

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

Samuel V. J. Robinson^{a,*}, Diane Edwards^b, Jess L. Vickruck^{a,**}, Lincoln R. Best^a, Paul Galpern^a

^a2500 University Drive NW, Calgary, AB

^b150 Ambrose Circle SW, Calgary, AB

Abstract

Ground-dwelling arthropods can be important generalist predators in agroecosystems, and can use non-crop features as overwintering habitats. However, it is unclear which types of landscape features constitute useful non-crop habitat, and at what spatial scale organisms gather resources. Additionally, the same landscape feature may act as a source or a destination for arthropods at different times of the year, but this is rarely considered. 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. *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 distincta* (Araneae: Lycosidae) and *Phalangium opilio* (Opiliones: Opiliones) showed weak patterns of seasonal migration, and were more influenced by large-scale geographic patterns rather than landscape composition. 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; ecosystem services; functional data analysis; seminatural land

*Corresponding Author

**Present address: Fredericton Research and Development Centre, 850 Lincoln Road, Fredericton, NB

Present address: Oregon State University; 1500 SW Jefferson Way, Corvallis, OR, USA

Email addresses: samuel.robinson@ucalgary.ca (Samuel V. J. Robinson), diane@abienvironmental.ca (Diane Edwards), jessica.vickruck@canada.ca (Jess L. Vickruck), lincoln.best@oregonstate.edu (Lincoln R. Best), paul.galpern@ucalgary.ca (Paul Galpern)

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 disperse 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 scale at which the landscape 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). 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 disperse into the crop, and a source at the end of the season as they disperse out of the crop. 3. Crops may act as a temporary feeding site for predators. Therefore, crops may act as a nearby destination for arthropods, but will also be negatively associated at more-distant 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). These data were collected as a continuation of an earlier study that examined pollination services in crops (Vickruck *et al.* 2019), and here we use pitfall trap data to examine the predatory arthropod community with a focus on canola

69 crops (*Brassica napus* L.). Canola is one of the most commonly-grown crops in southern Alberta, and
70 represented 15% of the total land cover within the spatial extent of our sampling region during 2017
71 (Figure 1). We did not collect information on soil fertilization, pesticide application, mowing, or tillage
72 (approximately 82% of planting in Vulcan County was done with zero-till in 2016; (Statistics Canada
73 2016)). Diverse crop rotations may increase predatory arthropod abundance (Bertrand *et al.* 2016;
74 Busch 2016), but this was beyond the scope of the study.

75 Traps in canola were installed in 27 fields at 25, 75, and 200 m along a transect heading away from
76 the nearest non-crop feature (wetland, grassy field edges, or remnant prairie), while the trap at 0 m
77 was installed in the non-crop feature itself. The remaining 90 sites had only a single trap. In-field
78 traps were placed in canola crops (68), wetlands (16), grassy field edges (11), and remnant prairie
79 grasslands (18). Traps were placed starting on May 17, and collections ended on August 29, with
80 collection occurring continuously and traps being emptied every 14 days on average (SD: 3). This
81 resulted in 850 unique collection events, taking place across a total of 11614 trapping days. We used
82 582 mL Solo® cups buried up to the rim and partially filled with propylene glycol, with 2 cm wire mesh
83 mounted over the rim to prevent vertebrates from falling into the traps. Specimens were identified to
84 species using appropriate taxonomic literature (Lindroth 1966; Dondale & Redner 1990; Edgar 1990;
85 Vogel 2004; Yigit *et al.* 2007).

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

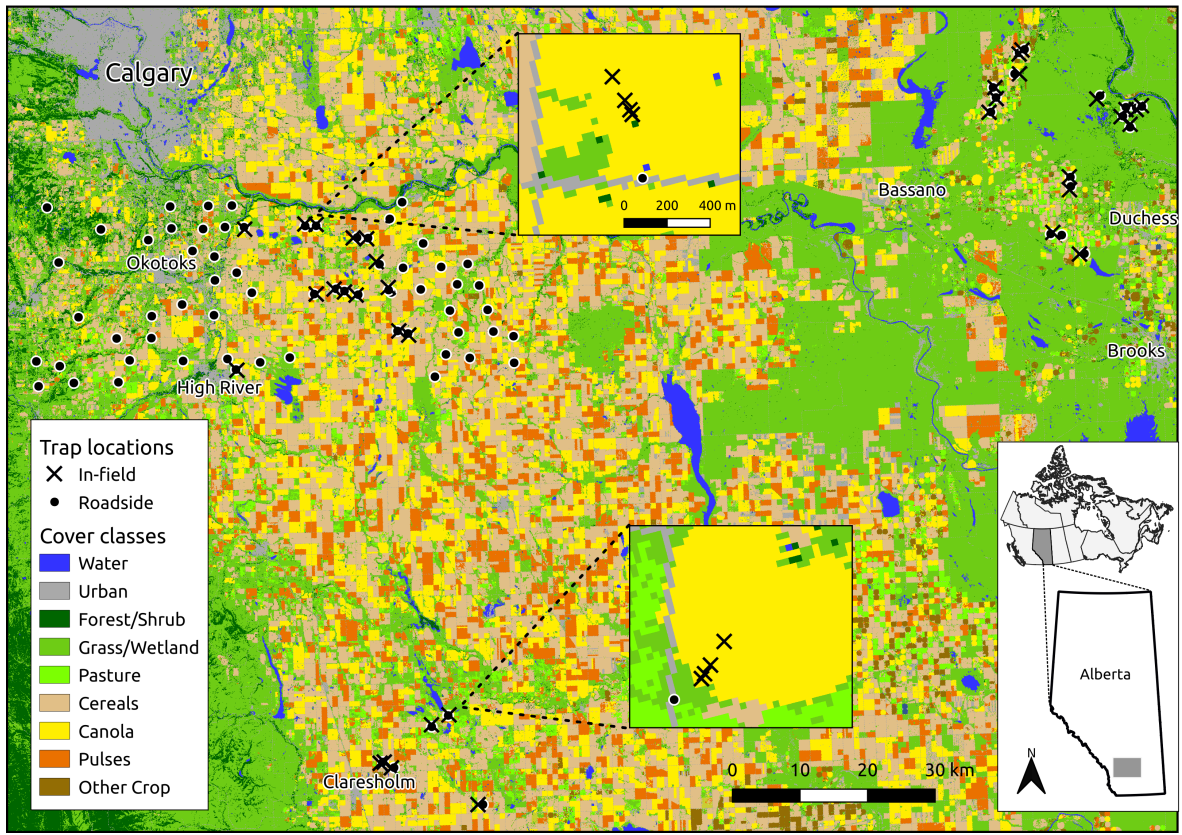


Figure 1: Classified land cover and location of pitfall traps during 2017. Inset map shows study location within Alberta provincial boundaries. Roadside traps were installed in road margins, while in-field traps were installed directly in canola fields, wetlands, or grassy field edges.

94 We used four highly-abundant species of predatory arthropods found in the pitfall traps, as common
95 species are more important for ecosystem service provision than rare species (Kleijn *et al.* 2015; Winfree
96 *et al.* 2015, but see 2018). *Pterostichus melanarius* is an introduced predatory ground beetle (Coleoptera:
97 Carabidae) that is a wide-ranging generalist known to prey upon crop pests (Cárcamo & Spence 1994;
98 Larsen *et al.* 2003; Busch 2016). It is commonly found in untilled grasslands (Purtauf *et al.* 2005) and
99 may use grassy field edges as larval habitat (Desender & Alderweireldt 1988). *Pardosa* are a genus of
100 wolf spiders (Araneae: Lycosidae) that use an active wandering predation strategy (Young & Edwards
101 1990), and are common across the Canadian prairies. Both *Pardosa distincta* and *Pardosa moesta* are
102 found in a wide variety of habitats, but are common in ungrazed pastures (Dondale & Redner 1990;
103 Cárcamo *et al.* 2014). *P. distincta* is also commonly found in disturbed environments (Collins *et al.*
104 1996; Wade & Roughley 2010), while *P. moesta* appear to prefer less frequent disturbances (Graham *et*
105 *al.* 2003; Kowal & Cartar 2011; but see Dondale & Redner 1990). Other *Pardosa* are known to use

road margins and wooded areas as habitat (Buddle 2000; Drapela *et al.* 2011). Finally, *Phalangium opilio* is an introduced harvestman (Opiliones: Phalangidae) that is found in drier disturbed areas (Bragg & Holmberg 2009). Juveniles hatch from eggs during the spring, becoming adults during the summer, and eggs are laid during the fall [adults do not overwinter; Bragg & Holmberg (2009)]. They are commonly found in human-altered landscapes (Muster & Meyer 2014; Van de Poel 2015) and are nocturnal generalist hunters and scavengers (Halaj & Cady 2000; Allard & Yeorgan 2005a), mainly eating small soft-bodied invertebrates (Allard & Yeorgan 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 nearby and far-away 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 ($\beta_i = f(\text{distance}_i)$), 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 scale of landscape relevant to a given organism may change over the course of its life (Addicott *et al.* 1987; Lima & Zollner 1996; Gardiner *et al.* 2010). It also allows for the possibility that small amounts of certain land cover types may be beneficial, but are detrimental at large scales, indicating that the cover type may

137 not constitute a completely usable habitat.

