

1 Non-crop sources of beneficial arthropods vary within-season across a 2 prairie agroecosystem

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7 Abstract

Ground-dwelling arthropods can be important generalist predators in agroecosystems, and can use non-crop features as overwintering habitats. However, it is unclear which types of landscape features constitute useful non-crop habitat, and at what spatial scale organisms gather resources. Additionally, the same landscape feature may act as a source or destination for arthropods at different times of the year, but this is rarely considered. We modeled the abundance of four highly-abundant species of Canadian prairie arthropods caught in pitfall traps, and used functional regression to simultaneously consider both their habitat preferences and the timing of sources and destinations. *Pterostichus melanarius* (Coleoptera: Carabidae) and *Pardosa moesta* (Arachnida: Lycosidae) appear to be attracted to canola (*Brassica napus* L.) during the early summer, then dispersed to grasslands, wetlands, and grassy road margins during the end of the summer. This suggests that grasslands and wetlands act as seasonal reservoir habitats for predatory arthropods, and that farmers should consider preserving existing habitat in order to maintain pest-control services across the season.

8 Key words: beetles; spiders; harvestmen; movement; natural enemies; functional regression

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1. Introduction

Arthropods are one of the most influential groups of animals in agricultural systems. Pest arthropods can cause large reductions in crop yield (Oerke 2005), which can result in negative downstream economic effects and food insecurity. However, beneficial arthropods living in non-crop patches can increase crop yields by providing ecosystem services, such as extra pollination or pest suppression (Losey & Vaughan 2006; Klein *et al.* 2007; Garibaldi *et al.* 2013). Seasonal “pulses” of food resources act as bottom-up drivers of arthropod communities in crop fields, meaning that agricultural land can increase arthropod abundance in adjacent non-crop land (Diekötter *et al.* 2010; Galpern *et al.* 2017). These movements of mobile arthropods in and out of crops are important for managing both crop yield and biodiversity in agroecosystems. In this context, finding “win-win” practices – that is, practices that result in better conservation outcomes while maintaining or improving crop yields – is of particular importance.

Uncultivated semi-natural land (SNL) can act as important habitat for beneficial arthropods (Duelli & Obrist 2003), which may spill over into adjacent cropland. Therefore, landscape management is a strategy to increase beneficial arthropod abundance in crops (Landis *et al.* 2000; Albrecht *et al.* 2010; Martin *et al.* 2020; but see Tschardt *et al.* 2016; Karp *et al.* 2018). For example, wild bee abundance in agricultural landscapes is largely driven by flower and nest availability (Roulston & Goodell 2011), and the effect of SNL on bee abundance and diversity is generally positive. Pest-suppressing predators, such as beetles or spiders, can be limited by water, food, and egg-laying sites (Lövei & Sunderland 1996; Purtauf *et al.* 2005; Gardiner *et al.* 2010), but the effect of SNL on their abundance and diversity is less consistent (Macfadyen & Muller 2013; Shackelford *et al.* 2013) as some taxa may use SNL as a travel corridor or overwintering site, but are not completely dependent on it for reproduction. Some taxa are not dependent on SNL at all, and thrive in cultivated landscapes, while others exclusively inhabit SNL and do not venture beyond the edge of cultivated fields. For example, carabid beetles are thought to reproduce in field margins, while the adults feed in fields (Desender & Alderweireldt 1988). Habitat preference also depends on the life history of the organisms in question, such as the seasonal timing of emergence, feeding, and reproduction, as well as their traits such as dispersal capability. Non-adjacent cropland can also influence arthropod abundance if the organisms are long-distance dispersers (Öberg *et al.* 2008). In this way, the spillover of beneficial arthropods into crops depends not only on the amount of adjacent SNL, but the specific habitat type, the time of the year, and the spatial scale at which an organism gathers resources.

Despite what is known about the spatial and temporal aspects of beneficial arthropod spillover, these are rarely considered together. First, some non-crop habitat may act as sources of arthropods during some times of the year, but as destinations during other times, meaning that the timing of spillover from non-crop habitat may not align with important periods in crop development. Arthropods can migrate from managed crops back into adjacent SNL at the end of the season (Desender & Alderweireldt 1988; Tscharnkte *et al.* 2005), but this is seldom considered. Second, the spatial “grain” of the landscape that is relevant to an organism depends on their traits and life history (Ahrenfeldt *et al.* 2015). For instance, bumblebee abundance can be influenced by both nearby and far-away SNL abundance (Westphal *et al.* 2006), but this is poorly studied for other groups of beneficial organisms (but see Sander *et al.* 2006). Finally, the feeding and life-history characteristics of many predatory ground beetles and spiders are often poorly-documented, especially in North America. This makes it difficult to make generalizations of which habitat types harbour beneficial arthropods, making it even more difficult to provide accurate information to farmers about land management practices.

In this study, we used pitfall traps to determine how landscape composition affects the seasonal abundance of predatory arthropods in a Canadian prairie agroecosystem. We considered the following hypotheses: 1. Untilled semi-natural land provides egg-laying and feeding areas for predatory arthropods, meaning that it should act as a *source* of arthropods during the early part of the season, and a *destination* during the later part of the season. 2. Crops provide food (pest insects) for predatory arthropods during the growing season. This should result in agricultural land becoming a destination for predators in the early part of the season as they migrate into the crop, and a source at the end of the season as they migrate out of the crop. 3. Crops may act as a temporary feeding site for predators. Therefore, crops may act as a local destination for arthropods, but will also be negatively associated at larger (landscape-level) scales. Using a large pitfall trapping dataset, we related seasonal changes in arthropod abundance to landscape composition at multiple spatial scales.

2. Methods

2.1. Data collection

We used a set of 198 pitfall traps installed in road margins (minimum of 5 m away from the road edge, 85 traps) and in-field locations (113) across southern Alberta, Canada in 2017 (Figure 1). The sites spanned a west-to-east gradient of four natural subregions, including foothills parkland, foothills fescue, mixedgrass, and dry mixedgrass (Natural Regions Committee 2006). Traps were placed starting

70 on May 16, and collections ended on August 28, with collection occurring continuously and traps being
71 emptied every 14 days on average (SD: 3). This resulted in 850 unique collection events, taking place
72 across a total of 11614 trapping days. In-field traps were placed in canola crops (68), wetlands (16),
73 grassy field edges (11), and remnant prairie grasslands (18). Traps in canola were installed at 25, 75,
74 and 200 m along a transect heading away from the nearest non-crop feature (wetland, grassy field
75 edges, or remnant prairie), while the trap at 0 m was installed in the non-crop feature itself. We used
76 582 mL Solo® cups buried up to the rim and partially filled with propylene glycol, with 2 cm wire mesh
77 mounted over the rim to prevent vertebrates from falling into the traps. Specimens were identified
78 to species using appropriate taxonomic literature (Dondale & Redner 1990; Edgar 1990; Vogel 2004;
79 Yigit *et al.* 2007).

80 We used counts of organisms in our pitfall traps as proxies of ecosystem services (specifically, pest
81 control). However, increased counts of organisms in pitfall traps can represent higher activity levels
82 (same number of organisms but more mobile) or higher abundances in the vicinity of the trap. This
83 makes it impossible to disentangle arthropod activity from density using single traps (Lang 2000; Zhao
84 *et al.* 2013), meaning that counts in the traps represent the “activity-density” of a given organism.
85 Despite this drawback, activity-density is generally positively related to pest consumption, at least in
86 carabids (Trichard *et al.* 2014; Boetzel *et al.* 2018; González *et al.* 2020), making it acceptable for our
87 study.

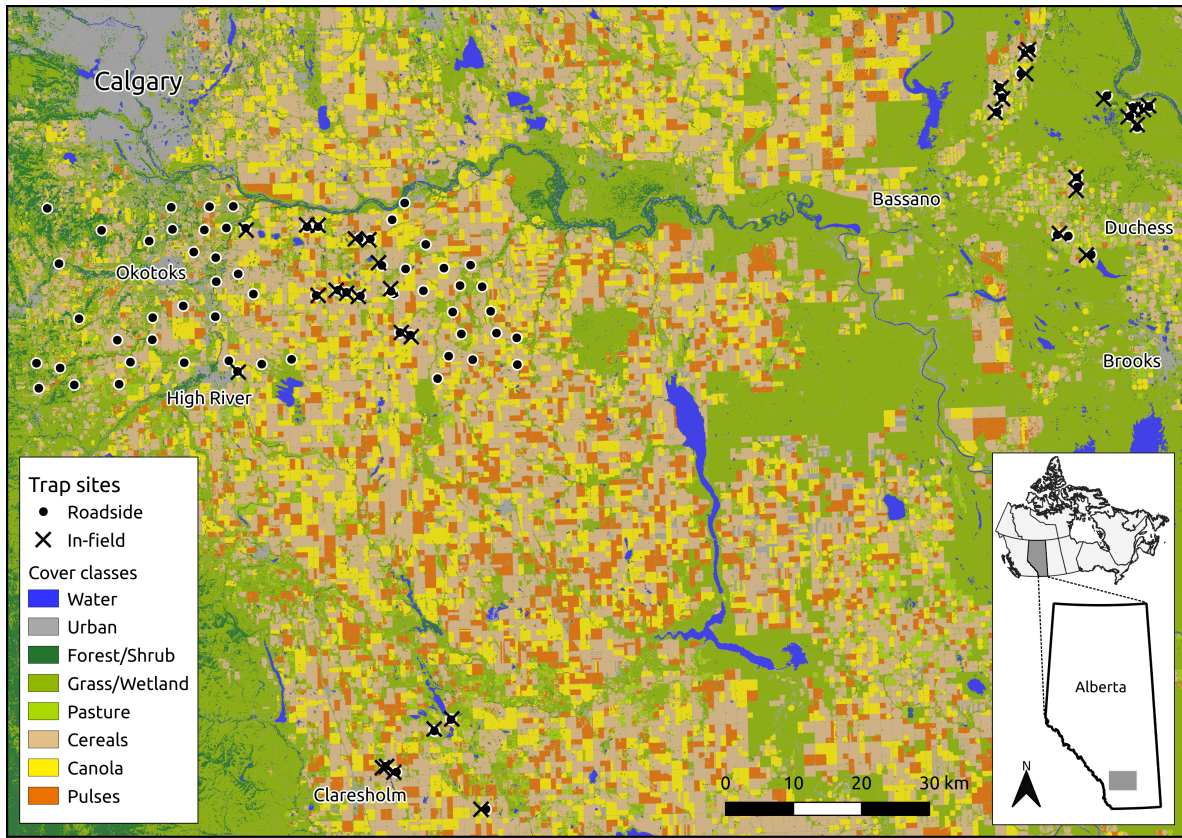


Figure 1: Classified land cover and location of pitfall traps during 2017. Inset map shows study location within Alberta provincial boundaries. Roadside traps were installed in road margins, while in-field traps were installed directly in canola fields, wetlands, or grassy field edges.

We used four highly-abundant species of predatory arthropods found in the pitfall traps, as common species are more important for ecosystem service provision than rare species (Winfree *et al.* 2015). *Pterostichus melanarius* is an introduced predatory ground beetle (Coleoptera: Carabidae) that is a wide-ranging generalist known to prey upon crop pests (Cárcamo & Spence 1994; Larsen *et al.* 2003; Busch 2016). It is commonly found in untilled grasslands (Purtauf *et al.* 2005) and may use grassy field edges as larval habitat (Desender & Alderweireldt 1988). *Pardosa* are a genus of wolf spiders (Araneae: Lycosidae) that use an active wandering predation strategy (Young & Edwards 1990), and are common across the Canadian prairies. Both *Pardosa distincta* and *Pardosa moesta* are found in a wide variety of habitats, but are common in ungrazed pastures (Dondale & Redner 1990; Cárcamo *et al.* 2014). *P. distincta* is also commonly found in disturbed environments (Collins *et al.* 1996; Wade & Roughley 2010), while *P. moesta* appear to prefer less frequent disturbances (Graham *et al.* 2003; Kowal & Cartar 2011; but see Dondale & Redner 1990). Other *Pardosa* are known to use

road margins and wooded areas as habitat (Buddle 2000; Drapela *et al.* 2011). Finally, *Phalangium*
opilio is an introduced harvestman (Opiliones: Phalangidae) that is found in drier disturbed areas
(Bragg & Holmberg 2009). Juveniles hatch from eggs during the spring, becoming adults during the
summer, and eggs are laid during the fall (adults do not overwinter; Bragg & Holmberg 2009). They
are commonly found in human-altered landscapes (Muster & Meyer 2014; Van de Poel 2015) and are
nocturnal generalist hunters and scavengers (Halaj & Cady 2000; Allard & Yeargan 2005b, a), mainly
eating small soft-bodied invertebrates (Acosta & Machado 2007).

