Differential effects of soil-based agricultural diversification on arthropods and crop yield

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Abstract

1. Agricultural diversification often promotes biodiversity and ecosystem services by increasing habitat diversity. However, responses to agricultural diversification are context dependent, differentially impacting functional groups of service-providing organisms and crop yields.
2. Conservation and no tillage are promoted as agricultural diversification practices that increase soil heterogeneity and habitat diversity. Here we investigated whether soil tillage practices in canola crop fields altered arthropod biodiversity or yield, and how effects of field-scale diversification compared to landscape-scale habitat context. We focused on effects of high, medium, or no tillage on five functional groups with unique diets and reproductive strategies: (i) herbivores, (ii) kleptoparasites, (iii) parasitoids, (iv) pollinators, and (v) predators.
3. Effects of agricultural diversification on arthropod abundance and diversity varied across functional groups. Pollinators responded to on-farm soil diversification, benefiting from medium tillage. Predators and herbivores responded most strongly to landscape-scale habitat composition and were more abundant in landscapes with more semi-natural habitat. However, variation in arthropod communities had little effect on canola crop yield, which was lowest in fields with no tillage.
4. *Policy implications:* Our results indicate that natural history differences among arthropod functional groups mediate how habitat availability affects biodiversity. Crop yields, however, showed no response to biodiversity of ecosystem service providers. Our research highlights the need to determine the contexts in which soil diversification practices meet a multi-faceted goal of simultaneously supporting natural biodiversity, ecosystem services, and crop yield.

Keywords: agricultural diversification, biodiversity, functional groups, crop yield, canola

Introduction

Enhancing crop yield while supporting biodiversity and ecosystem services is a challenge in agroecosystems. Management practices like intercropping and reduced tillage aim to support biodiversity and ecological services by increasing habitat diversity, although responses to such diversification practices vary among unique service-providing functional groups (Lefcheck et al., 2015; Mitchell et al., 2015). Indeed, there has been a call to determine simultaneous impacts of habitat change on multiple ecosystem services such as soil quality, pollination, and pest control (Bommarco et al., 2013; Tamburini et al., 2020). These impacts cannot be extrapolated from studies of single services due to interactions among organisms. It is thus key to determine how organisms in unique functional groups, that provide separate ecosystem services, differentially respond to agricultural diversification.

Reducing tillage is a practice that can diversify crop fields and support biodiversity by improving soil heterogeneity (Bommarco et al., 2013; Tamburini et al., 2020). However, effects of soil diversification on ecosystem service providers likely depend on how animal functional groups interact with soil. For example, tillage harms ground-nesting bees (Ullmann et al., 2016), but may benefit predators that shelter among weeds (Cranshaw, 2004). Impacts of soil diversification for unique functional groups may also depend on landscape context. Semi-natural habitat near farms can facilitate dispersal via habitat corridors or provide patches of suitable habitat amidst inhospitable matrixes (Kremen et al., 2007; Tscharntke et al., 2012). However, prior studies of field-level diversification show that organisms can benefit in relatively simple (Scheper et al., 2013; Tscharntke et al., 2012) and complex (Kennedy et al., 2013; Lichtenberg et al., 2017) landscapes. These complexities show that there is an urgent need to study effects of agricultural diversification on multiple functional groups at various scales.

Sustainable farming must also generate high crop yields. Because yield captures the total contribution of biotic communities and farming practices, it can be difficult to ascribe effects to single factors (Tamburini et al., 2019). Many studies use yield proxies corresponding to one ecosystem service, like pollen deposition, but such proxies do not always translate to crop yield (Bartomeus et al., 2015; Baylis et al., 2021; Birkhofer et al., 2018). Studies that use a single analytical framework to measure habitat diversification impacts on biodiversity and on multiple ecosystem functions can address this knowledge gap (Birkhofer et al., 2015; Byrnes et al., 2014). Such studies enable assessing how multiple elements of the biotic system, and farming practices, directly and indirectly alter crop production (Byrnes et al., 2014).

