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Holden, M.H., S.P. Ellner, D.-H. Lee, J.P. Nyrop, & J.P. Sanderson. 2012. Designing an effective trap cropping strategy: the effects of attraction, retention and plant spatial distribution. *Journal of Applied Ecology*. 49:3:715-722

Designing an effective trap cropping strategy: the effects of attraction, retention and plant spatial distribution

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Running title: Designing an effective trap cropping strategy

Summary

1. Trap cropping, the use of alternative host plants to reduce pest damage to a focal cash crop or other managed plant population, can be a sustainable strategy for pest control, but in practice it has often failed to reach management goals. Of the few successful trap cropping examples at a commercial scale, nearly all have included supplemental management strategies that reduce pest dispersal off the trap crop. In contrast, the trap cropping literature has focused extensively on trap plant attractiveness.
2. To test whether the dispersal of insects off trap plants is as important as the anecdotal evidence suggests, we developed a simple model to understand how a trap plant's spatial configuration within a field, its attractiveness, and its ability to retain pests affects pest density on a target cash crop.
3. The model predicts that when trap crop retention is low, trap cropping is ineffective and small increases in retention offer little improvement. However, when retention is high, small differences in retention dramatically affect trap cropping efficacy. In contrast, when the attractiveness of a trap crop is high, further increases in attractiveness have little effect on trap cropping efficacy.
4. Placing trap plants close together is most often detrimental to pest management because it leaves large portions of the field without nearby traps. However, planting the trap crop in rows often does not clump the landscape enough to cause this detrimental effect.
5. *Synthesis and applications*. The predictions from our model confirm the anecdotal evidence that trap cropping failures may be attributed to a focus on attraction at the expense of retention. A very high retention rate is required for effective reduction of pest densities. Therefore, additional practices that prevent insects from dispersing back into

the cash crop may be essential for effective trap cropping designs. These techniques include trap vacuuming, trap harvesting, sticky traps, planting a high proportion of trap plants or applications of pesticides or natural enemies to the trap crop.

Keywords: Cultural control, IPM, mass trapping, movement model, pest management, lattice model, trap plant, sustainable agriculture

Introduction

Habitat manipulation and diversification can be effective and sustainable strategies for pest management (Khan *et al.* 1997; Landis, Wratten, & Gurr 2000; Gurr *et al.* 2004), but often fail to produce the desired control (Podeva, Gomez & Martinez 2008; Simon *et al.* 2010). Trap cropping, the use of alternative host plants to attract, intercept and/or retain targeted insect pests for the purpose of reducing damage to a main crop, is one such strategy. Similar trapping designs have also been suggested as a potential method for control of invasive insects in natural ecosystems (El-Sayed *et al.* 2006; Mercader *et al.* 2011). For agricultural pest management, trap cropping potentially reduces crop damage inexpensively and simultaneously reduces conventional pesticide applications (Cavanagh *et al.* 2009; Lu *et al.* 2009). However, without assistance from other management inputs, including pesticide treatments, trap cropping has frequently failed to adequately reduce insect density, even when the pest shows a strong preference for the trap plant in laboratory or semi-field experiments (Shelton & Nault 2004; Shelton & Badenes-Perez 2006). In the most recent literature review on trap cropping, out of nearly 100 systems examined, only ten were considered successful examples of trap cropping on a commercially viable scale (Shelton & Badenes-Perez 2006). Why has trap cropping been applied with so little success, despite decades of study, and what can be done to improve future deployment?

To answer this question we must first note that there are two fundamental processes for a trap crop to successfully function as a sink for a target pest: attraction of the pest towards the trap plant and retention of pests that arrive. Therefore, a trap crop can fail due to deficiencies in either pest attraction or pest retention (Hilje, Costa & Stansly 2001). Although the two processes are explicit in a theoretical context, it is difficult to separate them empirically. In most cases, experiments provide only snap-shot data on how many pests accumulate on a trap crop over discrete time intervals. Measuring the process through continuous observations of insect movement to tease apart arrivals (related to attraction) and departures (retention) is time consuming, and in many cases logistically infeasible. Therefore, there have been no studies that explicitly test the relative effect of these two processes on trap cropping efficacy. In fact, the vast majority of the trap cropping literature is composed of small scale experiments to determine the attractiveness of new candidate trap plants over a short time scale (e.g. Edde & Phillips 2006); we are aware of no studies that explicitly measure retention. However, after decades of looking for the most attractive trap plants, little progress has been made towards successfully applying these highly attractive host plants in agricultural fields and greenhouses.

