calculating pairwise comparisons with a Tukey adjustment. The complete list of tested fixed effects and interactions for Models 7–8 can be found in Table 2.

All analyses were performed using packages *vegan* v2.6–8 (Oksanen et al., 2025), *lme4* v1.1–35.5 (Bates et al., 2015), *iNEXT* v3.0.1 (Hsieh et al., 2016) and *DHARMa* v0.4.7 (Hartig, 2020) in R v4.4.1 (R Core Team, 2019).

Table 1
Results of the generalized linear mixed effects models (GLMMs) testing the effects of tillage regime and distance from field margin on ground beetle abundance, richness and functional diversity.

Distribution	Dependent variable	Fixed effects	χ^2	P
Model 1				
Negative binomial	Ground beetle abundance	Tillage treatment	6.306	0.012
		Distance from margin*	1.636	0.201
		Tillage × Distance*	5.489	0.019
Model 2				
Poisson	Ground beetle richness	Tillage treatment	4.489	0.034
		Distance from margin*	1.578	0.209
Model 3				
Gaussian	Weighted ground beetle body size	Tillage treatment	0.001	0.975
		Distance from margin*	1.154	0.283
Model 4				
Gaussian	Weighted ground beetle feeding type	Tillage treatment	0.703	0.402
		Distance from margin*	1.497	0.221
Model 5				
Negative binomial	*Pterostichus melas* abundance	Tillage treatment	3.995	0.046
		Distance from margin*	4.801	0.028
		Tillage × Distance*	4.377	0.036
Model 6				
Negative binomial	*Harpalus rufipes* abundance	Tillage treatment	0.714	0.398
		Distance from margin*	2.187	0.139

* Ln-transformed.

Table 2
Results of the generalized linear mixed effects models (GLMMs) testing the effects of tillage regime, drought treatment and seed predator exclusion on weed biomass and richness.

Distribution	Dependent variable	Fixed effects	χ^2	P
Model 7				
Gaussian	Weed biomass*	Tillage treatment	2.374	0.123
		Drought treatment	23.016	<0.001
		Seed predator exclusion	15.516	<0.001
		Tillage × Drought	4.846	0.028
		Tillage × Exclusion	4.194	0.041
Model 8				
Gaussian	Weed richness	Tillage treatment	0.010	0.919
		Drought treatment	8.809	0.003
		Seed predator exclusion	2.718	0.099

* Square-root transformed.

Results

Ground beetle community features

We collected a total of 5390 ground beetles belonging to 45 different species or morphospecies. The most abundant species was the generalist predator *Pterostichus melas* (Creutzer) (1787 individuals, 33.2 % of the sample), with the mainly granivorous *Harpalus rufipes* (DeGeer) being the second most abundant species (1043 individuals, 19.4 % of the sample). Sample coverage was very high (99.6 % for both conservation and conventional tillage fields), indicating that the sampling effort was adequate (Fig. A.1).

Effects of tillage and distance from margin on ground beetle communities

There was a significant interaction of tillage regime and distance from field margin influencing ground beetle abundance (Table 1). Beetle abundance was generally higher in conservation tillage fields (28 % higher on average, overall), but it decreased going from field margin to center, while in conventional tillage field it increased going from margin to center (Fig. 1a). The effects of tillage and distance were also tested on the abundance of *P. melas* and *H. rufipes*, as the dominant predatory and granivorous species respectively. There was a significant interaction effect on *P. melas* (Table 1), with this species being generally more abundant in conservation tillage fields (36 % more abundant on average, overall) but decreasing significantly from field margin to center, while in conventional tillage fields it only slightly increased from margins to center (Fig. 1b). No significant effects of the explanatory variables on *H. rufipes* were found (Table 1).

Ground beetle species richness in general was also significantly higher in conservation tillage than in conventional tillage, with an 18 % increase (Table 1 and Fig. 2). Neither tillage regime nor distance from field margin significantly influenced ground beetle community-weighted body size or community weighted feeding type (Table 1). Additionally, the NMDS plot and ANOSIM did not show any effect of the explanatory variables on community composition (Fig. A.2).