Here, we assessed how soil diversification through reduced tillage, and landscape context, affected arthropods in unique functional groups, and how habitat and arthropod communities affected canola yield. Canola provides floral resources for pollinators and natural enemies, but attracts pests like aphids and flea beetles (Delaplane & Mayer, 2000; Morandin & Winston, 2005; Reddy, 2017). Yield may be altered by interactions among such beneficial and harmful arthropods (Lundin et al., 2020; Morandin & Winston, 2005; Ouvrard & Jacquemart, 2019; Reddy, 2017). We sampled insects and spiders in canola fields to answer three questions about effects of local and landscape habitat context on insect communities and yield. First, do effects of tillage on abundance and diversity of arthropods vary based on functional group? Second, which habitat scales do various functional groups respond most strongly to? Third, how do arthropods and habitat context directly and indirectly affect crop yield? We answered these questions by linking field data with structural equation models, enabling us to assess how abiotic and biotic factors interactively affected canola yield.

Materials and methods

Study sites

We sampled arthropod abundance and diversity in canola (*Brassica napus* and *B. rapa*) fields in eastern Washington and northern Idaho during the summers of 2013 and 2014 (Fig. S1). This heavily agricultural region has only scattered patches of semi-natural habitat. The primary crops grown are grains and legumes, but canola production has increased from 5K to over 75K acres in the last decade because it promotes soil quality and grower profits (Painter et al., 2006; USDA NASS, 2020). As a mass-flowering crop that blooms for up to a month, canola attracts diverse flower-feeding arthropods such as pollinators and natural enemies like predators and parasitoids (Delaplane & Mayer, 2000; Morandin & Winston, 2005). Canola fields are thus an effective model system for studying multiple ecosystem service providers.

We selected 15 canola fields each year with sizes from 0.7 to 142 ha (mean ± SD = 44.4 ± 41.0). Most fields were maintained by local farmers, but four were on research farms maintained by local universities or seed companies. Because farmers rotate canola with other crops, no field was sampled both years. Fields were sufficiently far apart (nearest neighbor distance of 5.4 ± 2.9 (min 1.9) km in 2013 and 6.8 ± 6.0 (min 2.8) km in 2014), relative to insect flight distances and the scale at which we measured the landscape (1 km), to be considered spatially independent.

Arthropod sampling

To target diverse arthropods that associate with canola flowers, we used two collection techniques: (i) traps typically used to sample bees and (ii) sweep netting. All sampling occurred along one field edge on days where daytime temperatures were above 13 ˚C and the wind speed below 4.5 m s-1. At 10:00, we conducted 100 sweeps at the level of the canola canopy,

immediately emptied net contents into a plastic bag, and stored them on ice. In the lab, we freeze-killed arthropods, then removed them and sorted to morphospecies (see below for sorting details). Bees were pinned, while specimens in other taxa were stored in ethanol.

Around noon at each site, we set out a line of bee traps that stayed in place for 24 h. This line included two blue vane traps (SpringStar) and six pan traps painted in colors that attract bees (Kearns & Inouye, 1993; Leong & Thorp, 1999). We used two each of white, fluorescent yellow, and fluorescent blue pan traps, randomizing color order within the line. Each trap contained unscented soapy water. We separated traps by 5 m, and located them ~0.5 m from the edge of the field. Traps and sweep netting began at the same spot. The following day, we collected trapped arthropods using a strainer, washed off excess soap, and stored the specimens in ethanol. In the lab, we washed and dried bees, and all specimens were sorted to genus and morphospecies based on morphological characteristics (Arnett et al., 2002; Arnett, 2000; Arnett & Thomas, 2000; Boyle & Philogène, 1983; Derraik et al., 2002, 2010; Michener, 2000; Stehr, 1987a,b). Both adults and immature forms were considered.

To aid interpretation, specimens were assigned to functional groups based on literature and information from local species (Arnett, 2000; Michener, 2000; Stehr, 1987a,b). We found five common functional groups: (i) pollinators, (ii) herbivores, (iii) predators, (iv) parasitoids, and (v) kleptoparasites (Table S1). This classification considers both diet and reproductive strategy. We also considered predators and parasitoids pooled together as “natural enemies”.