While the focus of the trap cropping literature has been on attraction, the few examples of successful trap cropping that do exist suggest that the retention of insects on the trap plant may be even more important. In fact, out of the ten systems labelled as commercial successes in the latest review, at least nine of them use supplemental management strategies that prevent insects from dispersing away from the trap crop (Shelton & Badenes-Perez 2006). The most common method, shared by four of these successes, is applications of pesticide directly to the trap crop. This has worked in systems ranging from lepidopteran pests of *Brassica oleracea* to *Acalymma vittata* and *Anasa tristis* on cucurbit crops (Hokkanen 1989; Srinivasan & Krishna Moorthy 1991; Pair 1997; Dogramaci *et al.* 2004). Since Shelton & Badenes-Perez's 2006 review, we found five new examples of successful large scale trap cropping, three of which also included pesticide applications to the trap crop (Leskey, Pinero & Prokopy 2008; Cavanagh *et al.* 2009; Lu *et al.* 2009). Of the other two systems, one involved regularly vacuuming an alfalfa *Medicago sativa* trap crop to reduce damage to organic strawberries *Fragaria ananassa* by *Lygus hesperus*

(Swezey, Nieto & Bryer 2009). The other example involved planting over 20 % of the landscape with trap plants, which also may lessen dispersal out of the trap crop (Michaud, Qureshi, & Grant 2007). The fact that most successful trap cropping designs employ supplemental management strategies to prevent dispersal of pests back into the cash crop suggests that past trap cropping failures may be due to a trap plant's inability to retain insects on its own.

It is inherently difficult to experimentally tease apart the effects of attraction and retention on pest density. Therefore, mathematical modelling is the best tool available for testing whether retention is actually as important as the above examples of successful trap cropping imply. We developed a simple model to determine the relative importance of attraction and retention on trap cropping efficacy, and also to determine how the spatial distribution of trap plants affects the relative importance of these two fundamental processes. Compared to most previous models (Cain 1985; Banks & Ekbom 1999; Potting, Perry & Powell 2005; Ma *et al.* 2009), our model is more general, sacrificing biological details that will be unique to particular systems in order to understand the relationship between retention and attraction. In addition, past modelling studies have assumed that large portions of the landscape are devoted to the trap crop, which is unrealistic for most trap cropping systems (Hokkanen 1991; Shelton & Badenes-Perez 2006). While a less complicated mathematical model of trap cropping has also been studied, it does not allow trap crops to attract insects (Hannunen 2005) and therefore cannot explain the interaction between attraction, retention, and plant spatial distribution on trap cropping efficacy.

In our model, we make conservative assumptions to favour the importance of attraction over retention, but even with these assumptions, for the vast majority of scenarios, the model predicts that high trap crop retention is more important than having a very attractive trap plant. Once the trap crop is somewhat more attractive than the cash crop, further gains in attraction do little to improve trap cropping efficacy. On the other hand, retention must be very high for trap cropping to be effective. In addition, when retention is high, increasing retention by even small amounts dramatically decreases pest densities on the cash crop. These results correspond to the empirical examples in the literature, which suggest that trap cropping is most effective when supplemental management strategies are deployed to prevent pest dispersal back into the cash crop. Therefore, practices such as applying insecticides (Hokkanen 1989; Srinivasan & Krishna Moorthy 1991; Pair 1997; Dogramaci *et al.* 2004; Cavanagh *et al.* 2009; Lu *et al.* 2009), sticky traps (Moreau & Isman 2011), natural enemies, or harvesting (Godfrey & Leigh 1994) or vacuuming trap crops (Swezey, Nieto & Bryer 2009) may be essential for a successful trap cropping strategy.

Materials and methods

We used two models. The first is a computer simulation of insect movement over a spatially explicit landscape with insect density tracked on each plant. The second model is an analytical approximation that describes average movement between the trap crop and cash crop. To simplify the analysis, we only looked at insect movement; reproduction and mortality are not considered. Hence, the variable of interest is the proportion of insects on the cash crop, which we refer to as cash crop pest proportion. In addition we assume that insect movement does not change with respect to insect density. While the above assumptions would affect some aspects of the model’s output, they do not affect the conclusions we draw in this paper, as explained in the discussion.

In the simulation model, after sufficient time has elapsed, the proportion of insects on the cash crop remains relatively constant. This can be viewed as the “final” proportion of insects on the cash crop, and is thus a measure of trap cropping efficacy. In the analytical model, the proportion of insects on the cash crop approaches an equilibrium which is analogous to the final cash crop pest proportion in the simulations. We show that the equilibrium in the analytic model approximates the simulated final proportion well, and we use it to show how the results from the simulation can be generalized for all combinations of parameter values.

