



# Aggregating fields of annual crops to form larger-scale monocultures can suppress dispersal-limited herbivores

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## Abstract

An important part of landscape ecology is determining how the arrangement (aggregation or fragmentation) of patches in space influences the population dynamics of foraging organisms. One hypothesis in agricultural ecology is that fine-grain spatial heterogeneity in cropping (many small agricultural fields) should provide better pest control than coarse-grain heterogeneity (few large agricultural fields); this hypothesis has been proposed as an explanation for the increased pest abundance associated with agricultural intensification. However, empirical studies have found mixed support for this hypothesis, and some, surprisingly, demonstrate a strong *decrease* in pest abundance with increased crop aggregation. We developed a spatially explicit simulation model of pest movement across an agricultural landscape to uncover basic processes that could reduce pest abundance in landscapes with fewer, larger fields. This model focuses on herbivore movement and does not include predation effects or other biological interactions. We found that field aggregation in the model led to severely reduced pest densities and further discovered that this relationship was due to an increased distance between fields and a decreased “target area” in more aggregated landscapes. The features that create a negative relationship between aggregation and pest densities rely on crop rotation and limited dispersal capabilities of the pests. These findings help to explain seemingly counter-intuitive empirical studies and provide an expectation for when field aggregation may reduce pest populations in agro-ecosystems.

**Keywords** Agroecology · Simulation model · Dispersal · Land use · Habitat fragmentation · Agricultural intensification

## Introduction

Understanding how the spatial arrangement of patches impacts the fitness of foraging organisms is important for predicting how changes in landscapes may drive changes in population dynamics. Ecologists have hypothesized that herbivore

population abundance should increase with the size of their host plant patches (Bowman et al. 2002). In the context of agricultural ecology, this suggests that herbivore pest abundance should be greater in landscapes with fewer, larger fields of host crops (more aggregated) than in landscapes with more, smaller fields of host crops (more fragmented) (Altieri and Letourneau 1982; Altieri 2002). Several well-characterized mechanisms suggest a positive relationship between field aggregation and pest densities, although some may be incorrectly applied (see Bowman et al. 2002 for a thorough exploration of these hypotheses and how they tie to expectations of pest density).

Despite the apparent theoretical support for more aggregated landscapes having higher pest densities, some empirical studies have found the opposite relationship. One striking example of this negative relationship between aggregation and pest abundance has been found in studies of the Andean potato weevil (*Premnotrypes* spp.), which is currently the most important pest for Andean potato farmers in Bolivia (Parsa 2010). Until the late 1900s, communities of farmers in the Andes aggregated all of their potato fields into a single large (~1 km square) sector, forming a monoculture (Parsa 2010).

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Potatoes and other crops were grown on communal land in a multiyear rotation. When changes to the social structure led each farmer to plant potatoes on his or her own small farm, the Andean potato weevil went from rare to devastating. Another study in the same system found that even at the current spatial scale of individual farmers with their own small fields, aggregation of potato fields can still lead to substantially reduced pests (Parsa et al. 2011). Thus, for the Andean potato weevil, crop aggregation appears to be a major factor in determining population size. The potato weevil system is far from the only empirical study that contradicts the expected positive relationship between field aggregation and herbivore abundance. Studies have found that the relationship between field aggregation and herbivore population densities can be positive, neutral, or negative, as found in reviews and meta-analyses of natural systems (Bender et al. 1998; Bowers and Matter 1997; Bowman et al. 2002), agricultural systems (Bommarco and Banks 2003; Bianchi et al. 2006; Poveda et al. 2008), and studies of habitat fragmentation (Debinski and Holt 2000). In addition, two recent theoretical studies found that the relationship between patch size and herbivore abundance could be positive, negative, or absent (Hambäck and Englund 2005; Segoli and Rosenheim 2012), and an additional theoretical study found a negative relationship between patch size and herbivore abundance (Vinatier et al. 2012).

Our study was initially motivated by the apparent contradiction between theoretical expectations and the findings of Parsa et al. (Parsa 2010, Parsa et al. 2011). However, we developed our model to ask a broader question: what mechanisms cause a negative relationship between herbivore abundance and patch aggregation in systems like the Andean potato weevil, in which patches are frequently destroyed and created (e.g., crop rotation), herbivore dispersal is limited relative to the distance between patches, and natural predators have little to no role in limiting herbivore abundance (Kaya et al. 2009). Throughout this study, we will use the definition of aggregation used in Parsa et al. (Parsa 2010, Parsa et al. 2011): the arrangement of crop fields to be adjacent to one another such that there are fewer, larger fields but the total area in host crop is the same. This means that aggregation simultaneously increases patch size and increases patch isolation.

Several theoretical studies have described mechanisms that rely on other attributes of natural systems. Segoli and Rosenheim (2012) illustrate how differences in dispersal capabilities between pests and natural enemies can determine whether pests are favored by small or large crop fields in the presence of natural enemies. While important, this mechanism depends on an effective predator, which in some cases (including the Andean potato weevil) may not be present. Hambäck and Englund (2005) describe how differences between how pests enter crop fields and how they leave can determine

whether or not pests tend to accumulate in small or large crop fields, regardless of the response by natural enemies or local population dynamics. While valuable, Hambäck and Englund (2005) focus on the dynamics within a single, static patch and do not address the landscape-scale mechanisms by which field aggregation can impact herbivore populations.

In their spatially explicit simulation study of pest management solutions for the banana weevil, *Cosmopolites sordidus*, Vinatier et al. (2012) found that increasing levels of field aggregation led to decreased weevil abundance. This is consistent with the empirical studies of the Andean potato weevil (Parsa 2010, Parsa et al. 2011); given that both pests are weakly dispersing flightless weevils, it is reassuring that the same pattern holds. We will build on the results presented by Vinatier et al. (2012) by probing the mechanisms underlying the effect of field aggregation on herbivore densities and by examining different modes of herbivore search for patches of host plants.

