

When can we expect natural habitats to enhance pest control by generalist predators? Insights from a simple, simulated agricultural landscape

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HIGHLIGHTS

- *In silico* landscape experiments reproduce conflicting results from field research.
- Food resources in natural habitats may be insufficient to enhance natural control.
- Predators overwintering in natural habitats require food resources in adjacent crops.
- Natural habitats can enhance natural control by being a source of alternate prey.
- Pest insects from natural habitats do not always increase crop pest loads.

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ABSTRACT

Many field studies have reported that natural habitats in the agricultural landscape are associated with increased predator abundance and/or decreased crop pest load. However, recently published *meta*-analyses have found mixed results, with natural habitats being associated with increased pest loads as often as decreased loads. We investigate possible reasons for these conflicting results using a mechanistic model that simulates the dynamics of a generalist, omnivorous predatory bug and a plant bug pest in a landscape consisting of a 1 km² annual field crop monoculture bisected by a 60 m wide natural habitat strip. The model simulates the movement of adult predators in the landscape via both trivial movement and long-distance dispersal, along with the movement of energy and egg reserves carried by those predators. We simulate multiple scenarios varying the presence or absence of floral resources and alternate prey in the natural habitat and crop, and the presence or absence of overwintering refuges for the predator and pest insect in the natural habitat. Food resources provided to the predator by the natural habitat did not enhance natural control in adjacent crops. When the natural habitat served as an overwintering refuge for predators, natural control of pests was enhanced if food resources were available in the crop for those predators. Availability of alternate prey was more important to the predator than floral resources. Early-season crop pest loads were always increased when pest insects overwintered in the natural habitat, however early-season availability of pest insects enhanced natural control across the whole-season. Overall, crop pest loads were highly variable across simulation scenarios, reproducing the conflicting results from field research.

1. Introduction

Preserving natural habitats in agricultural landscapes has long been advocated as a means of enhancing natural control and lessening the economic impact of pest insects in agricultural crops (e.g., Pickett & Bugg, 1998). It has also been advocated for having the additional benefit of slowing the loss of natural habitats worldwide, for which there is

increasing urgency (Burchfield et al., 2019). It makes ecological sense that a landscape with greater habitat diversity might enhance natural enemy abundance by increasing the likelihood that essential food resources and refuges will be available at critical times. Indeed, many individual studies have found a positive effect of landscape diversity on natural control of pest insects (e.g., Gardiner et al., 2009, Kheirodin et al., 2020). However, in a large *meta*-analysis, Karp et al. (2018) found

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a roughly equal frequency of increases and decreases in natural enemy abundance and pest loads in response to landscape diversity. Similarly, in a review of the effects of landscape complexity, Bianchi et al. (2006) found that while 74 % of studies on natural enemies found positive effects, 55 % of studies on pest impacts found either increased impacts or no effect. As a result, it remains problematic to advocate for the preservation of natural habitats in agricultural landscapes as a universally reliable way to decrease pest loads.

The conflicting results from landscape-scale studies should not necessarily be surprising. As pointed out in Begg et al. (2017), while enhanced natural control is a possible outcome of preserving natural habitats in the agricultural landscape, it is by no means a guaranteed outcome. For example, even if natural enemies overwinter in large numbers in a natural habitat and subsequently colonize adjacent crops, they may not be able to establish populations prior to outbreaks of a pest insect. In annual field crops, agronomic practices minimize insect densities at the beginning of the season, and it can take many weeks for insect populations to establish and start growing. Natural enemies that colonize during this period are confronted with resource scarcity and may not be able to sustain populations in the crop unless they carry substantial overwintering reserves, or the crop provides floral resources or alternate prey. Likewise, even if natural enemies consume floral resources or alternate prey provided by a natural habitat and subsequently move to adjacent crops, this may not increase their longevity and fecundity to a sufficient spatial extent to influence crop pest loads at a landscape scale.

As pointed out by Tschardt et al. (2016), another reason for the conflicting results of field studies is that natural habitats are frequently a source of pest insects, resulting in increased pest loads and yield losses. For example, *Lygus* spp., a major pest in cotton, are known to thrive on native and disturbed vegetation, which then become sources of infestations (e.g., Goodell et al., 2006). Theis et al. (2005) found that, while complex landscapes increased parasitism rates, they also increased cereal aphid abundance. Growers instinctively understand this risk through difficult experiences and routinely remove non-crop vegetation near their agricultural fields. In fact, in some cases even natural habitat that has been shown to benefit natural enemies has been removed by growers because they were considered to be a source of pest insects and/or disease vectors (e.g., County, 1997).

Unfortunately, controlled experiments are simply not feasible at landscape scale, making it exceedingly difficult to predict when natural habitats might increase or decrease pest loads in adjacent crops. Simulation-based research, however, offers the possibility of conducting landscape-scale experiments *in silico* (van der Werf et al., 2008, Parry et al., 2012, Alexandridis et al., 2021). Bianchi & van der Werf (2003, 2004) conducted simulation experiments examining how aphid control by coccinellids is affected by the availability of overwintering refuges (Bianchi & van der Werf, 2003) and alternate prey (Bianchi & van der Werf, 2004) in non-crop habitats. Their simulation experiments incorporate explicit predator–prey dynamics and dispersal rules for the predator and were conducted on a 400 by 400-meter square landscape of 10 m² cells, each being either crop or non-crop habitat. Their results predict that the presence of overwintering refuges greatly reduced aphid pest load if non-crop habitat represented at least 4 % of the landscape (Bianchi & van der Werf, 2003). This effect was enhanced if these overwintering refuges were dispersed across their simulated landscape rather than clumped (Bianchi & van der Werf, 2003) and was further enhanced when the non-crop habitat also supported alternate aphid prey (Bianchi & van der Werf, 2004). However, in their simulations non-crop habitat was either centered within or distributed throughout the 400 x 400 m² simulated wheat field, and so may not represent agricultural landscapes containing larger non-crop habitat elements separated by longer distances such as seen in the US in the Midwest, Plains, and California's central valley. Zamberletti et al. (2021) conducted experiments on a larger simulated landscape (defined as having an extent of 5.55 km) consisting of complex polygonal fields and their boundaries.

