

1 Beneficial arthropod habitat useage changes within-season: implications  
2 for pest control services in croplands

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7 **Abstract**

Ground-dwelling arthropods are important generalist predators in agro-ecosystems, 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 at. Additionally, the same landscape feature may act as source of arthropods spillover at different times of the year, but this is rarely considered. We modeled the activity-density of four highly-abundant species of Canadian prairie arthropods, and used functional regression to simultaneously consider both their habitat preferences and the timing of sources and sinks. *Pterostichus melanarius* (Coleoptera: Carabidae) and *Pardosa moesta* (Arachnida: Lycosidae) appear to be attracted to canola (*Brassica napus* L.) during the early summer, then disperse to grasslands, wetlands, and grassy road margins during the end of the summer. This suggests that grasslands and wetlands act as reservoir habitats for predatory arthropods, and that farmers should consider preserving existing habitat around croplands in order to maintain background levels of pest-control.

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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. On the other hand, spillover of beneficial arthropods from adjacent non-crop patches can deliver increased 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 from crop fields act as a bottom-up driver of their associated arthropod communities, meaning that agricultural land can act as a source of nutrients and individuals for adjacent non-crop land (Diekötter *et al.* 2010; Galpern *et al.* 2017). These important fluxes of mobile arthropods, both to crops and away from them, are key for managing both crop yield and biodiversity in agroecosystems. Finding “win-win” practices is of particular importance to land managers and conservationists; that is, practices that result in better conservation outcomes while maintaining or improving crop yields. Finally, agricultural land occupies 15 million km<sup>2</sup> (~36%) of land globally (Ramanakutty *et al.* 2018), suggesting that there remains great potential to achieve conservation outcomes by adjusting agricultural practices.

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. Predatory arthropods 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). This 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

39 *et al.* 2008). In this way, the spillover of beneficial arthropods into crops depends not only on the  
40 amount of adjacent SNL, but the specific habitat type, the time of the year, and the spatial scale at  
41 which an organism gathers resources.

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

55 In this study, we used pitfall traps to determine how landscape composition affects the seasonal  
56 activity-density of arthropods across a large Canadian prairie agroecosystem. We considered the  
57 following hypotheses: 1. Untilled semi-natural land provides egg-laying and feeding areas for predatory  
58 arthropods, meaning that it should act as a source of arthropods during the early part of the season,  
59 and a sink during the later part of the season. 2. Crops act as sources of food (pest insects) for  
60 predatory arthropods during the growing season. This should result in agricultural land becoming a  
61 sink for predators in the early part of the season as they migrate into the crop, and a source at the  
62 end of the season as they migrate out of the crop. 3. Crops may act as a temporary feeding site  
63 for predators. Therefore, crops may act as a local sink for arthropods, but will also be negatively  
64 associated at larger (landscape-level) scales. Using a large pitfall trapping dataset, we related seasonal  
65 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 ethylene 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 (Dondale & Redner 1990; Edgar 1990; Vogel 2004; Yigit *et al.* 2007).

We used counts of organisms in our pitfall traps as proxies of ecosystem service provision. 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; Zhao *et al.* 2013), meaning that counts in the traps represent the “activity-density” of a given organism. Despite this disadvantage, activity-density is generally positively related to ecosystem services, at least in carabids (Trichard *et al.* 2014; Boetzel *et al.* 2018; González *et al.* 2020), making it acceptable for our study.

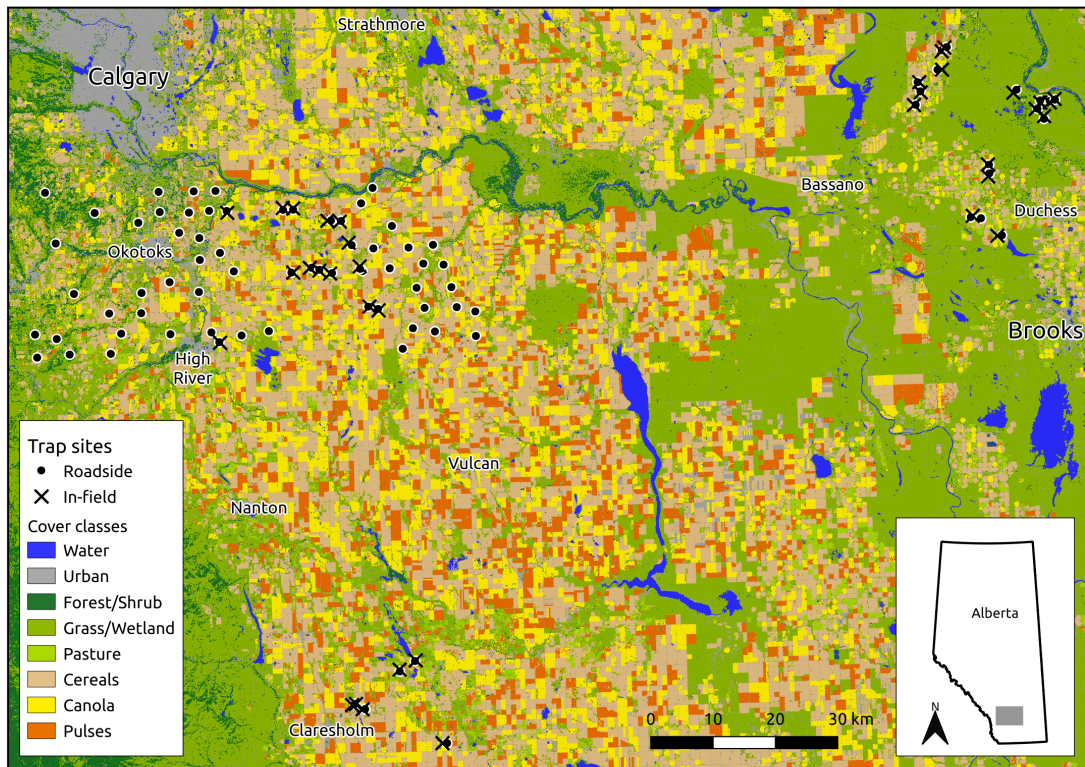


Figure 1: Location of pitfall traps during 2017, and classified cover f. Inset map shows study location within Alberta. Roadside traps were installed in road margins, while in-field traps were installed directly in canola fields or in adjacent wetland or grassy field edges.

