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Original Research

Effects of Flowering Inter-Crops on Ground Beetle (Coleoptera: Carabidae) Assemblages in Organic Raspberry and Strawberry Cultivation

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Abstract

Ground beetles contribute to the biological control of economically important pests in soft fruit crops, but their abundance and activity may be influenced by plantation management. A two-year field experiment in organic raspberry and strawberry plantations was undertaken in central Poland to investigate the effects of three flowering inter-crops on carabid assemblages. These included: (*i*.) an annual flower strip established along one side of the crop, (*ii*.) flower islands located within the crop, both composed of the same multi-species mixture of flowering plants, and (*iii*.) a perennial white clover living mulch grown in the inter-rows. Each treatment, including the control, was represented by a single 200 m² plot. Ground beetles were sampled using pitfall traps during three sampling periods: 1-31 August 2023, 1 September-10 October 2023 and 1-31 August 2024. A total of 470 carabids representing 12 genera were captured, including 264 individuals in raspberry and 206 in strawberry trials. The assemblages were composed predominantly of species commonly associated with agricultural habitats. In both crops, the eudominant species were *Harpalus rufipes* and *Pterostichus melanarius*, accounting for 20-27% and 36–56% of all individuals, respectively. Carabid assemblages were broadly similar in composition regardless of crop species, and temporal variation emerged as the primary driver of changes in their structure. The inter-cropping treatments neither increased the overall activity-density nor the species richness of ground beetles. Their influence was limited to the functional composition of assemblages, with the white clover living mulch significantly reducing the number of omnivorous carabids but leaving predatory species unaffected. The results suggest that, in landscapes already characterised by a high level of ecological complexity, the potential for further enhancement of carabid assemblages through additional biodiversity-supporting practices may be limited.

Keywords: biodiversity-enhancing practices, flower strip, living mulch, cover crop, carabid beetles, natural enemies, soil-dwelling insects, beneficial entomofauna, functional diversity

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Introduction

Ground beetles (Coleoptera: Carabidae) are an important component of beneficial farmland entomofauna, acting both as polyphagous predators of numerous pest species [1] and consumers of weed seeds [2]. Their role in the biological control of economically significant pests of soft fruit crops, including raspberries [3], strawberries [4] or blueberries [5], has been reported. Concurrently, carabids are considered bioindicators of the sustainability of agricultural management systems owing to their high susceptibility to anthropogenic pressure [6].

In Poland, there are approximately 500 species of ground beetles grouped into over 70 genera [7, 8]. Between 20 and 70 carabid species were recorded during faunistic studies performed across various agroecosystems; the vast majority of them were common ones, with *Harpalus rufipes*, *Poecilus cupreus*, *Poecilus versicolor*, *Pterostichus melanarius*, *Nebria brevicollis*, *Calathus ambiguus* and *Anchomenus dorsalis* being the most abundant [9-16]. However, in Poland, as in the rest of Europe, a worrying decline in the abundance and/or diversity of ground beetles on agricultural land has been observed, which has mainly been attributed to the negative impact of pesticides, intensive tillage and prevalence of monocultures in a landscape [10, 12, 13, 16-18]. This raises concerns about a consequent reduction in the natural pest regulation services provided by carabids.

Given the beneficial effects of vegetation richness on carabid assemblages [19], various inter-crops grown alongside main cash crops – not for direct economic return but rather as shelter for beneficial insects – have been widely investigated as a method of conserving ground beetles in agricultural land and enhancing natural pest control. However, the positive effects of flowering companion plants on ground beetle assemblages are based on different mechanisms than those reported for pollinators and parasitoids. Whilst the beneficial Hymenoptera exploit the increased nectar and/or pollen availability provided by flowering inter-crops [20], Carabidae – most of which are predatory or granivorous species – benefit indirectly from such habitat modifications. These include the provision of overwintering sites [21], refuges from intensive agricultural disturbances (e.g. tillage, pesticide use) [22], favourable microclimatic conditions [21], as well as increased availability of food resources in the form of supplementary seeds [23] and prey (greater invertebrate biomass [24]).

One such biodiversity-enhancing practice is the establishment of flower strips, which have been identified as important reservoirs for ground beetles in farmland [23, 25, 26]. Nonetheless, results concerning the role of these practices in shaping the abundance, diversity and pest control potential of carabids in agricultural land remain inconsistent. In a study by Pecheur et al. [27], rapid colonisation of annual flower strips by granivorous ground beetles was observed. However, this did not translate into any pronounced changes within Carabidae assemblages in adjacent cereal fields. Similarly, the presence of flower strips in winter wheat fields did not increase carabid activity-density, aphid suppression or crop yield [28]. In contrast, Li et al. [29] reported that flower strips significantly enhanced the abundance and diversity of carabids in the adjoining maize cultivation. Key factors determining the effectiveness of flower strips include their size (wider strips promote higher abundance and diversity of ground beetles, both within the strips themselves and in the adjacent crops) [29], plant density and diversity [28] and a complex age structure (i.e. a combination of older and younger floral patches) [30].

