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

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Abstract

1. 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 a destination for arthropods at different times of the year, but this is rarely considered.
2. We modeled the abundance of four common species of Canadian prairie arthropods caught in a set of 198 in-field and roadside pitfall traps (June to August of 2017). Functional regression was used in order to simultaneously consider both the habitat preferences and the timing of movement from the land cover classes.
3. *Pterostichus melanarius* (Coleoptera: Carabidae) and *Pardosa moesta* (Araneae: Lycosidae) were attracted to canola (*Brassica napus*) during the early summer, then dispersed to grasslands, wetlands, and grassy road margins at the end of the summer. In particular, *Pterostichus melanarius* aggregated in canola early in the growing season, suggesting that its role in suppressing crop pests may be underestimated. *Pardosa moesta* (Araneae: Lycosidae) and *Phalangium opilio* (Opiliones: Opilionidae) showed weak patterns of seasonal migration, and were more influenced by large-scale geographic patterns rather than landscape composition.
4. Synthesis and applications: Our results suggest that predatory arthropods migrate into canola crops during the early summer, and that grasslands and wetlands act as seasonal reservoir habitats. Farmers and land managers should consider preserving existing habitat in order to maintain pest-control services across the season.

Keywords: beetles; spiders; harvestmen; movement; ecosystem services; natural enemy; functional data analysis; seminatural land

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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 Tscharntke *et al.* 2016; Karp *et al.* 2018). For example, wild bee abundance in agricultural landscapes is driven by food 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 forages.

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; Tscharntke *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 on May 16, and collections ended on August 28, with collection occurring continuously and traps being emptied every 14 days on average (SD: 3). This resulted in 850 unique collection events, taking place across a total of 11614 trapping days. In-field traps were placed in canola crops (68), wetlands (16), grassy field edges (11), and remnant prairie grasslands (18). Traps in canola were installed at 25, 75, and 200 m along a transect heading away from the nearest non-crop feature (wetland, grassy field edges, or remnant prairie), while the trap at 0 m was installed in the non-crop feature itself. We used 582 mL Solo® cups buried up to the rim and partially filled with propylene glycol, with 2 cm wire mesh mounted over the rim to prevent vertebrates from falling into the traps. Specimens were identified to species using appropriate taxonomic literature (Lindroth 1966; Dondale & Redner 1990; Edgar 1990; Vogel 2004; Yigit *et al.* 2007).

We used counts of organisms in our pitfall traps as proxies of ecosystem services (specifically, pest control). However, increased counts of organisms in pitfall traps can represent higher activity levels (same number of organisms but more mobile) or higher abundances in the vicinity of the trap. This makes it impossible to disentangle arthropod activity from density using single traps (Lang 2000), meaning that counts from traps represent the "activity-density" of a given organism, not absolute density. Despite this drawback, activity-density is generally positively related to pest consumption, at least in carabids (Trichard *et al.* 2014; Boetzl *et al.* 2018; González *et al.* 2020), making it acceptable for our study.

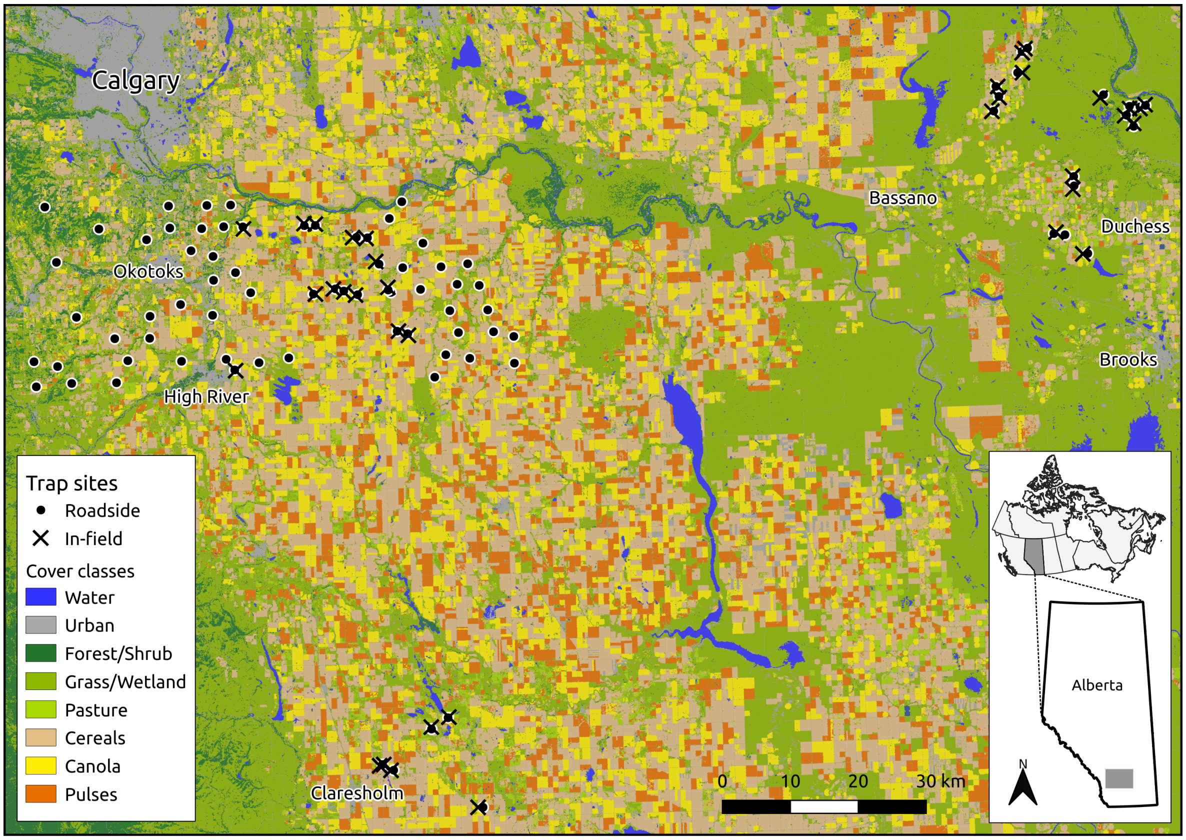

Figure 1: Classified land cover and location of pitfall traps during 2017. Inset map shows study location within Alberta provincial boundaries. Roadside traps were installed in road margins, while in-field traps were installed directly in canola fields, wetlands, or grassy field edges.

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: Phalangiidae) 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 2005a), mainly eating small soft-bodied invertebrates (Allard & Yeargan 2005b; 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 landscape 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 regression 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 ($\beta_i = f(distance_i)$), 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 not constitute a completely usable habitat.