89 We used four highly-abundant species of predatory arthropods found in the pitfall traps, as common  
 90 species are often more important for ecosystem service provision than rare species (Winfree *et al.* 2015),  
 91 but their habitat preferences are still poorly understood. *Pterostichus melanarius* is an introduced  
 92 predatory ground beetle (Coleoptera: Carabidae) that is a wide-ranging generalist known to prey  
 93 upon crop pests (Cárcamo & Spence 1994; Larsen *et al.* 2003; Busch 2016). It is commonly found in  
 94 untilled grasslands (Purtauf *et al.* 2005) and may use grassy field edges as larval habitat (Desender  
 95 & Alderweireldt 1988). *Pardosa* are wolf spiders (Araneae: Lycosidae) that use an active wandering  
 96 predation strategy (Young & Edwards 1990), and are common across the Canadian prairies. Both  
 97 *Pardosa distincta* and *Pardosa moesta* are found in a wide variety of habitats, but are common in  
 98 ungrazed pastures (Dondale & Redner 1990; Cárcamo *et al.* 2014). *P. distincta* is also commonly  
 99 found in disturbed environments (Collins *et al.* 1996; Wade & Roughley 2010), while *P. moesta* appear  
 100 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, *Phallangium 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 3); 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 ( $\beta$ ) 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 wider 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 ( $\theta$ ). 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 landcover in all annuli 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. This was deemed adequate, as 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 concurred with each other, so we removed them from the model or combined them. Concurrency 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” concurrency, 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

163 from the model, as it was negatively correlated with canola cover at distances less than 200m and  
 164 was positively correlated at distances over 500m, reflecting the most common crop rotations (canola  
 165  $\rightarrow$  wheat  $\rightarrow$  barley) and the commonly-used 800 m block structure of farmland in our study region  
 166 (quarter-sections). This resulted in a reduced set of landscape terms, none of which were strongly  
 167 concurred with each other (cropland: canola, pulses; SNL: grassland, pasture, woodland, roadside; see  
 168 Figure S1).

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### 170 **Box 1: Interpreting Functional Regression Plots**

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



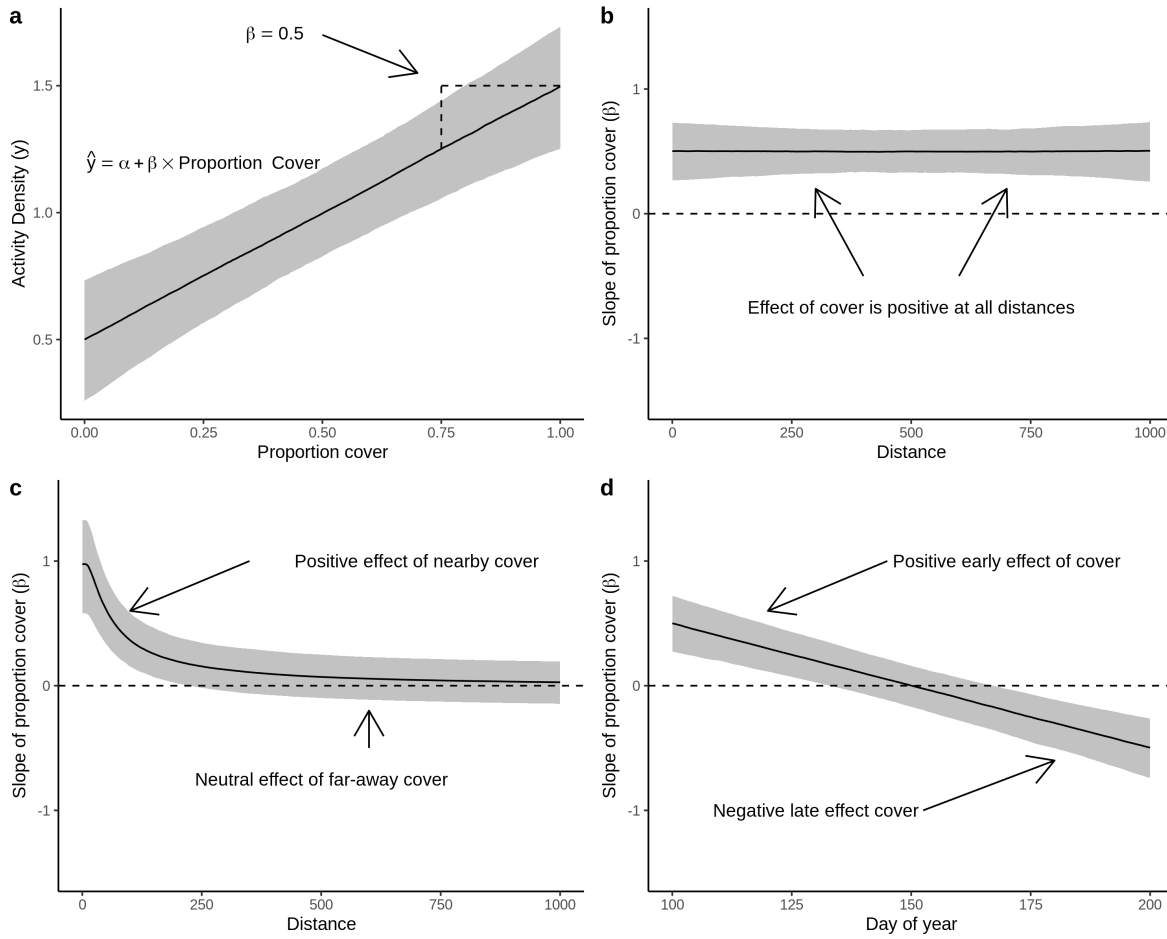


Figure 2: Examples of (functional) linear regression plots. **a)** shows a simple linear regression plot, with a single slope value for a single regressor. **b)** shows the equivalent plot in functional regression form, where the slope is a smoothed function that maps onto a function-valued regressor.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

186

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

195 Alternatively, a cover class could act as a sink by providing high-quality habitat at certain times of the  
196 year (e.g. egg laying/feeding), but act as a source at other times (e.g. during emergence). For brevity  
197 in the following Results section, we refer to local- and landscape-level effects, where local indicates the  
198 effects of landscape composition at scales of <500m, whereas landscape indicates scales >500 m. Simi-  
199 larly, we refer to early-, mid-, and late-season effects, where landscape composition affected abundance  
200 from June - July, July - August, or August - September, 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 3). Several landscape “fingerprints” were evident in  
205 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 3). 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).

