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Should increasing the field size of monocultural crops be expected to exacerbate pest damage?

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ABSTRACT

The intensification of agriculture, including the increase in the spatial extent of monocultures, is widely expected to result in an increase in crop damage by herbivorous pests. The theoretical basis for this expectation is, however, unclear. We used a simulation model to explore the relationship between the field size of monocultural crops and season-long mean expected pest densities. We investigated how the underlying relationship between field size and pest densities might be influenced by the presence/absence of an effective natural enemy; by the relative dispersal abilities of the pest and natural enemy; by the ability of the pest and natural enemy to overwinter within the crop habitat; and by the pest's rate of reproduction in the crop. Our model predicts that the relationship between field size and pest densities may, under commonly satisfied conditions, assume any of several forms (positive, negative, hump-shaped, or essentially constant), depending on the biology of the organisms. Each of the underlying relationships between field size of monocultural crops and expected pest densities may motivate adoption of a different set of pest management tactics. Whereas positive relationships motivate tactics that facilitate early natural enemy colonization of the interior of large monocultures (e.g., by supplementing food resources within the crop), negative relationships may instead motivate a suite of farm-design approaches that reduce pest colonization of crop interiors by achieving larger functional field sizes (e.g., aggregating multiple fields of the same crop).

1. Introduction

Modern agriculture has increased the field size of monocultural crops, simplified the agricultural landscape, and reduced the amount of non-crop habitats. It has been suggested that these changes in landscape configuration contribute to an increase in pest damage in crops (Matson et al., 1997; Bianchi et al., 2006). The conventional view is that an increase in field size will increase pest densities. Accordingly, decreasing field size or diversifying the cropping system is expected to reduce pest damage (Root, 1973; Altieri and Letourneau, 1982; Bowman et al., 2002; Bianchi et al., 2006).

Despite the wide acceptance of this prediction, its origin is unclear (Bowman et al., 2002). Island biogeography theory (MacArthur and Wilson, 1967) and the resource concentration hypothesis (Root, 1973) are commonly referred to, with varying degrees of explicitness, as the conceptual basis for the expected positive relationship between field size and pest density (Bowman et al., 2002). Island biogeography theory predicts that larger islands will have more species (MacArthur and Wilson, 1967), and this has been interpreted as implying that population densities should be higher in larger habitats. The resource concentration hypothesis predicts that specialist herbivores are more likely to find and remain on their host plants in larger monocultures, causing an increase in the density of only a few herbivore species, which reduces the persistence of generalist predators (Root, 1973). This view has received support from studies emphasizing the importance of biological control by natural enemies of agricultural pests. It has been suggested that the efficiency of biological control depends on the diversity of crop types and proximity to natural and semi-natural habitats (Altieri and Letourneau, 1982; Bianchi et al., 2006; Gardiner et al., 2009; Pluess et al., 2010). In addition, it has been suggested that natural enemies may be less able to disperse into agricultural crops than agricultural pests (Baggen and Gurr, 1998; Cronin and Reeve, 2005; Bianchi et al., 2006; Tscharntke et al., 2008).

Recent meta-analyses and reviews have, however, found only partial support for a positive relationship between field size and pest densities (Coll, 1998; Bommarco and Banks, 2003; Hamback and Englund, 2005; Bianchi et al., 2006; Poveda et al., 2008). Moreover, most experimental studies use a scale that is too small to be applied to commercial agriculture (Duelli et al., 1992; Bommarco and Banks, 2003; Rosenheim et al., 2011).

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Table 1
Range of values for the simulation parameters.