Scalar-on-function regression of activity-density was fit using generalized additive models (*mgcv* version 1.8.33; Wood 2017). Count data of arthropods were modeled using a negative binomial distribution with a log-link function and a single dispersion parameter (θ). To account for different lengths of trap exposure, log-days since trap placement were used as a fixed effect with their slope held at 1 ("offset" variable). Trapping location was included as a fixed effect with 5 levels (canola, field edge, grassland, road margin, and wetlands) to account for the effect of local cover independent of the surrounding landscape composition. Day of year was included as a 1-dimensional smooth, and easting and northing (km east and north of the trap extent centre point) were included as 2-dimensional smooths, in order to account for underlying spatial and temporal autocorrelation in the data.

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

Preliminary model fits revealed that some of the landscape terms in our model were strongly concurved with each other, so we removed them from the model or combined them. Concurvity is a nonlinear analogue of multicollinearity which can bias estimates of standard errors (Buja *et al.* 1989). There is no agreed-upon threshold of "unacceptable" concurvity, but 0.5 is commonly used (Dominici 2002; Ramsay *et al.* 2003). Forests and shrubland were combined into a single "woodland" category, and grassland and wetland were combined into a single "grassland" category, as they were strongly positively correlated at all distances, indicating similar feature classes. Cereal was removed from the model, as it was negatively correlated with canola cover at distances less than 200m and was positively correlated at distances over 500m, reflecting the most common crop rotations (canola → wheat → barley) and the commonly-used 800 m block structure of farmland in our study region (quarter-sections). This resulted in a reduced set of landscape terms, none of which were strongly concurved with each other (cropland: canola, pulses; SNL: grassland, pasture, woodland, roadside; see Figure S1).

Functional regression plots of landscape composition reveal which cover classes are acting as sources or destinations of a given arthropod, and at what spatial scale (Figure S7). Positive effects of nearby landscape cover classes indicate that arthropods are spilling over *from* it, therefore acting as a source. However, negative responses to nearby landscape cover classes can indicate one of two things: 1) It may indicate that arthropods are spilling over *into* it (therefore acting as a destination) or 2) it may indicate that no arthropods are available to spill over *from* it. We consider 1) to be the more likely scenario, as it is unlikely that any one cover class is *completely* unoccupied. For example, a cover class with low-quality habitat could act as an ecological trap (Galpern *et al.* 2017) if it acts as a destination but never as a source. Alternatively, a cover class could act as a destination by providing high-quality habitat at certain times of the year (e.g. egg laying/feeding), but act as a source at other times (e.g. during emergence).

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

3. Results

3.1. Landscape composition and trap catches

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

3.2. Ground beetle: *Pterostichus melanarius*

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

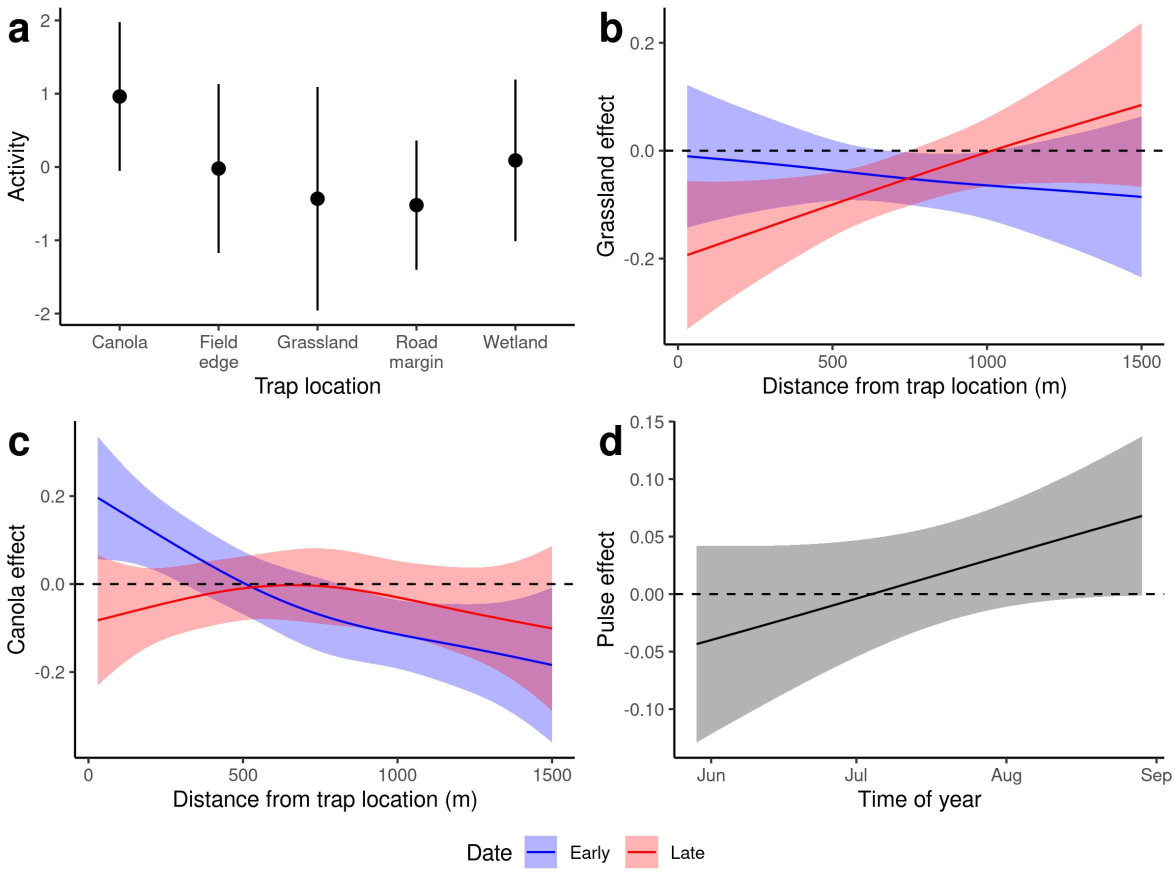

Figure 2: Landscape influence on *Pterostichus melanarius* activity-density. a) shows the effect of local trap location, and b-c) are functional regression plots of the proportion grassland and canola at distances away from each trap. d) is a functional regression plot over time, showing the effect of pulses at different times of the year. Lines and dots represent means, and bars and shaded regions represent 95 % confidence regions (1.96 x 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 3a, 4a). Activity-density of both *Pardosa* species had a strong temporal and spatial component, although the temporal component was dominant for *P. distincta*, whereas the spatial component was dominant for *P. moesta* (Figures S4 and S5; both p<0.001).

P. distincta activity-density was negatively affected by landscape-level pasture (Figure 3b), while woodlands had a negative effect late in the season (Figure 3c). This suggests that large amounts of pasture are unsuitable habitat for *P. distincta*, and that they migrate into woodlands later in the season.

