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Levels of predator movement between crop and neighboring habitats explain pest suppression in soybean across a gradient of agricultural landscape complexity

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ABSTRACT

Landscape complexity has been shown to play an important role in determining the levels of pests and predators found in agricultural fields. Although movement of predators between landscape habitats and crop fields is a crucial mechanism mediating landscape effects on pest control services, this has rarely been quantified in agroecosystems. Here we evaluated the relationship among agricultural landscape complexity, levels of predator movement and the suppression of soybean aphid, *Aphis glycines* Matsumara, in 27 soybean fields in Manitoba. Over a two-year period, we quantified soybean aphid suppression using predator manipulation treatments, predator movement using bi-directional Malaise traps, and landscape complexity using digital maps of the area within a 2 km radius of the focal fields studied. When aphids were exposed to predation, population growth was reduced by 73.7% on average (range: 38.3%–95.6%) compared to aphid populations protected with predator exclusion cages. Bi-directional Malaise trap and sweep-net sampling indicated that hover flies (Diptera: Syrphidae), followed by minute pirate bugs (Hemiptera: Anthocoridae), lady beetles (Coleoptera: Coccinellidae) and green lacewings (Neuroptera: Chrysopidae) were the numerically dominant predators. Focal fields were located in landscapes with a range of 0.3–40.3% of woodland, with soybean, cereals, and canola as the other major land-cover types present. Final aphid population size showed a negative association with the proportion of cereals and positive associations with the proportion of woodland and field border grass in the landscape. Levels of predator movement between soybean and neighboring habitats had negative associations with final aphid population size, and were the best predictors in the statistical models, either alone or combined with independent landscape complexity variables. Our results provide the first empirical evidence that landscape effects on pest suppression can be explained by the contribution of predators from extra-field habitats. From a management perspective, these results suggest that higher levels of pest suppression can be achieved by designing landscapes that facilitate predator movement to crops from extra-field habitats.

1. Introduction

There is increasing evidence that pest suppression by natural enemies (i.e. predators and parasitoids) is an economically important ecosystem service for the agriculture industry. For example, suppression of soybean aphid by natural enemies in four Midwestern US states was estimated to be worth $239 million/year over the two year-period from 2007 to 2008 (Landis et al., 2008). Tillage, pesticide application, and harvesting activities frequently disrupt natural enemy populations in crops, so that if natural biological control is to occur, natural enemies must recolonize crop fields from extra-field habitats (Wissinger, 1997; Landis et al., 2000). Recolonization of crops depends on the composition and arrangement of land-cover types (i.e. landscape complexity), through its effects on the abundance, community structure and dispersal capabilities of natural enemies (Marino and Landis, 1996; Thies and Tscharntke, 1999), ultimately affecting the levels of pest control observed in crop habitats (Landis et al., 2000; Bianchi et al., 2006). To date, higher habitat diversity (e.g. Gardiner et al., 2009), higher proportion of perennial habitats (including natural and semi-natural land covers; e.g. Thies and Tscharntke, 1999), and lower proportion of crop habitats (e.g. Thies et al., 2005) are characteristics of complex landscapes that have been associated with higher abundance and diversity of natural enemies and higher levels of pest suppression in crops.

The movement of natural enemies in sufficient numbers from landscape sources into crops at the appropriate time is crucial for pest suppression (Macfadyen and Muller, 2013; Costamagna et al., 2015;

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Macfadyen et al., 2015). It is therefore important to understand patterns of natural enemy movement since this knowledge could be used to improve biological control of pests in agroecosystems (Schellhorn et al., 2014). In general, natural and other non-crop areas are considered the main sources of predators that move into crop areas, but few studies have actually examined the movement patterns of natural enemies into crop fields and related them to landscape complexity. Macfadyen and Muller (2013) observed that predators and parasitoids move into canola from natural vegetation and Macfadyen et al. (2015) found that predators and parasitoids emigrate from natural areas to colonize cereal crops shortly after crop emergence. Predator movement between different crops could also be important for pest suppression. For example, Bastola et al. (2016) demonstrated that continuous bi-directional interchange of *Hippodamia convergens* Guerin-Meneville (Coleoptera: Coccinellidae) between cotton and alfalfa fields is important for conservation biological control of the cotton aphid, *Aphis gossypii*, Glover (Hemiptera: Aphididae). Further improvement of our understanding of patterns of predator movement across the agricultural landscape is required to guide future efforts to enhance natural pest control services in agroecosystems (Macfadyen and Muller, 2013; Schellhorn et al., 2014; Macfadyen et al., 2015).

