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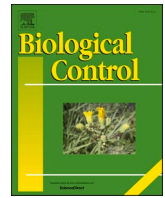
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# Compatibility of biological control and pesticides mediated by arthropod movement behavior and field spatial scale

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## HIGHLIGHTS

- Integrated pest management programs frequently rely on a combination of pesticide use with cultural controls, such as diversifying agroecosystems.
- Sublethal effects of pesticide exposure, such as impacts on natural enemy movement, are not well understood – especially across different habitat spatial scales.
- Using coupled partial differential equations, we explore the effects of pesticide use and reduced predator movement on pest suppression across a gradient of farm spatial scales.
- We find that in small fields, landscape diversification schemes that increase natural enemy abundance can be beneficial, but in mid-sized fields, sublethal pesticide effects on predator mobility have the most detrimental impact on pest control by natural predator communities.
- We also demonstrate that synergistic timing of predator activity and pesticide applications can reduce the need for further pesticide use.

## ABSTRACT

Integrated pest management programs frequently rely on a combination of pesticide use with cultural controls such as diversifying agroecosystems to control pest populations. Selective pesticides can impose both lethal and sublethal effects on natural enemies. However, understanding the compatibility of pesticide use with biological control strategies is critical for pest management success. The population dynamics of natural enemies subjected to the effects of pesticides, especially those that experience sublethal effects, is critical to this understanding. Although lethal effects of pesticides on natural enemies are well-studied, sublethal effects of pesticide exposure such as the impact on natural enemy movement is less well understood – especially across different habitat spatial scales. We present a simulation model using coupled partial differential equations to explore the sublethal effects of pesticide use, via reduced predator movement, on pest suppression across a gradient of farm spatial scales. Using a beetle-aphid model system, we find that in small fields, increased abundance of natural enemies can reduce the need for pesticide sprays. However, in mid-sized fields, we find that impaired predator mobility caused by pesticide sprays has a negative impact on biological control by the natural predator community. We also demonstrate how timing of predator introduction to a field can complement timing of pesticide sprays. We discuss the implications of these results for biological control planning and implementation.

## 1. Introduction

Landscape heterogeneity and spatial scale have long been recognized as important factors in the biological control of pests in agroecosystems (Wiens, 1989; Andow, 1991; Levin, 1992; Bommarco and Banks, 2003; Englund and Hambäck, 2004; Caballero-López et al., 2012; Banks and Gagic, 2016; Martin et al., 2016). In agroecosystems, vegetation diversification within fields or across landscapes is an effective means of facilitating biological control (Heimpel and Jervis, 2005; Gardiner et al., 2009; Schellhorn et al., 2014; Rusch et al., 2016). A common strategy in commercial agriculture is to incorporate natural vegetation into farms by retaining weeds, woody plants, and other non-crop vegetation in the

margins or adjacent to crop areas (Banks and Stark, 2004; Bianchi et al., 2006; Gardiner et al., 2009; Fonseca et al., 2017; Šálek et al., 2018). Vegetation adjacent to or within farmland may harbor predators and parasitoids, as well provision them with nectar and pollen, which may bolster biological control (Banks, 2000; Lee et al., 2006; Banks et al., 2008; Šálek et al., 2018; Gontijo, 2019), although net outcomes may vary (Jonsson et al., 2008; Rusch et al., 2013; Bianchi et al., 2017; Perez-Alvarez et al., 2018). The establishment of non-crop habitat that can shelter beetles in farming areas – or “beetle banks” – is a particularly important element of conservation biological control (MacLeod et al., 2004).

Root’s resource-concentration and natural enemies hypotheses have

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inspired decades of field studies and theory aimed at better understanding the mechanisms underlying the potential for vegetation diversification to enhance biological control of pests; many of these studies have focused on insect and arthropod movement behavior (Root, 1973; Hambäck and Englund, 2005; Finch and Collier, 2012). Because movement behavior is often scale-dependent (Turchin, 1998; Banks and Yasenak, 2003; Grez et al., 2008; Kindlmann et al., 2015), the effectiveness of vegetation diversity schemes aimed at suppressing pests may attenuate at larger scales, making it challenging to rely solely on landscape management prescriptions for most agroecosystems (Bommarco and Banks, 2003; Sálek et al., 2018). Thus, integrated pest management programs often rely critically on understanding the interplay between cultural controls and the use of pesticides.

