Strip cropping designed for maintaining productivity increases ground beetle biodiversity

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Abstract

Global biodiversity is declining at an unprecedented rate, with agriculture as a major driver. There is mounting evidence that intercropping can increase insect biodiversity while maintaining or increasing yield. Yet, intercropping is often considered impractical for mechanized farming systems. Strip cropping is pioneered by Dutch farmers as it is compatible with standard farm machinery. Here, we use ground beetle data from four experimental locations across four years of measurements because these are good agrobiodiversity indicators and hold keystone positions in agroecosystem foodwebs. We show that strip cropping systems that are designed for retaining productivity can also enhance ground beetle biodiversity, without incurring major yield loss. Strip cropped fields had on average 15% more ground beetle species and 30% more individuals than monocultural fields. The increase in field-level beetle species richness in organic agriculture through strip cropping approached increases found for other readily deployed biodiversity conservation methods, like shifting from conventional to organic agriculture (+19% - +23%). This makes strip cropping a useful tool for bending the curve of biodiversity loss without compromising food production.

Introduction

Insects account for 80% of the animal species in the world and, therefore, the recently reported unprecedented rate of insect decline is cause for alarm about the state of biodiversity on Earth (Dirzo *et al.*, 2014; Hallmann *et al.*, 2017; van Klink *et al.*, 2020). An array of biodiversity metrics provide strong evidence for declines of especially terrestrial insects across all continents (van Klink *et al.*, 2020). This includes declines in abundance of both common and rare species (Hallmann *et al.*, 2017; Seibold *et al.*, 2019; Pilotto *et al.*, 2020; van Klink *et al.*, 2023) and in total species richness and changes in assembly composition (Wagner *et al.*, 2021; Blowes *et al.*, 2022). In some areas, terrestrial insect biomass decreased by 75% in the last 30 years (Hallmann *et al.*, 2017), and a further 40% of all species is estimated to face extinction by 2100 (IPBES, 2019). Insects are essential for crop production through their role in decomposition, pollination, pest control and sustaining food webs. Therefore, erosion of insect communities can have potentially devastating effects on ecosystem functioning, provision of ecosystem services and ultimately on human civilization (IPBES, 2019). The main drivers of insect biodiversity decline are habitat loss due to conversion to agriculture, pollution, invasive species and climate change (Díaz *et al.*, 2019; Wagner *et al.*, 2021; Müller *et al.*, 2023).

Strategies for biodiversity conservation in conjunction with adequate food production require understanding of how biodiversity responds to agricultural management (Saunders, 2020). The idea of land sparing seeks to conserve natural habitats by separating high-yielding agriculture from protected natural habitats, while land sharing combines food production with biodiversity conservation on agricultural land (Green *et al.*, 2005; Loconto *et al.*, 2020). Combining both pathways is vital (Fischer *et al.*, 2008; Scariot, 2013) as land sparing counteracts land-use change

and land sharing makes agricultural landscapes better suited to support biodiversity and associated ecosystem services that support crop production (Dainese *et al.*, 2019). Ideally, sustainable agricultural practices retain yield and enhance biodiversity, preventing the need to convert natural habitats to agricultural land to maintain food production (Tscharntke *et al.*, 2021).

Increasing crop heterogeneity can facilitate biodiversity conservation in highly productive agricultural landscapes without compromising yield (Martin-Guay *et al.*, 2018; Sirami *et al.*, 2019). Crop diversification can enhance niche complementarity by creating heterogeneous habitats and increasing availability and diversity of resources (Lichtenberg *et al.*, 2017; Tamburini *et al.*, 2020). A promising crop diversification strategy is strip cropping, where crops are grown in alternating strips, wide enough for using standard agricultural machines yet narrow enough to facilitate ecological interactions among crops (Ditzler *et al.*, 2021). Crops that are grown in strips may benefit from increased resource use efficiency, and the suppression of pests and diseases (Tajmiri *et al.*, 2017b; Ditzler *et al.*, 2021; Juventia *et al.*, 2021; Alarcón-Segura *et al.*, 2022; Cuperus *et al.*, 2023; Karssemeijer *et al.*, 2023; Rakotomalala *et al.*, 2023; Croijmans *et al.*, 2024) without major yield compromises (Tajmiri *et al.*, 2017a, b; Mollaei *et al.*, 2020; van Oort *et al.*, 2020; Juventia *et al.*, 2021; Campanelli *et al.*, 2023). Growing multiple crops on a field may foster a larger diversity of organisms than monocultures through greater plant species richness that cascades into richer herbivore and predator communities (Crutsinger *et al.*, 2006; Cuperus et al., 2024). Moreover, the expected increase in available and potentially complementary niches within the agricultural field due to higher spatial diversity in crops can result in admixture of communities related to individual crops (Hummel *et al.*, 2012), or the creation of completely new communities by enhanced richness of agriculture-related species,

and/or the occurrence of species rarely found in agricultural fields (Rischen *et al.*, 2021). So far, it is not well understood if and how insect communities respond to strip cropping across distinct crops.

Here, we present data of four years of pitfall trapping of ground beetles at several moments during the growing season in 14 crops at four organic experimental farms across the Netherlands where strip cropping was compared to monocultures. Ground beetle community dynamics are sensititve to changes in farming practices and are frequently used to examine agricultural sustainability (Holland *et al.*, 2002; Makwela *et al.*, 2023). Furthermore, ground beetle species are important for maintaining ecolocal functions as they comprise scavengers and predators of (weed) seeds, detritivores (e.g., collembolas and earthworms) and herbivores (e.g., aphids and caterpillars). As such, they are often used as indicator group for wider insect diversity in agroecosystems (Gerlach et al., 2013). We first examine whether strip cropping fields have greater ground beetle richness and activity density than monocultural fields. Next, we present biodiversity metric changes for individual crops to assess the benefits of strip cropping for ground beetle biodiversity. We then evaluate whether ground beetle community changes are caused by admixture of communities, whether these assemblages promote species associated with agriculture or with natural ecosystems, and whether they contain rare species.

Results

A total of 49,199 ground beetles belonging to 71 species were caught using pitfall traps over four years at four different organically managed experimental locations in The Netherlands: 40,159 at Almere; 3,777 at Lelystad; 1,126 at Valthermond; and 4,137 at Wageningen (Table S1, S2).

Strip cropping enhances ground beetle richness

Strip cropping fields had on average 15% higher ground beetle taxonomic richness than monoculture fields after rarefaction to the number of samples of the least-sampled crop configuration (β_0 = 0.151, SE = 0.044, $p < 0.001$; Fig. 1c,d). However, strip cropping fields did not harbour more species than monocultural fields with the highest ground beetle richness (β_0 = -0.008, SE = 0.037, p = 0.821; Fig. 1d). The difference in field-level taxonomic richness could not be explained by an increase in the number of ground beetle species per crop in strip cropping compared to monocultures. At crop-level, the 5% increase in ground beetle taxonomic richness in strip cropping was not statistically significant (Fig. 1f). Similarly, crop-level absolute evenness, inverse Simpson index and Shannon entropy did not differ significantly among crop configurations (Fig. 1h-j, S1c,d, S2). The effect of crop configuration on crop-level taxonomic richness was variable and was not associated with location or crop species. The effect ranged from 56% more species in potato in monoculture at Wageningen in 2022, to 136% more species in barley in strip cropping at Wageningen in 2020 (Fig. 1k).

Strip cropping enhances ground beetle activity density

Ground beetle activity density was on average 30% higher in strip cropping fields than in monoculture fields (β_0 = 0.303, SE = 0.121, p = 0.012; Fig. 1e), based on rarefaction. However, there was no significant difference in activity density between the strip cropping fields and monocultures with crops that harboured the richest beetle communities (β_0 = -0.110, SE = 0.088, p = 0.215). Crop-level activity density of ground beetles was not affected by crop configuration (Fig. 1g, S1a,b).

Crop configuration alters ground beetle community composition

Ground beetle communities were significantly influenced by crop configuration, but the effects of location, year and crop dominated those of crop configuration (Fig. S3-S5, Table 1, S3). The context-dependency of configuration effects on ground beetle communities is illustrated in redundancy analyses of ground beetle assemblages per crop combination at Wageningen in 2021 and 2022 (Fig. S6). Here, we found distinct ground beetle communities among crop configurations for pumpkin, barley and potato in 2021, and for cabbage and oat in 2022. In the other cases the difference between crop configurations was not significant (Fig. S6, Table S4). Moreover, in all crop combinations except for potato-grass in 2021, the difference in ground beetle communities between the monocultures of the consitutuent crops were significant, while this was never the case for ground beetle communities of crops in strip cropping (Table S4). This indicates that strip cropping leads to overlapping crop-related communities. However, these results could be spatially biased as samples from different crops were in closer proximity of each other in strip cropping than among monocultures (Fig S7d).

Rare and common species indicators for strip cropping

Eleven ground beetle species were significantly associated with crop configuration: four species associated with strip cropping and seven with monocultures (Fig. 2, Table S5). Specifically, the rare *Harpalus griseus* (p=0.001, specificity=0.900) and the more common *Anchomenus dorsalis* (p=0.001, specificity=0.806) were strongly associated with strip cropping (Fig. 2, Table S5).

Discussion

It is well established that different crop types have distinct ground beetle communities (Holland and Luff, 2000; Eyre *et al.*, 2009) and that increasing habitat diversity by including multiple crops in a field can enhance ground beetle diversity (Puliga *et al.*, 2023; Cuperus et al., 2024). Our study shows that strip cropping increased field-level ground beetle richness by 15%. However, ground beetle richness in crops grown in strip cropping and in monocultures were mostly similar, and there were relatively few ground beetle species that were unique in strip cropping. In fact, our indicator species analysis showed that more species were associated with monocultures than with strip cropping. This indicates that the 15% increase in richness at the field level can be mostly attributed by the higher number of crops in strip cropped fields that harboured crop-specific ground beetle communities, and that there was only a limited mixture of ground beetle species among crops in strip crops. This is in line with findings from Anderson et al. (2024) who found that ground beetle movement is reduced by crop edges. Further research on movement behaviours of ground beetles at crop edges might help explain how ground beetles distribute themselves within a strip cropping field, and whether they utilize the different resources provided by a more diverse cropping system.

The 30% higher ground beetle activity density in strip cropping fields compared to monoculture fields may be explained by a more stable and diverse habitat with refuges and alternative resources in strip crops (Ratnadass *et al.*, 2012). Crop diversification enhances prey biomass for ground beetles (Lichtenberg *et al.*, 2017) and increases weed seed biomass as compared to monocultures (Carbonne et al., 2022; Ditzler *et al.*, 2023), both of which reduce bottom-up control by increased food provision. In addition, insectivorous farmland birds regularly prefer more diverse fields for foraging, consequently increasing top-down control (Josefsson *et al.*,

2017). Crop diversification might thus influence bottom-up and top-down control of ground beetles in opposing ways and the relative strength of each might explain the variation in responses of ground beetle activity density among locations and crops. Multi-taxa evaluation of future strip cropping studies will be a valuable approach to increase understanding of biomass flows and trophic interactions within agricultural systems.

The ground beetles *H. griseus* and *A. dorsalis* were specifically associated with strip cropping. The granivorous *H. griseus* may have benefitted from the relatively high weed abundance and diversity in the strip crops (Carbonne *et al.*, 2022; Ditzler *et al.*, 2023). *A. dorsalis* particularly associated with strip cropping at Almere, which could have been caused by the closeness of preferred hibernation locations such as grass-clover strips in the strip cropping configuration, compared to monoculture crops (Eyre *et al.*, 2009; Marrec *et al.*, 2017). Seven out of the eleven crop configuration indicator species in our study are typical eurytopic species, adapted to a wide range of environments and common to the Netherlands (Turin, 1991; Turin, 2000). *Amara aenea*, *Calathus melanocephalus*, *Loricera pilicornis* and *Trechus quadristriatus* were associated with monocultures. These polyphagous, generalist species are strongly adapted to crop monocultures characterised by large-scale physical disturbance through tillage and harvest (Kromp, 1999). Overall, our data indicate that multiple ground beetle species have a preference for a specific crop configuration.

Biodiversity gains in our study did in most cases not coincide with productivity losses (Table S6). Earlier studies on crop yield in the strip cropping fields in Lelystad and Wageningen during the years of pitfall trapping show a yield decrease when strip cropping cabbage (Carrillo-Reche

et al., 2023) and wheat (Ditzler *et al.*, 2023), whereas potato yield was unaffected by crop configuration (Ditzler *et al.*, 2023). In Almere bean and parsnip yields were higher in strip cropping, whereas oat and onion yield were lower (Juventia et al., accepted). In Valthermond crop productivity was similar for monocultures and strip cropping (Table S6). Therefore, strip cropping has the potential to reconcile farmland biodiversity conservation and agricultural production.

We show that changing crop configuration from monoculture to strip cropping enhances ground beetle richness by 15% and activity density by 30% within agricultural fields. These results show that strip cropping leads to increases in biodiversity that approach those achieved by shifting from conventional to organic farming practices (+19% richness, Lichtenberg et al., 2017; +23% richness, Gong et al., 2022) and by other in-field diversification measures (+23% richness, Lichtenberg et al., 2017; +24% richness, Beillouin *et al.* (2021)). While organic management or in-field diversification measures generally lead to lower productivity (Gong *et al.*, 2022), strip cropping can maintain crop productivity without taking land out of production (Tajmiri *et al.*, 2017a, b; Mollaei *et al.*, 2020; van Oort *et al.*, 2020; Juventia *et al.*, 2021; Campanelli *et al.*, 2023), although occasional yield reductions have been reported (Carillo-Reche et al., 2023; Ditzler et al., 2023). The biodiversity gain in our study was achieved without additional crop-level diversification strategies designed for biodiversity conservation, such as cover cropping or (flowering) companion plants. This increase in biodiversity stacks on top of already higher biodiversity achieved through organic management (Lichtenberg et al., 2017; Gong et al., 2022). Furthermore, the estimated richness effects of strip cropping, i.e., no change at crop level and 15% increase at field level, are conservative because they only consider the pairwise comparison of biodiversity of two or three crops in a strip cropping configuration to monocultures, whereas

the inclusion of more crops within strip cropping could further enhance ground beetle biodiversity. Also, measurements were conducted in relatively young strip cropping fields, which were not older than five years (less than a full rotation). Ground beetle communities might require more time to adapt to the new crop configuration (Rusch et al., 2013). The ground beetle communities in our study were dominated by farmland species and contained only few rare species. Nevertheless, even after only four years, specific species strongly associated with strip cropping were found. For Dutch farming systems, which are dominated by non-flowering crops, increased use of flowering crops or inclusion of semi-natural habitats with flowering plants might be necessary on top of strip cropping to increase biodiversity of groups such as pollinators. Strip cropping in combination with other in-field diversification measures, such as the establishment of more perennial semi-natural habitats (Sirami *et al.*, 2019; Rischen *et al.*, 2021) or uptake at larger spatial extents (Tscharntke et al., 2021) could further enrich agricultural landscape diversity and help bending the curve of biodiversity loss.