The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is a major pest of soybean, *Glycine max* (L.) Merr. (Fabales: Fabaceae), causing yield losses in both Asia and North America (Wu et al., 2004; Ragsdale et al., 2011). Interactions between soybean, soybean aphid, and its predators are influenced by the complexity of the surrounding landscape at different spatial scales. Gardiner et al. (2009) found higher soybean aphid suppression by predators associated with increased landscape diversity at a spatial scale of 1.5 km around soybean fields located in the North Central region of the USA. Additionally, working in the same region, Noma et al. (2010) found that soybean aphid abundance decreases with increasing landscape diversity at a spatial scale of 2 km. More recently, Maisonhaute et al. (2017) found a positive association between cumulative soybean aphid density and proportion of soybean in the landscape. In contrast, Stack Whitney et al. (2016) demonstrated a positive association between the proportion of forest in the landscape and soybean aphid abundance in Wisconsin, and Mitchell et al. (2014) found higher soybean aphid abundance in complex than in simple landscapes in Québec. These contradictory findings have also been reported in other systems. For example, Thies et al. (2005) reports higher crop colonization by cereal aphids with increasing landscape complexity in Europe. More research is still required before landscape effects can be generalized for soybean aphid, as well as for other agricultural pests.

In North America, the most common predators of soybean aphid include several species of lady beetles, minute pirate bugs, damsel bugs, brown lacewings, and larvae of hover flies and green lacewings (e.g. Ragsdale et al., 2011). Experimental manipulations have consistently shown that these generalist predators are important for suppressing soybean aphid populations (Costamagna and Landis, 2006; Gardiner et al., 2009), resulting in increased soybean yield (e.g. Costamagna et al., 2007). Direct field observations indicate that within this assemblage of predators, transient predators (i.e. predators that forage over multiple plants in short periods of time and may move many times through different habitats during a season) were better able to numerically respond to changes in aphid densities (Costamagna and Landis, 2007). Transient predators have an important advantage over less mobile predators, they can fly from one infested field to another, allowing them to utilise food resources more efficiently and provide control across multiple crops (Duelli et al., 1990; Grez and Prado, 2000). However, the movement of these predators between soybean and neighboring habitats has never been quantified.

In landscape studies, the implied assumption is that each patch of the same land-cover type within a landscape contributes similarly to the provision of predators to the focal fields studied. In reality, each patch could contribute very different numbers of predators due to different levels of disturbance, agronomic actions, or, in the case of semi-natural habitats, different plant species. We hypothesized that the level of predator movement between soybean and neighboring habitats would provide a more precise measure of the contribution of each landscape to soybean aphid suppression than the typical summary landscape complexity variables used in previous studies. The purpose of this study was to determine how landscape complexity and predator movement affects soybean aphid suppression in agricultural landscapes. The specific objectives of this study were to determine 1) if predators suppress soybean aphids in our region (Manitoba, Canada), 2) if landscape complexity is a good predictor of soybean aphid suppression, 3) if levels of predator movement between neighboring habitats predict soybean aphid suppression, and 4) if models combining both landscape complexity and predator movement variables result in better predictions of soybean aphid suppression than each set of variables independently.

2. Methods

2.1. Study landscapes and site selection

Field experiments were conducted in 27 landscapes (12 in 2013 and 15 in 2014; different fields each year), at twelve localities in Manitoba (Altona, Arnes, Carman, Elm Creek, Emerson, Gimli, Glenlea, La Broquerie, Letellier, Morris, Rosewood and Warren, Appendix A in Supplementary material). Agricultural landscapes were dominated by soybean, cereals (wheat, *Triticum* spp. L.; oat, *Avena sativa* L. and barley, *Hordeum vulgare* L.), canola, *Brassica napus* L., corn *Zea mays* L., and alfalfa, *Medicago sativa* L. (Appendix B in Supplementary material). Fields were selected to cover a range of landscape complexity, from agriculturally dominated landscapes to landscapes with moderate levels of woodland and riparian vegetation. The average size of the focal soybean field was 72.4 ± 50.7 ha (mean ± SD, range: 0.54–169 ha); about half of the fields were quarter sections (64 ha). The minimum and maximum distance between focal soybean fields were 4 and 200 km, respectively. Soybean phenology varied in the different landscapes, ranging between V6–V10 vegetative stages and beginning to bloom to full pod size reproductive stages (Ritchie et al., 1985, Appendix A in Supplementary material), at the time of our experiment.

2.2. Plant preparation

The widespread use of seed treated with insecticide in commercial fields prevented the use of field plants for this study. Experimental plants were seeded three weeks prior to the field study, and were grown in greenhouse conditions (16:8 h L: D; 23°–27 °C, and 60–75% RH) in square plastic pots (9 cm × 9 cm × 18 cm high) in the greenhouse of the Department of Plant Science, University of Manitoba. The potting mixture was made by mixing equal amounts of peat mix (Sunshine® Mix #4, Sun Gro Horticulture Canada Ltd. Seba Beach, Alberta, Canada), compost and sand by volume. Four soybean seeds were seeded near the four corners of each pot (3 cm below the potting mix level) and were watered three times per week. All plants used for field trials were in the V3 or V4 vegetative stages (Ritchie et al., 1985) and were exposed to natural sunlight conditions outside the greenhouse for 2 days (8 h/day), to increase their hardiness before field experiments. Two plants were removed from the pot before field deployment. A 30 cm bamboo stick was buried in the pot to support the two well grown plants using twist ties. The use of potted plants allowed standardization of plant variety, phenological stage and soil conditions among all focal soybean fields studied.

2.3. Predator manipulation experiment

Two predator manipulation treatments were used to test predation by natural enemies using predator exclusion field cages. In each focal soybean field, ten pots with soybean plants were randomly assigned