Simulation Model

Our simulation models insects moving in a rectangular arena containing two types of plants, cash plants and trap plants. These two plants differ in their ability to attract and retain insects. The number and spatial coordinates of the trap plants can be varied.

Insect movement occurs in two steps, dispersal from their initial location, and settling on a new plant. To model dispersal, at every time step insects on the cash crop leave with probability d_C and insects on the trap crop leave with probability d_T. Hence the retention of insects on a trap crop and cash crop is given by 1- d_T and 1- d_C respectively.

Dispersing insects choose a location for settlement within distance k of their initial location. For example, if k = 1, an insect can move to any plant next to its initial location, including diagonal movement. If k = 2, insects can move in any direction up to two plants away from their initial location. Small values of k correspond to instars or flightless/weak flying adults and large values of k correspond to stronger fliers such as lepidopteran and many coleopteran or hemipteran adults. Within the dispersal neighbourhood, the probability that an insect will settle on a trap plant is governed by the parameter a, trap crop attractiveness. Specifically, if there is a trap plant within k plants of the current insect location, the insect will be a times more likely to settle on the trap plant than each individual cash plant. For example, if nine insects disperse from a plant and can move to eight potential surrounding plants, one of which is a trap plant, then *a* = 2 means that on average the trap plant will get two insects and the seven cash plants will each receive one insect.

Insects on a plant next to an edge are not allowed to disperse out of the arena. Dispersal is still governed by the rules described above except the insect can now move to fewer plants. In movement models this is one commonly used method for dealing with edges; other solutions include wrapping the arena around to connect opposite borders or allowing insects to leave the system (Cain1985; Potting, Perry & Powell 2005) or reflecting insects back into the system that choose to move outside the boundary (Potting, Perry & Powell 2005). We experimented with several of these movement rules at the edge of the landscape, and while different rules did affect insect density at the edges, there was virtually no effect on the proportion of insects on the cash crop.

Note that the probability of dispersal (d_C and d_T) is solely based on the plant an insect is on, not on neighbouring plants. This is a standard assumption in the modelling literature (Potting, Perry & Powell 2005; Ma *et al.* 2009). In addition, we found no evidence to reject this assumption when we tested it experimentally (M. H. Holden, unpublished data) for greenhouse whitefly *Trialeurodes vaporariorum* movement between a single poinsettia *Euphorbia pulcherrima* (cash plant) and an eggplant *Solanum melongena*, which has been shown to be highly attractive to whitefly and proposed as a trap crop in greenhouses (Lee, Nyrop & Sanderson 2009).

We initialized the model with 10 insects on every cash plant, let the model run for 100 time steps, and calculated the proportion of insects on the cash crop at the end of the simulation. Each parameter combination was replicated five times, and the mean and standard error of the insect density on the cash crop was calculated. Note that a high insect density was chosen to save computing time by reducing the need for replication; because insects move independently in the model, changing insect density has no effect on any of the results presented.

The Simplified Mathematical Model

The parameters of the analytical model, match those in the simulation model. Insects disperse with probability d_T on trap crops and d_C on cash crops, movement of dispersing insects is determined by trap plant attractiveness, *a*, and the types of plants within the insect's dispersal range. In the simulation, this is achieved by evaluating the exact composition of the landscape within the insect's given dispersal distance. However, in the mathematical model an insect moves based on average local compositions of the landscape. To do this, we calculate the average of the number of cash plants within the insect's dispersal distance from a cash plant, averaged over all cash plants, $n_{C|C}$; the average number of cash plants within the dispersal distance from a trap plant, averaged over all trap plants, $n_{C|T}$; the average number of trap plants within the dispersal distance of a cash plant, averaged over all cash plants, $n_{T|C}$; and the average number of trap plants within the dispersal distance of a trap plant, averaged over all trap plants, $n_{T|T}$. Movement is then given by the attractiveness of the trap plant and on average how many trap plants and cash plants are within the dispersal range. Letting P_t be the proportion of insects on the cash crop at time *t*, yields the following equation,

$$P_{t+1} = (1-d_C)P_t + d_C \frac{n_{C|C}}{an_{T|C}+n_{C|C}} P_t + d_T \frac{n_{C|T}}{an_{T|T}+n_{C|T}} (1-P_t) \qquad \text{(eqn. 1)}$$

This equation says that the insects on the cash crop at the next time step (left hand side) is just the sum of the insects in the cash crop that did not move (first term on the right hand side), the insects that moved between cash plants (middle term), and the insects that moved from the trap crop to the cash crop (last term).