The use of pesticides in combination with biological control is an important tool in integrated pest management (Torres and Bueno 2018). Pesticides – even those deemed selective – can have both lethal (e.g., Roubos et al., 2014; Hill et al., 2017) and sublethal effects on natural enemy populations; the latter may include lowered reproductive output or impaired movement behavior (Stark and Banks 2003; Stark et al., 2007; Banks and Stark, 2011; Macfadyen et al., 2014; Banks et al., 2017; Amarasekare et al., 2016). The precise nature of the interaction between sublethal pesticide effects and diverse habitats at different spatial scales is still not well understood. Thus both the intensity and frequency of pesticide applications along with land use of plots in and around farm areas are factors that play an important role in determining the efficacy of integrated pest management schemes (Roubos et al., 2014; Nicholson and Williams, 2021). We present a simulation model, using coupled partial differential equations, that explores the interplay of pesticide use and predator movement on pest suppression across a gradient of farm spatial scales. We parameterize the model where possible with values from agroecosystem field and lab studies, and explore predator–prey dynamics throughout a simulated growing season.

## 2. Methods

### 2.1. Model agroecosystem

We simulate herbivore-predator dynamics in an agroecosystem consisting of crop fields of varying sizes, from 5 to 100 ha. In each field, we assume crops are colonized by a fast-growing aphid pest. A community of generalist predators, modeled after carabid beetles, consumes the pest during the growing season. This type of scenario is common in temperate agroecosystems, and has served as a model system for numerous field-based and theoretical explorations of predator–prey interactions in heterogeneous habitats (Root, 1973; Risch et al., 1983; Bommarco and Ekbom, 1996; Banks, 1998, 1999; Banks and Ekbom, 1999; Hannunen, 2005; Grez et al., 2008; Caballero-López et al., 2012). Carabid beetles (Coleoptera: Carabidae) are important predators in agroecosystems (Lövei & Sunderland, 1996). They are primarily ground-dwelling, overwintering in arable lands or nearby vegetation (Firle et al., 1998; Hanson et al., 2017); they often migrate from vegetation adjacent to crop fields as prey densities increase during the growing season. Both adults and larvae forage in crop fields for aphids and other soft-bodied insects throughout the growing season, preying on aphids that fall to the ground or climbing up on plants to chase down prey (Loughridge & Luff, 1983).

We consider scenarios in which the beetle community is (i) naturally occurring, (ii) fostered by conservation biological control strategies (e.g., established beetle banks), or (iii) introduced as in an augmentative biological control scheme. Fields are subject to pesticide sprays when the aphid pest exceeds a set threshold density. To test the interactions among pests, predators, and pesticide sprays, we simulate the fields using a system of coupled differential equations to describe aphid population growth and movement and carabid beetle consumption of aphid prey and movement. Beetle movement includes colonization and migration from adjacent non-crop vegetation (e.g. weeds or woody

plants) as well as foraging behavior, which changes with exposure to pesticides. We run these simulations for a gradient of different field spatial scales.

### 2.2. Mathematical model

We expand the model developed in Banks et al. (2020) to include threshold pesticide sprays and their effects on beetle predators. The resulting model is a system of 2-dimensional partial differential equations, describing dynamics and spatial movement of predators and prey in a rectangular field. At every point in the field, we describe the localized density of the aphid prey ( $A$ ) and two classes of beetle predators ( $B$  and  $B_S$ ). We separate the beetle predators based on pesticide exposure; the group  $B_S$  includes all beetles experiencing the effects of a pesticide spray, whereas the class  $B$  represents beetles unexposed to sprays.

*Prey:* The aphid population grows logistically at rate  $r$ , which incorporates individual birth and death processes, until reaching carrying capacity  $K$ . As the local population of aphids increases, they diffuse at rate  $d_A$ , causing them to spread throughout the field. We also incorporate the production of winged alates under crowded conditions, so that aphids may colonize nearby host plants. Aphid diffusion is enhanced by an additional rate  $d_{AB}(B + B_S)$ , which describes the increased production of winged alates and subsequent dispersal due to disturbance from predators. Aphids are consumed at rate  $\mu$  by beetle predators. We simplify the simulations by ignoring aphid migration to the field during the growing season; instead, we assume some initial distribution of aphids have already migrated to the field at the start of the season, to focus on local dynamics and redistribution.