Parameter	Values
Predator presence	Yes or no
Pest dispersal distance	5 cells/day (short) or 30 cells/day (long)
Predator dispersal distance	5 cells/day (short) or 30 cells/day (long)
Pest reproductive rate	0.1/day (low) or 0.4/day (high)
Pest overwinters in the crop	Yes or no
Predator overwinters in the crop	Yes or no

In a seminal paper, Hamback and Englund (2005) used a mathematical model to explore the disconnect between the resource concentration hypothesis, which predicts only positive density–area relationships, and the empirical record, which instead documents both increasing and decreasing relationships. Hamback and Englund's (2005) approach was to build a spatially implicit, single-species model of population growth that incorporated immigration and emigration functions that were themselves explicitly dependent upon patch size. Models incorporating a diversity of scale dependencies generated the full range of density–area relationships (positive, negative, and non-linear) observed for animals (mostly insects) in nature.

Here we aim to complement the approach taken by Hamback and Englund (2005) by moving to a modeling framework that will more readily allow us to relate our modeling results to aspects of agricultural pest management. We do this by moving to a spatially explicit setting and working with a tri-trophic species module: the crop, an herbivore (a crop pest), and its natural enemy. Our goal was to search for factors that might shape the relationship between the size of monocultural crops and pest densities. In particular, we focus on emergent properties of predator–prey systems that are scale dependent but that derive from processes that are entirely scale independent (i.e., are not tied to the size of the crop field). We explored a variety of scenarios including the presence or absence of effective natural enemies (henceforth 'predators'); pests that have stronger, similar or weaker dispersal abilities compared to their predators; pest reproductive rates in the crop that are low versus high; and pests and predators that could or could not overwinter in the crop habitat patch. We emphasize that this is not intended to be an exhaustive list of variables that might be important in shaping the relationship between field size and pest density; other potentially important variables are addressed in the discussion below. Our goal, however, was to ask whether or not an exploration of parameter space across even a conservatively small set of relevant variables would support the hypothesis of a single, robust relationship underlying the relationship between field size and pest density.

2. Methods

To explore factors affecting the relationship between the field size of monocultural crops and cumulative pest densities (henceforth 'pest densities') we simulated the population dynamics of pests and their predators in a monocultural crop. The experimental landscape consisted of a square crop field embedded in a matrix containing a constant pest population. The size of the crop field ranged from 100×100 cells to 400×400 cells, representing a crop field size of 1–16 ha. The size of the matrix surrounding the monoculture crop was adjusted so that it was always larger than the maximum dispersal distance of the pests and their predators. Our model assumes density-independent mobility and reproductive rates for both the pest and its predator. The values for each parameter are given in Table 1.

The processes of the simulation model are described in the flow chart (Fig. 1), and the MATLAB (Math Works, Inc., Natick, MA, USA) source file is given in Appendix A. We ran the model for 90 daily time steps (representing the duration of the crop's growing season). At each time step and in every cell, pest and predator populations were updated using the Lotka–Volterra equation and then allowed to disperse. The dispersal kernel was radially symmetric and characterized by a negative exponential decline into cells surrounding the cell initially occupied. With this dispersal kernel, 1% of the population reached the specified maximum dispersal distance during each time step (Table 1). Emigration from the focal crop to the matrix had a quantitative effect on the population dynamics in the smaller sized monocultures, but did not affect the overall trends reported below. Therefore, the model assumes that pests and their predators will not emigrate from the focal crop field once they have colonized it, and the crop field was defined as having reflective borders for resident insects.