Results

Simulation Results

The simulation model predicts that trap crop attractiveness and trap crop retention of insects have fundamentally different effects on final pest proportion. As the trap crop becomes more attractive, initially pest proportion on the cash crop decreases steeply. However, once the trap crop is relatively attractive, further increases in trap crop attractiveness have little effect on cash crop pest proportion (Fig. 1). This effect of attraction is stronger when trap crop retention is high (Fig. 1a compared to b). No matter how attractive the trap crop, more than 25 % of insects stay on the cash crop if trap crop retention is 0.9 (Fig. 1a). Increasing trap crop coverage from 1 - 2 % of the landscape reduces cash crop pest proportion for nearest neighbour dispersers but still leaves 25 % of the pest on the cash crop (Fig. 1a, dash dotted line compared to dashed line). Note that if retention is less than 0.9, trap cropping would be even less effective. On the other hand, if retention is 0.98, it is possible to reduce the proportion of insects on the cash crop to as low as 1 % (Fig. 1b). In this case, trap cropping is only ineffective if both 1 % of the landscape is devoted to trap crops and pests move infrequently and short distances (Fig. 1b, dashed line). However, increasing trap crop coverage, even to as little as 2 % of the total landscape, offers dramatic gains in trap crop efficacy for these less mobile pests (Fig. 1b, dashed dotted line).

Trap crop retention has the opposite effect on cash crop pest proportion compared to the patterns observed with respect to attraction. Initially, when trap crop retention is small, increases in retention have almost no effect on cash crop pest proportion. However, as the retention on the trap crop increases near values close to 100 %, small changes in trap crop retention lead to large changes in cash crop pest proportion (Fig. 2). We will refer to this trend as the nonlinear retention effect.

The severity of the nonlinear retention effect varies with cash crop retention, 1- d_C, dispersal distance, k, attractiveness of the trap crop, a, and the size and spatial configuration of the landscape. The nonlinear retention effect is strong for insects with intermediate to long distance dispersal over all landscapes that contain a small number of uniformly or randomly spread out trap crops. For insects that can only move one plant at a time, in a landscape with only 1 % trap crop coverage, trap cropping does not provide a meaningful drop in pest densities, even when retention rates approach 100 % (Fig. 1&2, dashed line). This is because the insects do not move enough to reach the trap crops. A higher dispersal distance, such that the insects can move within a five plant radius, leads to pest control only for high trap crop retention rates (Fig. 2, solid line). The same effect can be achieved if insects move short distances but do so more frequently. Increasing trap crop coverage to 2 % or more of the landscape allows for effective trap cropping as long as retention is near 100 % (Fig. 2, dotted line).

To summarize, if the insect moves infrequently and trap plants make up less than 1 % of the landscape, trap cropping is ineffective in all cases, even with 100 % retention. If trap crops make up more than 2 % of the landscape, or the insect is relatively mobile, trap cropping is only effective if trap crop retention is very high.

The spatial distribution of trap plants is also important for determining the final density of pests on the cash crops. When trap plants are clumped close together in a single patch in the middle of the landscape, pest proportion on the cash crop remains high for all trap crop retention rates, unless insects move long distances (Fig. 3a). Also note that for the clumped system, with long distance dispersal, the nonlinear relationship between pest proportion and trap crop retention is less severe. That is, the proportion of frequently moving pests on the cash crop gradually declines with an increase in trap crop retention for clumped trap crops (Fig. 3a, solid line) but only declines for retention near 100 % for uniformly spread out trap crops (Fig. 3c). Finally we note that for moderately clumped landscapes, such as the trap crop being planted in rows, the results are most similar to the uniformly located trap crop case (compare Fig 3b to 3c). That is, planting the trap crops in rows does not reduce trap cropping efficacy, except for insects that only disperse to nearest neighbor plants.

It should be noted that if the simulation runs long enough, corresponding to an average of more than 1,000 moves per insect, clumping trap crops actually dramatically reduces pest densities on the cash crop. However, this is an unrealistic situation in agricultural pest management, and hence extreme clumping of trap plants is likely to be disadvantageous in most cases.

