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Ground beetle conservation biocontrol: Potential for pest control ecosystem services using predation activity and trait-based analysis

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Ground beetle conservation biocontrol:

Potential for pest control ecosystem services using predation activity and trait-based analysis

by

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Abstract

Removal of non-crop vegetation (e.g., forest and grassland patches) to expand crop fields threatens the natural enemies of crop pests, like the ground beetle family (Coleoptera: Carabidae), that may use these areas for overwintering. An argument for maintaining non-crop vegetation is its potential to support the supply of ecosystem services, such as pest control, to the surrounding crop. A common proxy for this service is the activity-density of natural enemy species. Evidence that predators like ground beetles are attacking pests in crops has been less frequently studied as have the mechanisms for why non-crop vegetation may influence pest predation within the crop. Studying the traits of natural enemies that are both impacted by the environment and affect their predation activity, may provide a mechanism for how non-crop vegetation influences pest control. Traits, like the size of carabids, may influence both their dispersal from non-crop vegetation and their predatory activity. I sampled a gradient of distances from non-crop vegetation in 20 field sites. I estimated the potential for pest attacks by carabids through bite marks on *sentinel prey* (plasticine ‘caterpillars’ made to look like potential prey items) and measured the body size of 20,407 carabids. I also conducted prey choice experiments with the carabid *Pterostichus melanarius*. Generalized additive models show that the frequency of bite marks increased to 50 m into the crop before declining at 100 m, but carabids in pitfall traps increased linearly as distance from non-crop vegetation increased. Results also showed the smallest six quantiles of carabids increased in size with distance from non-crop vegetation areas and larger *P. melanarius* showed a trend towards preying upon larger prey than smaller prey, though we could not reject a null hypothesis of no effect (alpha=0.05; P=0.08). These findings show predation activity may be associated with non-crop vegetation and the carabid community size distribution, rather than being predicted by activity-density. These findings support conservation of non-crop vegetation to support the predation of a diverse array of pests.

Keywords: Carabidae; biocontrol; spill-over; ecosystem service; sentinel prey; activity-density, functional trait, response-effect

Preface

Chapter Two of this thesis will be submitted for publication as:

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Chapter 1: General Introduction

1.1 Land use change and conservation biocontrol

In northern North America, acting as the boundary between the boreal forests and the prairies, lies a mosaic landscape. Contemporarily, field crops meld with scattered groves of aspen (*Populus tremuloides*) and fescue grasslands. Within these stretches, wetlands punctuate the terrain. This is a place where many worlds coexist, each offering a glimpse into the others, and influencing those around it. This landscape is defined by its ongoing status of transition, contrasts, and balance. This, the Aspen Parkland Ecozone, was estimated to have only 10% of its natural habitat intact in 1999 with increasing agricultural activities, giving it a status of critically endangered (Ricketts et al., 1999). Nearly the entirety of the ecozone has been converted to agriculture, but remnants of its habitat persist in marginal areas and between crop fields (Ricketts et al., 1999; Riley et al., 2007). These non-crop vegetation areas offer a refuge for migratory birds, rare plants, and children seeking saskatoon berries, from the intensely managed field crops dominating the landscape (Bird, 1961; Carter, 1999; Ricketts et al., 1999; Riley et al., 2007).

The removal of non-crop vegetation areas, such as forested or grassy patches, to expand crop fields, is at odds with the conservation of landscape and species diversity (Díaz et al., 2019; Ricketts et al., 1999; Rumschlag et al., 2020). However, the trend towards larger areas for cropping is common in North America. For example, growers may remove treed windbreaks, cultivated as a response to the *dust bowl* of the 1930's, in favour of expanding cropping area and increasing yield (Brandle et al., 2004; Mayrinck et al., 2019; Osorio et al., 2019). Because of the widespread implementation of no-till or reduced till practices (where growers disturb the soil as little as possible) windbreaks to protect against soil erosion may be less necessary (Mayrinck et al., 2019; Osorio et al., 2019). However, removal of non-crop vegetation may also reduce habitat for rare plants and migratory birds (Boatman et al., 2004), decrease water filtering leading to watershed contamination by chemical crop inputs like pesticides (Brandle et al., 2004; Rumschlag et al., 2020), increase the spread of zoonotic disease (White & Razgour, 2020), and negatively impact ecosystem services such as carbon sequestration or natural pest control for the crops that are being expanded (Díaz et al., 2019; Mayrinck et al., 2019; Mitchell et al., 2014; Ricketts et al., 1999).

Even though non-crop vegetation is important for conservation, especially in endangered landscapes like the Aspen Parkland, some growers and landowners may believe non-crop vegetation provides ecosystem disservices. Growers may believe that non-crop vegetation acts a *reservoir* for crop pests, where the pests congregate in the non-crop vegetation for food or shelter and then *spill-over* into the crop to damage crop yield and quality (Tscharntke et al., 2005, 2016). This negative perception of non-crop vegetation areas may further incentivise their removal. However, spill-over of pests from non-crop vegetation is likely not as prevalent as growers may believe (Chaplin-Kramer et al., 2011; Innes et al., *In Progress*). Rather, what may be spilling into the crop from non-crop vegetation areas are ecosystem services, like pest control or pollination, from naturally occurring pollinators and beneficial predators (Boetzl et al., 2019; Gallé et al., 2019; Robinson et al., 2021).

Prior to my work, what is now the Agriculture, Biodiversity, and Conservation Lab at the University of Calgary started the Surveillance Networks for Beneficial Insects (SNBI) research program. The purpose of the SNBI was to survey beneficial arthropods in the Canadian Prairie Provinces and then, in a second phase, examine the effects of those beneficial arthropods on crop systems. Projects within the SNBI showed that native bees use wetlands as habitat reservoirs and will spill-over into the surrounding crop (Vickruck et al., 2019) and some beneficial predators (*natural enemies*), such as the ground beetle *Pterostichus melanarius* and the wolf spiders *Pardosa distincta* and *P. moesta,* also likely have spillover effects associated with different non-crop vegetation and at different times of the season (Robinson et al., 2021). However, the response of beneficial arthropods to landscape has temporal dependence and can be taxon-specific (Galpern et al., 2021; Robinson et al., 2021). It was also found that native bees have a diverse array of species dependent traits, such as phenology and nesting preferences, that may make their associations to certain landcover classes species, and trait, dependent (Galpern et al., 2021) though the importance of these traits were not measured for native bees or for beneficial predators in this system. Other findings from the lab and the program showed that landscape complexity and non-crop vegetative field boundaries can benefit crop yield (Galpern et al., 2020; Nguyen et al., 2022; Robinson et al., 2022). My research fits into this greater program by examining why we may see spillover trends in beneficial arthropods and what influence those arthropods have on the agroecosystem. I do this by examining a trait that may influence the dispersal of beneficial predatory arthropods, how that trait may influence predatory effects of the natural enemies, and then measuring the potential for predation activity within the landscape, all through the lens of conservation biocontrol.

The practice of conservation biocontrol focuses on retaining and restoring resources, such as non-crop vegetation areas, for natural enemies that will enact pest control services (Begg et al., 2017). Biodiversity is then supported by providing habitat in those non-crop areas for other organisms that require it (Begg et al., 2017). However, it remains challenging to predict the outcomes of conserving non-crop vegetation for pest control services. While conserving non-crop vegetation can increase the biodiversity of generalist predators and this, in turn, can increase crop yield (Barnes et al., 2020; Dainese et al., 2019; Geiger et al., 2010), the mechanisms of how increased biodiversity of generalist predators impacts yield are poorly understood.

1.2 Carabid generalist predators

Some of the most common generalist predators studied for their use in conservation biocontrol are found in the ground beetle family, Carabidae (Busch et al., 2021; Cividanes, 2021; Holland et al., 2016; Kromp, 1999; Roughley et al., 2006). Not a lot is known about the natural history of most carabid species in North America. *P. melanarius*, a common though introduced ground beetle throughout North America, is perhaps the most researched species in the Aspen Parkland Ecozone. New adult *P. melanarius* emerge in the early spring (Busch et al., 2021). The adult population peaks around the middle of July through to August, which is also when mating occurs (Busch et al., 2021). Carabid species overall may be divided between those with population peaks in the fall or those with peaks in the spring (Lövei & Sunderland, 1996). For *P. melanarius*, females oviposit in the early fall, with a preference for structurally complex environments as locations for oviposition (Busch et al., 2021). *P. melanarius* likely overwinter as larvae and pupation is triggered by warming spring weather (Busch et al., 2021). *P. melanarius* is generally considered more carnivorous than some other carabid taxa, like *Amara spp.*, which may be more granivorous, but overall carabids are regarded as diet generalists (Busch et al., 2021; Kromp, 1999; Kulkarni et al., 2015; Lövei & Sunderland, 1996).

The polyphagous feeding habits of carabid beetles have been used to justify their importance for conservation biological control for at least the last two decades (Busch et al., 2021; Cividanes, 2021; Holland et al., 2016; Kromp, 1999). A review from 1999 on the pest predation efficacy of carabids concluded that, while laboratory studies show that carabids will eat certain pest species, it was not known whether carabids can supply pest predation ecosystem services under typical agricultural conditions (Kromp, 1999). That same review also highlighted that future research should focus on determining the importance of field margins for overwintering by dispersing species of carabids. However, at least in Europe, the review argued that methods such as intercropping and landscape features such as treed areas can benefit carabid populations to differing degrees (Kromp, 1999). Since 1999, few studies have bridged the gap between testing whether carabids may consume a particular pest and quantifying their ability to provide pest control within an agricultural setting (Blaix et al., 2018; Chaplin-Kramer et al., 2011, 2019).

In Canadian agroecosystems, it is largely unknown what carabids are consuming. We can extrapolate from other global locations and laboratory studies to understand that carabids are likely consuming slugs, along with other agriculturally-important pests (Cross et al., 2015; Dunning et al., 1975; Kromp, 1999; Le Gall & Tooker, 2017; Solomon et al., 2001). We also know that they are likely eating weed seeds (Barbercheck & Wallace, 2021; Petit et al., 2014). Much of the information about the arthropod diet of carabids comes from laboratory settings, though evidence suggests that consumption in a laboratory setting does not always correlate with consumption in the field (Kheirodin et al., 2019; McKemey et al., 2003). Therefore, it is important to measure how carabids perform pest control and how much they rely on non-crop vegetation areas to perform predation in crops.

1.3 Functional traits and sentinel prey

Traditionally, research on biocontrol by carabids focuses on species identity and the diversity of species present (Blaix et al., 2018; Chaplin-Kramer et al., 2011, 2019; Kromp, 1999). These traditional studies also usually measure the *activity-density* of carabids as a proxy for either abundance or ecosystem service supply (Kromp, 1999; Lang, 2000; Thomas et al., 2006). Activity-density is measured when passive pitfall traps are used to capture carabids that fall into them (Lang, 2000; Thomas et al., 2006). The pitfall-traps rely on both the presence of the carabids (areas more densely populated with carabids may capture more in a pitfall) but also the movement activity of the carabids (if carabids move around more, they will be more likely to encounter a pitfall trap over the time that it is deployed. Conversely, if carabids do not move around, they may not fall into any traps even if they are present in the vicinity). This focus on species identity and use of activity-density as a proxy measurement for predation has largely ignored the mechanisms underlying predation (Boetzl et al., 2019; De Bello et al., 2021; Funk, 2021; Gallé et al., 2019, 2020; Kromp, 1999; Perović et al., 2018).

In this thesis, I explore two alternative methods to taxonomic surveys and measurements of activity-density that may assist in elucidating the mechanisms of pest predation by carabids and the impacts those mechanisms may have for ecosystem service supply. These are: 1. A *functional trait response-effect framework*, where traits of individual beetles that may assist in predatory effects in agroecosystems are measured (De Bello et al., 2021; Gallé et al., 2019, 2020; Perović et al., 2018) and 2. *Sentinel prey*, where prey items are artificially provided and predation on those items can be compared under different conditions (Lövei & Ferrante, 2017; Prasifka et al., 2006).

A *functional trait response-effect framework* allows researchers to determine the mechanisms of pest control (De Bello et al., 2021; Perović et al., 2018; Suding et al., 2008). Specifically, the functional trait of body size may respond to landscape features such as distance from non-crop vegetation areas – e.g., larger beetles may be able to disperse further (Perović et al., 2018). Body size of carabids may in turn have effects on prey consumption where larger beetles may eat more or larger prey than smaller ground beetles (Perović et al., 2018). The functional trait framework is also generalizable across agroecosystems in ways that taxonomic approaches are not; i.e., while certain species may not be present at all locations, making abundance comparisons challenging, the traits of the species that are present may be compared (De Bello et al., 2021).

Sentinel prey, the method of placing prey items artificially and measuring predation on those prey, allows researchers to understand patterns in prey consumption that may be otherwise elusive (Lövei & Ferrante, 2017). While ground beetles are assumed to be consuming pests, their predatory effects may not be dictated only by their activity-density as traditionally measured by number of beetles in pitfall traps (Lang, 2000; Thomas et al., 2006). Ground beetles, being polyphagous, often engage in intraguild predation where larger carabids will consume smaller carabids, potentially having a negative effect on pest control even when there is an abundance of ground beetles (McKemey et al., 2003; Rusch et al., 2015; Wang et al., 2019). Similarly, different habitats and different times of the season may be conducive to different activities for ground beetles, such as overwintering in non-crop vegetation areas or consuming seeds in the late summer when there is an abundance of seeds and a requirement of dietary fats (Petit et al., 2014; Robinson et al., 2021). Sentinel prey assists in determining when, where, and how much the activity of predation may be happening instead of measuring activity in general (Lövei & Ferrante, 2017).

1.4 Importance and significance

To summarize the background information that I have presented thus far, the removal of non-crop vegetation in agroecosystems presents a global challenge for conservation and is particularly impactful in areas where the native habitat is already endangered, such as the Aspen Parkland (Díaz et al., 2019; Ricketts et al., 1999; Riley et al., 2007). There is also a potential for non-crop vegetation to provide ecosystem services, like pest control, via the spillover of generalist predators, like carabids (Chaplin-Kramer et al., 2019; Dainese et al., 2019; Díaz et al., 2019). This supply of ecosystem services may be useful in incentivising growers and other stakeholders to reduce the removal of non-crop vegetation and even favour its restoration. Therefore, for the conservation of non-crop vegetation to be adopted by growers, I must answer the question **how does non-crop vegetation affect the potential for pest control ecosystem services by ground beetles in nearby crop fields?** This is not a novel question, but many researchers answer it with the assumption that species presence of ground beetles indicates pest predation is being supplied (Kromp, 1999; Lang, 2000; Thomas et al., 2006). Therefore, I answer this question with a potential mechanism and by parsing out the difference between activity-density of ground beetles and the potential to deliver the pest control ecosystem service. In this thesis I use sentinel prey to quantify the impacts of non-crop vegetation on potential predation activity by carabids. I then use a functional trait response-effect framework to parse out a mechanism of *how* non-crop vegetation impacts carabids and the potential predation they perform. The response-effect framework also allows for findings to be generalized between agroecosystems so growers may be able to better inform their conservation of non-crop vegetation without having to conduct a survey in their crop field.