Another inter-cropping approach aimed at increasing functional biodiversity in agricultural systems is the use of living mulches (undersown cover crops), which are grown simultaneously with the cash crop during at least part of the growing season. Nevertheless, as in the case of flower strips, studies evaluating their impact on carabid abundance, diversity, and biological control potential have produced inconsistent results.

In arable crops, Hüber et al. [31] found that maize-bean inter-cropping did not affect carabid activity-density or species richness. In vegetable cultivation, on the other hand, Ditner et al. [32] reported a significant increase in ground beetle abundance following the introduction of cornflower strips into the inter-rows of white cabbage. Similar observations were made by Theunissen et al. [33] and Booij et al. [34], who found that an increase in activity-density and diversity of Carabidae in cabbage fields inter-cropped with a white clover living mulch was accompanied by reduced pest pressure and lower crop damage. In a study by Depalo et al. [35] covering four European countries, the effects of legume cover crops introduced into cauliflower production were highly location-dependent, ranging from alterations in abundance of selected genera or overall diversity to no detectable changes in carabid assemblages. No decrease in cabbage caterpillar populations was detected, whilst aphid pressure was significantly reduced by the living mulch in one of the studied countries. Similarly inconsistent results were reported by Rämert [36], who found no steady effect of lucerne undersowing in carrot crops on carabid abundance across locations and years, although cover-cropped plots generally experienced lower levels of carrot fly damage.

Studies conducted in perennial cropping systems have also yielded contrasting results. In pear orchards, multi-species sown flowering ground covers supported higher activity-density of carabids than regularly mown swards [37], whereas the introduction of chrysanthemum living mulch into walnut orchards did not influence ground beetle abundance [38]. Conversely, Kosewska et al. [39] reported that both lucerne and white clover undersowing significantly reduced the abundance and species richness of Carabidae in energy willow plantations.

Despite the growing body of literature from arable, vegetable, and perennial crops outlined above, the impact of flowering inter-crops on ground beetle assemblages has not been conclusively established. Furthermore, to the authors' knowledge, no comparable results have yet been published from berry cropping systems, in spite of their different habit (herbaceous perennials or shrubs) and distinct management practices (e.g. annual mowing of plantations, higher planting density compared to orchards), which might alter the response of carabids to floral interventions.

The aim of the present study was to assess the impact of three flowering inter-crops, i.e. a white clover living mulch, a multi-species floral strip, and floral islands, on the activity-density, species richness, and functional composition of ground beetle assemblages in organic open-field raspberry and strawberry cultivation. It was hypothesised that the inter-cropping practices proposed would significantly enhance the activity-density and diversity of carabids within the crops, whilst increasing the representation of functionally beneficial guilds associated with biological pest and weed control.

Materials and Methods

A two-year open-field experiment (2022-2024) was conducted at the experimental site of the National Institute of Horticultural Research in Skierniewice, Central Poland (51°56'46.14''N 20°11'15.07''E). The area is located within the Mazovian Lowland and characterised by a transitional temperate climate with a mean annual temperature of 8.6ºC and average annual precipitation of 540 mm. The study site was situated in a suburb and surrounded mostly by single-family housing, farmland and semi-natural habitats within a radius of 250 m. In spring 2022, bare-root plants of the primocane-fruiting raspberry cv. Poemat (*Rubus idaeus*) and the mid-early summer-fruiting strawberry cv. Lycia (*Fragaria* × *ananassa*) were planted at spacings of 2.5×0.5 and 0.9×0.2 m, respectively. The first growing season (2022) was used for full plantation establishment, with all assessments performed over the following two years (2023-2024).

Three biodiversity-enhancing practices, including a living mulch, flower islands and a flower strip, were tested against a control without the inter-crops implemented. Each treatment was represented by a single plot of 200 m^2 (20×10 m), with a distance of approximately 50 m between the plots. Within each crop, the four treatments were randomly assigned to the four available plots. A 1.5-m-wide buffer zone at the edges of each plot was kept free from vegetation through regular mowing; in the further surroundings, a mixture of rye, buckwheat and leguminous plants was cultivated under a plough system.

The living mulch, which consisted of *Trifolium repens* (sowing rate: 1.5 g/m²) and *Festuca ovina* (0.5 g/m²), was intended to form a dense, nitrogen-fixing ground cover. The flower strip and islands were established using the same multi-species mixture comprising perennial plants – *Pulmonaria officinalis* (1 plant/m²) and *Stachys officinalis* (1 plant/m²) – as well as annual species – *Anethum graveolens* (1.0 g/m²), *Tagetes* spp. (0.5 g/m²), *Lobularia maritima* (0.3 g/m²), *Tropaeolum majus* (1 g/m²) and *Matthiola bicornis* (1.0 g/m²). This composition was selected to provide continuous pollen and nectar resources for beneficial insects throughout the growing season, to create a dense, multi-layered flower cover, and to avoid plant species posing phytosanitary risks to the berry crops.