Field and landscape variables

We assessed several agronomic and weather-related variables for each field: (i) field size, (ii) tillage, (iii) growing degree days, and (iv) cumulative precipitation. We determined field size

in ArcGIS by creating a polygon that traced each field's boundary, and subtracting the areas of all uncultivated patches. We determined these uncultivated patches by walking through fields and drawing patches on a map, ensuring that we covered sufficient area to see the entire field. We later converted these maps to ArcGIS polygons. To categorize each site's tillage regimen, we asked farmers about their practices. We categorized each field as having (i) full (4 to 7 passes that produce bare soil with no remaining stubble before seeding), (ii) intermediate (field tilled once and then planted into remaining stubble), or (iii) no (seed planted directly into the previous year's stubble) tillage. These represent the three main tillage regimes used in the study region.

To measure weather variables, we gathered daily temperature and precipitation estimates from PRISM (PRISM Climate Group, 2020). We calculated growing degree days and cumulative precipitation through (i) the day before we sampled arthropods at a field and (ii) shortly before harvest. Growing degree days indicate accumulated heat units that are likely to affect growth of a given taxonomic group. Temperatures below 5 ˚C can hinder canola growth (Dickson, 2014). We thus calculated growing degree days as the cumulative amount of heat above 5 ˚C since January 1. Because we did not know the exact harvest date for each field, and there were no catastrophic events in either year, we used August 15 as a cutoff for all harvest cumulative weather data.

We calculated landscape composition as the amount of semi-natural habitat within a 1 km radius of each field. This radius is ecologically relevant for pollinators, herbivores, and natural enemies (Greenleaf et al., 2007; Rusch et al., 2016). We determined land cover using CropScape data (USDA SARS, 2014a,b, 2015a,b) and ArcGIS to calculate the areas of each land cover type around each site. Semi-natural habitat included deciduous forest, evergreen forest, grassland, shrubland, and wetlands, while crop habitats were classified as agricultural.

Data analysis

To assess how each functional group responded to local- and landscape-scale habitat, we used a regression and model selection framework. We first calculated abundance, richness, and evenness (E_{var}, Smith & Wilson, 1996) for each functional group at each site as our response variables. We ran separate linear regressions for each functional group that included tillage, the proportion of semi-natural habitat within 1 km, their interaction, year, degree days through the day before sampling, cumulative precipitation through the day before sampling, and field size as fixed effects. These variables were not collinear. Because abundance data were overdispersed, we used negative binomial regressions (MASS package, Venables & Ripley, 2002). We analyzed richness and evenness data with linear models (identity link), although herbivore evenness had to be log-transformed due to heteroscedasticity. We then used information-theoretic model selection to determine the best fit models for each metric and functional group (MuMIn package, Barton, 2014), selecting models with AICc values within 2 of the smallest value (Burnham & Anderson, 1998). Low richness values, and thus lack of variation, prevented us from analyzing kleptoparasite and parasitoid evenness, but all other metrics were assessed.

We next assessed via structural equation modeling how arthropod biodiversity, as well as local- and landscape-level habitat factors, affected canola yields. We assembled three structural equation models that included abundance or diversity of the three most common functional groups (predators, herbivores, pollinators), habitat variables, abiotic factors, and canola yield (piecewiseSEM package, Lefcheck et al., 2019; Lefcheck, 2016). Due to power limitations, we separately analyzed effects of abundance, richness, and evenness. Each model included four structural equations, with the following response variables: (i) predator abundance or diversity, (ii) herbivore abundance or diversity, (iii) pollinator abundance or diversity, and (iv) yield.

Arthropod abundance equations were negative binomial regressions due to overdispersion of abundance data, yield and arthropod diversity equations used linear regression, and we log-transformed herbivore evenness. As with regressions, we assessed habitat through tillage level and the proportion of semi-natural habitat in the landscape around each field. Abiotic factors included year, degree days, and cumulative precipitation. Structural equation models with arthropod abundance or diversity as responses included degree days and cumulative precipitation through the day before sampling. The yield structural equation model included degree days and cumulative precipitation through harvest. To ensure best fit of our models, we iteratively added missing links ($P < 0.05$ with tests of directed separation) and pruned links with low influence (Fisher's C statistic $P > 0.3$, except we retained all tillage levels to enable pairwise comparisons) until the model contained all important and high-influence links (the "unconstrained" model). To assess all pairwise comparisons among the three tillage levels, we first constructed structural equation models with full tillage excluded. By testing significance of coefficients in these models (Fisher's C), we compared intermediate and no tillage with full tillage. We then tested whether intermediate and no tillage had differential impacts via multigroup analysis. We constructed a constrained model with the same variables as the reduced model, except that we replaced the separate intermediate and no tillage variables with one "intermediate or reduced tillage" variable. We then compared this constrained model to the unconstrained model via a likelihood ratio test.