Their simulation combined diffusion modelling with local predator–prey dynamics to predict the effects of varying amounts of hedgerows along these field boundaries. Their results predict that increasing the presence of hedgerows increases overall predator density, thereby keeping pest insects below pesticide treatment levels. However, their simulated predator only foraged in the crop without establishing populations there, limiting the applicability of their conclusions to other generalist insect predators.

The simulation studies described above take a mechanistic modelling approach. By this we mean that the effects of natural habitats on crop pest loads are not assumed *a priori* but rather are allowed to emerge on their own via the mechanisms of population growth, movement, and predation operating within the simulated landscape. Other simulation-based research on agricultural landscapes has taken a more correlative approach (e.g., Zhang et al., 2010, Johnson et al., 2014; Parry et al., 2022). That is, they either assume an amount and extent of pest control benefit provided by non-crop habitat or estimate that benefit statistically using field data. By conducting simulated experiments with varying landscape composition and/or agronomic management practices, these simulations predict the expected pest loads and/or economic impacts for target crops in the landscape. This approach can provide tremendous insight into the possible consequences of habitat and agronomic management decisions for a well know cropping system in which the response of pest populations to non-crop habitats has been well studied. However, they do not necessarily add to our understanding of *why* the presence and configuration of natural habitats within an agricultural landscape might increase or decrease crop pest loads and therefore can't be generalized to other cropping systems and landscapes.

In this paper we present the results of *in silico* experiments with a simulated landscape that expands upon the mechanistic approach applied by Bianchi & van der Werf (2003, 2004) and Zamberletti et al. (2021). Like the work by Bianchi & van der Werf (2003, 2004) we explore the potential effects on crop pest loads of overwintering refuges and alternate prey in natural habitats and implement explicit rules for dispersal from those natural habitats. Like Zamberletti et al. (2021) we include trivial-movement (represented via diffusion) in addition to long-distance dispersal behavior, and we simulate a larger landscape. In addition, our simulation includes the possibility of the natural habitat providing floral resources, the possible overwintering of the pest insect in the natural habitat, the possible provision of floral resources and alternate prey by the crop, and the movement of the alternate prey from the natural habitat to the crop. Finally, we explicitly represent the movement of egg and energy reserves within the landscape to account for the potential benefit of food resources consumed in the natural habitat on predator population growth in the adjacent crop.

Our focus is on the impact of large areas of natural habitat within the agricultural landscape and their potential impact on pest control by generalist predators in adjacent crops. To this end, we simulate a single, large area of natural habitat and its effects on a generalist predator and pest insect in an adjacent large acreage of an annual field crop. We derive parameters for population growth, predation, and movement by our generalist predator based on the existing literature for *Geocoris* spp. Using these baseline parameters, and by varying the resources provided by the natural habitat and adjacent crop – floral resources, alternate prey, overwintering of the predator, and/or overwintering of the pest insect – we explore the following questions:

- Under what conditions do food and/or overwintering resources provided by the natural habitat benefit predators to a sufficient spatial extent to decrease crop pest loads at the landscape scale?
- To what extent does pest overwintering in the natural habitat undermine the impact of food and/or overwintering resources provided to predators by that natural habitat?

2. Material & Methods

2.1. Overview

Our objective is a landscape-scale model of plant-herbivore-predator dynamics that captures the essential mechanisms and processes involved but does not include any direct assumptions regarding how natural habitats impact crop pest load. We use existing theoretical models and approaches wherever possible. Such an approach has been advocated by Alexandridis et al. (2021) to resolve the inherent tension between generality and realism in the design of landscape-scale simulations. To this end, we have developed a spatially explicit crop-pest-predator simulation with a reaction–diffusion system as its foundation. To this system we add two stochastic components to simulate (a) random colonization and (b) long-distance dispersal. Predator egg and energy reserves are explicitly represented and move with predators via diffusion and long-distance dispersal.

The simulation model is intended to represent a generic herbivorous plant bug on an annual field crop with a generalist, omnivorous predatory bug as its natural enemy. While we use existing literature for *Lygus* spp. pests and *Geocoris* spp. predators on cotton as a basis for parameters in the model (see Appendix B), we neither claim nor intend that our simulation model be seen as representing any specific real-world crop/predator system. The mathematical and computational details of our model are presented in Appendix A; sources and rationale for parameters are provided in Appendix B. Here we describe the key processes, assumptions, and parameters from primarily an ecological perspective.

2.2. Model structure

We simulate a simple agricultural landscape representing a 1 km² monoculture of an annual field crop, bisected by a 60-meter-wide natural habitat (Fig. 1). The natural habitat might, for example, represent a riparian habitat, a railroad right-of-way, or an irrigation channel. We choose this type and size of natural habitat because our focus is on the effects of large, landscape-scale habitat elements, not the effects of smaller scale vegetation diversification within or at the edges of a crop. The landscape is represented by a two-dimensional grid of 5x5 meter cells. Each cell implements the same vegetation/pest-insect/predator model. Within-cell dynamics are represented by a system of

differential equations (Section 2.2 below). Adult pest insects and predators randomly colonize all cells at a constant low rate. Adult pest insects and predators move between cells via two different modes: trivial movement, which occurs only between adjacent cells, represented by diffusion; and stochastic long-distance dispersal, using a probability distribution of flight distances (e.g., a “dispersal kernel”, see Bianchi et al., 2009). The simulation uses a time unit of 1 day and is updated using time increments small enough to ensure the stability of the numerical methods employed (see Appendix A for full implementation details).