However, trap location and the temporal random effect (Figure S4a) explained roughly 10 times more variance than landscape composition (R^2: 0.45 versus 0.045), meaning that while *P. distincta* may be locally abundant in certain cover types, it is highly general in its overall habitat preferences.

P. moesta activity-density responded to grassland, canola, and road margins. Grasslands had a local negative effect, but a positive landscape-level effect, indicating that while these cover types act as a local destination, the general amount of grassland in the area had a positive effect (Figure 4b). Local canola cover had a positive early effect on activity-density, but a negative local effect later in the season (Figure 4c). Local road margins also had a similar effect, acting as an early source and a late destination (Figure 4d). Pulses also had a positive effect at the landscape level (Figure 4e), but this explained very little variance in *P. moesta* activity-density (Table 1, R^2: 0.004). Similar to *P.distincta*, trap location and an East-West spatial random effect (Figure S5b) explained roughly 5 times more variance in *P. moesta* activity-density than landscape composition (R^2: 0.5 versus 0.096), meaning that *P. moesta* is also fairly general in its overall habitat preferences, and is influenced more heavily by larger-scale abiotic factors.

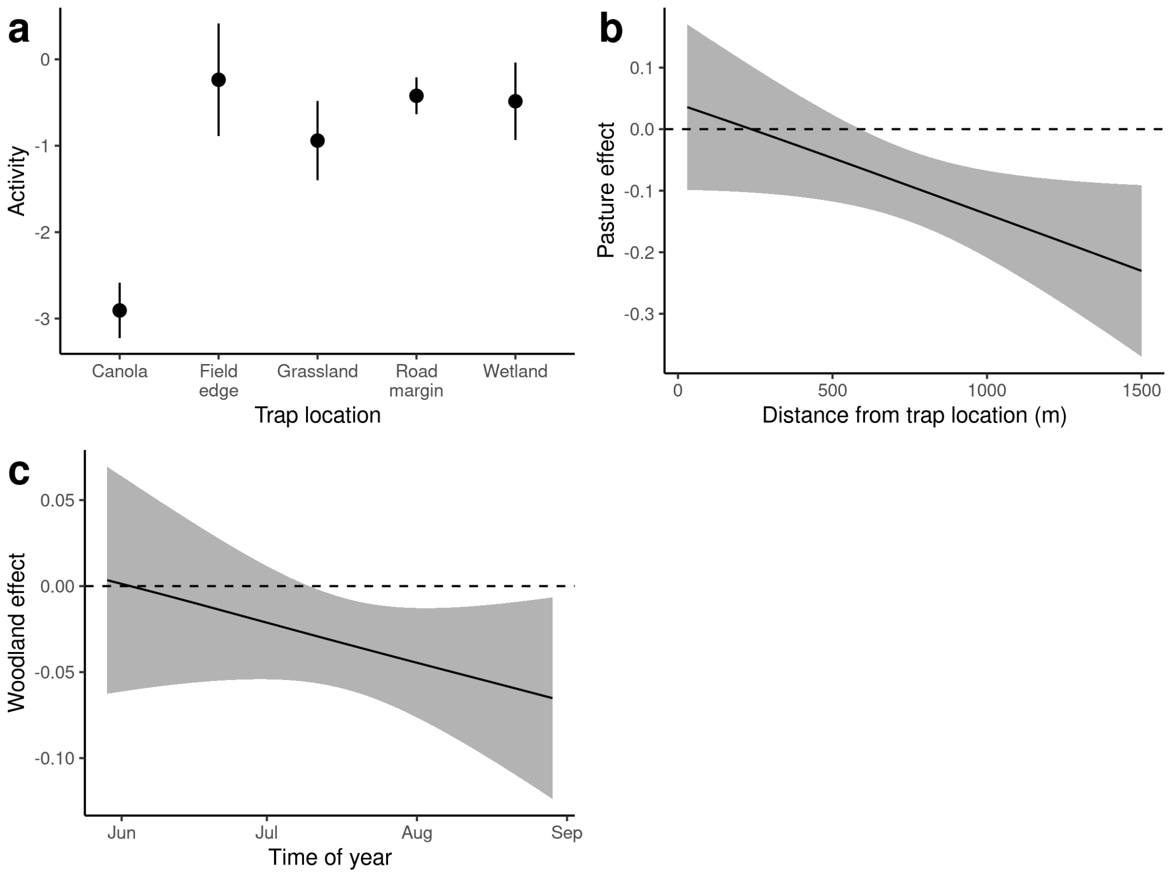

Figure 3: Landscape influence on *Pardosa distincta* activity-density. a) shows the effect of local trap location, b) is a functional regression plot of the proportion pasture at distances away from each trap, and c) is a functional regression plot over time, showing the effect of woodland at different times of the year. Lines and dots represent means, and bars and shaded regions represent 95 % confidence regions (1.96 x SE).