1.5 Study area

The studies presented in Chapters Two and Three took place in the Aspen Parkland Ecozone of central Alberta. The Aspen Parkland Ecozone is the largest transitional biome between boreal forest and prairie in the world and covers over 394,000 km^2 (Carter, 1999; Hoekstra & Molnar, 2010; Ricketts et al., 1999; Riley et al., 2007). It contains four major habitat classes; fescue grassland, wetlands, ravines, and woodlands of trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*), along with some conifers, and many understory shrubs and willows (Bird, 1961; Ricketts et al., 1999; Riley et al., 2007). Migratory bird species utilize the Aspen Parkland during migration and breeding along with many other plant and animal species that are reliant on the fragmented habitat (Ricketts et al., 1999; Riley et al., 2007). Over 90% of the Aspen Parkland has been converted to agriculture and it is one of the most anthropogenically impacted areas in the world (Bird, 1961; Ricketts et al., 1999; Riley et al., 2007).

While traditionally stewarded by the nations of treaties 1, 2, 4, 5, 6, 7, 8, and 10, land ownership in the Aspen Parkland Ecozone is typically separated into 64 ha ‘quarter sections’ and 87% of the landcover is privately owned (Carter, 1999; Riley et al., 2007). The quarter sections are often broken up for different purposes such as storage of equipment, homesteading, ranching, oil extraction, and cropping, though crop covers the most area (Riley et al., 2007). The most common crops used in rotation are canola (*Brassica napus*) and cereal grains (Agriculture and Agri-Food Canada, 2021; Riley et al., 2007). The dominant form of crop production utilizes crop protection chemicals and synthetic fertilizers, which can have deleterious environmental effects (Beingessner & Fletcher, 2020; Boatman et al., 2004; Geiger et al., 2010). ‘No-till’ agriculture, the practice of not disturbing the topsoil except when seeding, is common, as is ‘crop rotation’, where different crops are grown in subsequent years to limit pest damage and loss of soil nutrients (Agriculture and Agri-Food Canada, 2009; Harker et al., 2015). Growers may indicate an interest in sustainability due to wanting future generations to inherit land or land to be profitable into the future, though some believe their practices are sustainable enough for their goals due to the implementation of no-till and crop rotations (Beingessner & Fletcher, 2020). Ultimately, the driving factor in the dominant management practices is monetary (Beingessner & Fletcher, 2020).

The Aspen Parkland Ecozone is ideal for studying the impact of non-crop vegetation on the supply of pest control ecosystem services by carabids in crops. There are remnant and restored habitats of Aspen Parkland interspersed among the dominant crop fields and carabids are abundant in both the crops and the non-crop vegetation. Furthermore, the Aspen Parkland, being critically endangered due to the removal of its habitats in favour of crop expansion, would benefit from increased value to agriculture attributed to its remaining habitats.

1.6 Thesis outline

My objective for this thesis is to quantify how non-crop vegetation areas effect the predatory abilities of ground beetles within crops. I do this both through measuring potential predation activity and measuring traits that may affect predation both in relation to non-crop vegetation. Ultimately, I aim for this thesis to contribute to informing future policy or grower practices in the viability of conservation biocontrol.

The chapters of this thesis complement each other by determining the predatory outcome of the relationship carabid beetles have to non-crop vegetation areas and a functional mechanism potentially underlying the relationship. Knowledge of both the potential outcome of carabids in agroecosystems and the mechanisms underlying their effects are limited so I tackle each in separate chapters while also utilising and contrasting with more traditional methods of understanding carabid predation such as measuring activity-density and conducting laboratory analysis of predation. In Chapter Two I assessed the effect of non-crop vegetation on both the predatory activity and the activity-density of carabid beetles. I also provide what is likely one of the first metagenomic analyses of carabid arthropod diets in the Canadian Prairies. In Chapter Three I examine the effect of distance from non-crop vegetation on body size of ground beetles and then assess the effect of body size on prey choice. Chapter Three is complementary to

Chapter Two in that it explores underlying mechanisms for the predation activity outcomes of ground beetles. Chapter Four, the conclusion, is a summary of the broader significance of each study and the overall findings relating to my original objective of quantifying the effects of non-crop vegetation on ground beetles.

Both Chapters Two and Three were written as manuscripts, with the goal of publishing them (See Preface). As such, others have assisted in the research. Despite help from others, this thesis is fundamentally my work (See appendix for co-author contribution statements). I conceptualized the thesis, developed the methodology, investigated the question, collected and curated the data, conducted the formal analysis and visualization of the data, and wrote the original draft of and edited both chapters. Dr Paul Galpern provided expertise in the conceptualization of the project, the development of the methodology, the formal analysis and visualization of the data, edited the manuscripts, and provided resources such as lab space and funds. For Chapter Two, Dr Samuel Robinson also contributed to the formal analysis, visualization of the results, and editing of the chapter.

Chapter 2:

Predation activity by ground beetles is enhanced by non-crop vegetation

1. Introduction

Human-driven changes to agricultural landscapes threaten ecosystem services, such as pollination and pest control, that are critical for global food security (Díaz et al., 2019). For example, the removal of non-crop vegetation (e.g., wetlands, forests, grasslands) to expand fields is detrimental to the organisms that use these areas as habitat (Gallé et al., 2019; Mitchell et al., 2014; Vickruck et al., 2019; Zhang et al., 2007). Among these organisms are the *natural enemies* of crop pests, such as species from the ground beetle family (Coleoptera: Carabidae) which may supply ecosystem services because they prey upon on other insects that damage crops (Gallé et al., 2019; Kromp, 1999; Perović et al., 2018).

Non-crop vegetation areas in agroecosystems may serve as *reservoirs* for carabids by providing overwintering habitat, protection from predators, and food sources that in turn allow the carabids to provide pest control within the crop (Kromp, 1999; Robinson et al., 2021; G. Schneider et al., 2016). Evidence for predatory beetles that move into the crop from their non-crop vegetation reservoirs (*spill-over*) has been found in many cropping systems but is not observed in all agroecosystems (Tscharntke et al., 2005). The degree and causation of spill-over are often inconsistent between agroecosystems as well (Chaplin-Kramer et al., 2011; Gallé et al., 2019; Kromp, 1999; Tscharntke et al., 2005). Spill-over of carabids is likely to occur in western Canadian croplands (Robinson et al., 2021) but more research is required to determine the timing and direction of movement (i.e., when and why ground beetles move into or out of a crop). It is also unknown if spill-over of carabid beetles into the crop leads to increased predatory activity and therefore increased biocontrol potential.

Carabids are often thought to be capable of biocontrol, but this is not always tested in field settings (Blaix et al., 2018; Chaplin-Kramer et al., 2011; Kromp, 1999). There is evidence to show that carabids may consume aphids (Dunning et al., 1975) among other invertebrate pests (Kromp, 1999; Le Gall & Tooker, 2017; Solomon et al., 2001). Carabids may also be important consumers of weed seeds in agroecosystems (Ali & Willenborg, 2021; Barbercheck & Wallace, 2021; Diehl et al., 2012; Petit et al., 2014). However, much of this is known from lab-based studies or from field-based studies of carabid presence rather than a measurement of predatory activity or prey consumption. Studies on landscape and management effects, such as spill-over from non-crop vegetation areas, on carabids often use pitfall traps to measure activity-density of carabids at particular sites (Gallé et al., 2019; Gardiner et al., 2010; Thomas et al., 2006). Activity-density is then used as a proxy for biocontrol ecosystem service supply. The more time a ground beetle spends moving and the more net distance it covers, the more likely it is to encounter a pitfall trap (Thomas et al., 2006). However, pitfall traps do not indicate specific behaviours of the organisms they capture (e.g., foraging, migrating, breeding, avoiding predation, etc.), and therefore do not record evidence of an ecosystem service such as pest predation. Furthermore, generalist predators such as ground beetles are likely to engage in intraguild predation which may have negative impacts on pest control even if the abundance of carabids is high (Prasad & Snyder, 2006). Alternatives to pitfall trapping that seek evidence of pest predation directly include field observation, DNA or serological analysis, and prey labeling, all of which are either time intensive or expensive and can be biased, limited in total data, or fail to quantify rather than qualify predation (Lövei & Ferrante, 2017). Therefore, measurements of the effects of carabid-driven pest predation in agroecosystems have been limited (Kromp, 1999; Prasad & Snyder, 2006).

Sentinel prey may offer more clarity in measuring the potential for pest predation without the limits imposed by direct measurements of pest predation (as discussed above). Sentinel prey methods have been used to demonstrate in-field biocontrol potential by carabids (Howe et al., 2009; Lövei & Ferrante, 2017). These involve placing real or artificial prey items (sentinels) in locations where they may be exposed to predation and then recording evidence of predation. The use of sentinel prey permits standardization of experimental conditions (e.g., the type of prey) in a field setting to understand factors influencing predation (Howe et al., 2009; Lövei & Ferrante, 2017).

In this paper we use sentinel prey in addition to insect trapping methods to determine how non-crop vegetation may influence the supply of pest control ecosystem services. Our study aims to answer the question: **How does non-crop vegetation impact carabid predation activity in nearby crop fields?** We hypothesize that if non-crop vegetation areas are acting as reservoirs for carabid beetles, crop locations at greater distances from non-crop vegetation will have fewer resources (e.g., supplemental shelter or food) leading to fewer ground beetles in the crop, and consequently less predatory ground beetle activity. In other words, we hypothesize that ground beetle spill-over from non-crop vegetation, and subsequent predatory activity, will be dependent on the distance from non-crop vegetation. We propose two predictions consistent with this hypothesis: 1. The activity-density of ground beetles will decrease with distance from non-crop vegetation areas with non-crop vegetation areas having the highest carabid activity-density. 2. Ground beetle predatory activity will decline with greater distance from non-crop vegetation areas with non-crop vegetation areas having the most carabid predation activity. We evaluate these predictions in 20 field sites in temperate grassland agroecosystems of the Canadian Prairies.

2. Methods

2.1 Study system

Data were collected over two field seasons in 2021 and 2022 in the Aspen Parkland ecozone of Alberta, Canada. We collected from 20 field sites (the smallest was 14 ha and the largest was 74 ha, Figure 2.1), 10 growing barley (*Hordeum vulgare* L.) and 10 growing canola (*Brassica napus* L.). All canola crops were managed similarly, including the use of glyphosate (herbicide), selective deltamethrin (insecticide) spray, and neonicotinoid (insecticide) seed treatment. Half of the barley field sites were managed without the use of crop protection chemicals, and the other half of the barley field sites had herbicides and fungicides applied but no insecticides sprayed.

In-crop sample stations were stratified by distance away from non-crop vegetation areas into the crop. While linear transects are a traditional approach to stratifying sample sites by distances, the method fails to gain a continuous set of distances and it is more challenging to sample in a way that is representative of an entire crop field. A custom R algorithm (Galpern, *Personal Communication*) was used to allow sampling across the whole field, where sample stations were randomly selected from within each field site to maximise the distance between each station (Figure 2.1). For this study, 15 stations were selected in each of the 20 field sites (9 in the crop and 6 in the non-crop vegetation areas). This sampling regimen led to 300 different sample stations across all field sites (180 in the crop and 120 out of the crop), each at a unique distance from a non-crop vegetation margin or within non-crop vegetation areas (Figure 2.1). Sampling the whole field in this manner also achieved continuous variability in distance, which may be beneficial when working with small, terrestrial organisms such as carabids, where movement distances may also be small (Gardiner et al., 2010).

Sampling periods lasted 14 days each. Three successive sampling periods were done in each of the 10 barley sites. Three canola sites had one 14-day sample period and the other seven canola sites each had four successive sample periods.

2.2 Measuring activity-density

To test prediction 1, pitfall traps, made of plastic cups (10 cm diameter opening and 12 cm depth) partially filled with 100% propylene glycol as a preservative, were placed at each station and covered in a coarse mesh to prevent vertebrate bycatch. For measuring the change in activity-density of carabid beetles by distance into the crop, we counted beetles in 548 pitfall traps from 180 sample stations in crops. To measure the difference in activity-density of carabids between crop and non-crop stations, 915 collections were taken from pitfall traps, 549 in the crop and 366 in non-crop vegetation, collected over both field seasons (June through August 2021 and 2022). After 14 days of deployment, pitfall samples were collected and filtered from the propylene glycol and preserved in 95% EtOH. Every carabid beetle was removed from each pitfall sample. *Pterostichus melanarius* (Illiger, 1798), the most common species of ground beetle was counted and placed back into 95% EtOH storage. All other ground beetles were pinned, dried, and labelled for accession.

2.3 Determination of prey species

To support our choice of sentinel prey forms used for prediction 2 (see section 2.4), we investigated evidence for prey species of carabids. However, it is mostly unknown in the literature what prey items carabids eat in field settings, and data gaps are particularly evident in western Canada, our study system (e.g., Dunning et al., 1975; Kromp, 1999; Le Gall & Tooker, 2017; Solomon et al., 2001). Therefore, we conducted a metabarcoding analysis to test for all arthropod DNA in the gut contents of 240 *P. melanarius* individuals, the most common species of ground beetle in the system and a known potential predator (Busch et al., 2021).

We took *P. melanarius* from pitfall samples where available or collected live individuals in the field opportunistically. *P. melanarius* taken from pitfall traps were stored in 95% EtOH. The *P. melanarius* collected live were euthanized by freezing at -20^{o}C and then stored in 95% EtOH in -20^{o}C. Each *P. melanarius* was cleaned by washing in 75% EtOH. The whole gut of each *P. melanarius* was carefully dissected in a bleach sterilized environment using sterile tools and put in a DNA LoBind Tube (Eppendorf). Three individual guts, all from the same pitfall or field sample, were included in each tube. The tubes were filled halfway with 95% EtOH and stored in -20^{o}C before transport.