2.3. Within-cell dynamics

The within-cell model is a system of ten differential equations representing: the vegetation in the crop or natural habitat; three life-stages of pest insect; three life stages of predators; the adult predator energy and egg reserves; and an alternate prey population.

2.3.1. Vegetation

The crop is represented simply and exclusively as leaf surface area – i.e., as the surface upon which pest and predator dynamics occur. The model does not account for the impact of herbivory on crop growth. Leaf area increases via a natural growth function using parameters intended to simulate cotton: the maximum leaf area index (LAI) is 3.0; the crop reaches 90 % of the maximum LAI halfway through the season. LAI is initialized at 0.5, which is equivalent to 7 days of growth. Current leaf surface area of a cell is the current LAI x the ground area of the cell; at maximum LAI this is 75 m² of leaf surface per 5x5 meter cell. The natural habitat is initialized at an LAI of 3.0, equal to the maximum LAI for the crop, and remains constant throughout the season.

2.3.2. Pest insect

The pest insect is represented via three life stages: eggs, nymphs, and adults. The mean stage durations are 8, 21 and 14 days for eggs, nymphs, and adults respectively. Adults have an intrinsic oviposition rate of 4 eggs/day. Instantaneous birth and death rates are linear functions of the cumulative pest density up to that time, which provides for time-delayed influences on growth rate in a straightforward way. Birth rate and longevity reach a minimum at a specified critical cumulative pest density. The minimum oviposition rate is 1 egg/day; the minimum adult longevity is 5 days. Pest nymphs and adults are lost to predation in proportion to their relative abundance. The natural habitat is not a host plant for the pest insect, but we explore scenarios in which the natural habitat permits the pest to overwinter (see below); the pest insect does not lay eggs and its longevity is at minimum in the natural habitat.

2.3.3. Predators

Predators are represented by three stages: eggs, juveniles, and adults with a mean duration of 7, 14 and 14 days, respectively. Juvenile mortality is a decreasing linear function of their predation rate. Adult egg-laying and mortality are dependent on egg and energy reserves respectively, which are in turn dependent on predation rates – see further details on predator egg and energy reserves below (Section 2.2.4).

Predators exhibit a Type II Holling functional response. Their maximum prey consumption rate is 20 prey per day. Predators search a maximum of 2,000 cm² of leaf surface area per day. In annual field crops both the prey population and leaf surface area are dynamically changing. For example, leaf surface area may grow faster than the prey population early in the season, resulting in *decreasing* prey density over time. We explicitly represent growth in leaf surface area of the crop (Section 2.2.1) so that we can calculate the instantaneous predation rate based on the current prey *density*, not just its population size.

2.3.4. Predator energy and egg reserves

Adult egg-laying and mortality is mediated by the total energy and

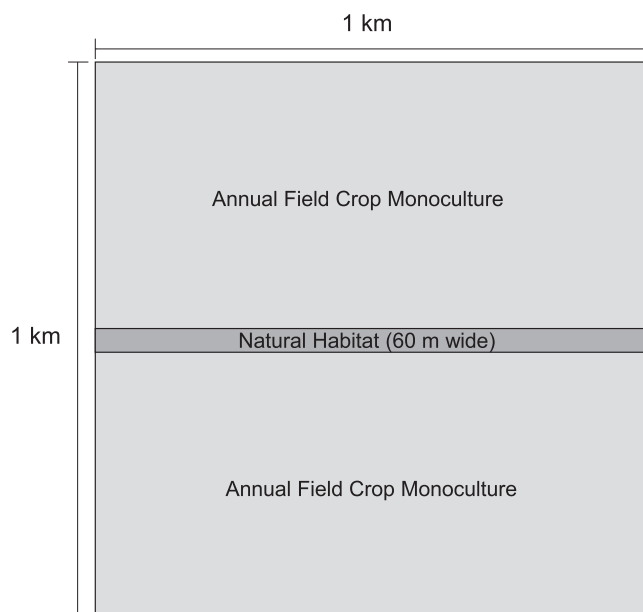


Fig. 1. Diagram of simulated landscape.

egg reserves of all adult predators within a cell, which are represented with their own differential equations. Representing energy and egg reserves explicitly allows for the movement of these reserves between cells within the simulated landscape. This, in turn, allows for the history of resource consumption by predators and not just the instantaneous local resource availability, to influence the numerical response in a cell.

The adult energy reserve of the predators within a cell decreases via mortality, emigration, and the daily maintenance energy cost. The energy reserve increases via:

1. *Consumption of prey and floral resources.* Each prey consumed contributes 1.25 day's-worth of maintenance energy to the reserve; it also contributes to the egg reserve as described below. All floral resources consumed go to the energy reserve. It is important to note that these assumptions are appropriate for simulating a generalist, omnivorous predator, but would not apply to other natural enemies such as many parasitoids.
2. *Emergence of new adults.* Adults emerge from the juvenile stage with 4 days'-worth of maintenance energy in their reserve.
3. *Immigration of adults via trivial-movement or dispersal.* Immigrating adults carry their portion of the energy reserve from the cell previously occupied.
4. *Colonization by adults.* Colonizing adults carry half the energy reserve of newly emerged adults – 2 days'-worth of maintenance energy.

Adult mortality is a function of the current energy reserves in the cell and increases linearly when energy reserves per predator fall below a minimum of 2 days'-worth of maintenance energy.

Egg reserves increase via predation at a rate of 0.75 eggs per prey consumed. The mean time between prey consumption and oviposition is approximately 3 days. Newly emerged and colonizing adults have no eggs on board; they must consume prey before producing eggs. As with the energy reserve, immigrating adults carry their portion of the egg reserve from the cell previously occupied.