Here, we develop a spatially explicit simulation model of herbivore movement across an agricultural landscape to determine how colonization challenges for herbivores could underlie a negative relationship between field size and herbivore abundance (i.e., lower pest abundance when crop fields are aggregated). Our goal was to develop a minimal model that included only features linked to the challenges herbivores face when colonizing new fields after crop rotation. These features include crop rotation, pests overwintering in the soil of their natal fields, and limited dispersal capabilities.

Our simulation does not include predators. The Andean potato weevil system lacks an effective predator, and ignoring higher trophic levels allows us to determine how a negative relationship between field aggregation and pest abundance could arise independently of predators. For similar reasons, our simulation does not include alternate host plants; while they are important in some systems, we wanted the simplest model that captured the dynamics of colonization, crop rotation, and dispersal limitation. Similarly, for simplicity, our simulation does not include density dependence; in an agricultural system, exploitative competition among pests is only relevant when pest abundances far exceed a tolerable level. However, adding density dependence strengthened instead of weakened the negative effect of aggregation on pest density (see supplements). The assumptions of no predation, no alternate hosts, and no density dependence are consistent with the model presented in Vinatier et al. (2012).

We focus on how herbivore movement rules control the rates of successful immigration to new crop plantings. We hold the total area planted in the host crop constant and assume that other agricultural practices are the same across all levels of aggregation; thus, we uncouple field aggregation from the other facets of agricultural intensification. Throughout this paper, when we discuss landscapes with a few large crop fields or landscapes with many small crop

fields, we are assuming that the same quantity of land is planted to the crop in either landscape.

To uncover the specific mechanisms underlying a negative relationship between pest density and field aggregation, we asked the following two questions: first, how does the aggregation of crop fields influence the distance that an herbivore must traverse to colonize a new field? Second, how does the aggregation of crop fields influence the probability of herbivores encountering a new field given that it is within their dispersal distance? For an herbivore with limited dispersal range and a potentially limited ability to orient in the direction of a crop field, the answers to these questions shape the likelihood of successful crop colonization.

## Materials and methods

### Model overview

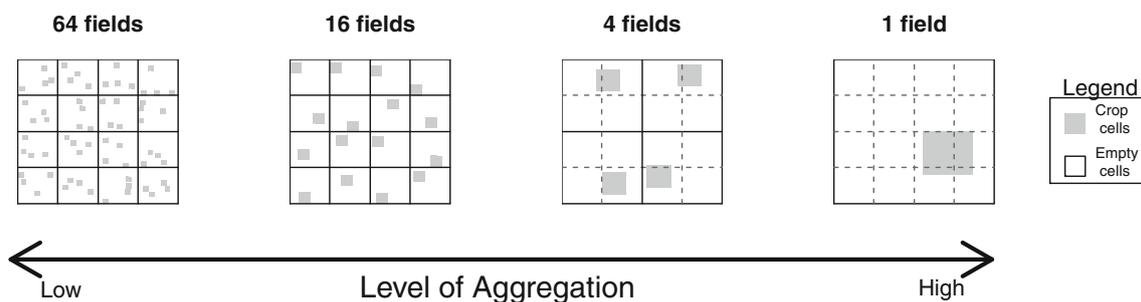
We constructed a spatially explicit simulation model in which a landscape of 16 small farms was represented as a square grid of  $104 \times 104$  cells (each farm consisting of  $26 \times 26$  cells). The landscape contained two components—crop fields (only for the host crop of the herbivore) and matrix (anything aside from the host crop). Within each of these landscapes, we simulated three generations of herbivore population dynamics. Different simulations used different rules for herbivore movement. This allowed us to determine how herbivore movement shaped the relationship between pest densities and field aggregation, what mechanisms caused that relationship, and in what biological systems we might expect to find the same relationship. Our model assumes univoltine herbivores, but simulations showed that the results were not qualitatively influenced by multivoltinism (data not shown). The model was implemented in MATLAB version 7.11.0 (MathWorks, Inc., Natick, MA, USA), and the source files can be found in an online supplement to this article. The parameterization of the landscapes in our model—the number and size of farms, percent land in host crop, and herbivore dispersal distance—was selected to approximately match those from the case

study of Parsa et al (2011) when cells are interpreted as being 5 m square (leading to farms of 130 m on a side, and four fields each  $20 \times 20$  m). However, because the simulation used general rules for movement and dispersal, the landscape scale and dispersal distance are only relevant in relation to one another, and thus the simulations also show what would happen in systems with larger farms and greater dispersal distances. As our interest is in understanding the effects of aggregation, the total number of host crop cells is kept the same in all treatments ( $1024$  cells or 9.5% of the landscape).

We simulated four aggregation scenarios (Fig. 1):

- “64 fields”: Each of the 16 farms had 4 crop fields that were each  $4 \times 4$  cells. This represented the averages found for Bolivian farms in Parsa (2010) ( $20 \times 20$  m fields).
- “16 fields”: Each of the 16 farms had a single crop field that was  $8 \times 8$  cells. This represented each Bolivian farmer planting his own crop fields adjacent to one another to form a  $40 \times 40$  m field.
- “4 fields”: The landscape was broken into four squares, each of which contained four farms. Each of those squares has a single field of  $16 \times 16$  cells. This represented groups of four Bolivian farmers cooperating to aggregate all of their crops into a single  $80 \times 80$ -m field but could represent aggregation within a farm for larger farms.
- “1 field”: The landscape had a single field of  $32 \times 32$  cells. This represented a group of 16 Bolivian farmers cooperating to aggregate all of their crops into a single  $160 \times 160$ -m field but could represent aggregation within a farm for larger farms.