138 Scalar-on-function regression of activity-density was fit using generalized additive models [*mgcv*
139 version 1.8.35; Wood (2017)]. Count data of arthropods were modeled using a negative binomial
140 distribution with a log-link function and a single dispersion parameter (θ). To account for different
141 lengths of trap exposure, log-days since trap placement were used as a fixed effect with their slope held
142 at 1 (“offset” variable). Trapping location was included as a fixed effect with 5 levels (canola, field
143 edge, grassland, road margin, and wetlands) to account for the effect of local cover independent of the
144 surrounding landscape composition. Day of year was included as a 1-dimensional smooth, and easting
145 and northing (km east and north of the trap extent centroid) were included as 2-dimensional smooths
146 in order to account for underlying spatial and temporal autocorrelation in the data.

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

161 To compare scalar-on-function (annular) regression to the more traditional (radial) regression
162 approach, we also fit radial models of abundance using the same cover classes. We fit models using
163 proportion cover in radii of increasing distances around each trap location (30 - 1500m, as above), and
164 chose the model with the lowest AIC as the “best” model. As in the annular regression model, trapping
165 location, log-days of trap placement, day of year, and easting and northing were also included in the
166 radial models.

167 Preliminary model fits revealed that some of the landscape terms in our model were strongly

168 concurred with each other, so we removed them from the model or combined them. Concurvity is a
 169 nonlinear analogue of multicollinearity which can bias estimates of standard errors (Buja *et al.* 1989).
 170 There is no agreed-upon threshold of "unacceptable" concurvity, but 0.5 is commonly used
 171 [dominici2002; ramsay2003]. <!-- Some landscape terms were strongly concurred , namely
 172 forest and shrubland (max: 0.71), canola and cereal (max: 0.74), and grassland and wetland
 173 (max: 0.63). --> For highly concurred classes, we examined the spatial nature of the concurvity
 174 using scatterplots of proportion cover within each annulus to determine whether the cover
 175 classes should be merged (if classes were consistently related) or removed (if classes
 176 were inversely related to one another). Forests and shrubland were combined into a "single woodland"
 177 category, and grassland and wetland were combined into a single "grassland" category, as they were
 178 strongly positively related to each other at all distances of annuli, indicating similar feature classes.
 179 Cereal was removed from the model, as it was highly concurred with canola; in particular, it was
 180 negatively associated with canola cover at annulus distances of less than 200m and was positively
 181 associated at distances over 500m, reflecting the most common crop rotations (canola → wheat →
 182 barley) and the commonly-used 800 m block structure of farmland in our study region (quarter-sections).
 183 This resulted in a reduced set of landscape terms, none of which were strongly concurred with each
 184 other (cropland: canola, pulses; SNL: grassland, pasture, woodland, roadside; see Figure S1).

185

Box 1: Interpreting Functional Regression Plots

186 Functional linear regression is a special case of linear regression, where the independent variable
 187 is predicted by a functional dependent variable, meaning that the slope is a function (vector) rather
 188 a fixed (scalar) value (Ramsay & Silverman 2004; Yen *et al.* 2014). Therefore, the interpretation of
 189 a functional regression plot is very different from that of a simple linear regression plot. Figure 2a
 190 shows a simple linear regression plot of a hypothetical relationship between trap *activity-density* (y)
 191 and a single predictor, *proportion cover* (x), which is measured in a circle of a fixed radius surrounding
 192 each trap. If we suppose that the relationship between x and y is similar at all radii at which x is
 193 measured, then Figure 2b shows the resulting functional linear regression plot, where the slope (β) is
 194 the same at all distances (we avoid the problem of overlapping concentric circles by using concentric
 195 *annuli*). In reality, it is more likely that nearby cover will be more influential on activity-density than
 196 far-away cover, which could result in a relationship similar to Figure 2c. As functional regression takes
 197 any continuous predictor of y , it is also possible to use proportion cover as a predictor of measurements
 198

199 taken across time, allowing the effect of a (fixed) proportion cover on activity density to vary over the
 200 course of the season (Figure 2d). Finally, the effect of proportion cover over distance and time may be
 201 modeled as a smoothed surface, representing the joint spatio-temporal influence of landscape cover on
 202 activity-density.

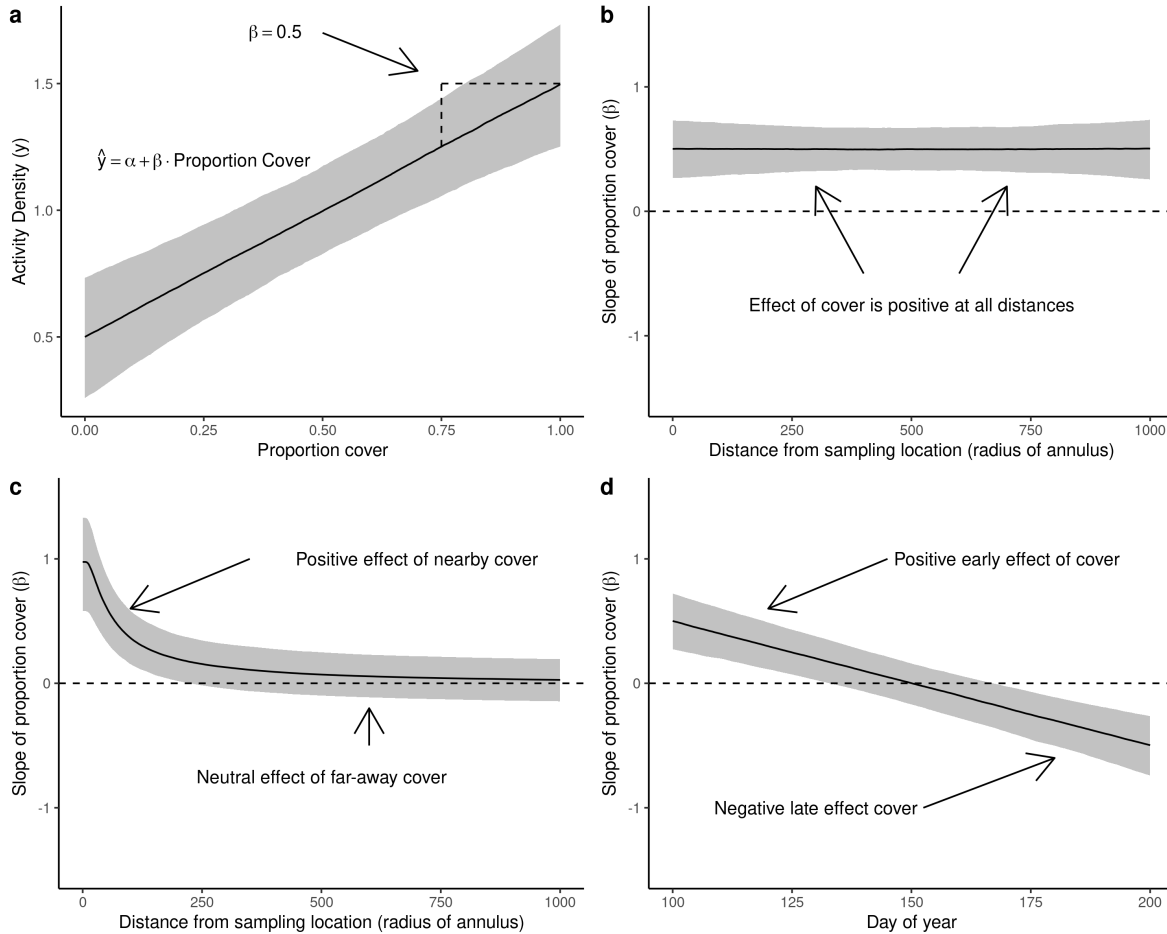


Figure 2: Examples of (functional) linear regression plots. **a)** shows a simple linear regression plot, with a single slope value for a single regressor. **b)** shows the equivalent plot in functional regression form, where the slope is a smoothed function that maps onto a function-valued regressor.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