2.3.5. Alternate prey

A second herbivore is incorporated as an alternate prey for the predator. This second herbivore is assumed to have negligible impact on crop growth/yield. The alternate prey population is represented via simple logistic growth relative to its density, with a growth rate of 0.09/day and a carrying capacity of one alternate prey per 125 cm² of leaf surface area. This results in a carrying capacity of 6000 alternate prey per cell when the crop reaches its maximum LAI, which is comparable to the maximum number of nymph and adult pest insects achieved in the absence of predators (6500 per cell). The predator consumes this alternate prey according to the same predation rules as detailed for the primary herbivore. Consumption of alternate prey adds to the adult predator energy and egg reserves at the same rate as the pest insect.

2.4. Movement and colonization

Trivial movement between adjacent cells is modelled via diffusion at a rate dependent on local cell conditions. For the pest insect, diffusion is 50 m²/day when cumulative pest density is zero and increases linearly to 200 m²/day when cumulative density is at its critical value (when birth and longevity are at a minimum, see Section 2.2.2). For the predator, diffusion is 200 m²/day when predation rate is zero and decreases linearly to 50 m²/day when predation rate is at its maximum of 20 prey/day. Alternate prey diffuse at a fixed rate of 100 m²/day. All insects move freely between the natural habitat and the adjacent crop.

Longer-distance dispersal is handled stochastically: whole numbers of adult predators and pest insects fly in a random direction and to a distance defined probabilistically by our dispersal kernel. Fig. 2 shows the probability distribution of flight distances for the parameters used in our simulation; see Appendix B for more details. We use the same parameters for the pest insect and the predator to exclude differential

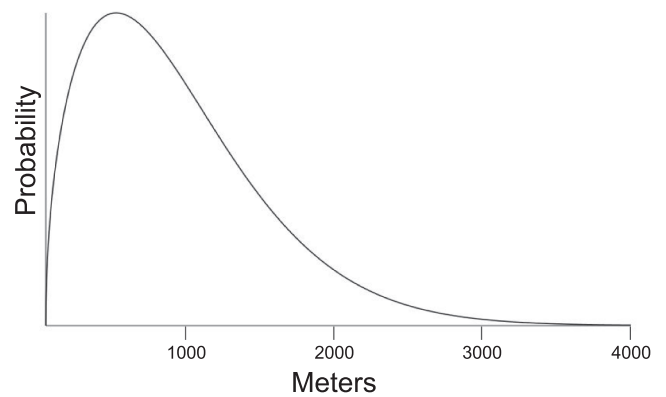


Fig. 2. Probability distribution of flight distances of dispersing adult predators and pest insects. See Appendix B for more details.

dispersal ability as a factor in the natural control potential of the predator. The rate of dispersal is anchored to the mortality rate, such that an equal number of adults disperse as die in a day. Triggers for dispersal in the field are of course more complex than this, but we make the simplifying assumption that correlating dispersal with mortality approximates the overall relationship of dispersal to local conditions.

Colonization is also handled stochastically. Whole numbers of adult pest insects and predators randomly colonize the simulated landscape at a low, uniform rate per unit area: pest insects at a rate of one adult per 1250 m² per day; predators at a rate of 1 adult per 10,000 m² per day. In the absence of overwintering in the natural habitat, colonization is the only source of predators and pest insects in our simulated landscape.

2.5. Resources

The natural habitat can provide: (a) overwintering for the predator; (b) overwintering for the pest insect; (c) floral resources to the predator (but not the pest insect); and/or, (d) alternate prey to the predator. Alternatively, the natural habitat can provide no resources. The crop can provide either floral resources or alternate prey to the predator, both floral resources and alternate prey, or no resources. The crop provides no overwintering resources to the predator or the pest insect.

Overwintering. When the natural habitat provides an overwintering refuge, pest insects overwinter in the natural habitat at a density of 10 adults per m² and predators overwinter at a density of 5 per m². Overwintering adults begin emerging on day 7 of the season with an average delay of 1 day before they emerge. All overwintering adults disperse upon emergence according to the same rules for dispersal described above. There is no overwintering in the crop.

Floral resources. When present, floral resources are available throughout the season. Predators start to shift from predation to floral resource consumption when the predation rate falls below 10 prey per day. Below 10 prey per day, the rate of consumption of floral resources grows linearly from 0 to 100 % as the predation rate drops to zero. Predators have a maximum energy reserve of 10 days'-worth of energy per predator; when floral resource consumption is at 100 %, predators reach this maximum reserve size in 0.1 days. The same rules for floral resource consumption apply in both the natural habitat and the crop.

Alternate prey. When the natural habitat supports alternate prey, they are initialized at a density of 10 per m². Alternate prey move to the adjacent crop via trivial movement only; no dispersal is simulated for alternate prey. When the crop supports alternate prey, they are initialized at a density of 0.25 in every 25 m².

2.6. Simulation scenarios

We ran simulations with the following configurations of resources in the natural habitat and/or the crop:

- The 1 km² of field crop provides no resources and is not bisected by a natural habitat.
- The crop is bisected by a natural habitat that provides no resources.
- The natural habitat provides floral resources, supports alternate prey, and/or provides an overwintering refuge for the predator.
- The natural habitat provides an overwintering refuge for the pest insect.
- The crop provides floral resources and/or supports alternate prey.

In total we ran 68 different simulation scenarios representing all permutations of the above resource configurations. All simulations were initialized at day 7 after planting of the field crop and run through day 180, representing a 6-month growing season. Note that the crop does not provide overwintering resources to the predator or the pest insect in any of these scenarios.

To evaluate the effects of resource combinations on crop pest load we use the average cumulative pest insect density across the whole 1 km² field (excluding the natural habitat) at day 90 and day 180, representing the early-season and whole-season pest loads for that scenario. To evaluate the effects of resource combinations on predators we use (a) the average density of adult predators at day 10 and day 90 across the whole 1 km² field (excluding the natural habitat) and (b) the average egg and energy reserves of adult predators at day 50. We also examine adult predator density relative to distance from the natural habitat at day 90.