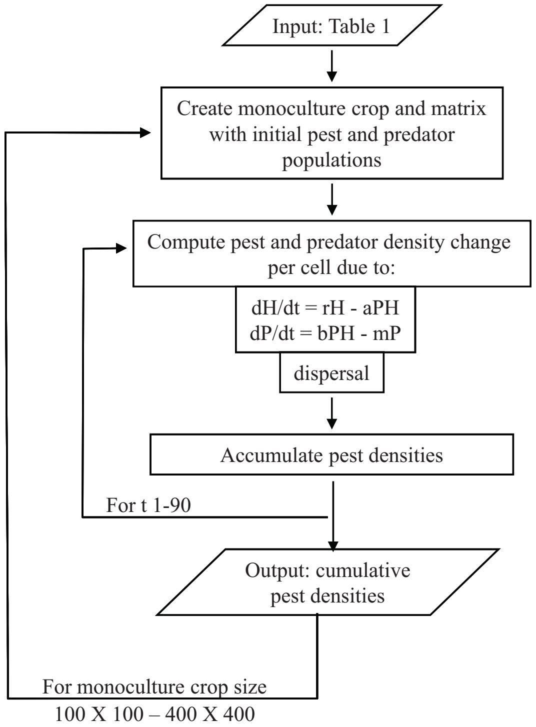

Fig. 1. Flow chart for the simulation model examining the relationship between monoculture crop size and cumulative pest densities. Letters represent: H = density of prey; P = density of predator; t = time step in days; r = pest reproductive rate; a = predation rate coefficient (0.1); b = reproductive rate of predator per pest consumed (0.01); m = predator mortality rate (0.05).

The model assumes that pest and predator populations are at a stable state in the matrix, and immigration is constant throughout the duration of each scenario. To simulate scenarios in which pests or predators can overwinter successfully in the crop field, we assumed that pests or predators could persist in the crop between growing seasons. In these cases, we assumed that the densities of pests and predators in the crop field were equal to their densities in the matrix at the beginning of the simulation.

The pest densities in the entire monoculture crop were accumulated across the duration of the simulation. Since the purpose of this model is to explore the relative change in pest densities with an increase in the field size of monocultural crops, we calculated and plotted cumulative pest densities as a percent of the maximum pest densities that were found in each scenario (i.e., for each scenario the monoculture crop size with the highest cumulative pest densities is plotted as 100%).

Table 2
Results from simulation model on the relationship between crop field size and cumulative pest densities.

Predator presence	Dispersal distance of the pest relative to the predator	Reproductive rate of pest	Overwintering of pest	Overwintering of predator	Relationship between monoculture size and cumulative pest load experienced by the crop
Yes	Shorter, similar, or longer	Low or high	Yes	No	Positive
Yes	Longer	High	No	No	Positive
No	Shorter, similar, or longer	Low or high	Yes or no	Yes or no	Negative
Yes	Similar	Low or high	No	No	Negative
Yes	Shorter	Low or high	No	No	Negative
Yes	Longer	Low	No	No	Hump-shape
Yes or no	Shorter, similar, or longer	Low or high	Yes	Yes	Constant

3. Results and discussion

3.1. Model predictions

Although the conventional view predicts a positive effect of field size on pest abundance, our model predicts a variety of effects, including positive, negative, hump-shaped, and constant relationships, depending on the biology of the interacting species (Table 2). In the next paragraphs, we will discuss in detail the different scenarios leading to each of the four possible outcomes.

3.1.1. Positive relationships

An increase in pest densities with increasing field size is expected under the conventional view (Root, 1973; Bowman et al., 2002; Bianchi et al., 2006). Our model predicts such a relationship in the following scenarios: (1) the pest overwinters in the crop and its predator does not; and (2) the pest and its predator do not overwinter in the crop, the pest has longer dispersal distances than the predator, and the pest has a high reproductive rate (Fig. 2a). In these scenarios the pest succeeds in rapidly occupying the interior of the crop while its predator does not (Fig. 3a). This enables the pest population to increase dramatically in the interior of the crop field, which is relatively 'predator-free' (Ohsaki and Sato, 1990).

When the pest overwinters in the crop and its predator does not, a reduction in pest densities is caused by the immigration of the predators into the crop. As the crop field size increases, it takes the predators longer to migrate into the interior of the fields, and the pest densities in the predator-free interior can increase. In the largest field sizes used in our simulations, the predator is not able to colonize the center of the fields at all, and pest populations are entirely released from predator control. Whereas overwintering in the crop is common in perennial crops, it is not common in annual crops (Wissinger, 1997), due to a variety of commonly employed agricultural practices (e.g., crop rotation, tillage; Thies et al., 2005).