Materials and methods

Study area

A multi-location study was conducted on four organic farms across the Netherlands (Fig. 1a). Three experimental farms were managed by Wageningen University & Research (Lelystad, Valthermond, Wageningen) and one commercial farm was managed by *Exploitatie Reservegronden Flevoland* (ERF B.V.) located in Almere. All four locations contained both strip cropping and monocultural crop fields, but differed in soil type, establishment year of the strip cropping experiment, number of crops grown, length of the crop rotation, number of sampled crops and sampling years, and farm and landscape characteristics such as percentage of on-farm

semi-natural habitat (SNH), mean field size, and landscape configuration (Fig. 1b, S7). The locations Almere and Lelystad were located in a homogeneous, open polder landscape characterized by intensive arable crop production and non-crop habitats consisting of grass margins, tree lines and watercourses. Valthermond was located in an open, reclaimed peat landscape with intensive arable crop production characterized by long and narrow fields separated by grassy margins and ditches and limited areas of woody elements. The site at Wageningen was located in a more complex landscape with smaller field sizes, and non-crop habitat consisting of woodlots, hedgerows, tree lines, ditches and farmyards.

Experimental lay-out

At Almere and Valthermond the crops in strip cropping were all grown alongside each other, whereas at Lelystad and Wageningen two alternating crops (crop pairs) were grown alongside each other (Fig. 1b, S7). At each location, strip cropping and monoculture fields were always paired on the same experimental field (Fig. S7). At Almere eight different crops were grown in alternating strips of 6 m width, including celeriac (*Apium graveolens* var. *rapaceum*), broccoli (*Brassica oleracea* var. *italic*), oat (*Avena sativa*), onion (*Allium cepa*), parsnip (*Pastinaca sativa*), faba bean (*Vicia faba*), potato (*Solanum tuberosum*) and a mix of ryegrass and white clover referred to as grass-clover (*Lolium perenne/Trifolium repens*) (Fig. S7a). At Lelystad four different crop pairs were grown in alternating strips of 3 m width, including carrot (*Daucus carota subsp. sativus)* and onion, white cabbage (*Brassica oleracea var. capitata*) and wheat (*Triticum aestivum*), sugar beet (*Beta vulgaris*) and barley (*Hordeum vulgare)*, and potato and ryegrass (Fig. S7b). At Valthermond eight different crops were grown in alternating strips of 6 m width, including potato, barley, barley mixed with broad bean (*Vicia faba*) in 2020, barley mixed

with pea (*Pisum sativum*) in 2021, sweet corn (*Zea mays convar. saccharata var. rugosa*), sugar beet, common bean (*Phaseolus vulgaris*), and grass-clover (Fig. S7c). At Wageningen three different crop pairs were grown in alternating strips of 3 m width, including white cabbage and wheat (2019 – 2021) or oat (2022), barley and pumpkin (*Cucurbita maxima*, 2020 - 2022) or bare soil due to crop failure (2019), and potato and ryegrass (Fig. S7d). The crop combinations and neighbors were selected based on literature, expert knowledge and experience of functionality in terms of expected advantages for yield and pest and disease control. Large scale monoculture plots (0.25 ha to 2.30 ha) served as reference, hereafter referred to as monoculture (Fig. S7). At Lelystad, Valthermond and Wageningen not each crop grown in strips was present as monoculture in each year, but only those crops for which a monoculture was present were sampled (Fig. 1k, Table S7). All fields were managed according to organic regulations, yet at each location fertilization and weed management reflected regional practices and were adjusted to local soil conditions. Flower strips were sown within the experimental fields at Almere and Valthermond (Fig. S7, Table S8).

Sampling

The ground beetle community was sampled using pitfall traps in all crops for which both a monoculture and strip cropping field were present, at each location and in multiple rounds per year between March and September. The sampled crops, number of rounds and number of pitfalls differed per year and per location (Table S7). Pitfall traps consisted of a plastic cup (8.5 cm diameter) placed in the soil so the top of the cup was level with the soil surface. Pitfalls were filled with water mixed with non-perfumed soap and covered with a black roof (12.5 cm diameter). Pitfall trap type was similar in all years and locations and traps were placed at the

same specific location per year. For all analyses, year series were made, in which all ground beetle catches from the same pitfall trap were pooled per year.

Statistical analyses

We used R, version 4.2.2 for all statistical analyses.

Effect of crop configuration on field-level richness and activity density

To analyse the difference in species richness and activity density between monocultures and strip cropping configurations at field level, we used rarefaction of samples within the same field. To rarify to an equal sampling intensity, we calculated the average cumulative number of species or individuals within x year series, where x is the largest number of year series available for the crop configuration comparison. Next, we calculated the relative change due to strip cropping by subtracting the number of species or individuals found in the monoculture field from the number found in the strip cropping field, and then dividing the result by the number of species or individuals in the monoculture. This gave the relative change centered around zero, where negative values indicated higher richness in monocultures and positive values higher richness in strip cropping. We then analysed this data using Generalized Linear Mixed Models (GLMM) with a Gaussian distribution, and assessed whether the intercept deviated significantly from zero. As random variables, we used location and year, with year nested in location. We ran these analyses using a dataset that included all comparisons among monocultural fields and strip cropping fields of all locations. To test whether strip cropping was more beneficial for beetle diversity than the most beetle rich monoculture, we separately analysed a dataset that only included the monocultural fields with the highest taxonomic richness or activity density among

the constitutive crops of the strip cropping field. Generalized linear models were run using the glmmTMB package and tested for model fit using the DHARMa package.

Effect of crop configuration on crop-level biodiversity

To quantify biodiversity we used five variables: (1) activity density, the total number of ground beetles found per year series; (2) taxonomic richness, the total number of species or genera (lowest taxonomic level available) found per year series; (3) the inverse Simpson index, the inverse of the sum of proportions of different species over the total abundance (Simpson, 1949); (4) absolute evenness, the number of effective species calculated by dividing the inverse Simpson index by the taxonomic richness (Williams, 1964); and (5) Shannon entropy (Shannon and Weaver, 1949). We chose absolute evenness as our measure for evenness, as this method removes the richness component from the inverse Simpson index and adheres to all requirements for an evenness index (Smith and Wilson, 1996; Tuomisto, 2012). We included both the inverse Simpson index and Shannon entropy as the former is more sensitive to changes in eveness and the latter to species richness (DeJong, 1975).

To analyse the effect of crop configuration on ground beetle activity density, taxonomic richness, evenness, inverse Simpson index and Shannon entropy we used GLMM. We constructed models for each response variable, using data from all four locations. In these models we included crop configuration (monoculture or strip cropping) as a fixed factor. We included location, year and crop as nested random variables in these models. To quantify and visualize the variation in responses between locations, years and crops, we ran generalized linear models (GLM) with a variable that combined these three variables into one, which was also included as a fixed factor.

Here, we also included the interaction between crop configuration and the combined variable for crop, location and year. For the model on activity density we used negative binomial distribution (log link function); for richness, evenness and Shannon entropy we used Gaussian distribution; and for inverse Simpson index we used gamma distribution (inverse link function). All models were tested for model fit using the DHARMa package.

Community composition of crop configurations and crops

To assess whether crop configurations have distinct ground beetle communities, we used permanova with a Hellinger transformation (with 999 permutations). We only used data from locations and years where pitfall catches had been identified to species level (Almere 2021/22, Lelystad and Wageningen). We considered four models, one for all locations combined and one for each location separately. In all models we included crop configuration and the nested variables of location (whenever applicable), year and crop as fixed factors. We also analysed the interaction between crop configuration and this nested structure of location, year and crop. To visualize crop-configuration-dependent ground beetle communities, we used redundancy analysis (RDA) on Hellinger transformed data. Here, we again conducted four analyses, one for all locations combined and one for each of the three considered locations. We only used crop configuration as a predictor, to force RDA to show any change in ground beetle community associated with crop configuration. As such, only one RDA axis was created per model, which was plotted against the first principal component describing the residual variation.

Due to the large influence of location and year on ground beetle communities, visualizing any general effects of strip cropping on these communities using all available data was challenging. To address this, we conducted RDA and visualized the effect of crop configuration on a subset of

the data from one location and one year. We chose the data from Wageningen in 2021 and 2022 for this analysis because it provided a set-up where strip cropping of two crops could be compared with their constituent monocultures within the same experimental fields. Here, we used both crop configuration, crop and their interaction term as explanatory variables for each crop pair separately. To analyse whether ground beetle communities significantly differed among combinations of crops and crop configurations, we ran pairwised permanova on all three fields and two years separately, using the "pairwiseAdonis" package.

Crop configuration specific species

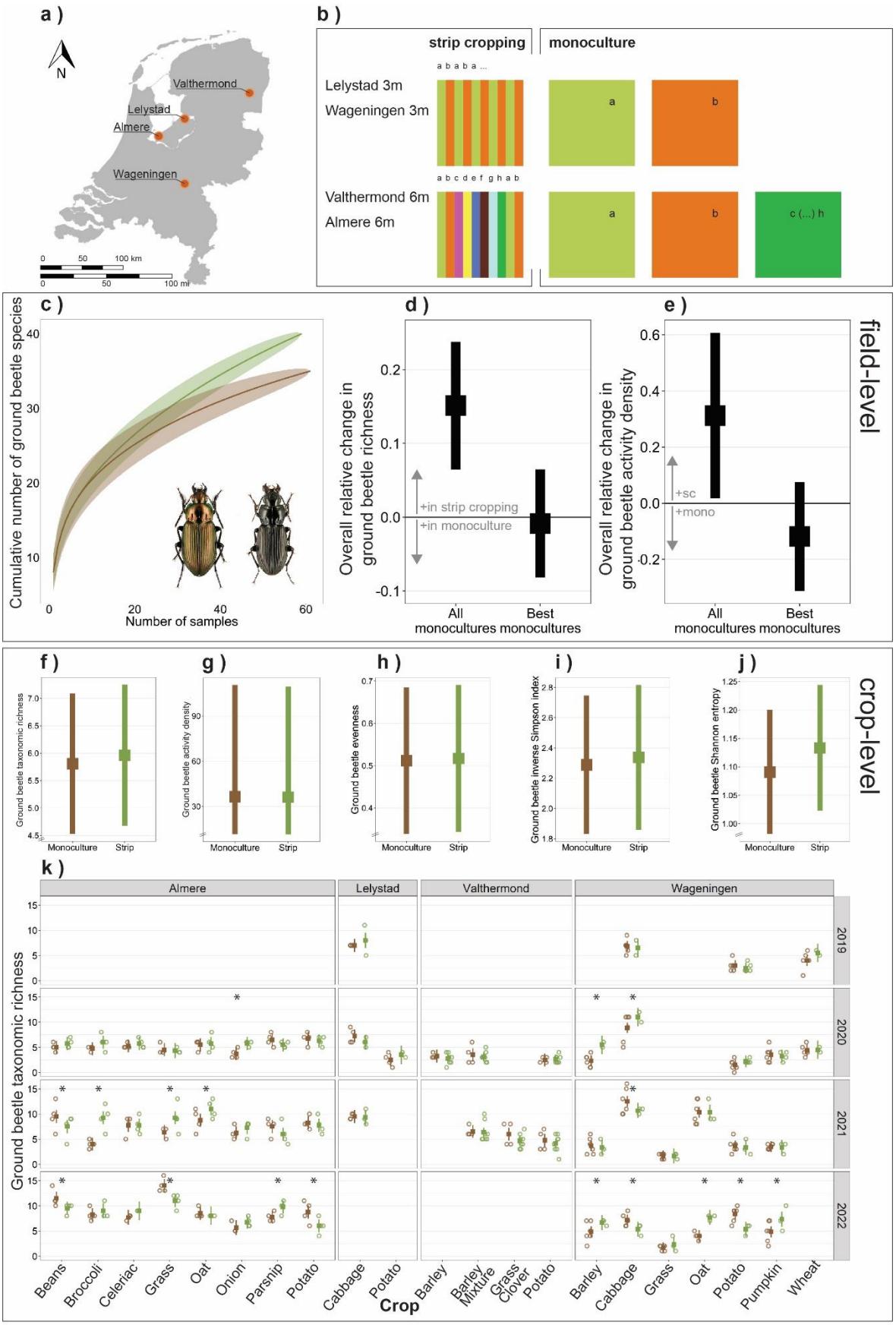
To assess whether there are crop-configuration-specific species we used indicator species analyses (ISA) (indicspecies package). Here, we excluded data from Almere in 2020, as they only contained genus-level identification. As this method does not allow for conditioning the data on location, we analysed the data for the different locations separately. To test whether species mainly occur in a monoculture or in strip cropping, we ran an ISA over the whole dataset per location. ISA uses two indicators: specificity and sensitivity of species to a certain crop configuration. Specificity refers to the predictive value of the species as indicator of the specific crop configuration, whereas sensitivity refers to the percentage of samples of the respective crop configuration that include the species. Both indicators do not take the abundance of species into account (de Cáceres, 2023).

Figures & Tables

Fig. 1. Effect of crop configuration (monoculture versus strip cropping) on ground beetle biodiversity (multi-panel).

Fig. 2. Effect of crop configuration on ground beetle indicator species.

Table 1. Effect of crop configuration on ground beetle community composition.


a)
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Overall relative change in ground beetle richness
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All monocultures
Best monocultures
e)
Overall relative change in ground beetle activity density
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All monocultures
Best monocultures
field-level
f)
Ground beetle taxonomic richness
Monoculture
Strip
g)
Ground beetle activity density
h)
Ground beetle evenness
i)
Ground beetle inverse Simpson index
j)
Ground beetle Shannon entropy
crop-level
k)
Almere
Lelystad
Valthermond
Wageningen
2019
2020
2021
2022
Ground beetle taxonomic richness
Beans
Broccoli
Celeriac
Grass
Oat
Onion
Parsnip
Potato
Cabbage
Potato
Barley
Barley Mixture
Grass Clover
Potato
Barley
Cabbage
Grass
Oat
Potato
Pumpkin
Wheat
Crop

385

Fig. 1. Effect of crop configuration (monoculture versus strip cropping) on ground beetle biodiversity. (a) Location of experimental sites in the Netherlands. **(b)** Field set-up of the two crop configurations: monoculture and strip cropping. At Lelystad and Wageningen, strip cropping consisted of 3-m wide crop strips of two crops (pairs), and multiple crop pairs were assessed. At Almere and Valthermond, strip cropping consisted of 6-m wide crop strips of eight crops combined (Fig. S7). **(c)** Sample-based species accumulation curves of all year series from monocultures (brown) and strip cropping (green), in Almere from 2021 and 2022. This was the only location where an equal number of samples were taken in the monocultures and in strip cropping on a similar area. Ground beetle species include *Poecilus cupreus* (left) and *Pterostichus melanarius* (right). Photo credit: Ortwin Bleich, retrieved from: www.eurocarabidae.de. **(d-e)** Overall relative change in field-level ground beetle **(d)** taxonomic richness and **(e)** activity density. Positive values indicate higher richness or activity density in strip cropping, negative values in monocultures. **(f-j)** Overall relative effect of crop configuration on ground beetle **(f)** taxonomic richness, **(g)** activity density, **(h)** absolute evenness, **(i)** inverse Simpson index, and **(j)** Shannon entropy. **(k)** Effect of crop configuration on ground beetle taxonomic richness for each combination of location, year and crop. Barley-mixture consists of a mixture of barley-bean (2020) or barley-pea (2021). Squares indicate estimated means, the bar indicates the 95% confidence interval. Asterisks indicate significant differences among the crop configurations. Empty panels indicate combinations of years and locations that were not sampled. When no estimated mean and confidence interval are shown, crops were not grown or sampled in that year. Open circles indicate individual year series to visualize sample size (Table S7).