Samples were sent to the Canadian Centre for DNA Barcoding (CCDB, Guelph, ON, Canada) for preparation and analysis. The CCDB performed PCR amplification using an arthropod specific primer pair, ZBJ-ArtF1c_t1/ZBJ-ArtR2_t1 that targets a 157 base-pair (bp) fragment of the barcode region of the cytochrome c oxidase subunit I (Zeale et al., 2011). Sequencing was done on an Ion Torrent S5 next-generation sequencer. The processed reads were compared to a Barcode of Life Data System (BOLD) reference library (www.boldsystems.org). Taxonomic identity was then assigned using a BLAST algorithm. We took a conservative approach and identifications were only accepted as unique and genuine if they were supported by at least 100 reads matching a reference sequence with ≥ 98% identity across at least 100 bp.

2.4 Sentinel prey to measure predation activity

To measure predatory activity rather than relying on the presence of ground beetles, we used sentinel prey ‘caterpillars’ (Figure 2.2) for testing prediction 2. Made of green plasticine, the sentinels were similar in size, shape, and colour to the potential prey items carabids naturally encounter (we used gut analysis to confirm this, as above; see Results). The sentinels were malleable and remained so through each of the 14-day trials which allowed the sentinels to record the shape of each mouthpart that bit them.

We first conducted pilot trials where we controlled the predator classes biting the sentinel prey to develop a bite mark reference for different potential predators. This enabled us to conclude that ground beetle predation had occurred on field deployed samples based on the size and shape of the mark left.

For the main field trials, each sentinel was taped to a clear acrylic card in level with the soil to avoid loss (Figure 2.2). This card was held in place with a flagging pole at each station within 40 cm of a pitfall trap. After 14 days the sentinels were replaced, and bite marks were tallied from each. To measure the change in predatory activity by distance into the crop and to examine the partial effect on predatory activity by distance into the crop and activity-density of carabids, 1038 sentinel prey caterpillars were counted from 180 stations within crops. To measure the change in number of bite marks on sentinel prey between crop and non-crop stations, 1732 sentinel prey caterpillars were counted, 1038 in the crop and 694 in non-crop vegetation.

2.5 Sentinel prey and activity-density statistical analyses

Negative binomial generalized additive models (GAMs) were fit to the data using the mgcv package (Wood, 2017) in R (R Core Team, 2023). To test prediction 1, the number of carabid beetles was the response variable, whereas the number of carabid bite marks was the response variable for prediction 2. Two tests of each prediction were completed (Table 2.1). One analyzed the effect of distance from non-crop vegetation on the number of carabids (Model 1) or the number of carabid bite marks on sentinel prey (Model 3) within crop stations. This test also included the interaction effect of distance with heat-time as measured by the median growing degree day (GDD) of each sample over 5ºC obtained from Agriculture and Irrigation, Alberta Climate Information Service, https://acis.alberta.ca (ACIS, 2022) for the closest weather station to each field site. A second test analyzed the difference between non-crop and crop station effects on the number of carabids (Model 2) or number of carabid bites (Model 4) which also included the interaction effect between status of being in the crop or non-crop with GDD.

All models included main effects of GDD, facilitating comparisons between samples collected in different years (Table 2.1). The GDD term was fit using a penalized thin-plate smoothing spline (Marra & Wood, 2011), that permitted a non-linear relationship if supported by the data. All models included penalized two-dimensional thin-plate spline smooths for the spatial location of the sample stations for each field site, which allowed for the control of potential spatial autocorrelation of data from having stations nearby others. A random intercept for each field site was included to account for the expected random difference between sites in their mean abundance of bite marks. A categorical term was included for the year of sampling to account for differences between the years (Table 2.1). The fit of each model was examined using the DHARMa package (Hartig, 2022).

3. Results

3.1 Activity-density as related to non-crop vegetation

Of the 915 pitfall samples used for analysis, only 60 had no carabids captured in them and 51 pitfalls had 100 or more carabid individuals captured in them. The mean number of carabids captured across all traps was 30.77 individuals.

Distance from non-crop vegetation was positively associated with the activity-density of carabid beetles in pitfall traps (Figure 2.3) and carabids were significantly less abundant in pitfall traps in non-crop vegetation areas (Figure 2.4). Growing degree day (GDD) had significant effects on the activity-density of carabids in the crop, with carabids increasing with GDD, but GDD had no main effect on carabids over the whole field when including those in the non-crop vegetation (Table 2.2). GDD had no interaction effects with distance or status of being in the crop or the non-crop vegetation areas for the activity-density of carabids. The model used to examine how activity-density changed over distance (M1) had an $R^2_{adj} = 0.325$ and explained 47.8% of the deviance. The model used to examine how activity density differed between crop and non-crop sites (M2) had an $R^2_{adj} = 0.292$ and explained 44.1% of the deviance.

3.2 Dietary analysis – Support for sentinel prey method

In all 80 samples of 240 whole guts from *P. melanarius*, three genera belonging to two families and two orders were detected. Most detections (99.96%) were of the predator DNA (*P. melanarius*), though this method would not allow for detection of cannibalism. However, from three samples two other genera were detected. Two different samples (0.03%) contained evidence of the ground beetle species *Amara littoralis* (Coleoptera: Carabidae) and one sample (0.01%) contained evidence of the pest genus *Euxoa ochrogaster* (Lepidoptera: Noctuidae), commonly referred to as the red backed cutworm moth. Negative controls did not produce identifiable sequence reads, suggesting that the results were not compromised by laboratory-introduced contamination.

3.3 Attacks on sentinel prey as related to non-crop vegetation

Of the 1732 sentinel prey collected and analyzed for use in this study, 40% had bite marks attributed to carabids. 2.4% of sentinel prey each had 30 or more carabid bite marks. The average number of carabid bites per sentinel prey across location and time of sampling was 2.96.

Overall, the number of carabid bite marks on sentinel prey decreased with distance from non-crop vegetation areas (Table 2.2) but increased from the non-crop vegetation areas until about 50 m into the crop before plateauing until 100 m and then declining below the initial measurements at the crop edge (Figure 2.5). The number of bite marks also changed significantly between the crop and non-crop stations and an interaction with GDD had a significant effect on this response (Table 2.2). Early season non-crop stations had slightly more bite marks on sentinel prey than crop stations while late season non-crop stations had fewer bites than crop stations (Figure 2.7). GDD also had a main effect on the number of bite marks on sentinel prey, with number of bite marks increasing over the season (Table 2.2). The activity-density of carabids significantly impacted the number of carabid bite marks both at a given distance into the crop (Figure 2.6) and overall, however, there was no interaction effect on bite marks between the activity-density of carabids and crop/non-crop status of the sample (Table 2.2). The model used to examine how bites change over distance (M3) had an $R^2_{adj} = 0.466$ and explained 55.5% of the deviance. The model used to examine how bites differ between crop and non-crop sites (M4) had an $R^2_{adj} = 0.606$ and explained 52.3% of the deviance.

3.4 Common results for all models

Only two field sites did not demonstrate significant spatial effects for any of the response variables while eight sites had spatial effects for at least two of the response variables, suggesting that there are “hot” and “cold” spots across the fields in these variables that are uncorrelated with the distance from the non-crop (Table 2.2). There were significant random effects between sites for all four models, demonstrating baseline levels of predation and/or activity-density that differed in each field site, but the year of sampling had no significant effects in any of the models (Table 2.2).

4. Discussion

Proximity to non-crop vegetation areas had a non-linear association with attacks on sentinel prey by ground beetles, and locations closer to non-crop areas had lower activity-densities of carabids. Between 50 and 100 metres away from non-crop vegetation, predation activity by carabids was heightened. Although we found that the frequency of sentinel prey attacks is associated with carabid activity-density, activity-density has a different relationship with distance from non-crop areas. Furthermore, there is evidence that carabid attacks on sentinel prey, but not activity-density, "spills" into the crop from the non-crop vegetation over the course of the season. Our results, therefore, suggest that non-crop vegetation may impact carabid predatory activity differently than other activities carabids may do in crop fields, such as searching for mates or avoiding predation.

4.1 Activity-density does not support spill-over

Carabids were trapped more often within the crop than the non-crop throughout the growing season and the number of carabids found in pitfalls increased with distance into the crop. These findings are not in support of our first prediction but also contradict much of the pre-existing evidence from the literature. We consider three possible explanations for our results: (a) spill-over of carabids is not happening in this system; (b) spill-over is happening but only from the crop into the non-crop; or (c) spill-over is happening, but our pitfall trapping methods could not detect it.

At ‘first glance’ our results appear to be most consistent with (a) that spill-over of carabids is not happening in this system. However, the change in carabids over the growing season (i.e., heat-time as measured by GDD) needs to be more closely examined. While activity-density of carabids in the crop increased over the season, activity-density did not increase significantly through the season overall. This finding might be expected in a system where the beetles are migrating from one area to another over time rather than a system where beetles are just increasing in abundance due to development driven by heat-time (Bale et al., 2002). If true, we should then also see a difference in activity-density between the crop and non-crop vegetation areas which we did not. We would also expect to trap more carabids nearer to the non-crop vegetation which we did not. Given that our evidence for spill-over of carabids is conflicting, we examine the literature. Another study found evidence of carabid spill-over happening in similar western Canadian field contexts, where *P. melanarius*, measured by its activity-density, appears to move into the non-crop vegetation post-harvest (Robinson et al., 2021). This migration of *P. melanarius* may support explanation (b) that spill-over is happening but in a direction opposite to what we expected.

It is possible that carabids exist primarily within the crop and are spilling into the non-crop which would indicate explanation (b) is occurring. In a similar western Canadian field context to our own, Robinson, et al. (2021) found evidence for *P. melanarius* spilling into non-crop vegetation late in the season. Support for non-crop vegetation areas as both a reservoir and a sink for natural enemies have been observed in European contexts (Tscharntke et al., 2005). However, many carabids, including the most common species in our system, *P. melanarius*, are particularly vulnerable to disturbances, such as spring spraying or fall harvesting, which occur in the crop and necessitate migration away from the crop during these periods (Busch et al., 2021; Cole et al., 2010). Possibly, what Robinson et al. (2021) observed when finding evidence for *P. melanarius* spilling into the non-crop vegetation areas was that non-crop vegetation may be a "reservoir" that is being repopulated towards the end of the growing season by beetles requiring overwintering areas. We did not complete any pitfall trapping as late in the season as Robinson, et al. (2021) which leads to explanation (c) that our pitfall trapping methods were not capable of detecting spill-over.

Two, non-mutually exclusive, possibilities for our pitfall traps not measuring spill-over, explanation (c) may be possible. Firstly, we may not have taken measurements at the correct times and secondly, pitfall traps may fail to measure absolute density when beetles move less and may measure activity when beetles move more (Robinson et al., 2021; Thomas et al., 2006). Many carabids are proven seed eaters, suggesting that the crop may be an attractant in the very early season when seeding is taking place (Ali & Willenborg, 2021; Petit et al., 2014). Because our data collection began post-seeding in the early growing season and concluded pre-harvest in the late growing season, it is possible that we did not capture the carabid migration from the non-crop vegetation reservoir into the crop before or around seeding time and that we did not measure carabid migration back into the non-crop vegetation post harvest. Furthermore, and perhaps most in line with our sentinel prey findings (See section 4.4), it is important to consider that traps measure activity-density (Thomas et al., 2006). If carabids are more active further into the crop, they would be more likely to encounter a pitfall trap. Increased activity could be due to a lack of shelter or food causing carabids in those areas to move more in search of those resources. We may expect to see a decline in these resources away from non-crop vegetation areas. These resources may also respond to changes over the season.

Our findings indicate activity-density increased over the growing season in the crop, but there were no interaction effects with heat-time and distance from non-crop vegetation or status of being in the crop or non-crop. The main effect of GDD shows that possibly more adult carabids emerged over time or carabids became more active later in the season or carabids moved from the non-crop into the crop. However, carabids showed no change in the locations of highest or lowest activity-density across the season, i.e., there was no evidence that carabids migrated within the field. A lack of migration is, again, in contrast to other findings that indicate carabids likely do spill into and out of crops (Robinson et al., 2021; G. Schneider et al., 2016; Tscharntke et al., 2005). These results may indicate that carabids may be active earlier and later than we expected, possibly more in conjunction with seeding and harvesting (Ali & Willenborg, 2021; Petit et al., 2014; Robinson et al., 2021) and that activity-density does not always indicate abundance (Thomas et al., 2006).

4.2 Prey species identified through gut analysis

The detection of *E. ochrogaster* (red backed cutworm moth) DNA shows that *P. melanarius*, the most abundant carabid species, will consume these larval lepidopterans at least some of the time and therefore that plasticine sentinel caterpillars are a plausible prey item. Given the high levels of decay that may have occurred in the gut samples and the amplification of *P. melanarius* DNA recorded, these findings are certainly incomplete and reliable only to the genus level. However, the genus *Euxoa* is likely to be found in canola only as an economically important surface-feeding canola pest (Gavloski et al., 2011). Detections of prey species that we were able to confirm suggest that carabids will consume economically important pests within crop fields in this region.

This gut analysis may be one of the first studies to investigate the western Canadian diet of this abundant carabid, although a low number of prey detections limits our ability to generalize. For example, predation by ground beetles on *Euxoa* spp. may provide economic benefits due to the negative impact cutworms have on crops.

Detection of *Amara* DNA in the *P. melanarius* gut sample may be due to *P. melanarius* participating in intraguild predation. It is known that many carabids will engage in intraguild predation, and it has also been demonstrated previously in *P. melanarius* in North America (Prasad & Snyder, 2006). Intraguild predation can potentially negatively impact the effectiveness of carabids as natural enemies (Prasad & Snyder, 2006). Our results underline that the impact of *P. melanarius* for pest control ecosystem services in western Canada is likely to be complex and mediated by its trophic interactions among predatory insects. We, therefore, echo calls for additional research to understand how community structure influences service supply (De Heij & Willenborg, 2020; Prasad & Snyder, 2006).

4.3 Predatory activity does support spill-over

Spill-over of predatory activity did happen from the non-crop stations into the crop. The spill-over was over time where early in the season the non-crop vegetation had more attacks on sentinel prey and later into the season the crop had more attacks on sentinel prey. Once in the crop, carabids were more likely to attack the sentinels in a *halo* region around the non-crop vegetation areas, between 25 m and 100 m, while the furthest points into the crop showed the least predatory activity. These findings are consistent with our second prediction. Activity-density of carabids had a positive effect on predation activity only at high numbers and only near non-crop vegetation. In contrast, high activity-density away from non-crop vegetation had a negative effect on predation activity. Carabids were more active further into the crop but engaged less in predation possibly because their activity (e.g., avoiding predators) inhibited engaging in predation.