Biological weed control

The complete list of weed species recorded during this study is reported in Table A.2. Regarding weed biomass, tillage regime had significant interactions with both seed predator exclusion and drought treatment (Table 2). In conservation tillage fields, weed biomass was significantly higher (27 % on average) than in conventional tillage in normal seed predator access conditions, but it decreased (31 %) with seed predator exclusion, while the much lower biomass of conventional fields did not change significantly with exclusion (Fig. 3a). Drought, on the other hand, tended to increase weed biomass in both types of fields, but the effect was significant only for conservation tillage fields, which saw a disproportionately higher increase in biomass (35 %), reaching significantly higher values than conventional tillage in drought conditions (26 %) (Fig. 3b). There was no significant interaction between seed predator exclusion and drought treatment on weed biomass, and the only variable significantly affecting weed species richness was the drought treatment, which increased richness (Table 2 and Fig. 3c).

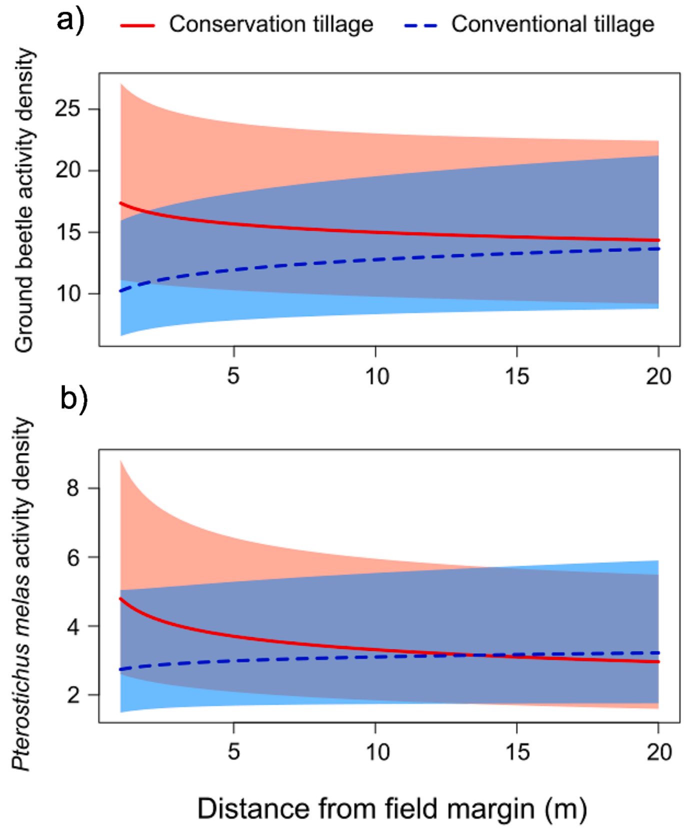

Fig. 1. Effect of tillage regime and distance from field margin on (a) overall ground beetle activity density and (b) Pterostichus melas activity density, with 95 % confidence intervals.

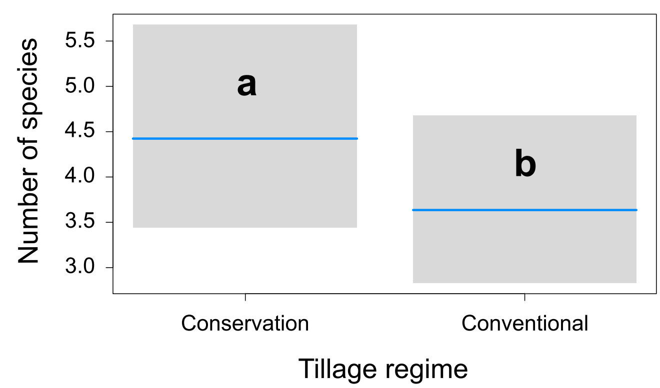

Fig. 2. Effect of tillage regime on the number of ground beetle species by trap, with 95 % confidence intervals. Different letters indicate statistically significant differences according to post-hoc pairwise comparisons with Tukey adjustment.