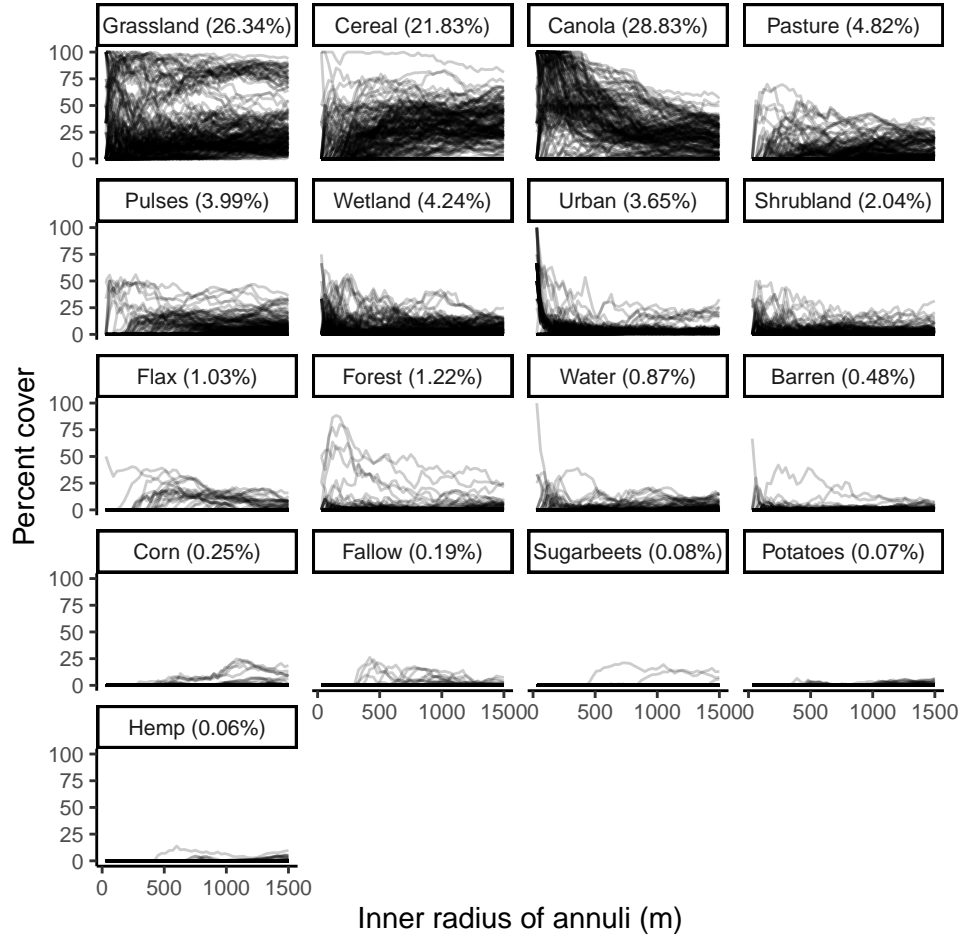


Figure 3: Landscape composition in annuli surrounding each trap location. Sites are represented by individual lines. Mean cover for each class is listed in each sub-figure heading.

### 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 4a). 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 4b), 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 4c). Pulses acted as a late-season source, indicating that *P. melanarius* may migrate out of the crop after (or during) harvest (Figure 4d). 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 S2). Landscape composition and trap location explained 22% of the variance in activity-density, while the spatial and temporal smoothers accounted for 41% (Table 1).

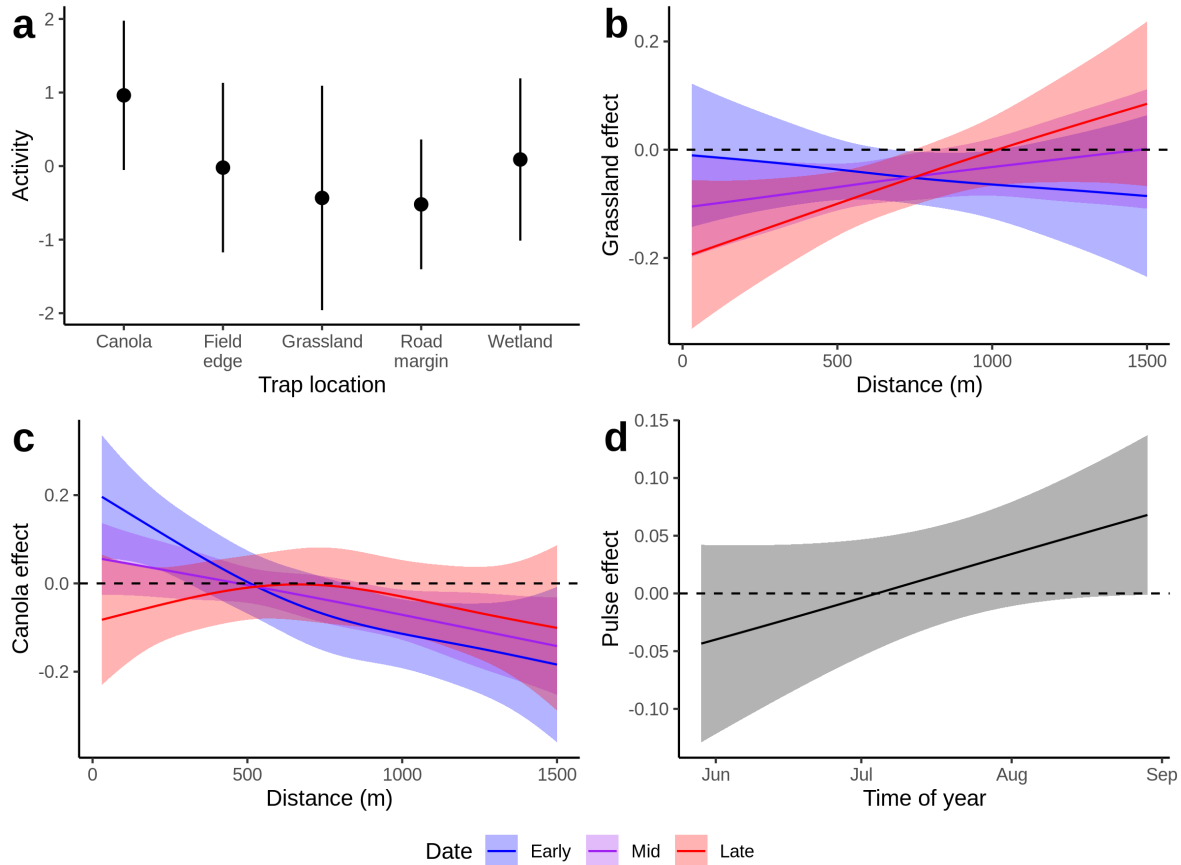


Figure 4: Landscape influence on *Pterostichus melanarius* activity-density. a) shows the effect of local trap location, and b-c) are functional regression plots of the proportion grassland and canola at distances away from each trap. d) is a functional regression plot over time, showing the effect of pulses at different times of the year. Lines and dots represent means, and bars and shaded regions represent 95 % confidence regions ( $1.96 \times SE$ ). Coloured regions represent early-, mid-, and late-season effects (blue = June, purple = July, 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 5a, 6a). 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 S3 and S4; both

234  $p < 0.001$ ).