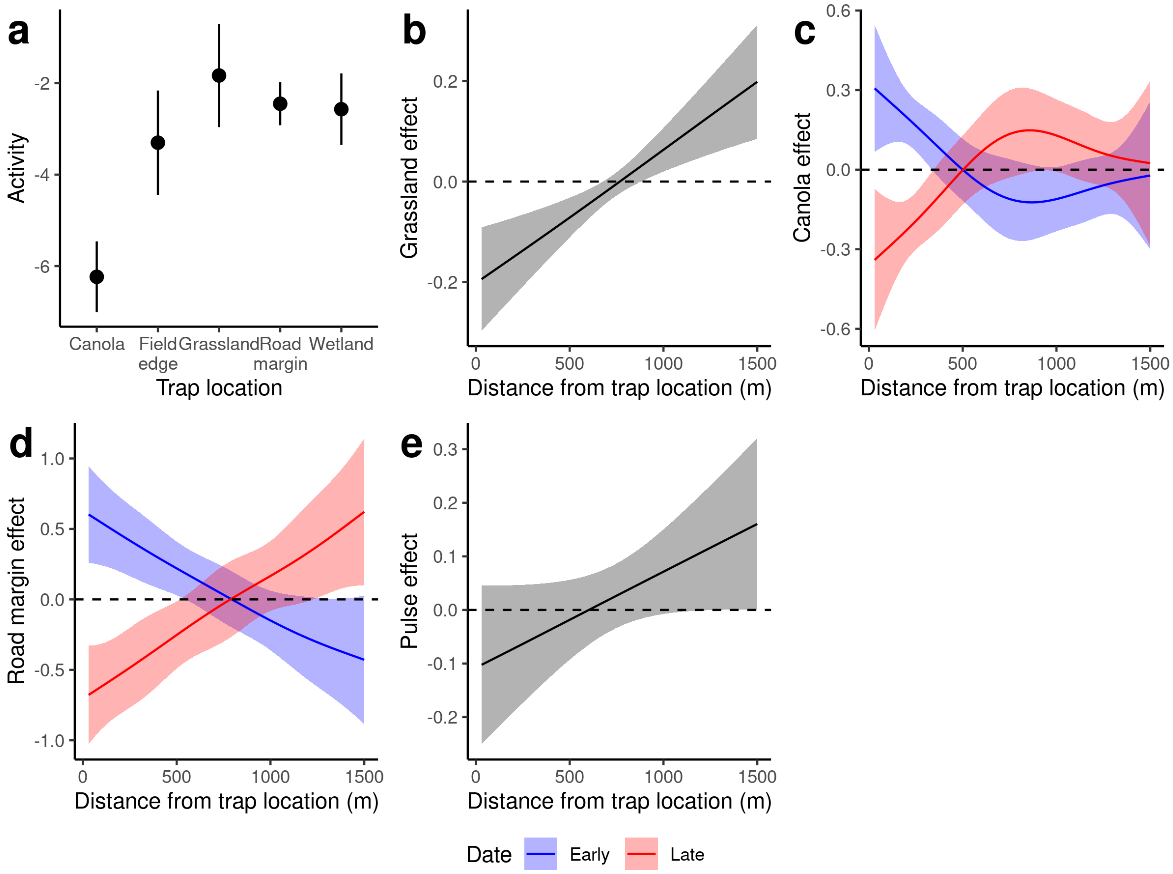

Figure 4: Landscape influence on *Pardosa moesta* activity-density. a) shows the effect of local trap location, and b-e) are functional regression plots of the proportion grassland, canola, road margins, and pulses at distances away from each trap. Lines and dots represent means, and bars and shaded regions represent 95 % confidence regions (1.96 x 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 5a), 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 5b,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), indicating that their activity-density is also influenced by larger-scale abiotic factors.

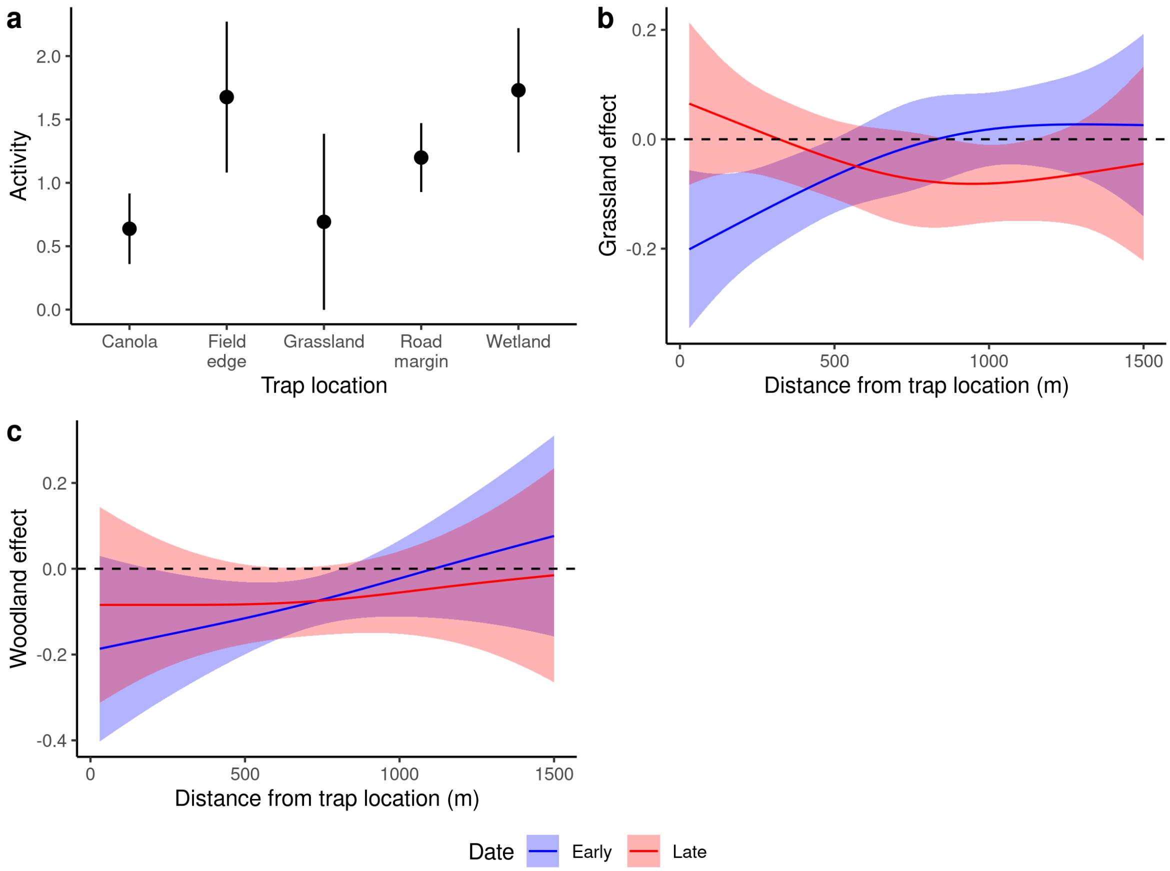

Figure 5: Landscape influence on *Phalangium opilio* activity-density. a) shows the effect of local trap location, and b-c) are functional regression plots of the proportion grassland and woodland at distances away from each trap. Lines and dots represent means, and bars and shaded regions represent 95 % confidence regions (1.96 x SE). Coloured regions represent early- and late-season effects (blue = June, red = August).

4. Discussion

Our prediction of SNL having late-season effects on beneficial arthropods was supported (Table 2). Specifically, grassland had a negative effect on *P. melanarius* activity-density, woodlands on *P. distincta* activity-density, and road margins on *P. moesta* activity-density, all during late summer (August - September). This suggests that these arthropods migrate to these habitats at the end of the summer to prepare for oviposition or overwintering. However, *P. opilio* showed no evidence of this, instead showing a negative effect of grassland *early* in the season, suggesting that a) they aggregate in 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	*Pterostichus melanarius*	*Pardosa distincta*	*Pardosa moesta*	*Phalangium opilio*
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
Pterostichus melanarius	· Moves to canola during early season · Disperses to grassland during late season	High
Pardosa distincta	· Negative effect of pasture · May move locally to field edges	Low
Pardosa moesta	· Moves to canola during early season · Disperses to road margins and grassland during late season ·Moves to grasslands across the season.	Medium
Phalangium opilio	· Moves to grassland early in the season	Low

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

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

1999; Bourassa *et al.* 2011), which may influence the degree to which landscape-level proportion cover impacts activity-density.