It is both possible that food resource densities were increased or decreased in the halo region of potential carabid predation; either option may have implications for predation by carabids. If there was a lack of prey availability in the halo region of the crop, carabids may be 'hungrier' within the halo. Carabids may then have been more likely to bite the sentinels compared to ground beetles that had more food access. However, many prey arthropods do not appear to have low or high densities in correlation with non-crop vegetation (Chaplin-Kramer et al., 2011; Innes et al., Unpublished results). Weed seeds may be an important food source for carabids (Ali & Willenborg, 2021; Barbercheck & Wallace, 2021; Diehl et al., 2012), and they may decline in density with increasing distance from non-crop vegetation areas (Wilson & Aebischer, 1995). Carabids may have been more satiated in the areas we observe them attacking sentinels the most. If seed densities were high in the halo region, it is possible that carabids may have been specifically going into the halo areas of the crop to do predation (Blaix et al., 2018) while utilizing other areas of the crop for non-predatory activities. However, carabids are highly polyphagous and unlikely to choose food based on availability (Guenay-Greunke et al., 2023). It is likely that carabids gain additional resources from the halo region other than food. These resources may be shelter or moisture that, rather than attracting predation activity, act as a catalyst for such behaviours possibly by decreasing stress (Alford et al., 2023; De Heij et al., 2023; De Heij & Willenborg, 2020). Therefore, more of a functional or behavioural analysis of carabids is needed to understand why they do more predation in the halo region.

4.4 Activity-density and optimal foraging

Our findings are not consistent with our hypothesis that predation activity will be driven by spill-over of carabids. However, these findings are consistent with pitfall abundance of carabids measuring activity rather than density of carabids. The sentinel prey method is less indicative of overall activity than pitfall traps are, even though both methods require encounters, because sentinel prey measure a specific type of activity of carabids. In some scenarios, carabid activity may have a negative effect on the potential for carabid predation. If carabids are moving around further into the crop (i.e., away from the non-crop vegetation), it may be due to stressors, like predation risk, that reduce time available for foraging or hunting. Our findings are consistent with others that show when resources are abundant and diverse, insects spend less time moving, and turn more, moving less net distance across a landscape (Kindlmann & Dixon, 1993; Pyke, 1978; Zimmerman, 1979). The resources provided by non-crop vegetation, such as shelter from increased weed plant abundance (Barbercheck & Wallace, 2021; Blaix et al., 2018; Diehl et al., 2012), may cause carabids to engage in predation more by providing opportunities to spend less time on immediate survival and reproduction (i.e., avoiding predation, searching for egg laying habitat, etc.).

It is likely the spill-over into the crop of predatory activity by carabids is a result of many ecosystem factors such as soil moisture retention, plant habitat increasing safety from predators of carabid beetles, and location of food abundance (Haan et al., 2020; Kromp, 1999; Vankosky et al., 2017). The internal areas of the crop may be less subjected to weeds due to their distance from weed sources in the non-crop vegetation (Wilson & Aebischer, 1995) and occasional exposure to herbicides. Weeds may provide both shelter and food for carabids (Barbercheck &

Wallace, 2021; Blaix et al., 2018; Diehl et al., 2012) and the lack of them may increase carabid stress and activity while decreasing carabid predation.

As the crop grows over the season (i.e., with increasing heat-time), the crop itself likely starts to provide more resources for carabids (Holland et al., 2016; Kromp, 1999; Perović et al., 2018). Protection from predators and moisture retention is less likely to be provided by the crop in the early season when the crop plants are small, and the soil is exposed. Heat-time, measured by growing degree days, influences not only vegetation, but insect development as well. As GDDs accumulate, more insects are physiologically able to develop (Bale et al., 2002). Heat-time may provide increased food and shelter within the crop for carabids and may also result in more total carabids.

Some research has found a halo effect of crop yield near non-crop vegetation within a similar ~50 m distance as our study found the halo region in predatory activity (Robinson et al., 2022). While this yield halo could be due, in part, to pest control supplied by carabid beetles, it may also be that both yield and carabids are responding to other resources, such as moisture retention, provided by non-crop vegetation (Brandle et al., 1984; Jong & Kowalchuk, 1995).

5. Conclusion

Carabid beetle attacks on sentinel prey decrease with distance from non-crop vegetation areas, though there is an increase in predatory activity within a halo region of the crop near to the non-crop vegetation. These trends are most likely due to resource provisioning from the non-crop vegetation year-round, especially in the winter, and seasonally available resources from the crop (e.g., shelter) that are amplified by indirect resources from the non-crop, like moisture retention (Brandle et al., 1984; Jong & Kowalchuk, 1995), and weed seeds (Ali & Willenborg, 2021;

Barbercheck & Wallace, 2021; Blaix et al., 2018; Diehl et al., 2012). While carabids may spread out throughout the crop, they are more likely to attack sentinel prey nearer to non-crop vegetation areas. Non-crop vegetation areas are beneficial in that they increase predatory activity by ground beetles.

Our study exemplifies why abundance of carabids in traps may indicate more about general activity of individuals in the landscape rather than presumed provisioning of services. Therefore, pitfall traps and presence of carabids should not be used to indicate the supply of ecosystem services and measures of the effects of potential for carabid predation, such as sentinel prey, need to be considered. Further research should focus on these more direct measures of carabid predatory activity when examining the supply of pest control ecosystem services.

For carabids to supply pest control, they will require non-crop vegetation areas to be accessible. Non-crop vegetation areas may also enhance the habitat for carabids within the crop by providing weed seeds that may increase shelter and food sources (Blaix et al., 2018; Kulkarni et al., 2015). There are also likely to be resources provided to the crop sourced from non-crop vegetation areas, such as soil moisture retention, that in turn benefit carabids indirectly (Brandle et al., 1984; Jong & Kowalchuk, 1995) possibly by also increasing shelter provided by the crop plants themselves. Ultimately, we answer our research question: non-crop vegetation increases carabid predatory activity within a halo region of the crop. Favouring crop expansion over retention or restoration of non-crop vegetation will potentially have negative impacts on pest control ecosystem services.

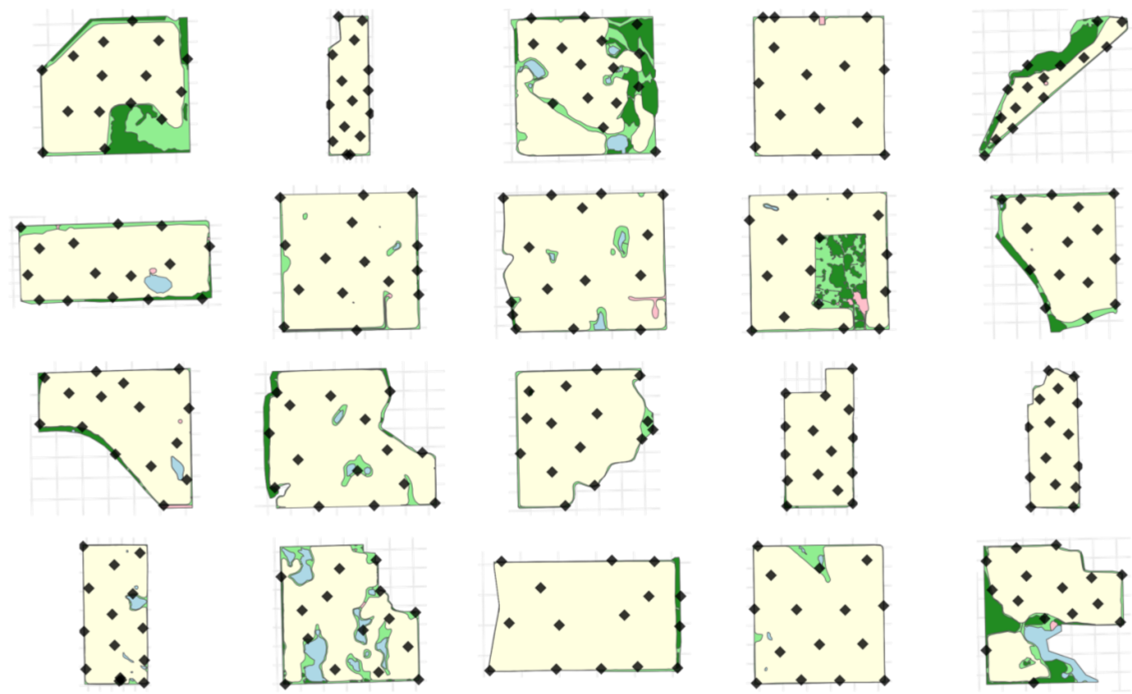

Figure 2.1: Maps of all 20 field sites sampled in this study, showing the pattern of sampling across crop and non-crop locations. Maps are not drawn to scale. Light yellow areas represent the crop, light green are grassy patches, dark green are forested areas, light blue are wetlands, and pink patches are anthropogenic infrastructure (e.g., roads, gravel pits, oil wells). Black diamonds show the sampling stations in each field. Latitude and longitude are not provided to maintain confidentiality.

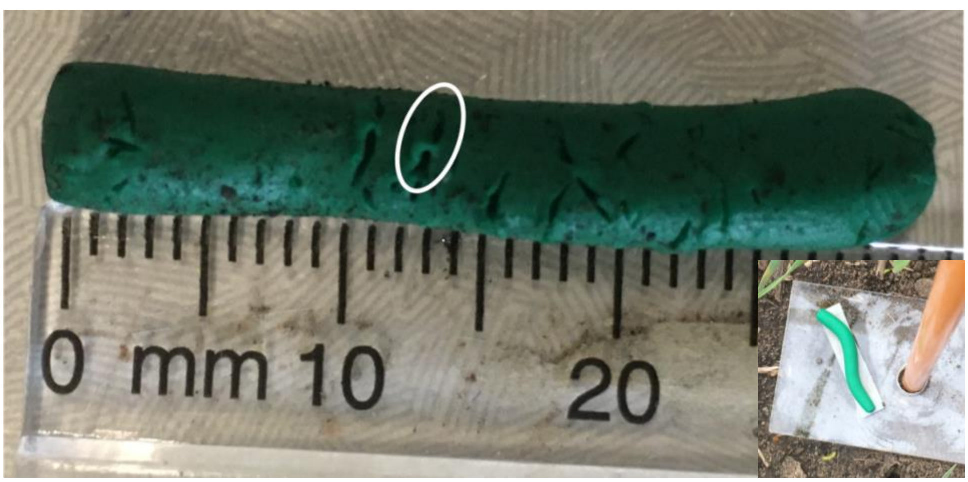

Figure 2.2: Artificial sentinel prey ‘caterpillar’ with carabid beetle bite marks. A single bite mark is circled in white as an example. The inset shows a sentinel as placed in the field on a clear acrylic card which is held in place with a flagging pole.

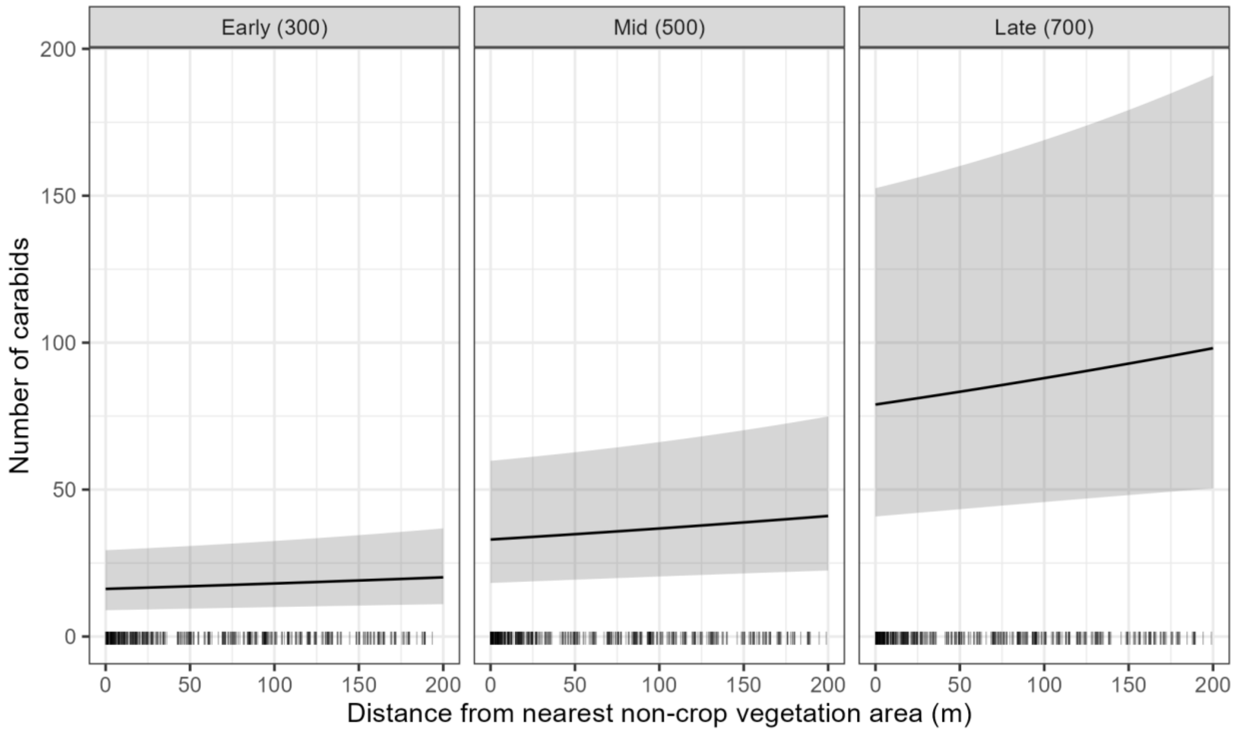

Figure 2.3: The model predicted effects on the number of carabid beetles recorded in pitfall traps at different distances (m) from non-crop vegetation areas from all 20 field sites modelled using a negative binomial generalized additive model (M1). Growing degree days (GDD) are used to show the estimate for the early-season (GDD 300), mid-season (GDD 500), and late-season trends (GDD 700). Black ticks on the x axis are sampling locations, demonstrating coverage of a broad range of distances from non-crop vegetation. Grey ribbons show the 95% confidence interval of the mean fit (black line). Stations greater than 200 m into the crop (n=15) have been removed to improve visualization.

