

1 Differential effects of soil conservation practices on arthropods and crop yield

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3 Running title: Tillage impacts on arthropods and crop yield

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19 **Abstract**

- 20 1. Many agricultural management tactics, such as reduced tillage, aim to promote biodiversity  
21 and ecosystem services. Responses to such tactics can be context dependent, however, and  
22 differentially impact (i) functional groups of service-providing organisms and (ii) crop yields.
- 23 2. In canola (*Brassica napus* Linnaeus, *B. rapa* L) crop fields we assessed how soil tillage and  
24 landscape context affected arthropod biodiversity and crop yield. We assessed effects of full  
25 (multiple tillage passes that leave soil surface bare), intermediate (tilled once and some  
26 stubble remains), or no (seed planted directly into last year's stubble) tillage on functional  
27 groups with unique diets and reproductive strategies: (i) herbivores, (ii) kleptoparasites, (iii)  
28 parasitoids, (iv) pollinators, and (v) predators.
- 29 3. Effects of tillage and landscape context on arthropod abundance and diversity varied across  
30 functional groups. Pollinators responded strongest to tillage, benefitting from intermediate  
31 tillage. Predators and herbivores responded strongly to landscape context, as both were more  
32 abundant in landscapes with more semi-natural habitat. Our results suggest natural history  
33 differences among functional groups mediate effects of landscape context on biodiversity.  
34 However, variation in arthropod communities had little effect on canola crop yield.
- 35 4. *Policy implications:* The effects of soil management practices on aboveground arthropods are  
36 complex, and practices thought to increase some aspects of agricultural sustainability may  
37 not be beneficial in other contexts. Identifying practices such as intermediate tillage that may  
38 increase soil quality and arthropod diversity is key to designing agricultural ecosystems that  
39 will effectively benefit both biodiversity and human wellbeing.

40 **Keywords:** sustainable agriculture, biodiversity, crop yield, tillage, pollinators, natural enemies,  
41 soil habitat

## 42 **Introduction**

43       Agricultural management tactics such as intercropping and reduced tillage are implemented  
44 in an effort to support biodiversity and ecological services in agroecosystems without sacrificing  
45 yield. Reduced tillage, for example, supports biodiversity by creating soil habitat availability and  
46 heterogeneity (de Graaff et al. 2019; Tamburini et al. 2020). However, responses of organisms to  
47 practices such as tillage often vary among service-providing functional groups (Lefcheck et al.  
48 2015; Mitchell et al. 2015). This has led to calls to better assess impacts of habitat change on  
49 multiple ecosystem services such as soil quality, pollination, and crop yield (Bommarco et al.  
50 2013; Tamburini et al. 2020). Given the complexity of agricultural food webs, studies should  
51 also assess how organisms in unique functional groups respond to management.

52       Effects of in-field soil management practices on ecosystem service providers likely depend  
53 on how animal functional groups interact with soil. For example, tillage can harm ground-nesting  
54 bees (Ullmann et al. 2016) and predators that shelter among weeds (Cranshaw 2004), but often  
55 has little to no impact on herbivorous pests that feed on crops (Tooker et al. 2020). While  
56 reduced tillage is implemented to limit soil erosion and conserve soil moisture, it can also affect  
57 soil chemical and physical profiles, and availability of flowering plants that feed beneficial  
58 insects (Kennedy and Schillinger 2006). However, impacts of soil management practices on  
59 distinct functional groups may also depend on the landscape context. Semi-natural habitat near  
60 farms can facilitate dispersal of organisms to crops (Kremen et al. 2007; Tscharrntke et al. 2012)  
61 and responses of organisms to particular practices may depend on the landscape context. Indeed,  
62 some studies show benefits of sustainable agricultural practices accrue most strongly in relatively  
63 simply landscapes, while others show the greatest benefits in complex landscapes (Tscharrntke et  
64 al. 2012; Kennedy et al. 2013; Scheper et al. 2013; Lichtenberg et al. 2017).

65           While supporting biodiversity is often a goal of agricultural production systems, crops must  
66 also generate high yield. Because yield captures the total contribution of biotic communities and  
67 farming practices, it can be difficult to ascribe yield to single factors (Tamburini et al. 2019).  
68 Studies are thus needed that use a single analytical framework to assess how habitat availability  
69 and diversification affect biodiversity and yield, both directly and through indirect interactions  
70 among organisms and management practices (Byrnes et al. 2014; Birkhofer et al. 2015; Weekers  
71 et al. 2022). Such studies may be particularly useful when conducted at field-level scales that  
72 involve commercial production and representative growing practices for a given region.