The wolf spiders *Pardosa distincta* and *Pardosa moesta* both responded to landscape composition, but it explained only a small fraction of their activity-density (R^2: 0.045, 0.096). This means that both species of *Pardosa* appear to have very general habitat preferences, but may be somewhat influenced by certain cover types. Pasture had a negative effect at the landscape scale, and woodland had a late-season negative effect, suggesting that *P. distincta* move to woodlands for overwintering or winter foraging (Aitchison 1984; Buddle 2000). *Pardosa* are found in areas close to disturbed roadside strips (Drapela *et al.* 2008, 2011; Kowal & Cartar 2011), but *P. distincta* appears to be less sensitive to disturbances than *P. moesta* (Collins *et al.* 1996; Wade & Roughley 2010). Moring & Stewart (1994) showed that *P. distincta* were active in grassy habitats, which we found partial evidence of, as *P. distincta* tended to have higher activity-density in trap locations with higher grass cover (Figure 3a). Canola had an early-season positive effect on *P. moesta*, indicating that *P. moesta* and *P. melanarius* may both use canola as foraging grounds. We also found that road margins had a positive early-season and a negative late-season effect (similar to Drapela *et al.* 2008). Grassland and pulses also had a local negative effect but a positive landscape-level effect; this suggests that they may constitute suitable habitat for *P. moesta* and attract them away from other cover types. Wolf spiders (Lycosidae) employ a wandering-active predation strategy (Young & Edwards 1990), meaning that nearby landscape composition may be more influential to *Pardosa* than large-scale composition (Öberg *et al.* 2007, 2008). While trapping location explained a large proportion of variance for both species (0.29 and 0.38), several landscape features were also important at large spatial scales, including grass and wetland, pasture, pulses, and road margins. Therefore, *Pardosa* dispersal distances may be further than previously thought, either through ballooning as juveniles (Richter 1970; Greenstone 1982) or through other long-distance travel.

Phalangium opilio activity-density responded to grass and wetland cover, as well as wooded landscapes. Other studies have found that *P. opilio* is mostly found in human-altered landscapes with a large proportion of farming (Muster & Meyer 2014; Van de Poel 2015). Since most of our study area was in or near farmed land, the lack of variation is understandable, but there were a few notable landscape-level patterns that emerged. *P. opilio* activity-density was higher in grassy field edges and wetlands, but grasslands and wetlands had a local negative effect on *P. opilio* until late in the season. 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 (rainfall or temperature) are more important influences on 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).

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

5. Authors' contributions

SVJR and PG conceived of the project. JV, DE, and LB conducted field work and taxonomic work. SVJR designed the statistical analysis and wrote the manuscript. JV, DE, LB, and PG all gave critical feedback on the manuscript, and give their approval for the final version.

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References

Acosta, L. & 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., Klatt, B., Arildsen, J., Trandem, N., Andersson, G. & Tscharntke, 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.

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

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

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

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

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

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

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

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

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

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

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

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

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

Diekötter, T., Kadoya, T., Peter, F., Wolters, V. & Jauker, F. (2010). Oilseed rape crops distort plant-pollinator interactions. *Journal of Applied Ecology*, 47, 209–214.

Dominici, F. (2002). On the use of generalized additive models in time-series studies of air pollution and health. *American Journal of Epidemiology*, 156, 193–203.

Dondale, C. & Redner, J. (1990). The insects and arachnids of Canada. In: *Part 17: The wolf spiders, nurseryweb spiders and lynx spiders of Canada and Alaska. Araneae: Lycosidae, Pisauridae and Oxyopidae*. Agriculture Canada.

Drapela, T., Frank, T., Heer, X., Moser, D. & Zaller, J.G. (2011). Landscape structure affects activity density, body size and fecundity of *Pardosa* wolf spiders (Araneae: Lycosidae) in winter oilseed rape. *European Journal of Entomology*, 108, 609–614.

Drapela, T., Moser, D., Zaller, J.G. & Frank, T. (2008). Spider assemblages in winter oilseed rape affected by landscape and site factors. *Ecography*, 31, 254–262.

Duelli, P. & Obrist, M.K. (2003). Regional biodiversity in an agricultural landscape: The contribution of seminatural habitat islands. *Basic and Applied Ecology*, 4, 129–138.

Edgar, A.L. (1990). Opiliones (Phalangida). In: *Soil biology guide* (ed. Dindal, D.L.). John Wiley & Sons, Eastbourne, UK, pp. 529–581.

Fournier, E. & Loreau, M. (2002). Foraging activity of the carabid beetle *Pterostichus melanarius* Ill. in field margin habitats. *Agriculture, Ecosystems & Environment*, 89, 253–259.

Gagic, V., Kleijn, D., Báldi, A., Boros, G., Jørgensen, H.B. & Elek, Z. *et al.* (2017). Combined effects of agrochemicals and ecosystem services on crop yield across Europe. *Ecology Letters*, 20, 1427–1436.

Galpern, P. & Gavin, M.P. (2020). Assessing the potential to increase landscape complexity in Canadian prairie croplands: A multi-scale analysis of land use pattern. *Frontiers in Environmental Science*, 8.

Galpern, P., Johnson, S.A., Retzlaff, J.L., Chang, D. & Swann, J. (2017). Reduced abundance and earlier collection of bumble bee workers under intensive cultivation of a mass-flowering prairie crop. *Ecology and Evolution*, 7, 2414–2422.

Gardiner, M., Landis, D., Gratton, C., Schmidt, N., O'Neal, M. & Mueller, E. *et al.* (2010). Landscape composition influences the activity density of Carabidae and Arachnida in soybean fields. *Biological Control*, 55, 11–19.

Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R. & Cunningham, S.A.

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

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

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

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

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

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

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

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

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

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

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

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

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

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.

Lindroth, C.H. (1966). The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part 4. *Opuscula Entomologica Supplementum*, 409–648.

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.

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.

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

Purtauf, T., Roschewitz, I., Dauber, J., Thies, C., Tscharntke, 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.

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

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.

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.

Tscharntke, 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.

Tscharntke, T., Rand, T.A. & Bianchi, F.J.J.A. (2005). The landscape context of trophic interactions: Insect spillover across the crop–noncrop interface. *Annales Zoologici Fennici*, 42, 421–432.

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

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

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

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

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

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

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

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

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

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

Appendix A: Supplementary Material

	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.