The perennial living mulch was established once in 2022, in every inter-row in the raspberry plots and in every second inter-row in the strawberry plots. It was subsequently managed by regular mowing after white clover flowering. The flower strip was sown along the longer outer edge of the experimental plot. The flower islands consisted of two floral patches in raspberry cultivation and four patches in strawberry cultivation; these were located in the centre of the plot, aligned with the crop rows and partially replacing them. Both the flower strip and flower islands were renewed annually by soil cultivation and reseeding around 10 May. Their species composition was maintained through manual weeding when necessary. The spatial arrangement and dimensions of all inter-crops are shown in Fig. 1. The control represented a traditional berry cropping system without any additional sown vegetation.

The experiment was conducted under an organic production system, yet no plant protection products were applied in order to avoid any adverse impact on beneficial organisms. The crop rows were hand-weeded, whereas the inter-rows – except those covered with living mulch – were maintained as bare soil by repeated mechanical tillage (2-3 operations per growing season).

Samples of ground beetle assemblages were collected continuously during three sampling periods: 1-31 August 2023, 1 September-10 October 2023 and 1-31 August 2024. Beetles were captured using plastic pitfall traps [40] with a capacity of approx. 460 mL. The traps were filled to half their volume with brine (25% NaCl solution in tap water), which served both as a preservative and a killing agent [41]. One trap was dug into the ground in the inter-row space at the centre of each experimental plot so that the rim was level with the soil surface. An area within a radius of 15 cm around each trap was carefully cleared of vegetation. The traps were covered with a raised lid that allowed beetles to enter whilst protecting the contents from rainfall. The traps were emptied and refilled weekly, and the ground beetles collected were rinsed with water and identified to species level based on their morphological traits [42-46] using a Delta Optical SZ-630T stereoscopic microscope (Delta Optical Ltd, Mińsk Mazowiecki, Poland).

All recorded species were classified as either omnivorous (mixed feeders consuming both plant

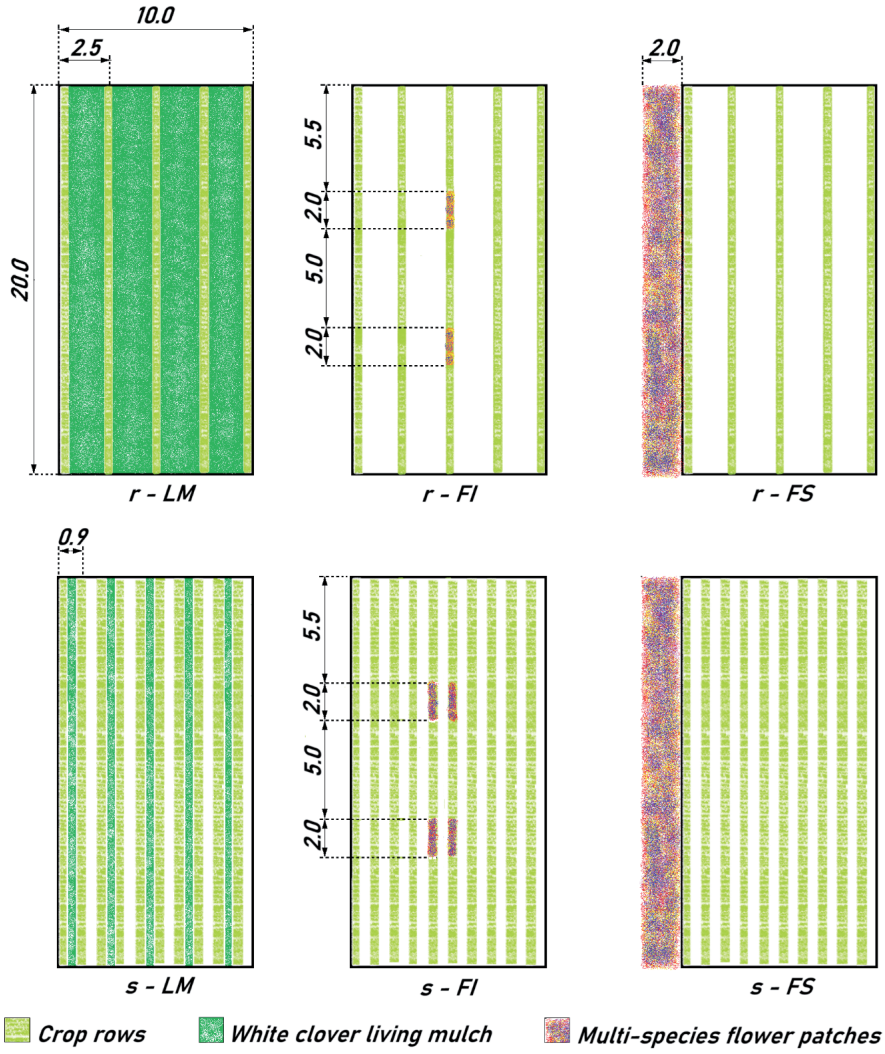

Fig. 1. Schematic drawing illustrating the spatial arrangement of three inter-crops: a living mulch (*LM*), flower islands (*FI*), and a flower strip (*FS*) in raspberry (*r*) and strawberry (*s*) cultivation. All dimensions are given in metres; the distances between the plots are not to scale.

and animal material) or predatory (feeding on animal material) according to the available literature [43, 47-54]. In the descriptive analysis of dominance structure at the crop level, the following classes were adopted: eudominant (>10.0%), dominant (5.1-10.0%), subdominant (2.1-5.0%), recedent (1.1-2.0%) and subrecedent species (<1.0% of individuals in the assemblage) [55]. Moreover, from the species-level abundance data, six diversity indices were computed in order to characterise richness, heterogeneity and evenness of carabid communities under different inter-cropping practices. These were: Shannon, Simpson, Fisher's alpha, Chao1, Berger-Parker dominance and Buzas-Gibson's evenness [56].