73           Here we assessed how soil tillage affected arthropod functional groups in canola (*Brassica*  
74 *napus* Linnaeus, *B. rapa* L) crops of the Pacific Northwest USA, and how landscape context and  
75 tillage interacted with arthropods to affect yield. Canola provides floral food for pollinators and  
76 natural enemies, but attract pests like aphids (Aphididae) and flea beetles (Chrysomelidae). We  
77 first asked if effects of tillage on arthropod abundance and diversity varied by functional group.  
78 We hypothesised functional groups with soil dependence, like pollinators and kleptoparasites,  
79 would be most strongly impacted by tillage (Rowen et al. 2020). Second, we asked if responses  
80 of functional groups to tillage depended on landscape context, given variation in mobility and  
81 habitat needs of unique organisms (Lichtenberg et al. 2017; Marja et al. 2022). Third, we asked  
82 whether variation in arthropod communities interacted with tillage and landscape context to  
83 affect yield (Delaplane and Mayer 2000; Morandin and Winston 2005; Reddy 2017). Reduced  
84 tillage often decreases crop yield (e.g., Lundin 2019; Tamburini et al. 2020), but enhanced pest  
85 control or pollination could counteract this. This allowed us to assess how agricultural practices  
86 directly and indirectly affected multiple ecosystem services and biodiversity across landscapes.

87

## 88 **Materials and Methods**

### 89 *Study sites*

90 We sampled arthropods in spring canola fields in eastern Washington and northern Idaho  
91 during 2013 and 2014 (Fig. S1; Table S1). This heavily agricultural region has patches of semi-  
92 natural habitat amidst considerable acreage of grains, legumes, and canola (Painter et al. 2006;  
93 USDA NASS 2020). As a mass-flowering crop that blooms for up to a month, canola attracts  
94 flower-feeding arthropods such as pollinators and natural enemies like predators and parasitoids  
95 (Delaplane and Mayer 2000; Morandin and Winston 2005). Canola fields are thus an effective  
96 model system for studying multiple ecosystem service providers across unique functional groups.

97 We selected 15 fields each year ranging from 0.7 to 142 ha (mean  $\pm$  SD = 44.4  $\pm$  41.0). The  
98 short canola bloom period and relatively small number of spring canola fields in the region  
99 limited further sampling. Most fields were maintained by local farmers with four maintained by  
100 local universities or seed companies. All seed was treated with a neonicotinoid, and some sites  
101 applied a pyrethroid insecticide once after bloom to control flea beetles and cabbage seed pod  
102 weevils (*Ceutorhynchus obstrictus* [Marsham]). Most farmers also applied an herbicide  
103 treatment (glyphosate) before bloom. Fields were spaced at least 2 km apart, which was  
104 sufficiently far relative to insect flight distances to consider them spatially independent.

105

### 106 *Arthropod sampling*

107 We used two collection techniques to sample diverse arthropods that associate with canola:  
108 (i) traps typically used to sample bees and (ii) sweep nets. All sampling occurred along one field  
109 edge on days with daytime temperatures above 13 °C and wind speed below 4.5 m/s. Sampling  
110 locations were haphazardly selected along accessible field edges, where we could work without

111 damaging crops and where traps on the ground would not be covered in vegetation. At 10:00, we  
112 conducted 100 continuous sweeps in the canola canopy, emptied net contents into a plastic bag,  
113 and stored them on ice. In the lab, we freeze-killed arthropods, then sorted them to  
114 morphospecies. Bees were pinned and specimens in other taxa were stored in ethanol.