To characterize landscape composition surrounding the traps, we used publicly available classified
landscape data (30 m resolution; Agriculture and Agri-Food Canada 2018). AAFC cropland landscape
classifications from 2017 were very accurate for cultivated fields (~90%), but were less accurate for non-
crop areas (~70%). We combined functionally similar landscape categories (cereals: *Triticum aestivum*
and *Hordeum vulgare*, pulses: *Pisum sativum* and *Lens culinaris*, forest: coniferous and broadleaf).
At each site, we extracted the proportion of each cover class within 30m annuli (rings), with the
inner radius of each annulus ranging from 30 to 1470m in increments of 30m (total of 49 annuli, 1.5
km maximum). The ten most-common cover classes surrounding our sites represented 98% of the
total land cover in our study region: grassland, cereal, canola, pasture, pulses, wetland, urban (road
margins), shrubland, flax, and forests (Figure S2); flax was removed, as only a single site had nearby
flax cover.

2.2. Analysis

Functional regression (Ramsay & Silverman 2004; Yen *et al.* 2014) was used to incorporate land-
scape information at different distances, allowing assessment of both local and regional landscape
composition (Galpern & Gavin 2020). Scalar-on-function regression is a special type of linear regres-
sion model ($y = X\beta + e$), where the columns of the model matrix X contain some continuous predictor
of the scalar y , and the values of the coefficients (β) are modeled as a smooth function $f(x)$ of the
predictors. In our case, the proportion of landscape cover (X) within each annulus surrounding the
trap is a function of distance away from the trap, meaning that the coefficients are a smoothed function
of distance ($\beta_i = f(\text{distance}_i)$), and represent the additive effect of a given type of landscape cover at
distances away from the trap (i.e. $X\beta$). This allows for the possibility that the size of the landscape
“grain” relevant to a given organism may change over the course of its life stages (Addicott *et al.* 1987;
Lima & Zollner 1996; Gardiner *et al.* 2010). It also allows for the possibility that certain land cover
types may be locally beneficial, but detrimental at large scales, indicating that the cover type may

131 not constitute a completely usable habitat.

132 Scalar-on-function regression of activity-density was fit using generalized additive models (*mgcv*
133 version 1.8.31; Wood 2017). Count data of arthropods were modeled using a negative binomial distri-
134 bution with a log-link function and a single dispersion parameter (θ). To account for different lengths
135 of trap exposure, log-days since trap placement were used as a fixed effect with their slope held at 1
136 (“offset” variable). Trapping location was included as a fixed effect with 5 levels (canola, field edge,
137 grassland, road margin, and wetlands) to account for the effect of local cover independent of the sur-
138 rounding landscape composition. Day of year was included as a 1-dimensional smooth, and easting and
139 northing (km east and north of the trap extent centre point) were included as 2-dimensional smooths,
140 in order to account for underlying spatial and temporal autocorrelation in the data.

141 For each landscape cover class, we used three scalar-on-function terms. First, we used the propor-
142 tion cover in the annuli surrounding each trap location (spatial effect of cover class). Second, we used
143 the average proportion cover across days of the year (temporal effect of cover class). Finally, we used
144 a tensor-product interaction of landscape cover and day of year (spatio-temporal interaction of cover
145 class). We used 10 basis dimensions for the spatial and temporal landscape smoothers, and 16 basis di-
146 mensions for the spatio-temporal interaction. The effective degrees of freedom for all smoothing terms
147 were far below the number of basis dimensions, indicating that no additional basis dimensions were
148 needed (see Tables S2, S4, S6, S8). To remove unimportant terms from the model, we used thin-plate
149 regression splines with shrinkage, a continuous analog to stepwise model selection where weaker terms
150 are completely removed from the model rather than reduced to a line (Marra & Wood 2011). The
151 deviance residuals from each model were visually inspected for normality and equal variance (Hilbe
152 2011; Wood 2017). Finally, we calculated the proportion of explained variance (R^2) for each set of
153 terms (Nakagawa *et al.* 2013, 2017).

154 Preliminary model fits revealed that some of the landscape terms in our model were strongly
155 concurred with each other, so we removed them from the model or combined them. Concurvity is
156 a nonlinear analogue of multicollinearity which can bias estimates of standard errors (Buja *et al.*
157 1989). There is no agreed-upon threshold of “unacceptable” concurvity, but 0.5 is commonly used
158 (Dominici 2002; Ramsay *et al.* 2003). Forests and shrubland were combined into a single “woodland”
159 category, and grassland and wetland were combined into a single “grassland” category, as they were
160 strongly positively correlated at all distances, indicating similar feature classes. Cereal was removed
161 from the model, as it was negatively correlated with canola cover at distances less than 200m and

162 was positively correlated at distances over 500m, reflecting the most common crop rotations (canola
 163 \rightarrow wheat \rightarrow barley) and the commonly-used 800 m block structure of farmland in our study region
 164 (quarter-sections). This resulted in a reduced set of landscape terms, none of which were strongly
 165 concurred with each other (cropland: canola, pulses; SNL: grassland, pasture, woodland, roadside; see
 166 Figure S1).

167

168 **Box 1: Interpreting Functional Regression Plots**

169 Functional linear regression is a special case of linear regression, where both the independent
 170 variable is predicted by a functional dependent variable, meaning that the slope is a function (vector)
 171 rather a fixed (scalar) value (Ramsay & Silverman 2004; Yen *et al.* 2014). Therefore, the interpretation
 172 of a functional regression plot is very different from that of a simple linear regression plot. Figure 2a
 173 shows a simple linear regression plot of a hypothetical relationship between trap *activity-density* (y)
 174 and a single predictor, *proportion cover* (x), which is measured in a circle of a fixed radius surrounding
 175 each trap. If we suppose that the relationship between x and y is similar at all radii at which x is
 176 measured, then Figure 2b shows the resulting functional linear regression plot, where the slope (β) is
 177 the same at all distances (we avoid the problem of overlapping concentric circles by using concentric
 178 *annuli*). In reality, it is more likely that nearby cover will be more influential on activity-density than
 179 far-away cover, which could result in a relationship similar to Figure 2c. As functional regression takes
 180 any continuous predictor of y , it is also possible to use proportion cover (measured within an annulus of
 181 a fixed radius) as a predictor of measurements taken across time, allowing the effect of proportion cover
 182 to vary over the course of the season (Figure 2d). Finally, the effect of proportion cover over distance
 183 and time may be modeled as a smoothed surface, representing the joint spatio-temporal influence of
 184 landscape cover on activity-density.

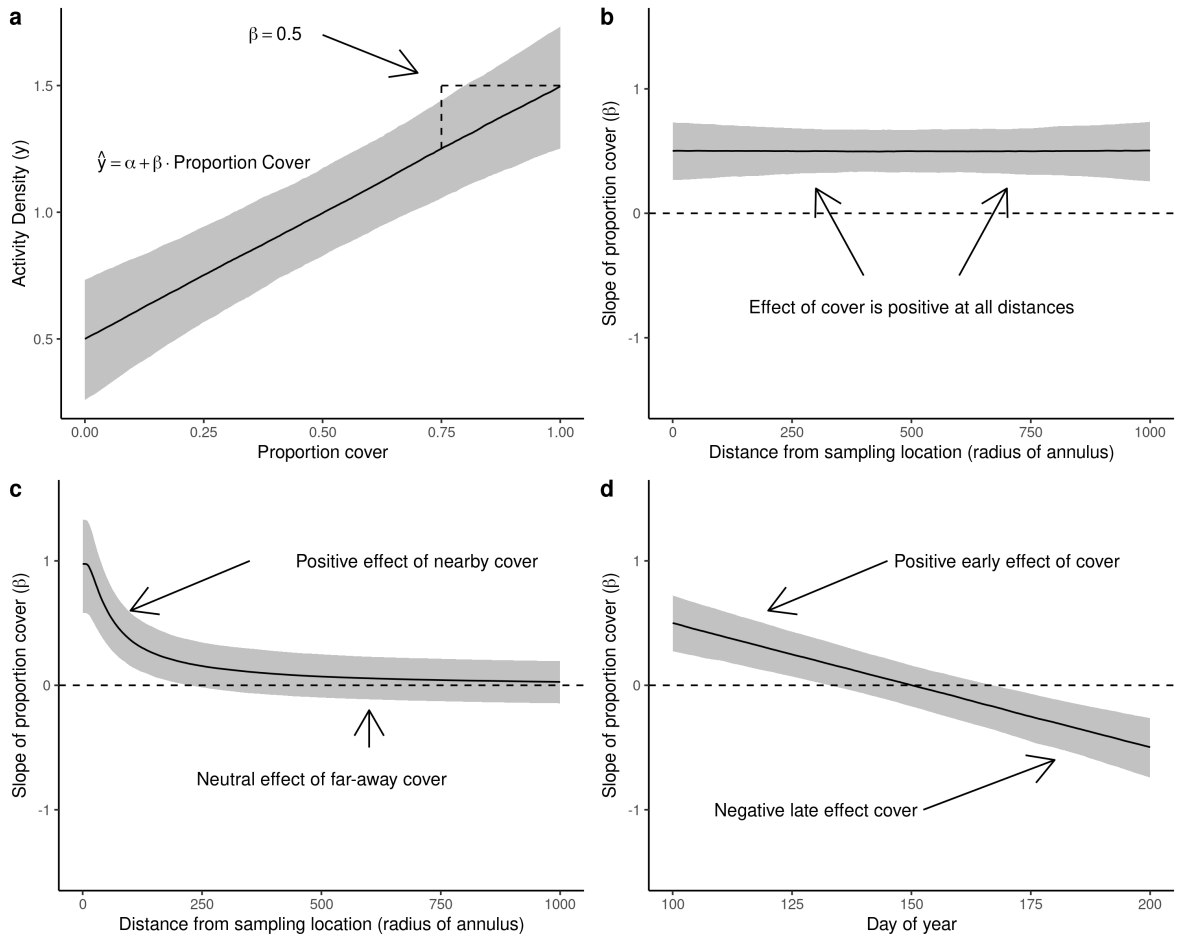


Figure 2: Examples of (functional) linear regression plots. **a)** shows a simple linear regression plot, with a single slope value for a single regressor. **b)** shows the equivalent plot in functional regression form, where the slope is a smoothed function that maps onto a function-valued regressor. **c)** and **d)** show functional linear regression plots where the slope varies with the location of the regressor.

185

186 Functional regression plots of landscape composition reveal which cover classes are acting as sources
 187 or destinations of a given arthropod, and at what spatial scale. Positive effects of nearby landscape
 188 cover classes indicate that arthropods are spilling over *from* it, therefore acting as a source. However,
 189 negative responses to nearby landscape cover classes can indicate one of two things: 1) It may indicate
 190 that arthropods are spilling over *into* it (therefore acting as a destination) or 2) it may indicate that
 191 no arthropods are available to spill over *from* it. We consider 1) to be the more likely scenario, as it is
 192 unlikely that any one cover class is *completely* unoccupied. For example, a cover class with low-quality
 193 habitat could act as an ecological trap (Galpern *et al.* 2017) if it acts as a destination but never

194 as a source. Alternatively, a cover class could act as a destination by providing high-quality habitat
195 at certain times of the year (e.g. egg laying/feeding), but act as a source at other times (e.g. during
196 emergence).

197 In the Results section, we refer to local- and landscape-level effects, where local indicates the effects
198 of landscape composition at scales of <500 m, whereas landscape indicates scales >500 m. Similarly,
199 we refer to early- and late-season effects, where landscape composition affected activity-density on
200 June 20th or August 20th, respectively.