Within each simulation, the same aggregation treatment was applied to the landscape for all years. At the start of the simulation, ten herbivores were placed in each crop cell. This represented herbivores that overwintered in these locations before the simulation began; because there was no density dependence, the initial density of herbivores is irrelevant,



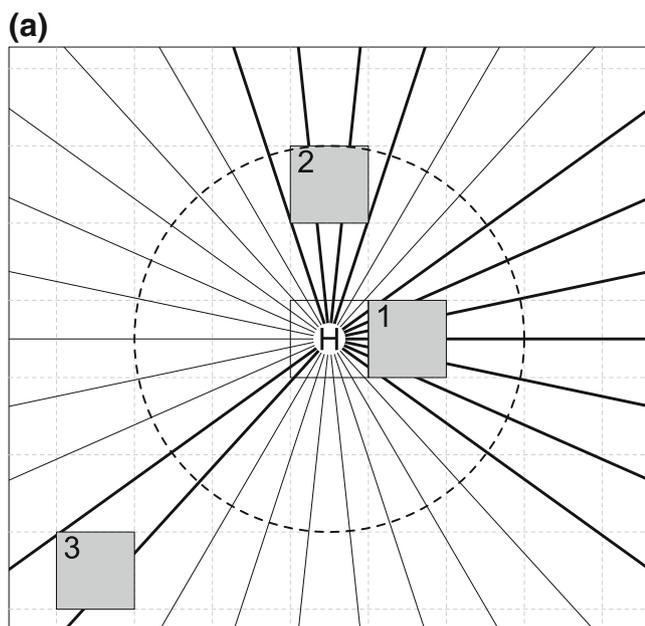
**Fig. 1** Examples of landscape configurations at all four levels of aggregation. Gray space represents host crop fields; white space represents matrix. In the 64 and 16 field treatments, each farm has its own fields; farms are separated by solid black lines. In the four-field

treatment, groups of four farms are aggregating their fields—dotted lines separate farms that are sharing fields; solid lines separate farms that are not. In the 1 field treatment, all 16 farms are aggregating their fields into one contiguous cropped area, so all farms are separated by dotted lines

and ten was chosen for convenience. The simulation then executed the following steps:

1. The previous year's crop fields were removed, herbivores allowed to "overwinter" by remaining in their current location, and crop fields were rotated (placed in new locations as described below). In this way, the landscape was changed but herbivore locations remained the same.
2. Herbivores moved from the cells in which they overwintered, following one of two sets of movement rules (see below); within a simulation, the same rule was used for all herbivores for all years. Herbivores that stopped on crop cells survived to the next step; herbivores that stopped on matrix cells died.
3. Herbivores reproduced and died, leaving four herbivore young that survived to adulthood. This number was selected to ensure that populations had the potential to grow under herbivore-friendly scenarios but would not invariably explode; sensitivity analysis using different reproduction rates gave the same qualitative patterns. These resulting offspring were assumed to overwinter in their natal cell.
4. The year ended and the simulation began again from step 1.

Each simulation was run for 3 years, and we used data from the final year for statistical comparisons among the different scenarios. Sensitivity analysis using 15-year simulations showed that population levels in year 3 were predictive of longer-term population dynamics.



**Fig. 2** Examples of the movement rules using a smaller and more simplified landscape. The central "H" cell is an overwintering cell containing herbivores; the gray cells contain crops; the dotted circle represents the hypothetical maximum dispersal distance for limited dispersal scenario. **a** Example of undirected movement. The rays

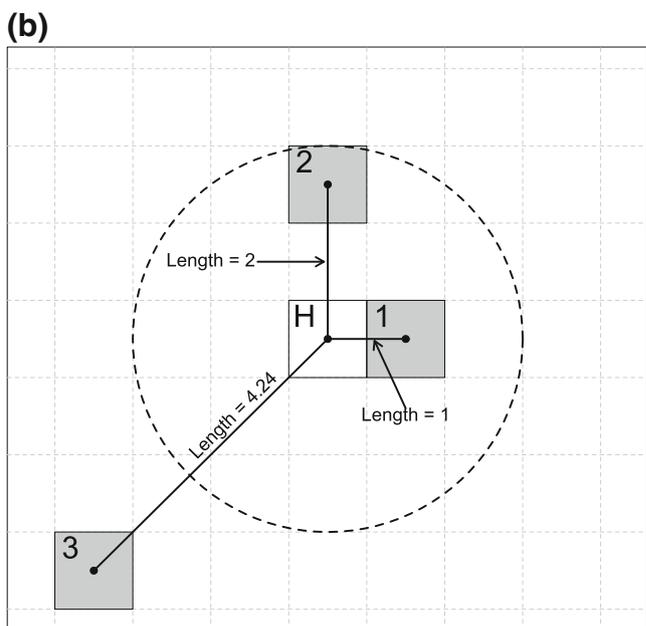
## Crop rotation

To represent crop rotation, each year the landscape contained crop fields in new locations. The location of each crop field was chosen at random from all options that (a) placed the crop field entirely within the original farm (or collection of farms, in the case of the one field and four field scenarios where farms were collectively aggregating their fields) and (b) avoided having any cell of the current year's field overlap with a cell from the last year's field. This second rule, which is an implementation of crop rotation, ensured that after overwintering, the herbivores had to travel at least a short distance to the nearest crop field (which is one of the motivations behind crop rotation).

This means that each simulation has a sequence of 4 years of landscapes, an initial landscape that represents "year minus one" and was used to place the herbivores for the initialization of the model, and then 3 years of landscapes in which each had crop field locations that did not overlap with the previous year's.