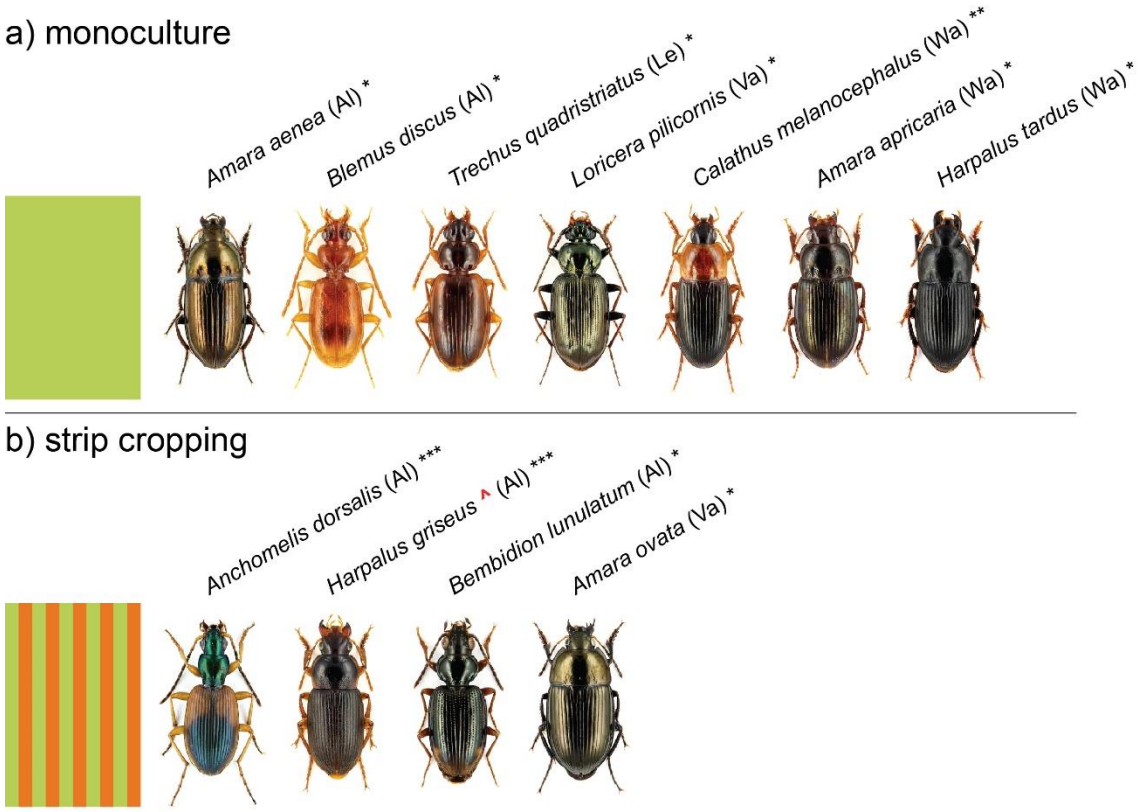

Fig. 2. Ground beetle species associated with crop configuration (monoculture (a) versus strip cropping (b)). Results obtained by indicator species analyses with the four locations analysed separately (Table S6). Locations are indicated between brackets (Al=Almere; Le = Lelystad; Va = Valthermond; Wa = Wageningen). Data from Almere in 2020 was excluded from the analysis as ground beetles were identified up to genus level only. An asterisk indicates the significance of the association between ground beetle specie and crop configuration (*: $\alpha < 0.05$; **: $\alpha < 0.01$; ***: $\alpha < 0.001$). Rare species indicated by red "^" (Turin, 2000). Photo credit: Ortwin Bleich, retrieved from: www.eurocarabidae.de.

Table 1. Effect of crop configuration on ground beetle community composition. Results from permanova analysis using Hellinger's transformation for data from the three locations with species level data (see Table S4 for analyses per location). Crops were a nested variable within years, as these differed among years. Years were nested in locations, as the years that were studied differed among locations. Bold letters indicate significant effects (α = 0.05).

Location	Predictor	Df	Sum sq	R2	F	P
All locations	Crop configuration	1	1.68	0.01	7.32	**0.001**
	Location	2	47.7	0.29	103.8	**0.001**
	Location : Year	6	10.7	0.06	7.72	**0.001**
	Location : Year : Crop species	31	33.3	0.20	4.67	**0.001**
	Crop configuration : Location	2	0.63	0.00	1.37	0.149
	Crop configuration : Location : Year	6	2.31	0.01	1.67	**0.012**
	Crop configuration : Location : Year : Crop species	31	14.8	0.09	2.08	**0.001**
	Residual	*245*	*56.3*	*0.34*		
	Total	*324*	*167.4*	*1.00*		

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Availability of data and materials Data will be made publicly available upon acceptance in the 4TU repository.

References

Alarcón-Segura, V., Grass, I., Breustedt, G., Rohlfs, M., Tscharntke, T., 2022. Strip intercropping of wheat and oilseed rape enhances biodiversity and biological pest control in a conventionally managed farm scenario. Journal of Applied Ecology 59, 1513-1523.

Anderson, M.E., Harman, R.R., Kim, T.N., 2024. Ground beetle movement is deterred by habitat edges: a mark-release-recapture study on the effectiveness of border crops in an agricultural landscape. Journal of Insect Science 24(3), ieae062.

Batáry, P., Dicks, L.V., Kleijn, D., Sutherland, W.J., 2015. The role of agri-environment schemes in conservation and environmental management. Conservation Biology 29, 1006-1016.

Beillouin, D., Ben-Ari, T., Malézieux, E., Seufert, V., Makowski, D., 2021. Positive but variable effects of crop diversification on biodiversity and ecosystem services. Global Change Biology 27, 4697-4710.

Blowes, S.A., Daskalova, G.N., Dornelas, M., Engel, T., Gotelli, N.J., Magurran, A.E., Martins, I.S., McGill, B., McGlinn, D.J., Sagouis, A., Shimadzu, H., Supp, S.R., Chase, J.M., 2022. Local biodiversity change reflects interactions among changing abundance, evenness, and richness. Ecology 103, e3820.

Campanelli, G., Iocola, I., Leteo, F., Montemurro, F., Platani, C., Testani, E., Canali, S., 2023. Strip cropping in organically managed vegetable systems: agronomic and environmental effects. Renewable Agriculture and Food Systems 38, e31.

Carbonne, B., Bohan, D.A., Foffová, H., Daouti, E., Frei, B., Neidel, V., Saska, P., Skuhrovec, J., Petit, S., 2022. Direct and indirect effects of landscape and field management intensity on carabids through trophic resources and weeds. Journal of Applied Ecology 59, 176-187.

Carrillo-Reche, J., Le Noc, T., van Apeldoorn, D.F., Juventia, S.D., Westhoek, A., Shanmugam, S., Kristensen, H.L., Hondebrink, M., Himanen, S.J., Kivijärvi, P., Lepse, L., Dane, S., Rossing, W.A.H., 2023. Finding guidelines for cabbage intercropping systems design as a first step in a meta-analysis relay for vegetables. Agriculture, Ecosystems & Environment 354, 108564.

CBD, 2020. Global biodiversity outlook 5. CBD, Montreal, Canada.

Croijmans, L., van Apeldoorn, D.F., Sanfilippo, F., Zangpo, T., Poelman, E.H., 2024. Crop species diversity levels with attract and reward strategies to enhance Pieris brassicae parasitism rate by Cotesia glomerata in strip intercropping. Functional Ecology 38, 654-667.

Crutsinger, G.M., Collins, M.D., Fordyce, J.A., Gompert, Z., Nice, C.C., Sanders, N.J., 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. Science 313, 966-968.

Cuperus, F., Ozinga, W.A., Bianchi, F.J.J.A., Croijmans, L., Rossing, W.A.H., van Apeldoorn, D.F., 2023. Effects of field-level strip and mixed cropping on aerial arthropod and arable flora communities. Agriculture, Ecosystems & Environment 354, 108568.

Cuperus, F., Allema, B., Bianchi, F.J.J.A., Rossing, W.A.H., van Apeldoorn, D.F., 2024. Cauliflower strip cropping promotes ground-dwelling arthropod richness and spider abundance. Agriculture, Ecosystems & Environment 374, 109137.

Dainese, M., Martin, E.A., Aizen, M.A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L.G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L.A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D.S., Kennedy, C.M., Kleijn, D., Kremen, C., Landis, D.A., Letourneau, D.K., Marini, L., Poveda, K., Rader, R., Smith, H.G., Tscharntke, T., Andersson, G.K.S., Badenhausser, I., Baensch, S., Bezerra, A.D.M., Bianchi, F.J.J.A., Boreux, V., Bretagnolle, V., Caballero-Lopez, B., Cavigliasso, P., Ćetković, A., Chacoff, N.P., Classen, A., Cusser, S., da Silva e Silva, F.D., de Groot, G.A., Dudenhöffer, J.H., Ekroos, J., Fijen, T., Franck, P., Freitas, B.M., Garratt, M.P.D., Gratton, C., Hipólito, J., Holzschuh, A., Hunt, L., Iverson, A.L., Jha, S., Keasar, T., Kim, T.N., Kishinevsky, M., Klatt, B.K., Klein, A.-M., Krewenka, K.M., Krishnan, S., Larsen, A.E., Lavigne, C., Liere, H., Maas, B., Mallinger, R.E., Martinez Pachon, E., Martínez-Salinas, A., Meehan, T.D., Mitchell, M.G.E., Molina, G.A.R., Nesper, M.,

Nilsson, L., O'Rourke, M.E., Peters, M.K., Plećaš, M., Potts, S.G., Ramos, D.d.L., Rosenheim, J.A., Rundlöf, M., Rusch, A., Sáez, A., Scheper, J., Schleuning, M., Schmack, J.M., Sciligo, A.R., Seymour, C., Stanley, D.A., Stewart, R., Stout, J.C., Sutter, L., Takada, M.B., Taki, H., Tamburini, G., Tschumi, M., Viana, B.F., Westphal, C., Willcox, B.K., Wratten, S.D., Yoshioka, A., Zaragoza-Trello, C., Zhang, W., Zou, Y., Steffan-Dewenter, I., 2019. A global synthesis reveals biodiversity-mediated benefits for crop production. Science Advances 5, eaax0121.

de Cáceres, M., 2023. Indicator Species Analysis using 'indicspecies'.

DeJong, T.M., 1975. A comparison of three diversity indices based on their components of richness and evenness. Oikos 26, 222-227.

Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Agard, J., Arneth, A., Balvanera, P., Brauman, K.A., Butchart, S.H.M., Chan, K.M.A., Garibaldi, L.A., Ichii, K., Liu, J., Subramanian, S.M., Midgley, G.F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R.R., Shin, Y.-J., Visseren-Hamakers, I., Willis, K.J., Zayas, C.N., 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. Science 366, eaax3100.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. Science 345, 401-406.

Ditzler, L., Rossing, W.A.H., Schulte, R.P.O., Hageman, J., van Apeldoorn, D.F., 2023. Prospects for increasing the resolution of crop diversity for agroecosystem service delivery in a Dutch arable system. Agriculture, Ecosystems & Environment 351, 108472.

Ditzler, L., van Apeldoorn, D.F., Schulte, R.P.O., Tittonell, P., Rossing, W.A.H., 2021. Redefining the field to mobilize three-dimensional diversity and ecosystem services on the arable farm. European Journal of Agronomy 122, 126197.

European Commission, 2020. The European Green Deal. Publications Office.

Eyre, M.D., Labanowska-Bury, D., Avayanos, J.G., White, R., Leifert, C., 2009. Ground beetles (Coleoptera, Carabidae) in an intensively managed vegetable crop landscape in eastern England. Agriculture, Ecosystems & Environment 131, 340-346.

Fischer, J., Brosi, B., Daily, G.C., Ehrlich, P.R., Goldman, R., Goldstein, J., Lindenmayer, D.B., Manning, A.D., Mooney, H.A., Pejchar, L., Ranganathan, J., Tallis, H., 2008. Should agricultural policies encourage land sparing or wildlife-friendly farming? Frontiers in Ecology and the Environment 6, 380-385.

Gerlach, J., Samways, M., Pryke, J., 2013. Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. Journal of Insect Conservation 17, 831-850.

Gong, S., Hodgson, J.A., Tscharntke, T., Liu, Y., van der Werf, W., Batáry, P., Knops, J.M.H., Zou, Y., 2022. Biodiversity and yield trade-offs for organic farming. Ecology Letters 25, 1699-1710.

Green, R.E., Cornell, S.J., Scharlemann, J.P.W., Balmford, A., 2005. Farming and the fate of wild nature. Science 307, 550-555.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., de Kroon, H., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLOS ONE 12, e0185809.

Holland, J.M., Frampton, G., Brink, van den Heiligenberg, H., 2002. Carabids as indicators within temperate arable farming systems: implications from SCRAB and LINK integrated farming systems projects. In: Holland, J.M. (Ed.), The agroecology of carabid beetles. Intercept, pp. 251-270.

Holland, J.M., Luff, M.L., 2000. The effects of agricultural practices on Carabidae in temperate agroecosystems. Integrated Pest Management Reviews 5, 109-129.

Hummel, J.D., Dosdall, L.M., Clayton, G.W., Harker, K.N., O'Donovan, J.T., 2012. Ground beetle (Coleoptera: Carabidae) diversity, activity density, and community structure in a diversified agroecosystem. Environmental Entomology 41, 72-80.

IPBES, 2019. Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES Secretariat, Bonn, Germany.

Josefsson, J., Berg, Å., Hiron, M., Pärt, T., Eggers, S., 2017. Sensitivity of the farmland bird community to crop diversification in Sweden: does the CAP fit? Journal of Applied Ecology 54, 518-526.

Juventia, S.D., van Apeldoorn, D.F. Strip cropping increases yield and revenue: multi-year analysis of an organic system in the Netherlands. *Frontiers in Sustainable Food Systems, in press.*

Juventia, S.D., Rossing, W.A.H., Ditzler, L., van Apeldoorn, D.F., 2021. Spatial and genetic crop diversity support ecosystem service delivery: A case of yield and biocontrol in Dutch organic cabbage production. Field Crops Research 261, 108015.

Juventia, S.D., Selin Norén, I.L.M., van Apeldoorn, D.F., Ditzler, L., Rossing, W.A.H., 2022. Spatio-temporal design of strip cropping systems. Agricultural Systems 201, 103455.