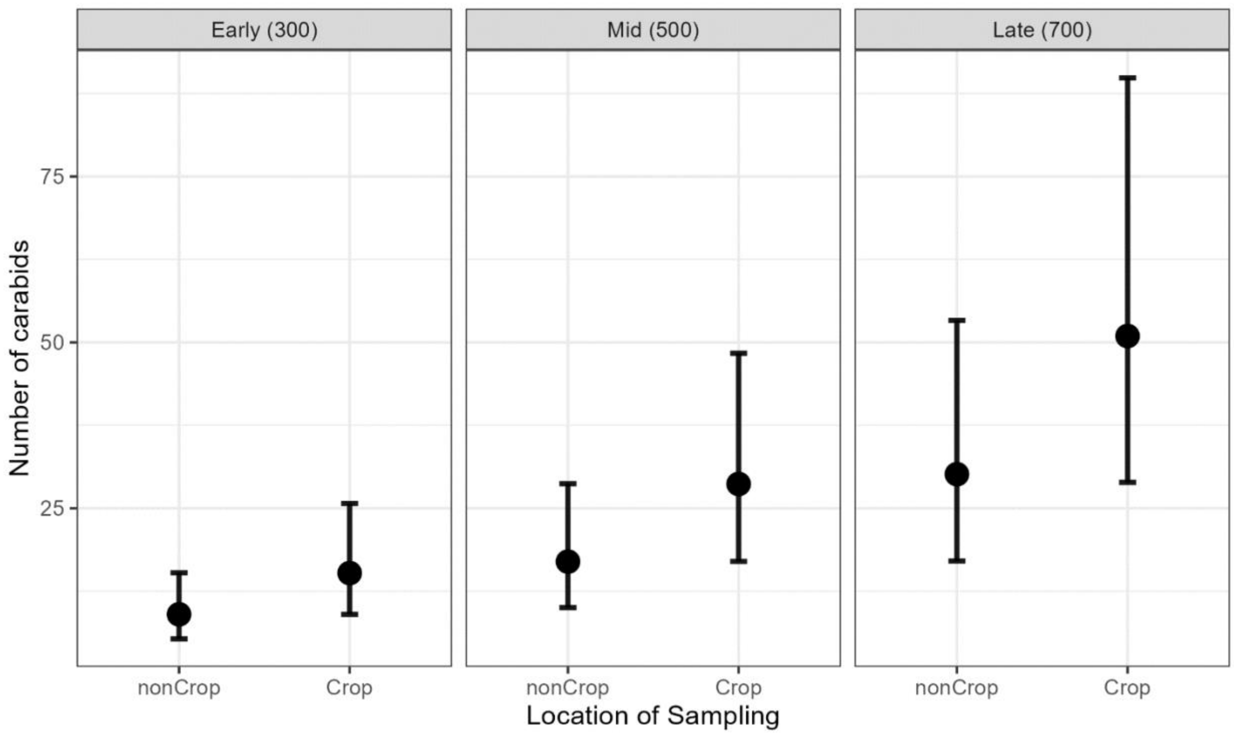

Figure 2.4: The model predicted effects on the number of carabid beetles recorded in pitfall traps from sample stations either in non-crop vegetation areas or the crop from all 20 field sites determined using a negative binomial generalized additive model (M2). Growing degree days (GDD) are used to show the estimate for the early-season (GDD 300), mid-season (GDD 500), and late-season trends (GDD 700). Error bars show the 95% confidence interval of the mean estimate (black point).

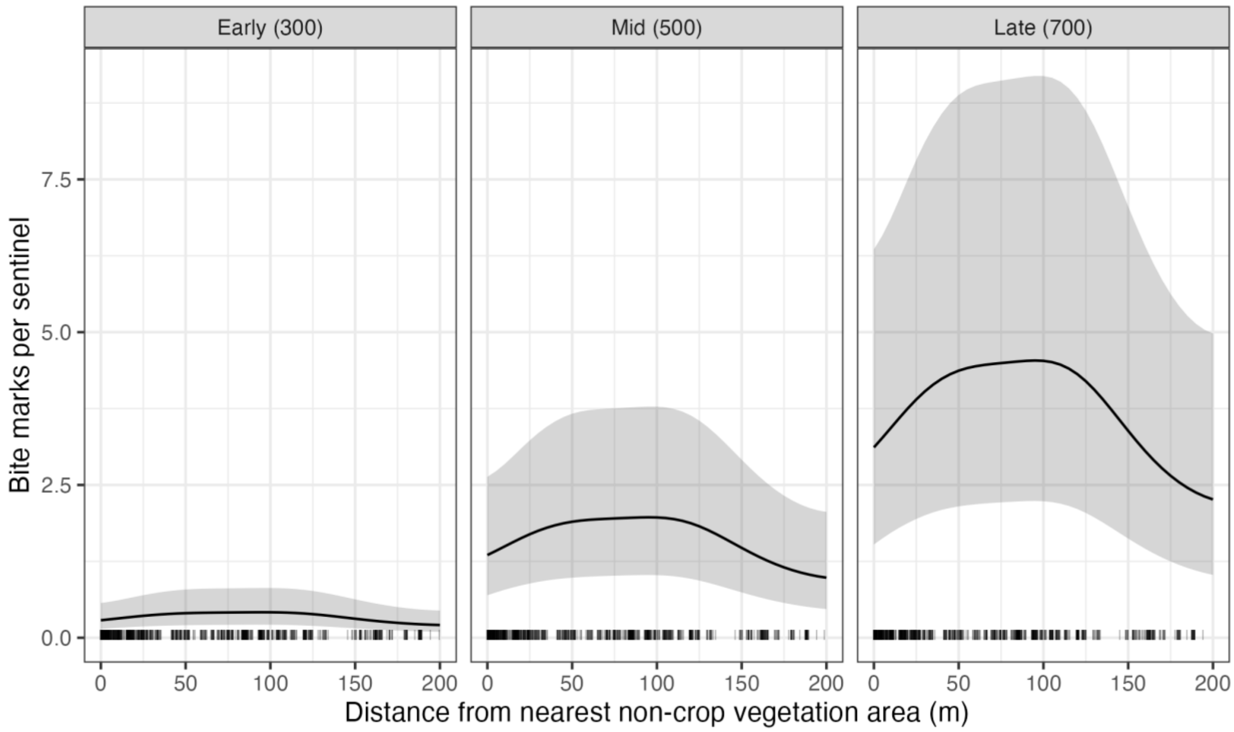

Figure 2.5: The model predicted effects on the number of bite marks recorded on sentinel prey at different distances (m) from the non-crop vegetation areas from all 20 field sites modelled using a negative binomial generalized additive model (M3). Growing degree days (GDD) are used to show the estimate for the early-season (GDD 300), mid-season (GDD 500), and late-season trends (GDD 700). Black ticks on the x axis are sampling locations, demonstrating coverage of a broad range of distances from non-crop vegetation. Grey ribbons show the 95% confidence interval of the mean fit (black line). Stations greater than 200 m into the crop (n=15) have been removed to improve visualization.

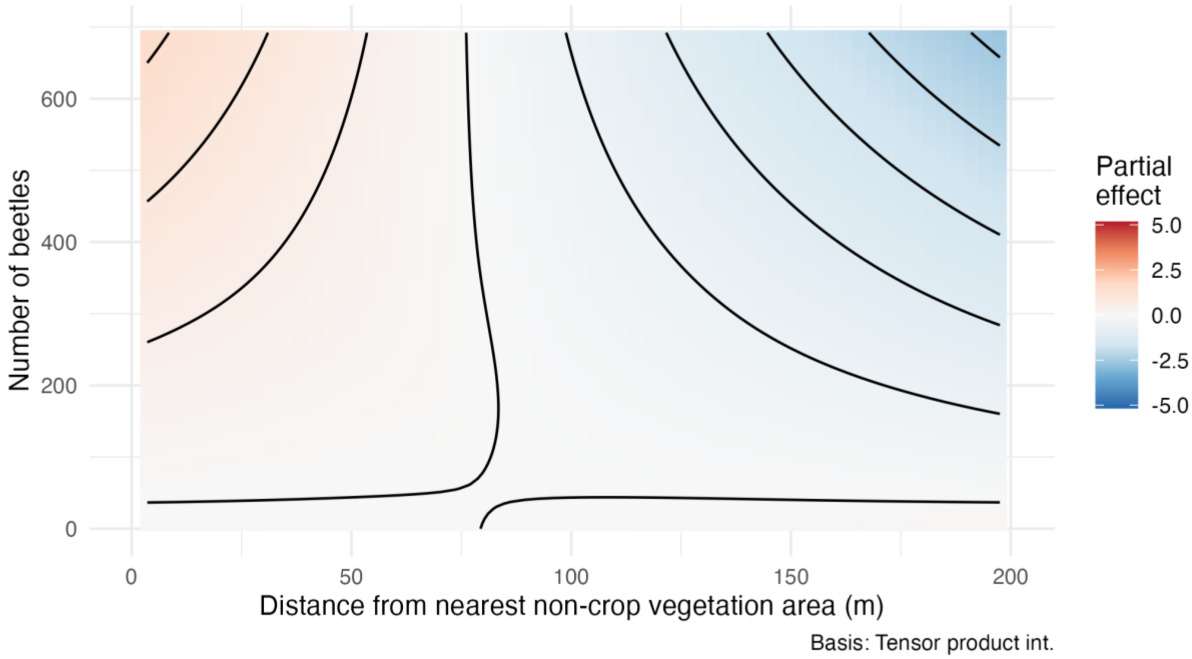

Figure 2.6: The partial effect on the number of bite marks recorded on sentinel prey from sample stations at different distances away from non-crop vegetation areas and with different abundances of carabid beetles modelled using a negative binomial generalized additive model (M3). Red colour indicates a positive partial effect while blue indicates a negative partial effect on predatory activity. Stations greater than 200 m into the crop (n=15) have been removed to improve visualization.

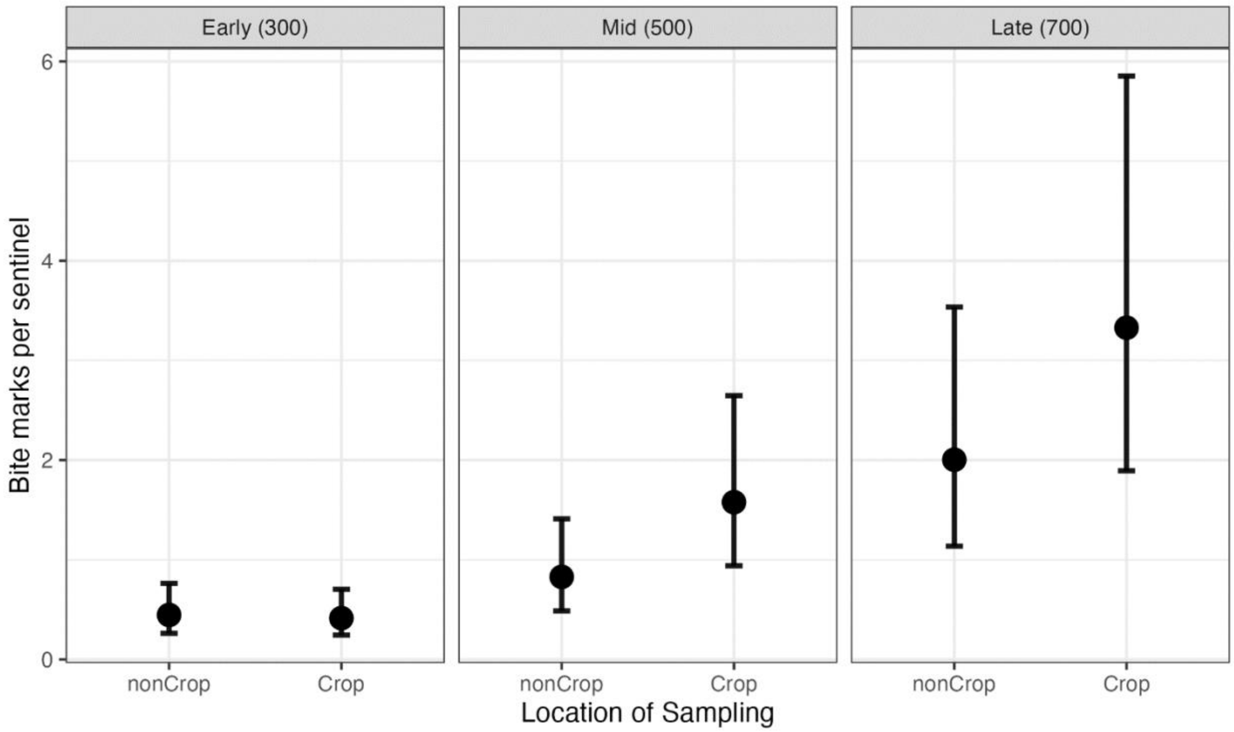

Figure 2.7: The model predicted effects on the number of bite marks recorded on sentinel prey from sample stations either in non-crop vegetation areas or the crop from all 20 field sites modelled using a negative binomial generalized additive model (M4). Growing degree days (GDD) are used to show the estimate for the early-season (GDD 300), mid-season (GDD 500), and late-season trends (GDD 700). Error bars show the 95% confidence interval of the estimated mean (black point).

Table 2.1: All terms that were included in each model to test carabid predation activity and spill-over in an agroecosystem, with descriptions and reasoning for inclusion. Formula notation used to represent smooth model terms is that used by the mgcv package for R (Wood, 2017). Increased penalization (or shrinkage) achieves variable selection, effectively allowing terms to drop out of the model if they are unrelated to the response (Marra & Wood, 2011).

Term description	***Models***	***Formula notation for smooth terms***	***Notes***
Distance from non-crop vegetation area	1, 3	s(…, bs = "ts")	Allows non-linearity; with increased penalization
Heat-time i.e., median growing degree day (GDD)	1, 2, 3, 4	s(…, bs= "ts")	Allows non-linearity; with increased penalization
Interaction between distance from non-crop vegetation and heat-time	1, 3	ti(…, …, bs = "ts")	Allows non-linearity in interaction between terms of different scale; with increased penalization
Year of sampling	1, 2, 3, 4	[parametric term]	Categorical
Location of sampling centred within each field in relation to other sample stations in the same field site	1, 2, 3, 4	s(…, …, by = …, bs= "ts")	Accounts for unmodelled spatial variability that may create spatial autocorrelation; with increased penalization
Abundance of carabid beetles	3, 4	s(…, bs= "ts")	Allows non-linearity; with increased penalization
Interaction between distance from non-crop vegetation areas and abundance of carabid beetles	3, 4	ti(…, …, bs= "ts")	Allows non-linearity in interaction between terms of different scale; with increased penalization
Mean differences between field sites	1, 2, 3, 4	s(…, bs= "re")	Random intercept
Sample location either within the crop or within non-crop vegetation	2, 4	[parametric term]	Categorical
Interaction between heat-time and location of sampling either within the crop or the non-crop	2, 4	s(…, by= …, bs="ts")	Allows for non-linearity in heat-time as it relates to the categorical crop/non-crop status of sampling location; with increased penalization

Table 2.2: Estimates for activity-density of carabid beetles (Model 1) or number of bite marks on sentinel prey (Model 3) by distance into crop from non-crop vegetation areas and activity-density of carabids (Model 2) or number of bite marks (Model 4) on sentinel prey as effected by status of being in the crop or the non-crop vegetation areas. NA indicates we did not include the term in the model and bolded estimates indicate the estimate was significant for the model ($p<0.05$).