3. Results

Our 68 scenarios produced a wide range of effects on crop pest loads (Figs. 3 & 4). In the absence of crop-based resources, resources provided by the natural habitat had negligible effects on whole-season pest load. Availability of floral resources in the crop had minimal impacts on whole-season pest load. Availability of alternate prey in the crop produced large impacts on whole-season pest load, resulting in reductions between 10 % and 70 % (Fig. 3A). The effect of alternate prey in the crop was greatly enhanced if the alternate prey was also supported by the natural habitat. This effect was further enhanced if the predator overwintered in the natural habitat and if the crop provided floral resources in addition to alternate prey.

Overwintering of the pest insect in the natural habitat did not increase whole-season pest load (Fig. 3B) relative to a landscape with no natural habitat. In fact, whole-season pest load was decreased by as much as 40 % if both the natural habitat and crop were host to alternate prey, even with pest insects overwintering in the natural habitat. Early-season pest load, on the other hand, was increased by as much as 20-fold when the pest overwintered in the natural habitat (Fig. 4). Early-season pest load was largely unaffected by resources provided to the predator by either the natural habitat or the crop.

To explore the effects of natural habitat and crop resources on predators we examine the average density of adult predators in the crop at the beginning (day 10) and midpoint (day 90) of the season for selected scenarios (Fig. 5). When predators did not overwinter in the natural habitat, their abundance at the beginning of the season was always low and tended to remain low unless the crop provided alternate prey. The number of predators increased by mid-season only when alternate prey were available in the crop or the pest overwintered in the natural habitat. When the natural habitat provided an overwintering refuge for predators, their numbers were always high at the beginning of the season. However, with one exception, predator abundance declined by mid-season to that seen in scenarios with no overwintering refuge. Only when both the natural habitat and crop served as hosts for the alternate prey did this higher early-season predator abundance persist to mid-season.

To explore the relationship between egg and energy reserves of adult predators and resources provided by the natural habitat or crop, we examine the average reserves of adult predators in the crop at day 50 for the same selected scenarios (Fig. 6). Energy reserves of adult predators

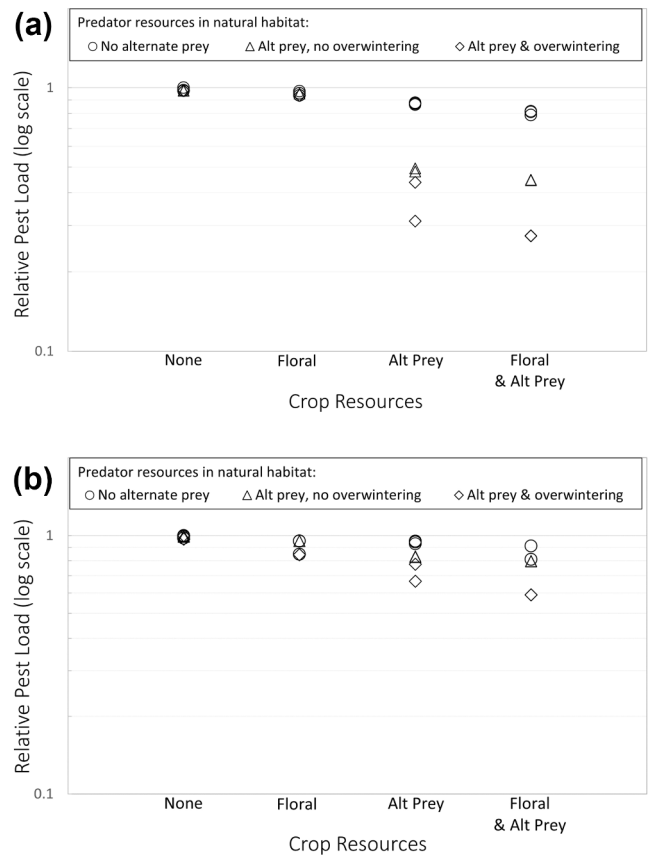


Fig. 3. Relative whole-season pest load for each crop resource combination when (A) pest insects do not overwinter in the natural habitat and (B) when pests do overwinter. Values are calculated relative to whole-season pest load for a crop with no bisecting natural habitat and that provides no resources for the predator. Scenarios are grouped with respect to the presence of alternate prey and/or predator overwintering refuges in the natural habitat: no alternate prey (circle), alternate prey without predator overwintering (triangle), alternate prey and predator overwintering (diamond). Complete results for all scenarios are available in Appendix C.

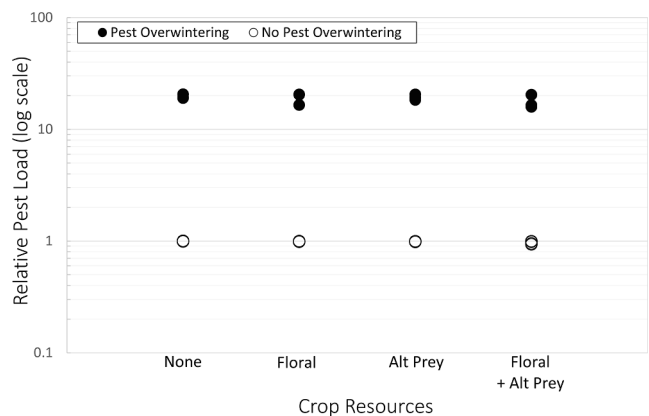


Fig. 4. Relative early-season pest load (first 90 days) for each crop resource combination when the pest insect overwinters in the natural habitat (closed circle) and when it does not (open circle). Values are calculated relative to early-season pest load for a crop with no bisecting natural habitat and that provides no resources for the predator. Complete results for all scenarios are available in Appendix C.