Results

Overall, we collected 22,879 individuals across 131 taxa. This included 15,256 herbivores (20 taxa), 154 kleptoparasites (8 taxa), 1,080 parasitoids (6 taxa), 4,217 pollinators (64 taxa), and 739 predators (31 taxa). The most abundant taxonomic groups were thrips (7,184 individuals;

herbivores), aphids (4,078; herbivores), sciaroid flies (2,041 individuals; herbivores), two halictid bee morphotaxa (813 and 581 individuals; pollinators), chalcidoid wasps (727 individuals; parasitoids), and chrysomelid beetles (576 individuals; herbivores). The most common predators were melyrid beetles (229 individuals).

Functional groups with known trophic relationships had correlated metrics (Table S2). We found positive correlations in abundance and diversity of (i) pollinators and kleptoparasites, and (ii) parasitoids, predators, and herbivores (and between natural enemies and herbivores).

Effects of tillage and landscape on arthropod communities

Effects of habitat context on arthropod abundance and diversity varied across functional groups. Broadly, pollinators and kleptoparasites were affected by tillage while herbivores and predators responded most strongly to landscape composition. This pattern did not reflect a correlation between field- and landscape-scale habitat measures, as semi-natural habitat did not differ based on tillage regimen (Kruskal-Wallis test: $X^2_2 = 2.47$, $P = 0.29$). This pattern was also not due to trade-offs in promoting pollinators versus predators or parasitoids, as abundance and evenness of these groups (and of pollinators and natural enemies as a group) were positively correlated (Table S2).

Pollinator richness was higher in fields with intermediate tillage than fields with no tillage (Fig. 1a; Tables S3, S4). Kleptoparasite abundance was higher in fields with either form of conservation tillage (intermediate or no tillage) than in heavily-tilled fields in one of four best models (and significant at $\alpha < 0.10$ in a second model; Fig. 1b; Tables S4, S5). Pollinator abundance and evenness, and kleptoparasite richness, were not affected by local or landscape

habitat context (Tables S3, S5, S6). There were too few kleptoparasite species (median 2 per site) to assess evenness.

Landscapes with more semi-natural habitat promoted greater herbivore abundance (Fig. 2a) regardless of tillage regime (Table S5). Herbivore diversity was unaffected by either tillage or landscape composition (Tables S3, S6). Predator (Fig. 2b) abundance also increased as canola fields were surrounded by more semi-natural habitat (Table S5). Fields in landscapes with more habitat also had predator communities with lower evenness (Table S6). Parasitoids were unaffected by habitat context at either local or landscape scale (Tables S3, S5, S6).

Effects of tillage, landscape and arthropod communities on crop yields

Structural equation models showed that field-scale habitat diversity (and weather) directly impacted canola yield. In all analyses, yield was lower in fields with no tillage than in fields with full or intermediate tillage, and lower in 2014 than in 2013 (Fig. 3, Tables S7, S8). Landscape composition did not impact canola yield, however. In the arthropod richness structural equation model, yields were also lower at drier sites, and in areas that had experienced warmer weather (more growing degree days) at the time we sampled arthropods (Table S7). These two weather variables were not correlated (Table S2).

We found minimal evidence for indirect effects of habitat context on crop yield, via arthropod communities (Fig. 3; Tables S7, S8). This indirect effect was due to higher landscape-scale habitat availability promoting more diverse herbivore communities, as fields with more herbivore species had lower yields. However, arthropod abundance and evenness, and pollinator and natural enemy richness, did not impact yield. Consistent with pairwise correlations, fields

with higher herbivore richness and abundance also had higher predator richness and abundance (Table S7).