Mathematical Model Results:

The simplified mathematical model accurately predicts the long term behaviour of the simulation model (Fig. 4). The advantage of this model is that we can solve it exactly, describe final pest proportion on the cash crop for all parameter combinations, and use it to confirm the results from the simulation and prove their generality. In this model, for all parameter combinations, small changes in retention always have a greater effect on cash crop pest proportion when retention is high (see Appendix S1 in Supporting Information). In addition, for all parameter combinations, the severity of this nonlinear effect increases as *an*, trap plant attractiveness times the ratio of the number of trap plants to cash plants, decreases (Fig. 5 &

Appendix S1). So if trap plants are not numerous or not extremely attractive, the severity of this nonlinear effect means that trap crops must retain nearly 100 % of the insects to provide meaningful control. As a general rule of thumb, trap plants with moderately high retention, 0.85 - 0.90, can provide meaningful pest control if $an > 2$ (Appendix S1). For example, if trap plants make up 10 % of the landscape, the trap crop must be close to twenty times more attractive than the cash crop in order for moderately high retention to provide meaningful control. Otherwise only retention very close to 100 % leads to effective trap cropping. The guideline above presumes that a cash crop pest proportion of 0.2 or less is effective trap cropping. If tolerated pest proportions are lower or higher, the structure of the rule remains unchanged, but the critical value that an must be greater than differs. In this case, the new value can be derived using the methods in Appendix S1.

The mathematical model also shows why clumping trap plants is normally detrimental to pest management, but may be beneficial for controlling long distance dispersers. This is because clumping trap plants decreases the proportion of insects on the cash crop at equilibrium, for all parameter values (see Appendix S1). However, this equilibrium is only reached on a reasonable timescale if the insects move long distances. Clumping trap plants close together leaves a large portion of the field without traps, so insects that disperse short distances never get to the trap crop. Our simulations verified that while clumping decreased the number of pests on the cash crop in the long run, it actually increased pest densities on the cash crop in the short term.

Discussion:

Our simple model provides potential reasons for past trap cropping failures and gives guidelines for its future use in pest management. A key result of our model is that small changes in trap crop retention have a major effect on the proportion of insects on the cash crop when retention is high, but almost no effect when retention is low. This is because when retention is high there are many insects on the trap crop. Decreasing retention, by even a small amount, sends many insects back onto the cash crop. On the other hand, when retention is low, there are fewer insects on the trap crop, so a decrease in retention has less impact.

This effect of retention implies that attractive trap plants may be ineffective, even if their retention rate is moderately high. Our model shows that in order for a trap crop to meaningfully reduce populations on a cash crop it must be very good at retaining insects. This result coincides with every successful commercial trap cropping example we were able to review, since all of them used supplemental management strategies that would prevent insects from dispersing back into the cash crop. The combination of the modelling result and the evidence from the literature, both supporting the importance of retention, is especially concerning because experiments and field studies have rarely addressed trap crop retention.

To our knowledge only two studies have attempted to measure even proxies for insect retention by trap crops (Borden & Greenwood 2000; Badenes-Perez, Shelton & Nault 2005). Borden & Greenwood studied baited trees as trap plants to prevent damage by spruce and bark beetles, and concluded that the increased retention of baited trees potentially contribute to the trap crop’s commercial success. This confirms that artificially increasing retention with semiochemicals, which have been shown to arrest insects in controlled experiments (Metcalf 1994), may improve trap cropping at a larger spatial scale. Placing sticky traps judiciously within a trap crop is another way of explicitly increasing retention. Traditionally the deployment of sticky traps has been infeasible on large spatial scales (Epsky, Morrill & Mankin 2004) but placing them within an isolated trap crop may allow growers to take advantage of near perfect sticky trap retention rates, which has allowed them to outperform traditional trap plants in some small scale experiments (Gu *et al.* 2008; Moreau & Isman 2011).

The most common approach to preventing damage caused by poor trap crop retention is removing the pest while it is on the trap crop. In fact, out of the 14 successful trap cropping studies we were able to review, 11 used this strategy, seven by pesticide applications to the trap crop (Hokkanen 1989; Srinivasan & Krishna Moorthy 1991; Pair 1997; Dogramaci *et al.* 2004; Leskey, Pinero & Prokopy 2008; Cavanagh *et al.* 2009; Lu *et al.* 2009), one by a trap plant that increased pest parasitism by natural enemies (Khan *et al.* 1997), one by cutting the trap plants (Godfrey & Leigh 1994), one by using disease resistant plants that allowed the insect vector to rid itself of the disease while feeding on the trap crop, preventing dispersal of the disease back into the cash crop (Gonsalves & Ferriera 2003), and one by vacuuming insects off of the trap crop (Swezey, Nieto & Bryer 2009).