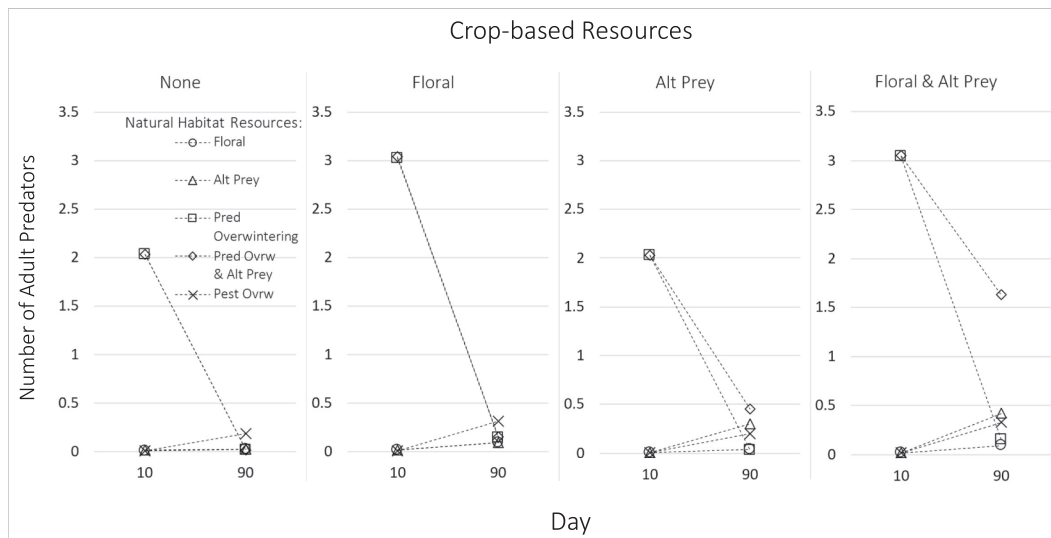


Fig. 5. Average number of adult predators in the crop at day 10 and day 90 for selected combinations of natural habitat and crop resources.

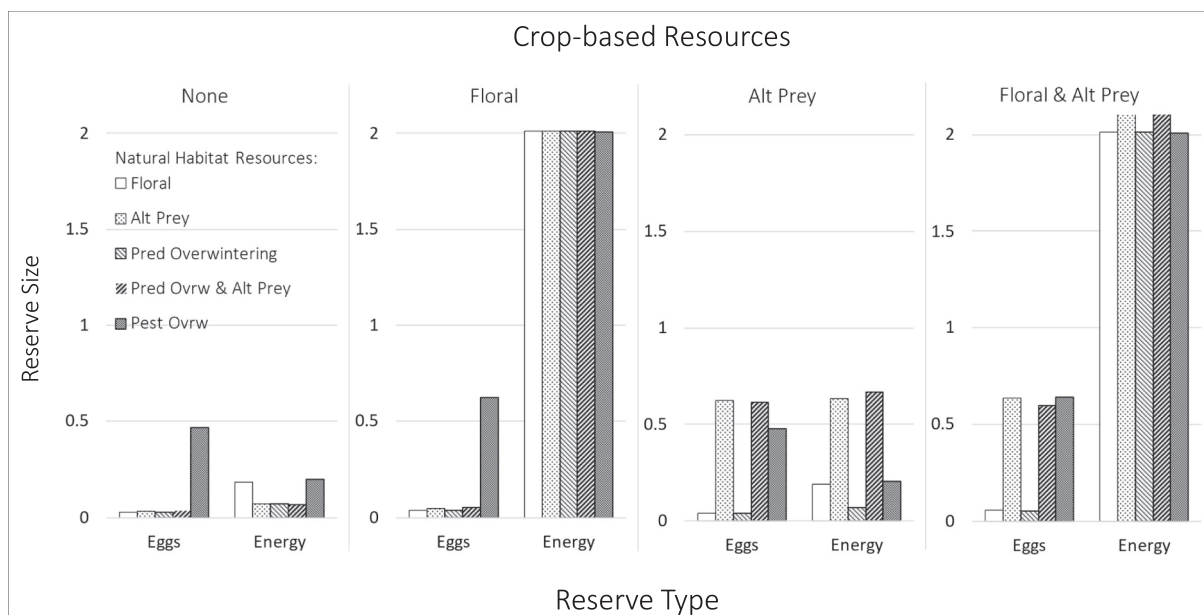


Fig. 6. Adult egg and energy reserves at day 50 for selected combinations of natural habitat and crop resources.

were always increased by the presence of floral resources in the crop but were not affected by floral resources in the natural habitat. Egg reserves were increased whenever there were prey available in the crop, be they the pest insect or alternate prey. In the absence of floral resources in the crop, energy reserves tended to follow egg reserves; this is because our simulated generalist predator obtained both egg and maintenance energy from consuming prey. The scenarios in which egg reserves were highest correspond to the same scenarios in which predator abundance was highest at the midpoint of the season (see Fig. 4).

While floral resources in the natural habitat had negligible effects on whole-season pest loads, spatial patterns reveal an effect on adult predators near the natural habitat at day 90 (Fig. 7). When the natural habitat provided floral resources, adult predator density was two to four times higher within 100 m of the natural habitat. There was no similar spatial effect when the natural habitat provided alternate prey or an overwintering refuge.

4. Discussion

In our simulation scenarios, the presence of a natural habitat produced a wide range of effects on pest load in the adjacent crop depending on the combination of resources provided to the predator and pest insect by the natural habitat and/or the crop. These effects included dramatic increases in half-season pest loads, moderate to large decreases in whole-season pest loads, as well as negligible effects. Thus, our results are consistent with the wide variety of outcomes reported by Karp et al. (2018). It is notable that we obtained this wide range of results in this relatively simple simulated landscape in which both the landscape configuration and the attributes of predator and prey were kept constant. This suggests that the variable results of field studies on landscape heterogeneity should be seen as a natural and expected result of the complex spatial-temporal dynamics of insects in agricultural landscapes.