*Predators:* Over the period we consider, we assume that beetle birth and death processes are negligible. Beetle predators have a baseline diffusion rate  $d_B$ , which describes random movement while they forage. They exhibit directed movement with velocity  $V$ , which incorporates the speed and direction of the beetles' movement. The velocity develops dynamically, incorporating prey-taxis towards aphid pests at rate  $d_{VA}$ . Change in velocity is smoothed by intraguild competition at rate  $d_{VB}$ , describing beetles whose direction is changed by running into other beetles. Exposed beetles follow these same principles, but their diffusion and prey-taxis terms are reduced by the quantity  $1 - \epsilon$ . This corresponds to a percent reduction in movement speeds, describing how exposure to pesticide sprays impedes the beetle's movement while hunting aphids, but does not include any effects of pesticide exposure on intraguild competition rates. We assume that  $\epsilon > 0$ , or that pesticides always cause a reduction in predator mobility, instead of potentially causing increased activity.

Unexposed beetles may be present in the field at the start of a season (e.g. due to farming practices such as no-till or conservation management), and beetles can also migrate into the field within the season in two different ways. Beetles fostered at, or naturally residing near, field margins may walk into the field at the edge at rate  $M_E$ . Beetles introduced by managers through augmentative control uniformly drop into the field interior at rate  $M_I$ . We assume that migrating beetles have not been exposed to the pesticide before arrival to the field, and so there are no migration terms for the exposed beetle population.

The described dynamics for this model are given by the equations:

$$\frac{\partial A}{\partial t} = rA \left(1 - \frac{A}{K}\right) + \nabla \cdot [d_A \nabla A + d_{AB}(B + B_S) \nabla A] - \mu A(B + B_S) \quad \nabla A \cdot n = 0$$

$$\frac{\partial B}{\partial t} = \nabla \cdot d_B \nabla B - \nabla \cdot (VB) + M_I \quad \nabla B \cdot n = M_E$$

$$\frac{\partial B_S}{\partial t} = \nabla \cdot (1 - \epsilon) d_B \nabla B_S - \nabla \cdot (V_S B_S) \quad \nabla B_S \cdot n = 0$$

$$\frac{\partial V}{\partial t} = d_{VA}\nabla A + d_{VB}\Delta(V + V_S) \quad V \cdot n = 0, \frac{\partial V^\perp}{\partial n} = 0$$

$$\frac{\partial V_S}{\partial t} = (1 - \epsilon)d_{VA}\nabla A + d_{VB}\Delta(V + V_S) \quad V_S \cdot n = 0, \frac{\partial V_S^\perp}{\partial n} = 0$$

The boundary conditions (right column) correspond to the assumption that aphids and exposed beetles cannot migrate at field edges, unexposed beetles migrate into the field at rate  $M_E$ , and direction is maintained at field edges (Arditi et al., 2001).

In addition to these dynamics, we implement a threshold pesticide spray. At the end of every day, we check to see whether or not the field’s aphid density exceeds some threshold value  $A_{max}$ . When the threshold is exceeded, we implement a pesticide spray. After a spray, 90 % of aphids die immediately and 90 % of unexposed beetles are exposed to the pesticide. Newly-exposed beetles are selected uniformly across the field and transferred from the population  $B$  into the population  $B_S$ . For tractability, we assume that beetles exposed to the pesticide cannot recover from its effects during the simulation. The directed motion of unexposed beetles is unaffected by the pesticide spray, and we assume that newly-exposed beetles lose their prior direction. Importantly, we neglect all lethal effects of the pesticide on exposed beetles, although some pesticides might drastically reduce the predator community, in order to isolate the impact of sublethal pesticide effects in our system.

### 2.3. Numerical scenarios

We parameterize our model from available literature where possible, as in Banks et al. (2020); values and sources are listed in Table 1. To study the combined effects of pesticide sprays and predator communities, we modify related model parameters. Different predator communities are modeled through changes in edge migration ( $M_E$ ), interior supplements ( $M_I$ ), and initial abundance ( $B_0$ ). Different use of pesticides sprays is modeled through changes in threshold levels ( $A_{max}$ ) and penalties to predator movement ( $\epsilon$ ). All scenarios are conducted in a single field for a 60-day “season,” which starts after the aphid pest’s initial colonization. The scenarios are simulated using finite difference