235 *P. distincta* activity density was negatively affected by landscape-level pasture (Figure 5b), while  
236 woodlands had a negative effect late in the season (Figure 5c). 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 S3a) 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 sink, the general amount of grassland in the area had a positive effect (Figure 6b). Local  
244 canola cover had a positive early effect on activity-density, but a negative local effect later in the season  
245 (Figure 6c). Local road margins also had a similar effect, acting as an early source and a late sink  
246 (Figure 6d). Pulses also had a positive effect at the landscape level (Figure 6e), but this explained very  
247 little variance in *P. moesta* activity density (Table 1,  $R^2$ : 0.004). Similar to *P. distincta*, trap location  
248 and an East-West spatial random effect (Figure S4b) explained roughly 5 times more variance in *P.*  
249 *moesta* activity density than landscape composition ( $R^2$ : 0.5 versus 0.096), meaning that *P. moesta*  
250 is also fairly general in its overall habitat preferences, and is influenced more heavily by larger-scale  
251 abiotic factors.

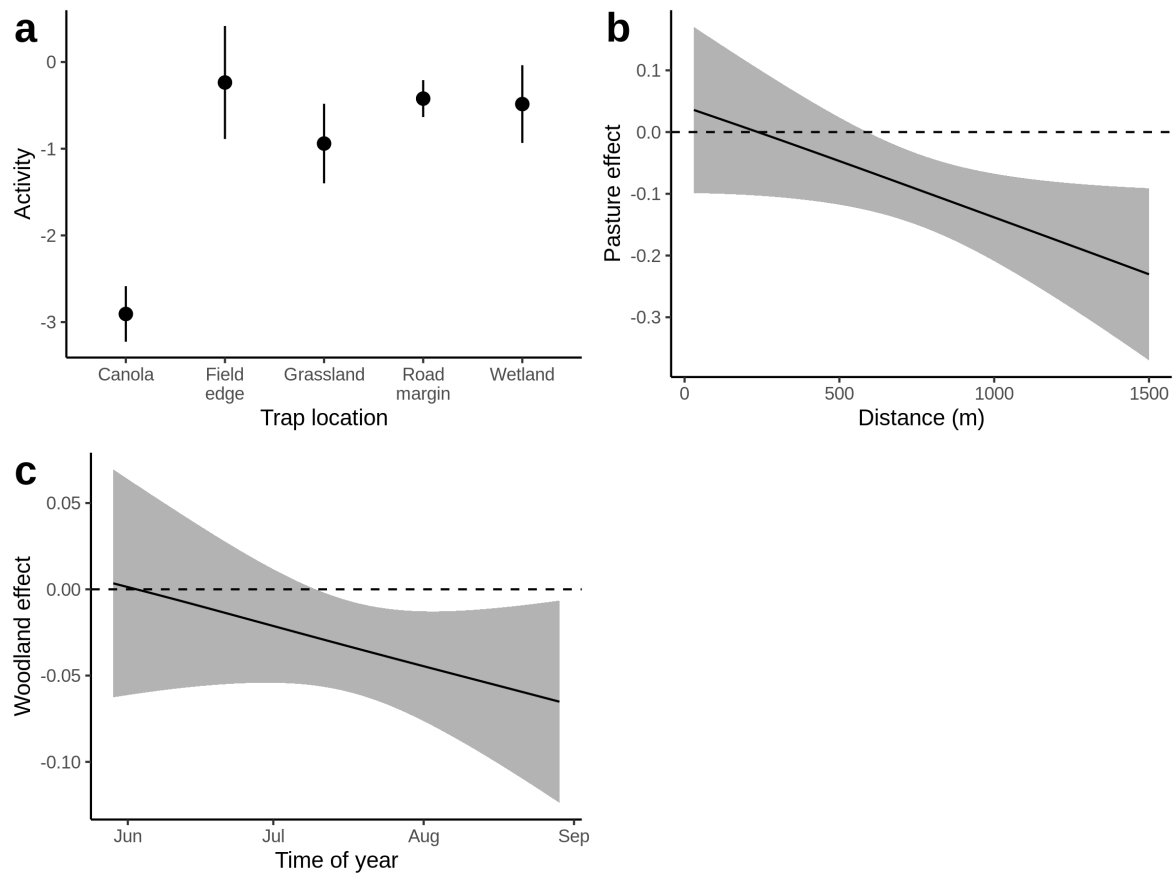


Figure 5: Landscape influence on *Pardosa distincta* activity-density. a) shows the effect of local trap location, b) is a functional regression plot of the proportion pasture at distances away from each trap, and c) is a functional regression plot over time, showing the effect of woodland at different times of the year. Lines and dots represent means, and bars and shaded regions represent 95 % confidence regions ( $1.96 \times \text{SE}$ ). Coloured regions represent early-, mid-, and late-season effects (blue = June, purple = July, red = August).