201 3. Results

202 3.1. Landscape composition and trap catches

203 Grassland, cereal, and canola were the three most-abundant landcover classes surrounding our
204 traps, accounting for 77% of land cover (Figure S2). Several landscape “fingerprints” were evident
205 in the landscape annuli, with cereal cover increasing with distance away, along with a corresponding
206 decrease in canola cover. Study sites were originally chosen for sampling arthropods surrounding
207 canola agroecosystems, so canola was a dominant signal in the landscape, but there was also a large
208 amount of variation in grassland and pasture surrounding each site (Figure S2). Grassland cover was
209 largely constant with distance, but a cluster of sites had uniformly high or low cover of grassland with
210 distance. The pitfall traps caught a total of 18968 *Pterostichus melanarius*, 5397 *Pardosa distincta*,
211 2350 *Pardosa moesta*, and 34090 *Phalangium opilio* (mean trapping rates per day: 1.58, 0.49, 0.22,
212 2.92, SD: 5.69, 1.08, 1.09, 5.48, respectively).

213 3.2. Ground beetle: *Pterostichus melanarius*

214 *P. melanarius* activity-density was strongly influenced by trap location and landscape composition
215 (Tables S1, S2). Canola crops had a marginally higher activity-density of *P. melanarius* than other trap
216 locations (Figure 3a). Grassland cover was the most important land cover type in explaining activity-
217 density (R^2 : 0.104, Table 1), and local grassland had a negative effect late in the summer (Figure 3b),
218 suggesting that *P. melanarius* may move into grasslands later in the year. Local canola had a positive
219 effect in the early season, but landscape-level canola had a negative effect, indicating that areas with
220 widespread canola coverage had lower *P. melanarius* activity-density (Figure 3c). Pulses acted as a
221 late-season source, indicating that *P. melanarius* may migrate out of the crop after (or during) harvest
222 (Figure 3d). Finally, *P. melanarius* activity-density had a strong temporal and spatial component

(both $p < 0.001$), indicating that phenology and local geographic factors were important drivers of ground beetle activity-density (Figure S3). Landscape composition and trap location explained 22% of the variance in activity-density, while the spatial and temporal smoothers accounted for 41% (Table 1).

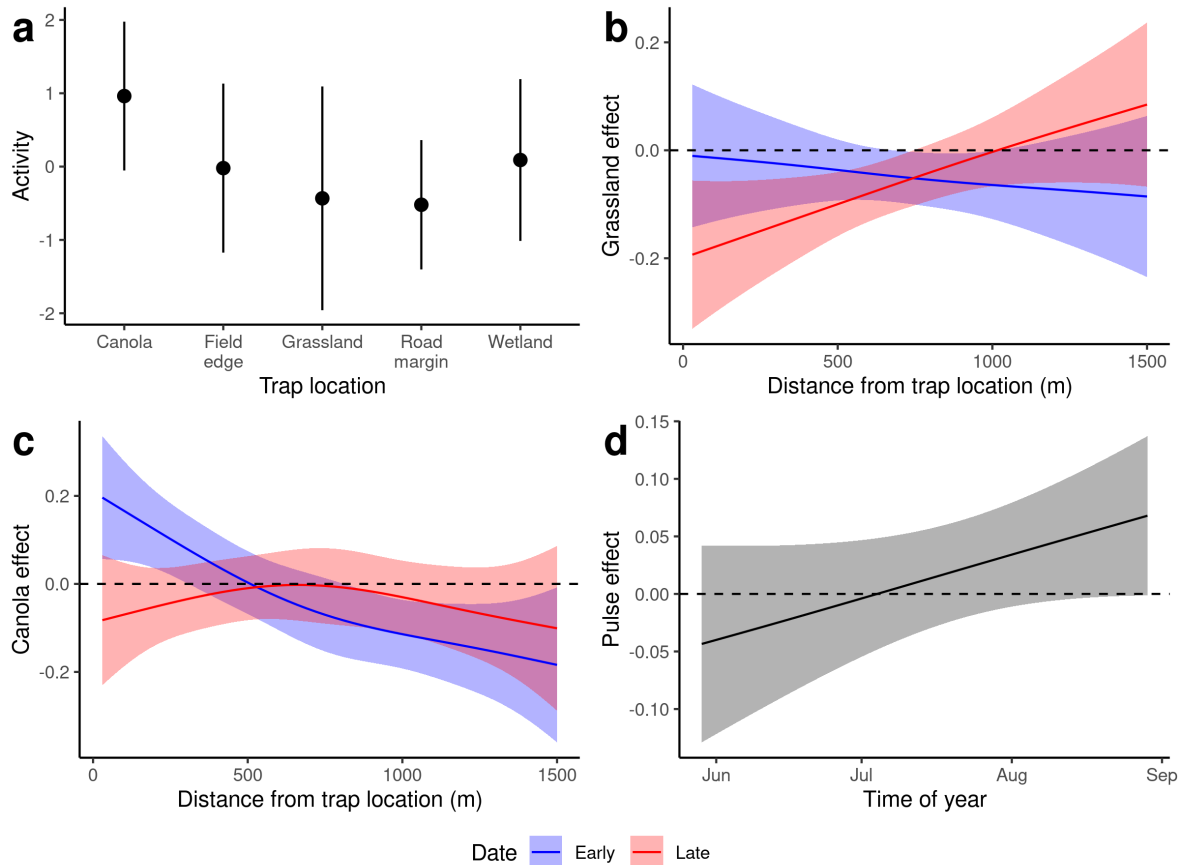


Figure 3: Landscape influence on *Pterostichus melanarius* activity-density. a) shows the effect of local trap location, and b-c) are functional regression plots of the proportion grassland and canola at distances away from each trap. d) is a functional regression plot over time, showing the effect of pulses at different times of the year. Lines and dots represent means, and bars and shaded regions represent 95 % confidence regions ($1.96 \times \text{SE}$). Coloured regions represent early- and late-season effects (blue = June, red = August).

3.3. Wolf spiders: *Pardosa distincta* and *Pardosa moesta*

Activity-density of *P. distincta* and *P. moesta* was influenced by trap location and landscape composition (Tables S3, S4, S5, S6), but landscape composition had relatively weak effects on both species (R^2 : 0.0446, 0.0963). Unlike *P. melanarius*, both *Pardosa* species had far lower activity-density in canola than any other cover type (Figures 4a, 5a). Activity-density of both *Pardosa* species had a strong temporal and spatial component, although the temporal component was dominant for

233 *P. distincta*, whereas the spatial component was dominant for *P. moesta* (Figures S4 and S5; both
234 $p < 0.001$).

235 *P. distincta* activity-density was negatively affected by landscape-level pasture (Figure 4b), while
236 woodlands had a negative effect late in the season (Figure 4c). This suggests that large amounts
237 of pasture are unsuitable habitat for *P. distincta*, and that they migrate into woodlands later in the
238 season. However, trap location and the temporal random effect (Figure S4a) explained roughly 10 times
239 more variance than landscape composition (R^2 : 0.45 versus 0.045), meaning that while *P. distincta*
240 may be locally abundant in certain cover types, it is highly general in its overall habitat preferences.

241 *P. moesta* activity-density responded to grassland, canola, and road margins. Grasslands had a
242 local negative effect, but a positive landscape-level effect, indicating that while these cover types act
243 as a local destination, the general amount of grassland in the area had a positive effect (Figure 5b).
244 Local canola cover had a positive early effect on activity-density, but a negative local effect later in
245 the season (Figure 5c). Local road margins also had a similar effect, acting as an early source and
246 a late destination (Figure 5d). Pulses also had a positive effect at the landscape level (Figure 5e),
247 but this explained very little variance in *P. moesta* activity-density (Table 1, R^2 : 0.004). Similar to
248 *P. distincta*, trap location and an East-West spatial random effect (Figure S5b) explained roughly 5
249 times more variance in *P. moesta* activity-density than landscape composition (R^2 : 0.5 versus 0.096),
250 meaning that *P. moesta* is also fairly general in its overall habitat preferences, and is influenced more
251 heavily by larger-scale abiotic factors.

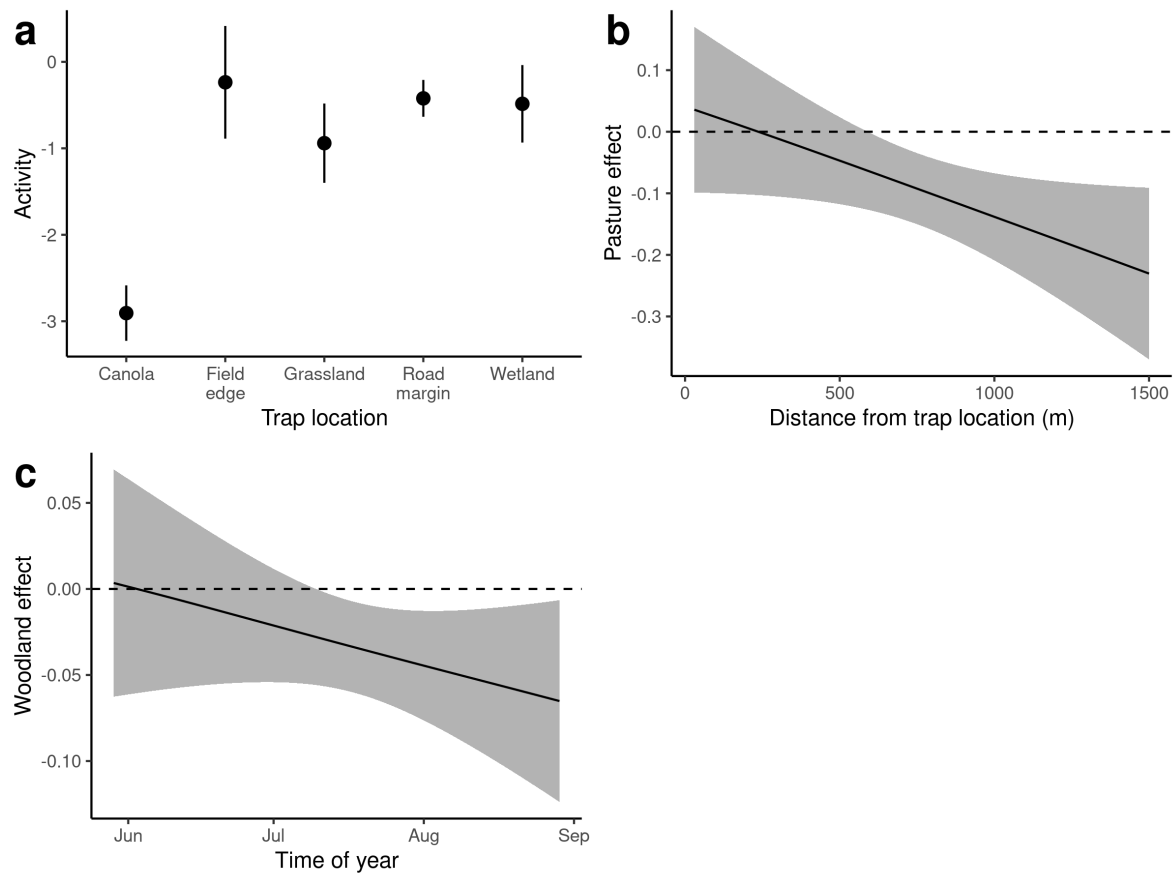


Figure 4: Landscape influence on *Pardosa distincta* activity-density. a) shows the effect of local trap location, b) is a functional regression plot of the proportion pasture at distances away from each trap, and c) is a functional regression plot over time, showing the effect of woodland at different times of the year. Lines and dots represent means, and bars and shaded regions represent 95 % confidence regions ($1.96 \times \text{SE}$).