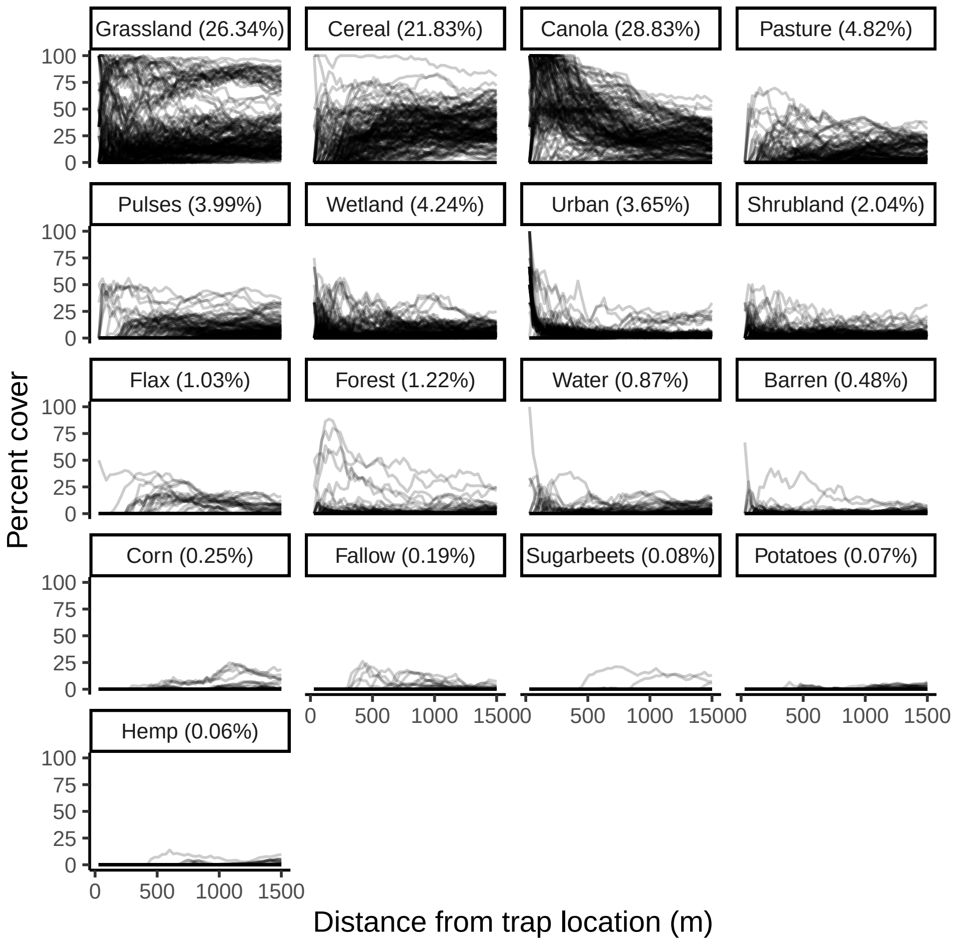

Figure S2: Percent cover of landscape cover classes in annuli surrounding each trap location. Sites are represented by individual lines. Mean cover for each class is listed in each sub-heading.

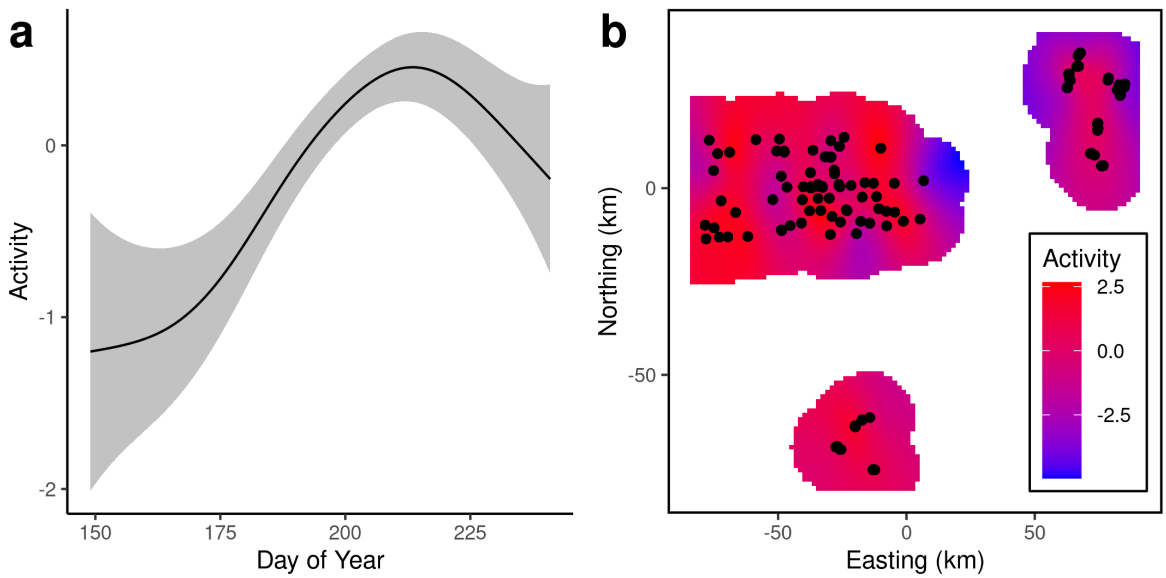

Figure S3: Temporal and spatial components of *Pterostichus melanarius* activity-density (after accounting for landscape composition and trap location). a) shows the effect of day of year, and b) shows the spatially smoothed effect of site location.

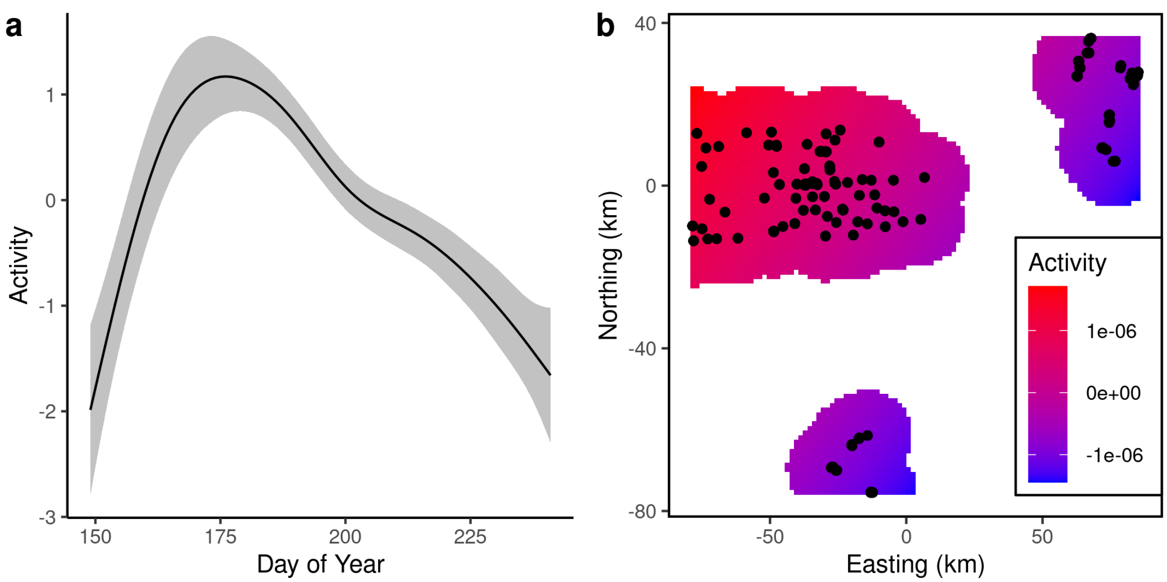

Figure S4: Temporal and spatial components of *Pardosa distincta* activity-density (after accounting for landscape composition and trap location). a) shows the effect of day of year, and b) shows the spatially smoothed effect of site location.