Karssemeijer, P.N., Croijmans, L., Gajendiran, K., Gols, R., van Apeldoorn, D.F., van Loon, J.J.A., Dicke, M., Poelman, E.H., 2023. Diverse cropping systems lead to higher larval mortality of the cabbage root fly (*Delia radicum*). Journal of Pest Science 97, 337-353.

Kromp, B., 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. Agriculture, Ecosystems & Environment 74, 187-228.

Lichtenberg, E.M., Kennedy, C.M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., Bosque-Pérez, N.A., Carvalheiro, L.G., Snyder, W.E., Williams, N.M., Winfree, R., Klatt, B.K., Åström, S., Benjamin, F., Brittain, C., Chaplin-Kramer, R., Clough, Y., Danforth, B., Diekötter, T., Eigenbrode, S.D., Ekroos, J., Elle, E., Freitas, B.M., Fukuda, Y., Gaines-Day, H.R., Grab, H., Gratton, C., Holzschuh, A., Isaacs, R., Isaia, M., Jha, S., Jonason, D., Jones, V.P., Klein, A.-M., Krauss, J., Letourneau, D.K., Macfadyen, S., Mallinger, R.E., Martin, E.A., Martinez, E., Memmott, J., Morandin, L., Neame, L., Otieno, M., Park, M.G., Pfiffner, L., Pocock, M.J.O., Ponce, C., Potts, S.G., Poveda, K., Ramos, M., Rosenheim, J.A., Rundlöf, M., Sardiñas, H., Saunders, M.E., Schon, N.L., Sciligo, A.R., Sidhu, C.S., Steffan-Dewenter, I., Tscharntke, T., Veselý, M., Weisser, W.W., Wilson, J.K., Crowder, D.W., 2017. A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. Global Change Biology 23, 4946-4957.

Loconto, A., Desquilbet, M., Moreau, T., Couvet, D., Dorin, B., 2020. The land sparing – land sharing controversy: Tracing the politics of knowledge. Land Use Policy 96, 103610.

Makwela, M.M., Slotow, R., Munyai, T.C., 2023. Carabid beetles (Coleoptera) as indicators of sustainability in agroecosystems: A systematic review. Sustainability 15.

Martin-Guay, M.-O., Paquette, A., Dupras, J., Rivest, D., 2018. The new Green Revolution: Sustainable intensification of agriculture by intercropping. Science of The Total Environment 615, 767-772.

Mollaei, M., Fathi, A.A., Ganbalani, G., Hassanpour, M., Golizadeh, A., 2020. Effects of strip intercropping of canola with faba bean, field pea, garlic, or wheat on control of cabbage aphid and crop yield. Plant Protection Science 57, 59-65.

Müller, J., Hothorn, T., Yuan, Y., Seibold, S., Mitesser, O., Rothacher, J., Freund, J., Wild, C., Wolz, M., Menzel, A., 2023. Weather explains the decline and rise of insect biomass over 34 years. Nature.

Pilotto, F., Kühn, I., Adrian, R., Alber, R., Alignier, A., Andrews, C., Bäck, J., Barbaro, L., Beaumont, D., Beenaerts, N., Benham, S., Boukal, D.S., Bretagnolle, V., Camatti, E., Canullo, R., Cardoso, P.G., Ens, B.J., Everaert, G., Evtimova, V., Feuchtmayr, H., García-González, R., Gómez García, D., Grandin, U., Gutowski, J.M., Hadar, L., Halada, L., Halassy, M., Hummel, H., Huttunen, K.-L., Jaroszewicz, B., Jensen, T.C., Kalivoda, H., Schmidt, I.K., Kröncke, I., Leinonen, R., Martinho, F., Meesenburg, H., Meyer, J., Minerbi, S., Monteith, D., Nikolov, B.P., Oro, D., Ozoliņš, D., Padedda, B.M., Pallett, D., Pansera, M., Pardal, M.Â., Petriccione, B., Pipan, T., Pöyry, J., Schäfer, S.M., Schaub, M., Schneider, S.C., Skuja, A., Soetaert, K., Spriņģe, G., Stanchev, R., Stockan, J.A., Stoll, S., Sundqvist, L., Thimonier, A., Van Hoey, G., Van Ryckegem, G., Visser, M.E., Vorhauser, S., Haase, P., 2020. Meta-analysis of multidecadal biodiversity trends in Europe. Nature Communications 11, 3486.

Puliga, G.A., Arlotti, D., Dauber, J., 2023. The effects of wheat-pea mixed intercropping on biocontrol potential of generalist predators in a long-term experimental trial. Annals of Applied Biology 182, 37-47.

Rakotomalala, A.A.N.A., Ficiciyan, A.M., Tscharntke, T., 2023. Intercropping enhances beneficial arthropods and controls pests: A systematic review and meta-analysis. Agriculture, Ecosystems & Environment 356, 108617.

Ratnadass, A., Fernandes, P., Avelino, J., Habib, R., 2012. Plant species diversity for sustainable management of crop pests and diseases in agroecosystems: a review. Agronomy for Sustainable Development 32, 273-303.

Rischen, T., Frenzel, T., Fischer, K., 2021. Biodiversity in agricultural landscapes: different non-crop habitats increase diversity of ground-dwelling beetles (Coleoptera) but support different communities. Biodiversity and Conservation 30, 3965-3981.

Saunders, M.E., 2020. Conceptual ambiguity hinders measurement and management of ecosystem disservices. Journal of Applied Ecology 57, 1840-1846.

Scariot, A., 2013. Land sparing or land sharing: the missing link. Frontiers in Ecology and the Environment 11, 177-178.

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., Weisser, W.W., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574, 671-674.

Shannon, C.E., Weaver, W., 1949. The mathematical theory of communication. University of Illinois Press, Urbana, IL, US.

Simpson, E.H., 1949. Measurement of diversity. Nature 163.

Sirami, C., Gross, N., Baillod, A.B., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miguet, P., Vuillot, C., Alignier, A., Girard, J., Batáry, P., Clough, Y., Violle, C., Giralt, D., Bota, G., Badenhausser, I., Lefebvre, G., Gauffre, B., Vialatte, A., Calatayud, F., Gil-Tena, A., Tischendorf, L., Mitchell, S., Lindsay, K., Georges, R., Hilaire, S., Recasens, J., Solé-Senan, X.O., Robleño, I., Bosch, J., Barrientos, J.A., Ricarte, A., Marcos-Garcia, M.Á., Miñano, J., Mathevet, R., Gibon, A., Baudry, J., Balent, G., Poulin, B., Burel, F., Tscharntke, T., Bretagnolle, V., Siriwardena, G., Ouin, A., Brotons, L., Martin, J.-L., Fahrig, L., 2019. Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. Proceedings of the National Academy of Sciences 116, 16442-16447.

Smith, B., Wilson, J.B., 1996. A consumer's guide to evenness indices. Oikos 76, 70-82.

Tajmiri, P., Fathi, S.A.A., Golizadeh, A., Nouri-Ganbalani, G., 2017a. Effect of strip-intercropping potato and annual alfalfa on populations of *Leptinotarsa decemlineata* Say and its predators. International Journal of Pest Management 63, 273-279.

Tajmiri, P., Fathi, S.A.A., Golizadeh, A., Nouri-Ganbalani, G., 2017b. Strip-intercropping canola with annual alfalfa improves biological control of *Plutella xylostella* (L.) and crop yield. International Journal of Tropical Insect Science 37, 208-216.

Tamburini, G., Bommarco, R., Wanger, T.C., Kremen, C., van der Heijden, M.G.A., Liebman, M., Hallin, S., 2020. Agricultural diversification promotes multiple ecosystem services without compromising yield. Science Advances 6, eaba1715.

Tscharntke, T., Grass, I., Wanger, T.C., Westphal, C., Batáry, P., 2021. Beyond organic farming – harnessing biodiversity-friendly landscapes. Trends in Ecology & Evolution 36, 919-930.

Tuomisto, H., 2012. An updated consumer’s guide to evenness and related indices. Oikos 121, 1203-1218.

Turin, H., 2000. De Nederlandse Loopkevers—verspreiding en oecologie.

Turin, H., Alebeek, F., F.A.N, 2007. Loopkevers (Coleoptera: Carabidae) in agrarische milieus – een faunakarakteristiek. Entomologische Berichten 67 (2007) 6.

van Klink, R., Bowler, D., Gongalsky, K., Shen, M., Swengel, S., Chase, J., 2023. Disproportionate declines of formerly abundant species underlie insect loss. Nature 628, 1-6.

van Klink, R., Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A., Chase, J.M., 2020. Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. Science 368, 417-420.

van Oort, P.A.J., Gou, F., Stomph, T.J., van der Werf, W., 2020. Effects of strip width on yields in relay-strip intercropping: A simulation study. European Journal of Agronomy 112, 125936.

Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R., Stopak, D., 2021. Insect decline in the Anthropocene: Death by a thousand cuts. Proceedings of the National Academy of Sciences 118, e2023989118.

Williams, C.B., 1964. Patterns in the balance of nature. Academic Press, London, UK.

WWF (Ed), 2020. Living Planet Report 2020 - Bending the curve of biodiversity loss. Gland, Switzerland.

Supplementary figures

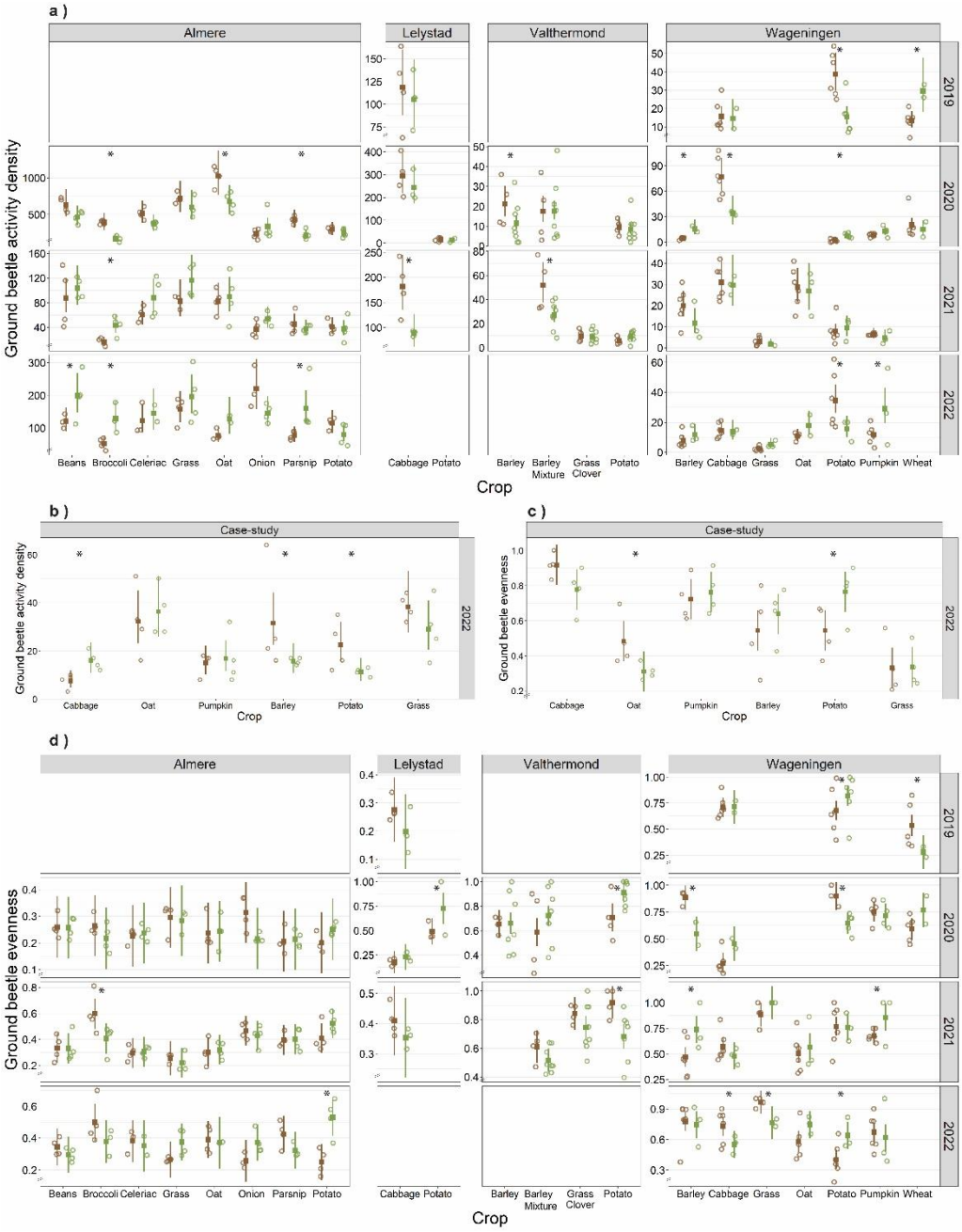


Fig. S1. Effect of crop configuration on ground beetle activity density and absolute evenness. Effect of crop configuration on activity density **(a)** and absolute evenness **(d)** per combination of location (columns), year (rows) and crop (x-axis); and the effect of crop configuration on activity density **(b)** and absolute evenness **(c)** in the case-study in Wageningen, consisting of two early spring sampling rounds in 2022. Activity density here is the total number of ground beetles captured in year series, which might differ in sampling frequency (Table S1). Absolute evenness is calculated from the total number of ground beetles captured in year series. Empty panels indicate combinations of years and locations that were not

sampled. Squares indicate estimated means, the bar indicates the 95% confidence interval. When no estimated mean and confidence interval are shown, then those crops were not grown or sampled in that year. Asterisks indicate significant differences among the crop configurations (α = 0.05). Open circles indicate individual year series (Table S1).