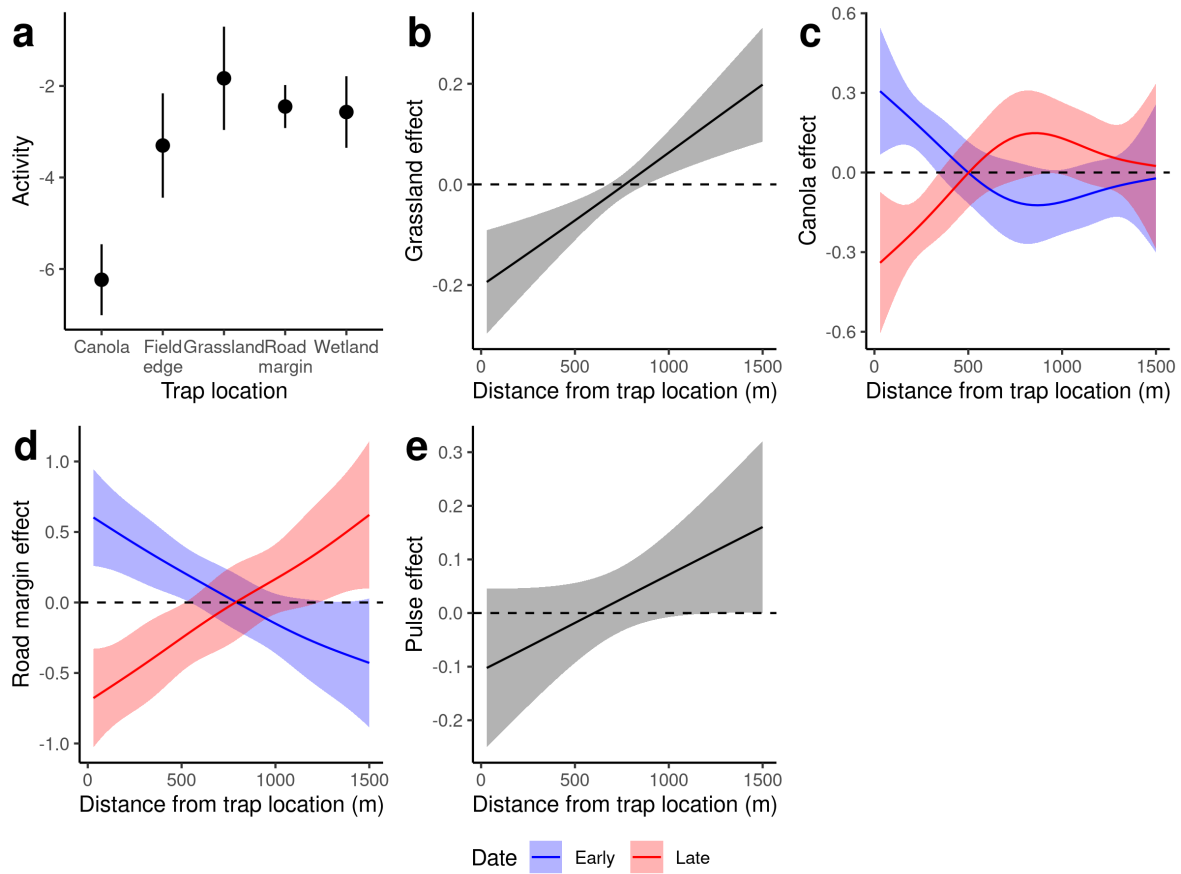


Figure 5: Landscape influence on *Pardosa moesta* activity-density. a) shows the effect of local trap location, and b-e) are functional regression plots of the proportion grassland, canola, road margins, and pulses at distances away from each trap. Lines and dots represent means, and bars and shaded regions represent 95 % confidence regions ($1.96 \times SE$). Coloured regions represent early- and late-season effects (blue = June, red = August).

3.4. Harvestman: *Phalangium opilio*

P. opilio activity-density was somewhat influenced by trap location, with field edges and wetlands having the highest activity-density (Figure 6a), but this effect was swamped by the effect of landscape and the spatiotemporal random effects (Table 1), meaning that *P. opilio* activity-density is only mildly influenced by local cover type. Nearby grassland and woodland both had negative effects on *Phalangium opilio* activity-density, but only early in the season (Figures 6b,c), suggesting that *P. opilio* may preferentially migrate to these cover classes. The temporal random effect was overwhelmingly the most important predictor of *P. opilio* activity-density (R^2 : 0.44), showing that activity-density increased during the spring, and showed very little decline during the rest of the season (Figure S6a). Similar to *P. moesta*, *P. opilio* also showed a distinct East-West spatial random effect (Figure S6b),

262 indicating that their activity-density is also influenced by larger-scale abiotic factors.

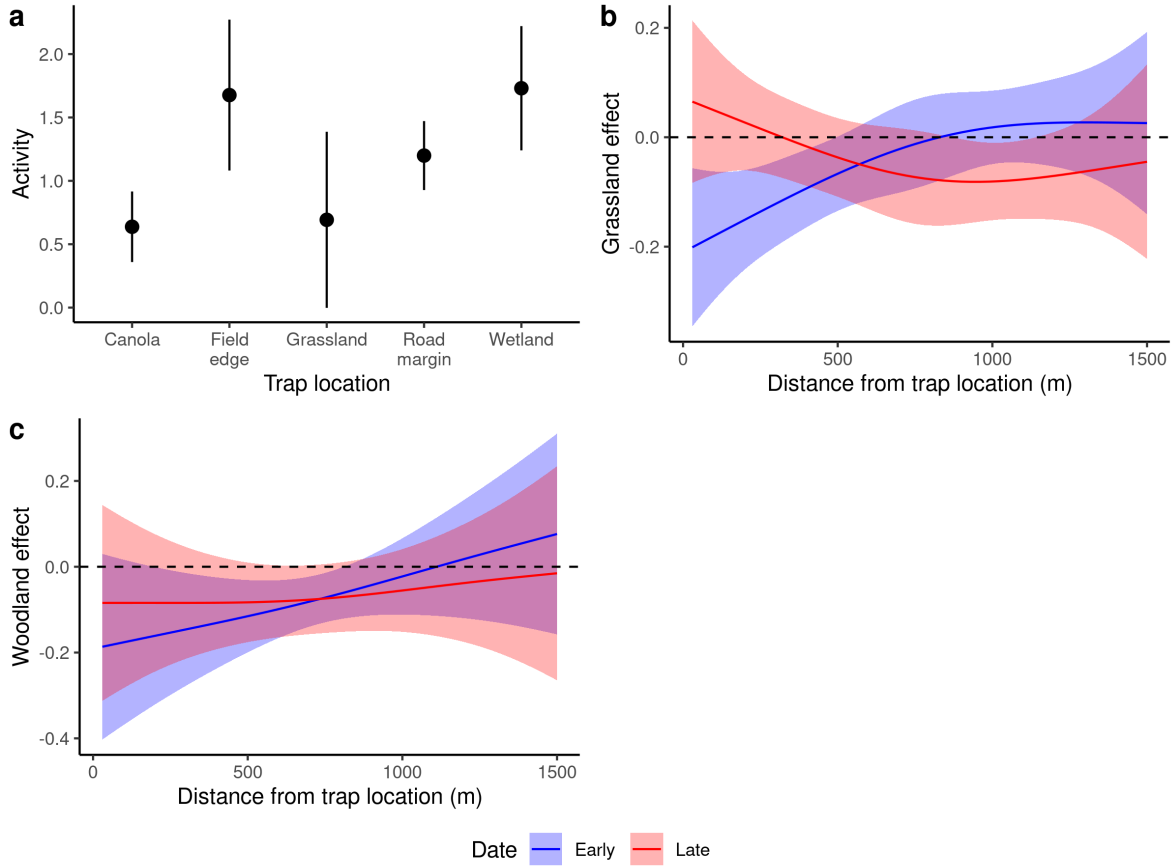


Figure 6: Landscape influence on *Phalangium opilio* activity-density. a) shows the effect of local trap location, and b-c) are functional regression plots of the proportion grassland and woodland at distances away from each trap. Lines and dots represent means, and bars and shaded regions represent 95 % confidence regions ($1.96 \times \text{SE}$). Coloured regions represent early- and late-season effects (blue = June, red = August).

263 4. Discussion

264 Our prediction of SNL having late-season effects on beneficial arthropods was supported (Table
 265 2). Specifically, grassland had a negative effect on *P. melanarius* activity-density, woodlands on *P.*
 266 *distincta* activity-density, and road margins on *P. moesta* activity-density, all during late summer
 267 (August - September). This suggests that these arthropods migrate to these habitats at the end of the
 268 summer to prepare for oviposition or overwintering. However, *P. opilio* showed no evidence of this,
 269 instead showing a negative effect of grassland *early* in the season, suggesting that a) they aggregate in
 270 grasslands or b) grasslands do not constitute suitable habitat for *P. opilio*, resulting in low spillover.

Table 1: R^2_{GLMM} for model components, representing the proportion of total variance explained by each term. R^2 was calculated using methods from Nakagawa et al. 2013 and Nakagawa et al. 2017.

Term	<i>Pterostichus melanarius</i>	<i>Pardosa distincta</i>	<i>Pardosa moesta</i>	<i>Phalangium opilio</i>
Trap Location	0.080	0.294	0.379	0.026
Day of Year	0.040	0.160	0.000	0.436
Spatial Location	0.373	0.000	0.125	0.085
Grassland	0.104	0.000	0.017	0.086
Canola	0.030	0.002	0.037	0.000
Pasture	0.000	0.032	0.002	0.000
Woodland	0.000	0.009	0.001	0.017
Pulses	0.005	0.000	0.004	0.001
Road margins	0.000	0.001	0.034	0.002
Residual	0.369	0.502	0.400	0.348

Table 2: Synthesis of model results. Pest control potential is based on likelihood of early-season aggregation to canola crops.

Species	Summary	Pest control potential
<i>Pterostichus melanarius</i>	<ul style="list-style-type: none"> · Moves to canola during early season · Disperses to grassland during late season 	High
<i>Pardosa distincta</i>	<ul style="list-style-type: none"> · Negative effect of pasture · May move locally to field edges 	Low
<i>Pardosa moesta</i>	<ul style="list-style-type: none"> · Moves to canola during early season · Disperses to road margins and grassland during late season · Moves to grasslands across the season. 	Medium
<i>Phalangium opilio</i>	<ul style="list-style-type: none"> · Moves to grassland early in the season 	Low

271 There was little evidence of SNL acting as early-season sources, aside from road margins having a
 272 positive early effect on *P. moesta* activity-density. However, some cover classes had a positive effect
 273 at the landscape level (grassland and road margins on *P. moesta*), suggesting earlier or larger-scale
 274 dispersal away from these cover classes. Canola had a positive effect on *P. melanarius* and *P. moesta*
 275 in the early season, suggesting that these organisms aggregate to canola crops and disperse at the end
 276 of the season (mass effects *sensu* Shmida & Wilson 1985). Canola also had negative landscape-level
 277 effects on *P. melanarius* while pasture had negative effects on *P. distincta*, meaning that these cover
 278 types likely represent only partial habitat for these arthropods. Finally, the influence of landscape
 279 composition tended to be limited to a radius of about 500m, indicating that large-scale *and* local
 280 land cover can be important to beneficial arthropod abundance. There was also a strong temporal
 281 component to most of the landscape effects, meaning that it is important to consider how destinations
 282 and sources may change over the season.

283 The predatory ground beetle *Pterostichus melanarius* responded to landscape composition, pri-
 284 marily to canola, pulses, and grass and wetland cover. Grassland and wetland cover had a negative
 285 late-season effect, suggesting that they act as a destination for *P. melanarius* at the end of the summer.
 286 Other studies have found similar results, suggesting that untilled land is important off-field habitat
 287 for carabids (Desender & Alderweireldt 1988; Fournier & Loreau 2002; but see Hatten *et al.* 2007).
 288 In particular, Purtauf *et al.* (2005) found that carabid density increased with proportion of nearby
 289 grasslands, so our negative late-season effect of grasslands may represent *P. melanarius* moving to
 290 overwintering habitat at the end of the season. However, *P. melanarius* is also found in a wide variety
 291 of habitats, and tends to prefer agricultural fields (Larsen *et al.* 2003). Our models confirmed this,
 292 as they showed that canola and pulse crops had positive effects on *P. melanarius* activity-density
 293 early in the season. Early in the season, canola crops had a local positive effect, but a landscape-level
 294 negative effect, which may indicate that they provide only temporary feeding habitat. The effect of
 295 pulse crops on carabid abundance is not well-studied, but our results suggest that pulses may represent
 296 a potential food resource for *P. melanarius*, albeit a weak one (Table 1). Carabids are predators of
 297 pea-leaf weevils (*Sitona lineatus*) on other Fabaceae (Hamon *et al.* 1990), and *P. melanarius* can prey
 298 upon other carabids that are predators of *S. lineatus*, such as *Bembidion quadrimaculatum* (Vankosky
 299 *et al.* 2011), so this effect may be direct or indirect. We did not consider the influence of previous
 300 years' crops, although carabids tend to be more abundant in areas of high crop rotation (Bertrand *et*
 301 *al.* 2016; Busch 2016). Finally, *P. melanarius* has long- and short-winged morphs with very different

302 dispersal abilities (Niemelä & Spence 1999; Bourassa *et al.* 2011), which may influence the degree to
303 which landscape-level proportion cover impacts activity-density.