Discussion

Our study shed some light on the effects of tillage on ground beetle

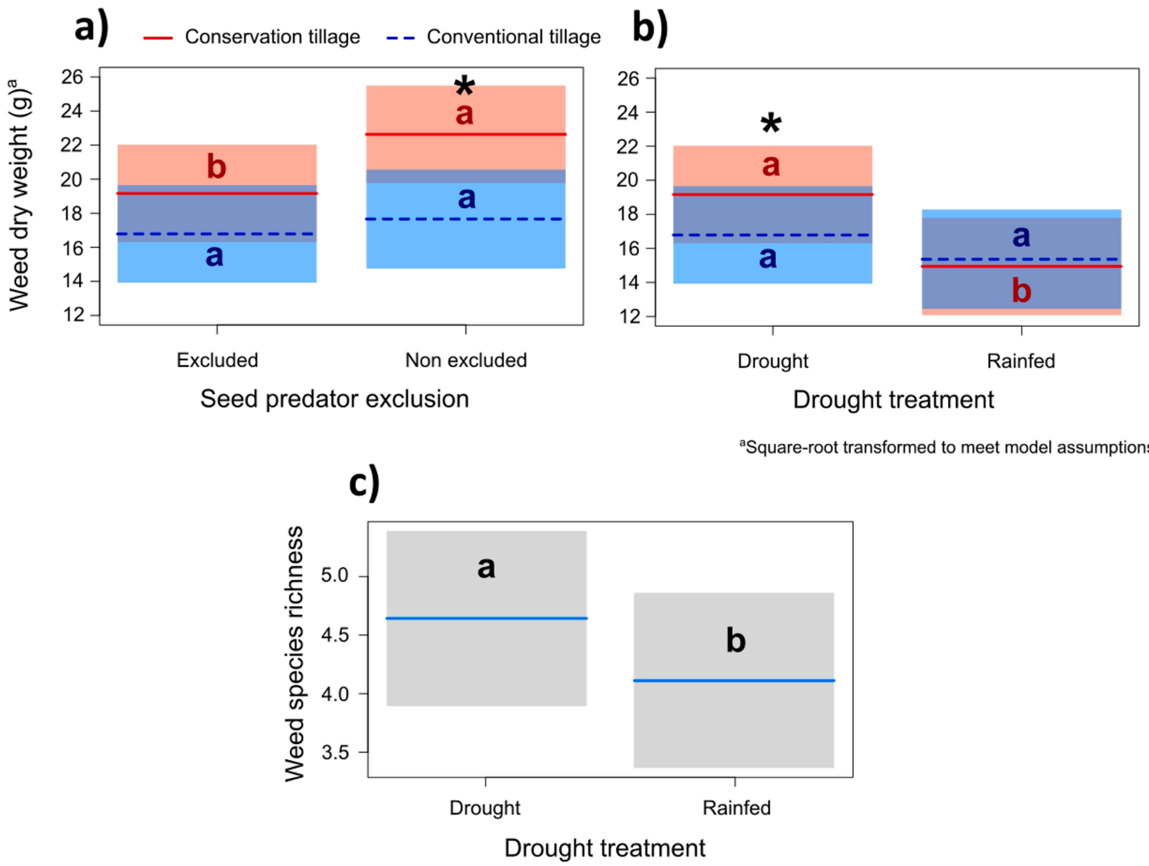

Fig. 3. Effect of the interaction of tillage regime and seed predator exclusion (a) and of tillage regime and drought treatment (b) on weed biomass (measured as weed dry weight), and effect of drought treatment on the number of weed species (c), with 95 % confidence intervals. Different letters indicate statistically significant differences between exclusion treatments for conservation (red) and conventional tillage (blue) and for the entire dataset (black), while asterisks indicate significant differences between tillage regimes within the same predator exclusion or drought treatment, all according to post-hoc pairwise comparisons with Tukey adjustment. Weed dry weight was square-root transformed in order to meet model assumptions.

communities, as well as on the combined influence of tillage and drought on weed control performed by ground beetles and other arthropods. Conservation tillage positively influenced ground beetles in general, as expected, but it also affected their in-field distribution patterns, with potential implication for ecosystem services distribution. Contrary to what we hypothesized, seed predator presence increased weed biomass in conservation tillage; the significance and implications of our findings are discussed in the following sections.