Data Analysis

Ground beetle activity-density data and biodiversity indices were analysed using general linear models with crop type (raspberry or strawberry), treatment (control, living mulch, flower islands or flower strips) and sampling session (1-31 August 2023, 1 September-10 October 2023 or 1-31 August 2024) as explanatory variables. Normality and homogeneity of variance of the input data were assessed using the Shapiro-Wilk and Brown-Forsythe tests, respectively. Three response variables – total number of carabids, number of predatory carabids and number of omnivorous carabids – were *ln*-normalised to meet model assumptions; back-transformed means and confidence intervals are presented in the results section.

Differences in ground beetle assemblages amongst crops, inter-cropping treatments and sampling sessions were visualised using non-metric multidimensional scaling (NMDS) [57] and tested with two-way permutational multivariate analysis of variance (PERMANOVA) [58]. Two separate PERMANOVA models were performed: the first included the effects of crop and sampling session, whilst the second tested the effects of inter-crop and sampling session, both of

which included interactions of the factors incorporated. Prior to the analyses, species-level activity-density data were *ln(x+1)*-normalised. Homogeneity of multivariate dispersions was verified for all factors using the PERMDISP test [59]. All analyses were based on the chord distance measure with 9,999 random permutations.

Statistical significance was tested at $\alpha \leq 0.05$. For general linear models, however, a tolerance of +0.01 was applied to the assessment of their overall fit, also permitting cautious interpretation of marginally significant models. Basic calculations and regression analyses were conducted in PQStat v.1.8.6 (PQStat Software, Poznań, Poland), whereas advanced ecological analyses (biodiversity indices, NMDS, PERMANOVA, PERMDISP) were performed in PAST v.5.2.1 (Natural History Museum, Oslo, Norway).

Results and Discussion

During the three sampling sessions performed between 2023 and 2024, a total of 470 ground beetles belonging to 12 genera were captured in pitfall traps, 264 of them in raspberry (Table 1) and 206 in strawberry trials (Table 2). In raspberries, the eudominant species were *Harpalus rufipes* and *Pterostichus melanarius*; the dominant species were *Calathus fuscipes* and *Nebria brevicollis*, whilst *Broscus cephalotes* was classified as a subdominant species. The remaining Carabidae specimens, present in small numbers, were considered either recedent or subrecedent species. Meanwhile, in strawberries, the most abundant species were *H. rufipes* and *P. melanarius* (eudominants), as well as *B. cephalotes* and *C. fuscipes* (dominants), followed by *Carabus granulatus* and *Poecilus cupreus* (subdominants). The remaining species, represented by single individuals, were classified as subrecedents. In both crops, all specimens collected belonged to species commonly found in Poland [9-16].

The composition of ground beetle assemblages determined in the trials is generally consistent with that reported from raspberry [60, 61] and strawberry plantations [62-66] in Northern Europe by other authors, both in terms of the prevalence of species commonly associated with agricultural habitats and the predominance of only a few taxa. The strong dominance of *H. rufipes* is of particular interest, as this species, apart from its beneficial role as a natural enemy of pests [3, 5] and weed seed consumer [2], has been reported to occasionally damage soft fruits, strawberries in particular, potentially decreasing their marketable yield [67-69]. However, no evidence of such damage was found in the agronomic assessment of the three inter-cropping systems tested [70]; heavy slug pressure was observed instead [70], which the carabids might have helped control [71-73].

Table 1. Species composition and activity-density of ground beetles (Carabidae) captured in raspberry cultivation under different inter-cropping practices during three sampling sessions.