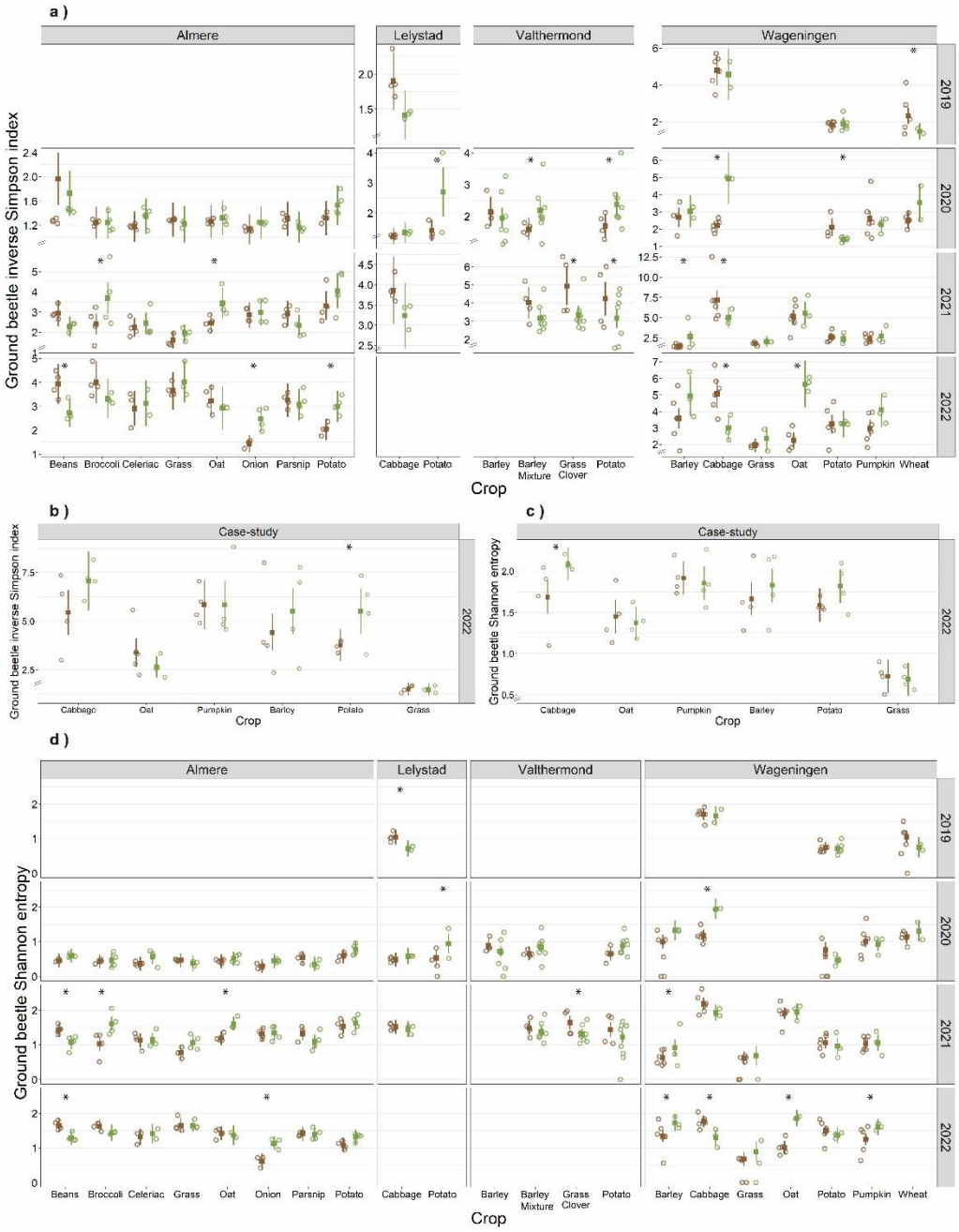


Fig. S2. Effect of crop configuration on ground beetle inverse Simpson index and Shannon entropy. Effect of crop configuration on inverse Simpson index **(a)** and Shannon entropy **(d)** per combination of location (columns), year (rows) and crop (x-axis); and the effect of crop configuration on inverse Simpson index **(b)** and Shannon entropy **(c)** in the case-study in Wageningen, consisting of two early spring sampling rounds in 2022. Inverse Simpson index and Shannon entropy were calculated from the total number of ground beetles captured in year series. Empty panels indicate combinations of years and

locations that were not sampled. Squares indicate estimated means, the bar indicates the 95% confidence interval. When no estimated mean and confidence interval are shown, then those crops were not grown or sampled in that year. Asterisks indicate significant differences among the crop configurations (α = 0.05). Open circles indicate individual year series (Table S1).

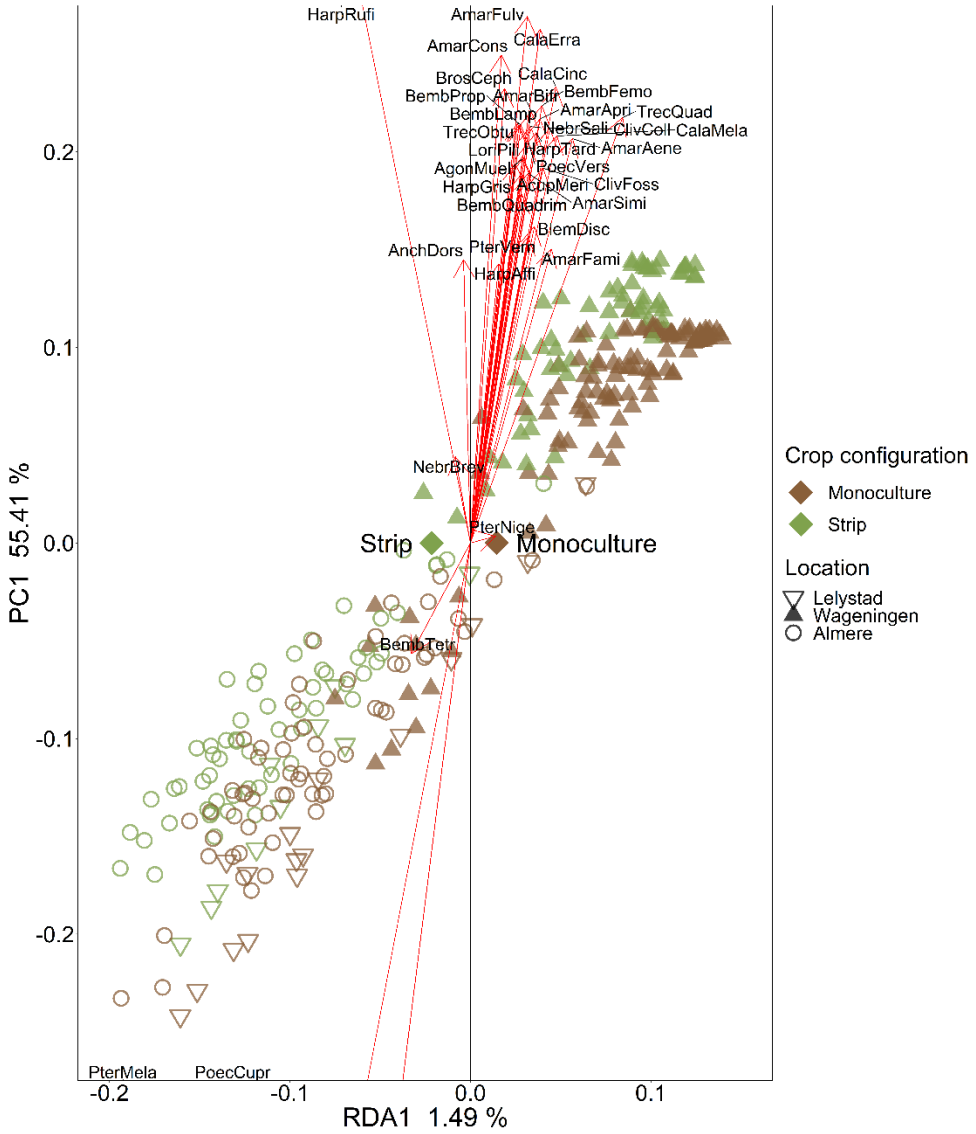


Fig. S3. The effect of crop configuration on ground beetle community composition. Data from all datasets that included species level data (Almere (○), Lelystad (▽), Wageningen (▲)) are used for visualizing the first RDA and PC axis. Each axis shows the percentage explained variation. Colour of the dots indicates crop configuration (brown = monoculture, green = strip cropping), and the direction of each crop configuration on the RDA axis (x-axis) is mentioned. Red arrows indicate species placement and name codes are given close to the tip of the arrow, meaning of the name codes can be found in Table S3.

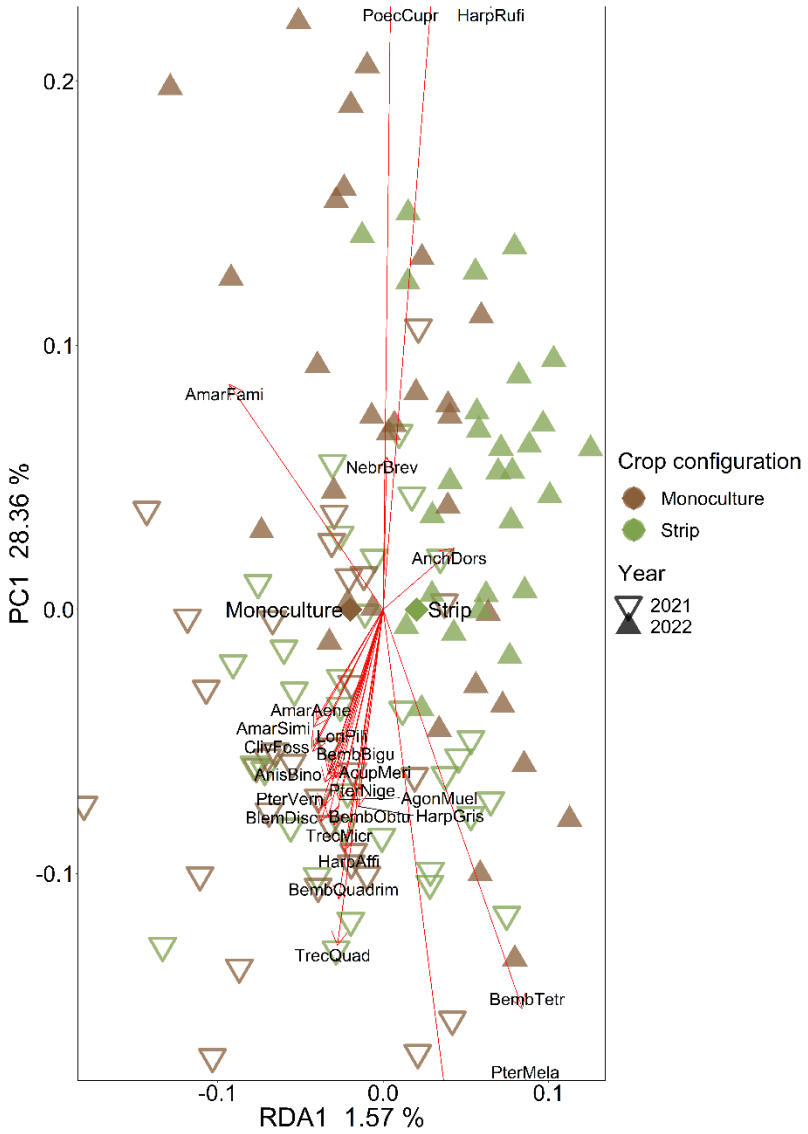


Fig. S4. The effect of crop configuration on ground beetle community composition in Almere. The first RDA and PC axis are visualized. Each axis shows the percentage explained variation. Shape of the dots indicates year (▽ = 2021, ▲ = 2022), colour of the dots indicates crop configuration (brown = monoculture, green = strip cropping), and the direction of each crop configuration on the RDA axis (x-axis) is mentioned. Red arrows indicate species placement and name codes are given close to the tip of the arrow, meaning of the name codes can be found in Table S3.

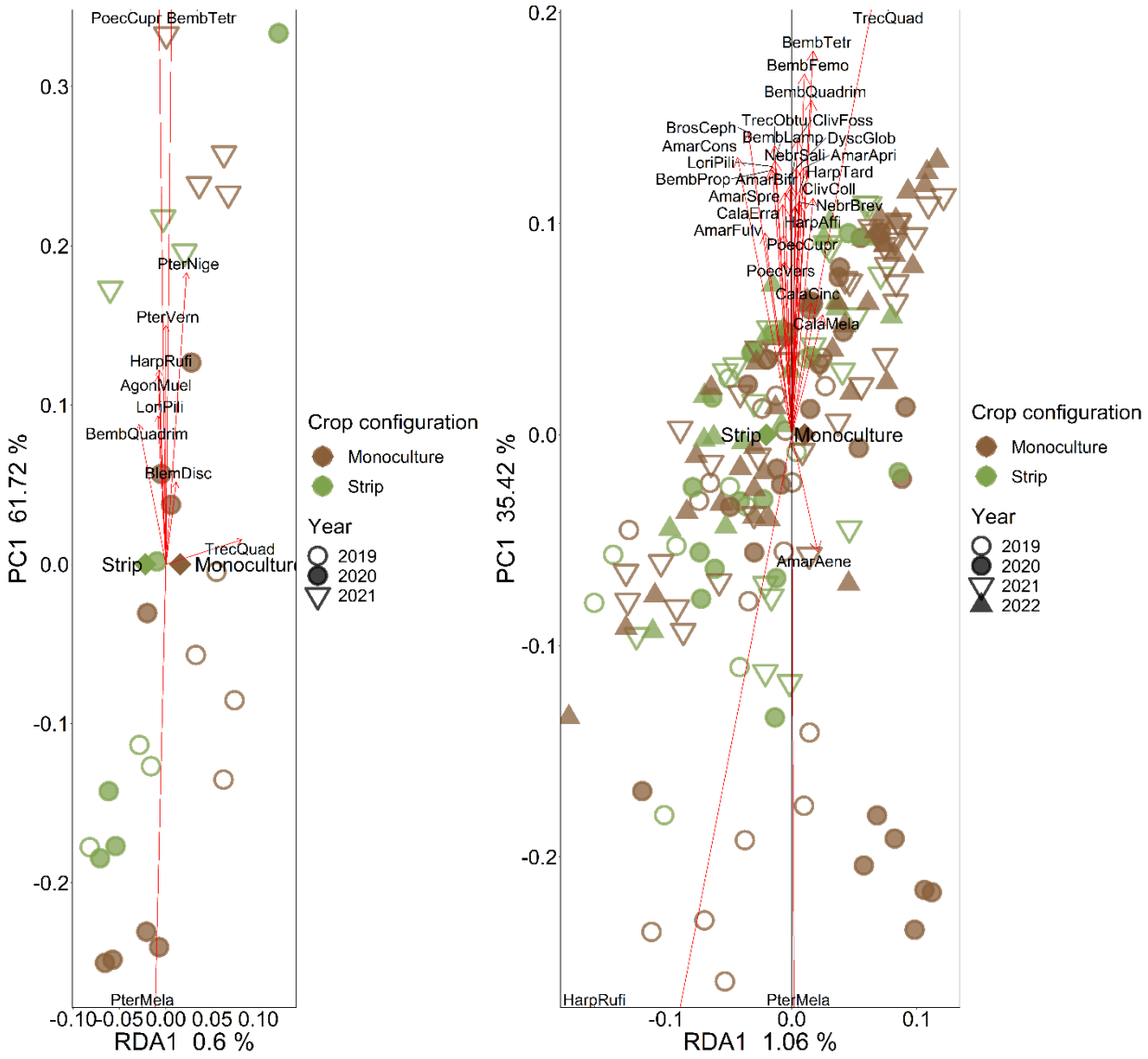


Fig. S5. The effect of crop configuration on ground beetle community composition in Lelystad (left) and Wageningen (right). The first RDA and PC axis are visualized. Each axis shows the percentage explained variation. Shape of the dots indicates year (○ = 2019, ● = 2020, ▽ = 2021, ▲ = 2022), colour of the dots indicates crop configuration (brown = monoculture, green = strip cropping), and the direction of each crop configuration on the RDA axis (x-axis) is mentioned. Red arrows indicate species placement and name codes are given close to the tip of the arrow, meaning of the name codes can be found in Table S3.