When the pest and its predator do not overwinter in the crop, the pest has a high reproductive rate, and the pest's dispersal abilities are stronger than those of its predators, the pest can disperse further into the interior of the crop field and again utilize this predator-free area. The high reproductive rate allows the pest population to build up rapidly and then disperse further into additional predator-free areas. It has been suggested that a similar result can also be caused if a predator requires a key resource (e.g., a non-host/prey source of nutrition, such as nectar or honeydew; or an alternate host) that is found only outside the crop (Freeman Long et al., 1998). In this case, even if the pest and its predator have similar dispersal abilities, the predator population can only sustain itself near the interface of the crop field and the surrounding matrix, enabling the pest to find refuge in the predator-free interior. This is a central issue in biological control when using parasitoids, since in many cases they require nectar from non-crop habitats.

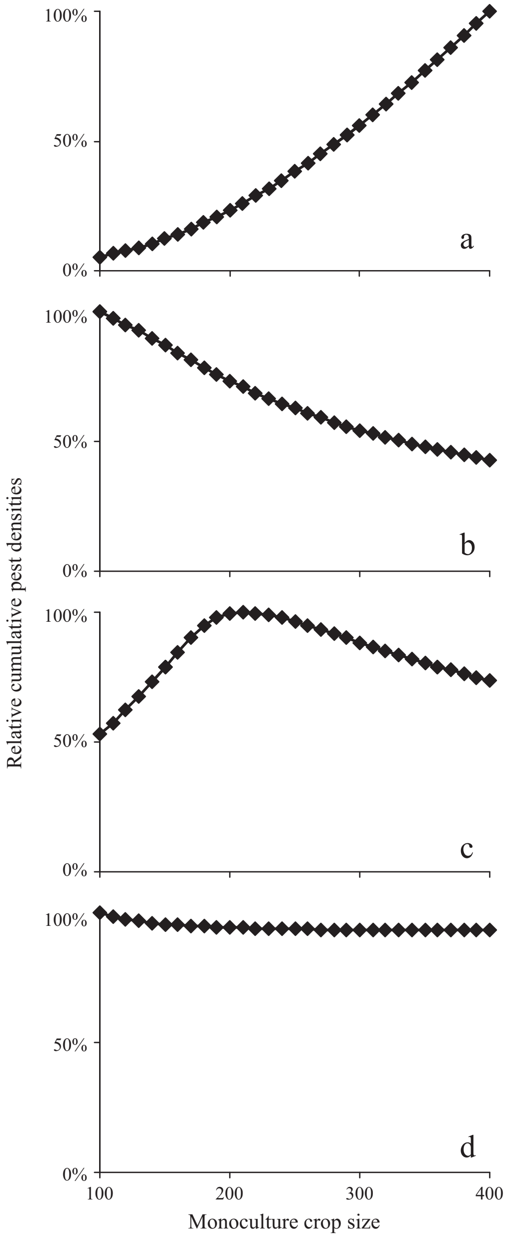

Fig. 2. Possible relationships between the field size of a monocultural crop and cumulative pest densities (presented as a percentage of the maximum cumulative pest densities observed in the scenario) when both the pest and its enemy do not overwinter in the crop field. (a) The pest has a longer dispersal distance than the predator, and the pest has a high reproductive rate. (b) Both the pest and its predator have similar dispersal distances, and the pest has a high reproductive rate. (c) The pest has a longer dispersal distance than its predator, and the pest has a low relative reproductive rate. (d) The pest has a longer dispersal distance than its predator, and the pest has a low relative reproductive rate.