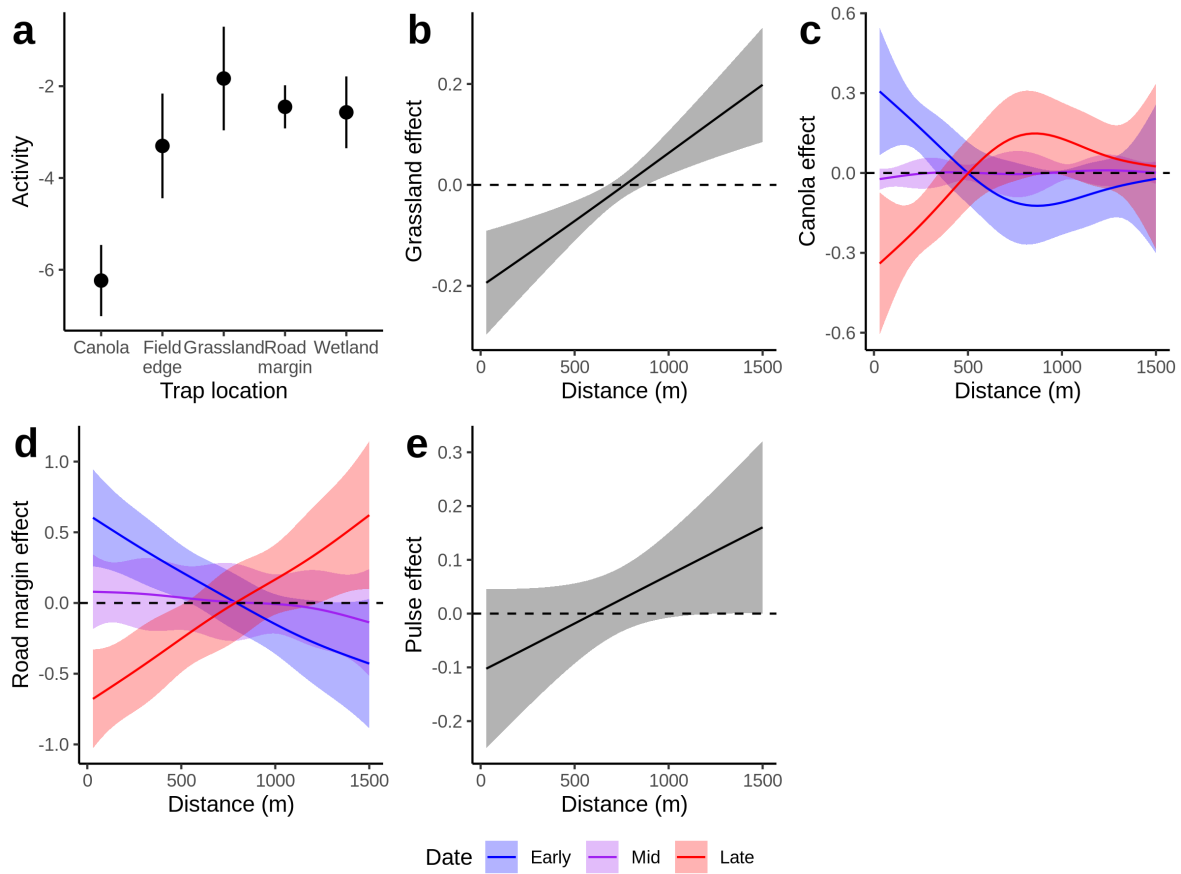


Figure 6: Landscape influence on *Pardosa moesta* activity-density. a) shows the effect of local trap location, and b-e) are functional regression plots of the proportion grassland, canola, road margins, and pulses at distances away from each trap. Lines and dots represent means, and bars and shaded regions represent 95 % confidence regions (1.96 x SE). Coloured regions represent early-, mid-, and late-season effects (blue = June, purple = July, 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 7a), 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 7b,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 S5a). Similar to *P. moesta*, *P. opilio* also showed a distinct East-West spatial random effect (Figure S5b),

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

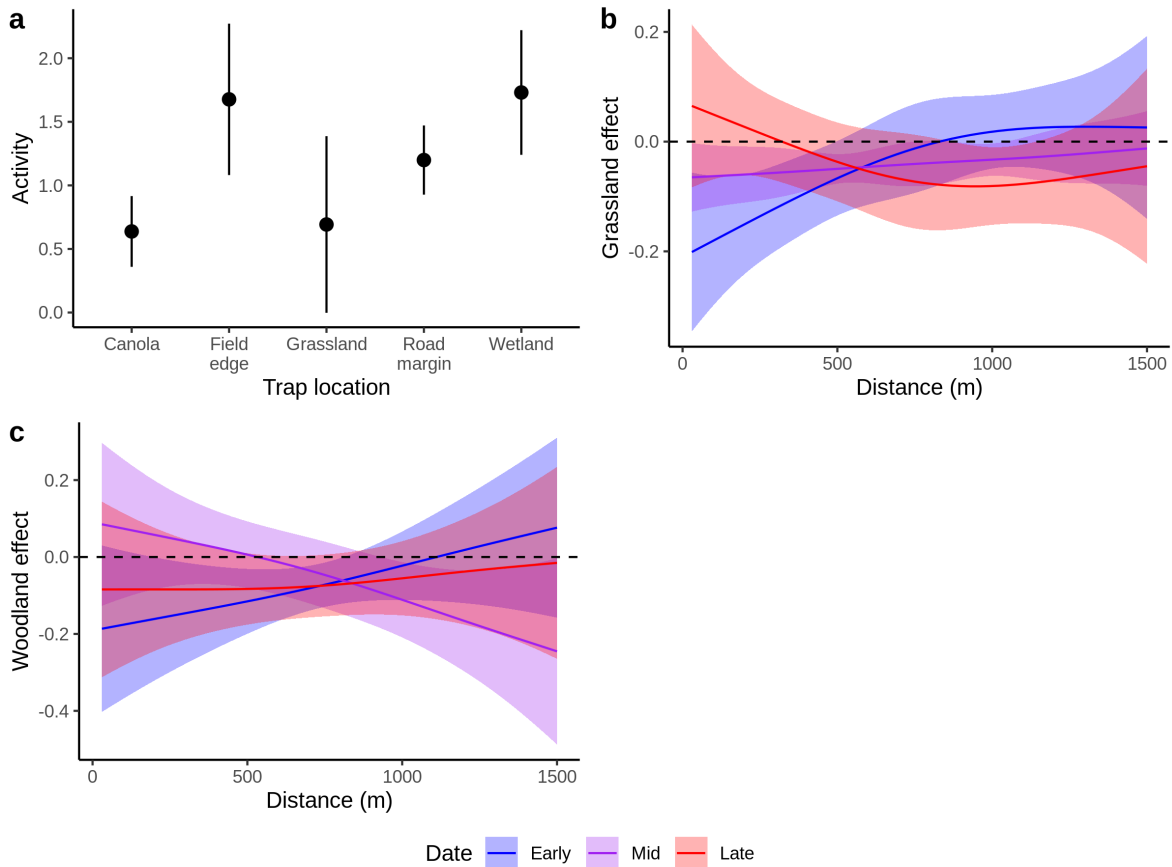


Figure 7: Landscape influence on *Phalangium opilio* activity-density. a) shows the effect of local trap location, and b-c) are functional regression plots of the proportion grassland and woodland at distances away from each trap. Lines and dots represent means, and bars and shaded regions represent 95 % confidence regions (1.96 x SE). Coloured regions represent early-, mid-, and late-season effects (blue = June, purple = July, red = August). **SHOULD WE TAKE OUT THE MID (PURPLE) TIME SEQUENCE, IN THE INTEREST OF READABILITY? THIS WOULD WORK FINE FOR ALL OTHER FIGURES, EXCEPT FOR c OF THIS ONE.**

#### 263 4. Discussion

264 We found support for our predictions of SNL having late-season effects on beneficial arthropods;  
 265 specifically, grassland had a negative effect on *P. melanarius* activity-density, woodlands on *P. distincta*  
 266 activity density, and road margins on *P. moesta* activity density, all during late summer (August -  
 267 September). This suggests that these arthropods migrate to these habitats at the end of the summer to  
 268 prepare for oviposition or overwintering. However, *P. opilio* showed no evidence of this, instead showing  
 269 a negative effect of grassland *early* in the season, suggesting that a) they aggregate in grasslands or



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. Bio-control potential is based on likely early-season aggregation to canola crops.