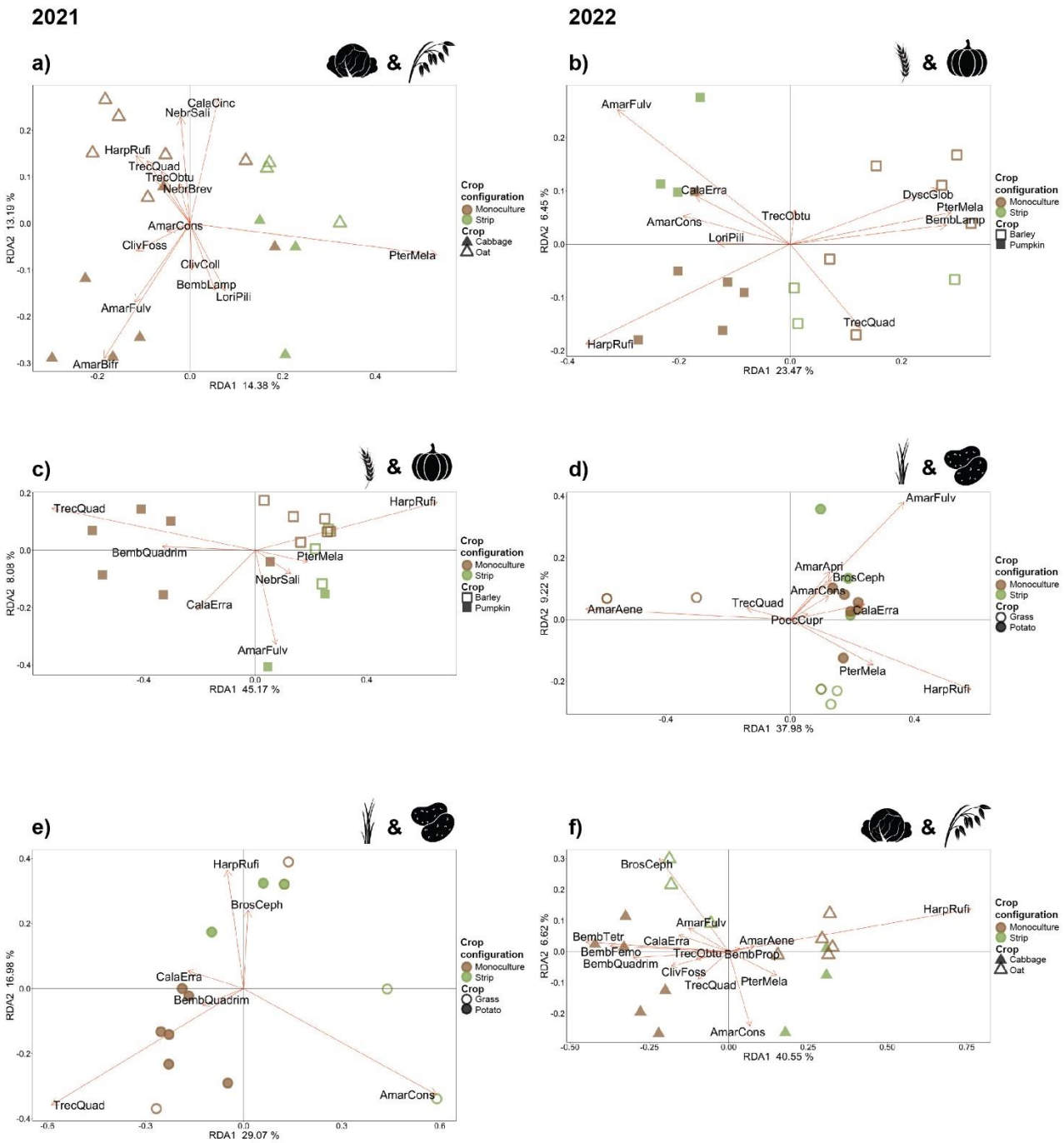
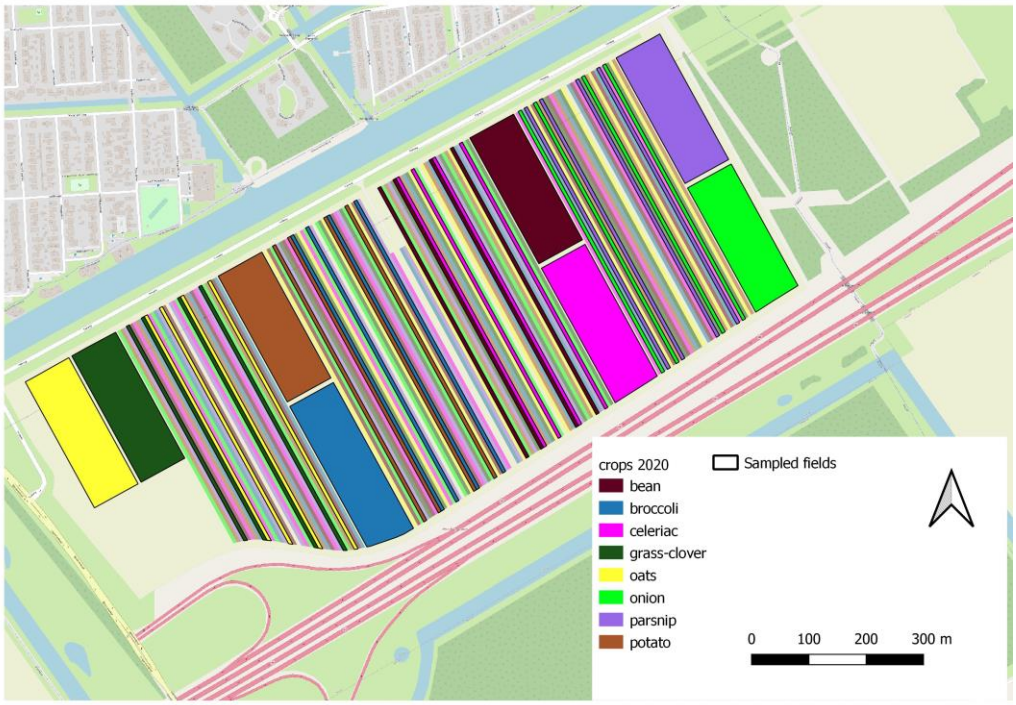


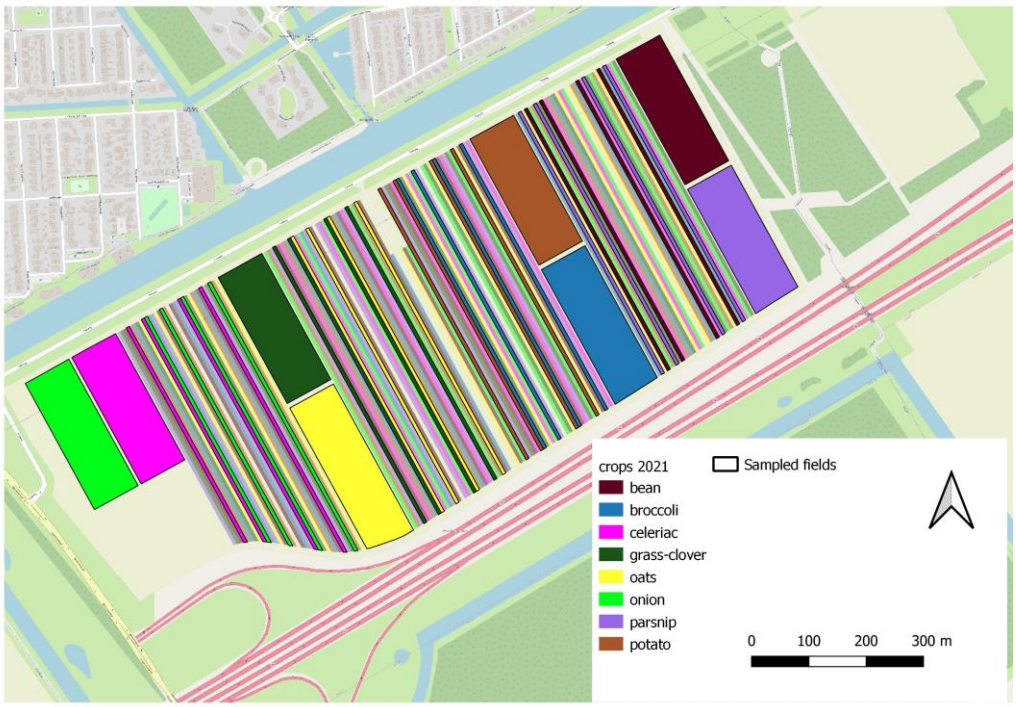
Fig. S6. Effect of crop configuration and crop on ground beetle community composition in Wageningen. Here, we use data from Wageningen in 2021 (left column; panels a, c, e) and 2022 (right column; panels b, d, f) from three fields including three crop pairs being cabbage and oat (panel a and f), barley and pumpkin (panel b and c), and grass and potato (panel d and e). The first and second RDA axis are visualized. Each axis shows the percentage explained variation. Colour of the dots indicates crop configuration (brown = monoculture, green = strip cropping), shapes indicates crop (□ = barley, ■ =

pumpkin, ○ = grass, ● = potato, △= oat, ▲ = cabbage). The red lines and abbreviated names indicate how specific ground beetles species correlate with the RDA axes, species names are given in Table S3.

Fig. S7. Field maps

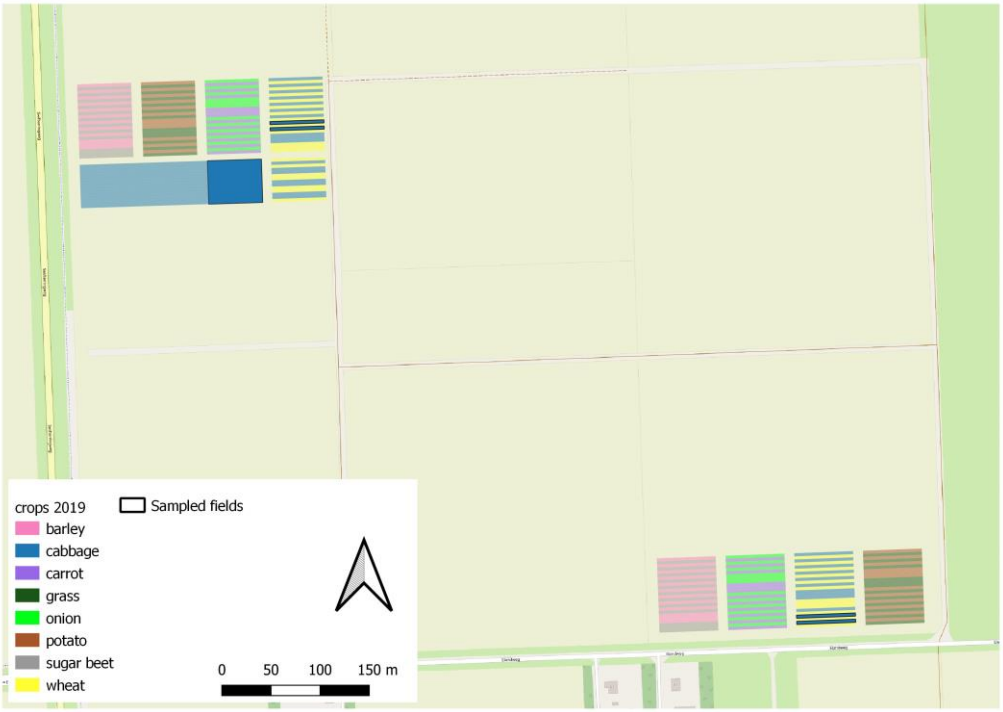
A Almere



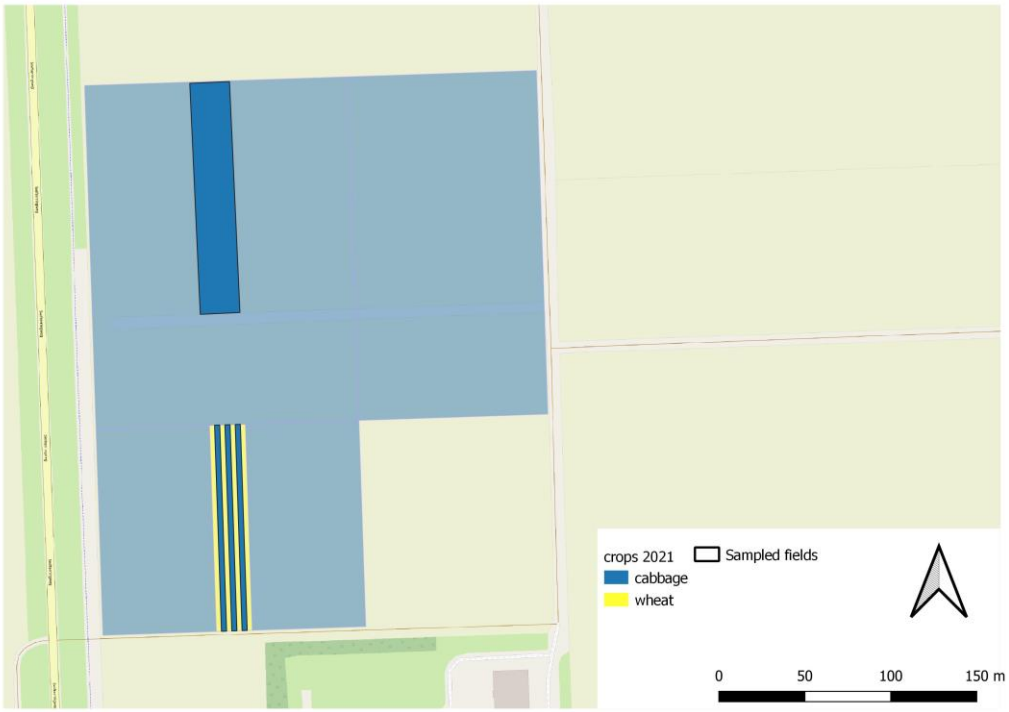


A Almere (continued)