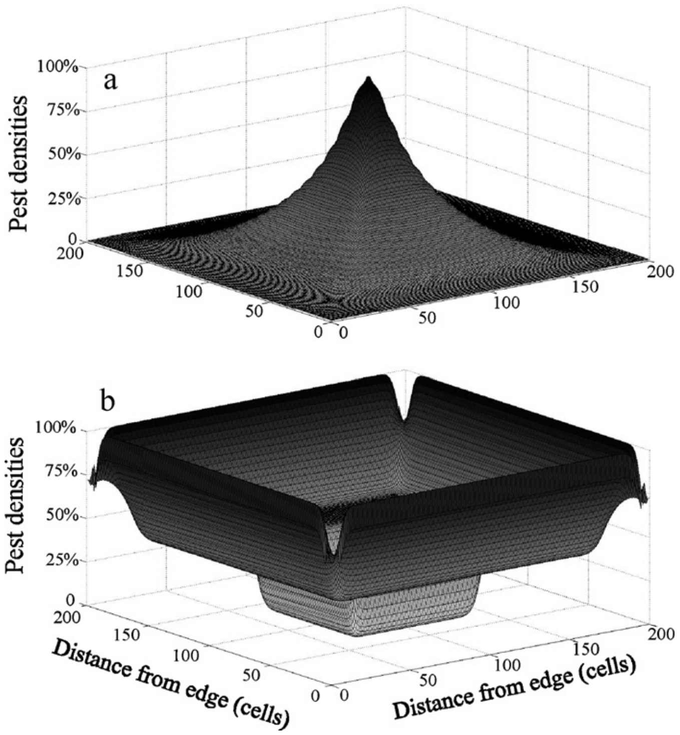

Fig. 3. Cumulative pest densities observed at different locations within a monocultural crop field. In both cases, it is assumed that the pest has a high reproductive rate in the crop and that neither the pest nor the predator can overwinter within the crop habitat; thus both must colonize the crop field. (a) Here the pest has a high dispersal ability and the predator has a low dispersal ability. As a result, pest densities build up in the interior of the crop field, because pests can colonize there effectively but predators cannot. Under this scenario, increasing field size is expected to increase pest damage. (b) Here the pest and predator have similarly low dispersal abilities. In this case, neither the pest nor the predator can effectively colonize the interior of the crop field. Under this scenario, increasing field size is expected to decrease pest damage.

3.1.2. *Negative relationships*

A decrease in pest densities with increasing monoculture field size is predicted by our model in scenarios where: (1) there are no effective predators; or (2) the pest and its predator do not overwinter in the crop, and the pest does not have longer dispersal distances than its predator (Fig. 2b). In these cases the pest population in the crop is determined by pest immigration from the matrix into the crop. Because the boundary (perimeter) of the crop is proportional to the crop's linear dimension, whereas the area of crop is proportional to the square of the crop's linear dimension, the ratio of the two (perimeter/area) declines as crop size increases, reducing the proportion of the crop's interior that is strongly colonized by the pest.

In the scenarios without effective predators, the lower pest densities in the larger crop fields are due to dispersal limitations into the interior of the crop. Although the pest densities are reduced in the larger fields, the lack of predators can cause pest densities to be extremely high, even in the interior of the larger crops.

In these scenarios, pests are concentrated in the edges of the crop field and have smaller densities in the interior of the field (Fig. 3b). Such a pattern has been documented by several studies (Alomar et al., 2002; Reay-Jones, 2010). For example, stink bug densities and the damage they cause are greater in the edges of cotton crops and decrease towards the interior (Toews and Shurley, 2009; Reeves et al., 2010).

3.1.3. *Hump-shaped relationships*

An increase in pest densities with initial increases in crop field size followed by a decrease of pest densities with further increases in field size is predicted by our model when the pest and its predator do not overwinter in the crop, the pest has a low reproductive rate, and the pest has higher dispersal abilities than its predator (Fig. 2c). The initial increase in pest densities is caused by the longer dispersal distance of the pest that enables its densities to increase and build up in the predator-free interior of the crop field. However, due to the pest's low reproductive rate, its densities cannot increase enough to continue spreading effectively into the more interior parts of the larger fields. A hump-shaped relationship between pest densities and field size has been predicted and documented in aphids (Hamback and Englund, 2005; Hamback et al., 2007). In addition, some studies have documented a hump-shaped relationship between pest densities and distance from the crop edge (Duelli et al., 1992; Reay-Jones et al., 2010), suggesting a likely hump-shaped relationship between pest densities and crop size.