203

204 Functional regression plots of landscape composition reveal which cover classes are acting as sources
 205 or destinations of a given arthropod, and at what spatial scale (Figure 2). Positive effects of nearby
 206 landscape cover classes indicate that arthropods are spilling over *from* it, therefore acting as a source.
 207 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 **near** and **far** landscape effects, where near indicates the effects of landscape composition at scales of <500 m, and far indicates scales of >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 78% 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 3a). Grassland cover was the most important land cover type in explaining activity-density (R^2 : 0.104, Table 1), and near grassland had a negative effect late in the summer (Figure 3b), suggesting that *P. melanarius* may move into grasslands later in the year. Near canola

237 had a positive effect in the early season, but landscape-level canola had a negative effect, indicating
 238 that areas with widespread canola coverage had lower *P. melanarius* activity-density (Figure 3c).
 239 Pulses acted as a late-season source, indicating that *P. melanarius* may disperse out of pulses after
 240 (or during) harvest (Figure 3d). Finally, *P. melanarius* activity-density had a strong temporal and
 241 spatial component (both $p < 0.001$), indicating that phenology and large-scale geographic factors were
 242 important drivers of ground beetle activity-density (Figure S3). Landscape composition and trap
 243 location explained 19% of the variance in activity-density, while the spatial and temporal smoothers
 244 accounted for 51% (Table 1).

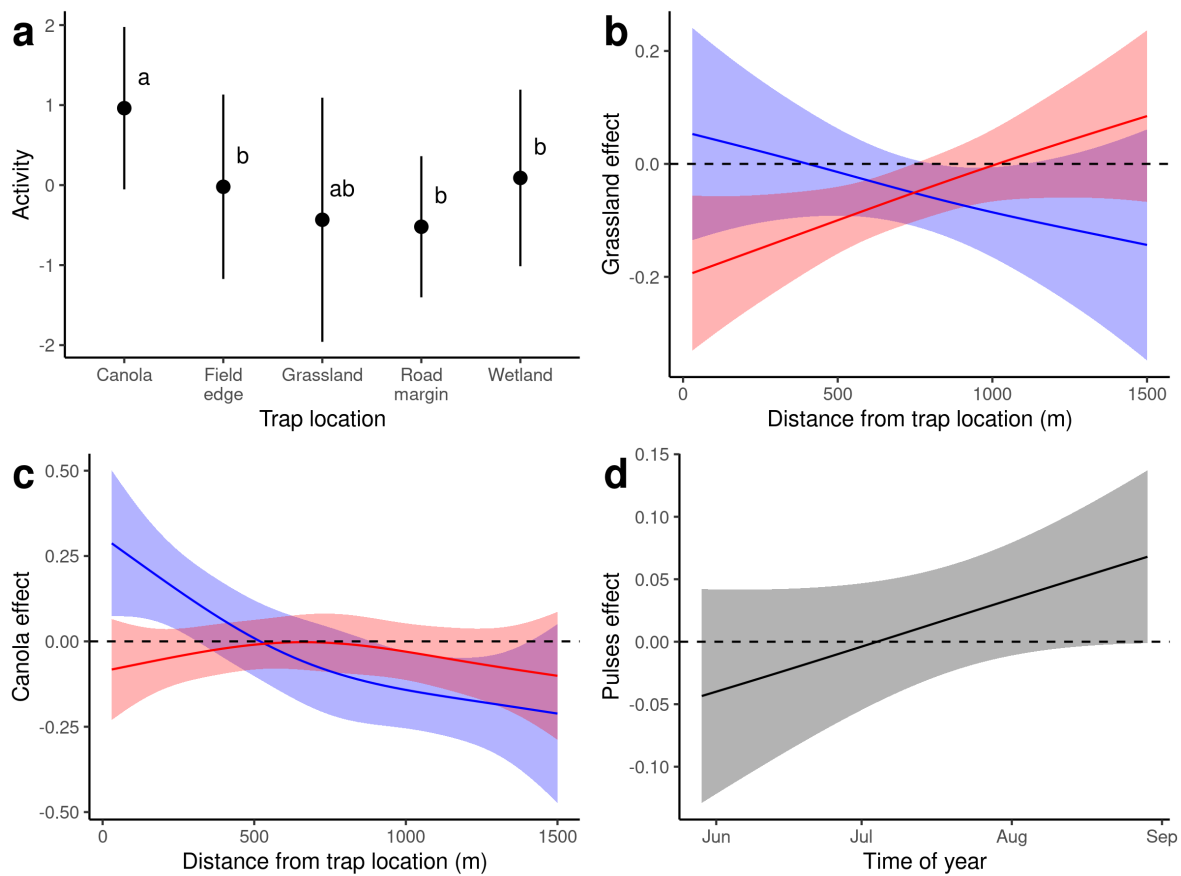


Figure 3: Landscape influence on *Pterostichus melanarius* activity-density. a) shows the effect of trap location, and b-c) are functional regression plots of the proportion grassland and canola at distances away from each trap. d) is a functional regression plot over time, showing the effect of pulses at different times of the year. Lines and dots represent means, and bars and shaded regions represent 95 % confidence regions ($1.96 \times \text{SE}$). Coloured regions represent early- and late-season effects (blue = June 20, red = August 20).

245 3.3. Wolf spiders: *Pardosa distincta* and *Pardosa moesta*

246 Activity-density of *P. distincta* and *P. moesta* was influenced by trap location and landscape
247 composition (Tables S3, S4, S5, S6), but landscape composition had relatively weak effects on both
248 species (R^2 : 0.0252, 0.0445). Unlike *P. melanarius*, both *Pardosa* species had far lower activity-density
249 in canola than any other cover type (Figures 4a, 5a). Activity-density of both *Pardosa* species had
250 a strong temporal and spatial component, although the temporal component was dominant for *P.*
251 *distincta*, whereas the spatial component was dominant for *P. moesta* (Figures S4 and S5; both $p < 0.001$).

252 *P. distincta* activity-density was negatively affected by far pasture (Figure 4b), suggesting that
253 large amounts of pasture are unsuitable habitat for *P. distincta*. There was also a negative effect of
254 woodlands late in the summer (Figure 4c) that did not depend on spatial scale, indicating that *P.*
255 *distincta* may disperse into woodlands at this time. However, trap location and the temporal smoother
256 (Figure S4a) explained roughly 10 times more variance than landscape composition (R^2 : 0.51 versus
257 0.025), meaning that while *P. distincta* may be abundant in certain cover types, its overall habitat
258 preferences are fairly general.

259 *P. moesta* activity-density responded to grassland, canola, and road margins. Grasslands had a
260 near negative effect, but a positive far effect, indicating that these cover types act as a local destination,
261 the general amount of grassland in the area had a positive effect (Figure 5b). Near canola cover had a
262 positive early effect on activity-density, but a negative effect later in the season (Figure 5c). Near road
263 margins also had a similar effect, acting as an early source and a late destination (Figure 5d). Pulses
264 also had a positive effect at the landscape level (Figure 5e), but this explained very little variance in *P.*
265 *moesta* activity-density (Table 1, R^2 : 0.01). Similar to *P. distincta*, trap location and an East-West
266 spatial smoother (Figure S5b) explained roughly 5 times more variance in *P. moesta* activity-density
267 than landscape composition (R^2 : 0.52 versus 0.045), meaning that *P. moesta* is also fairly general in its
268 overall habitat preferences, and is influenced more heavily by larger-scale abiotic factors.