**Table 1**  
List of model parameters, with biological meaning and values used in our simulations.

	Biological Meaning	Value	Source
$r$	Aphid growth rate	0.21	Mid-level growth rate from Asin and Pons (2001), selected for aphid populations to establish quickly but not at maximal rates
$K$	Aphid carrying capacity	10,000	Selected to greatly exceed $A_{max}$
$\mu$	Consumption of aphids by beetles	1	Selected (with $B_0$ ) for aphid population similar to Curtsdotter et al. (2019)
$d_A$	Aphid diffusion (via winged alates)	$8.87 \times 10^{-6}$	From Bommarco et al. (2007)
$d_{AB}$	Aphid diffusion increased by beetles	$6.81 \times 10^{-6}$	From Weisser et al. (1999)
$d_B$	Beetle diffusion (via random foraging)	$[10^{-3}, 10^{-2}]$	Variability around observation from Allema (2014)
$d_{VA}$	Beetle movement towards aphids	$[10^{-9}, 10^{-7}]$	Variability not to exceed predator speeds from Wallin and Ekbom (1994)
$d_{VB}$	Beetle movement away from competition	$10^{-4}$	Scaled to balance (not outweigh) change in speed caused by $d_{VA}$
$\epsilon$	Penalty to sprayed predator movement	0.9	Assumed efficacy
$A_{max}$	Aphid threshold for pesticide sprays	500	Assumed threshold
$M_E$	Beetle migration at field edge (natural)	$[.1, .9]$	Variability around beetle abundances from Curtsdotter et al. (2019)
$M_I$	Beetle addition to field interior (introduced)	–	Calculated to match average predator abundance from $M_E$

approximation of model equations on Linux 5.4.0–121-generic #137-Ubuntu running MATLAB 9.8.0.1417392 (R2020a), and code for simulations is available upon request.

We first assess the need for threshold pesticide sprays, as determined by the natural or managed predator community. We investigate the effect of different migration rates at the edge of the field (taking  $M_E$  to be 0.1, 0.5, or 0.9), assuming no predators overwinter in the field. This describes the use of pesticide sprays alongside naturally occurring predator communities, which may be sparse or abundant. We also consider different management strategies that affect the timing of predator arrival but maintain the same average predator abundance over the season (changing  $B_0$  to 0.359 for fields with beetle banks or setting  $M_I$  to 322.05 for predators introduced midseason). This connection between predator management choices and model parameters is summarized in Table 2.

In the presence of pesticide sprays, we also test the change in biological control imposed by the predator community. We isolate the effect of pesticide-induced movement penalties by comparing aphid consumption between an entirely-exposed population with a 90 % penalty to movement ( $\epsilon = .9$ ) and an entirely-exposed population with 0 % penalty to movement ( $\epsilon = 0$ ). We make this comparison in the absence of additional pesticide sprays or any unexposed beetles. We then quantify the practical effect of this movement penalty by comparing the need for additional pesticide sprays under these different movement penalties. We also make this comparison over a longer 90-day season and repeat for multiple random initial pest distributions, to assess average timing over many pesticide sprays.