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

270 b) grasslands do not constitute suitable habitat for *P. opilio*, resulting in low spillover. There was  
 271 little evidence of SNL acting as early-season sources, aside from road margins having a positive early  
 272 effect on *P. moesta* activity-density. However, some cover classes had a positive effect at the landscape  
 273 level (grassland and road margins on *P. moesta*), suggesting earlier or wider-scale dispersal away  
 274 from these cover classes. Canola had a positive effect on *P. melanarius* and *P. moesta* in the early  
 275 season, suggesting that these organisms aggregate to canola crops and disperse at the end of the season  
 276 (mass effects *sensu* Shmida & Wilson 1985). Canola also had negative landscape-level effects on *P.*  
 277 *melanarius* while pasture had negative effects on *P. distincta*, meaning that these cover types likely  
 278 represent only partial habitat for these arthropods. Finally, the influence of landscape composition  
 279 tended to be limited to a radius of about 500m, indicating that large-scale *and* local land cover can be  
 280 important to beneficial arthropod abundance. There was also a strong temporal component to most  
 281 of the landscape effects, meaning that it is important to consider how sinks and sources may change  
 282 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 *P. melanarius* migrates into it at the end of the summer. Other stud-  
 286 ies have found similar results, suggesting that untilled land is important off-field habitat for carabids  
 287 (Desender & Alderweireldt 1988; Fournier & Loreau 2002; but see Hatten *et al.* 2007). In particular,  
 288 Purtauf *et al.* (2005) found that carabid density increased with proportion of nearby grasslands, so our  
 289 negative late-season effect of grasslands may represent *P. melanarius* moving to overwintering habitat  
 290 at the end of the season. However, *P. melanarius* is also found in a wide variety of habitats, and tends  
 291 to prefer agricultural fields (Larsen *et al.* 2003). Our models confirmed this, as they showed that  
 292 canola and pulse crops had positive effects on *P. melanarius* activity-density early in the season. Early  
 293 in the season, canola crops had a local positive effect, but a landscape-level negative effect, which may  
 294 indicate that they provide only temporary feeding habitat. The effect of pulse crops on carabid abun-  
 295 dance is not well-studied, but our results suggest that pulses may represent a potential food resource  
 296 for *P. melanarius*, albeit a weak one (Table 1). Carabids are predators of pea-leaf weevils (*Sitona*  
 297 *lineatus*) on other Fabaceae (Hamon *et al.* 1990), and *P. melanarius* can prey upon other carabids  
 298 that are predators of *S. lineatus*, such as *Bembidion quadrimaculatum* (Vankosky *et al.* 2011), so this  
 299 effect may be direct or indirect. We did not consider the influence of previous years' crops, although  
 300 carabids tend to be more abundant in areas of high crop rotation (Bertrand *et al.* 2016; Busch 2016).

301 The wolf spiders *Pardosa distincta* and *Pardosa moesta* both responded to landscape composition,  
 302 but it explained only a small fraction of their activity-density ( $R^2$ : 0.045, 0.096). This means that both  
 303 species of *Pardosa* appear to have very general habitat preferences, but may be somewhat influenced  
 304 by certain cover types. Pasture had a negative effect at the landscape scale, and woodland had a  
 305 late-season negative effect, suggesting that *P. distincta* move to woodlands for overwintering or winter  
 306 foraging (Aitchison 1984; Buddle 2000). *Pardosa* are found in areas close to disturbed roadside strips  
 307 (Drapela *et al.* 2008, 2011; Kowal & Cartar 2011), but *P. distincta* appears to be less sensitive  
 308 to disturbances than *P. moesta* (Collins *et al.* 1996; Wade & Roughley 2010). Moring & Stewart  
 309 (1994) showed that *P. distincta* were active in grassy habitats, which we found partial evidence of, as  
 310 *P. distincta* tended to have higher activity-density in trap locations with higher grass cover (Figure  
 311 5a). Canola had an early-season positive effect on *P. moesta*, indicating that *P. moesta* and *P.*  
 312 *melanarius* may both use canola as foraging grounds. We also found that road margins had a positive  
 313 early-season and a negative late-season effect (similar to Drapela *et al.* 2008). Grassland and pulses  
 314 also had a local negative effect but a positive landscape-level effect; this suggests that they may  
 315 constitute suitable habitat for *P. moesta* and attract them away from other cover types. Wolf spiders  
 316 (Lycosidae) employ a wandering-active predation strategy (Young & Edwards 1990), meaning that  
 317 nearby landscape composition may be more influential to *Pardosa* than large-scale composition (Öberg  
 318 *et al.* 2007, 2008). While trapping location explained a large proportion of variance for both species  
 319 (0.29 and 0.38), several landscape features were also important at large spatial scales, including grass  
 320 and wetland, pasture, pulses, and road margins. Therefore, *Pardosa* dispersal distances may be further  
 321 than previously thought, either through ballooning as juveniles (Richter 1970; Greenstone 1982) or  
 322 through other long-distance travel.

323 *Phalangium opilio* activity-density responded to grass and wetland cover, as well as wooded land-  
 324 scapes. Other studies have found that *P. opilio* is mostly found in human-altered landscapes with  
 325 a large proportion of farming (Muster & Meyer 2014; Van de Poel 2015). Since most of our study  
 326 area was in or near farmed land, the lack of variation is understandable, but there were a few notable  
 327 landscape-level patterns that emerged. *P. opilio* activity-density was higher in grassy field edges and  
 328 wetlands, but grasslands and wetlands had a local negative effect on *P. opilio* until late in the season.  
 329 These indicate that while grass and wetlands could act as a reservoir, spillover into other land cover  
 330 types may be limited, as *P. opilio* avoids heavily grazed areas, possibly due to low humidity (Šajna  
 331 *et al.* 2011). *P. opilio* is also found in large numbers at the edges of forests, and may migrate from

332 forests into farmlands (Van de Poel 2015). We found the opposite pattern: forests had a weak negative  
 333 effect on *P. opilio*, at least early in the year. Unlike the other arthropods, most of the variation in  
 334 activity-density for *P. opilio* was explained by day of year ( $R^2 = 0.44$ ), indicating strong seasonal emer-  
 335 gence cues. However, there was also a strong East-West spatial random effect in both *P. opilio* and  
 336 *P. moesta*, meaning that wider-scale geographic patterns (possibly related to rainfall or temperature)  
 337 also influence their activity-density.