304 The wolf spiders *Pardosa distincta* and *Pardosa moesta* both responded to landscape composition,
305 but it explained only a small fraction of their activity-density (R^2 : 0.045, 0.096). This means that both
306 species of *Pardosa* appear to have very general habitat preferences, but may be somewhat influenced
307 by certain cover types. Pasture had a negative effect at the landscape scale, and woodland had a
308 late-season negative effect, suggesting that *P. distincta* move to woodlands for overwintering or winter
309 foraging (Aitchison 1984; Buddle 2000). *Pardosa* are found in areas close to disturbed roadside strips
310 (Drapela *et al.* 2008, 2011; Kowal & Cartar 2011), but *P. distincta* appears to be less sensitive
311 to disturbances than *P. moesta* (Collins *et al.* 1996; Wade & Roughley 2010). Moring & Stewart
312 (1994) showed that *P. distincta* were active in grassy habitats, which we found partial evidence of, as
313 *P. distincta* tended to have higher activity-density in trap locations with higher grass cover (Figure
314 4a). Canola had an early-season positive effect on *P. moesta*, indicating that *P. moesta* and *P.*
315 *melanarius* may both use canola as foraging grounds. We also found that road margins had a positive
316 early-season and a negative late-season effect (similar to Drapela *et al.* 2008). Grassland and pulses
317 also had a local negative effect but a positive landscape-level effect; this suggests that they may
318 constitute suitable habitat for *P. moesta* and attract them away from other cover types. Wolf spiders
319 (Lycosidae) employ a wandering-active predation strategy (Young & Edwards 1990), meaning that
320 nearby landscape composition may be more influential to *Pardosa* than large-scale composition (Öberg
321 *et al.* 2007, 2008). While trapping location explained a large proportion of variance for both species
322 (0.29 and 0.38), several landscape features were also important at large spatial scales, including grass
323 and wetland, pasture, pulses, and road margins. Therefore, *Pardosa* dispersal distances may be further
324 than previously thought, either through ballooning as juveniles (Richter 1970; Greenstone 1982) or
325 through other long-distance travel.

326 *Phalangium opilio* activity-density responded to grass and wetland cover, as well as wooded land-
327 scapes. Other studies have found that *P. opilio* is mostly found in human-altered landscapes with
328 a large proportion of farming (Muster & Meyer 2014; Van de Poel 2015). Since most of our study
329 area was in or near farmed land, the lack of variation is understandable, but there were a few notable
330 landscape-level patterns that emerged. *P. opilio* activity-density was higher in grassy field edges and
331 wetlands, but grasslands and wetlands had a local negative effect on *P. opilio* until late in the season.
332 These indicate that while grass and wetlands could act as a reservoir, spillover into other land cover

types may be limited, as *P. opilio* avoids heavily grazed areas, possibly due to low humidity (Šajna *et al.* 2011). *P. opilio* is also found in large numbers at the edges of forests, and may migrate from forests into farmlands (Van de Poel 2015). We found the opposite pattern: forests had a weak negative effect on *P. opilio*, at least early in the year. Unlike the other arthropods, most of the variation in activity-density for *P. opilio* was explained by day of year ($R^2 = 0.44$), indicating strong seasonal emergence cues. However, there was also a strong East-West spatial random effect in both *P. opilio* and *P. moesta*, meaning that larger-scale geographic patterns (possibly related to rainfall or temperature) also influence their activity-density.

Many other studies have considered the overall effect of SNL on ecosystem service provision, but we have highlighted the different spatial and temporal aspects of these services. We have shown how a relatively straightforward statistical technique can be used to consider multiple spatial scales of landscape composition, providing richer inference about the processes acting on beneficial arthropods. Our results show empirical evidence of arthropod migration between cover types at different times of year, which is rarely considered beyond single-field studies. Since we did not directly track individual movements, future studies should directly examine arthropod movement and life-history within matrices of cover types, with the goal of integrating landscape ecology and behavioural processes into a single model (Lima & Zollner 1996). This would also allow direct inference about landscape categories that were combined in our dataset, allowing us to consider different landscape categories independently. Finally, future work should explicitly link landscape structure, arthropod abundance, and ecosystem services (Gagic *et al.* 2017).

5. Applications

Our work has three main applications. First, it adds to the basis of scientific evidence showing that SNL can act as reservoir habitats in intensely-managed agroecosystems. Based on our findings, farmers and land managers should consider preserving existing grassland and wetland habitat to act as habitat for pest-suppressing arthropods in crops. While local habitat appears valuable, even landscape-level habitat can be valuable, as it can increase the number of beneficial arthropods at larger spatial scales (e.g. Figures 3, 5). Secondly, our work suggests that *P. melanarius* and *P. moesta* should be investigated for their role as predators in canola crops (Table 2). They appear to aggregate in canola crops early in the season, meaning that they have the potential to provide valuable pest-control services to growers. Finally, we demonstrate that timing and spatial scale of spillover should be considered

363 in future landscape studies of ecosystem services. We show important differences in the timing of
364 landscape effects on activity-density (early-season vs. late-season spillover) that are typically ignored,
365 but should be considered when assessing how SNL can deliver ecosystem services.

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372 Association.

	Trap location	s(day)	s(E,N)	s(Distance):Grassland	s(Time):Grassland	ti(Distance,Time):Grassland	s(Distance):Canola	s(Time):Canola	ti(Distance,Time):Canola	s(Distance):Pasture	s(Time):Pasture	ti(Distance,Time):Pasture	s(Distance):Woodland	s(Time):Woodland	ti(Distance,Time):Woodland	s(Distance):Pulses	s(Time):Pulses	ti(Distance,Time):Pulses	s(Distance):Urban	s(Time):Urban	ti(Distance,Time):Urban
Trap location	1	0.01	0.01	0.04	0.01	0.01	0.44	0.11	0.07	0.17	0.05	0.01	0.01	0	0	0.07	0.01	0	0.04	0.01	0
s(day)	0.07	1	0.06	0.01	0.4	0.02	0.02	0.43	0.23	0.01	0.21	0.02	0.04	0.21	0.02	0.02	0.28	0.03	0.03	0.42	0.22
s(E,N)	0.25	0.08	1	0.43	0.18	0.05	0.29	0.14	0.05	0.53	0.22	0.07	0.75	0.31	0.07	0.47	0.22	0.04	0.4	0.18	0.03
s(Distance):Grassland	0.24	0.02	0.14	1	0.36	0.02	0.29	0.1	0.02	0.21	0.1	0.01	0.27	0.09	0.01	0.12	0.04	0.01	0.34	0.13	0.01
s(Time):Grassland	0.05	0.6	0.11	0.97	1	0.01	0.1	0.13	0.04	0.09	0.14	0.01	0.17	0.24	0.03	0.06	0.07	0.01	0.29	0.39	0.13
ti(Distance,Time):Grassland	0.07	0.09	0.01	0.04	0.13	1	0.05	0.09	0.25	0.04	0.06	0.03	0.02	0.13	0.08	0.01	0.04	0.05	0.02	0.11	0.04
s(Distance):Canola	0.72	0.02	0.1	0.14	0.07	0.01	1	0.39	0.1	0.29	0.09	0.03	0.03	0.01	0	0.34	0.12	0.01	0.34	0.12	0
s(Time):Canola	0.47	0.67	0.04	0.1	0.13	0.03	0.93	1	0.35	0.21	0.23	0.02	0.02	0.02	0.01	0.28	0.39	0.02	0.24	0.28	0.11
ti(Distance,Time):Canola	0.54	0.27	0.03	0.05	0.07	0.15	0.36	0.38	1	0.19	0.15	0.09	0.01	0.02	0.02	0.07	0.15	0.06	0.06	0.09	0.07
s(Distance):Pasture	0.33	0.02	0.09	0.13	0.06	0.02	0.28	0.09	0.05	1	0.41	0.1	0.05	0.03	0	0.08	0.02	0.02	0.16	0.06	0.01
s(Time):Pasture	0.21	0.34	0.06	0.12	0.22	0.03	0.21	0.16	0.14	0.8	1	0.06	0.06	0.16	0.03	0.07	0.06	0.02	0.14	0.19	0.06
ti(Distance,Time):Pasture	0.14	0.24	0.04	0.02	0.1	0.05	0.08	0.09	0.18	0.33	0.57	1	0.02	0.09	0.03	0.01	0.03	0.03	0.03	0.09	0.06
s(Distance):Woodland	0.04	0.02	0.14	0.33	0.14	0.01	0.06	0.03	0.01	0.04	0.03	0	1	0.37	0.05	0.02	0.01	0	0.25	0.11	0.01
s(Time):Woodland	0.02	0.26	0.04	0.21	0.26	0.05	0.04	0.05	0.01	0.03	0.06	0.01	0.92	1	0.27	0.02	0.03	0.01	0.2	0.24	0.14
ti(Distance,Time):Woodland	0.01	0.08	0.04	0.06	0.09	0.05	0	0.04	0.02	0.01	0.03	0.01	0.11	0.41	1	0	0.01	0.04	0.01	0.08	0.06
s(Distance):Pulses	0.18	0.01	0.08	0.08	0.04	0.01	0.35	0.16	0.02	0.12	0.05	0.01	0.03	0.02	0	1	0.37	0.06	0.22	0.09	0
s(Time):Pulses	0.09	0.35	0.02	0.05	0.06	0.01	0.23	0.31	0.08	0.07	0.08	0.01	0.01	0.02	0	0.8	1	0.02	0.14	0.16	0.07
ti(Distance,Time):Pulses	0.05	0.19	0.02	0	0.04	0.04	0.04	0.13	0.15	0.02	0.06	0.02	0.01	0.03	0.01	0.05	0.38	1	0.01	0.07	0.03
s(Distance):Urban	0.36	0.03	0.11	0.36	0.16	0.01	0.45	0.19	0.05	0.22	0.1	0.02	0.21	0.09	0.01	0.26	0.09	0.01	1	0.36	0.02
s(Time):Urban	0.1	0.62	0.04	0.27	0.39	0.01	0.27	0.32	0.08	0.14	0.16	0.01	0.18	0.26	0.02	0.14	0.21	0.02	0.88	1	0.47
ti(Distance,Time):Urban	0.03	0.62	0.04	0.03	0.29	0.03	0.04	0.24	0.06	0.03	0.16	0.04	0.03	0.26	0.07	0.02	0.23	0.04	0.07	0.55	1

Figure S1: Concurvity estimates for reduced cover classes used in models.