Term	*Term type*	*H_0 interpretation*	*Activity-density – Crop (M1)*	*Activity-density – crop vs. non-crop (M2)*	*Predation activity – crop (M3)*	*Predation activity – crop vs. non-crop (M4)*
INTERCEPT	parametric	intercept=0	**3.35**	**3.21**	0.24	0.28
DISTANCE	smooth	no effect	**0.78**	NA	**4.21**	NA
STATION (non-crop)	parametric	no effect	NA	**-0.07**	NA	**-0.27**
GDD	smooth	no effect	**6.69**	5.95	**5.34**	**4.99**
DISTANCE* GDD	smooth	no interaction effect	<0.01	NA	<0.01	NA
GDD*STATION (crop)	smooth	no interaction effect	NA	<0.01	NA	**3.09**
GDD*STATION (non-crop)	smooth	no interaction effect	NA	<0.01	NA	**<0.01**
CARABID ABUNDANCE	smooth	no effect	NA	NA	**0.95**	**2.09**
CARABID ABUNDANCE* DISTANCE	smooth	no interaction effect	NA	NA	**1.16**	NA
CARABID ABUNDANCE* STATION (crop)	smooth	no interaction effect	NA	NA	NA	<0.01

CARABID ABUNDANCE* STATION (non-crop)	smooth	no interaction effect	NA	NA	NA	<0.01
YEAR (2022)	parametric	no effect	-0.52	-0.07	-0.40	-0.24
SITE A	smooth	no spatial effect	**1.39**	**1.28**	5.44	**1.45**
SITE B	smooth	no spatial effect	0.47	<0.01	<0.01	**1.76**
SITE C	smooth	no spatial effect	1.15	**1.52**	1.31	0.78
SITE D	smooth	no spatial effect	**4.49**	6.48	<0.01	<0.01
SITE E	smooth	no spatial effect	<0.01	11.19	**3.89**	4.29
SITE F	smooth	no spatial effect	**1.49**	**1.75**	<0.01	1.42
SITE G	smooth	no spatial effect	<0.01	1.33	**1.48**	0.99
SITE H	smooth	no spatial effect	0.55	<0.01	<0.01	1.12
SITE I	smooth	no spatial effect	1.34	1.11	**1.52**	1.01
SITE J	smooth	no spatial effect	0.34	<0.01	**1.57**	0.92
SITE K	smooth	no spatial effect	**1.75**	**1.45**	<0.01	0.73
SITE L	smooth	no spatial effect	<0.01	**1.48**	0.30	<0.01
SITE M	smooth	no spatial effect	<0.01	7.64	0.14	1.12
SITE N	smooth	no spatial effect	<0.01	0.49	<0.01	**9.88**
SITE O	smooth	no spatial effect	**4.58**	0.73	<0.01	0.71
SITE P	smooth	no spatial effect	**1.14**	**1.80**	<0.01	0.89
SITE Q	smooth	no spatial effect	**1.54**	**1.62**	0.83	**1.36**
SITE R	smooth	no spatial effect	**1.42**	**5.67**	**1.37**	**1.37**
SITE S	smooth	no spatial effect	**1.35**	**1.57**	<0.01	**7.31**
SITE T	smooth	no spatial effect	0.46	1.00	**1.46**	**9.22**
BETWEEN SITES	random intercept	$\sigma_{intercept} = 0$	**16.14**	**16.09**	**14.32**	**15.24**

*Estimates for parametric terms are coefficients and for smooth and random intercept terms are Effective Degrees of Freedom (EDF).

Chapter 3:

Ground beetle conservation biocontrol mediated by size

1. Introduction

1.1 Agricultural intensification

Agricultural intensification is driving losses in biodiversity and ecosystem services (Awkerman et al., 2011; Boatman et al., 2004; Chagnon et al., 2015; Rumschlag et al., 2020; Schmitz et al., 2014). Current intensification trends include the application of chemical pesticides (insecticides and herbicides) and the removal of non-crop vegetative landcover. Even though agricultural intensification has known environmental impacts, ceasing these practices jeopardizes crop yields and farm profits (Chagnon et al., 2015; Oerke, 2006). For example, without pest control, animal pests would cause an 18% loss in crop yield averaged globally, underlining that protecting crops from pests is vital to maintaining food security (Oerke, 2006). There are alternatives to agricultural intensification that still promote yield and are cost effective for growers (Barnes et al., 2020; Chagnon et al., 2015). Pest control ecosystem services, provided by natural enemy arthropods that prey on crop pests, provide a complement to insecticides (Barnes et al., 2020; Chagnon et al., 2015). However, with continued agricultural intensification, the risk to pest control ecosystem services is likely to increase (Díaz et al., 2019).

Increasing abundance and diversity of natural enemies of pests in crops have been shown to increase pest control (Cahenzli et al., 2019; Martin et al., 2019; Meyer et al., 2019; Östman et al., 2003). However, it is also possible that pest control potential does not only change with abundance of predators but instead predators alter where they perform predation in relation to resources provided by non-crop vegetation areas. These areas of increased predation (around 50 m to 100 m into the crop) can be described as a *halo* region. Studies using remote sensing and precision agricultural data have shown that crop yield does exhibit haloes surrounding non-crop vegetation, although the factors driving this halo remain uncertain. These have been hypothesized to include factors associated with proximity to the non-crop areas such as moisture retention, soil fertility, shade, as well as predation by pest control arthropods that use the non-crop as habitat (Nguyen et al., 2022; Robinson et al., 2022).

It is challenging to predict the outcomes for pest control when agricultural intensity changes (e.g., non-crop vegetation is removed to increase the cultivated area). Often the abundance or activity-density of taxonomic groupings of carabids are examined when studying the relationship of carabid pest predation to non-crop vegetation. However, when using a taxonomic approach, the mechanisms of pest control, apart from taxonomic identity, are difficult to determine. Because the species makeup within crop fields will differ between agroecosystems, it is also difficult to incorporate findings from taxonomic approaches across cropping systems. A trait-based approach to study pest control, rather than a traditional taxonomic one, may help address this challenge because examining traits may reveal the mechanisms associated with pest control supply (De Bello et al., 2021; Funk, 2021; Gallé et al., 2019; Perez-Alvarez et al., 2021).

1.2 Functional traits

When assessing functional traits of organisms two methods are commonly used, a species trait approach, where the species of an individual is determined and then traits are assigned by species identity (e.g., life cycle traits or feeding guilds; Gallé et al., 2019), or an individual trait approach, where traits are measured on individuals (e.g., size of the individual) (e.g.,

Rudolf, 2012). Individual trait-based analysis emphasizes how organisms perform their functions rather than focusing on taxonomic identities (De Bello et al., 2021; Perez-Alvarez et al., 2021). By using this approach, traits (e.g., morphological, or behavioural characteristics) with mechanistic implications (e.g., traits for predation or dispersal) can be determined and furthermore, relationships between those traits and the external environment can be identified (Perez-Alvarez et al., 2021). The environment may 'filter' traits; a process by which the presence of individuals in a crop field is influenced by the suitability of their traits for conditions in or near that field (Perez-Alvarez et al., 2021; Perović et al., 2018). Subsequently, the traits of a community of organisms found in the field may influence the supply of ecosystem services such as pest control (Perez-Alvarez et al., 2021). Trait-mediated filtering by environmental conditions, and the consequences of the resulting trait pool for ecosystem service supply have been referred to as a "response-effect" framework (Damour et al., 2018; De Bello et al., 2021; Perović et al., 2018; Robleño et al., 2018; Suding et al., 2008).

Here we use an individual trait-based approach to determine if carabid traits have been filtered by landscape features (i.e., the trait-mediated *response* to environment) and whether to ask if these traits have the potential to affect pest control services (i.e., the trait-mediated *effect* of predators on prey). Specifically, we choose to focus on the trait of body size because of its implications for dispersal and predation (Perović et al., 2018).

Here we use data collected from field sites and a laboratory experiment to test two hypotheses: 1 Larger carabids will be relatively more abundant than smaller ground beetles as distance increases from non-crop vegetation areas, which provide resources to carabids, because larger ground beetles have increased dispersal abilities. 2. Larger ground beetles require greater amounts of energy from prey items and have an increased ability to hunt larger prey items leading to a preference towards larger prey items.

2. Methods

2.1 Study system

To test the first hypothesis, 20 field sites (10 canola and 10 barley), in the Aspen Parkland ecozone of Alberta, Canada, were sampled over the growing seasons (June through August) of 2021 and 2022. These sites and the sample stations within them have been previously described (Chapter 2). Each canola crop was managed similarly, including the use of herbicides (e.g., glyphosate) and insecticides (e.g., selective deltamethrin spraying and neonicotinoid seed treatments). None of the barley sites had insecticides applied though half of the barley sites were managed with the application of fungicides and herbicides while the other half had no chemical crop protection products applied. Both barley and canola are common crops in rotation across this region and the layout of non-crop vegetation in fields typically remains the same between seasons.

In each of the 20 field sites, nine sample stations were inside the crop for a combined 180 sample stations. Stations were stratified by distance away from non-crop vegetation areas. Transects are the traditional approach to sampling by distance into a crop (Mitchell et al., 2014; Vickruck et al., 2019), however this method is difficult in fields, such as those in this study, that are irregular in shape due to the presence of non-crop vegetation patches distributed throughout. Transects also may fail to gain a continuous set of distances and are challenged to represent an entire field. To achieve an even distribution of sampling stations, given these challenges, a custom sampling algorithm was created in R (Galpern, *Personal Communication*) to allow sampling across the whole field. Sample stations were randomly selected from within each field site to assign each station a unique distance from the nearest non-crop vegetation area and to maximize the distance between stations.

2.2 Sampling and sorting

Pitfall traps, made of plastic cups that had a diameter of 10 cm and a depth of 12 cm and each partially filled with 100% propylene glycol, were used at each sample station to capture carabids for hypothesis 1. Pitfalls were collected from each field site after being deployed for 14-day sample periods. Three successive sampling periods were completed for the 10 barley sites. Seven canola sites had four sample periods each while the last three canola sites each had one. At the time of collection, the contents of each pitfall were filtered from the propylene glycol and preserved in 95% EtOH.

All carabids were sorted out of each sample. *Pterostichus melanarius* (Illiger, 1798), the most common ground beetle in this system, was identified using the key from Lindroth (1961). The length of the elytra, a reliable proxy measurement of ground beetle size (Juliano, 1986; Perez-Alvarez et al., 2021), of *P. melanarius* individuals, due to their larger size and ease of manipulation, were measured using digital calipers. All other carabids were pinned but were not identified to species as the functional trait of interest could be measured from individuals. These carabids were imaged using a digital camera and the length of the elytra was measured using ImageJ (C. A. Schneider et al., 2012). All carabid samples are stored in the University of Calgary Invertebrate Collection.

To test the second hypothesis, we used a lab experiment to expose carabid beetles of different sizes to prey of different sizes and examine which prey were chosen for consumption. *P. melanarius* were collected from dry pitfalls and opportunistically within sites. The beetles were maintained prior to the trial at room temperature with constant water and food foraging opportunities (canola seeds, moistened cat/dog food, sugar-water solution).

2.3 Statistical analysis of size

To test the effect of distance from non-crop vegetation on the size of carabids (i.e., elytra length of carabids), nine quantile generalized additive models (QGAMs) were fit to the data using the qgam package in R (Fasiolo et al., 2021). The 10th through to the 90th quantile at increments of 10% were chosen to represent trends that may be evident across the body size distribution. QGAMs were chosen, rather than simpler quantile linear models, because they allow for non-linear two-dimensional smoothing, useful for spatial trends, in addition to modelling parametric linear terms and random effects (Fasiolo et al., 2021). The primary variable of interest for testing Hypothesis 1 was distance from non-crop vegetation. This was modelled as a linear parametric term (Table 3.1). To compare across the two years of sample collection, the median growing degree day (GDD) of each sample was also included in each model as a linear term and as an interaction with distance (Table 3.1), with data obtained from Agriculture and Irrigation, Alberta Climate Information Service, https://acis.alberta.ca (ACIS, 2022) using the closest weather station to each site. Each model also included two-dimensional smooths on the spatial location of the sample stations within each site to control for potential spatial variability and spatial autocorrelation in each quantile of body size (Table 3.1). To account for a possible mean difference in a quantile of body size between sites, a random intercept was included in each model for the site of sampling. The year of sampling was also included as a categorical term to control for mean differences among the years that may exist (Table 3.1).

2.4 Laboratory feeding experiment

Trichoplusia ni (Lepidoptera: Noctuidae) eggs, which are a similar species to many of the lepidopteran prey species found in croplands where the live *P. melanarius* were collected

(Dosdall & Mason, 2010; Philip et al., 2018), were obtained from the Great Lakes Forestry Centre (GLFC), Insect Production and Quarantine Laboratories of Natural Resources Canada. *T. ni* were maintained in accordance with the standard operating procedure for rearing *T. ni* from the GLFC (Ebling & Dedes, 2015). For trials, frozen and then thawed caterpillars were arranged into four distinct size categories (individuals that were not distinctly within one of the four categories were not used). These were placed in a trial arena (Figure 3.1).

For each trial, one live *P. melanarius* individual was placed in the center of the arena (Figure 3.1), facing a predetermined direction that had two of the potential prey sizes at a 45° angle and two of the potential prey sizes at a 135° angle. The trial beetle was rotated 90° clockwise for each subsequent trial, to control for biased preference for any prey size by direction. The beetle was allowed to move freely around the arena after placement. Once the beetle bit a prey item, the size category of the chosen prey was recorded, and the elytra of the beetle were measured using digital calipers. Beetles were trialed only once, and prey were refreshed with those of equal size after being bitten or upon desiccation.