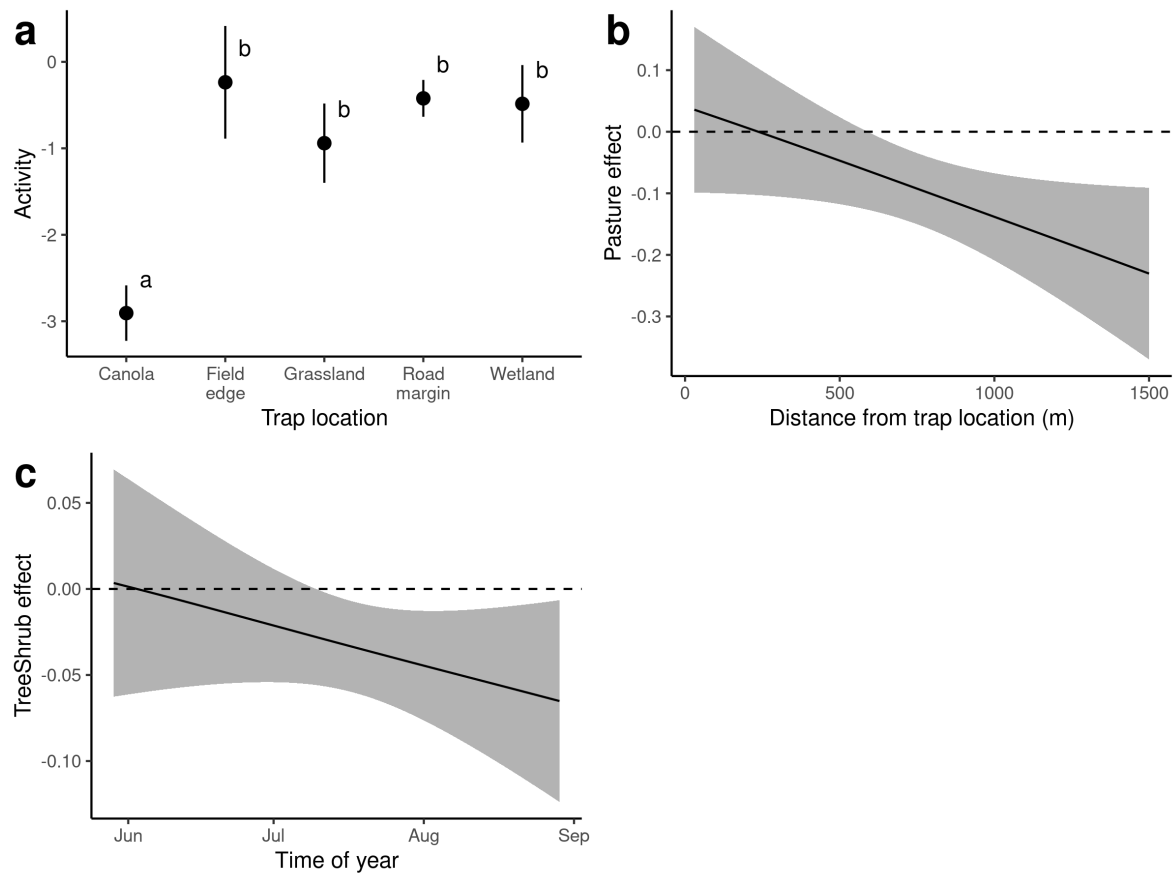


Figure 4: Landscape influence on *Pardosa distincta* activity-density. a) shows the effect of trap location, b) is a functional regression plot of the proportion pasture at distances away from each trap, and c) is a functional regression plot over time, showing the effect of woodland at different times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

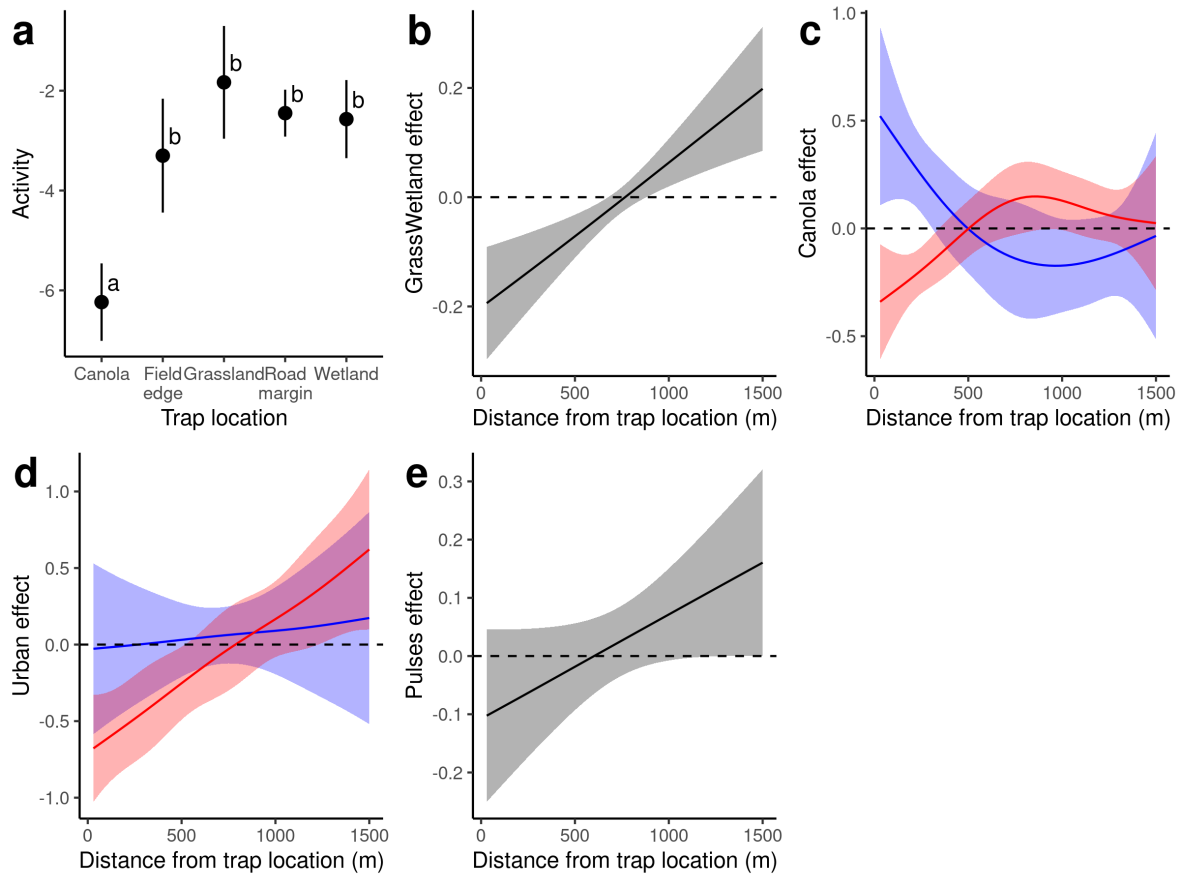


Figure 5: Landscape influence on *Pardosa moesta* activity-density. a) shows the effect of trap location, and b-e) are functional regression plots of the proportion grassland, canola, road margins, and pulses at distances away from each trap. Lines and dots represent means, and bars and shaded regions represent 95 % confidence regions ($1.96 \times SE$). Coloured regions represent early- and late-season effects (blue = June 20, red = August 20).

269 3.4. Harvestman: *Phalangium opilio*

270 *P. opilio* activity-density was somewhat influenced by trap location, with field edges and wetlands
 271 having the highest activity-density (Figure 6a), but this effect was dwarfed by the spatial and temporal
 272 smoothers (Table 1), meaning that *P. opilio* activity-density is only mildly influenced by landscape
 273 composition. Nearby grassland and woodland both had negative effects on *Phalangium opilio* activity-
 274 density Figures 6b,c), but the effect of grassland was negative only early in the season (only weakly for
 275 woodland: $p=0.07$), suggesting that *P. opilio* may preferentially disperse to these cover classes. The
 276 temporal smoother was overwhelmingly the most important predictor of *P. opilio* activity-density (R^2 :
 277 0.42), showing that activity-density increased during the spring, and showed very little decline during
 278 the rest of the season (Figure S6a). Similar to *P. moesta*, *P. opilio* also showed a distinct East-West

279 spatial smoother (Figure S6b), indicating that their activity-density is also influenced by larger-scale
 280 abiotic factors.