115         Around 12:00, we set out a line of bee traps that stayed in place for 24 h. This line included  
116 two blue vane traps (SpringStar) and six pan traps painted in colours that attract bees (white,  
117 fluorescent yellow, fluorescent blue; Kearns and Inouye 1993; Leong and Thorp 1999). We  
118 separated traps by 5 m and located them ~0.5 m from the field edge. Traps and sweep netting  
119 began at the same spot. The following day, we collected trapped arthropods using a strainer,  
120 washed off excess soap, and stored the specimens in ethanol. In the lab, we washed and dried  
121 bees, and all specimens were sorted to genus and morphospecies based on morphological  
122 characteristics (Boyle and Philogène 1983; Stehr 1987a, 1987b; Arnett 2000; Arnett and Thomas  
123 2000; Michener 2000; Arnett et al. 2002; Derraik et al. 2002, 2010). Both adults and immature  
124 forms of all arthropod groups were considered.

125         Specimens were also assigned to five functional groups using literature and information  
126 from local species (Stehr 1987a, 1987b; Arnett 2000; Michener 2000): (i) pollinators, (ii)  
127 herbivores, (iii) predators, (iv) parasitoids, and (v) kleptoparasites (Table S2). This classification  
128 considered both diet and reproductive strategy. Herbivores included major regional canola pests  
129 (thrips [Thysanoptera], aphids, flea beetles, cabbage seedpod weevils, and *Lygus* bugs Hahn;  
130 Reddy 2017). Kleptoparasites are regulators of bee communities, and may reflect overall levels  
131 of pollinator biodiversity (Sheffield et al. 2013). We also considered predators and parasitoids  
132 pooled together as “natural enemies”.

133

134 *Field and landscape variables*

135       For each site we assessed agronomic and weather factors that can affect insects: (i) tillage,  
136 (ii) field size, (iii) growing degree days, and (iv) cumulative precipitation (e.g., Skellern et al.  
137 2017; Smith et al. 2020; Forcella et al. 2021; Fragoso et al. 2021; Aldercotte et al. 2022). We  
138 asked farmers directly to categorise each site's tillage regime. A field had either (i) full (4 to 7  
139 passes producing bare soil with no stubble before seeding; n = 6), (ii) intermediate (field tilled  
140 once with some stubble remaining before seeding; n = 13), or (iii) no (soil not tilled and seed  
141 planted directly into the previous year's stubble; n = 11) tillage. These represent the three main  
142 tillage regimes used in the region. Because canola is planted very shallow, spring tillage in the  
143 region is recommended to be limited to 2 to 5 cm (Brown et al. 2009). We determined field size  
144 in ArcGIS by creating a polygon tracing the boundary and subtracting the areas of all  
145 uncultivated patches (typically remnant prairie within and adjacent to fields; originally mapped  
146 by hand). We gathered daily temperature and precipitation values from PRISM (PRISM Climate  
147 Group 2020) and calculated growing degree days and cumulative precipitation through the day  
148 before we sampled arthropods. These environmental measures can cause inter-annual variation in  
149 arthropod populations (Skellern et al. 2017; Forcella et al. 2021). Growing degree days were  
150 calculated as the cumulative amount of heat above 5 °C since January 1 (Dickson 2014).

151       We also calculated the amount of semi-natural habitat within 1 km of each field, a radius  
152 that is ecologically relevant for pollinators, herbivores, and natural enemies (Greenleaf et al.  
153 2007; Rusch et al. 2016). We determined land cover using CropScape data (USDA SARS 2014a,  
154 2014b, 2015a, 2015b) to calculate area of each land cover type around each site. Semi-natural  
155 habitat included forests, grassland, shrubland, and wetlands, while crop habitats were classified

156 as agricultural. Landscapes around our sites ranged from 0% to 36% semi-natural habitat, and  
157 was independent of tillage regime (Kruskal-Wallis test:  $X^2_2 = 2.47$ ,  $P = 0.29$ ).

158

### 159 *Data analysis*

160 We used model selection to test how functional groups responded to tillage and landscape  
161 context. We calculated three community metrics – (i) abundance, (ii) richness, and (iii) evenness  
162 ( $E_{var}$ , Smith and Wilson 1996) – for each functional group at each site. Evenness captures how  
163 individuals are distributed across taxa and indicates the degree that rare taxa affect ecosystem  
164 functioning (Crowder et al. 2010; Winfree et al. 2015). We ran linear regressions for each  
165 functional group with tillage, proportion semi-natural habitat, their interaction, year, degree days,  
166 cumulative precipitation, and field size as fixed effects. These variables were not collinear (Table  
167 S4). As abundance data were overdispersed, we used negative binomial regressions (MASS  
168 package, Venables and Ripley 2002). We analysed richness and evenness with linear models  
169 (identity link), but herbivore evenness was log-transformed due to heteroscedasticity. All  
170 analyses met model assumptions. We used information-theoretic model selection to assess model  
171 fit for functional group metrics (MuMIn package, Barton 2014), and selected models with AICc  
172 values within 2 of the lowest value (Burnham and Anderson 1998). Low richness, and thus lack  
173 of variation, prevented us from analysing kleptoparasite and parasitoid evenness; all other  
174 metrics were assessed. There were 13 total models, one for each functional group and  
175 community metric, each with 30 observations (28 for predator evenness).