Species	1-31 Aug 2023				1 Sep-10 Oct 2023				1-31 Aug 2024			
	UTC	LM	FI	FS	UTC	LM	FI	FS	UTC	LM	FI	FS
Broscus cephalotes (Linnaeus, 1758)	1	1	2	1	2	—	1	—	—	—	1	—
Calathus cinctus (Motschulsky, 1850)*	1	—	—	—	—	—	—	—	—	—	—	—
Calathus fuscipes (Goeze, 1777)*	12	1	—	—	—	1	—	1	—	—	—	7
Clivina fossor (Linnaeus, 1758)*	—	—	3	—	—	—	—	—	—	—	1	—
Harpalus affinis (Schrank, 1781)*	1	1	—	—	—	—	—	1	—	—	—	—
Harpalus distinguendus (Duftschmid, 1812)*	—	—	—	1	—	—	—	—	—	—	—	—
Harpalus griseus (Panzer, 1797)*	—	—	—	2	—	—	—	—	—	—	—	—
Harpalus rubripes (Duftschmid, 1812)*	1	—	—	—	—	—	—	—	—	—	—	—
Harpalus rufipes (De Geer, 1774)*	13	2	3	5	—	1	2	4	6	10	6	1
Loricera pilicornis (Fabricius, 1775)	—	—	1	—	—	—	—	—	—	—	—	—
Nebria brevicollis (Fabricius, 1792)	—	—	—	2	—	10	2	2	—	—	—	—
Poecilus cupreus (Linnaeus, 1758)*	—	—	—	—	—	—	—	—	—	—	2	—
Poecilus lepidus (Leske, 1785)*	—	—	1	—	—	—	—	—	—	—	—	—
Pterostichus melanarius (Illiger, 1798)	10	4	1	5	61	26	7	18	4	5	3	4

Note: UTC – control, LM – living mulch, FI – flower islands, FS – flower strip. Species marked with an asterisk (*) were classified as omnivorous; the remaining were classified as predators.

Table 2. Species composition and activity-density of ground beetles (Carabidae) captured in strawberry cultivation under different inter-cropping practices during three sampling sessions.

Species	1-31 Aug 2023				1 Sep-10 Oct 2023				1-31 Aug 2024			
	UTC	LM	FI	FS	UTC	LM	FI	FS	UTC	LM	FI	FS
Amara aenea (De Geer, 1774)*	—	—	—	—	1	—	—	1	—	—	—	—
Bembidion articulatum (Panzer, 1796)	—	2	—	—	—	—	—	—	—	—	—	—
Broscus cephalotes (Linnaeus, 1758)	—	1	—	—	1	—	—	—	—	1	7	3
Calathus fuscipes (Goeze, 1777)*	—	2	1	1	6	2	3	—	—	1	—	—
Carabus granulatus (Linnaeus, 1758)	—	—	—	1	—	—	—	9	—	—	—	—
Chlaenius nitidulus (Schrank, 1781)	—	—	—	—	—	—	—	—	—	—	2	—
Clivina fossor (Linnaeus, 1758)*	—	—	—	—	—	—	—	—	—	—	1	—
Harpalus rufipes (De Geer, 1774)*	6	1	3	8	1	2	1	6	7	4	5	12
Nebria brevicollis (Fabricius, 1792)	—	—	—	—	1	11	3	7	—	—	—	—
Poecilus cupreus (Linnaeus, 1758)*	—	1	—	—	—	—	1	3	1	—	—	—
Poecilus lepidus (Leske, 1785)*	—	—	—	—	—	—	—	—	—	—	1	—
Pterostichus melanarius (Illiger, 1798)	1	7	1	9	6	12	15	15	2	3	3	1

Note: UTC – control, LM – living mulch, FI – flower islands, FS – flower strip. Species marked with an asterisk (*) were classified as omnivorous; the remaining were classified as predators.

The under-representation of the smallest beetles measuring less than 7 mm in the present study is noteworthy, with only six records obtained for *Bembidion articulatum* and *Clivina fossor*, accounting for 1.3% of the total catch (Tables 1 and 2). In contrast, recalculation of the data on ground beetle assemblages in strawberry crops presented by Kosewska et al. [66] and Tuovinen et al. [65] reveals a substantially greater contribution of small-bodied species, reaching approximately 15% and 40%, respectively. It is very unlikely that the smallest carabids were present to such a small extent in the studied plantations. Rather, this group may have been under-sampled by the trapping method employed. One possible cause is the use of brine as a preservative and killing agent in pitfall traps. Schmidt et al. [41], when comparing the effectiveness of brine against other fillings for pitfall traps, found that brine, although it did not significantly reduce the total number of carabids caught, did limit the number of genera recorded. The authors suggested that the high specific gravity of brine may facilitate the flotation of trapped arthropods on the liquid surface, potentially increasing the likelihood of escape and thereby reducing trap efficiency. Although Schmidt et al. [41] did not analyse the effect of body size, it may be hypothesised that this mechanism promotes survival of small-bodied species [74], which generally benefit from a more favourable ratio of surface tension force to their body mass whilst floating.

As shown in Table 3, the inter-cropping treatments neither affected the total carabid activity-density ($F_{3,17}$ = 0.85, p = 0.49, η_p^2 (partial eta-squared) = 0.13) nor the activity-density of predatory species ($F_{3,17}$ = 0.91, p = 0.46, η_p^2 = 0.14). Nonetheless, a large (η_p^2 = 0.38) and statistically significant ($F_{3,17}$ = 3.50, p<0.05) effect of the inter-cropping factor on the numbers of omnivorous ground beetles was observed, with fewer individuals from this guild having been captured in the living mulch treatment compared to the flower strip or control treatments. In order to assess whether the effect of inter-cropping treatment on omnivorous carabid activity-density varied across sampling sessions, an additional general linear model including the treatment × sampling session interaction was fitted. The interaction was not statistically significant ($F_{6,11}$ = 0.79, p = 0.59). Accordingly, the lower activity-density of omnivorous carabids observed in the living mulch treatment was not detectably confined to a single sampling period or to a particular late-summer or early-autumn phase of carabid activity or inter-crop development.