Discussion

Soil-based habitat diversification can affect arthropod biodiversity, with impacts varying by functional group or landscape context, due to differences in resource needs or dispersal among taxa (Bommarco et al., 2013; Harmon-Threatt, 2020). Because many of these arthropods provide ecosystem services or are pests, biodiversity impacts are predicted to affect crop yield. We found that agricultural landscapes can simultaneously support pollinators and predators, but that different functional groups respond to habitat context at separate scales. Pollinators were affected by field-scale diversification via reduced tillage, while landscapes with more semi-natural habitat promoted herbivores and predators. Although habitat context affected arthropod biodiversity, arthropods did not strongly impact crop yield. Our results show that agricultural diversification can impact crop yield directly, but does not always indirectly improve yield by promoting higher arthropod biodiversity (Dainese et al., 2019; Ricketts et al., 2016).

We found that pollinator and kleptoparasite, but not herbivore, predator, or parasitoid, guilds responded to tillage intensity. We expected reduced tillage would promote pollinators and kleptoparasites that depend on them by destroying fewer ground-nesting bee nests and enabling soil stratification (Tamburini et al., 2020; Ullmann et al., 2016). However, we found intermediate tillage supported a more diverse pollinator community than no tillage. One potential explanation is that untilled soil contains too thick a layer of decaying crop stems for bees to dig through (Stinner & House, 1990). However, tillage impacts, and presence of kleptoparasites that are

typically found in the vicinity of bee nests, do suggest that bees are nesting in canola crop fields or nearby grain or legume fields, which is often assumed to not occur (Kleijn et al., 2011).

Effects of tillage on natural enemies and herbivores are more well studied than for bees, although results have been mixed for each group (Furlan et al., 2021; Rowen et al., 2020; Tooker et al., 2020). When reduced tillage promotes natural enemies, likely mechanisms are increased availability of weeds that provide nectar, or surface mulch that provides shelter and prey (Clark et al., 1993; Stinner & House, 1990). The first mechanism is likely not operating in our system because canola provides abundant nectar and weeds were controlled with glyphosate. The second mechanism may also not be relevant because crops rotated with canola do not contribute much mulch (Hammel, 1996). When reduced tillage promotes herbivores, it mainly does so due to less soil disturbance or by promoting larger or more diverse weed communities (Rowen et al., 2020). Neither mechanism applies to our study, since we mainly sampled herbivores that reside near the tops of plants rather than in soil, and weeds were controlled. Thus, it is not surprising that tillage intensity did not affect natural enemies or herbivores. This highlights the importance of studying mechanisms underlying habitat-biodiversity relationships, including how species' natural histories relate to both food and shelter resources within a habitat (Carvalheiro et al., 2021).

We found that landscapes with more semi-natural habitat promoted predators and herbivores. Heterogeneous landscapes offer opportunities for mobile consumers to exploit patchy resources (Tscharntke et al., 2012). Predators and our main herbivores (aphids and thrips) routinely travel long distances in search of suitable habitat patches. In contrast, most of our pollinators (bees) are central place foragers that repeatedly return to a single nest and visit food patches only within their flight range of this nest. Indeed, bees visiting canola flowers in Alberta tended to travel only a few meters from their nest when surrounded by canola flowers (Robinson,

2019). Thus, most of the bees we collected likely were nesting in or near the fields we sampled, and were affected more by tillage than landscape composition. This result mirrors meta-analyses that suggest that highly mobile organisms are more likely to respond to landscape-scale habitat patterns than less mobile organisms (Lichtenberg et al., 2017; Schneider et al., 2014).

While we show local and landscape habitat patterns affected arthropod communities, these communities minimally impacted crop yields, similar to studies that have found no relationship between multi-diversity and multifunctionality (Birkhofer et al., 2018). We did find that yield was lower in fields with higher herbivore richness. Inspection of herbivore abundances at each site (Table S9) suggests two potential drivers. First, sites with higher herbivore richness could have higher pest abundance (Table S2). Second, sites with higher herbivore richness could be more likely to contain a specific damaging pest. Our data shows high-herbivore-richness fields contained large numbers of aphids, a key canola pest (Reddy, 2017). We also found more chrysomelids, curculionids, meloids, scraptiids, pentatomids, and yponomeutids in sites with higher herbivore richness. However, the only canola pests in these groups are seedpod weevils (Curculionidae), which damage a later crop stage than we sampled (Reddy, 2017).