## 3. Results

### 3.1. Effects of biological control on required frequency of pesticide sprays

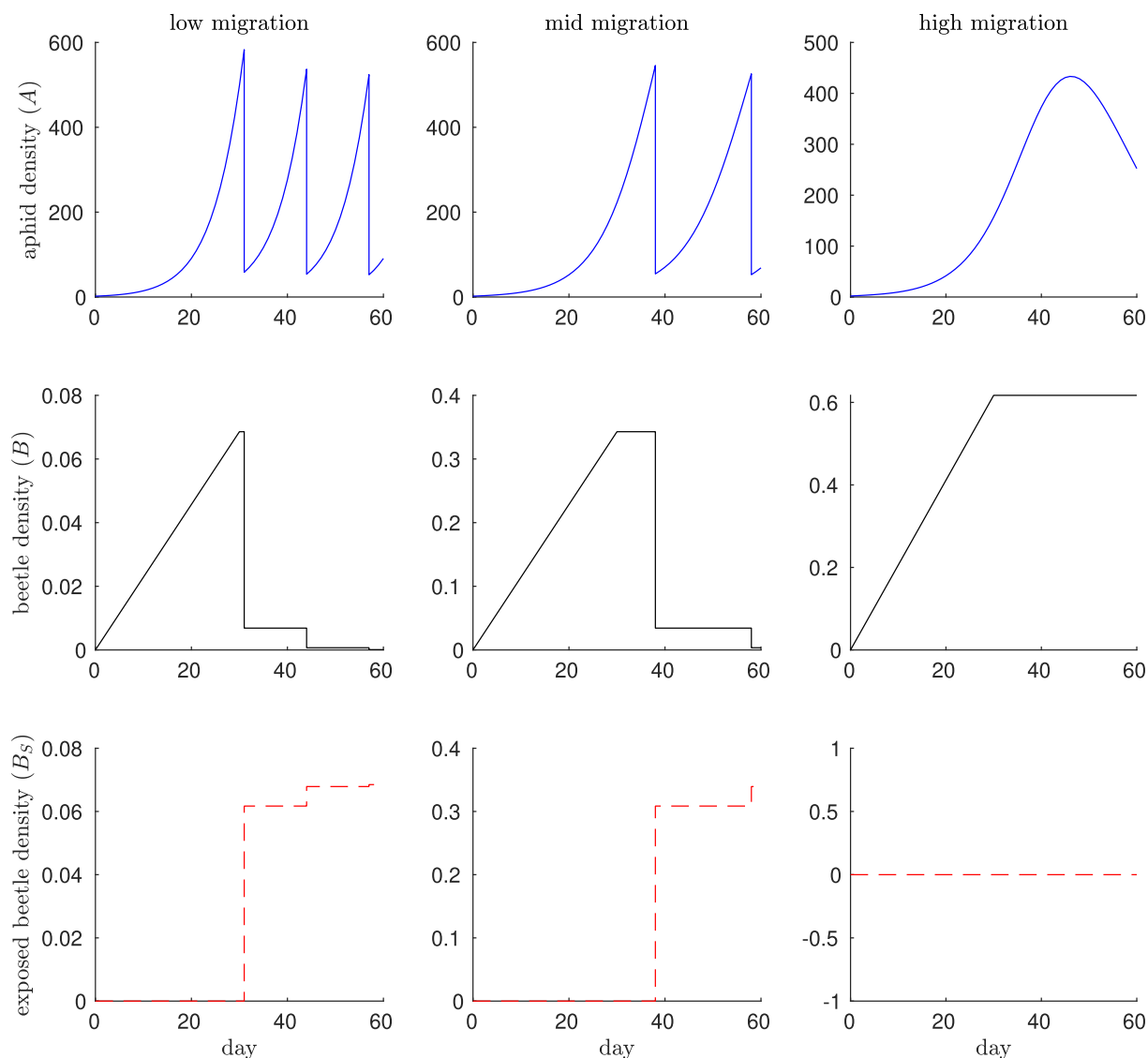
The frequency of pesticide sprays necessary to suppress aphids is mitigated by beetle migration rates; at the scale of 5 ha, fields with low and medium beetle immigration require frequent sprays, whereas at the same scale, fields with high beetle immigration are able to rely solely on biological control for pest suppression (Fig. 1). For 50 ha fields, frequency of required sprays varies with control strategies (Fig. 2). Augmentative control requires the fewest number of sprays, while natural and within-field beetle banks fare only slightly better than fields in which no predators are present.

### 3.2. Effects of pesticide spray on biological control

The relationship between loss of biological control (increasing aphid density) and pesticide-exposed predator movement is linear, except in the very smallest and the very largest fields, where increasing predator diffusion has a saturating effect (Fig. 3). In mid-sized fields (25 ha), pesticide-exposed predator movement has the highest effect on loss of biological control. This translates to an intermediate effect of pesticide sprays on days of biological control lost (decreasing time between

**Table 2**  
Model implementation of assumed predator management strategies. Quantities indicated by (\*) are calculated to match average predator densities from the natural predator community with  $M_E = 0.9$ .

Predator Management	Model implementation
Natural predator community	No predators in field initially Migration at field edge, $M_E$ from 0.1 to 0.9 Migration begins after aphid colonization
Augmentative control	No predators in field initially Added to field interior, $M_I$ at 322.05* Augmentation begins when aphid density is high
Conservation control	Predators initially in field at average density 0.359* Migration at field edge, $M_E$ at 0.225* Migration begins after aphid colonization



**Fig. 1.** Average population densities in a small 5 ha field over a 60-day season for aphids (top row), natural beetle predators (middle row), and exposed beetle predators (bottom row). The three columns correspond to different predator migration rates, ranging from low (left) to high (right).