3.1.4. *Constant relationship*

We considered the relationship between pest densities and monoculture crop size to be essentially 'constant' when pest densities changed by $\leq$20% as crop field size increased in linear dimension by 4-fold. Our model predicts this relatively constant relationship in cases where both the pest and its predator overwinter in the crop (Fig. 2d). In this scenario, the overwintering populations of pests and predators dominate the densities within the crop, such that the contributions of immigrants generated only very weakly positive, negative or hump-shaped patterns.

A similar result can also be achieved when the pest overwinters in the crop and reaches and maintains its carrying capacity (Bianchi and Van Der Werf, 2003), or in situations where the pest has very high dispersal abilities enabling them to achieve very quickly a uniform distribution across the landscape, and the predator is either absent or also has a similarly high dispersal ability (Hamback and Englund, 2005; Gavish-Regev et al., 2008). Many studies have shown, directly and indirectly, that pest densities are not affected by field size (Bach, 1988; Thies et al., 2005; Bianchi et al., 2006; Poveda et al., 2008).

3.2. *Continuous effects of parameters*

In the previous sections we demonstrated how scenarios with qualitative differences in the assumed underlying biology (see Table 1) can lead to predictions of four different relationships between crop field size and pest densities. In the next two sections, we demonstrate how continuous changes in a single parameter value (first, pest reproductive rate; second, pest dispersal distance) can produce similarly continuous changes in the form of the relationship between crop field size and pest densities.

3.2.1. *Effect of reproductive rate*

Progressive reductions in the pest reproductive rates can transform a positive relationship between crop field size and pest densities into, first, a hump-shape relationship and, eventually, a negative relationship (Fig. 4a).

Some of these scenarios might seem more important from the perspective of applied agricultural ecology than others. For instance, it might be suggested that scenarios that involve low pest reproduction in the crop are less important, because such an herbivore might be unlikely to achieve pest status in that focal crop. However, herbivores can become economically significant pests in crops that represent poor hosts for them (e.g., even if the crop habitat is a sink for the pest population), if the crop field is adjacent to a potent source habitat. For example, *Lygus* spp. bugs have high reproductive rates in alfalfa, from which they can disperse *en masse*