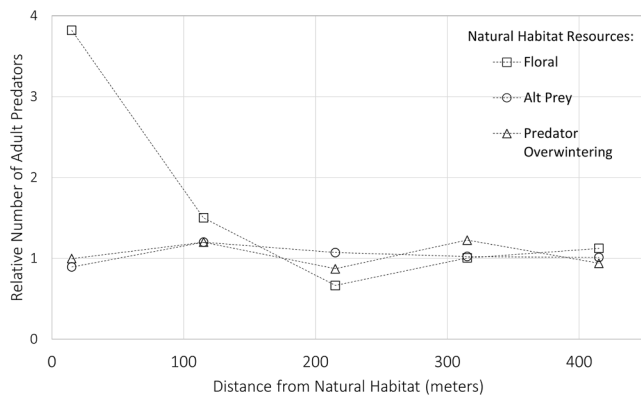


Fig. 7. Relative numbers of adult predators at day 90 versus distance from the natural habitat for different resources provided by the natural habitat. Values plotted are the density at that distance from the natural habitat divided by the density at that location for a crop without a bisecting natural habitat.

4.1. Predator overwintering

Overwintering of predators in the natural habitat had negligible effects on pest load unless the crop also provided resources. Although adult predator density was higher at the beginning of the season when they overwintered in the natural habitat, this benefit of a nearby overwintering refuge disappeared by mid-season in the absence of crop-based resources (Fig. 5). This suggests that that unless resources are available in the crop, predators colonizing from nearby overwintering refuges may be lost to mortality and emigration prior to build-up of the pest insect. Simply increasing the number of early-season colonizers may not be sufficient in and of itself to enhance natural control. We are simulating a generalist predator and have assumed a modest energy reserve and no egg reserve upon emergence from overwintering, which is a reasonable assumption for most natural enemies. Some natural enemies emerge with greater reserves of energy and eggs. For example, the egg parasitoid *Anagrus epos* emerges with a full complement of eggs and does not feed as an adult, but this is relatively uncommon. For these types of natural enemies, the benefit of overwintering refuges alone is likely to be higher.

Other simulation studies by Bianchi & van der Werf (2003) and Banks et al. (2008) concluded that overwintering refuges on their own can increase suppression of aphids by coccinellids in adjacent crops. However, these simulations were initialized with relatively high densities of aphid prey in the crop. In contrast, our simulations were initialized with zero pest insects in the crop and a low, uniform rate of colonization from outside the system. Additionally, the simulated crop leaf area in our model is growing rapidly during the first half of the season, keeping pest insect densities and, therefore, predation rates low. Under these conditions, which we believe are like those found in annual field crops, our simulated overwintering predator was confronted with a severe scarcity of resources in the absence of floral resources or alternate prey in the crop.

4.2. Floral resources

The availability of floral resources in the natural habitat and or the crop had negligible effects on crop pest load. Consumption of floral resources was unable to sufficiently increase the longevity or fecundity of our simulated generalist predator to impact crop pest loads. Since we simulated floral resources as being available all season long and to provide high energy value with short bouts of feeding, we believe we have, if anything, overestimated the potential benefit of floral resources. We simulate a generalist, omnivorous predator for whom the availability of floral resources is advantageous but not essential. Larger impacts of floral resources on crop pest load would be expected for natural

enemies, like many parasitoids, for whom floral resources are essential for adult survival (Heimpel & Jervis, 2005).

Despite not having an impact on crop pest load, floral resources in the natural habitat did increase the abundance of adult predators within the first 100 m from the habitat (Fig. 5). These results are consistent with other findings from field and modeling studies. For aphid parasitoids in wheat, Tylisanakis et al. (2004) found that while the availability of floral resources increased parasitoid fecundity in general, parasitism rates were only increased within 15 m of floral resources. Modeling studies by Banks et al. (2008), Bianchi & Wackers (2008), and Begg et al. (2017) also found that the benefits of floral resources to natural enemies diminish rapidly with distance. In our simulation, the benefits of floral resources extended to a greater distance than observed in other research but were still insufficient to have an impact on whole-season pest load. This suggests that, while floral resources provided by natural habitats may benefit some predators in a landscape, this does not guarantee decreased pest loads at a sufficient spatial scale to benefit large acreages of crop. An important caveat is that the movement of our simulated generalist predator responds to prey density, not floral resources. It is reasonable to hypothesize that natural enemies that require floral resources are likely to have movement rules that respond to the availability of floral resources, possibly making them more likely to visit floral resources adjacent to the crop.

4.3. Alternate prey

Alternate prey in the natural habitat on its own had negligible effects on crop pest load in our simulations. Bianchi & van der Werf (2004) found that alternate prey increased predator reproduction throughout a simulated wheat field even if only available in hedgerows; however, in their scenarios much of the crop was within 100 m of a simulated hedgerow bringing all predators into relatively close proximity with alternate prey resources. In our simulated landscape, the availability of alternate prey in the natural habitat was unable to increase predator fecundity to a sufficient spatial extent to impact whole-season pest loads across a large acreage of crop.