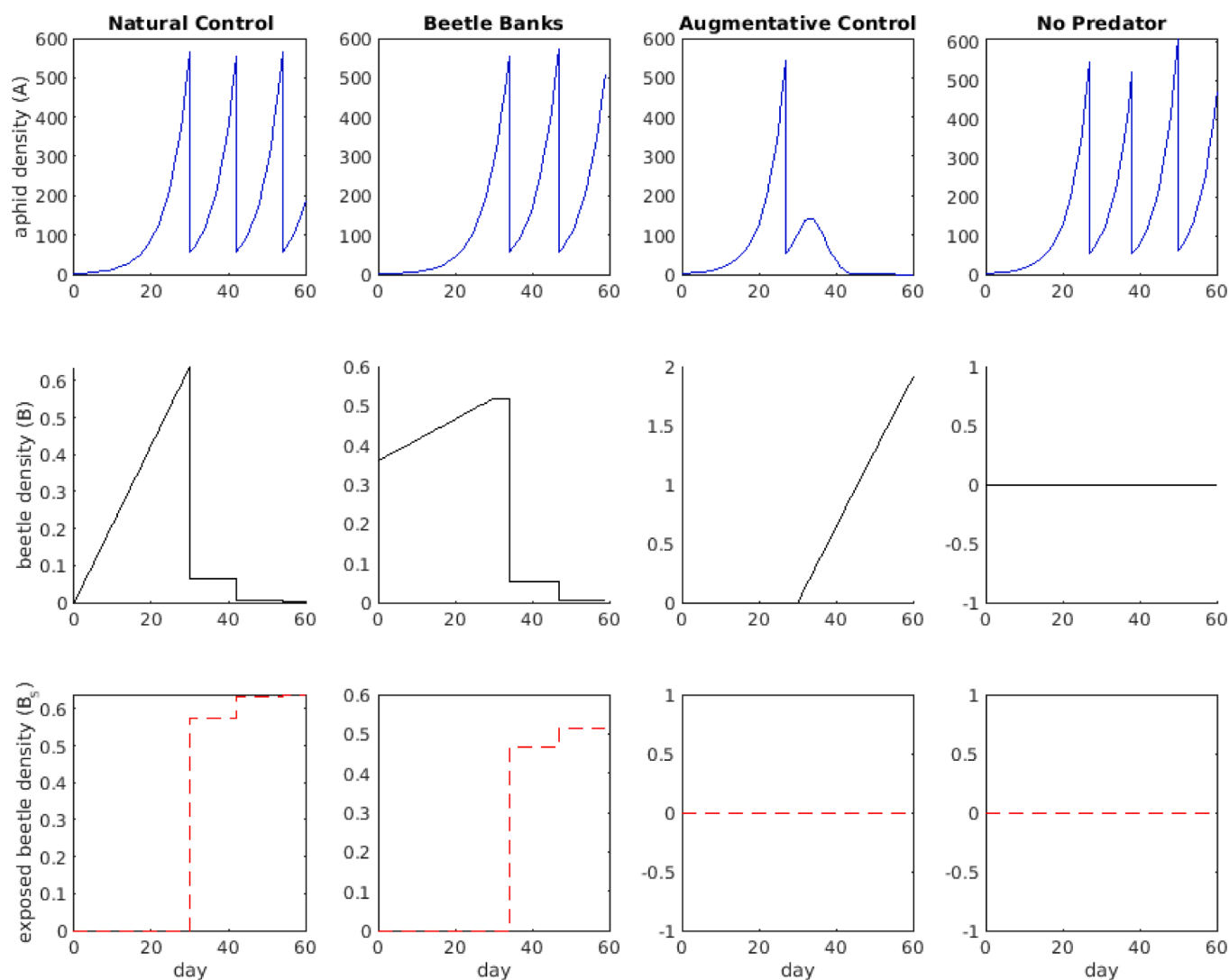
sprays). There is higher compatibility of pesticide sprays and biological control in 5 ha and 100 ha fields than at intermediate spatial scales (Table 3), but a minimal effect on days of biological control lost overall.

#### 4. Discussion

Results of our simulations demonstrate that an abundance of natural beetle predators can reduce the frequency of threshold sprays in small fields (Fig. 1). At small spatial scales, when beetle immigration is low, more pesticide sprays are required, with greater frequency, to maintain pest suppression. When beetle migration rates are high, the naturally-occurring predator population eliminates the need for pesticide sprays to suppress prey. Importantly, these results are only found for small fields; in larger fields, there is not a substantial effect of predator migration rate on pesticide spray regimes (see Supplemental Figures). This difference illustrates the interplay between field spatial scale and predator mobility. In small fields, predators migrating to the field can efficiently cover the interior of the field and control aphids. In contrast, high migration rates at the edge of large fields allow for uncontrolled aphid growth on the field interior, necessitating frequent pesticide sprays. This highlights the potential for management strategies that facilitate natural predator migration, such as weedy field margins (e.g.