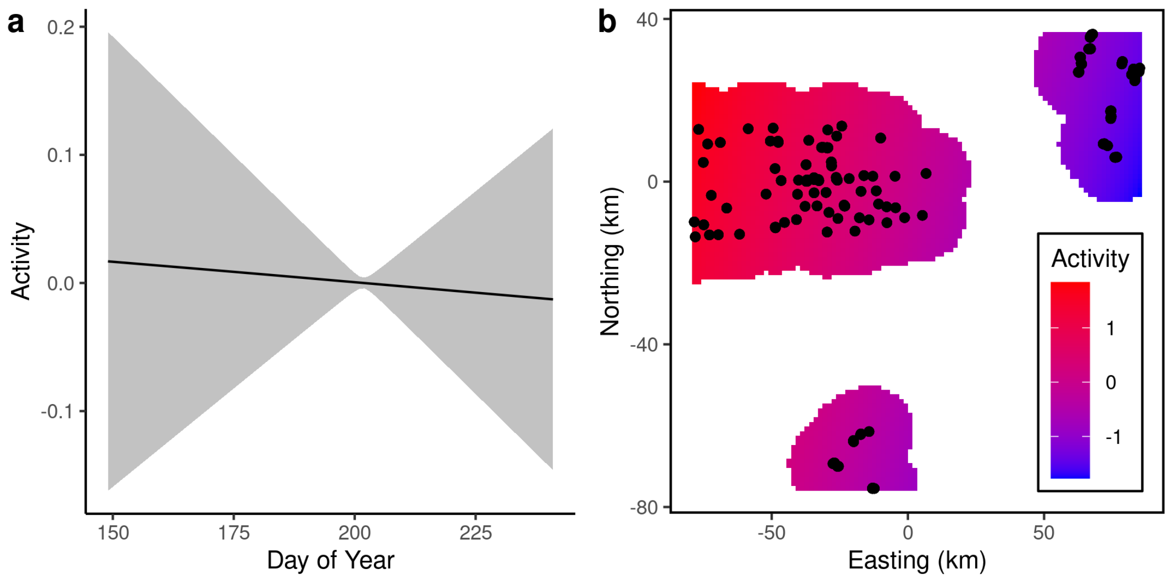

Figure S5: Temporal and spatial components of *Pardosa moesta* activity-density (after accounting for landscape composition and trap location). a) shows the effect of day of year, and b) shows the spatially smoothed effect of site location.

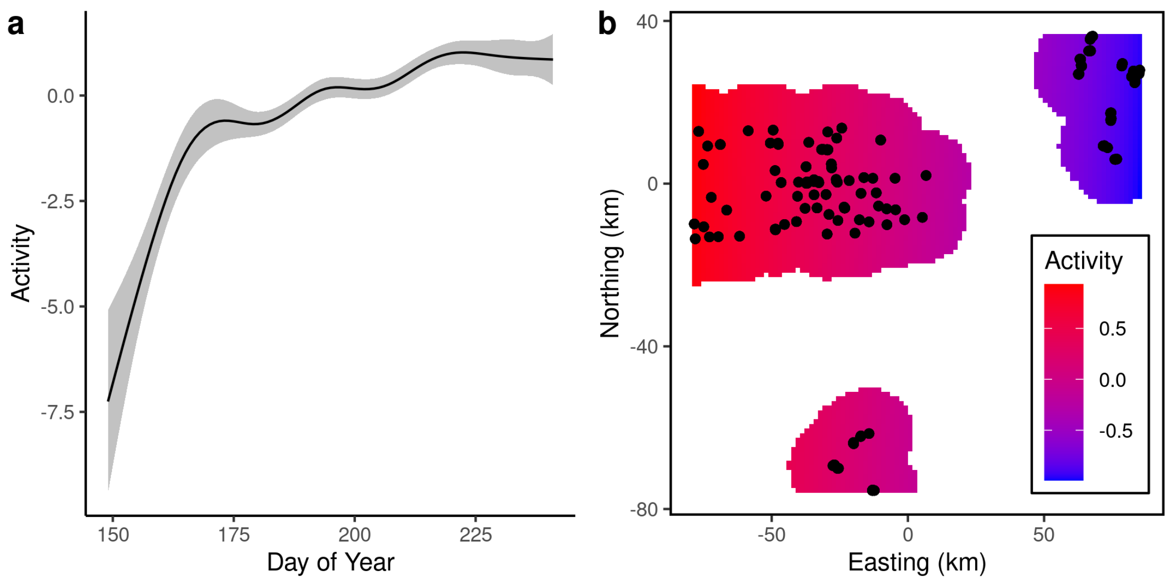

Figure S6: Temporal and spatial components of *Phalangium opilio* activity-density (after accounting for landscape composition and trap location). a) shows the effect of day of year, and b) shows the spatially smoothed effect of site location.

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	0.769
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	0.824
ti(Distance,Day):Canola	1.64	8.86	**0.002**
s(Distance):Pasture	<0.01	<0.01	0.979
s(Day):Pasture	0.67	0.92	0.23
ti(Distance,Day):Pasture	<0.01	<0.01	0.907
s(Distance):Woodland	<0.01	<0.01	0.439
s(Day):Woodland	<0.01	<0.01	0.939
ti(Distance,Day):Woodland	<0.01	<0.01	0.983
s(Distance):Pulses	<0.01	<0.01	0.498
s(Day):Pulses	1.27	3.96	**0.033**
ti(Distance,Day):Pulses	1.4	2.24	0.16
s(Distance):Urban	<0.01	<0.01	0.277
s(Day):Urban	<0.01	<0.01	0.582
ti(Distance,Day):Urban	<0.01	<0.01	0.591

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	0.958
s(Distance):Grassland	<0.01	<0.01	0.966
s(Day):Grassland	<0.01	<0.01	0.94
ti(Distance,Day):Grassland	<0.01	<0.01	0.616
s(Distance):Canola	<0.01	<0.01	0.927
s(Day):Canola	<0.01	<0.01	0.645
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	0.799
s(Distance):Woodland	0.01	0.01	0.098
s(Day):Woodland	1.61	7.74	**0.005**
ti(Distance,Day):Woodland	0.56	0.98	0.153
s(Distance):Pulses	<0.01	<0.01	0.693
s(Day):Pulses	<0.01	<0.01	0.921
ti(Distance,Day):Pulses	<0.01	<0.01	0.43
s(Distance):Urban	<0.01	<0.01	0.725
s(Day):Urban	0.7	1.03	0.224
ti(Distance,Day):Urban	<0.01	<0.01	0.919