176 We next assessed how arthropod biodiversity, tillage, and landscape context affected  
177 canola crop yield; farmers provided yield data for their sites directly. We ran separate linear  
178 regressions with abundance, richness, or evenness that also included tillage, proportion semi-



179 natural habitat, their interaction, and year. For each set of models, we selected the best fit models  
180 as those with AICc values within 2 of the smallest value.

181

## 182 **Results**

183 We collected 22,879 individuals across 131 taxa, with 15,256 herbivores (20 taxa, 82% of  
184 individuals were pest species), 154 kleptoparasites (8 taxa), 1,080 parasitoids (6 taxa), 4,217  
185 pollinators (64 taxa), and 739 predators (31 taxa). The most abundant herbivores were thrips,  
186 aphids, sciaroid flies, and chrysomelids (7,184, 4,078, 2,041, and 576 individuals, respectively).  
187 The most common pollinators were two halictid bee morphospecies (813 and 581 individuals).  
188 The most common natural enemies were chalcidoid wasps (727 individuals, parasitoid) and  
189 melyrid beetles (229 individuals, predator).

190

### 191 *Effects of tillage and landscape on arthropod communities*

192 Overall, pollinators and kleptoparasites were affected by tillage while herbivores and  
193 predators responded most strongly to landscape composition. Pollinator richness was higher in  
194 fields with intermediate tillage than fields with no tillage (Fig. 1a; Tables S5, S6). Kleptoparasite  
195 abundance was higher in fields with intermediate or no tillage than in heavily-tilled fields in one  
196 of four best models (and significant at  $\alpha < 0.10$  in a second model; Fig. 1b; Tables S6, S7).  
197 Pollinator abundance and evenness, and kleptoparasite richness, were not affected by tillage or  
198 landscape context (Tables S5, S7, S8). In contrast, more semi-natural habitat promoted herbivore  
199 and predator abundance regardless of tillage regime (Fig. 2; Table S7). Herbivore diversity and  
200 predator richness were unaffected by tillage or landscape context (Tables S5, S8). These results  
201 did not qualitatively change if the site in the landscape with the most semi-natural habitat was

202 removed (Table S7). Parasitoids were unaffected by tillage or landscape context (Tables S5, S7,  
203 S8). Tillage and landscape composition never had an interactive effect.

204 Environmental variables had mixed effects on arthropod abundance and diversity (Tables  
205 S5, S7, S8). Precipitation generally had stronger impacts on arthropod communities than degree  
206 days. Greater detritivore abundance, kleptoparasite abundance and richness, pollinator  
207 abundance, and predator richness occurred at sites with lower precipitation. Parasitoid abundance  
208 and pollinator evenness had the opposite pattern. Detritivore abundance, kleptoparasite richness,  
209 parasitoid abundance, and predator richness were highest at cooler sites. Larger fields were  
210 associated with greater kleptoparasite abundance and richness but lower pollinator evenness.

211 Differential responses of arthropod functional groups may indicate trade-offs when aiming  
212 to manage biodiversity, but we found stronger evidence for synergies than trade-offs. Functional  
213 groups with known trophic relationships often had correlated metrics (Table S3). For example,  
214 we found positive correlations in abundance and diversity between pollinators and  
215 kleptoparasites, and among parasitoids, predators, and herbivores. Abundance and evenness of  
216 pollinators was also positively correlated with abundance and evenness of natural enemies, as  
217 well as individual natural enemy groups (predators or parasitoids) (Table S3).