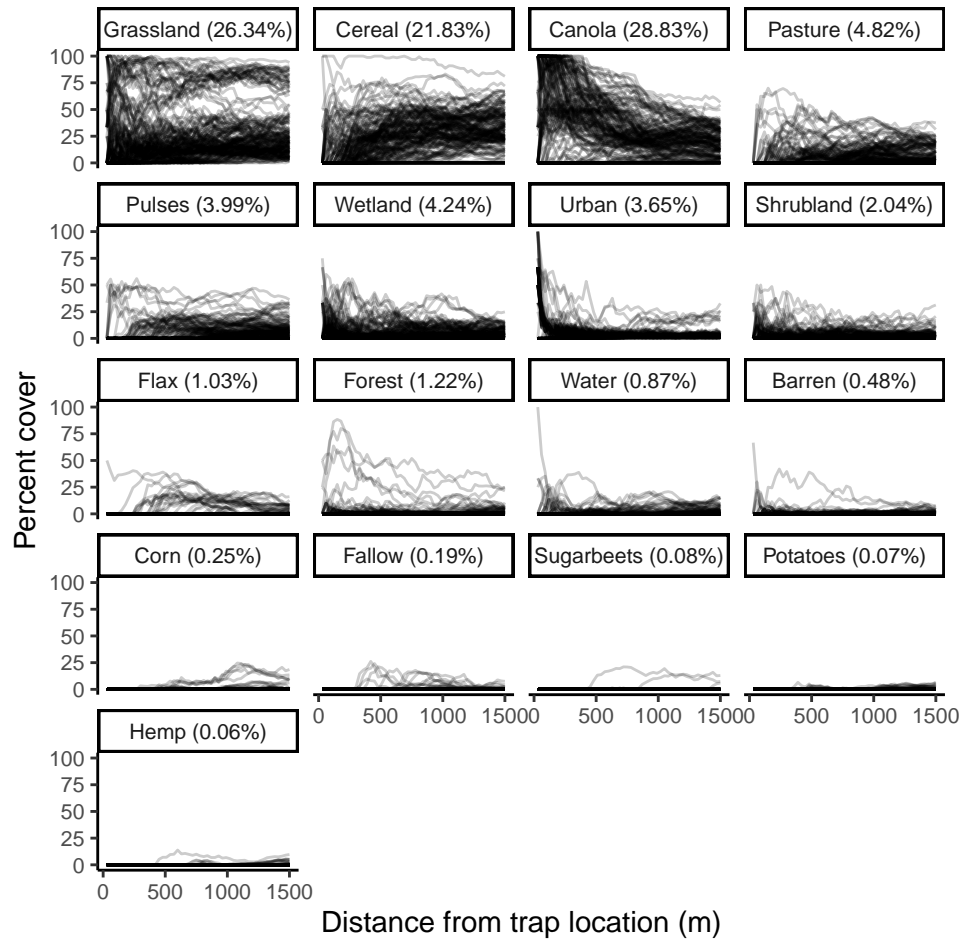


Figure S2: Percent cover of landscape cover classes in annuli surrounding each trap location. Sites are represented by individual lines. Mean cover for each class is listed in each sub-heading.

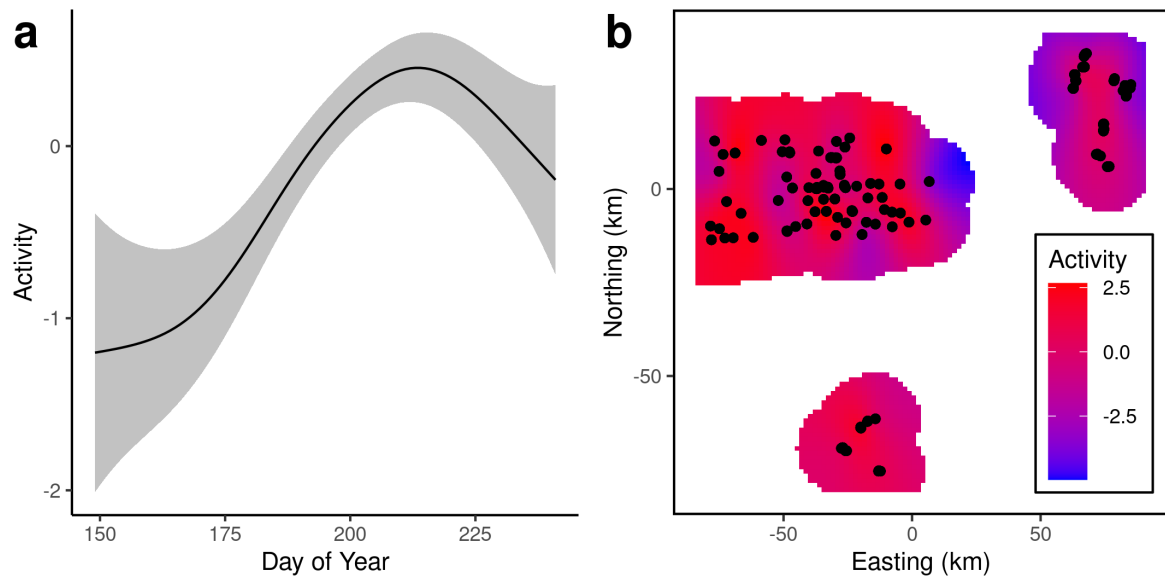


Figure S3: Temporal and spatial components of *Pterostichus melanarius* activity-density (after accounting for landscape composition and trap location). a) shows the effect of day of year, and b) shows the spatially smoothed effect of site location.

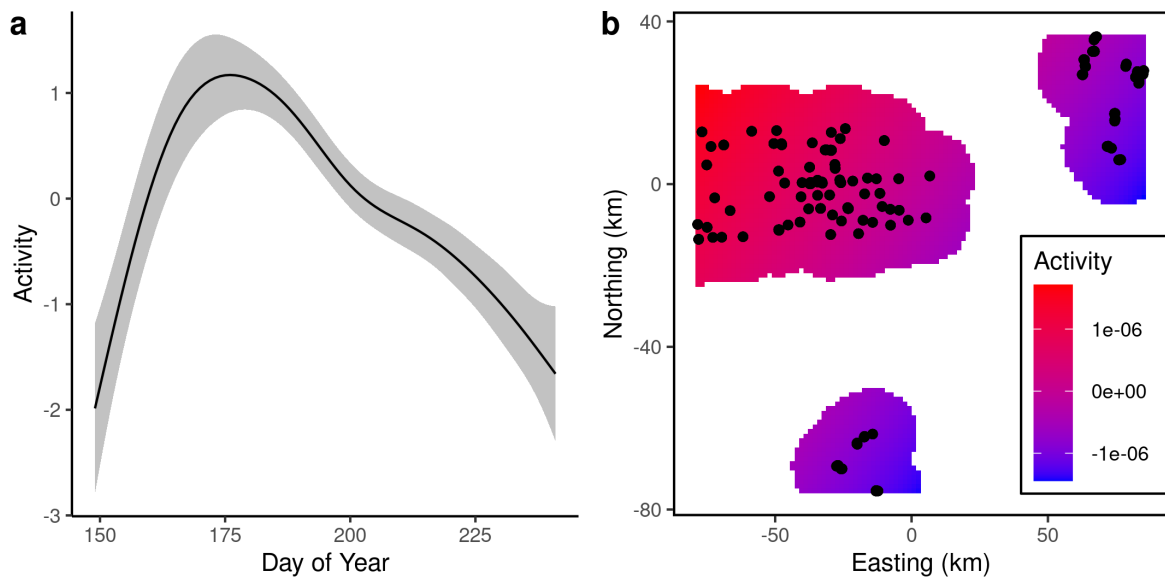


Figure S4: Temporal and spatial components of *Pardosa distincta* activity-density (after accounting for landscape composition and trap location). a) shows the effect of day of year, and b) shows the spatially smoothed effect of site location.

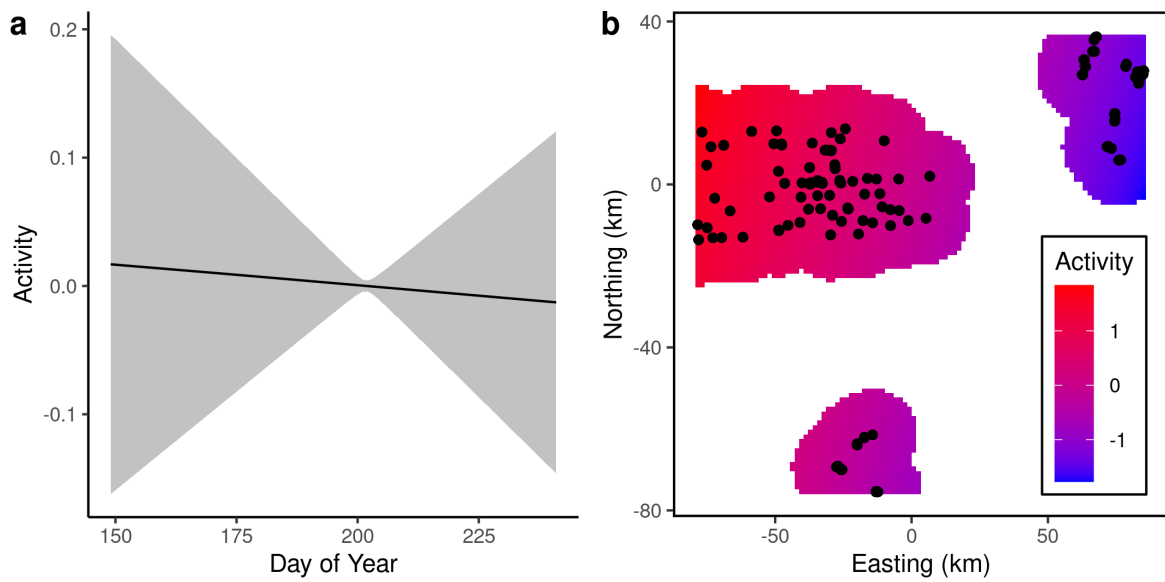


Figure S5: Temporal and spatial components of *Pardosa moesta* activity-density (after accounting for landscape composition and trap location). a) shows the effect of day of year, and b) shows the spatially smoothed effect of site location.

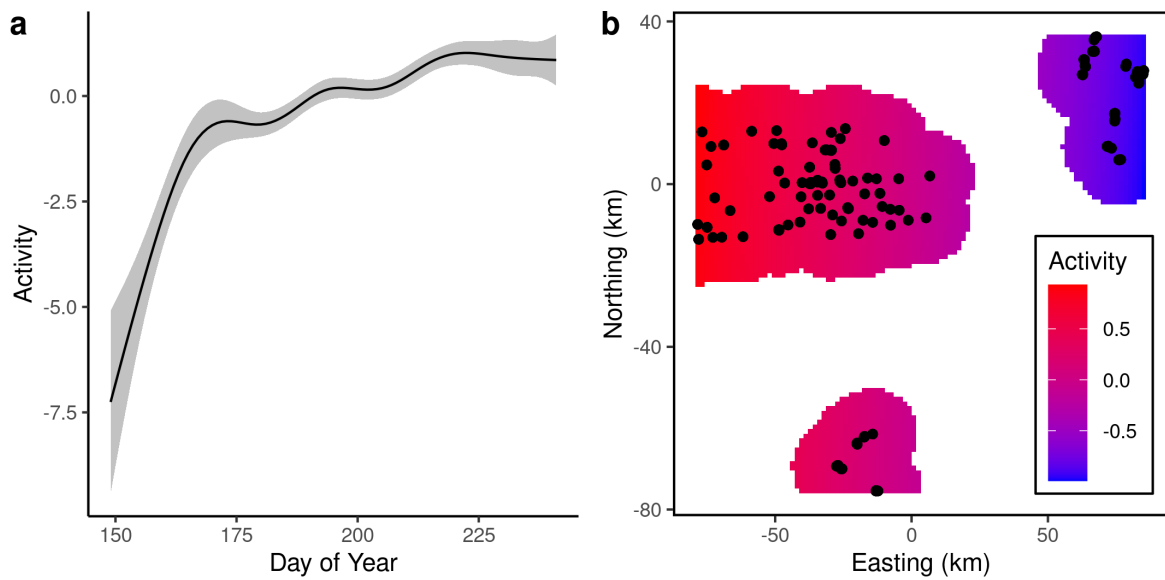


Figure S6: Temporal and spatial components of *Phalangium opilio* activity-density (after accounting for landscape composition and trap location). a) shows the effect of day of year, and b) shows the spatially smoothed effect of site location.

Table S1: Trap location (cover type that trap was located in) intercept estimates for *Pterostichus melanarius*

Trap location	β	S.E.	Z	p
Canola	0.96	0.52	1.86	0.063
Road margin	-0.52	0.45	-1.16	0.247
Grassland	-0.43	0.78	-0.56	0.578
Field edge	-0.02	0.59	-0.04	0.972
Wetland	0.09	0.56	0.16	0.874

Table S2: Smooth terms for *Pterostichus melanarius*. *s* indicates a thin-plate spline, *ti* indicates a tensor-product interaction. All terms except for day and (E,N) are functional regression fits.