Previous studies have likewise shown that flowering inter-crops may influence the functional composition of carabid assemblages without necessarily affecting their overall activity-density [30, 75]. What requires further explanation, however, is the observed decline in omnivorous carabids in the living mulch treatment, which may be attributable to several non-mutually exclusive factors.

One possible explanation is that the white clover living mulch effectively suppressed weed growth [76], thereby reducing the availability of seeds that represent a key dietary resource for many omnivorous carabid species [77] and potentially contributing to the lower activity-density recorded. The observed changes

Table 3. Effects of three inter-crops on the numbers of ground beetles (Carabidae) captured in raspberry and strawberry cultivation. The values presented are GLM-estimated means (95% CI) for the treatment effect, controlling for variability between the two crops and sampling sessions (1-31 Aug 2023, 1 Sep-10 Oct 2023, 1-31 Aug 2024).

Treatment	Number of ground beetles		
	Omnivorous	Predatory	Total
Control	8.50 (5.70-12.81)[b]	5.93 (3.13-11.36)	17.64 (11.36-27.39)
Living mulch	4.31 (2.89-6.42)[a]	9.68 (5.10-18.54)	16.61 (10.70-25.79)
Flower islands	5.10 (3.42-7.61)[ab]	5.70 (3.00-10.91)	12.68 (8.08-19.69)
Flower strip	8.67 (5.75-12.94)[b]	9.58 (5.05-18.36)	19.89 (12.81-30.88)

Note: Means sharing the same letter in the column are not significantly different (Fisher's LSD test, $\alpha = 0.05$).

may also have been due to differences in vegetation cover density between the experimental plots, which could have affected the activity of carabids. As is well documented, the number of ground beetles caught in pitfall traps depends not only on their abundance but also on their activity in a given area; greater activity increases the likelihood of beetles being captured (by accidentally falling into the trap) [78]. Captures in pitfall traps can vary significantly between sites with different vegetation densities, even when the actual population density remains similar [79], whereas an increase in vegetation density reduces the number of carabids trapped [80]. In this study, the living mulch covered most of the cultivation area, whilst the control and flower strip or islands featured mostly bare soil, potentially decreasing carabid activity in the living mulch treatment, but not necessarily reducing their abundance. Finally, as suggested by Kosewska et al. [39], white clover living mulch may be less favourable for some ground beetle species due to the altered microclimatic conditions it creates, for example, increased humidity and reduced soil-surface temperatures [80]. However, none of these mechanisms were directly investigated in the present experiment and should therefore be regarded as literature-supported hypotheses rather than demonstrated explanations.

Of the six diversity indices calculated for the Carabidae assemblages, none responded significantly to the inter-cropping treatment (detailed results presented in Table S1 in the Supplementary Material). A non-metric multidimensional scaling (NMDS) ordination, which visualises differences in the composition of carabid assemblages across different berry crops, inter-cropping treatments and sampling periods, is presented in Fig. 2. A stress value of 0.16 indicates an acceptable fit of the ordination. The high proportion of variance explained by the first NMDS axis ($R^2 = 0.61$) implies that it captures the primary ecological gradient structuring the ground beetle communities, whilst the contribution of the second axis ($R^2 = 0.17$) is of lesser importance.

Visual inspection of Fig. 2 reveals a pronounced effect of sampling time that dominated the distribution of points in the NMDS space. The September/October 2023 samples (green symbols) form a distinct cluster along the NMDS1 axis, separate from the August samples from 2023 (red symbols) and 2024 (yellow symbols), which show some degree of overlap. Nonetheless, any particular pattern dependent on the inter-crop factor is difficult to discern.

Vectors depicting *H. rufipes*, *P. melanarius* and *B. cephalotes* are located near the centre of the coordinate system, suggesting that these species were common and uniformly distributed across all samples, and thus made only a minor contribution to the differences between carabid assemblages. It was mainly the remaining, less abundant and unevenly distributed species that contributed to the arrangement of points in the ordination (Fig. 2).

The results of PERMANOVA largely supported these findings, indicating no statistically significant effect of the crop, the inter-cropping treatment or their interaction with time. Instead, a strong and statistically significant effect due to the sampling period was observed, showing the dominant influence of temporal variability (Table 4).

Taken together, the results provided above give no evidence that the flowering inter-crops examined enhanced ground beetle activity-density and diversity, thereby failing to support the hypothesis that the inter-cropping practices could enhance the activity-density and diversity of ground beetles. Previous studies have reported contrasting effects of biodiversity-enhancing practices on carabid assemblages within agricultural fields, ranging from positive [29, 32, 33, 37] and negative [39] responses to little or no detectable effects [27, 28, 31, 36, 38]. The findings of the present work are most consistent with the latter observations. The increase in marketable yield recorded in the corresponding agronomic study [70] should, therefore, be attributed to the activity of beneficial insect groups other than ground beetles.