Banks and Stark, 2004; Plath et al., 2021), to be effective in reducing the need for frequent pesticide sprays in smaller fields. In a meta-analysis of farm practices in California's Central Valley, Nicholson and Williams (2021) found that pesticide use was reduced on farms with higher crop diversity; in particular, pesticides were used less frequently and with less intensity. This supports our current findings – along with other recent ecological models based on farm data (e.g. Meehan and Gratton, 2016) – that there is high potential for compatibility of pesticide use and biological control in integrated pest management schemes in fields adjacent to diverse vegetation that support large populations of mobile natural enemies, though those benefits wane in larger fields.

When comparing across different biological control strategies, we find that control in the natural predator scenario is no more effective than the scenario in which no predators are present (Fig. 2 a vs d); the same number of sprays is required over the season, although aphid growth is reduced. The use of beetle banks reduces the number of required sprays, but predators are still unable to suppress prey (Fig. 2b). This demonstrates that in large fields, strategies that feature low abundance or inefficient predators, such as natural landscape or beetle banks, that trigger an initial pesticide spray will likely require consistent subsequent sprays. The most effective scenario is for predators introduced through augmentative control, after the first threshold spray. The



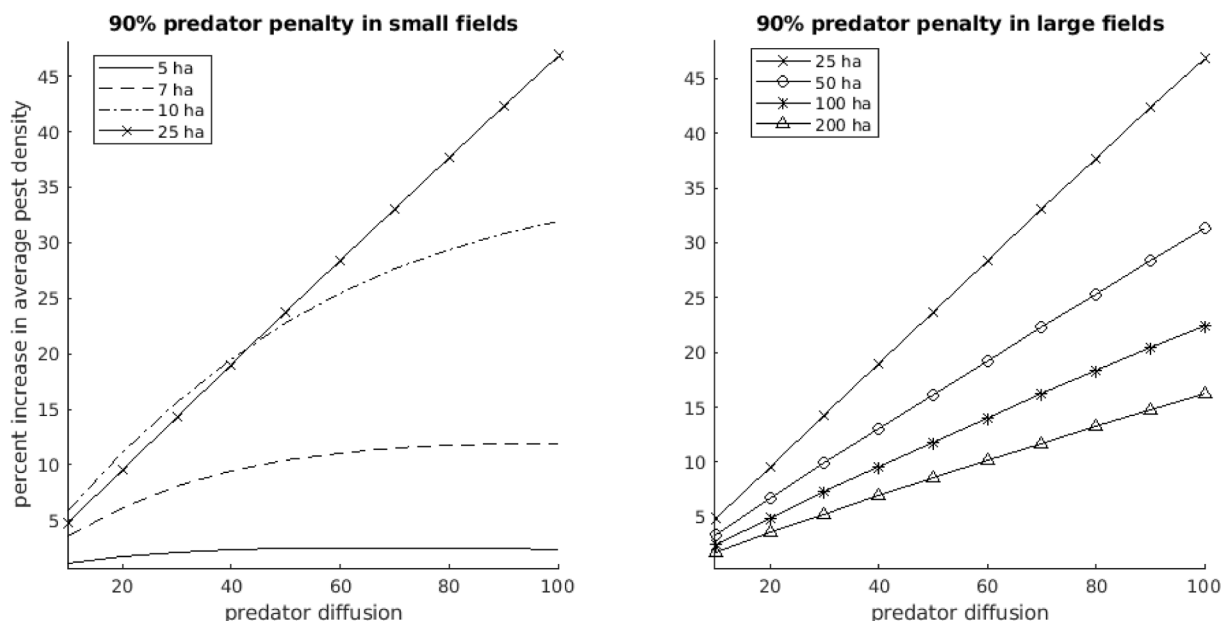
**Fig. 2.** Average population densities in a large 50 ha field over a 60-day season for aphids (top row), natural beetle predators (middle row), and exposed beetle predators (bottom row). The columns correspond to different management strategies, from left to right: natural biological control, within-field beetle banks, augmentative biological control, and a baseline comparison without predators.

combination of decreased aphid abundance due to the initial spray with subsequent rapid introduction of predators results in effective control of the aphid population (Fig. 2c). Taken together, these results demonstrate more generally how the timing of predator introductions can interact synergistically with pesticide sprays to reduce or eliminate the need for further or additional applications.