Specifically, our results on ground beetle communities are relevant to Northern hemisphere agroecosystems, as ground beetles are highly characteristic of the Holarctic realm (Kryzhanovsky, 2022) and are among the most common ground-dwelling arthropods in the agroecosystems of this region (Müller et al., 2022); European agroecosystems, in particular, are the most likely to harbor ground beetle communities similar to what we reported (Lövei & Sunderland, 1996), and behaving in similar ways. The implications of our results on weed control by seed predators, on the other hand, might have even wider geographical relevance (at least considering areas with similar environmental features as our own), given that ground-dwelling invertebrates tend to be amongst the most important weed seed predators in many parts of the world (Boadi et al., 2024; Jacob et al., 2006; Pinos et al., 2023).

Effects of tillage on ground beetle communities

While it is well known that tillage has generally negative impacts on ground beetle communities (Boscutti et al., 2015), its effects on their diversity can be variable due to a number of other interacting environmental factors, including landscape features (Müller et al., 2022). Our data indicates that tillage regime influenced ground beetle activity density and species richness, but did not influence community composition and functional diversity. This pattern agrees with previous findings from intensified agricultural landscapes (Belaoussoff et al., 2003), which often report a mostly positive effect of the reduction of tillage (and of the associated microhabitat disruptions) on ground beetle abundance and diversity (Müller et al., 2022), but also a relatively homogeneous fauna dominated by a few adaptable species (Aguilera et al., 2020; Deppe & Fischer, 2023; Rischen et al., 2022). We found an inhomogeneous distribution of activity density of ground beetles within fields, also coherent with studies reporting aggregated distributions for these insects (Jowett et al., 2019; Trichard et al., 2014). Skewed species-abundance distributions, in which the numerically dominant species disproportionately influence community patterns, are very common (McGill et al., 2007; Winfree et al., 2015), and this was also the case for our data, as overall ground beetle in-field distribution patterns were similar to the distribution patterns of the dominant species *P. melas*. Specifically, we found that in-field distribution patterns for this species and the community in general had opposite trends for conventional and conservation tillage.

In the case of conservation tillage fields, the higher ground beetle activity density at the margins might be explained by the fact that field margins can be considered a transition zone between a semi-natural and a crop habitat. The relatively low disturbance of conservation tillage fields allows easier colonization by wild plant species (Boscutti et al., 2015), turning this transitional zone into less of an ecotone and more of an ecocline (van der Maarel, 1990), at least when compared with more disturbed conventional tillage fields. This ecocline can thus host a mix of plant species from both the adjacent semi-natural habitats and the crop field itself, which in the case of conservation tillage might be particularly rich in ruderal species, taking advantage of the relatively low soil disturbance. The resulting higher plant and invertebrate species richness might represent a valuable source of food items and microhabitats for ground beetles, and especially for generalists linked with agricultural landscapes, which may reach particularly high densities (Jowett et al., 2021; Maksimovich et al., 2023). The opposite trend in conventional tillage fields is likely linked with the higher soil disturbance. Tilled environments are more hostile to plants and invertebrates (i.e. potential ground beetle food sources) from neighboring habitats and, at the same time, field-specific resources are likely to be scarcer at the margins than in the center, resulting in a sharper ecotone with a lower ability to support wild species (Dutoit et al., 2007). This suggests that biocontrol services provided by ground beetles might also be lower at the margins for conventionally tilled fields and higher at the margin for conservation tillage fields, and that field shape and size might be an important factor to consider when deciding for conventional or conservation tillage. Specifically, conservation tillage would be particularly useful to improve ground beetle services in small or complex-shaped fields, in which the proportion of edge area is higher, while for larger and less complex fields the difference between conservation and conventional tillage would likely be negligible in terms of ground beetle services enhancement, and in some cases conventional tillage might have an edge over conservation tillage (Lami et al., 2020).