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

## 350 5. Applications

351 Our work has three main applications. First, it adds to the basis of scientific evidence showing  
 352 that SNL can act as reservoir habitats in intensely-managed agroecosystems. Based on our findings,  
 353 farmers and land managers should consider preserving existing grassland and wetland habitat to act  
 354 as a background source of pest-control in crop fields. While local habitat appears valuable, even  
 355 landscape-level habitat can be valuable, as it can increase the number of beneficial arthropods at  
 356 larger spatial scales (e.g. Figures 4, 6). Secondly, our work suggests that *P. melanarius* and *P. moesta*  
 357 should be investigated for their role as predators in canola crops. They appear to aggregate in canola  
 358 crops early in the season, meaning that they have the potential to provide valuable pest-control services  
 359 to growers. Finally, we demonstrate that timing and spatial scale of spillover should be considered  
 360 in future landscape studies of ecosystem services. We show important differences in the timing of  
 361 landscape effects on activity-density (early-season vs. late-season spillover) that are typically ignored,

<sup>362</sup> but should be considered when assessing how SNL can deliver ecosystem services.



	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.

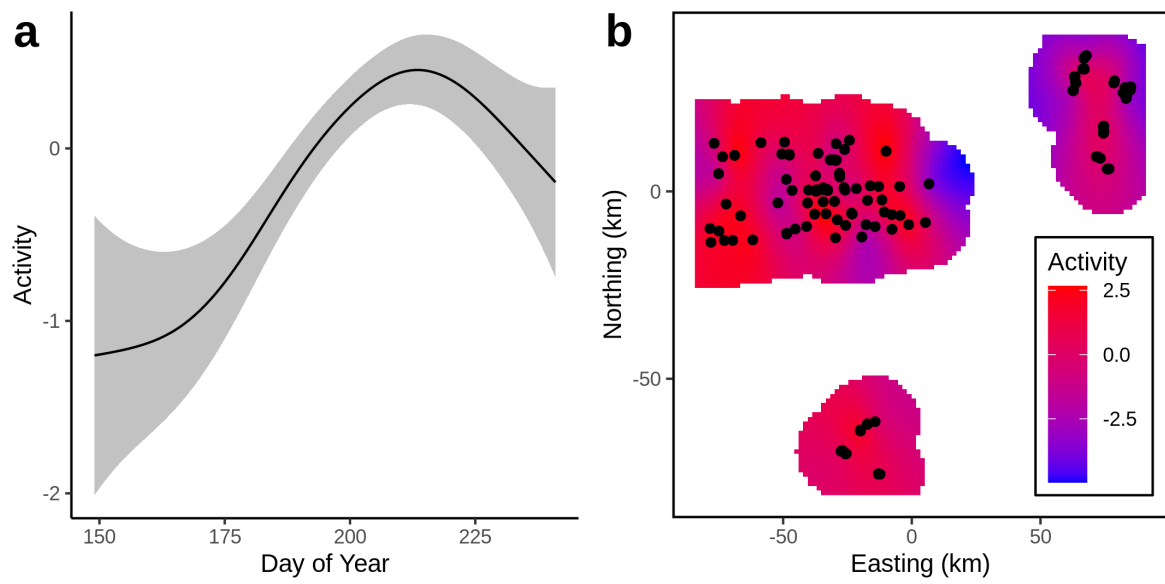


Figure S2: Temporal and spatial components of *Pterostichus melanarius* activity-density (after accounting for landscape composition and trap location). a) shows the effect of day of year, and b) shows the spatially smoothed effect of site location.

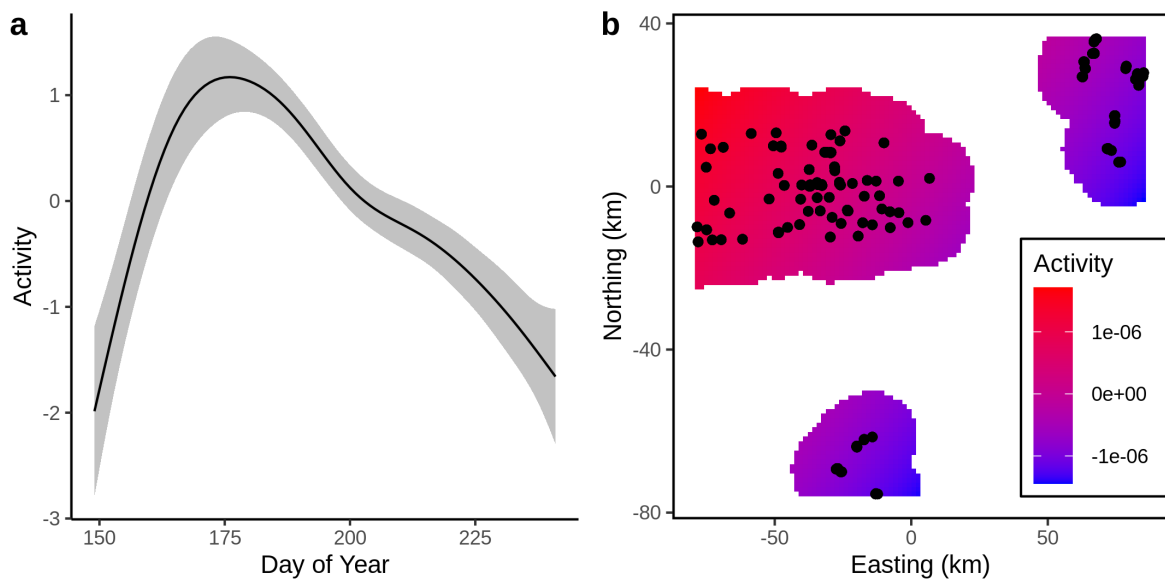


Figure S3: Temporal and spatial components of *Pardosa distincta* activity-density (after accounting for landscape composition and trap location). a) shows the effect of day of year, and b) shows the spatially smoothed effect of site location.