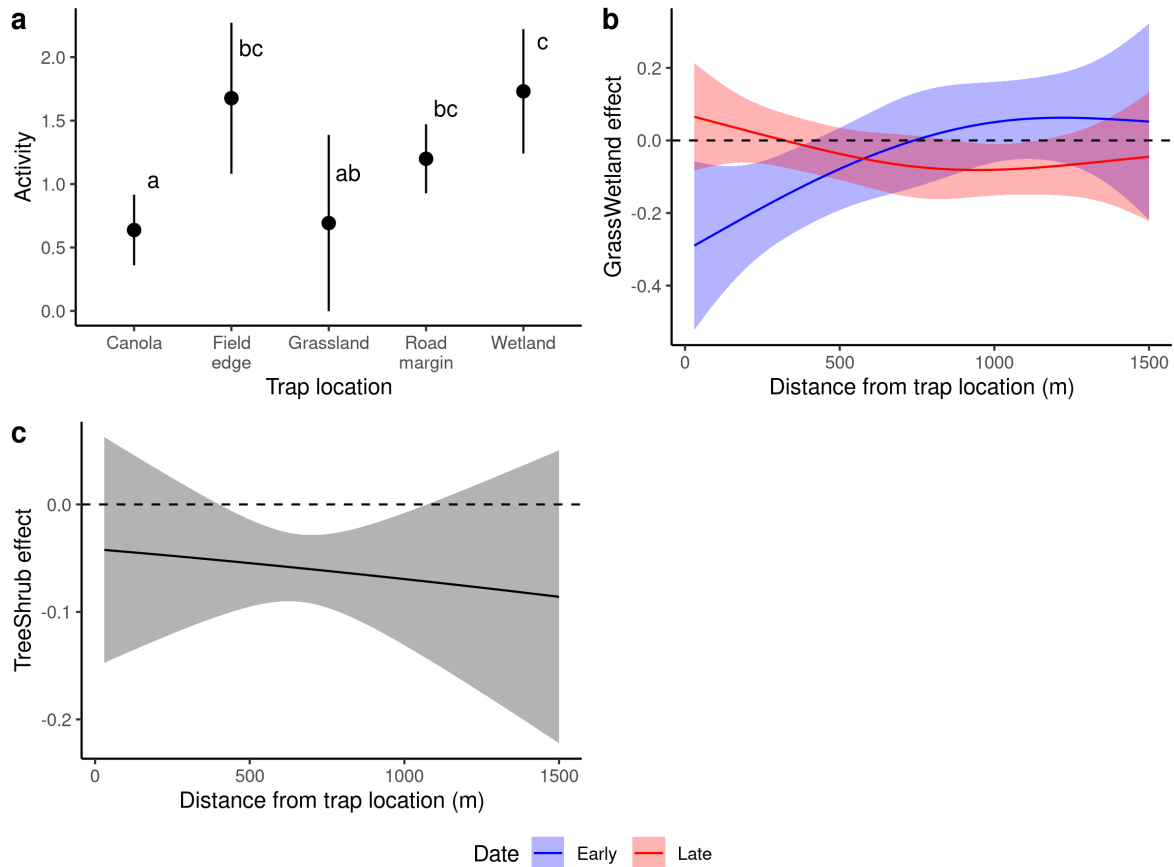


Figure 6: Landscape influence on *Phalangium opilio* activity-density. a) shows the effect of trap location, and b-c) are functional regression plots of the proportion grassland and woodland at distances away from each trap. Lines and dots represent means, and bars and shaded regions represent 95 % confidence regions ($1.96 \times \text{SE}$). Coloured regions represent early- and late-season effects (blue = June 20, red = August 20).

281 3.5. Comparison of annular and radial models

282 Functional regression provided a better abundance model for two out of the four species (*P.*
 283 *melanarius* and *P. distincta*), while radial regression performed better for *P. moesta*, and the null
 284 model (no landscape terms) was the best model for *P. opilio* (Table 3). The best radial model of *P.*
 285 *melanarius* used a landscape radius of 1230 m, lending strength to the interpretation of the functional
 286 model where far-away landscapes have an influence on *P. melanarius* abundance. The best landscape
 287 radii identified for *P. distincta* and *P. moesta* were much smaller (270 and 180 m, respectively), so it
 288 may be that the functional regression incorrectly identified effects of far-away land cover classes on

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	0.142	0.322	0.385	0.019
Day of Year	0.053	0.186	0.066	0.425
Spatial Location	0.454	0.039	0.138	0.235
Grassland	0.008	0.005	0.000	0.001
Canola	0.001	0.007	0.013	0.000
Pasture	0.006	0.000	0.001	0.003
Woodland	0.013	0.000	0.008	0.002
Pulses	0.004	0.009	0.010	0.000
Road margins	0.018	0.005	0.013	0.000
Residual	0.301	0.428	0.367	0.314

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

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

Table 3: Comparison of models. The null model includes trap location and a spatial and a temporal smoother, but contains no landscape terms. The annular model includes the terms in the null model plus scalar-on-function landscape terms. The radial model includes the terms the null model plus radial landscape smoothers. Radius indicates the radius of landscape composition used in the best-fitting radial model.

Species	Null Model		Annular Model		Radial Model		
	AIC	edf	AIC	edf	AIC	edf	Radius (m)
<i>Pterostichus melanarius</i>	4732.1	51.3	4717.3	71.0	4733.1	58.6	1230
<i>Pardosa distincta</i>	3897.1	29.3	3882.5	43.6	3885.0	36.0	270
<i>Pardosa moesta</i>	2013.3	13.2	2008.2	23.1	1975.4	49.9	180
<i>Phalangium opilio</i>	6562.2	33.2	6566.7	45.8	6565.3	38.0	90

abundance. However, none of the radial models accounted for the temporal effects of specific land cover classes, so it is difficult to compare the models directly. Interestingly, the radial model of *P. moesta* provided a much better fit than the functional regression model (δAIC : -33), suggesting that a simpler model may be more appropriate for some species than others. Finally, the null model (no landscape terms) provided the best model of *P. opilio* abundance, indicating that the organism has very general landscape preferences.

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 disperse 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. 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 nearby landscapes are

312 associated with beneficial arthropod abundance. There was also a strong temporal component to most
313 of the landscape effects, meaning that it is important to consider how destinations and sources may
314 change over the season.

315 The predatory ground beetle *Pterostichus melanarius* responded to landscape composition, primarily
316 to canola, pulses, and grass and wetland cover. Grassland and wetland cover had a negative late-season
317 effect, suggesting that they act as a destination for *P. melanarius* at the end of the summer. Other
318 studies have found similar results, suggesting that untilled land is important off-field habitat for carabids
319 (Desender & Alderweireldt 1988; Fournier & Loreau 2002; but see Hatten *et al.* 2007). In particular,
320 Purtauf *et al.* (2005) found that carabid density increased with proportion of nearby grasslands, so our
321 negative late-season effect of grasslands may represent *P. melanarius* moving to overwintering habitat
322 at the end of the season. However, *P. melanarius* is also found in a wide variety of habitats, and tends
323 to prefer agricultural fields (Larsen *et al.* 2003). Our models confirmed this, as they showed that canola
324 and pulse crops had positive effects on *P. melanarius* activity-density early in the season. Early in the
325 season, canola crops had a near positive effect, but a landscape-level negative effect, which may indicate
326 that they provide only temporary feeding habitat. The effect of pulse crops on carabid abundance is
327 not well-studied, but our results suggest that pulses may represent a potential food resource for *P.*
328 *melanarius*, albeit a weak one (Table 1). Carabids are predators of pea-leaf weevils (*Sitona lineatus*)
329 on other Fabaceae (Hamon *et al.* 1990), and *P. melanarius* can prey upon other carabids that are
330 predators of *S. lineatus*, such as *Bembidion quadrimaculatum* (Vankosky *et al.* 2011), so this effect may
331 be direct or indirect. We did not consider the influence of previous years' crops, although carabids tend
332 to be more abundant in areas of high crop rotation (Bertrand *et al.* 2016; Busch 2016). Finally, *P.*
333 *melanarius* has long- and short-winged morphs with very different dispersal abilities (Niemelä & Spence
334 1999; Bourassa *et al.* 2011), which may influence the degree to which landscape-level proportion cover
335 impacts activity-density.