218

### 219 *Effects of tillage, landscape and arthropod communities on crop yields*

220 Tillage strongly affected canola yield, and yield was lower in fields with no tillage than  
221 with full or intermediate tillage (Fig. 3a, Tables S6, S9). Landscape composition did not impact  
222 canola yield, however. We found little evidence for effects of landscape context or arthropod  
223 communities on yield (Tables S6, S9; S10). Higher landscape-scale habitat availability promoted

224 more diverse herbivore communities, which lowered yield (Fig. 3b; Tables S6, S9). However,  
225 arthropod abundance and evenness, and richness of other functional groups, did not impact yield.

226

## 227 **Discussion**

228 Soil management may differentially affect functional groups due to differences in resource  
229 needs or dispersal among taxa (Bommarco et al. 2013; Harmon-Threatt 2020). Because many of  
230 these arthropods provide ecosystem services or are pests, biodiversity can affect crop yield. We  
231 found that agricultural landscapes can simultaneously support pollinators and predators, but  
232 different functional groups respond to habitat variability at different scales. Pollinators were  
233 most affected by tillage within fields, while landscape context most strongly affected herbivores  
234 and predators. Yet, no arthropod group strongly impacted crop yield. Our results show that  
235 agriculture practices alter crop yield directly, but not always indirectly by affecting arthropods  
236 (as in Ricketts et al. 2016).

237 We found that pollinator and kleptoparasite, but not herbivore, predator, or parasitoid taxa  
238 responded to tillage. Reduced tillage may promote pollinators and kleptoparasites by destroying  
239 fewer ground-nesting bee nests (Kennedy and Schillinger 2006; Ullmann et al. 2016), but we  
240 found intermediate tillage supported a more diverse pollinator community than no tillage. One  
241 potential explanation is that untilled soil contains a thick layer of crop stems that prevent ground  
242 nesting (Stinner and House 1990). However, our observed impacts of tillage along with the  
243 presence of kleptoparasites suggests that many bee species nest in canola crop fields, which is  
244 often assumed to not occur (Kleijn et al. 2011).

245 Effects of tillage on natural enemies and herbivores are more well studied than for bees  
246 (Rowen et al. 2020; Tooker et al. 2020; Furlan et al. 2021). Reduced tillage can benefit natural

247 enemies by promoting weeds that provide nectar or surface mulch that provides shelter and prey  
248 (Stinner and House 1990; Clark et al. 1993). These mechanisms are likely not operating in our  
249 system as canola provides abundant nectar, farmers controlled weeds, and crops in the region do  
250 not contribute much mulch (Hammel 1996). When reduced tillage promotes herbivores, it mainly  
251 does so due to less soil disturbance or by promoting weeds (Rowen et al. 2020). Neither  
252 mechanism applies here, since we mainly sampled herbivores that reside near the tops of plants  
253 rather than in soil, and farmers manged weeds. Thus, it is not surprising that tillage did not affect  
254 natural enemies or herbivores. This highlights the necessity of studying mechanisms mediating  
255 how species' life histories relate to food and shelter resources (Carvalho et al. 2021).

256 Heterogeneous landscapes provide opportunities for consumers to exploit patchy resources  
257 (Tscharntke et al. 2012), and landscapes with more semi-natural habitat had more predators and  
258 herbivores. Predators and our main herbivores (aphids and thrips) routinely travel long distances  
259 in search of suitable habitat (Loxdale and Lushai 1999; Schellhorn et al. 2014). In contrast, most  
260 pollinators are central place foragers that repeatedly return to a single nest. Indeed, bees visiting  
261 canola flowers tend to travel only a few metres from their nest (Robinson 2019). Thus, most of  
262 the bees we collected likely were nesting in or near the canola fields we sampled, and were thus  
263 affected more by tillage than landscape composition. This result mirrors meta-analyses that  
264 suggest that highly mobile organisms are more likely to respond to landscape-scale habitat  
265 patterns than less mobile organisms (Schneider et al. 2014; Lichtenberg et al. 2017).