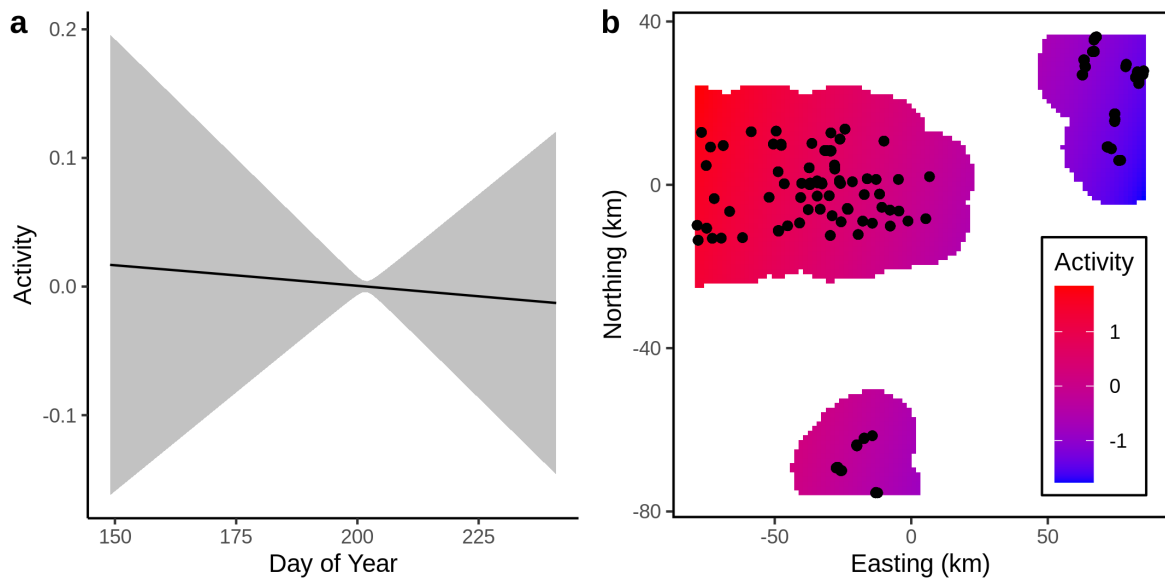


Figure S4: Temporal and spatial components of *Pardosa moesta* activity-density (after accounting for landscape composition and trap location). a) shows the effect of day of year, and b) shows the spatially smoothed effect of site location.

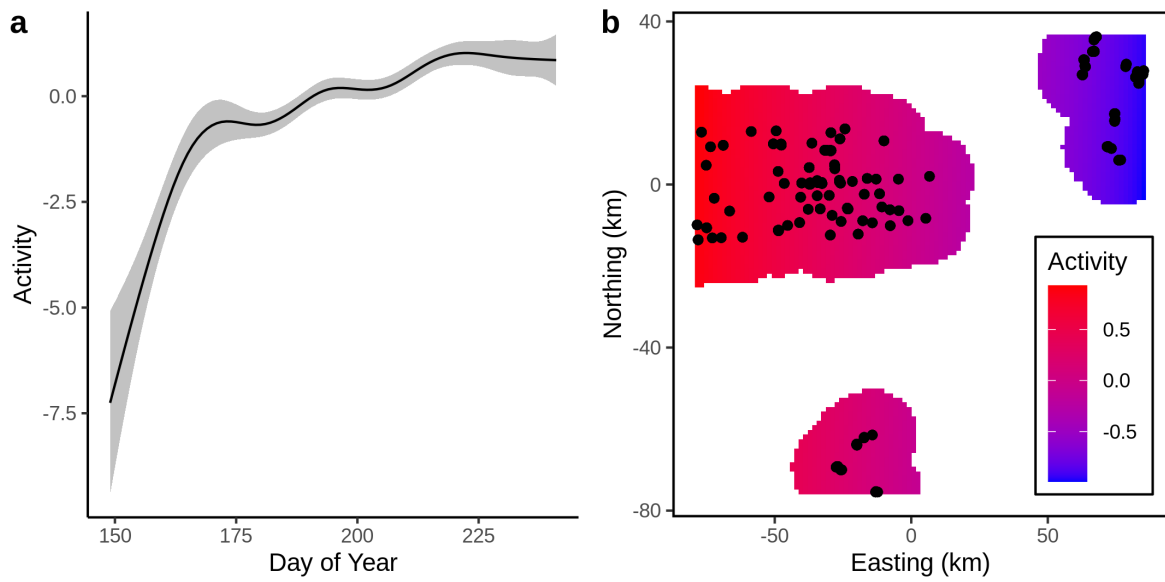


Figure S5: Temporal and spatial components of *Phalangium opilio* activity-density (after accounting for landscape composition and trap location). a) shows the effect of day of year, and b) shows the spatially smoothed effect of site location.

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

Trap location	$\beta$	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.	$\chi^2$	p
s(Day)	3.48	31.11	<b>&lt;0.001</b>
s(E,N)	39.47	309.8	<b>&lt;0.001</b>
s(Distance):Grassland	1.51	11.24	<b>&lt;0.001</b>
s(Day):Grassland	<0.01	<0.01	0.769
ti(Distance,Day):Grassland	0.93	3.87	<b>0.026</b>
s(Distance):Canola	1.71	7.36	<b>0.004</b>
s(Day):Canola	<0.01	<0.01	0.824
ti(Distance,Day):Canola	1.64	8.86	<b>0.002</b>
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	<b>0.033</b>
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	$\beta$	S.E.	Z	p
Canola	-2.91	0.16	-17.77	<b>&lt;0.001</b>
Road margin	-0.42	0.11	-3.88	<b>&lt;0.001</b>
Grassland	-0.94	0.23	-4.02	<b>&lt;0.001</b>
Field edge	-0.24	0.33	-0.71	0.477
Wetland	-0.49	0.23	-2.12	<b>0.034</b>

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.	$\chi^2$	p
s(Day)	5.59	120.42	<b>&lt;0.001</b>
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	<b>&lt;0.001</b>
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	<b>0.005</b>
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	$\beta$	S.E.	Z	p
Canola	-6.24	0.40	-15.76	<b>&lt;0.001</b>
Road margin	-2.45	0.24	-10.22	<b>&lt;0.001</b>
Grassland	-1.83	0.58	-3.18	<b>0.001</b>
Field edge	-3.30	0.58	-5.67	<b>&lt;0.001</b>
Wetland	-2.57	0.40	-6.44	<b>&lt;0.001</b>

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.	$\chi^2$	p
s(Day)	0.05	0.04	0.349
s(E,N)	1.96	50.7	<b>&lt;0.001</b>
s(Distance):Grassland	1.87	14.39	<b>&lt;0.001</b>
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	<b>&lt;0.001</b>
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	<b>0.039</b>
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	<b>&lt;0.001</b>

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

Trap location	$\beta$	S.E.	Z	p
Canola	0.64	0.14	4.49	<b>&lt;0.001</b>
Road margin	1.20	0.14	8.64	<b>&lt;0.001</b>
Grassland	0.69	0.35	1.95	0.051
Field edge	1.68	0.30	5.52	<b>&lt;0.001</b>
Wetland	1.73	0.25	6.92	<b>&lt;0.001</b>

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.	$\chi^2$	p
s(Day)	7.2	141.89	< <b>0.001</b>
s(E,N)	1.95	59.8	< <b>0.001</b>
s(Distance):Grassland	1.69	50.17	< <b>0.001</b>
s(Day):Grassland	<0.01	<0.01	0.685
ti(Distance,Day):Grassland	1.39	5.79	<b>0.013</b>
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	< <b>0.001</b>
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

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