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	0.944
ti(Distance,Day):Grassland	<0.01	<0.01	0.976
s(Distance):Canola	<0.01	<0.01	0.341
s(Day):Canola	<0.01	<0.01	0.627
ti(Distance,Day):Canola	2.22	21.63	**<0.001**
s(Distance):Pasture	<0.01	<0.01	0.936
s(Day):Pasture	<0.01	<0.01	0.835
ti(Distance,Day):Pasture	1.6	2.96	0.109
s(Distance):Woodland	<0.01	<0.01	0.646
s(Day):Woodland	0.95	2.23	0.085
ti(Distance,Day):Woodland	<0.01	<0.01	0.414
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	0.984
s(Distance):Urban	<0.01	<0.01	0.846
s(Day):Urban	0.63	0.8	0.252
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	0.466
s(Day):Canola	<0.01	<0.01	0.882
ti(Distance,Day):Canola	<0.01	<0.01	0.675
s(Distance):Pasture	0.36	0.42	0.291
s(Day):Pasture	<0.01	<0.01	0.436
ti(Distance,Day):Pasture	<0.01	<0.01	0.585
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	0.073
s(Distance):Pulses	<0.01	<0.01	0.716
s(Day):Pulses	<0.01	<0.01	0.713
ti(Distance,Day):Pulses	1.23	1.88	0.187
s(Distance):Urban	0.79	1.94	0.088
s(Day):Urban	<0.01	<0.01	0.419
ti(Distance,Day):Urban	0.36	0.53	0.224

Appendix B: Interpreting Functional Regression Plots

Functional linear regression is a special case of linear regression, where both the independent variable is predicted by a functional dependent variable, meaning that the slope is a function (vector) rather a fixed (scalar) value (Ramsay & Silverman 2004; Yen *et al.* 2014). Therefore, the interpretation of a functional regression plot is very different from that of a simple linear regression plot. Figure S7a shows a simple linear regression plot of a hypothetical relationship between trap *activity-density* (y) and a single predictor, *proportion cover* (x), which is measured in a circle of a fixed radius surrounding each trap. If we suppose that the relationship between x and y is similar at all radii at which x is measured, then Figure S7b shows the resulting functional linear regression plot, where the slope (β) is the same at all distances (we avoid the problem of overlapping concentric circles by using concentric *annuli*). In reality, it is more likely that nearby cover will be more influential on activity-density than far-away cover, which could result in a relationship similar to Figure S7c. As functional regression takes any continuous predictor of y, it is also possible to use proportion cover (measured within an annulus of a fixed radius) as a predictor of measurements taken across time, allowing the effect of proportion cover to vary over the course of the season (Figure S7d). Finally, the effect of proportion cover over distance and time may be modeled as a smoothed surface, representing the joint spatio-temporal influence of landscape cover on activity-density.

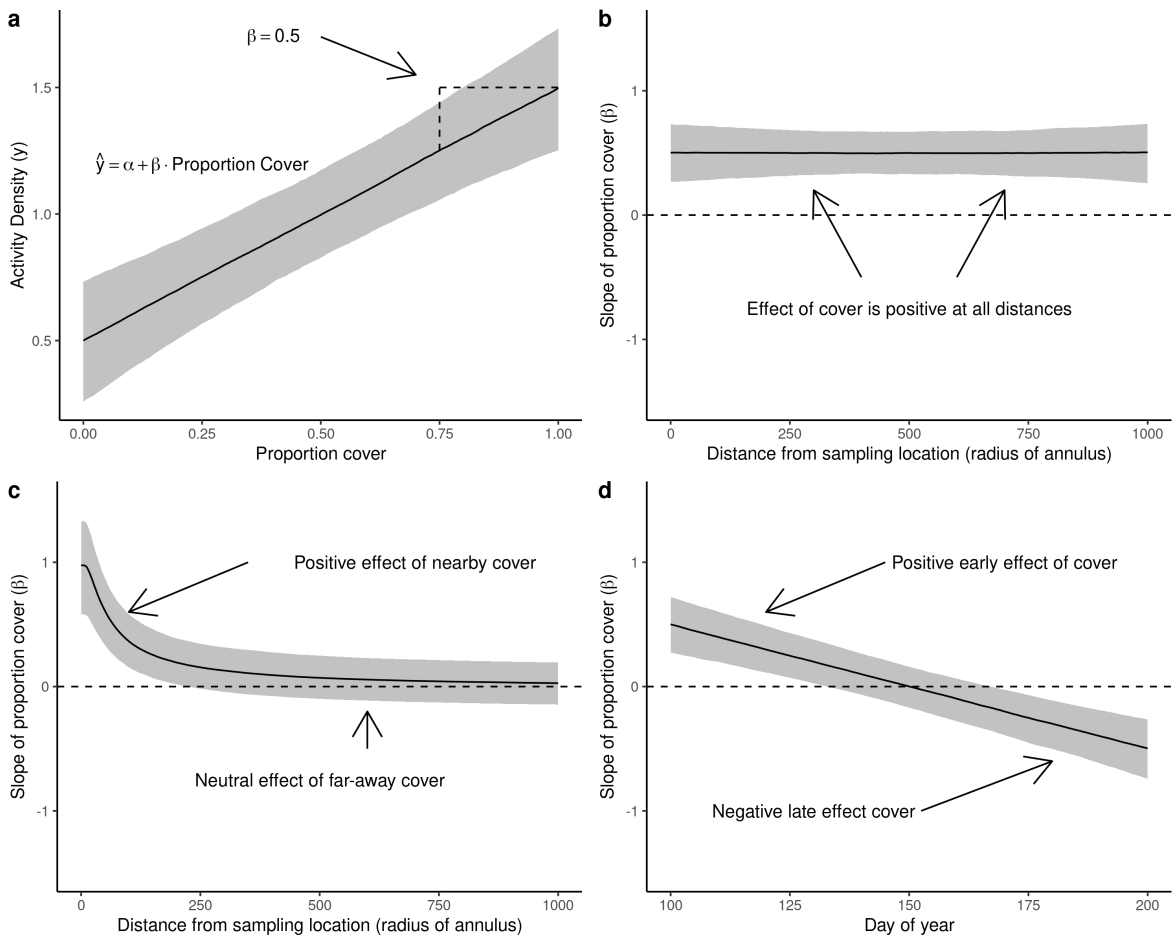

Figure S7: Examples of (functional) linear regression plots. **a)** shows a simple linear regression plot, with a single slope value for a single regressor. **b)** shows the equivalent plot in functional regression form, where the the slope is a smoothed function that maps onto a function-valued regressor. **c)** and **d)** show functional linear regression plots where the slope varies with the location of the regressor.