2.5 Statistical analysis of prey choice

Data for hypothesis 2 were analyzed using an ordered categorical generalized additive model (GAM) with four ordered categories for prey size (i.e., 1=smallest, 2, 3 and 4=largest) as the response variable (Wood, 2017). Two models were tested, the first was a simple model with the linear effect of elytra length of *P. melanarius* on the prey category chosen. The second model was the same as the first except it included a categorical term for the angle the prey was from the beetle. Model fit was assessed using the DHARMa package for R (Hartig, 2022) and models were compared using AIC. The null hypotheses that a model term had no effect on the size category of prey chosen was tested using alpha = 0.05.

3. Results

3.1 Response of size of carabids to distance

20,407 carabids were measured from 180 different sample locations at different distances. The QGAMs indicated that distance from non-crop vegetation and GDD both had significant positive effects on the elytra length of carabid beetles that were found in smaller quantiles of the distribution (0.1, 0.2, 0.3, 0.4, 0.5, and 0.6; Table 3.2, Figure 3.2). The interaction between GDD and distance also had a significant negative effect on the elytra length of carabid beetles in the smallest six quantiles of the distribution (Table 3.2). In the 0.7 and 0.8 quantiles distance, GDD, and the interaction between distance and GDD had no effect on elytra length (Table 3.2, Figure 3.2). In the 0.9 quantile of elytra length distribution, GDD had a significant negative effect on elytra length but the interaction of distance and GDD had no effect (Table 3.2, Figure 3.2). Year had no effect on elytra length at any quantile while there were significant random differences between all sites at all quantiles (Table 3.2). Many field sites also demonstrated significant spatial variability uncorrelated with distance from non-crop vegetation at various quantiles (Table 3.2).

3.2 Effect of size on prey choice

Seventy-seven *P. melanarius* were tested in the size-choice experiment for the second hypothesis. The more complex model that included an effect of the angular difference between beetle and prey had a higher AIC than the simple model that only included the effect of elytra length on the prey size category (Table 3.3). Therefore, the simple model was chosen for interpretation.

P. melanarius beetles with longer elytra are predicted to trend towards an increasing probability of choosing the largest prey (beta ± standard error = 0.71 ± 0.41; Table 3.3) A plot of model predictions (Figure 3.3) confirms this trend is being driven by the largest size class. However, we were unable to reject the null hypothesis for the absence of an effect (alpha=0.05; P = 0.08; Table 3.3). A similar trend was not observed for the other three smaller size classes of prey (Figure 3.3).

4. Discussion

4.1 Distance from non-crop vegetation areas filters predator size

There are fewer smaller carabid beetles at greater distances from the crop margin, an effect that becomes statistically evident only when looking at trends across the smallest six quantiles of body size (i.e., 0.1 to 0.6). This effect is strongest when examining the smallest tenth of all carabids (i.e., q=0.1), where the mean size of this subset increases steeply over distance into the crop (Figure 3.2). These trends suggest that smaller ground beetles may be found at higher densities in non-crop vegetation areas and are unable, due to their smaller, less mobile body size, to travel far from non-crop vegetation into the centre of a crop field. These findings are consistent with our first hypothesis that size mediates dispersal of carabids from non-crop vegetation source habitats.

Carabids in the largest 30% of the body size distribution showed no restrictions in dispersal due to their size (Table 3.2, Figure 3.2). We consider two possible explanations for the absence of size limited dispersal in the largest beetles: (a) large ground beetles, as opposed to small ground beetles have no relationship with non-crop vegetation or (b) the largest ground beetles were not limited by their dispersal within the distance context of this sampled landscape. For explanation (a) it may be possible that the largest ground beetles have no relationship with non-crop vegetation and instead they are always capable of existing throughout the crop matrix. However, this is unlikely because migration out of the crop post-harvest has been shown in this system for *P. melanarius* (Robinson et al., 2021) which likely falls between the 80th and 90th percentiles of carabid size in this system (Busch et al., 2021). Therefore, explanation (b) may be more plausible where it is likely the largest carabids are effectively not limited in their dispersal on this landscape. This explanation is consistent with other research that finds a skew towards larger body sizes of arthropods in more homogenous agricultural landscapes (Perez-Alvarez et al., 2021).

4.2 Size of predator filters on size of prey

Larger *P. melanarius* trended to be more likely to prey on larger prey than smaller prey (Figure 3.3) though the p-value for this effect was not significant (alpha=0.05; P = 0.08; Table 3.3). A strict interpretation of the model therefore suggests that all prey sizes were equally likely to be chosen regardless of predator size. However, visualization does suggest that larger ground beetles may prefer larger prey items (Figure 3.3). While these findings are trending towards support for our second hypothesis, that larger ground beetles show a preference for larger prey, the absence of statistical significance demands caution in interpretation. For example, it is possible that *P. melanarius* being a large carabid relative to others in the family (Busch et al., 2021) has no preferences for prey sizes because it can consume all available prey. The presence of a suggestive trend, nonetheless, suggests future research would be beneficial to examine effects of body size on prey size filtering across the carabid family.

4.3 Within field prey filtering – Implications for pest control

Our findings suggest a diverse size range of predators are not able to access pests further into the crop. Given that larger carabids are likely to be found further into the crop and that larger predators may choose larger prey over smaller prey, it would be interesting to examine whether there is a filtering effect on prey traits within the field. If smaller prey (often those that are younger and more numerous) are overlooked by predators at further distances into the crop, many crop pests may be more capable of damage further into the crop by being allowed to exist in their larval feeding stage for longer. There is evidence in the literature that changes in the size composition of carabid communities can influence pest suppression (Perez-Alvarez et al., 2021; Rouabah et al., 2023; Rusch et al., 2015) but little research has examined the filtering effects of carabid body size on the traits of prey either in the lab or the field. Greater richness and evenness of carabid sizes likely increases pest suppression and increasing predator size may indicate an increase in pest suppression as well (Perez-Alvarez et al., 2021; Rouabah et al., 2014, 2023). However, other research has found contradictory effects where mean body size of ground-dwelling predators (including carabids) was negatively correlated with predation pressure (Rusch et al., 2015). Rusch et al. (2015) suggests intraguild predation of smaller ground-dwelling predators by larger ground-dwelling predators has a negative impact on pest suppression.

Increasing functional diversity in other systems has been shown to enhance pest control ecosystem services from carabids (Perez-Alvarez et al., 2021) and our laboratory findings may provide preliminary evidence for why this is, though intraguild predation may also play an important role in pest control ecosystem services (Rusch et al., 2015). By not focusing on species identity and rather on functional traits, the conclusions of this study can be compared in other systems where these specific pest control providers do not exist. It is likely beneficial for the sustainability of our food systems globally to maintain non-crop vegetation areas, because doing so will enhance the size diversity of carabid predators and possibly strengthen consumption pressure on pests at earlier stages of development.

5. Conclusion

5.1 Size (maybe) matters

The agroecosystem landscape has filtering effects on the body size of carabids (i.e., larger ground beetles are capable of dispersing further than smaller ground beetles from non-crop vegetation) and body size of carabids possibly influences prey choice or intraguild predation (Rusch et al., 2015). From an applied perspective, maintaining a diversity of ground beetle sizes within the crop is likely to ensure the broadest range of pests are consumed. To increase the effect of pest control in crop fields, increasing the amount of non-crop vegetation in the landscape is likely to bolster the diversity of sizes of ground beetles and may therefore have a greater alleviating effect on the impact of pests. Furthermore, reducing non-crop vegetation in favour of crop expansion may create fields where the largest carabids are unable to disperse throughout them and ultimately reduce potential pest control ecosystem services to the crop. This response-effect framework may help us draw conclusions across broad ecological contexts. Marginal areas of agroecosystems are integral to the maintenance of functional diversity of carabid predators.

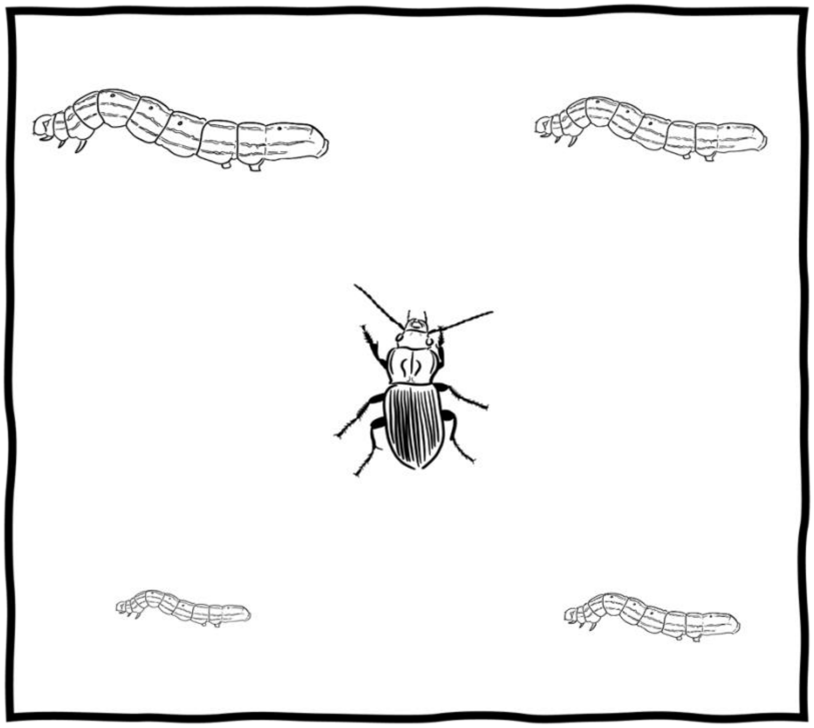

Figure 3.1: A diagram (not to scale) of the set-up of the arena experiment where the dark bounding box are the walls containing the insects. One live *Pterostichus melanarius* was placed in the center facing two frozen-thawed prey, *Trichoplusia ni*, caterpillars and given the option to bite any of the four caterpillars in the arena.

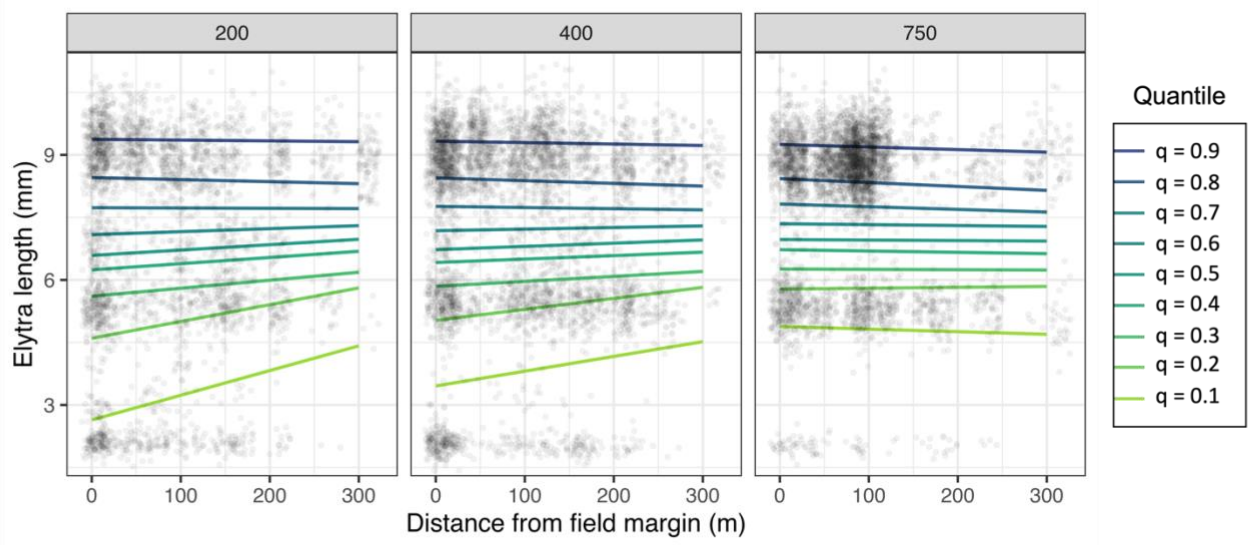

Figure 3.2: The elytra length of carabid beetles (mm) is related to the distance from marginal non-crop vegetation areas (m), and this varies over time (i.e., growing degree days; early season = 200, mid-season = 400, and late season = 750). Grey circles indicate individual ground beetles measured (N=20,407). Lines indicate the predicted fit at each of nine quantiles of the carabid elytra length distribution (0.1 to 0.9 at 0.1 increments).

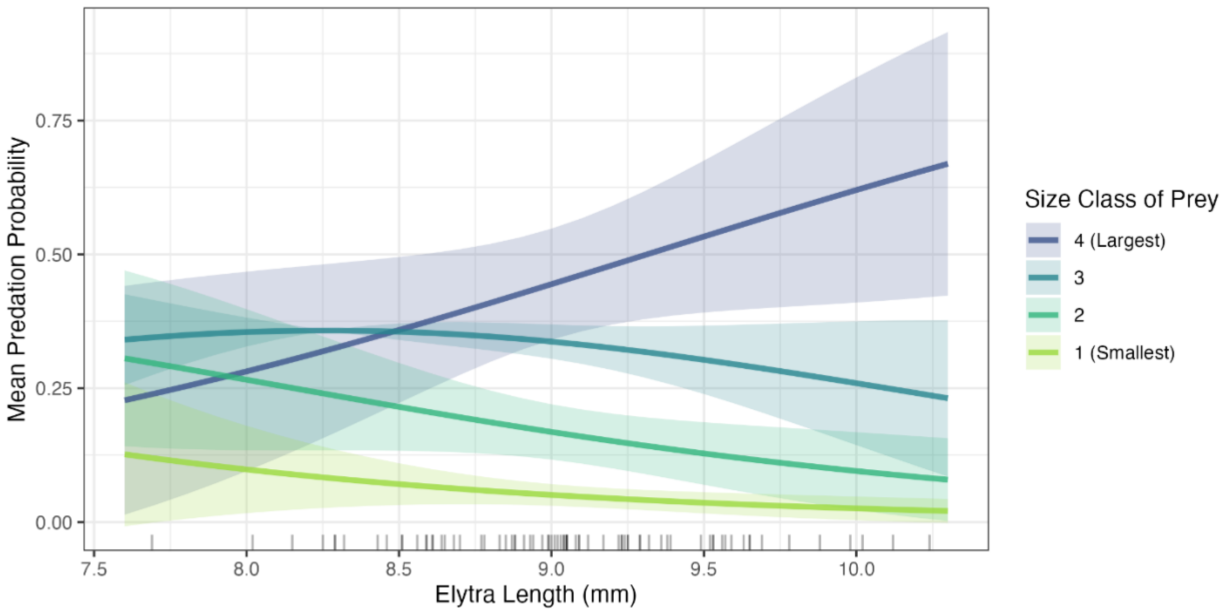

Figure 3.3: The predicted mean probability of predation on different size categories (1 through 4; 1 being the smallest and 4 the largest) of *Trichoplusia ni* (Lepidoptera: Noctuidae) caterpillar prey as effected by the elytra length (mm) of the predator *Pterostichus melanarius* (Coleoptera: Carabidae). Modeled using ordered categorical generalized additive models. Ribbons show the 95th percent confidence interval of the estimated mean as modeled for each prey size category. Grey tick marks on the x axis indicate the elytra lengths of each *P. melanarius* tested (N=77).