Abundance and diversity of “beneficial” pollinators and predators also did not affect canola yield. Canola has high variability in pollinator dependence (Ouvrard & Jacquemart, 2019), and the ≥ 15 varieties in our study may not be pollinator dependent, or the study region is windy enough to ensure high pollen dispersal. Benefits from predators may have also been limited by insecticide use, as farmers grow insecticide-coated seeds that provide plants with systemic insecticide coverage. If these insecticides effectively controlled herbivore pests, benefits from having more predators present might not be noticeable (Janssen & van Rijn, 2021). However, it is also possible that pollinators or predators correlate with common measures of single

ecosystem services, such as pollen deposition or consumption of sentinel pests on a small subset of plants. If such patterns were present, they did not scale up to the entire field (as found by Birkhofer et al., 2018; Sutter et al., 2018; Tamburini et al., 2020), and thus are unlikely to affect farmer decisions.

Tillage intensity and weather did affect crop yields. Reduced tillage has previously been found to reduce yield for crops including oilseed rape (Lundin, 2019; Tamburini et al., 2020). Indeed, multiple farming practices aimed at diversifying habitat or reducing human impacts (e.g., organic farming) sometimes result in lower yield than their conventional counterparts (Ponisio et al., 2015; Tamburini et al., 2020). Despite the yield loss seen here, reduced tillage can provide other benefits such as improving soil infiltration, reducing erosion, decreasing evaporative water loss from soil, and improving soil quality (Hammel, 1996; Kennedy & Schillinger, 2006). These factors might ultimately increase yield of other crops or reduce farmers' costs. This highlights the complex decisions that underlie farm management decisions.

Overall, our study shows that field-scale diversification of soil habitat impacted pollinators, while landscape-scale habitat availability promoted predators and herbivores. These differences likely reflect natural history differences among these functional groups, and highlight the need to understand how biodiversity patterns are simultaneously affected by multiple mechanisms at various scales. However, these habitat impacts on biodiversity only minimally impacted yield. It is often assumed that enhancing biodiversity promotes ecosystem services, although evidence from arthropod-mediated ecosystem services such as pollination and pest control is mixed (e.g., Birkhofer et al., 2018; Dainese et al., 2019; Ricketts et al., 2016). Without clear evidence that a conservation action such as reduced tillage is likely to increase crop yield, adoption by farmers will likely remain low (Kleijn et al., 2019). Thus, data-driven management of agricultural

landscapes to simultaneously support natural biodiversity and boost crop yield requires much more research to determine the contexts in which given management practices, and soil diversification practices in particular, do or do not meet this multi-faceted goal.

Author contributions

EML and DWC conceived the ideas and designed methodology; EML collected and analyzed the data; IM identified arthropods; EML and AJC led the writing of the manuscript; All authors contributed critically to the drafts and gave final approval for publication.

Statement on inclusion

Our study design and results interpretation incorporated local knowledge from stakeholders, and results were communicated with stakeholders through outreach.

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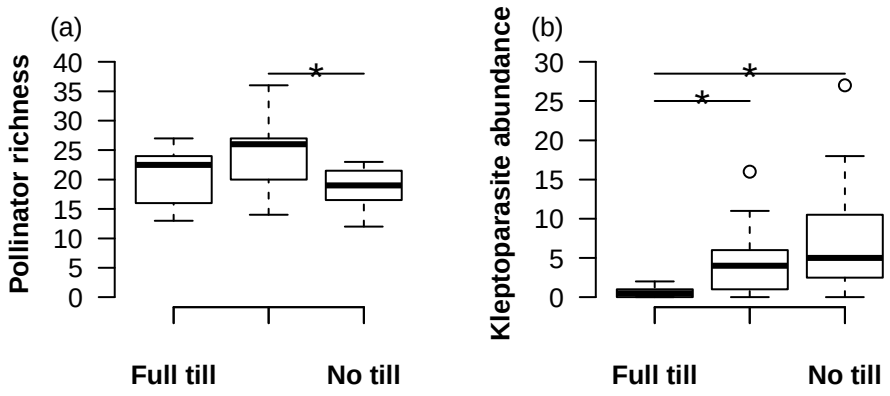

Fig. 1: Box and whisker plots of (a) pollinator richness and (b) kleptoparasite abundance as a function of tillage intensity. Lines with asterisks indicate groups that are statistically different from each other.