In our model, if attraction is extremely high and there are many trap plants in the field then the effect of retention on pest proportion is less dramatic because insects move from one trap plant to another as opposed to back into the main crop. We showed if trap plants are evenly spread across the landscape, then the attractiveness of the trap crop must be greater than twice the ratio of cash plants to trap plants in order to avoid the dramatic retention effect. This means that growers who are willing to sacrifice a large portion of their landscape to the trap crop do not need near-perfect trap crop retention for pest control. Indeed, all of the successful trap cropping examples that did not include physically manipulating retention or removing pests from the trap crop used at least triple the typical proportion of the landscape dedicated to a trap crop (Ramert *et al.* 2001; Michaud, Qureshi, & Grant 2007), offering support for our general rule of thumb. However, since most trap cropping systems devote less than 10 % of the landscape to trap plants

(Hokkanen 1991; Shelton & Badenes-Perez 2006), trap crop retention must be extremely high for successful pest control in most agricultural systems.

Despite the fact that virtually all cases of successful trap cropping involve manipulating the system to prevent dispersal away from the trap crop, the majority of studies in the trap cropping literature focus on finding the most attractive trap plant (Edde & Phillips 2006; Shelton & Badenes-Perez 2006). The results of our model suggest that maximizing attraction is relatively unimportant. Increasing attractiveness is only beneficial if the trap crop is relatively unattractive. Once a trap crop is relatively attractive compared to the cash crop, efforts would be better spent on management strategies that prevent insects from dispersing back into the cash crop.

In our model, placing trap plants closer together usually undermines trap cropping efficacy. However, our simulations show that planting the trap crop in rows does not clump the landscape enough to have this negative effect, except for nearest neighbour dispersers. This result offers some hope for trap cropping because clumping trap plants in rows within a field or on the perimeter is the most practical and common spatial arrangement.

Our model is simplified in order for it to remain tractable. However, all of our simplifying assumptions favour the importance of attraction over retention, suggesting our result on the importance of retention is likely robust. For example, our model did not include reproduction, but including it would lead to the trap crop acting as a breeding ground for dispersal back into the main field (Hilje, Costa & Stansly 2001). Therefore, preventing insects from dispersing back onto the cash crop is even more important when reproduction is considered. Similarly, including density dependent movement would increase dispersal off the trap crop, making the removal of insects from the trap crop more crucial as well. We also did not allow for insects migrating into a field with a border trap crop (Boucher *et al.* 2003) because the goal of a border crop is to prevent insects from entering the cash crop, making retention even more important in this scenario. Lastly, the importance of retention would also increase if the attractiveness of the trap crop declined as damage increased over time. Therefore, all of our assumptions minimize the importance of insects dispersing back into the cash crop, yet still lead to retention being the most important factor in developing an effective trap cropping strategy.

Increasingly there has been a call for sustainable forms of pest management. While trap cropping is a promising option, at best it has had little success in agricultural systems (Shelton & Badenes-Perez 2006). Although it is difficult to determine exactly why a trap crop succeeds or fails to control a pest, our model, along with examples in the literature, suggests that a potential reason for so many failures is the trap crop's inability to retain insects. Fixing this problem may be achieved by management practices that prevent insects from dispersing back into the cash crop. While high effort or costly supplemental agronomic practices may be a barrier for growers to actively adopt trap cropping in the field, this effort may be necessary to reach desired management outcomes. Therefore, we recommend that future trap cropping research include empirical studies on the effect of retention in trap cropping, the development of new supplemental strategies to prevent dispersal away from the trap crop, and the improvement of currently successful strategies so that they can be more widely adopted.

Acknowledgements

M.H.H. is supported by a National Science Foundation Graduate Research Fellowship. We thank Anthony Shelton, Rebecca Loughner, Ben Dalziel, Candace Low, Katherine Marchetto, Wopke van der Werf and two anonymous reviewers for helpful comments.