Table 3.1: All terms that were included in each quantile generalized additive model to test effects on carabid sizes with descriptions and reasoning for inclusion.

Term Description	***Model Term***	***Notes***
Distance from non-crop vegetation area	[parametric term]	Effect of distance was represented linearly to explore overall trends
Heat-time i.e., median growing degree day (GDD)	[parametric term]	Effect of heat-time was represented linearly to explore overall trends
Interaction between distance from non-crop vegetation and heat-time	[parametric term]	Interaction effect of heat-time and distance was represented linearly to explore overall trends
Year of sampling	[parametric term]	Categorical
Location of sampling centred within each site in relation to other sample stations in the same site	s(…, …, by = …)	Accounts for any spatial variability and spatial autocorrelation that may exist
Random differences between sites	s(…, bs= “re”)	Fits a random intercept for each field site.

Table 3.2: Estimates for effect on the size of carabid beetles by different terms included in nine quantile non-parametric additive models (q=0.1-q=0.9, each number corresponds with the percentile that model tested). Random intercept and smooth term estimates are effective degrees of freedom. Bolded estimates indicate significance for the model ($p<0.05$).

Term	***Term Type***	***H_0 Interpretation***	***q = 0.1***	***q = 0.2***	***q = 0.3***	***q = 0.4***	***q = 0.5***	***q = 0.6***	***q = 0.7***	***q = 0.8***	***q = 0.9***
Intercept	Parametric	Intercept =0	**2.50**	**4.45**	**6.03**	**6.93**	**7.51**	**8.02**	**8.57**	**9.05**	**9.60**
Distance	Parametric	No effect	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	<0.01	<-0.01	<-0.01
GDD	Parametric	No effect	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	<0.01	<-0.01	**<-0.01**
Year (2022)	Parametric	No effect	-0.678	-0.279	-0.655	-0.867	-1.061	-1.032	-0.872	-0.587	-0.179
Distance: GDD	Parametric	No interaction effect	**<-0.01**	**<-0.01**	**<-0.01**	**<-0.01**	**<-0.01**	**<-0.01**	<-0.01	<-0.01	<-0.01
Between Sites	Random Intercept	$\sigma_{intercept} = 0$	**14.674**	**15.817**	**14.955**	**15.343**	**15.513**	**15.386**	**15.017**	**14.033**	**12.474**
Site A	Smooth	No spatial effect	**3.42**	**4.01**	**7.60**	**7.52**	**8.11**	**8.13**	**8.21**	**7.22**	**6.27**
Site B	Smooth	No spatial effect	**7.04**	**7.94**	**8.11**	**8.05**	**8.11**	**8.10**	**8.07**	**8.12**	**7.68**
Site C	Smooth	No spatial effect	**6.07**	**7.91**	**7.97**	**8.03**	**7.99**	**8.01**	**7.96**	**7.86**	**8.18**
Site D	Smooth	No spatial effect	**7.84**	**8.06**	**8.16**	**8.20**	**7.49**	**7.19**	5.64	2.22	2.31
Site E	Smooth	No spatial effect	**6.59**	**7.44**	**8.14**	**8.33**	**8.35**	**8.39**	**8.40**	**8.55**	**8.63**
Site F	Smooth	No spatial effect	**6.55**	**6.86**	**6.40**	**6.60**	**6.67**	**6.55**	**6.36**	**6.91**	**7.14**
Site G	Smooth	No spatial effect	**7.90**	**8.05**	**8.05**	**7.24**	**7.72**	**7.47**	**6.21**	**5.66**	**5.06**
Site H	Smooth	No spatial effect	**7.69**	**7.49**	**7.82**	**7.71**	**7.84**	**8.00**	**8.04**	**8.11**	**8.29**

Site I	Smooth	No spatial effect	**7.80**	**8.06**	**8.05**	**7.74**	**7.93**	**7.97**	**7.87**	**7.03**	**5.55**
Site J	Smooth	No spatial effect	2.17	**5.75**	**6.87**	**7.38**	**6.52**	**2.02**	2.00	2.03	4.45
Site K	Smooth	No spatial effect	**2.62**	**2.00**	**2.01**	2.01	2.01	2.00	2.00	2.01	2.02
Site L	Smooth	No spatial effect	**3.43**	**5.06**	**5.40**	**5.73**	**6.67**	**6.51**	**6.69**	**6.86**	4.67
Site M	Smooth	No spatial effect	**3.33**	**5.56**	**3.55**	**4.23**	**4.52**	**4.97**	**5.39**	**5.77**	**5.32**
Site N	Smooth	No spatial effect	**6.90**	**6.14**	**5.22**	**6.01**	**7.39**	**7.76**	**7.88**	**7.92**	**8.24**
Site O	Smooth	No spatial effect	**7.28**	2.05	2.04	2.01	2.01	**2.01**	**2.59**	**5.26**	**4.62**
Site P	Smooth	No spatial effect	**6.48**	**6.99**	**7.08**	**7.37**	**7.43**	**7.57**	**7.58**	**5.87**	**5.69**
Site Q	Smooth	No spatial effect	**6.40**	**5.20**	**5.23**	**5.10**	**5.30**	**5.29**	4.96	4.55	2.02
Site R	Smooth	No spatial effect	**6.36**	**6.94**	**7.96**	5.28	**6.19**	**6.71**	**6.91**	**8.28**	**8.62**
Site S	Smooth	No spatial effect	**7.28**	**5.85**	**6.03**	**6.19**	**6.56**	**7.64**	**7.86**	**7.85**	**7.45**
Site T	Smooth	No spatial effect	**7.07**	**7.71**	**7.69**	**7.79**	**7.93**	**7.93**	**7.40**	**6.77**	5.42

Table 3.3: The estimates and standard errors for the terms included in each model to test the probability of a particular size class of prey being chosen by the predator *Pterostichus melanarius*. The p-values for the estimates are included. The AIC values for both models are also shown.

Term	***Model 1 beta***	***Standard error***	***p-value***	***Model 2 beta***	***Standard error***	***p-value***
Intercept	-4.49	3.71	0.23	-4.45	3.73	0.23
Elytra length (mm)	0.71	0.41	0.08	0.71	0.41	0.08
Prey angle-135	NA	NA	NA	-0.05	0.43	0.92
AIC		186.30			188.29	

Chapter 4: Conclusion

1.1 Summary of findings

The findings of my thesis can be broken down into four key points: (1) potential for carabid predatory activity increased to around 50 m into the crop, plateaued, and decreased around 100 m into crop. The increase and subsequent decrease in predation are evidence of a *halo effect* caused by the non-crop vegetation impacting the activity of the carabids within the crop. (2) Even though there is a halo effect of predation, it does not appear to be driven by the presence of carabids. The number of carabids I trapped (which indicates the *activity-density* of carabids, because passive trapping methods such as pitfalls rely on both the presence of the individual but also the individual moving and encountering the trap) increased with distance into the crop. (3) Though the average activity-density of the entire carabid family increased into the crop only the largest carabids dispersed throughout the whole field while smaller carabids could not. (4) Larger carabids may trend towards choosing to consume larger prey, though this last finding was not statistically significant (alpha=0.05; P = 0.08). Ultimately these findings all contribute to the original objective of this thesis which was to ***quantify how non-crop vegetation areas affect the predatory abilities of ground beetles within crops.***

In Chapter Two, I show how predatory activity of carabids may not be driven only by activity-density but also by proximity to non-crop vegetation areas. Carabid activity-density increased over the growing season within the crop and with distance into the crop, but depending on the sampling distance into the crop, higher activity-density may have increased, decreased, or had no effect on the potential for carabid predation. We also observed a halo effect of carabid predation around non-crop vegetation that is not reflected by the model of carabid activity-density. Non-crop vegetation has an impact on the potential for predation activity by ground beetles within the crop and more non-crop vegetation within agroecosystems is likely to benefit those predatory activities. These findings contribute to my original objective by quantifying the relative change in carabid predation activity with distance away from non-crop vegetation. The findings show that predation activity and therefore the potential supply of pest control ecosystem services cannot be accurately predicted from the activity-density of carabids. These findings may be indicative of non-crop vegetation providing resources within the crop that are influenced by growing time, such as weed plant cover, that in turn provide favourable conditions for predation activity by ground beetles, potentially by decreasing predation stress (Alford et al., 2023; De Heij et al., 2023; Lövei & Sunderland, 1996).

The resources from non-crop vegetation may influence certain activities more than others. For example, activity-density (potentially indicative of movement activity) may be lessened in areas of high carabid predation activity because if the carabids are less stressed about getting consumed themselves they may be more ‘willing’ to forage and hunt and may also spend less time moving to avoid predation (De Heij et al., 2023). Sentinel prey appears to be a potentially more accurate proxy than activity-density for the supply of pest control ecosystem services.

Future research would have to further examine the plant communities within the crop to determine the relationship carabids may have with weed plants (Barbercheck & Wallace, 2021). Parsing out density and activity from activity-density would also be illuminating in determining how we may predict predation activity and potential ecosystem services from presence of carabids in pitfall traps.

In Chapter Three, I show how proximity to non-crop vegetation filters the body size functional trait of ground beetles and provide an example of how body size may relate to predation. The findings show that the smallest quantiles of carabid size increase in size with distance into the crop and with time while the largest quantiles of carabids do not change with distance or time. Smaller carabids are likely less capable of dispersing as far into the crop as larger carabids, and larger carabids disperse into the crop faster while smaller carabids take longer to move the same distance. Larger ground beetles are indicated to not reach a limit to their dispersal within the landscape studied. We also found that larger *P. melanarius* may be more likely to consume larger prey (beta ± standard error = 0.71 ± 0.41), though we were unable to reject the null hypothesis of no effect (alpha=0.05; P = 0.08). These findings together show how non-crop vegetation may mediate pest predation ecosystem services through the body size of carabids by showing how body size changes in response to distance from non-crop vegetation and then how body size may impact the pests that get preyed upon. If large prey are preferentially preyed upon where there are more large carabids (i.e., further into the crop) then smaller prey may persist longer in those areas. The size of an insect herbivore can be indicative of its age; later instars are larger than earlier instars. A pest may have more time to cause crop damage in areas where only large carabids can reach before the pest reaches the size limit to where it is large enough to be preferentially preyed upon.

While some papers have examined the size functional trait of carabids (Gallé et al., 2020; Perez-Alvarez et al., 2021; Rouabah et al., 2014; Rusch et al., 2015), few have examined how the size of the predator may be able to influence a functional trait of the pest community. This chapter advances the original objective by indicating a potential mechanism for how non-crop vegetation can influence pest predation. However, there are limitations to the findings; the findings of prey size preference were both statistically inconclusive and completed in a controlled laboratory setting with only a single, dominant species. Threat of predation on the carabids (which may affect smaller carabids, like those in the genus *Bembidion,* more than larger carabids) and the availability of prey choices may have impacts on the prey preferences of the ground beetles (De Heij et al., 2023; De Heij & Willenborg, 2020; Vankosky et al., 2011). Next steps to measure the effects of carabid size on the size of the pest community may be to examine the functional traits of pests captured in the agroecosystem.

Behaviour is likely a driving factor behind the predatory effects of carabids and more research should consider the driving forces behind carabid behaviour, which may include both environmental factors and individual traits, rather than focusing on factors that influence only activity-density. Ultimately, what I find is that non-crop vegetation impacts carabid predation positively and that more effort should be made to construct and retain non-crop vegetation in the Canadian Prairie Provinces.

1.2 Biocontrol implications

Taken together, both Chapters exemplify the importance of non-crop vegetation in the potential provisioning of pest control ecosystem services by ground beetles. Carabids are likely capable of providing pest control ecosystem services when afforded non-crop vegetation because non-crop vegetation may create favourable conditions for predation in the crop and provide resources for a diverse range of carabid sizes that may then bolster predation on a diverse array of pests. By supporting carabids and their predatory activity via non-crop vegetation, growers may be able to limit or even eliminate pesticide use. Limiting the use of pesticides would have benefits for conservation by reducing non-target exposures to the chemicals and may also benefit growers who would not have to spend as much time or money on spraying (Chagnon et al., 2015). Valuing non-crop vegetation areas as suppliers of pest control ecosystem services may also help to conserve the remnant habitat of the Aspen Parkland Ecozone. In conserving or restoring non-crop vegetation areas we may be able to better serve species such as those protected under the Canadian Migratory Bird or Species at Risk Acts and other conservation interests (Migratory Birds Convention Act, 1994; Species at Risk Act, 2002; Ricketts et al., 1999; Riley et al., 2007). We may also be able to bolster the supply of other ecosystem services such as water filtration, by having a robust root system, or carbon sequestration, though having more perennial vegetation (Mayrinck et al., 2019). To increase the sustainability of agricultural systems in the Canadian Prairies supporting non-crop vegetation will likely provide benefits for growers and for conservation interests.

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Appendix: Co-author Contribution Statements

Chapter 2

T.J.N.: Conceptualization, Methodology, Data Curation, Investigation, Formal Analysis, Writing – Original Draft, Writing – Review & Editing, Visualization. **S.V.J.R.** Formal Analysis, Visualization, Writing – Review & Editing. **P.G.** Conceptualization, Methodology, Resources, Formal Analysis, Writing – Review & Editing

Chapter 3

T.J.N.: Conceptualization, Methodology, Data Curation, Investigation, Formal Analysis, Writing – Original Draft, Writing – Review & Editing, Visualization. **P.G.** Conceptualization, Methodology, Resources, Investigation, Visualization, Formal Analysis, Writing – Review & Editing