Effects of tillage, drought and seed predator exclusion on weed control

The higher susceptibility of conservation tillage fields to weed infestations compared with conventional tillage is well known (Chauhan et al., 2012; Peigné et al., 2007). Therefore, it was expected that weed biomass would increase more under conservation tillage in drought conditions, which tend to favor drought-resistant weed species over crops (Karkanis et al., 2018; Valerio et al., 2011). These same adaptations to drought are also the likely explanation for the general increase in weed species richness under drought treatment in both tillage regimes. The projected higher weed problems in conventional tillage under climate change conditions implied by these results, and their implications for weed management, were more thoroughly explored in Lami et al. (2025) with a dedicated analysis starting from the same dataset.

In contrast with our expectations, seed predator exclusion did not favor weeds in terms of biomass production. In fact, there were no significant differences between exclusion and control plots in conventional tillage, while in conservation tillage, which had higher weed biomass to begin with, seed predator exclusion was associated with a reduction in biomass. An element to consider is the fact that herbivorous insects attacking weeds may have included flying species that were not efficiently stopped by barriers, while ground-dwelling natural enemies of those herbivores, including predatory and omnivorous ground beetles (Firlej et al., 2013; Lövei & Sunderland, 1996), would have been excluded; this would have led to an increased herbivore pressure on weeds within barriers compared with controls. Still, another factor might be at play, involving the direct relationship between seed predators and weeds. Invertebrate seed predators are generally considered valuable assets in the biological control of weeds, especially in conservation tillage (Baraibar et al., 2011; Sarabi, 2019). However, it has been shown in past research that in certain conditions seed predation (or herbivory in general) can indeed fail to reduce weeds (Ortega et al., 2012), and can even increase them (Myers & Risley, 1999). This phenomenon arises especially in cases where weed density (and consequently seed density) is very high, leading to a very strong competition for germination and resources between seeds. In such cases, the removal of potential competitors allows a larger number of seeds to develop into adult plants, or a smaller number of plants to grow larger given the increased resource availability (Garren & Strauss, 2009). This would also explain why the effect on biomass is stronger for conservation tillage fields, in which weed density is higher, leading to higher seed density and competition. As our own data and a steadily increasing body of research predict that weed infestations will only grow more severe in climate change conditions (Peters et al., 2014), cases in which seed predation becomes inefficient or even facilitates weeds are bound to become more common. Strategies such as thick mulching, sowing density manipulation, crop rotations and cover cropping (MacLaren et al., 2020) may thus become increasingly important in order to limit weed abundance to a level at which seed predation can efficiently contribute to weed control (Honek et al., 2003) without resorting to environmentally damaging herbicides. This is especially true for conservation tillage fields, in which the increase in weed infestations caused by drought will likely be more severe.

Conclusions

Aside from generally confirming the positive effect of conservation tillage on ground beetle abundance and diversity, we showed that:

a) Tillage had an impact on the in-field distribution of the dominant ground beetle species and of the community in general, which potentially means that the related ecosystem services would also be differentially distributed within conservation and conventional tillage fields;
b) Seed predator presence had an unexpected negative effect on weed control in conservation tillage fields, a phenomenon possibly linked with the high number of weed seeds that can compete for resources in conservation tillage conditions.

These facts indicate that i) the effectiveness of conservation tillage in preserving beneficial ground beetles might also depend on field shape and size; and ii) it is pivotal to find sustainable ways of limiting weeds to a level at which seed predation can efficiently contribute to weed control, also considering the projected increasing weed densities in climate change drought scenarios (especially in conservation tillage). Finally, our results can also inform future research by acting as a reminder that i) when studying the effects of disturbance on organisms, it is important to consider not only community features, but also spatial distribution; and ii) in specific environmental conditions, what is normally a beneficial ecosystem service may end up facilitating harmful organisms.

CRediT authorship contribution statement

Francesco Lami: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Francesco Boscutti:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition. **Giacomo Santoiemma:** Writing – review & editing, Investigation. **Lorenzo Marini:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2025.11.001.

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