B Lelystad

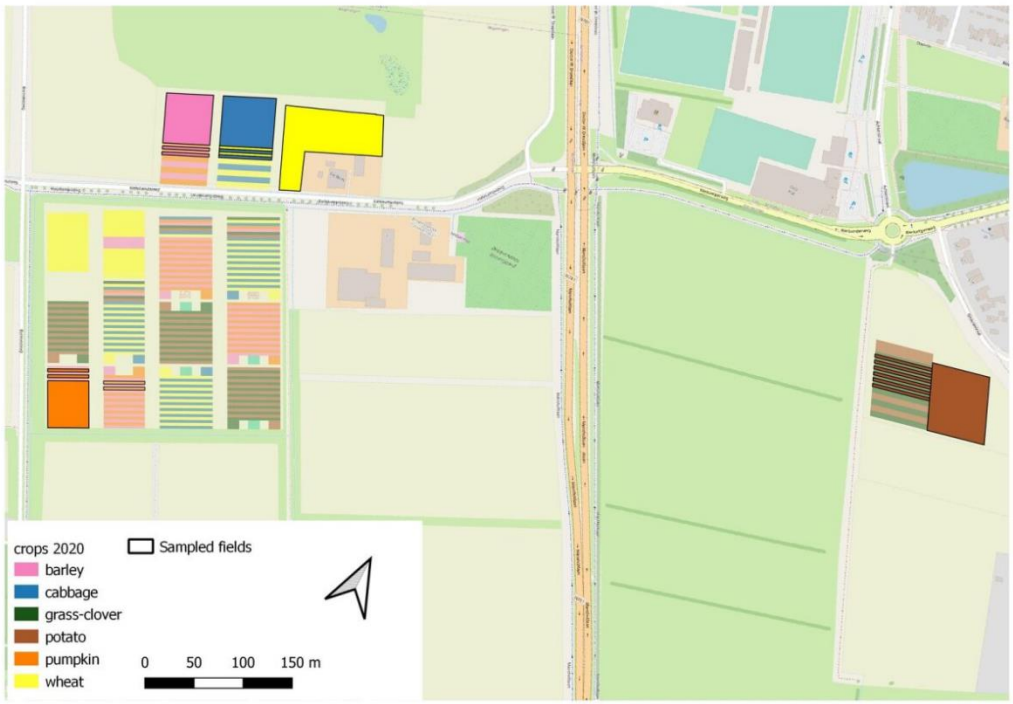


B Lelystad (continued)

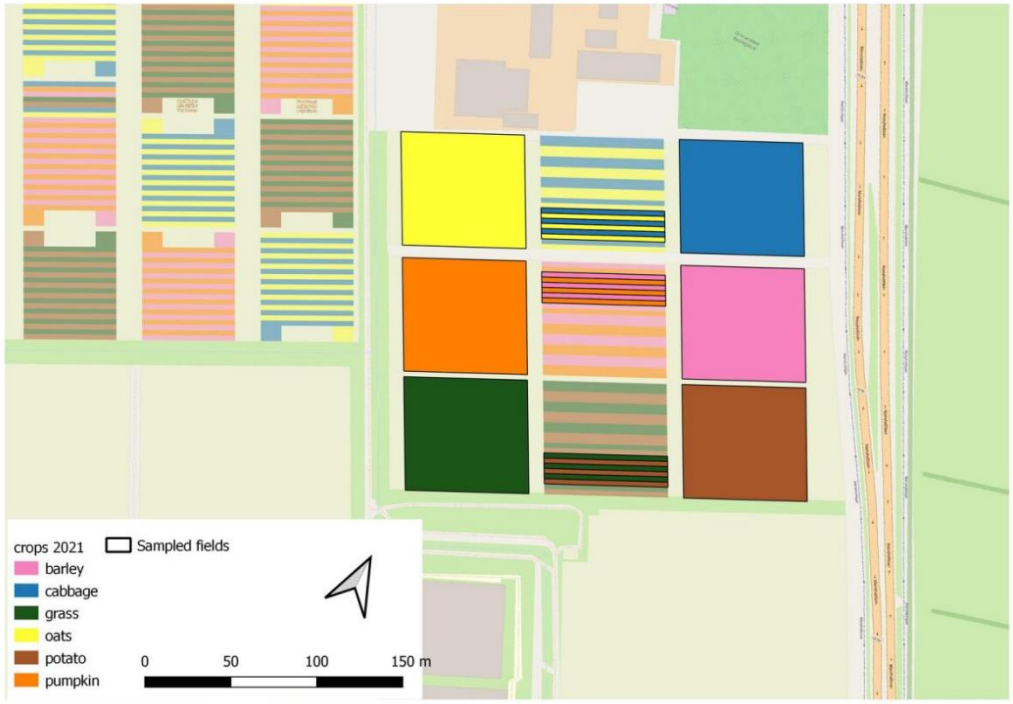


C Valthermond

D Wageningen



D Wageningen (continued)



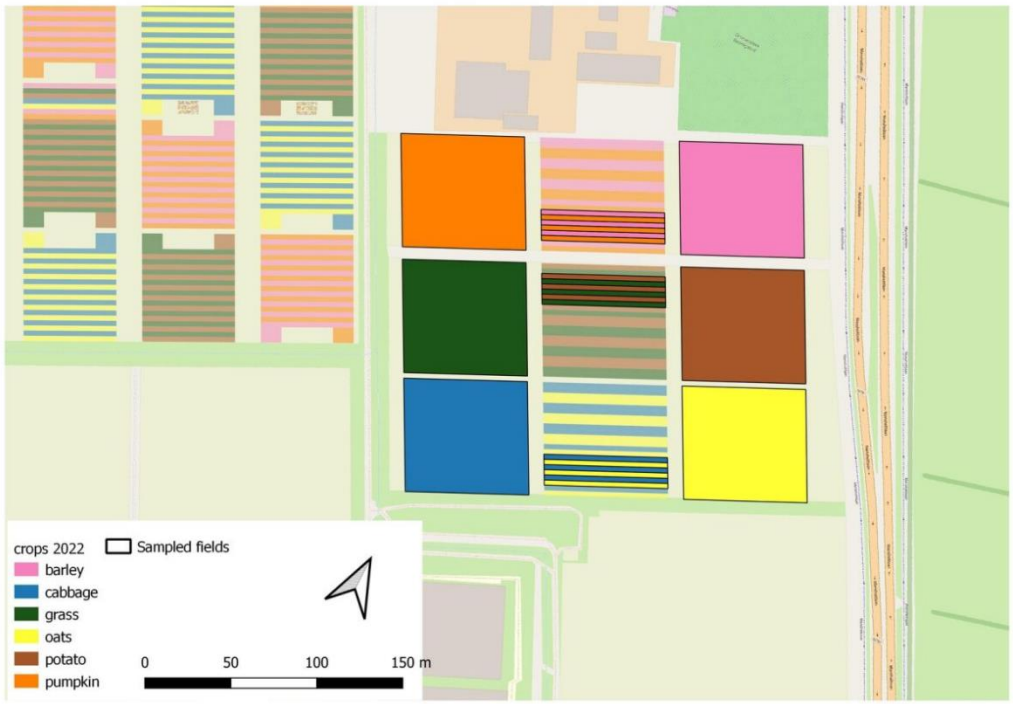


Fig. S7. Field maps of experimental lay-out per year and location. Field maps are shown in chronological order (oldest to newest) per location: Almere **(a)**, Lelystad **(b)**, Valthermond **(c)** and Wageningen **(d)**. Colors indicate distinct crops, whereas diagonal lines indicate a crop mixture (only for Valthermond). Brighter colours with black lining around the field indicate areas in which samples included in this study were taken.

Supplementary tables

Table S1. All ground beetle species found among the four locations, and their species codes as used in several figures.

Subfamily	Genus	Species	Species code
Carabinae	Carabus	*Carabus granulatus*	CaraGran
	Nebria	*Nebria brevicollis*	NebrBrev
		Nebria salina	NebrSali
	Notiophilus	*Notiophilus aquaticus*	NotiAqua
		Notiophilus biguttatus	NotiBigu
		Notiophilus palustris	NotiPalu
Harpalinae	Acupalpus	*Acupalpus meridianus*	AcupMeri
	Agonum	*Agonum muelleri*	AgonMuel
	Amara	*Amara aenea*	AmarAene
		Amara anthobia	AmarAnth
		Amara apricaria	AmarApri
		Amara aulica	AmarAuli
		Amara bifrons	AmarBifr
		Amara communis	AmarComm
		Amara consularis	AmarCons
		Amara famelica	AmarFame
		Amara familiaris	AmarFami
		Amara fulva	AmarFulv
		Amara ovata	AmarOvat
		Amara plebeja	AmarPleb
		Amara similata	AmarSimi
		Amara spreta	AmarSpre
		Amara tibialis	AmarTibi
	Anchomenus	*Anchomenus dorsalis*	AnchDors
	Anisodactylus	*Anisodactylus binotatus*	AnisBino
	Badister	*Badister bullatus*	BadiBull
		Badister sodalist	BadiSoda
	Bradycellus	*Bradycellus harpalinus*	BradHarp
	Calathus	*Calathus cinctus*	CalaCinc

Subfamily	Genus	Species	Species code
		Calathus erratus	CalaErra
		Calathus fuscipes	CalaFusc
		Calathus melanocephalus	CalaMela
		Calathus rotundicollis	CalaRotu
	Harpalus	*Harpalus affinis*	HarpAffi
		Harpalus distinguendus	HarpDist
		Harpalus griseus	HarpGris
		Harpalus rubripes	HarpRubr
		Harpalus rufipes	HarpRufi
		Harpalus signaticornis	HarpSign
		Harpalus tardus	HarpTard
	Microlestes	*Microlestes minutulus*	MicrMinu
	Oxypselaphus	*Oxypselaphus obscurus*	OxypObsc
	Panagaeus	*Panagaeus bipustulatus*	PanaBipu
	Poecilus	*Poecilus cupreus*	PoecCupr
		Poecilus versicolor	PoecVers
	Pterostichus	*Pterostichus anthracinus*	PterAnth
		Pterostichus melanarius	PterMela
		Pterostichus niger	PterNige
		Pterostichus strenuus	PterStre
		Pterostichus vernalis	PterVern
	Stenolophus	*Stenolophus teutonus*	StenTeut
	Stomis	*Stomis pumicatus*	StomPumi
	Syntomus	*Syntomus truncatellus*	SyntTrun
Loricerinae	Loricera	*Loricera pilicornis*	LoriPili
Scaritinae	Broscus	*Broscus cephalotes*	BrosCeph
	Clivina	*Clivina collaris*	ClivColl
		Clivina fossor	ClivFoss
	Dyschirius	*Dyschirius globosus*	DyscGlob
Trechinae	Asaphidion	*Asaphidion flavipes*	AsapFlav
	Bembidion	*Bembidion aenea*	BembAene
		Bembidion biguttatum	BembBigu
		Bembidion femoratum	BembFemo

Subfamily	Genus	Species	Species code
		Bembidion lampros	BembLamp
		Bembidion lunulatum	BembLunu
		Bembidion obtusum	BembObtu
		Bembidion proprans	BembProp
		Bembidion quadrimaculatum	BembQuadrim
		Bembidion tetracolum	BembTetr
	Blemus	*Blemus discus*	BlemDisc
	Trechoblemus	*Trechoblemus micros*	TrecMicr
	Trechus	*Trechus obtusus*	TrecObtu
		Trechus quadristriatus	TrecQuad

Table S2. Total number of ground beetles caught per species (or genus), per location. For some locations, ground beetles were identified up to genus level, these are underlined. "N/A" indicates that this taxa was identified to a different taxonomic level for the specific location. Locations are indicated with abbreviations (Al=Almere; Le = Lelystad; Va = Valthermond; Wa = Wageningen).

	Species	Al	Le	Va	Wa	Total
1	*Pterostichus sp.*	25258	N/A	68	N/A	25326
2	*Pterostichus melanarius*	5556	2731	144	765	9196
3	*Poecilus cupreus*	2876	233	N/A	66	3175
4	*Harpalus rufipes*	1409	15	168	1143	2735
5	*Poecilus sp.*	1769	N/A	82	N/A	1851
6	*Harpalus sp.*	947	N/A	308	N/A	1255
7	*Bembidion tetracolum*	345	397	N/A	44	786
8	*Amara aenea*	15	0	8	654	677
9	*Pterostichus niger*	167	228	5	1	401
10	*Nebria brevicollis*	320	2	0	24	346
11	*Bembidion sp.*	300	N/A	32	N/A	332
12	*Anchomenus dorsalis*	151	1	161	8	321
13	*Trechus sp.*	303	N/A	N/A	N/A	303
14	*Trechus quadristriatus*	69	76	0	137	282
15	*Amara familiaris*	124	0	0	97	221
16	*Harpalus affinis*	131	3	1	57	192

17	*Bembidion quadrimaculatum*	87	8	N/A	68	163
18	*Clivina fossor*	49	9	2	66	126
19	*Calathus melanocephalus*	0	0	67	42	109
20	*Amara fulva*	0	0	6	98	104
21	*Calathus cinctus*	0	0	20	73	93
22	*Calathus erratus*	0	0	6	87	93
23	*Poecilus versicolor*	4	2	N/A	80	86
24	*Loricera pilicornis*	22	6	20	37	85
25	*Blemus discus*	34	45	0	0	79
26	*Pterostichus vernalis*	57	9	N/A	6	72
27	*Amara spreta*	0	0	0	71	71
28	*Bembidion proprans*	4	0	N/A	64	68
29	*Clivina collaris*	0	2	2	64	68
30	*Amara consularis*	0	0	0	54	54
31	*Bembidion lampros*	3	1	N/A	44	48
32	*Nebria sp.*	42	N/A	N/A	N/A	42
33	*Amara apricaria*	0	0	0	41	41
34	*Amara bifrons*	1	0	1	36	38
35	*Bembidion femoratum*	0	0	N/A	36	36
36	*Broscus cephalotes*	0	0	0	35	35
37	*Amara similata*	24	0	0	6	30
38	*Harpalus tardus*	0	0	2	26	28
39	*Agonum muelleri*	5	3	7	11	26
40	*Nebria salina*	0	0	0	23	23
41	*Trechus obtusus*	2	0	0	18	20
42	*Harpalus griseus*	9	0	2	4	15
43	*Acupalpus meridianus*	8	3	0	3	14
44	Unknown carabidae	10	1	0	3	14
45	*Amara ovata*	0	0	9	1	10
46	*Dyschirius globosus*	0	0	0	10	10
47	*Anisodactylus binotatus*	6	0	0	2	8
48	*Amara communis*	0	0	0	7	7
49	*Bembidion biguttatum*	7	0	N/A	0	7
50	*Amara sp.*	5	N/A	N/A	N/A	5

51	*Clivina sp.*	5	N/A	N/A	N/A	5
52	*Harpalus distinguendus*	0	0	N/A	5	5
53	*Harpalus signaticornis*	0	0	N/A	5	5
54	*Bembidion obtusum*	4	0	N/A	0	4
55	*Trechoblemus micros*	4	0	0	0	4
56	*Amara anthobia*	0	0	3	0	3
57	*Badister bullatus*	2	0	0	1	3
58	*Badister sodalis*	3	0	0	0	3
59	*Bembidion lunulatum*	3	0	N/A	0	3
60	*Oxypselaphus obscurus*	3	0	0	0	3
61	*Stomis pumicatus*	3	0	0	0	3
62	*Acupalpus sp.*	2	N/A	N/A	N/A	2
63	*Amara aulica*	1	0	0	1	2
64	*Calathus fuscipes*	0	0	2	0	2
65	*Calathus rotundicollis*	0	0	0	2	2
66	*Carabus granulatus*	2	0	0	0	2
67	*Harpalus rubripes*	0	1	N/A	1	2
68	*Notiophilus palustris*	2	0	0	0	2
69	*Pterostichus strenuus*	2	0	N/A	0	2
70	*Stenolophus teutonus*	0	0	0	2	2
71	*Amara famelica*	0	0	0	1	1
72	*Amara plebeja*	1	0	0	0	1
73	*Amara tibialis*	0	0	0	1	1
74	*Asaphidion flavipes*	0	0	0	1	1
75	*Bembidion aenea*	0	1	N/A	0	1
76	*Bradycellus harpalinus*	1	N/A	N/A	N/A	1
77	*Carabus sp.*	1	N/A	N/A	N/A	1
78	*Microlestes minutulus*	0	0	0	1	1
79	*Notiophilus aquaticus*	0	0	0	1	1
80	*Notiophilus biguttatus*	0	0	0	1	1
81	*Panagaeus bipustulatus*	0	0	0	1	1
82	*Pterostichus anthracinus*	1	0	N/A	0	1
83	*Syntomus truncatellus*	0	0	0	1	1

Table S3. Effect of crop configuration on ground beetle community composition. Results from permanova analyses using Hellinger's transformation for data from the three locations with species level data. "Crop species" is a nested variable within years, as these differed among years. Years were nested in locations, as the years that were studied differed among locations. P-values in bold typeset indicate significant effects (α = 0.05).