Amongst the factors that could have limited the expected positive effects of the studied inter-crops on ground beetle assemblages, an organic management system stands out, having been demonstrated in some research as sufficient to support carabid populations [81, 82]. The landscape context is also noteworthy, particularly the presence of semi-natural habitats

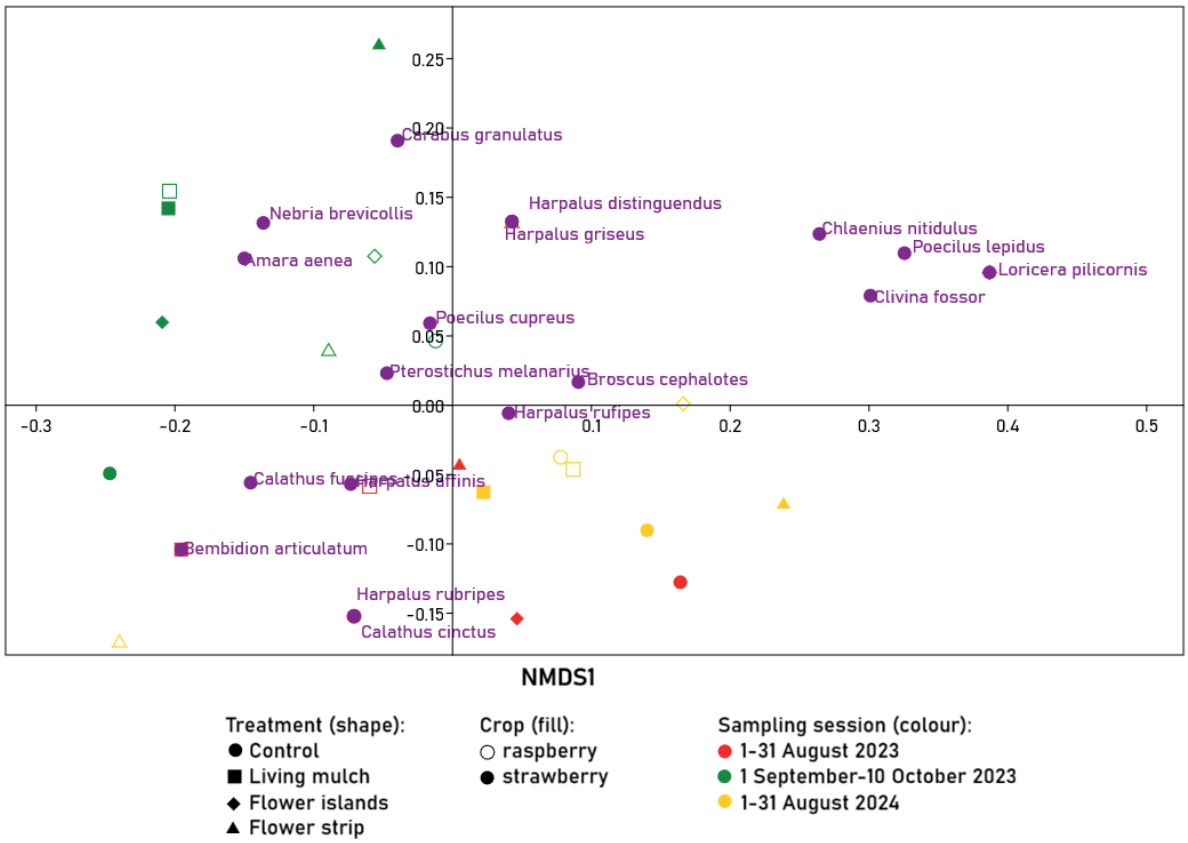

Fig. 2. Analysis of Carabidae community composition using non-metric multidimensional scaling (NMDS). The ordination was based on the chord similarity index (stress = 0.16). Red, green and yellow symbols depict samples of carabid assemblages from raspberry and strawberry plantations managed under different inter-cropping practices, collected during three sampling sessions (see legend). Labelled purple points represent the weighted average positions (centroids) of particular carabid species.

surrounding the crop, which are known to provide shelter, overwintering sites and food resources for carabid beetles [18, 19, 83]. The site where the experiment was conducted had been managed under an organic farming system for over a decade and is rich in semi-natural habitats such as hedgerows, scrubs and grassy margins. Consequently, plant resources and refuges were available not only within the experimental plots but also in their surroundings. This relatively high availability of non-crop habitats may have supported resilient carabid assemblages and reduced the ecological contrast between the control and inter-cropping treatments. Previous studies likewise show that local biodiversity-enhancing measures may have weaker effects when food resources, refuges and overwintering sites are already available in the surrounding landscape [84, 85].