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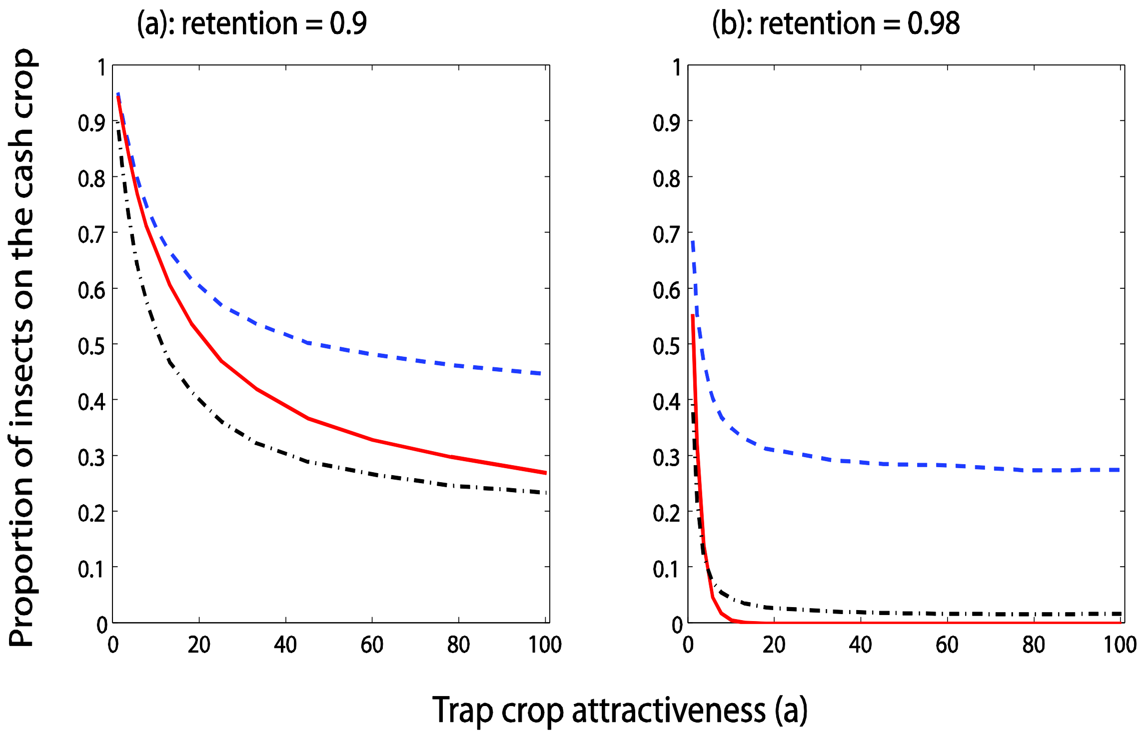

Figure 1. A plot of the mean proportion of insects on the cash crop, versus trap crop attractiveness *a*, with trap crop retention fixed at (a) 0.9 and (b) 0.98. The dashed line is for nearest neighbour dispersing insects and the solid line is for nearest five neighbour dispersal, both over a landscape with 1 % trap plants. The dash dotted line is for nearest neighbour dispersing insects but over a landscape that contains 2 % trap crops. For all plots retention on the cash crop is 0.5. The 1 % landscape is a 30 x 30 arena with 9 uniformly spread trap crops. The 2 % landscape is a 28 x 28 arena with 16 uniformly spread trap crops. Standard errors were less than 0.01 and hence error bars are not shown.