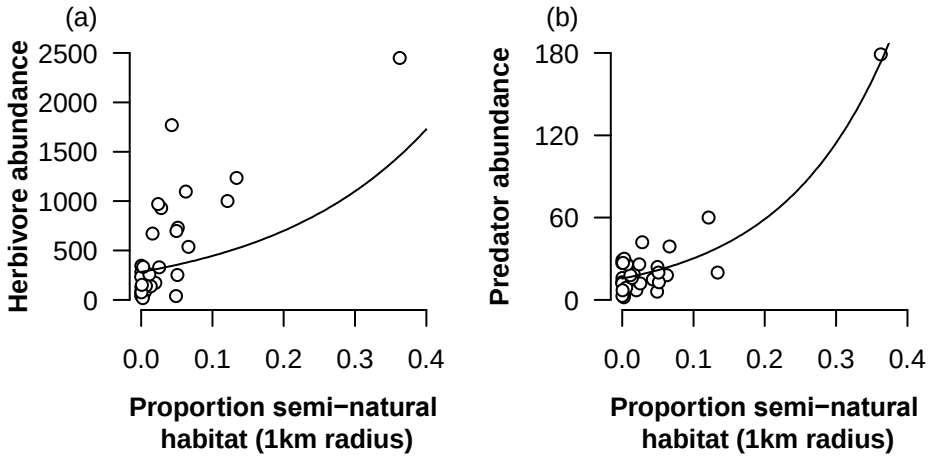

Fig. 2: (a) Herbivore and (b) predator abundance increase with landscape-scale habitat availability (proportion of semi-natural habitat in a 1 km radius around a site). Curves show best-fit lines from negative binomial regressions.

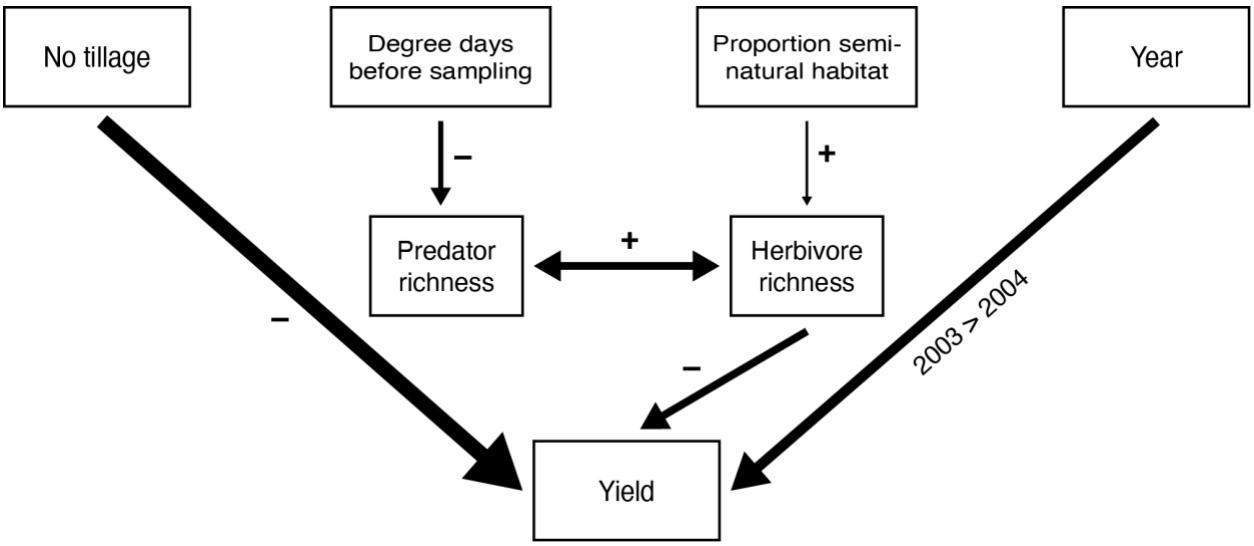

Fig. 3: Summary of the three structural equation models determining direct and indirect impacts of habitat diversity, abiotic factors, and the arthropod community on canola yield. Wider lines represent links with larger magnitude effects (standardized coefficients). Complete SEM results are in Tables S7 and S8.