336 The wolf spiders *Pardosa distincta* and *Pardosa moesta* both responded to landscape composition,
337 but it explained only a small fraction of their activity-density (R^2 : 0.025, 0.045). This means that both
338 species of *Pardosa* appear to have very general habitat preferences, but may be somewhat influenced by
339 certain cover types. Pasture had a negative effect at the landscape scale, and woodland had a late-season
340 negative effect, suggesting that *P. distincta* move to woodlands for overwintering or winter foraging
341 (Aitchison 1984; Buddle 2000). *Pardosa* are found in areas close to disturbed roadside strips (Drapela
342 *et al.* 2008; Drapela *et al.* 2011; Kowal & Cartar 2011), but *P. distincta* appears to be less sensitive

343 to disturbances than *P. moesta* (Collins *et al.* 1996; Wade & Roughley 2010). Moring & Stewart
 344 (1994) showed that *P. distincta* were active in grassy habitats, which we found partial evidence of, as
 345 *P. distincta* tended to have higher activity-density in trap locations with higher grass cover (Figure 4a).
 346 Canola had an early-season positive effect on *P. moesta*, indicating that *P. moesta* and *P. melanarius*
 347 may both use canola as foraging grounds. We also found that road margins had a positive early-season
 348 and a negative late-season effect Drapela *et al.* (2011). Grassland and pulses also had a negative nearby
 349 effect but a positive faraway effect; this suggests that they may constitute suitable habitat for *P. moesta*
 350 and attract them away from other cover types. Wolf spiders (Lycosidae) employ a wandering-active
 351 predation strategy (Young & Edwards 1990), meaning that nearby landscape composition may be
 352 more influential to *Pardosa* than large-scale composition (Öberg *et al.* 2007, 2008). While trapping
 353 location explained a large proportion of variance for both species (0.32 and 0.38), several landscape
 354 features were also important at large spatial scales, including grass and wetland, pasture, pulses, and
 355 road margins. Therefore, *Pardosa* dispersal distances may be further than previously thought, either
 356 through ballooning as juveniles (Richter 1970; Greenstone 1982) or through other long-distance travel.

357 *Phalangium opilio* activity-density responded to grass and wetland cover, as well as wooded
 358 landscapes. Other studies have found that *P. opilio* is mostly found in human-altered landscapes with
 359 a large proportion of farming (Muster & Meyer 2014; Van de Poel 2015). Since most of our study
 360 area was in or near farmed land, the lack of variation is understandable, but there were a few notable
 361 landscape-level patterns that emerged. *P. opilio* activity-density was higher in grassy field edges and
 362 wetlands, but grasslands and wetlands had a negative nearby effect on *P. opilio* until late in the season.
 363 These indicate that while grass and wetlands could act as a reservoir, spillover into other land cover
 364 types may be limited, as *P. opilio* avoids heavily grazed areas, possibly due to low humidity (Šajna
 365 *et al.* 2011). *P. opilio* is also found in large numbers at the edges of forests, and may disperse from
 366 forests into farmlands (Van de Poel 2015). We found the opposite pattern: forests had a weak negative
 367 effect on *P. opilio*, at least early in the year. Unlike the other arthropods, most of the variation in
 368 activity-density for *P. opilio* was explained by day of year ($R^2 = 0.42$), indicating strong seasonal
 369 emergence cues. However, there was also a strong East-West pattern in the spatial smoother for both
 370 *P. opilio* and *P. moesta*, meaning that larger-scale geographic patterns (rainfall or temperature) are
 371 more important influences on their activity-density.

372 Many other studies have considered the overall effect of SNL on ecosystem service provision, but
 373 we have highlighted the different spatial and temporal aspects of these services. We have shown how

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

384 Our work has three main applications. First, it adds to the basis of scientific evidence showing
385 that SNL can act as reservoir habitats in intensely-managed agroecosystems. Based on our findings,
386 farmers and land managers should consider preserving existing grassland and wetland habitat to act
387 as habitat for pest-suppressing arthropods in crops. While nearby habitat appears valuable, even
388 faraway habitat can be valuable, as it can increase the number of beneficial arthropods at larger spatial
389 scales (e.g. Figures 3, 5). Secondly, our work suggests that *P. melanarius* and *P. moesta* should be
390 investigated for their role as predators in canola crops (Table 2). They appear to aggregate in canola
391 crops early in the season, meaning that they have the potential to provide valuable pest-control services
392 to growers. Finally, we demonstrate that timing and spatial scale of spillover should be considered
393 in future landscape studies of ecosystem services. We show important differences in the timing of
394 landscape effects on activity-density (early-season vs. late-season spillover) that are typically ignored,
395 but should be considered when assessing how SNL can deliver ecosystem services.

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	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	0.02	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: Concurrency estimates for reduced cover classes used in models.

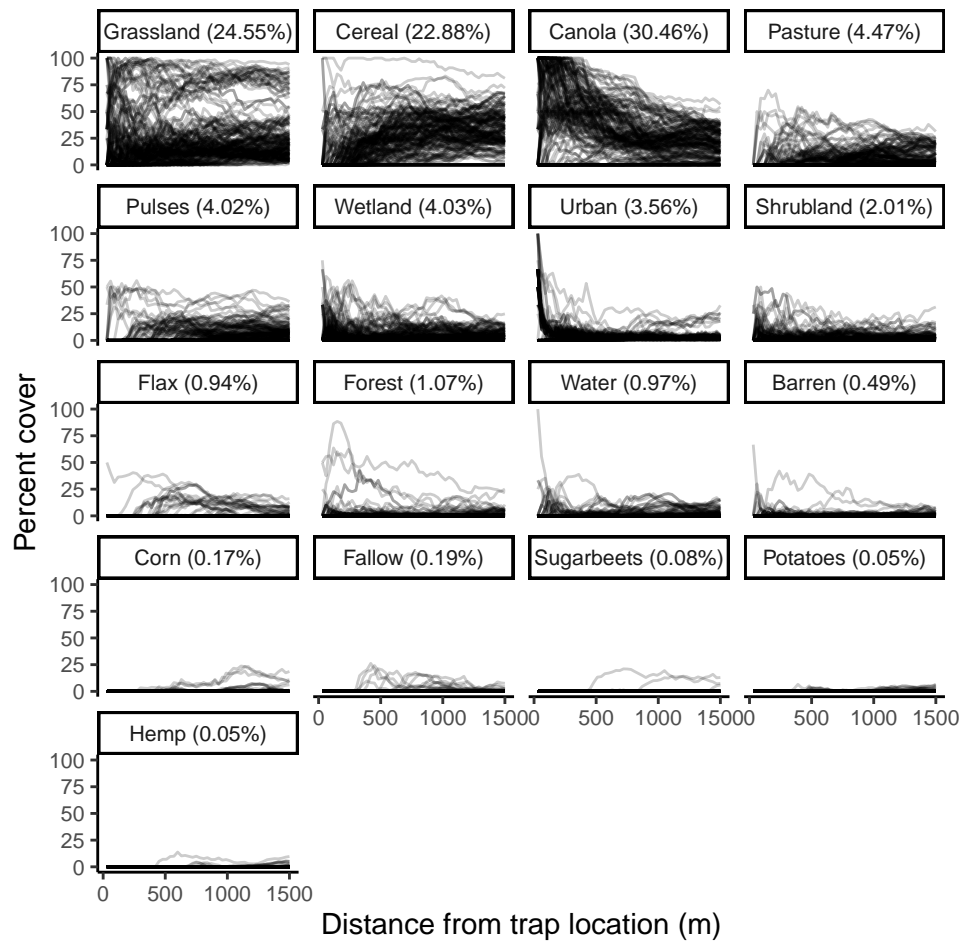


Figure S2: Percent cover of landscape cover classes in annuli surrounding each trap location. Sites are represented by individual lines. Mean cover for each class is listed in each sub-heading.