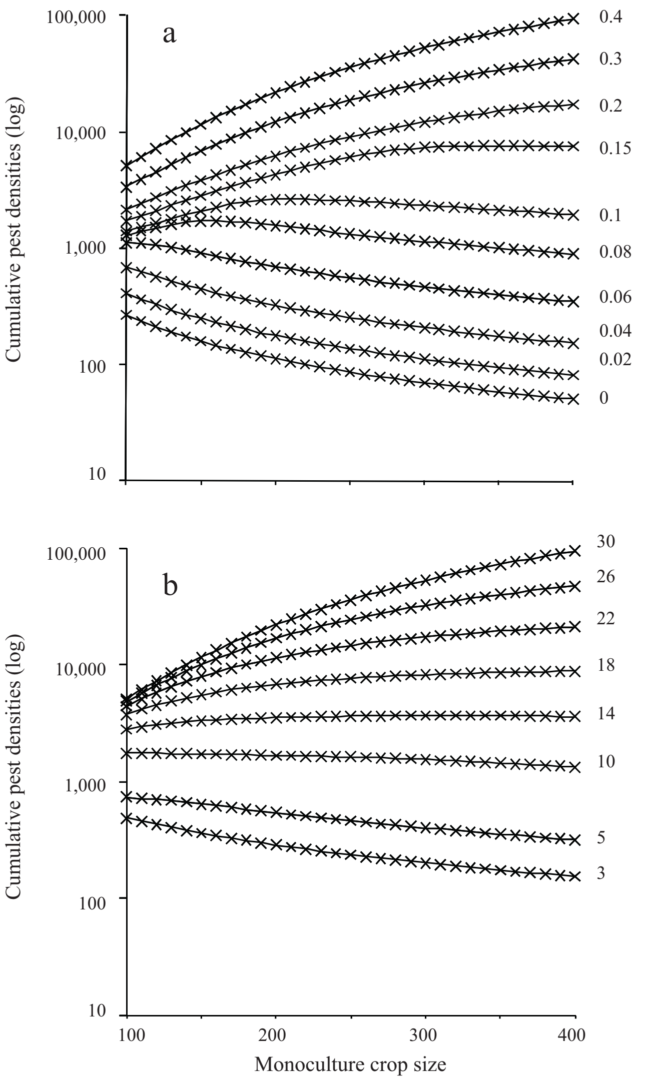

Fig. 4. Effect of continuous changes in (a) pest reproductive rate and (b) pest dispersal distance on the relationship between crop field size and pest densities, when both the pest and its enemy do not overwinter in the field. (a) The pest has a longer dispersal distance than the predator (reproductive rates are displayed on the graph). (b) The predator has a low dispersal distance and the pest has high reproductive rates (dispersal distances of the pest are displayed on the graph).

into neighboring cotton crops when the alfalfa crop is harvested (Graham et al., 1986; Goodell et al., 2002; Carrière et al., 2006). In cotton, *Lygus* reproduction may be quite poor, but nevertheless immigrants can impose severe damage to the crop, even when they are present at modest densities (Barman et al., 2010).

3.2.2. *Effect of dispersal distance*

Similarly, progressive increases in the dispersal distance of the pest can transform a negative relationship between pest densities and monoculture crop size into, first, a hump-shaped or constant relationship and, eventually, a positive relationship (Fig. 4b). This supports the widespread suggestion that dispersal distances play a central role in determining the effect of crop field size on pest damage.

3.3. *Origins of the conventional view*

The main result of our modeling study is that a wide range of relationships may be expected between pest densities and the size of a crop field. Why then has there been such broad acceptance of just one expected form of the relationship, namely that pest damage will be amplified by increases in field size? We suggest two possible reasons: one that is scientific and one that is cultural.

The scientific basis for a positive relationship between crop field size and pest densities is sometimes attributed to island biogeography theory or to the resource concentration hypothesis (MacArthur and Wilson, 1967; Root, 1973; Bowman et al., 2002). However, island biography theory assumes that population densities are independent of habitat area. Moreover, Root (1973) commented that “Field size is an important variable, and large, commercial acreages in intensively cultivated regions probably differ greatly from the small gardens followed in this study.” In addition, we hypothesize that the conventional view may have been formed in part under the expectations that (i) every pest has an effective natural enemy, (ii) herbivores have larger dispersal distances than their predators, or (iii) natural enemies rely on key resources found only outside the crop. However, these assumptions need not be satisfied universally.

There may also be a cultural explanation underpinning the expected worsening of pest problems as crop field size increases. The industrialization of agriculture, associated with an ongoing displacement of smaller, diversified family farms by larger and larger, corporate farming operations, has changed the fabric of farming communities in ways that many view as being injurious to rural society (Altieri and Nicholls, 2005). By extension, then, the tendency may have been to view other aspects of this scaling up of agricultural production as being similarly deleterious. This might explain how this ecological ‘folklore’ (Bowman et al., 2002) came to be accepted in the agricultural literature. Andow (1983) has similarly suggested that the debate over the effects of agricultural intensification is often shaped by economic, social, and political considerations.

3.4. *Implications for pest management and farmscape design*

An increased spatial scale of agricultural production is an ongoing response to positive economies of scale (Giampietro, 1997). Our model predicts that the main mechanism underlying a positive relationship between crop field size and pest densities is the ability of agricultural pests to colonize predator-free areas. We suspect that many annual agroecosystems will exhibit this positive relationship, because pests and their predators are usually unable to overwinter in annual crops (Wissinger, 1997), crops are usually high quality resources for pests, which enables pests to achieve high reproductive rates, and pests may often have longer dispersal distances than their predators (due to dispersal limitation per se or due to predators requiring key resources found only outside of the crop).