## Movement rules

Two contrasting dispersal behaviors were modeled. Under "undirected dispersal," herbivores were assumed to be ignorant of the content of all cells except the one they occupied, and thus herbivores dispersed in all directions in search of host plants (Fig. 2a), using a linear search as in Englund and Hambäck (2007). To implement this rule, we drew a set of



radiating outwards are used for the undirected movement rule and for calculating the  $p_c$ . In actual simulations, 1860 rays were used, and the limited dispersal distance was 20 cell widths. **b** Example of directed movement

1860 rays radiating out from each cell. For each ray, we composed an ordered list of the crop cells that intersected that ray within the dispersal distance of the herbivores, and 1/1860 of the herbivores in the host cell were assigned to the first three crop cells in each of those lists, as described below. Note that our model did not round to the nearest integer number of herbivores and instead tracked fractions of herbivores. Under “directed dispersal,” herbivores were assumed to be aware of all crop cells in the landscape (perfect information, as in Milinski and Parker 1991) and were sent to the nearest crop cells (Fig. 2b). In both cases, the edges of the landscape were absorbing—with undirected dispersal, herbivores that left the landscape died; with directed dispersal, there were no crop cells beyond the edge of the landscape for herbivores to find using directed dispersal. This was necessary given our unlimited dispersal distance scenarios below.

Dispersal was treated as a single event, but some fractions of herbivores rejected the first or second crop cells that their movement rules provided. For both dispersal behaviors, 70% of herbivores accepted the first crop cell encountered and settled there, 20% continued to follow their original movement rules until they encountered the next crop cell, and the final 10% only settled when reaching their third crop cell. Under “directed dispersal,” for each overwintering cell, a list of all crop cells was made and sorted from near to far. Seventy percent of the herbivores from a given overwintering cell moved to first cell in that list, 20% moved to the second cell, and 10% moved the third cell. If any of those cells was beyond the dispersal distance of the herbivores, then the herbivores that would have traveled to those cells died. If two or more crop cells were equidistant, they each received equal proportions of the allotted herbivores. These values were selected to produce spatial patterns similar to those in the Andean potato weevil system (S. Parsa, pers. comm.). However, changing how many crop cells herbivores rejected did not qualitatively change the results of the model for either movement rule. This was tested with 100% accepting the first crop cell they encountered, 85 and 15% accepting the first and second crop cell, and 40, 20, 10, 10, 10, 5, and 5% accepting the first through seventh crop cells.

Within a simulation, all herbivores used the same dispersal rule. For each field placement and each dispersal distance, we ran the simulation for directed dispersal and then again for undirected dispersal.

## Dispersal distance

To determine what role dispersal limitation plays in the relationship between herbivore abundance and field aggregation, we looked at two dispersal distances for each of the two movement rules. Under “limited dispersal,” herbivores could only travel a distance of 20 cell widths. When cells represent a distance of 5 m, this corresponds to a dispersal distance of

100 m. A previous study of the Andean potato weevil found dispersal up to 300 m; we used 100 m as a typical dispersal distance assuming that the dispersal kernel would be leptokurtic (Chavez 1997). For the directed movement rule, this meant that herbivores traveled to the nearest three cells containing crops that were within 20 cells of their overwintering cell. In the undirected movement rule, this meant that herbivores traveled outwards from their overwintering cell in all directions until they encountered one, two, or three crop cells or reached a distance of 20 cell lengths.

Under “unlimited dispersal,” herbivores could travel across the entire simulated landscape. In directed movement, this meant that herbivores traveled to the three nearest cells containing crops, regardless of distance. In undirected movement, this meant that herbivores traveled outwards from their overwintering cell in all directions until they encountered one, two, or three crop cells or reached the edge of the landscape and died.

## Movement example

The movement rules and dispersal distance rules can best be understood by examining two simple examples (Fig. 2a, b). A central cell (“H”) contained crops in the previous year and now contains herbivores that overwintered there, while several nearby cells contain crops.

For the undirected movement rule (Fig. 2a), a series of rays is drawn radiating outwards from the focal cell, and herbivores in the cell are distributed evenly to each ray (allowing fractions). All cells along each ray are checked: 70% of herbivores assigned to that ray are placed in the first crop cell encountered, 20% in the second, and 10% in the third. Any herbivores that are not placed in a crop cell (e.g., because that ray intersected fewer than three crop cells) die. In the limited dispersal scenario, only cells within the maximum dispersal distance of the overwintering cell (here 2.5 cell widths, for visual clarity) are checked. Here there are 30 rays, of which seven, four, and two intersect crop cells 1, 2, and 3, respectively. So in the landscape in Fig. 2a, of the herbivores in the overwintering cell H, 7/30 are placed in cell 1, and 4/30 are placed in cell 2. In the limited dispersal scenario, all other herbivores die, because cell 3 is beyond their maximum dispersal distance (Fig. 2b). In the unlimited dispersal scenario, 2/30 of the herbivores in the overwintering cell are placed in cell 3, and all the remaining herbivores would die. In actual simulations, 1860 rays were used, and the limited dispersal distance was 20 cell widths. The process described here was repeated with each cell containing overwintering herbivores.

For the directed movement rule, distances are calculated from the overwintering cell to all crop cells. Seventy percent of the herbivores in the overwintering cell are placed in the nearest crop cell (cell 1), 20% in the next nearest (cell 2), and 10% in the third nearest (cell 3). In the limited dispersal

scenario, only cells within the dispersal distance (here 2.5 cell widths, for visual clarity) are considered. Any herbivores that are not placed in a cell (because fewer than three crop cells were within the dispersal distance) die; in this case, 10% of the original herbivores (those that rejected cells 1 and 2) die.

### Simulation execution and analysis

We carried out our simulations as a  $4 \times 2 \times 2$  factorial design, crossing aggregation level (64 fields, 16 fields, 4 fields, 1 field), movement type (undirected versus directed), and dispersal distances (limited versus unlimited). For each combination of treatments, we carried out 30 3-year-long simulations. For any given aggregation treatment, the same set of 30 randomly generated 4-year landscapes was used for all movement rules and dispersal distances. This allowed better comparisons between dispersal distances and movement rules in the same level of aggregation, as there were no stochastic differences between them.

To understand the interplay between field aggregation level and the distance that herbivores might need to travel, we measured the minimum dispersal distance from each cell that had contained crops the previous year (and thus could be an overwintering site) to the nearest cell containing crops in the present year. These minimum dispersal distances were calculated for each year of 125 randomly generated 3-year landscapes for each level of aggregation.