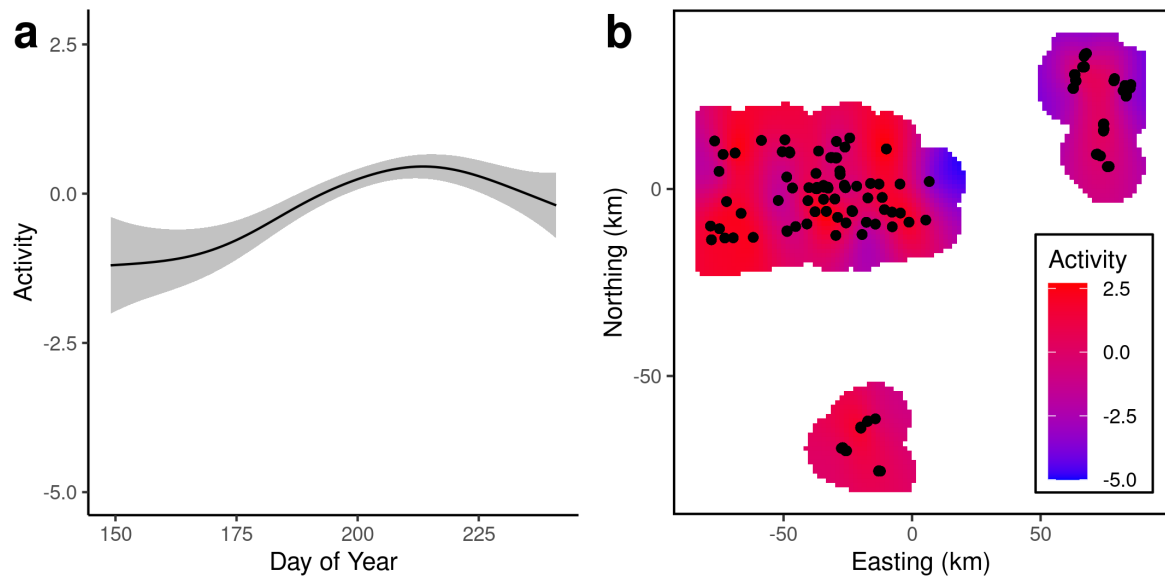


Figure S3: Temporal and spatial components of *Pterostichus melanarius* activity-density (after accounting for landscape composition and trap location). a) shows the effect of day of year, and b) shows the spatially smoothed effect of site location.

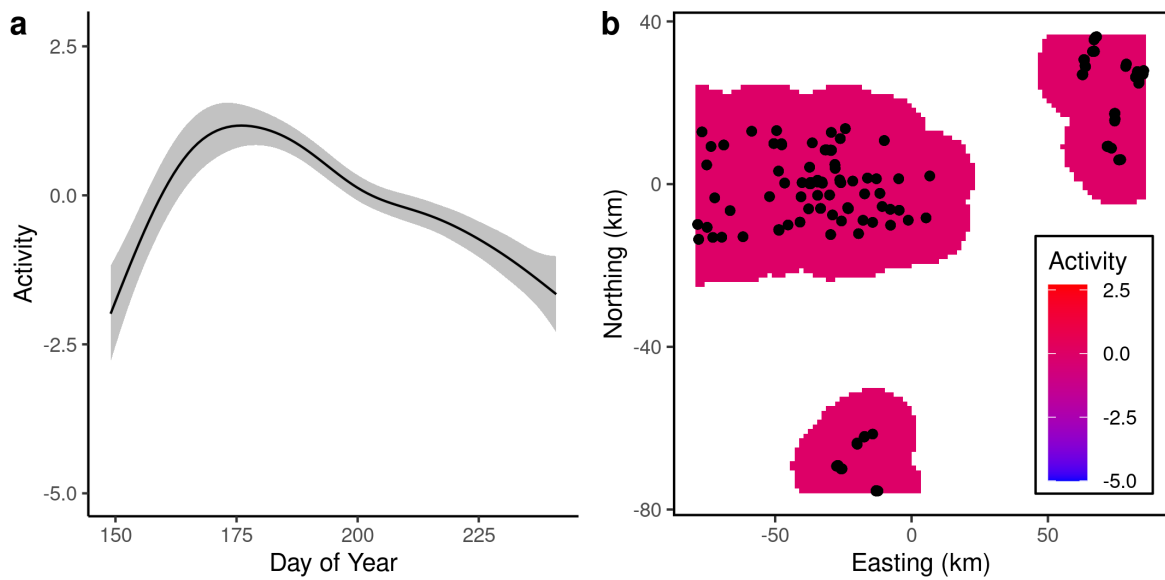


Figure S4: Temporal and spatial components of *Pardosa distincta* activity-density (after accounting for landscape composition and trap location). a) shows the effect of day of year, and b) shows the spatially smoothed effect of site location.

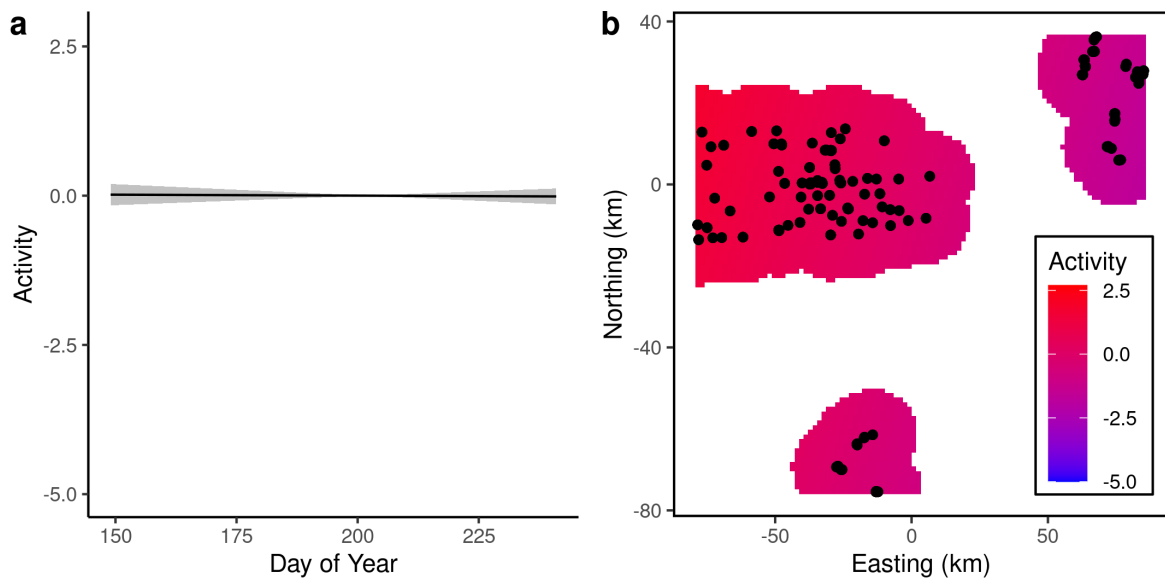


Figure S5: Temporal and spatial components of *Pardosa moesta* activity-density (after accounting for landscape composition and trap location). a) shows the effect of day of year, and b) shows the spatially smoothed effect of site location.

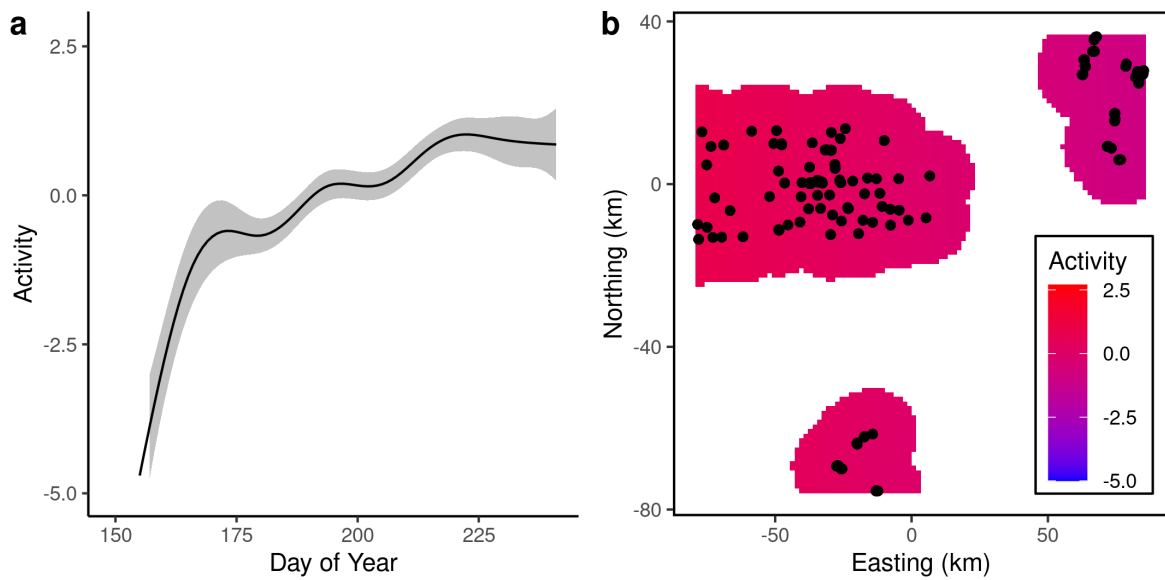


Figure S6: Temporal and spatial components of *Phalangium opilio* activity-density (after accounting for landscape composition and trap location). a) shows the effect of day of year, and b) shows the spatially smoothed effect of site location.