266 While we show local and landscape habitat patterns affected arthropod communities, these  
267 communities minimally impacted crop yields, similar to studies that have found no relationship  
268 between multi-diversity and multifunctionality (Birkhofer et al. 2018). We did find that yield  
269 was lower in fields with higher herbivore richness. Inspection of herbivore abundances at each

270 site (Table S11) suggests two potential drivers. First, sites with higher herbivore richness could  
271 have higher pest abundance (Table S3). Second, sites with higher herbivore richness could be  
272 more likely to contain a specific damaging pest. Our data shows high-herbivore-richness fields  
273 contained large numbers of aphids, a key canola pest (Reddy 2017). We also found more  
274 chrysomelids, curculionids, meloids, scaptiids, pentatomids, and yponomeutids in sites with  
275 higher herbivore richness. However, the only canola pests in these groups are seedpod weevils  
276 (Curculionidae), which damage a later crop stage than we sampled (Reddy, 2017).

277 Abundance and diversity of pollinators and predators also did not affect yield. Canola has  
278 high variability in pollinator dependence (Ouvrard and Jacquemart 2019), and the varieties in our  
279 study may not be pollinator dependent (Perrot et al. 2018), or the study region is windy enough  
280 to ensure pollen dispersal. Variation in pollinator dependence may explain differences between  
281 our results and studies that find increased yield of oilseed crops with higher pollinator abundance  
282 (Catarino et al. 2019). Benefits from pollinators and predators may have also been limited by  
283 insecticide use (neonicotinoid treated seeds) that may control pests and may reduce pollinator  
284 abundance. It is also possible that pollinators or predators correlate with common measures of  
285 single ecosystem services, such as pollen deposition or consumption of sentinel pests on a small  
286 subset of plants. If such patterns were present, they did not scale up to the entire field.

287 Tillage intensity did affect crop yields, similar to studies showing reduced tillage reducing  
288 yield for oilseed rape and other crops (Lundin 2019; Tamburini et al. 2020). Indeed, multiple  
289 sustainability-oriented farming practices sometimes result in lower yield than their conventional  
290 counterparts (Smith et al. 2020; Tamburini et al. 2020). Despite yield loss seen here, reduced  
291 tillage can provide other benefits such as improving soil infiltration, reducing erosion, decreasing  
292 evaporative water loss from soil, and improving soil quality (Hammel 1996; Kennedy and

293 Schillinger 2006). These factors might ultimately increase yield of other crops or reduce farmers'  
294 costs. This highlights the complex decisions that underlie farm management.

295 Overall, our study highlights the need to understand how biodiversity patterns and crop  
296 yields are simultaneously affected by multiple mechanisms, including via soil management, at  
297 various scales. We showed that tillage impacted pollinators, while landscape context strongly  
298 affected predators and herbivores. These differences likely reflect natural history differences  
299 among functional groups. However, these habitat impacts on biodiversity minimally impacted  
300 yield. It is often assumed that enhancing biodiversity promotes ecosystem services, although  
301 evidence from arthropod-mediated ecosystem services such as pollination and pest control is  
302 mixed (e.g., Ricketts et al. 2016; Birkhofer et al. 2018; Dainese et al. 2019). Without clear  
303 evidence that a conservation action such as reduced tillage is likely to increase crop yield,  
304 adoption by farmers will likely remain low (Kleijn et al. 2019). Thus, data-driven management  
305 of agricultural landscapes to simultaneously support natural biodiversity and boost crop yield  
306 requires much more research to determine the contexts in which given management practices,  
307 and soil diversification practices in particular, do or do not meet this multi-faceted goal.

308

### 309 **Conflict of Interest Statement**

310 We declare no conflict of interest.

311

### 312 **Author Contribution**

313 EML and DWC conceived research. EML conducted experiments. IM identified arthropods.

314 EML analysed data and conducted statistical analyses. EML, AJC and DWC wrote the

315 manuscript. DWC secured funding. All authors read and approved the final manuscript.

316

317 **Data Availability Statement**

318           Data will be published via SCAN and Zenodo.

319

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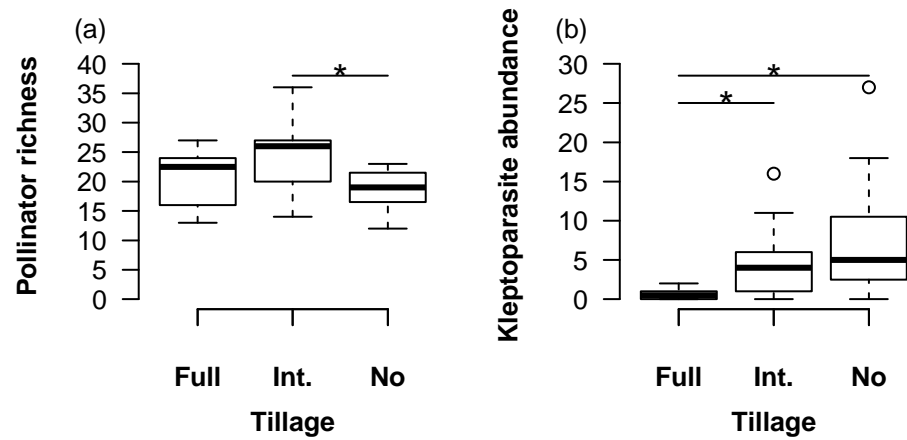