To understand the effect of field aggregation on the ability of herbivores to find crop fields, we devised a measure to represent the effect of field aggregation on the “target size” of crops for herbivores using the undirected dispersal rule. This measure, the radial encounter probability ( $p_e$ ), is the probability that a herbivore starting from a given cell and heading outwards in a straight line in a random direction would encounter a crop cell before reaching the edge of the landscape. This is related to the diameter-dependent immigration described in Englund and Hambäck (2007)—however,  $p_e$  is the result of the size of patches, the distances to patches (which combine to give the angle subtended by a particular patch) and the number of patches; it is a single index that encapsulates how hard it is for a particular randomly searching insect to find suitable food.

We measured  $p_e$  from every potential overwintering site for each year of 125 generated 4-year landscapes for each aggregation level.  $p_e$  for a given overwintering cell was measured by creating 1860 rays radiating out of the cell over a uniform, circular distribution and calculating the proportion of those rays that collided with at least one of the new crop cells before striking the edge of the landscape. A simple example of this using only 30 rays and a smaller landscape is seen in Fig. 2a: here 13 of the 30 rays intersect cells containing crops, so  $p_e \approx 0.43$ . To compare different treatment combinations, we emphasize effect sizes instead of  $p$ -values.  $P$ -values are very

dependent on sample size, and in simulation studies, sample size can be increased arbitrarily until the desired  $p$ -value is obtained; for this reason, it is important to use effect size instead (White et al. 2014).

## Results

### Influence of field aggregation on herbivore densities

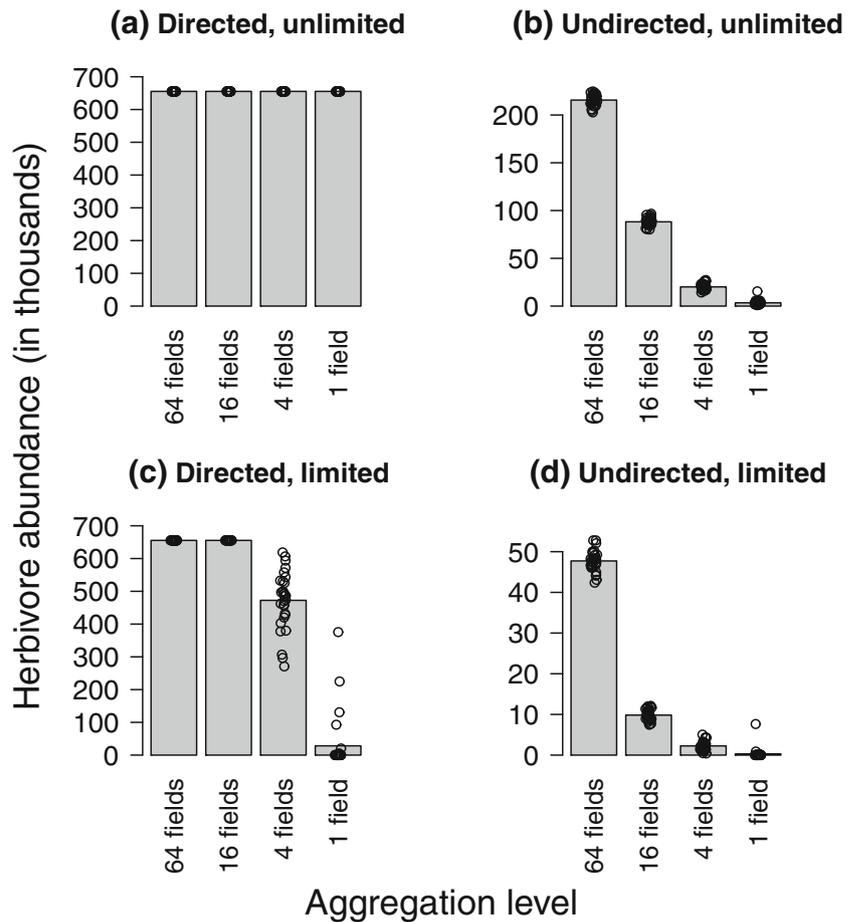
Our simulations suggest that the effect of crop field aggregation on herbivore population densities depends critically on the movement behavior of the herbivore (Fig. 3). As a baseline, we first examined the case in which herbivores were given perfect knowledge of crop cell locations and an unlimited dispersal distance (Fig. 3a). In this case, all herbivores traveled to the nearest crop field, regardless of distance, and mean herbivore abundance was unaffected by the level of field aggregation. In contrast, when herbivores were given an unlimited dispersal distance, but had no knowledge of crop cell locations and radiated out uniformly from their overwintering locations, mean herbivore abundance decreased as fields were aggregated into a smaller number of larger units (Fig. 3b). When herbivores had perfect knowledge of crop cell locations but were constrained to a maximum dispersal distance of 20 cells, the aggregation of fields again caused a strong decrease of herbivore densities (Fig. 3c). Finally, aggregation of fields caused the strongest decreases in herbivore densities when dispersing herbivores had no knowledge of crop cell location and were limited to a dispersal distance of 20 cells (Fig. 3d). Thus, the effect of crop field aggregation was observed only when herbivores faced constraints on their abilities to locate and reach new fields: as we added more constraints, either informational (ignorance of the location of crop fields) or physiological (short maximum dispersal distance), field aggregation imposed stronger limits to herbivore population growth.