Smoothing term	E.d.f.	χ^2	p
s(Day)	3.48	31.11	<0.001
s(E,N)	39.47	309.8	<0.001
s(Distance):Grassland	1.51	11.24	<0.001
s(Day):Grassland	<0.01	<0.01	0.768
ti(Distance,Day):Grassland	0.93	3.87	0.026
s(Distance):Canola	1.71	7.36	0.004
s(Day):Canola	<0.01	<0.01	0.822
ti(Distance,Day):Canola	1.64	8.86	0.002
s(Distance):Pasture	<0.01	<0.01	1
s(Day):Pasture	0.67	0.92	0.228
ti(Distance,Day):Pasture	<0.01	<0.01	0.975
s(Distance):Woodland	<0.01	<0.01	0.433
s(Day):Woodland	<0.01	<0.01	1
ti(Distance,Day):Woodland	<0.01	<0.01	1
s(Distance):Pulses	<0.01	<0.01	0.49
s(Day):Pulses	1.27	3.96	0.034
ti(Distance,Day):Pulses	1.4	2.24	0.163
s(Distance):Urban	<0.01	<0.01	0.276
s(Day):Urban	<0.01	<0.01	0.559
ti(Distance,Day):Urban	<0.01	<0.01	0.567

Table S3: Trap location (cover type that trap was located in) intercept estimates for *Pardosa distincta*

Trap location	β	S.E.	Z	p
Canola	-2.91	0.16	-17.77	<0.001
Road margin	-0.42	0.11	-3.88	<0.001
Grassland	-0.94	0.23	-4.02	<0.001
Field edge	-0.24	0.33	-0.71	0.477
Wetland	-0.49	0.23	-2.12	0.034

Table S4: Smooth terms for *Pardosa distincta*. *s* indicates a thin-plate spline, *ti* indicates a tensor-product interaction. All terms except for day and (E,N) are functional regression fits.

Smoothing term	E.d.f.	χ^2	p
s(Day)	5.59	120.42	<0.001
s(E,N)	<0.01	<0.01	1
s(Distance):Grassland	<0.01	<0.01	1
s(Day):Grassland	<0.01	<0.01	0.965
ti(Distance,Day):Grassland	<0.01	<0.01	0.599
s(Distance):Canola	<0.01	<0.01	1
s(Day):Canola	<0.01	<0.01	0.635
ti(Distance,Day):Canola	0.75	2.18	0.077
s(Distance):Pasture	1.76	14.9	<0.001
s(Day):Pasture	0.46	0.66	0.202
ti(Distance,Day):Pasture	<0.01	<0.01	0.795
s(Distance):Woodland	0.01	0.01	0.1
s(Day):Woodland	1.61	7.74	0.005
ti(Distance,Day):Woodland	0.56	0.98	0.154
s(Distance):Pulses	<0.01	<0.01	0.675
s(Day):Pulses	<0.01	<0.01	0.922
ti(Distance,Day):Pulses	<0.01	<0.01	0.418
s(Distance):Urban	<0.01	<0.01	0.716
s(Day):Urban	0.7	1.03	0.224
ti(Distance,Day):Urban	<0.01	<0.01	0.977

Table S5: Trap location (cover type that trap was located in) intercept estimates for *Pardosa moesta*.

Trap location	β	S.E.	Z	p
Canola	-6.24	0.40	-15.76	<0.001
Road margin	-2.45	0.24	-10.22	<0.001
Grassland	-1.83	0.58	-3.18	0.001
Field edge	-3.30	0.58	-5.67	<0.001
Wetland	-2.57	0.40	-6.44	<0.001

Table S6: Smooth terms for *Pardosa moesta*. *s* indicates a thin-plate spline, *ti* indicates a tensor-product interaction. All terms except for day and (E,N) are functional regression fits.

Smoothing term	E.d.f.	χ^2	p
s(Day)	0.05	0.04	0.349
s(E,N)	1.96	50.7	<0.001
s(Distance):Grassland	1.87	14.39	<0.001
s(Day):Grassland	<0.01	<0.01	0.943
ti(Distance,Day):Grassland	<0.01	<0.01	1
s(Distance):Canola	<0.01	<0.01	0.334
s(Day):Canola	<0.01	<0.01	0.614
ti(Distance,Day):Canola	2.22	21.63	<0.001
s(Distance):Pasture	<0.01	<0.01	1
s(Day):Pasture	<0.01	<0.01	0.84
ti(Distance,Day):Pasture	1.6	2.96	0.112
s(Distance):Woodland	<0.01	<0.01	0.626
s(Day):Woodland	0.95	2.23	0.085
ti(Distance,Day):Woodland	<0.01	<0.01	0.41
s(Distance):Pulses	1.48	3.94	0.039
s(Day):Pulses	0.4	0.5	0.221
ti(Distance,Day):Pulses	<0.01	<0.01	1
s(Distance):Urban	<0.01	<0.01	0.886
s(Day):Urban	0.63	0.8	0.249
ti(Distance,Day):Urban	3.15	20.23	<0.001

Table S7: Trap location (cover type that trap was located in) intercept estimates for *Phalangium opilio*

Trap location	β	S.E.	Z	p
Canola	0.64	0.14	4.49	<0.001
Road margin	1.20	0.14	8.64	<0.001
Grassland	0.69	0.35	1.95	0.051
Field edge	1.68	0.30	5.52	<0.001
Wetland	1.73	0.25	6.92	<0.001

Table S8: Smooth terms for *Phalangium opilio*. *s* indicates a thin-plate spline, *ti* indicates a tensor-product interaction. All terms except for day and (E,N) are functional regression fits.

Smoothing term	E.d.f.	χ^2	p
s(Day)	7.2	141.89	< 0.001
s(E,N)	1.95	59.8	< 0.001
s(Distance):Grassland	1.69	50.17	< 0.001
s(Day):Grassland	<0.01	<0.01	0.685
ti(Distance,Day):Grassland	1.39	5.79	0.013
s(Distance):Canola	<0.01	<0.01	0.449
s(Day):Canola	<0.01	<0.01	0.901
ti(Distance,Day):Canola	<0.01	<0.01	0.657
s(Distance):Pasture	0.36	0.42	0.286
s(Day):Pasture	<0.01	<0.01	0.428
ti(Distance,Day):Pasture	<0.01	<0.01	0.561
s(Distance):Woodland	1.44	14.8	< 0.001
s(Day):Woodland	<0.01	<0.01	0.601
ti(Distance,Day):Woodland	1.81	4.06	0.074
s(Distance):Pulses	<0.01	<0.01	0.703
s(Day):Pulses	<0.01	<0.01	0.71
ti(Distance,Day):Pulses	1.23	1.88	0.188
s(Distance):Urban	0.79	1.94	0.091
s(Day):Urban	<0.01	<0.01	0.404
ti(Distance,Day):Urban	0.36	0.53	0.224

References

- Acosta, L.E. & Machado, G. (2007). Harvestmen: The biology of Opiliones. In: *Diet and foraging* (ed. Pinto-da-Rocha, M., R.). Harvard University Press, pp. 309–338.
- Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S. & Soluk, D.A. (1987). Ecological neighborhoods: Scaling environmental patterns. *Oikos*, 49, 340–346.
- Agriculture and Agri-Food Canada. (2018). *Annual Crop Inventory*. Available at: <https://open.canada.ca/data/en/dataset/ba2645d5-4458-414d-b196-6303ac06c1c9>. Last accessed.
- Ahrenfeldt, E.J., Klatt, B.K., Arildsen, J., Trandem, N., Andersson, G.S. & Tscharnkte, T. *et al.* (2015). Pollinator communities in strawberry crops - variation at multiple spatial scales. *Bulletin of Entomological Research*, 105, 497–506.
- Aitchison, C.W. (1984). Low temperature feeding by winter-active spiders. *The Journal of Arachnology*, 12, 297–305.
- Albrecht, M., Schmid, B., Obrist, M.K., Schüpbach, B., Kleijn, D. & Duelli, P. (2010). Effects of ecological compensation meadows on arthropod diversity in adjacent intensively managed grassland. *Biological Conservation*, 143, 642–649.

389 Allard, C.M. & Yeargan, K.V. (2005a). Diel activity patterns and microspatial distribution of
390 the harvestman *Phalangium opilio* (Opiliones, Phalangiidae) in soybeans. *Journal of Arachnology*, 33,
391 745–752.

392 Allard, C.M. & Yeargan, K.V. (2005b). Effect of diet on development and reproduction of the
393 harvestman *Phalangium opilio* (Opiliones: Phalangiidae). *Environmental Entomology*, 34, 6–13.

394 Bertrand, C., Burel, F. & Baudry, J. (2016). Spatial and temporal heterogeneity of the crop mosaic
395 influences carabid beetles in agricultural landscapes. *Landscape Ecology*, 31, 451–466.

396 Boetzel, F.A., Krimmer, E., Krauss, J. & Steffan-Dewenter, I. (2018). Agri-environmental schemes
397 promote ground-dwelling predators in adjacent oilseed rape fields: Diversity, species traits and distance-
398 decay functions. *Journal of Applied Ecology*, 56, 10–20.

399 Bourassa, S., Spence, J., Hartley, D.J. & Lee, S.I. (2011). Wing-dimorphism and population
400 expansion of *pterostichus melanarius* (Illiger, 1798) at small and large scales in central Alberta, Canada
401 (Coleoptera, Carabidae, Pterostichini). *ZooKeys*, 147, 545–558.

402 Bragg, P.D. & Holmberg, R.G. (2009). The harvestmen (Arachnida, Opiliones) of British Columbia.
403 *Journal of the Entomological Society of British Columbia*, 106, 29–37.

404 Buddle, C.M. (2000). Life history of *Pardosa moesta* and *Pardosa mackenziana* (Araneae, Lycosi-
405 dae) in central Alberta, Canada. *The Journal of Arachnology*, 28, 319–328.

406 Buja, A., Hastie, T. & Tibshirani, R. (1989). Linear smoothers and additive models. *The Annals*
407 *of Statistics*, 17, 453–510.

408 Busch, A.K. (2016). Life history of *Pterostichus melanarius* (Coleoptera: Carabidae) and its
409 importance for biological control in field crops. Master's thesis. Pennsylvania State University.

410 Cárcamo, H.A. & Spence, J.R. (1994). Crop type effects on the activity and distribution of ground
411 beetles (Coleoptera: Carabidae). *Environmental Entomology*, 23, 684–692.

412 Cárcamo, H., Pinzón, J., Leech, R. & Spence, J. (2014). Spiders (Arachnida: Araneae) of the
413 Canadian Prairies. In: *Arthropods of Canadian Grasslands (Volume 3): Biodiversity and Systematics*
414 *Part 1* (eds. Cárcamo, H.A. & Giberson, D.J.). Biological Survey of Canada, pp. 75–137.

415 Collins, J.A., Jennings, D.T. & Forsythe, H.Y. (1996). Effects of cultural practices on the spider
416 (Araneae) fauna of lowbush blueberry fields in Washington county, Maine. *The Journal of Arachnology*,
417 24, 43–57.

418 Desender, K. & Alderweireldt, M. (1988). Population dynamics of adult and larval carabid beetles
419 in a maize field and its boundary. *Journal of Applied Entomology*, 106, 13–19.