Some management approaches devised to deal with the worsening of pest problems in large fields focus on means of enhancing the colonization and efficiency of predators in the otherwise predator-free areas. These schemes include (1) overcoming dispersal constraints (e.g., making augmentative releases of natural enemies); (2) supplementation of key resources needed by predators (e.g., selection of crop cultivars that produce resources for predators, or the application of supplemental resources for predators); and (3) increasing in-field diversification (e.g., use of hedgerows, intercropping, or cover crops). Similarly, pest problems in large crop fields may also be ameliorated by preventing the overwintering of pests in the crop field (e.g., use of tillage or crop rotation; Altieri and Letourneau, 1982; Corbett and Rosenheim, 1996).

A hump-shaped relationship between crop field size and pest densities is predicted in similar scenarios, except that the pest has lower reproductive rates. Therefore, it is plausible that similar schemes may be effective, even without applying them in the interior parts of the crops.

If, however, the relationship between field size and pest densities is negative, a different set of management approaches, which has largely been overlooked in the literature, may be available for implementation. Based on predictions from our model, we recommend exploring the benefits of increasing the size of crop fields in the following scenarios: (1) the crop is a sink for pests; and (2) the pest is not able to overwinter in the crop and cannot colonize the interior of large crops, due to low dispersal. We propose that negative relationships will be relatively common in annual agroecosystems when (1) the crop is intrinsically a poor-quality host plant for a particular herbivore, or when the crop has been bred to express substantial resistance against pests (e.g., solid-stemmed wheat cultivars that reduce wheat stem sawfly's fecundity and survivorship; Carcamo et al., 2005), or (2) for crops that are attacked by pests that disperse by walking (e.g., gastropods and many beetles; Hof and Bright, 2010; Reineke et al., 2011).

Larger field sizes may, in some cases, not only reduce average damage from pests, but may also provide additional benefits in reducing the cost of applying pest management tactics. In larger fields where pests are concentrated near the field periphery, control measures such as trap cropping or pesticide applications may be usefully applied just to the field edges (Cavanagh et al., 2009; Toews and Shurley, 2009; Reay-Jones et al., 2010). Alternately, it might be possible to plant crop cultivars that are resistant to pests, but are more costly or produce lower yields (Bennett et al., 2006), only in edges of the fields, thereby reducing the total cost of coping with damaging pests.

In addition, crop rotations at a large spatial scale may increase the spatio-temporal variability of the agricultural matrix so greatly that pest populations face a diminished ability to track their key host plant resources across years. This may be especially important in systems where the pests migrate cyclically between annual agricultural crops and permanent habitats (Wissinger, 1997).

Of course, there may be costs associated with schemes that increase the spatial scale of monocultural crops, even under conditions when resulting pest densities are expected to be reduced. Increasing crop field size may cause a reduction in the control ability of natural enemies, cause habitat loss, and reduce natural biodiversity (Altieri and Letourneau, 1982; Daily, 1997; Bianchi et al., 2006). However, if the pests cannot colonize or build up in the interior parts of large crop fields, or if predators are inherently limited in their ability to suppress the target pest, then the loss of natural enemies may be of secondary importance. Furthermore, by implementing farmscapes that involve coordination between farmers, same crop types can be grown adjacent to each other and effectively create large monoculture crops (Ehler, 2000; Carrière et al., 2006) without causing further habitat loss or reduction of natural biodiversity. For example, it has been suggested that aggregation of five potato fields in the Andes could reduce the densities of a key pest by 50% (Parsa et al., 2011). There are many examples of agricultural intensification reducing species richness and diversity (Firbank et al., 2008). However, agricultural intensification can comprise different components (i.e., habitat fragmentation, habitat loss, habitat isolation, loss of landscape complexity, etc.). Our model suggests that field size per se may not be consistently responsible for at least those negative effects of agricultural intensification related to the intensity of damage by herbivorous pests (Fahrig, 2003; Hendrickx et al., 2007).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.agee.2012.01.010.

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