### Mechanisms underlying difficulties of colonizing aggregated landscapes

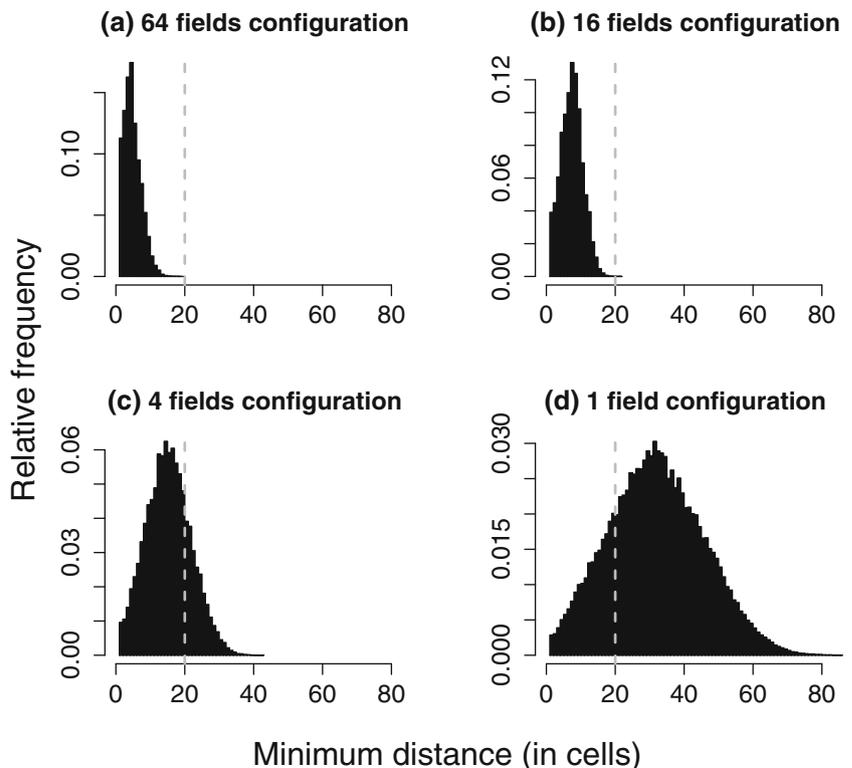
We used the simulation model to explore the mechanisms underlying the effect of increasing crop field aggregation on herbivore colonization success.

First, the minimum distances from the crop cells of one year and the crop cells of the next became substantially greater with increasing field aggregation (Fig. 4). As a result, a greater proportion of dispersal-limited herbivores in the landscapes with higher levels of crop field aggregation would be expected to die without being able to reach a host plant, as distances to crop fields exceeded their maximum dispersal capabilities (23.3% for the four-field configuration; 80.9% for the one-field configuration). It is this effect that makes limited

**Fig. 3** Herbivore population size after 3 years of simulated movement and reproduction as a function of field aggregation level. **a** Directed herbivore movement with unlimited dispersal distance capability. **b** Undirected herbivore movement with unlimited dispersal distance capability. **c** Directed herbivore movement with maximum dispersal of 20 cells. **d** Undirected herbivore movement with maximum dispersal of 20 cells. Note the different scales on the y-axes. Bars represent average weevil abundance across 30 simulations, and open circles represents herbivore abundance for each simulation



**Fig. 4** Distribution of minimum distances an herbivore would have to travel from its overwintering site (prior year's crop field) to colonize a new (current year) crop field, calculated for all crop cells for 5 years in 125 generated landscapes. Dotted vertical lines represent maximum herbivore dispersal distance (20 cells). Panels show distributions for landscapes from lowest level of aggregation (a, 64 fields in the landscape) to highest (d, a single field in the landscape). For low levels of field aggregation (**a, b**), all and nearly (respectively) all potential overwintering sites were within 100 m of the following year's host crop cells. For high levels of field aggregation (**c, d**), a notable proportion and a majority (respectively) of potential overwintering sites were more than 100 meters from the following year's host crop cells



dispersal an important modulator of the effect of field aggregation on herbivore densities (compare Fig. 3a with Fig. 3c).

Second, the distribution of radial encounter probabilities ( $p_e$ ) calculated using the previous year's crop cells as points of origin shows an overall reduction with increasing levels of crop field aggregation (Fig. 5). This corresponds to a smaller “target” with more aggregated fields, when herbivores were using the undirected dispersal rule. It is this effect that makes directed versus undirected dispersal an important modulator of the effect of field aggregation on herbivore densities (compare Fig. 3a with Fig. 3b).

## Robustness

The model was tested with different durations (up to 15 years), initial population sizes, herbivore generations per year, reproductive rates, and additional landscape features that served as permanent herbivore refuges, and all resulted in the same qualitative patterns described above (data not shown).

## Discussion

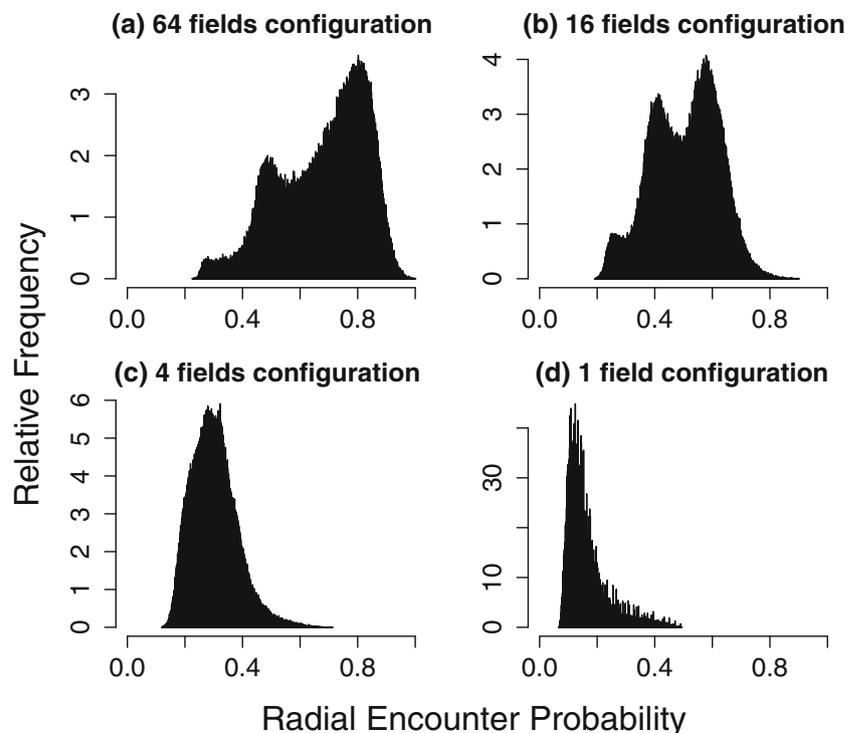
Our simulations demonstrate novel mechanisms by which the aggregation of annual crop fields leads to herbivore population suppression when herbivores have constraints on their foraging abilities and crops are rotated each year. Aggregating fields increased isolation by increasing the distance herbivores had to travel to reach host plants and