- 420 Diekötter, T., Kadoya, T., Peter, F., Wolters, V. & Jauker, F. (2010). Oilseed rape crops distort
421 plant-pollinator interactions. *Journal of Applied Ecology*, 47, 209–214.
- 422 Dominici, F. (2002). On the use of generalized additive models in time-series studies of air pollution
423 and health. *American Journal of Epidemiology*, 156, 193–203.
- 424 Dondale, C.D. & Redner, J.H. (1990). The insects and arachnids of Canada. In: *Part 17: The wolf*
425 *spiders, nurseryweb spiders and lynx spiders of Canada and Alaska. Araneae: Lycosidae, Pisauridae*
426 *and Oxyopidae*. Agriculture Canada.
- 427 Drapela, T., Frank, T., Heer, X., Moser, D. & Zaller, J.G. (2011). Landscape structure affects
428 activity density, body size and fecundity of *Pardosa* wolf spiders (Araneae: Lycosidae) in winter
429 oilseed rape. *European Journal of Entomology*, 108, 609–614.
- 430 Drapela, T., Moser, D., Zaller, J.G. & Frank, T. (2008). Spider assemblages in winter oilseed rape
431 affected by landscape and site factors. *Ecography*, 31, 254–262.
- 432 Duelli, P. & Obrist, M.K. (2003). Regional biodiversity in an agricultural landscape: The contri-
433 bution of seminatural habitat islands. *Basic and Applied Ecology*, 4, 129–138.
- 434 Edgar, A.L. (1990). Opiliones (Phalangida). In: *Soil biology guide* (ed. Dindal, D.L.). John Wiley
435 & Sons, Eastbourne, UK, pp. 529–581.
- 436 Fournier, E. & Loreau, M. (2002). Foraging activity of the carabid beetle *Pterostichus melanarius*
437 Ill. in field margin habitats. *Agriculture, Ecosystems & Environment*, 89, 253–259.
- 438 Gagic, V., Kleijn, D., Báldi, A., Boros, G., Jørgensen, H.B. & Elek, Z. *et al.* (2017). Combined
439 effects of agrochemicals and ecosystem services on crop yield across Europe. *Ecology Letters*, 20,
440 1427–1436.
- 441 Galpern, P. & Gavin, M.P. (2020). Assessing the potential to increase landscape complexity in
442 Canadian prairie croplands: A multi-scale analysis of land use pattern. *Frontiers in Environmental*
443 *Science*, 8.
- 444 Galpern, P., Johnson, S.A., Retzlaff, J.L., Chang, D. & Swann, J. (2017). Reduced abundance and
445 earlier collection of bumble bee workers under intensive cultivation of a mass-flowering prairie crop.
446 *Ecology and Evolution*, 7, 2414–2422.
- 447 Gardiner, M.M., Landis, D.A., Gratton, C., Schmidt, N., O’Neal, M. & Mueller, E. *et al.* (2010).
448 Landscape composition influences the activity density of Carabidae and Arachnida in soybean fields.
449 *Biological Control*, 55, 11–19.
- 450 Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R. & Cunningham,

451 S.A. *et al.* (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance.
452 *Science*, 339, 1608–1611.

453 González, E., Seidl, M., Kadlec, T., Ferrante, M. & Knapp, M. (2020). Distribution of ecosystem
454 services within oilseed rape fields: Effects of field defects on pest and weed seed predation rates.
455 *Agriculture, Ecosystems & Environment*, 295, 106894.

456 Graham, A.K., Buddle, C.M. & Spence, J.R. (2003). Habitat affinities of spiders living near a
457 freshwater pond. *Journal of Arachnology*, 31, 78–89.

458 Greenstone, M.H. (1982). Ballooning frequency and habitat predictability in two wolf spider species
459 (Lycosidae: Pardosa). *The Florida Entomologist*, 65, 83–89.

460 Halaj, J. & Cady, A.B. (2000). Diet composition and significance of earthworms as food of har-
461 vestmen (Arachnida: Opiliones). *The American Midland Naturalist*, 143, 487–491.

462 Hamon, N., Bardner, R., Allen-Williams, L. & Lee, J. (1990). Carabid populations in field beans
463 and their effect on the population dynamics of *Sitona lineatus* (L.). *Annals of Applied Biology*, 117,
464 51–62.

465 Hatten, T.D., Bosque-Pérez, N.A., Labonte, J.R., Guy, S.O. & Eigenbrode, S.D. (2007). Effects of
466 tillage on the activity density and biological diversity of carabid beetles in spring and winter crops.
467 *Environmental Entomology*, 36, 356–368.

468 Hilbe, J.M. (2011). *Negative binomial regression*. Cambridge University Press.

469 Karp, D.S., Chaplin-Kramer, R., Meehan, T.D., Martin, E.A., DeClerck, F. & Grab, H. *et al.*
470 (2018). Crop pests and predators exhibit inconsistent responses to surrounding landscape composition.
471 *Proceedings of the National Academy of Sciences*, 115, E7863–E7870.

472 Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A. & Kremen, C.
473 *et al.* (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the*
474 *Royal Society B: Biological Sciences*, 274, 303–313.

475 Kowal, V.A. & Cartar, R.V. (2011). Edge effects of three anthropogenic disturbances on spider
476 communities in Alberta’s boreal forest. *Journal of Insect Conservation*, 16, 613–627.

477 Landis, D.A., Wratten, S.D. & Gurr, G.M. (2000). Habitat management to conserve natural
478 enemies of arthropod pests in agriculture. *Annual Review of Entomology*, 45, 175–201.

479 Lang, A. (2000). The pitfalls of pitfalls: A comparison of pitfall trap catches and absolute density
480 estimates of epigeal invertebrate predators in arable land. *Journal of Pest Science*, 73, 99–1006.

481 Larsen, K.J., Work, T.T. & Purrington, F.F. (2003). Habitat use patterns by ground beetles

(Coleoptera: Carabidae) of northeastern Iowa. *Pedobiologia*, 47, 288–299.

Lima, S.L. & Zollner, P.A. (1996). Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution*, 11, 131–135.

Losey, J.E. & Vaughan, M. (2006). The economic value of ecological services provided by insects. *BioScience*, 56, 311.

Lövei, G.L. & Sunderland, K.D. (1996). Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology*, 41, 231–256.

Macfadyen, S. & Muller, W. (2013). Edges in agricultural landscapes: Species interactions and movement of natural enemies. *PLoS ONE*, 8, e59659.

Marra, G. & Wood, S.N. (2011). Practical variable selection for generalized additive models. *Computational Statistics & Data Analysis*, 55, 2372–2387.

Martin, A.E., Collins, S.J., Crowe, S., Girard, J., Naujokaitis-Lewis, I. & Smith, A.C. *et al.* (2020). Effects of farmland heterogeneity on biodiversity are similar to – or even larger than – the effects of farming practices. *Agriculture, Ecosystems & Environment*, 288, 106698.

Moring, J.B. & Stewart, K.W. (1994). Habitat partitioning by the wolf spider (Araneae, Lycosidae) guild in streamside and riparian vegetation zones of the Conejos River, Colorado. *The Journal of Arachnology*, 22, 205–217.

Muster, C. & Meyer, M. (2014). *Ferrantia*. Travaux scientifiques du musée national d’histoire naturelle de luxembourg. Musée national d’histoire naturelle, Luxembourg.

Nakagawa, S., Johnson, P.C.D. & Schielzeth, H. (2017). The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of The Royal Society Interface*, 14, 20170213.

Nakagawa, S., Schielzeth, H. & O’Hara, R.B. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142.

Natural Regions Committee. (2006). *Natural regions and subregions of Alberta*. Government of Alberta, Edmonton.

Niemelä, J. & Spence, J.R. (1999). Dynamics of local expansion by an introduced species: *Pterostichus melanarius* Ill. (Coleoptera, Carabidae) in Alberta, Canada. *Diversity and Distributions*, 5, 121–127.

Oerke, E.C. (2005). Crop losses to pests. *The Journal of Agricultural Science*, 144, 31–43.

Öberg, S., Ekbom, B. & Bommarco, R. (2007). Influence of habitat type and surrounding landscape

on spider diversity in Swedish agroecosystems. *Agriculture, Ecosystems & Environment*, 122, 211–219.

Öberg, S., Mayr, S. & Dauber, J. (2008). Landscape effects on recolonisation patterns of spiders in arable fields. *Agriculture, Ecosystems & Environment*, 123, 211–218.

Purtauf, T., Roschewitz, I., Dauber, J., Thies, C., Tscharnkte, T. & Wolters, V. (2005). Landscape context of organic and conventional farms: Influences on carabid beetle diversity. *Agriculture, Ecosystems & Environment*, 108, 165–174.

Ramsay, J.O. & Silverman, B.W. (2004). *Functional data analysis*. Springer series in statistics. 2nd edn. Springer.

Ramsay, T.O., Burnett, R.T. & Krewski, D. (2003). The effect of concurvity in generalized additive models linking mortality to ambient particulate matter. *Epidemiology*, 14, 18–23.

Richter, C.J.J. (1970). Aerial dispersal in relation to habitat in eight wolf spider species (Pardosa, Araneae, Lycosidae). *Oecologia*, 5, 200–214.

Roulston, T.H. & Goodell, K. (2011). The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology*, 56, 293–312.

Sander, A.-C., Purtauf, T., Wolters, V. & Dauber, J. (2006). Landscape genetics of the widespread ground-beetle *Carabus auratus* in an agricultural region. *Basic and Applied Ecology*, 7, 555–564.

Shackelford, G., Steward, P.R., Benton, T.G., Kunin, W.E., Potts, S.G. & Biesmeijer, J.C. *et al.* (2013). Comparison of pollinators and natural enemies: A meta-analysis of landscape and local effects on abundance and richness in crops. *Biological Reviews*, 88, 1002–1021.

Shmida, A. & Wilson, M.V. (1985). Biological determinants of species diversity. *Journal of Biogeography*, 12, 1–20.

Šajna, N., Kušar, P., Novak, L.S. & Novak, T. (2011). Benefits of low-intensity grazing: Co-occurrence of umbelliferous plant (*Hladnikia pastinacifolia* RCHB.) and opilionid species (*Phalangium opilio* L.) in dry, calcareous grassland. *Polish Journal of Ecology*, 59, 777–786.

Trichard, A., Ricci, B., Ducourtieux, C. & Petit, S. (2014). The spatio-temporal distribution of weed seed predation differs between conservation agriculture and conventional tillage. *Agriculture, Ecosystems & Environment*, 188, 40–47.

Tscharnkte, T., Karp, D.S., Chaplin-Kramer, R., Batáry, P., DeClerck, F. & Gratton, C. *et al.* (2016). When natural habitat fails to enhance biological pest control – five hypotheses. *Biological Conservation*, 204, 449–458.

Tscharnkte, T., Rand, T.A. & Bianchi, F.J.J.A. (2005). The landscape context of trophic interac-

544 tions: Insect spillover across the crop–noncrop interface. *Annales Zoologici Fennici*, 42, 421–432.

545 Van de Poel, S. (2015). Harvestman communities in small forest patches in European agricultural
546 landscapes. Master’s thesis. University of Antwerp.

547 Vankosky, M.A., Cárcamo, H.A. & Dosdall, L.M. (2011). Identification of potential natural enemies
548 of the pea leaf weevil, *Sitona lineatus* L. in western Canada. *Journal of Applied Entomology*, 135, 293–
549 301.

550 Vogel, B.R. (2004). A review of the spider genera *Pardosa* and *Acantholycosa* (Araneae, Lycosidae)
551 of the 48 contiguous United States. *Journal of Arachnology*, 32, 55–108.

552 Wade, D.J. & Roughley, R.E. (2010). Arthropods of Canadian grasslands (Volume 1): Ecology
553 and interactions in grassland habitats. In: (eds. Shorthouse, J.D. & Floate, K.D.). Biological Survey
554 of Canada, pp. 237–249.

555 Westphal, C., Steffan-Dewenter, I. & Tschardtke, T. (2006). Bumblebees experience landscapes at
556 different spatial scales: Possible implications for coexistence. *Oecologia*, 149, 289–300.

557 Winfree, R., W. Fox, J., Williams, N.M., Reilly, J.R. & Cariveau, D.P. (2015). Abundance of
558 common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters*,
559 18, 626–635.

560 Wood, S.N. (2017). *Generalized additive models: An introduction with R*. CRC press.

561 Yen, J.D.L., Thomson, J.R., Paganin, D.M., Keith, J.M. & Mac Nally, R. (2014). Function regres-
562 sion in ecology and evolution: FREE. *Methods in Ecology and Evolution*, 6, 17–26.

563 Yigit, N., Bayram, A., Corak, I. & Danisman, T. (2007). External morphology of the male har-
564 vestman *Phalangium opilio* (Arachnida: Opiliones). *Annals of the Entomological Society of America*,
565 100, 574–581.

566 Young, O.P. & Edwards, G.B. (1990). Spiders in United States field crops and their potential effect
567 on crop pests. *The Journal of Arachnology*, 18, 1–27.

568 Zhao, Z.-H., Shi, P.-J., Hui, C., Ouyang, F., Ge, F. & Li, B.-L. (2013). Solving the pitfalls of
569 pitfall trapping: A two-circle method for density estimation of ground-dwelling arthropods. *Methods*
570 *in Ecology and Evolution*, 4, 865–871.