Location	Predictor	Df	Sum Sq	R2	F	P
Almere	Crop configuration	1	0.20	0.01	2.34	**0.025**
	Year	1	2.48	0.13	28.6	**0.001**
	Year : Crop species	14	5.66	0.30	4.68	**0.001**
	Crop configuration : Year	1	0.13	0.01	1.50	0.138
	Crop configuration : Year : Crop species	14	2.88	0.15	2.38	**0.001**
	Residual	88	*7.61*	*0.40*		
	Total	119	*19.0*	*1.00*		
Lelystad	Crop configuration	1	0.03	0.01	0.68	0.534
	Year	2	1.78	0.55	18.9	**0.001**
	Year : Crop species	1	0.12	0.04	2.45	0.082
	Crop configuration : Year	2	0.26	0.08	2.80	**0.026**
	Crop configuration : Year : Crop species	1	0.14	0.04	2.91	**0.039**
	Residual	*19*	*0.90*	*0.28*		
	Total	*26*	*3.22*	*1.00*		
Wageningen	Crop configuration	1	1.48	0.02	4.30	**0.001**
	Year	3	6.40	0.07	6.22	**0.001**
	Year : Crop species	16	27.7	0.29	5.05	**0.001**
	Crop configuration : Year	3	1.90	0.02	1.85	**0.006**
	Crop configuration : Year : Crop species	16	11.8	0.12	2.15	**0.001**
	Residual	*138*	*47.3*	*0.49*		
	Total	*177*	*96.6*	*1.00*		

Table S4. Effect of crop configuration and crop species on ground beetle community composition. Results from pairwise permanova analyses for crop pairs pumkin-barley, cabbage-oat, and potato-grass in 2021 (a) and 2022 (b) in Wageningen. Values show F-values for the comparison between the crop configurations and crops in crossing rows and columns. Bold numbers indicate significant differences between combinations of crop configurations and crops (α = 0.05).

Table S4a. 2021

F-value		Pumpkin		Barley	
		Mono	Strip	Mono	Strip
Pumpkin	Mono				
	Strip	**3.64**			
Barley	Mono	**10.39**	1.40		
	Strip	**5.82**	1.21	**4.23**	

F-value		Potato		Grass	
		Mono	Strip	Mono	Strip
Potato	Mono				
	Strip	**5.00**			
Grass	Mono	1.70	0.57		
	Strip	**8.38**	5.06	1.94	

F-value		Cabbage		Oat	
		Mono	Strip	Mono	Strip
Cabbage	Mono				
	Strip	1.47			
Oat	Mono	**2.08**	**3.52**		
	Strip	2.06	2.07	2.92	

Table S4b. 2022

F-value		Pumpkin		Barley	
		Mono	Strip	Mono	Strip
Pumpkin	Mono				
	Strip	1.42			
Barley	Mono	**3.84**	**2.90**		
	Strip	1.82	2.18	0.76	

F-value		Potato		Grass	
		Mono	Strip	Mono	Strip
Potato	Mono				
	Strip	1.42			
Grass	Mono	**7.14**	3.26		
	Strip	**4.01**	3.24	3.58	

F-value		Cabbage		Oat	
		Mono	Strip	Mono	Strip
Cabbage	Mono				
	Strip	**5.35**			
Oat	Mono	**8.72**	**1.82**		
	Strip	1.59	3.56	**5.05**	

Table S5. Effect of crop configuration on ground beetle indicator species. Results from indicator species analyses with the four locations being analysed separately. Data from Almere in 2020 data was excluded from the analysis as ground beetles were identified up to genus level in 2020. Specificity refers to the predictive value of the species as indicator of the specific crop configuration whereas sensitivity refers to the percentage of samples of the respective crop configuration that included the species. "Stat" refers to the indicator value, which is the square root of the product of specificity and sensitivity. Bold letters indicate a significant association between species and crop configurations per location (α = 0.05).

Almere					
Species	Specificity	Sensitivity	Stat	p	
MONO					
Amara aenea	0.733	0.219	0.401	**0.031**	*
Blemus discus	0.833	0.156	0.361	**0.030**	*
Anisodactylus binotatus	0.833	0.094	0.280	0.182	
Badister sodalis	0.750	0.094	0.265	0.281	
Bembidion obtusum	0.750	0.094	0.265	0.274	
STRIP					
Anchomenus dorsalis	0.806	0.656	0.727	**0.001**	***
Harpalus griseus	0.900	0.250	0.474	**0.001**	***
Bembidion lunulatum	1	0.094	0.306	**0.040**	*
Amara aulica	1	0.031	0.177	0.496	
Amara bifrons	1	0.031	0.177	0.511	
Amara plebeja	1	0.031	0.177	0.498	
Pterostichus anthracinus	1	0.031	0.177	0.515	

Lelystad					
Species	Specificity	Sensitivity	Stat	p	
MONO					
Trechus quadristriatus	0.774	0.325	0.502	**0.006**	*
Pterostichus vernalis	0.798	0.063	0.223	0.195	
Poecilus versicolor	1	0.025	0.158	0.222	
Bembidion aeneum	1	0.013	0.112	0.485	
STRIP					
Anchomenus dorsalis	1	0.044	0.211	0.128	

Harpalus affinis	1	0.033	0.183	0.247
Nebria brevicollis	1	0.022	0.149	0.539
Amara aenea	1	0.011	0.105	1
Amara familiaris	1	0.011	0.105	1
Bembidion lampros	1	0.011	0.105	1
Harpalus rubripes	1	0.011	0.105	1
Badister sodalis	1	0.011	0.105	1

Valthermond

Species	Specificity	Sensitivity	Stat	p	
MONO					
Loricera pilicornis	0.750	0.292	0.468	**0.044**	*
Amara aenae	0.769	0.167	0.358	0.138	
Clivina fossor	1.000	0.083	0.289	0.103	
Amara anthobia	0.800	0.083	0.258	0.278	
Amara bifrons	1.000	0.042	0.204	0.341	
Harpalus affinis	1.000	0.042	0.204	0.354	
Clivina collaris	0.667	0.042	0.167	1.000	
Harpalus tardus	0.667	0.042	0.167	1.000	
STRIP					
Amara ovata	1.000	0.188	0.433	**0.042**	*
Harpalus griseus	1.000	0.042	0.204	0.548	
Calathus fuscipes	1.000	0.042	0.204	0.553	
Amara fulva	1.000	0.021	0.144	1.000	

Wageningen

Species	Specificity	Sensitivity	Stat	p	
MONO					
Calathus melanocephalus	0.823	0.063	0.228	**0.004**	**
Amara apricaria	0.792	0.036	0.168	**0.025**	*
Bembidion tetracolum	0.782	0.036	0.167	0.083	.
Harpalus tardus	0.781	0.036	0.167	**0.041**	*
Bembidion femoratum	0.757	0.025	0.137	0.137	

Harpalus signaticornis	0.945	0.016	0.125	0.072	.
Pterostichus vernalis	1.000	0.014	0.117	0.056	.
Anchomelis dorsalis	1.000	0.014	0.117	0.068	.
Dyschirius globosus	0.792	0.016	0.114	0.195	
Harpalus griseus	0.740	0.008	0.078	0.621	
Calathus rotundicollis	1.000	0.005	0.074	0.507	
Stenolophus teutonus	1.000	0.005	0.074	0.508	
Amara communis	1.000	0.003	0.052	1.000	
Acupalpus meridianus	1.000	0.003	0.052	1.000	
Badister bullates	1.000	0.003	0.052	1.000	
STRIP					
Harpalus distinguendus	0.808	0.012	0.097	0.215	
Pterostichus niger	1.000	0.003	0.054	0.504	
Amara tibialis	1.000	0.003	0.054	0.488	
Amara aulica	1.000	0.003	0.054	0.488	
Amara famelica	1.000	0.003	0.054	0.512	
Notiophilus aquaticus	1.000	0.003	0.054	0.482	
Demetrias atricapillus	1.000	0.003	0.054	0.481	
Bradycellus harpalinus	1.000	0.003	0.054	0.492	
Microlestes minutulus	1.000	0.003	0.054	0.514	
Badister sodalis	1.000	0.003	0.054	0.483	

Table S6. Effect of crop configuration on crop yield. Yield results were retrieved from published and unpublished studies on effects of strip cropping on crop yield in similar locations, years, and crops as this study. Mean crop yield is presented in ton per hectare (t/ha). When known, standard deviations of mean crop yield are given (± SD). When a crop is indicated with NC (not collected) the crop yield was not collected due to an inconsistent sampling method (potato, 2020, Almere), crop failure (broccoli, 2020, Almere; celeriac, 2021, Almere), unavailable machine-harvest data (grass, Almere, 2020, 2021, 2022) and undocumented reasons (barley/beans, 2020, Valthermond). Unavailable data include cabbage (2019) and potato (2020) in Lelystad; and pumpkin (2020, 2021, 2022), barley (2020, 2021, 2022), oat (2021, 2022), potato (2021, 2022), grass (2021, 2022), and cabbage (2022) in Wageningen.

Location	Year	Crops	Reference	Yield (t/ha)	
				Mono	Strip
Almere	2020	Beans	Unpublished data from Juventia and van Apeldoorn, in preparation (see: attached manuscript under embargo)	2.80	3.45
		Broccoli		NC	NC
		Celeriac		54.44	69.57
		Grass		NC	NC
		Oat		6.05	5.08
		Onion		41.06	42.14
		Parsnip		27.50	35.36
		Potato		NC	NC
	2021	Beans	Unpublished data from Juventia and van Apeldoorn, in preparation (see: attached manuscript under embargo)	4.72	6.50
		Broccoli		9.30	4.90
		Celeriac		NC	NC
		Grass		NC	NC
		Oat		8.76	8.25
		Onion		39.03	37.39
		Parsnip		36.88	65.01
		Potato		24.68	27.88
	2022	Beans	Unpublished data from Juventia and van Apeldoorn, in preparation (see: attached manuscript under embargo)	4.12	4.36
		Broccoli		1.12	1.59
		Celeriac		45.38	51.45
		Grass		NC	NC
		Oat		6.27	6.70
		Onion		57.89	48.62
		Parsnip		20.6	21.09
		Potato		31.08	31.60
Lelystad	2020	Cabbage	Carillo-Reche et al., 2023	44.0 ± 12.8	46.3 ± 13.0
	2021	Cabbage	Carillo-Reche et al., 2023	85.6 ±18.2	75.9 ± 23.4
Valthermond	2020	Barley	Unpublished data	5.3	5.1
		Barley / Beans		NC	5.1
		Potato		20.9	20.5
	2021	Barley / Beans	Unpublished data	3.1	3.4
		Grass / Clover		8.3	7.9

		Potato		23.7	20.7
Wageningen	2019	Cabbage	Carillo-Reche et al., 2023	36.8 ± 15.8	34.6 ± 6.5
		Wheat	Ditzler et al., 2023	2.8 ± 0.2	2.1 ± 0.3
		Potato	Ditzler et al., 2023	29.3 ± 5.7	30.6 ± 8.8
	2020	Cabbage	Carillo-Reche et al., 2023	25.7 ± 9.3	19.3 ± 6.6
		Wheat	Ditzler et al., 2023	0.9 ± 0.2	1.0 ± 0.4
		Potato	Ditzler et al., 2023	23.4 ± 6.1	26.1 ± 8.9
	2021	Cabbage	Carillo-Reche et al., 2023	32.1 ± 7.1	27.9 ± 13.1

Table S7. Sampling effort. The total numbers of pitfall traps placed per location, year and crop. Rounds indicate the number of times pitfall traps were placed and were pooled within year series.

Location	Year	Crops	Rounds	Pitfall traps per round	
				Mono	Strip
Almere	2020	Beans	3	4	4
		Broccoli		4	4
		Celeriac		4	4
		Grass		4	3
		Oat		4	4
		Onion		4	4
		Parsnip		4	4
		Potato		4	4
	2021	Beans	4	4	4
		Broccoli		4	4
		Celeriac		4	4
		Grass		3	4
		Oat		4	4
		Onion		4	4
		Parsnip		4	4
		Potato		4	4
	2022	Beans	5	4	4
		Broccoli		4	3
		Celeriac		3	2
		Grass		4	4
		Oat		4	2
		Onion		3	4
		Parsnip		4	4
		Potato	4	4	4
Lelystad	2019	Cabbage	5	4	3
	2020	Cabbage	7	4	3

Location	Year	Crops	Rounds	Pitfall traps per round	
				Mono	Strip
		Potato	2	4	2
	2021	Cabbage	6	4	3
Valthermond	2020	Barley	7	6	6
		Barley / Beans		6	6
		Potato		6	6
	2021	Barley / Beans	8	6	6
		Grass / Clover		6	6
		Potato		6	6
Wageningen	2019	Cabbage	4	6	2
		Wheat	2	6	2
		Potato	3	6	6
	2020	Cabbage	8	6	2
		Wheat	3	5	2
		Potato	1	6	5
		Pumpkin	2	6	4
		Barley		6	2
	2021	Cabbage	7	6	3
		Oat		6	3
		Potato	2	6	3
		Grass		6	3
		Pumpkin		6	3
		Barley		6	3
	2022	Cabbage	2	6	3
		Oat		5	3
		Potato		6	3
		Grass		6	3
		Pumpkin		6	3
		Barley		6	3

Table S8. Plant species composition of flower strips adjacent to the strip cropping fields in Lelystad and Valthermond (see location in Fig. S7).

	Species
1	*Achillea millefolium* (common yarrow)
2	*Anethum graveolens* (dill)
3	*Cichorium intybus* (common chichory)
4	*Foeniculum vulgare* (fennel)
5	*Pastinaca sativa* (parsnip)
6	*Angelica sylvestris* (wild angelica)
7	*Anthriscus sylvestris* (cow parsley)
8	*Fagopyrum esculentum* (buckwheat)
9	*Papaver Rhoeas* (common poppy red wild form)
10	*Chrysanthemum segetum* (corn marigold)
11	*Ammi majus* (greater ammi)
12	*Centaurea cyanus* (cornflower, single flowered wild form)