decreasing the chance that they would head towards host plants by choosing a random foraging direction. Together these effects mean that colonization of new crop fields by herbivores is substantially more difficult when crop fields are more aggregated. These mechanisms likely explain the surprising results found in empirical studies of the Andean potato weevil system and may be important in other systems where herbivores face foraging constraints and colonization is a key population bottleneck.

The results of this paper (and the empirical studies that inspired it) may seem counterintuitive to some readers. There is a common expectation that large monocultures increase pest densities (Bowman et al. 2002). This expectation has a foundation in the resource concentration hypothesis (Root 1973) and the importance of non-cropland for natural enemies (Root 1973). Additionally, this expectation may be reinforced by the association of vulnerable high-yield cultivars and chemical fertilizer with monocultures, both of which may lead to increased herbivory (Harris 1980, Throop and Lerda 2004, Turcotte et al. 2014).

As described in the introduction, empirical studies have found only mixed support for this expectation. Mismatches between expectation and evidence may emerge because the resource concentration and natural enemies' hypotheses are relevant only in some circumstances, and high yield cultivars and chemical fertilizers are not necessarily tied to large monocultures (Bowman et al. 2002). However, there is an additional limitation to the intuition—it seems to be based on a mental model of increasing both the size of crop fields and the total

**Fig. 5** Distribution of  $p_e$ , the crop cell radial encounter probability, for herbivores dispersing in a landscape with varying levels of crop field aggregation, measured from crop cell overwintering sites.  $p_e$  of a single cell is the probability that an herbivore starting in that cell and walking in a random direction will encounter a crop cell before reaching the edge of a landscape. For low levels of field aggregation (a, b), most directions eventually lead to crop cells. For high levels of field aggregation (c, d), most directions lead to the edge of the landscape before encountering a crop cell. The multimodality of the distributions in **a** and **b** occurs because radial encounter probabilities are different for herbivores on the edge, corner, or middle farms



area of the landscape planted in that crop. Just as Ioannou et al. (2011) found when looking at the effects of prey aggregation on predation levels, the results are drastically different when the total area of crop (or in the case of Ioannou et al. (2011), prey population size) is held constant. In this case, aggregation leads to both increased field size and increased isolation.

If, in this simulation, we were to increase the size of each crop field without decreasing the number of fields, the average distance herbivores would have to travel would decrease and the average radial encounter probability would increase as field size was increased. Both effects would make it easier for herbivores to colonize new fields, leading to increased population sizes (although density per crop cell might decrease in the short-term, given the increased number of cells). However, increasing the amount of land planted in a single crop is a decision by the farmer that would be driven by an array of economic factors in addition to the ecological ones. In contrast, aggregating fields does not presume a change in the farmer's decisions about how much of any crop to grow. The key to our simulation is that because total area in crops is held constant, aggregating crop fields decreases the total number of fields. And while, on its own, increasing patch size should increase connectivity, decreasing the number of patches much more drastically decreases connectivity.

Our model ignores predators and disease, for reasons explained above. However, changing the size and distance between fields may also influence the ability of predators or pathogens to reach pests (for example, see Segoli and Rosenheim 2012). Further modeling is needed to incorporate the interactions of predators and disease with field aggregation, as these antagonists may themselves be influenced by patch connectivity and are likely to be influenced by pest population sizes.

Our model assumes no alternate host plants—in fact, it assumes that any herbivore not finding a crop cell dies. The real world can be more complicated; some herbivores can feed on alternative plants, and even the main host plants may not be constrained solely to cultivated fields. The dynamics depicted with our model are the result of food “deserts,” in which crop fields serve as oases. If alternative oases exist, then aggregating and reducing the connectivity of the man-made ones will not have the same impact on herbivore populations. We tested a version of the model in which each farm had a single permanent source cell (corresponding to the potato storage units in the Andean system) that served as a source of herbivores during each cropping cycle. Simulations including this feature showed the same effect of aggregation, although pest abundances were higher overall and the impact of aggregation was somewhat reduced (results not shown). This is obviously only one of a vast array of potential alternative landscapes with more complicated source features. It is beyond the scope of this study to explore the consequences of various landscape complications, but we can make general predictions based on our results: as alternate hosts and “volunteer” hosts increase

connectivity between fields, aggregating fields will no longer guarantee isolation between fields, and so aggregation should have less of an impact on herbivore populations. However, the exact consequences will likely depend on the specifics of the system, including the prevalence, desirability, and spatial arrangement of these alternate cells, as well as differential competition and predation in these alternate cells as opposed to the host fields.

The model described in this paper did not address the possibility that farmers would intentionally place their fields in ways to reduce pest densities; it instead used a “blind” agroscape configuration in which fields were planted randomly from all allowed choices described in the “Crop rotation” section. This was an intentional decision, as farmers often have multiple constraints on where they plant their fields that might preclude optimizing field configurations for pest reduction, and our goal was to demonstrate the overall importance of the scale of aggregation. However, the variation in herbivore densities within each field aggregation treatment shows the substantial impact a farmer can make by careful placement of their fields, especially with moderate or high levels of aggregation; if farmers intentionally place their fields to reduce pest densities (by planting as far from the previous crop as possible), the improvements due to aggregation would be considerably stronger than the mean response of our simulations.