These results further emphasize the role that spatial scale plays in mediating the compatibility of conservation biological control and pesticide use; the greatest difference among control strategies occurs in intermediate-sized fields (25 ha), in which pesticide penalties imposed on predator movement necessitate sprays two days earlier than strategies without movement penalties (Table 2). However, two days is a relatively small difference on the temporal scale of the simulation, which is run across 90 days, so the total number of required sprays is unchanged. However, these small differences may be important for scenarios in which growers are managing pests that can transmit viruses even while at lower densities (Perring et al., 1999; Harris and Marmorosch, 2013). In cases where multiple pesticide sprays are required to control the pest population, the predator community does not significantly affect the aphid abundance. Importantly, these results are specific to our model for aphid-beetle dynamics, which necessarily includes simplifying assumptions. In addition to sublethal effects on

mobility, natural predator communities often suffer increased direct mortality from pesticide sprays (Roubos et al., 2014; Hill et al., 2017), which further decreases the compatibility between natural predator communities and pesticide sprays. Control may be further complicated by predator recovery from pesticide effects, changes to beetle competition with pesticide exposure, or additional species interactions – especially among vector and non-vector insects in the field (Chisholm et al., 2019; Crowder et al., 2019). Furthermore, aphid prey themselves may respond to an interaction between vegetation diversity and pesticide exposure in the field (Banks and Stark, 2004), creating another layer of complexity. Finally, incorporating carabid beetle birth and death processes alongside an explicit model of both below- and above-ground dynamics (corresponding to larval and adult activity, respectively) would enhance our understanding of how strategies such as no-till agriculture affect predator-pesticide compatibility (Jowett et al., 2020). Overall, it is clear that further field and theoretical studies exploring multi-trophic interactions are needed.

Natural or anthropogenic disruption or decoupling of predator-prey interaction has been shown to negatively affect the ability of natural enemies to suppress prey (Desneux and O’Neil, 2008; Schmitz and Barton, 2014). In addition to direct, lethal effects, pesticide exposure can cause sublethal effects to arthropods that affect their population



**Fig. 3.** The percent increase in average aphid density when predatory beetles incur a 90 % movement penalty, compared to beetles without any movement penalty. The average is calculated across a 60 day season for a range of beetle mobilities (diffusion constant  $d_c$ ) and differently sized fields. For readability, the left subplot shows results for smaller fields and the right subplot shows results for larger fields. Results for a 25 ha field are shown in both subplots, to facilitate comparison.

**Table 3**

The average and maximum days of pest control lost (decrease in number of days between pesticide sprays) when predators suffer a 90 % movement penalty, compared to beetles without movement penalties over a 90 day season. The average is reported from 25 replicates using random initial aphid distributions.

Farm Size	Number of sprays	Average number of days between sprays (with penalty)	Average number of days between sprays (without penalty)	Maximum number of days lost between sprays
5 ha	2	21.92	22	0.08
10 ha	3	19.78	20.5	1.44
25 ha	4	14.33	15	2.00
50 ha	5	12.75	13.25	2.00
100 ha	5	12	12.25	1.00

dynamics; in some cases, predators may find pests exposed to pesticides less appealing as prey (Plata-Rueda et al., 2019; Silva et al., 2020). Such disruptions to the foraging behavior of predators can disrupt predator-prey interactions sufficiently to facilitate pest outbreaks. The current results suggest that the nuances of predator behavioral responses to pesticide exposure, coupled with field spatial scale, are important details when determining population outcomes. In our simulations, beetles with higher baseline levels of mobility exhibit less prey suppression when movement ability is reduced (Fig. 3). This can be attributed to the initial efficiency of the predators prior to the imposed mobility reduction; predators with lower mobility already cover the field slowly, so an additional penalty has minimal effect. The largest loss of control occurs in fields at intermediate spatial scales (25 ha); for smaller fields, the minimum mobility required to cover the field is lower and so reductions to mobility have less of an effect on predators overall. In contrast, beetles with all levels of mobility have an increasingly difficult time controlling prey in larger fields (Fig. 3b) – but this also means reductions to mobility can have less of an effect on pest control overall. Additionally, these results neglect the potential for predator stimulation after pesticide exposure (Cutler et al., 2022; Guedes et al., 2022), which could further affect the efficacy of control at different spatial scales. Taken together, our results suggest there is a marked need for further research into the interaction between predator mobility and pesticide exposure in

assessing the efficacy of biological control in integrated pest management systems.

**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.

**Data availability**

Data will be made available on request.

**Appendix A. Supplementary data**

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocontrol.2022.105125>.

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