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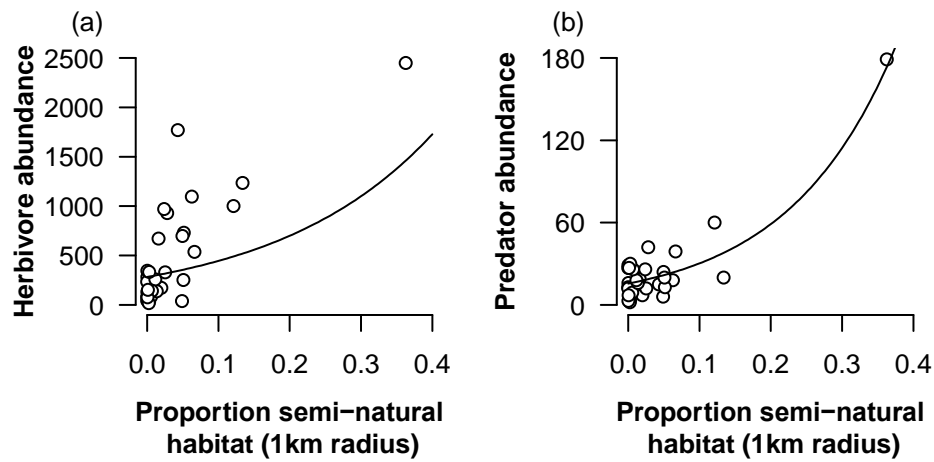
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535 **Fig. 1:** Box and whisker plots of (a) pollinator richness and (b) kleptoparasite abundance as a  
536 function of tillage intensity. “Int.” is intermediate tillage. Lines with asterisks indicate groups  
537 that are statistically different from each other.

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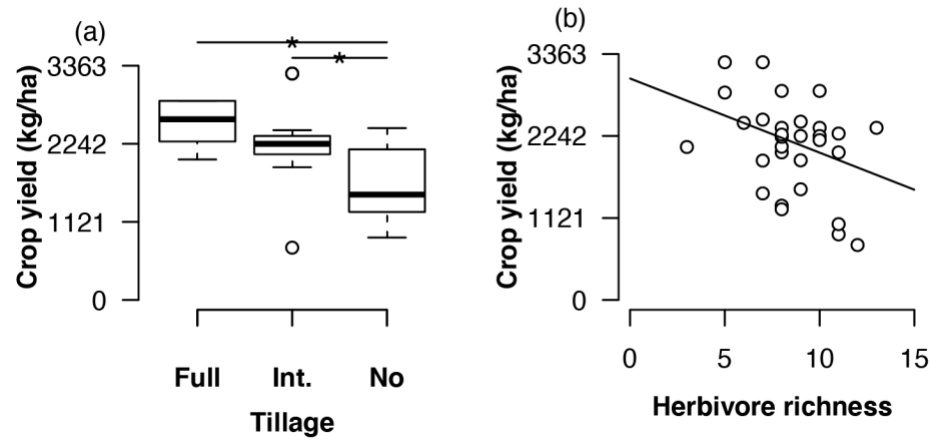
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541 **Fig. 2:** (a) Herbivore and (b) predator abundance increase with landscape-scale habitat  
542 availability (proportion of semi-natural habitat in a 1 km radius around a site). Curves show best-  
543 fit lines from negative binomial regressions.

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545

546 **Fig. 3:** Canola yield (a) was lowest with no tillage and (b) decreased as herbivore richness

547 increased. “Int.” is intermediate tillage. Lines with asterisks (a) indicate groups that are

548 statistically different from each other. The curve (b) shows the best-fit line from linear

549 regression.