The scarce response of carabid assemblages may also lie in the design of the inter-cropping treatments employed in this study. The annual flower strip and islands were intended primarily to enhance nectar and pollen availability for pollinators and other flower-visiting beneficial insects. Consequently, the species composition of floral patches was maintained each year through cultivation and reseeding as well as manual weeding during the growing season. However, ground beetles respond positively to the ageing of flower strips [86], at least during the first years after establishment. This may be linked to the increase in vegetation density resulting from the natural succession of grasses and other non-sown plants [21], which improves overwintering and refuge opportunities. More importantly, soil cultivation associated with the establishment of annual flower strips has been shown to exert a strongly detrimental effect on ground beetles, reducing their overwintering success by nearly 70% [87]. The use of annual floral patches may, therefore, have been suboptimal for promoting Carabidae assemblages. A combined approach incorporating flower strips of varying ages might represent a more suitable strategy [30].

The temporal correspondence between the biodiversity-enhancing practices examined herein and the resource requirements of carabid beetles during successive parts of the growing season also warrants consideration. Whereas the perennial living mulch provided vegetation cover throughout the seasonal activity period of Carabidae, the flower strip and islands were renewed annually around 10 May. Consequently, dense vegetation cover developed only towards the end of June, whilst a substantial supply of seeds became available in the second half of July. This timing should be considered in relation to the seasonal activity of

Table 4. Effects of the crops, inter-cropping treatments and sampling sessions on Carabidae assemblage composition tested by means of two-way permutational multivariate analyses of variance (PERMANOVA).

Source of variation	Df	Sum of squares	Pseudo-*F*	*p*-value	R^2 (effect size)
Analysis I: crop and sampling period effects					
Crop	1	0.18	0.77	0.57	0.03
Sampling session	2	1.73	3.69	<0.001	0.26
Crop × sampling session	2	0.66	1.41	0.17	0.10
Residual	18	4.21			
Total	23	6.77			
Analysis II: treatment and sampling period effects					
Treatment	3	0.70	0.98	0.48	0.10
Sampling session	2	1.73	3.59	<0.001	0.53
Treatment × sampling session	6	1.46	1.01	0.47	0.22
Residual	12	2.88			
Total	23	6.77			

The analyses were based on the chord similarity index with 9,999 random permutations.

the species most abundantly represented in the study. According to Luff [88], adults of *H. rufipes* are active from April to November, and females oviposit in August. *P. melanarius* exhibits two activity peaks, from mid-June to early July and from late July to mid-August, with an important reproductive phase occurring in late summer [89]. The floral patches were therefore already well established during a substantial part of the activity and reproductive periods of both dominant species. Their temporal suitability may, however, have been lower for some of the less abundant taxa. For example, the principal reproductive period of *P. cupreus* extends from April to July, and the availability of food resources within wildflower strips during this period has been shown to improve female nutritional condition and prolong reproduction [90]. The mixture used in the present study could therefore potentially be improved by including plant species that establish and produce seeds earlier in the season, possibly combined with earlier sowing where agronomically feasible. Such modifications could extend the period during which floral patches provide suitable cover and food resources for carabid species differing in their seasonal activity and reproductive phenology.

In closing, it is important to clearly state that the results presented in this study should be interpreted in light of the limited spatial replication of the experiment. Within each crop, each inter-cropping treatment was represented by one 200 m^2 plot, which was monitored during three sampling periods spanning two growing seasons. Although all plots were situated within the same study site and broader landscape context, repeated sampling did not constitute independent spatial replication, and plot-specific variation could not be fully separated from treatment effects. Consequently, this experimental design limits the strength of treatment-level inference and the extent to which the findings can be generalised. Moreover, the relatively low overall catch of 470 individuals, with most species represented by only a few specimens, may have further limited the ability to detect weaker species-specific treatment responses.

Conclusions

(1) Carabid assemblages in raspberry and strawberry plantations were composed of common species associated with agricultural habitats, with a strong dominance of *Harpalus rufipes* and *Pterostichus melanarius*.

(2) The species composition of ground beetle assemblages was broadly similar in raspberry and strawberry crops.

(3) Under the conditions of the present study, neither the multi-species flower strip and floral islands nor the white clover living mulch increased the overall activity-density or diversity of Carabidae. The inter-cropping treatments affected only the functional composition of assemblages, reducing the activity-density of omnivorous species in the living mulch treatment, whilst the activity-density of predatory carabids remained unaffected.

(4) Temporal variation was the primary factor shaping carabid assemblages, exerting a stronger influence than crop species or inter-cropping treatment.

(5) Future research should focus on developing biodiversity-enhancing practices that simultaneously benefit flower-visiting beneficial insects and ground-dwelling natural enemies. In particular, habitat-

management strategies should combine abundant floral resources for pollinators and parasitoids with structurally complex, permanent refuges that provide favourable overwintering, foraging and dispersal opportunities for carabid beetles.

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AI Usage Statement Disclosure

During the preparation of this work, the authors utilised ChatGPT (GPT-5.6, OpenAI) to assist with English language editing, specifically to check spelling, grammar and punctuation, as well as to refine the wording of selected passages. All AI-assisted revisions were reviewed and approved by the authors, who take full responsibility for the final content of the article.

Conflict of Interest

The authors declare no conflict of interest.

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Supplementary Materials

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