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

Trap location	β	S.E.	Z	p
Canola	0.35	0.22	1.62	0.105
Road margin	-1.83	0.17	-10.59	<0.001
Grassland	-1.36	0.64	-2.11	0.035
Field edge	-0.89	0.36	-2.51	0.012
Wetland	-0.61	0.31	-1.93	0.054

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)	1.14	16.18	<0.001
s(E,N)	39.05	343.41	<0.001
s(Distance):Grassland	<0.01	<0.01	0.161
s(Day):Grassland	1.58	7.11	0.007
ti(Distance,Day):Grassland	<0.01	<0.01	0.925
s(Distance):Canola	<0.01	<0.01	0.339
s(Day):Canola	<0.01	<0.01	0.495
ti(Distance,Day):Canola	0.76	1.82	0.075
s(Distance):Pasture	1.33	6.06	0.009
s(Day):Pasture	<0.01	<0.01	0.541
ti(Distance,Day):Pasture	1.02	2.34	0.091
s(Distance):Woodland	<0.01	<0.01	0.292
s(Day):Woodland	1.8	12.06	0.001
ti(Distance,Day):Woodland	1.87	12.68	<0.001
s(Distance):Pulses	1.57	4.83	0.035
s(Day):Pulses	<0.01	<0.01	0.759
ti(Distance,Day):Pulses	0.59	1.22	0.139
s(Distance):Roads	<0.01	<0.01	0.329
s(Day):Roads	0.52	0.66	0.237
ti(Distance,Day):Roads	3.49	26.8	<0.001

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

Trap location	β	S.E.	Z	p
Canola	-3.48	0.21	-16.95	<0.001
Road margin	-0.62	0.18	-3.45	0.001
Grassland	-1.54	0.35	-4.42	<0.001
Field edge	-0.72	0.34	-2.09	0.037
Wetland	-1.06	0.27	-3.91	<0.001

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)	5.92	207.13	<0.001
s(E,N)	14.44	48.23	<0.001
s(Distance):Grassland	<0.01	<0.01	0.722
s(Day):Grassland	0.04	0.04	0.333
ti(Distance,Day):Grassland	2.42	7.68	0.014
s(Distance):Canola	1.57	6.51	0.012
s(Day):Canola	<0.01	<0.01	0.482
ti(Distance,Day):Canola	0.3	0.41	0.212
s(Distance):Pasture	0.28	0.33	0.274
s(Day):Pasture	<0.01	<0.01	0.55
ti(Distance,Day):Pasture	<0.01	<0.01	0.578
s(Distance):Woodland	<0.01	<0.01	0.988
s(Day):Woodland	<0.01	<0.01	0.727
ti(Distance,Day):Woodland	<0.01	<0.01	0.623
s(Distance):Pulses	1.51	6	0.016
s(Day):Pulses	<0.01	<0.01	0.544
ti(Distance,Day):Pulses	0.97	5.63	0.01
s(Distance):Roads	1.45	7.19	0.007
s(Day):Roads	<0.01	<0.01	0.455
ti(Distance,Day):Roads	<0.01	<0.01	0.938

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

Trap location	β	S.E.	Z	p
Canola	-5.89	0.42	-13.90	<0.001
Road margin	-1.77	0.28	-6.37	<0.001
Grassland	-2.10	0.52	-4.03	<0.001
Field edge	-3.15	0.60	-5.22	<0.001
Wetland	-2.63	0.43	-6.13	<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)	1.12	20.9	<0.001
s(E,N)	1.99	66.86	<0.001
s(Distance):Grassland	<0.01	<0.01	0.953
s(Day):Grassland	<0.01	<0.01	0.768
ti(Distance,Day):Grassland	<0.01	<0.01	0.499
s(Distance):Canola	1.58	6.56	0.015
s(Day):Canola	<0.01	<0.01	0.478
ti(Distance,Day):Canola	1.03	2.33	0.094
s(Distance):Pasture	<0.01	<0.01	0.968
s(Day):Pasture	0.88	1.35	0.208
ti(Distance,Day):Pasture	<0.01	<0.01	0.949
s(Distance):Woodland	1.23	7.26	0.005
s(Day):Woodland	<0.01	<0.01	0.511
ti(Distance,Day):Woodland	<0.01	<0.01	0.413
s(Distance):Pulses	1.44	7.72	0.005
s(Day):Pulses	<0.01	<0.01	0.557
ti(Distance,Day):Pulses	<0.01	<0.01	0.711
s(Distance):Roads	<0.01	<0.01	0.265
s(Day):Roads	1.41	4.97	0.025
ti(Distance,Day):Roads	2.88	10.68	0.002

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

Trap location	β	S.E.	Z	p
Canola	-0.22	0.15	-1.43	0.153
Road margin	0.20	0.12	1.59	0.112
Grassland	-0.13	0.34	-0.39	0.695
Field edge	0.84	0.31	2.71	0.007
Wetland	0.80	0.25	3.26	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)	7.18	147.87	< 0.001
s(E,N)	17.81	220.24	< 0.001
s(Distance):Grassland	0.72	1.87	0.084
s(Day):Grassland	<0.01	<0.01	0.4
ti(Distance,Day):Grassland	<0.01	<0.01	0.956
s(Distance):Canola	<0.01	<0.01	0.711
s(Day):Canola	<0.01	<0.01	0.793
ti(Distance,Day):Canola	<0.01	<0.01	0.575
s(Distance):Pasture	<0.01	<0.01	0.659
s(Day):Pasture	1.3	3.01	0.089
ti(Distance,Day):Pasture	0.87	3.29	0.038
s(Distance):Woodland	<0.01	<0.01	0.813
s(Day):Woodland	<0.01	<0.01	0.633
ti(Distance,Day):Woodland	2.24	5.16	0.059
s(Distance):Pulses	<0.01	<0.01	0.714
s(Day):Pulses	<0.01	<0.01	0.512
ti(Distance,Day):Pulses	<0.01	<0.01	0.622
s(Distance):Roads	0.62	1.05	0.163
s(Day):Roads	0.03	0.03	0.266
ti(Distance,Day):Roads	<0.01	<0.01	0.639

608 Appendix B: R Code

```
#Code to run functional regression using gam function from mgcv 1.8-35

gam(count ~ offset(log(trapdays)) + trapLoc + s(day) + s(E,N)+
  #Canola
  s(distanceMatrix,by=Canola) + #Functional regression of distance
  s(dayMatrix,by=Canola) + #FR of time
  ti(distanceMatrix,dayMatrix,by=Canola) + #FR of distance and time
  #Pasture
  s(distanceMatrix,by=Pasture)+ #Functional regression of distance
  s(dayMatrix,by=Pasture) + #FR of time
  ti(distanceMatrix,dayMatrix,by=Pasture) + #FR of distance and time
  #Other land cover classes here
  #...
```

```

#...

#...

s(distanceMatrix,by=Roads) +
s(dayMatrix,by=Roads)+
ti(distanceMatrix,dayMatrix,by=Roads),
family= 'nb'
)
# where:
#
# count = N x 1 vector of activity density from traps (count)
# trapdays = N x 1 vector of number of days that the trap was installed for (numeric)
# trapLoc = N x 1 vector of trap location type (factor)
# day = N x 1 vector of day of year that the trap was installed on (numeric)
# E,N = N x 1 vector(s) of Easting and Northing (numeric)
# distanceMatrix = N x M matrix of distances, where the Nth row contains a vector
#   of distances to the annuli (numeric)
# dayMatrix = N x M matrix of days, where the Nth row contains a vector of days
#   that spans the range of days of the year (numeric)
# Canola, Pasture, ... = N x M matrix of cover measurements, where the Nth row
#   contains a vector of proportion cover measurements within each annulus (numeric)
# 'nb' = Negative binomial family

```