Availability of alternate prey in the crop was the only factor to result in significant decreases in whole season pest load, with the largest decreases obtained if the natural habitat was also a host to alternate prey. In this latter scenario, alternate prey colonized the crop early in the season and provided a clear enhancement to natural control of the pest. This outcome is consistent with other work demonstrating the importance of alternate prey availability to natural enemies. In studies of tropical rice production, Settle et al. (1996) demonstrated that the availability of alternate prey significantly increased the early-season abundance of generalist predators. Their hypothesis that early-season availability of alternate prey “gives the predator populations a ‘head start’ on later-developing pest populations” is corroborated by the results of our simulation experiments. In studies of leafminers and their parasitoids in natural habitats, Blitzer & Welter (2011) demonstrate a similar effect: early season abundance of the leafminer *Liriomyza helianthi* leads to higher parasitism rates later in the season on *Calycomyza platyptera*, a second leafminer species. Likewise, in laboratory cage experiments Emery & Mills (2020) demonstrated an indirect interaction between *Acyrtosiphon pisum* and *Aphis gossypii* via predation by *Hippodamia convergens*. This concept has been successfully applied in greenhouse IPM by using “banker plants” that provide early access to alternate prey to prevent later aphid outbreaks (Peyton Miller & Rebek, 2018). Other simulation studies have also demonstrated the effect of alternate prey availability on target pests. In a simulation model of coccinellids in wheat, Bianchi & van der Werf (2004) found that the availability of non-pest aphids in hedgerows enabled the predator to achieve high reproduction rates prior to build up of the target pest. In a theoretical model, Chakraborty et al. (2017) also found that the presence of alternate prey enhanced control of the pest insect so long as the pest insect did not have a large refuge from which to recolonize the

system.

4.4. Pest overwintering

Overwintering of the pest in the natural habitat resulted in large increases in crop pest load over the first half of the season. No combination of predator resources in either the natural habitat or the crop was able to prevent this increase. Early-season is a critical time for pest damage in many crops and the negative effect of pest overwintering on yield likely outweighs any potential benefit of the natural habitat to natural enemies in those crops. This corroborates the concern of many growers and agricultural researchers that natural vegetation is as likely to exacerbate pests as to benefit natural enemies.

Surprisingly, overwintering of the pest insect in the natural habitat did *not* increase whole-season pest load and even decreased pest load in some scenarios (Fig. 3). Likewise, early-season egg reserves (Fig. 6) and midseason predator abundance (Fig. 5) were similar whether the crop supported alternate prey or the pest overwintered in the natural habitat. In fact, our results suggest a direct causal link between greater early-season availability of prey, larger early-season egg reserves (Fig. 6), higher midseason predator abundance (Fig. 5), and lower whole-season crop pest load (Fig. 3). Bianchi & van der Werf (2004) demonstrate a similar effect in their simulations of coccinelids in wheat in which earlier colonization of wheat by pest aphids enabled coccinelids to maximize their reproduction early in the season even in the absence of alternate prey. This suggests that for a predatory insect, early-season availability of pest insects is simply another resource that can sustain their populations and result in greater pest suppression over the course of the whole season. As demonstrated by Speisman et al. (2020) in their metapopulation model, early-season availability of prey – whether it be alternate prey or the target pest – provides temporal resource continuity, which is critical to maintaining predator abundance at levels sufficient to contain incipient pest outbreaks.

5. Conclusions

Our results suggest that resources provided by natural habitats are likely insufficient *on their own* to enhance control by generalist predators but can result in lower pest loads when combined with crop-based resources, most importantly alternate prey. Overwintering of pests in a natural habitat is likely to undermine any enhancement of natural control during the early-season, but this effect can be overcome later in the season. These results support the hypotheses proposed by Tcharntke et al. (2016) for why natural habitats might not enhance control by natural enemies: if the natural habitat is a source of insect pests; if resources provided by the crop are more important than those provided by the natural habitat; and if the attributes of the natural habitat do not lead to increased natural enemy populations in the crop.

Our model is, of course, simply a hypothesis which may or may not be corroborated by field research. We endeavored to select parameter values that were supported by the available literature wherever possible and/or that were weighted in favor of showing a positive effect of natural habitat resources on the simulated predator. The actual values in the field for most of the parameters are simply not known and are likely to vary widely across different pest-predator combinations, and our results are subject to whatever unintended biases may have been introduced by our model parameterization. Nevertheless, our findings do suggest three hypotheses that are worthy of testing in the field. Specifically, we hypothesize that nearby natural habitats are most likely to promote pest control by generalist, omnivorous predators under the following conditions:

- 1) The predator overwinters in natural habitats *and* the crop provides alternate prey to support those predators at initial colonization.
- 2) The crop is host to an alternate prey *and* that alternate prey occurs in, and colonizes the crop from, adjacent natural habitats.

Our most intriguing result is that early-season availability of *any* prey – including a pest insect – may enhance natural control with respect to whole-season pest loads. This leads to our third hypothesis:

- 3) For long-season crops in which early-season pest load has minimal impacts on yield, overwintering of pests in nearby natural habitats may enhance natural control.

The opposite would be expected, however, for short-season crops or those where early-season pest load decreases yield. In this situation, overwintering of pests in nearby natural habitats produces large pest loads not easily overcome by any benefit of that habitat to natural enemies.

Ultimately, our results demonstrate that there is no single answer for whether natural habitat promotes or undermines natural control of pest insects. Rather, natural habitats can do either, or have no impact, depending on the specific attributes of the crop and insect species involved. However, our results also indicate that developing a detailed understanding of the mechanisms operating in agricultural landscapes, and how they respond to differences in landscape composition and insect attributes, may eventually yield reliable predictions regarding when natural habitats will result in lower crop pest loads. This will require focused field research that informs, and is informed by, mechanistically explicit models such as the one presented here.

CRedit authorship contribution statement

Andrew Corbett: Writing – original draft, Validation, Software, Methodology, Formal analysis, Conceptualization. **Jay A. Rosenheim:** Conceptualization, Writing – review & editing, Investigation, Methodology. **Frances Sivakoff:** Conceptualization, Writing – review & editing, Investigation, Methodology.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

A.C. conceived and implemented the simulation model; all authors participated in parameterization of the model; A.C. ran simulations, processed the output, and interpreted the results with input and assistance on statistical analysis from J.A.R and F.S.S.; A.C. led the writing of the manuscript with revisions from J.A.R. and F.S.S; all authors gave final approval for publication.

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Appendices A to C. Supplementary data

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