The original representation of the model focused on a very small scale agricultural landscape; even the most aggregated scale involved a single crop field with size corresponding to  $160 \times 160$  m. While this reflects the scale of agriculture in the Andean potato weevil system, many other systems of interest are much larger. However, as described above, our model defines distances in cells, not in meters. If we were to examine a system in which the insects traveled 10 km in their life, and the same 9.5% of the landscape was in the host crop, then we would run the model with identical parameterization. This would obtain results similar to those presented here (differing only due to stochastic variation between simulations), but they would describe expectations for farmers with four fields that were 500 m on a side and that could be aggregated up to a single field 4 km on a side. The specific sizes of fields and distances traveled do not matter, just the ratio between the two and the fraction of landscape that is host crop. While beyond the scope of this study, it would be valuable to explore how changing the fraction of the landscape planted in host crop modulates the relationship between aggregation and herbivore populations.

Two other theoretical models have found mechanisms that complement those described here. Hambäck and Englund (2005) constructed a general spatially implicit mathematical model that suggested that the relationship between patch size and equilibrium densities of organisms depends on how immigration and emigration scale with patch size. Organisms with area-dependent immigration and perimeter-dependent

emigration (such as aphids) were predicted to exhibit increased density with increased patch size, but organisms with diameter-dependent immigration and perimeter-dependent emigration (organisms that enter and exit patches from the edges) were predicted to exhibit decreased density with increased patch size. Our model complements that of Hambäck and Englund; while Hambäck and Englund explain how the relative rates of entering and leaving a single patch varies with patch size (a patch-centric, single-patch framework), our model explains how varying patch size through aggregation can make finding and reaching patches more difficult (an herbivore-centric and landscape-scale framework).

Segoli and Rosenheim (2012) developed a spatially explicit two-species simulation model that focused on relative dispersal abilities of predators and herbivores, and how increasing field size influenced the interplay of two trophic levels. Under some scenarios, larger fields were associated with lower herbivore densities, because the fields became too large for low-mobility herbivores to colonize the center of the field effectively, especially when predators were at least as mobile as their prey. Under other scenarios, when the herbivores were more mobile than the predators, larger fields provided larger safe zones that were beyond the reach of predators. The Segoli and Rosenheim (2012) study examined only a single agricultural field at a time, and assumed that the entire surrounding matrix functioned uniformly as a source of herbivores and predators (two-species, single-patch framework). For many herbivores, however, sources are often patchy, reflecting the previous year's fields, and for some herbivores, predation is relatively unimportant (as in Parsa et al. 2011). Here we complement the Segoli and Rosenheim (2012) model with simulations of a single-species system, incorporating a larger spatial scale with a more realistic representation of the heterogeneity of the agricultural matrix through time (one species, landscape-scale framework). In addition to accounting for landscape-driven factors, we elucidated those processes driving the patch-size versus pest abundance relationship that do not depend on the presence of predators.

While our model was developed independently of the model presented by Vinatier et al. (2012), our findings confirm and expand upon theirs. Both studies used spatially explicit simulations of herbivores moving through agricultural landscapes to look at the role of crop aggregation in determining herbivore population density. The specifics of the methods differed, but the patterns produced were similar: increased crop aggregation led to decreased herbivore abundance. Vinatier et al. (2012) offer their suspicions as to the cause: changes in the distance between crop fields. Our work confirms their suspicion and provides an additional mechanism behind the pattern: the changes in “target size” as measured in radial encounter probability.

The findings of our paper provide simple, novel mechanistic explanations for the empirically observed phenomenon that

increased field aggregation sometimes leads to decreased pest abundances. Having aggregated (fewer, larger, and more isolated) patches makes it more difficult for herbivores to colonize new crop fields, which is especially important if patch disturbance is frequent (as in agriculture of annual plants, in which patch disturbance occurs at least once a year). These mechanisms are likely driving the patterns observed in the Andean potato weevil system that inspired this study, but as our model is fairly general and the mechanisms simple, our findings may be applicable in other systems. For a typical herbivore in an agricultural landscape, the challenge of finding a suitable patch of host plants will depend on number of factors:

1. How mobile is the insect? The more mobile the insect, the less severe the problem of reaching a patch is.
2. How effective is the insect at detecting food sources? The better the insect is at detecting suitable food, the less severe the problem of finding a patch is.
3. How often are fields changed from one crop species to another? For annuals, crop rotation is often a major feature of agricultural practices, and herbivores may need to colonize new patches relatively frequently. For perennials, rotations are likely to be infrequent, and colonizing new patches may be less important for herbivores. Our tests of multivoltinism showed the same qualitative effect of aggregation as our univoltine case; because multivoltinism is effectively the same as less frequent crop rotation, the patterns we describe do not require crop rotation to be on a yearly time scale.
4. How specialized is the herbivore? For specialized species like the Andean potato weevil that forage on only one or a few host species, finding the right fields may be fairly challenging. For more generalized pests, the “matrix,” which we treated as being a food desert for our herbivores, may be replete with alternate food sources.
5. How widely planted is the suitable host plant? Even relatively mobile herbivores may be challenged to find patches of a rare crop species that are widely separated across the landscape.

The most general result of our study—that aggregation of a resource into a smaller number of larger patches makes finding or reaching new patches more difficult—is relevant to more than just agro-ecology. Ioannou et al. (2011) provides analogous findings for prey aggregation as a defense against predation. Using both models and behavioral experiments with three-spined sticklebacks, Ioannou et al. (2011) showed that when prey are clumped together, the visual angle subtended by the prey in an environment decreased, increasing search times for the predators. This result is directly analogous to the radial encounter probability in our study, although in Ioannou et al. (2011), the angle relates to visual

hunters instead of random dispersers. In the Ioannou et al. (2011) study, prey density and predator mobility were high enough that reaching the prey “herds” was not a challenge. However, for less mobile predators and scarce or clumped prey, both of the mechanisms described in our study could be relevant for other predator-prey systems.

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