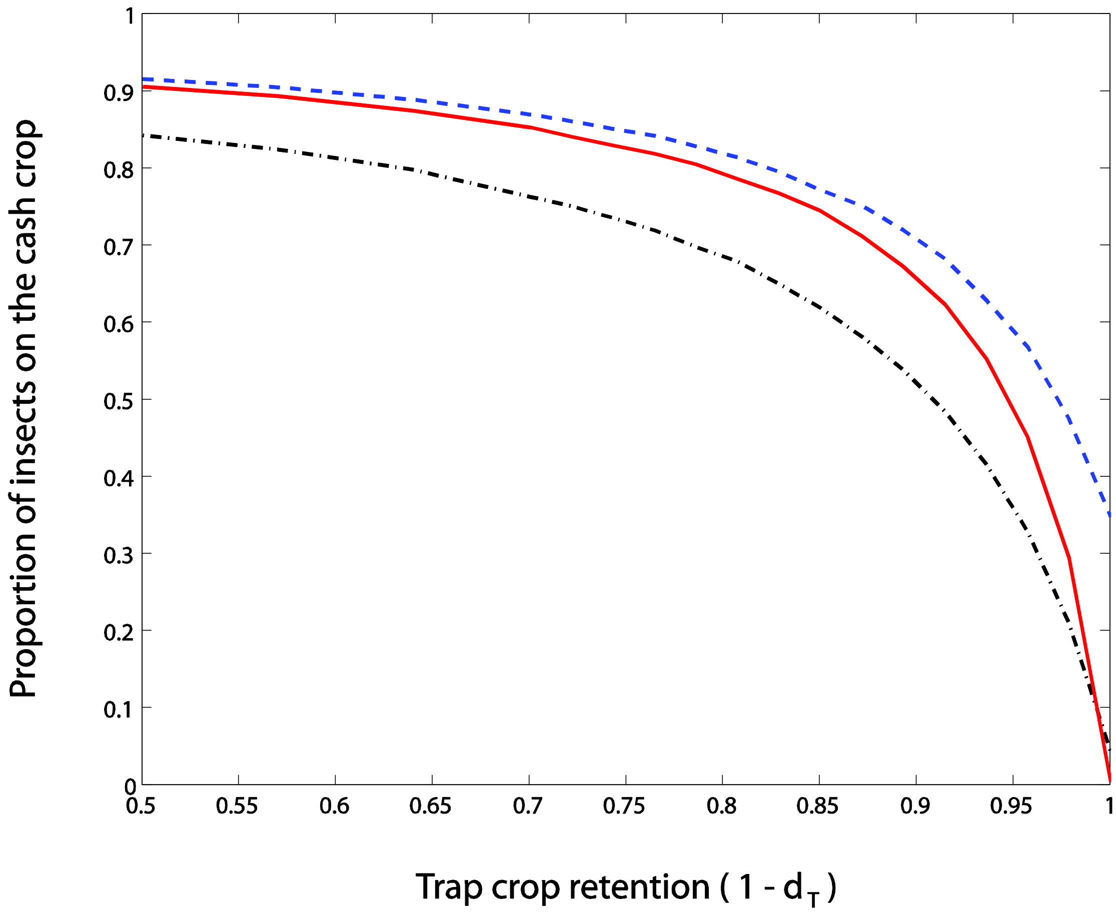

Figure 2. A plot of the mean proportion of insects on the cash crop versus trap crop retention, 1-d_T. The dashed line is for nearest neighbour dispersal and the solid line is for nearest five neighbour dispersal, both over a landscape with 1 % trap crops. The dash dotted line is for nearest neighbour dispersing insects but over a landscape that contains 2 % trap plants. For all plots retention on the cash crop is 0.5. The 1 % trap crop landscape is a 30 x 30 arena with 9 uniformly located traps. The 2 % landscape is a 28 x 28 arena with 16 uniformly located traps. Standard errors were less than 0.01 and hence error bars are not shown.

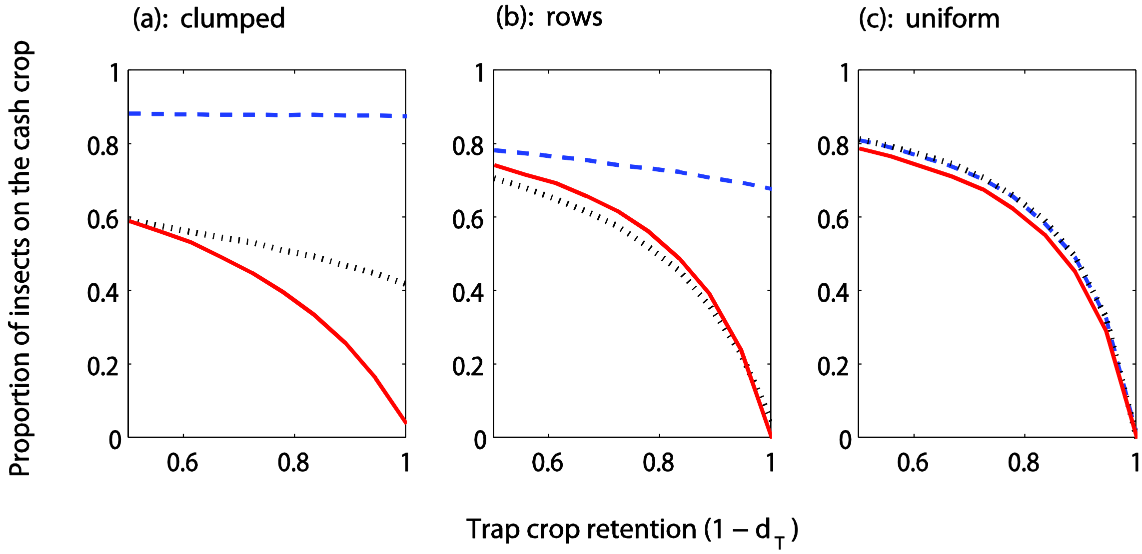

Figure 3. The proportion of insects on the cash crop vs. trap crop retention after 100 time steps for insects moving (a) over a landscape containing one clump of trap plants, (b) over strips/rows of trap plants, and (c) over uniformly located trap plants. Dashed, dotted, and solid lines are for nearest 1, 5 and 10 neighbour dispersal respectively. Attractiveness of the trap crop and cash crop retention are fixed at 10 and 0.5 respectively for all plots. Clumped trap plants constitute a 6 x 12 grid of 72 trap plants in a 36 x 72 arena (3 % of the landscape), strip trap plants are simulated as two evenly spaced rows of 36 trap plants, and uniformly located trap plants are 72 evenly spaced plants.

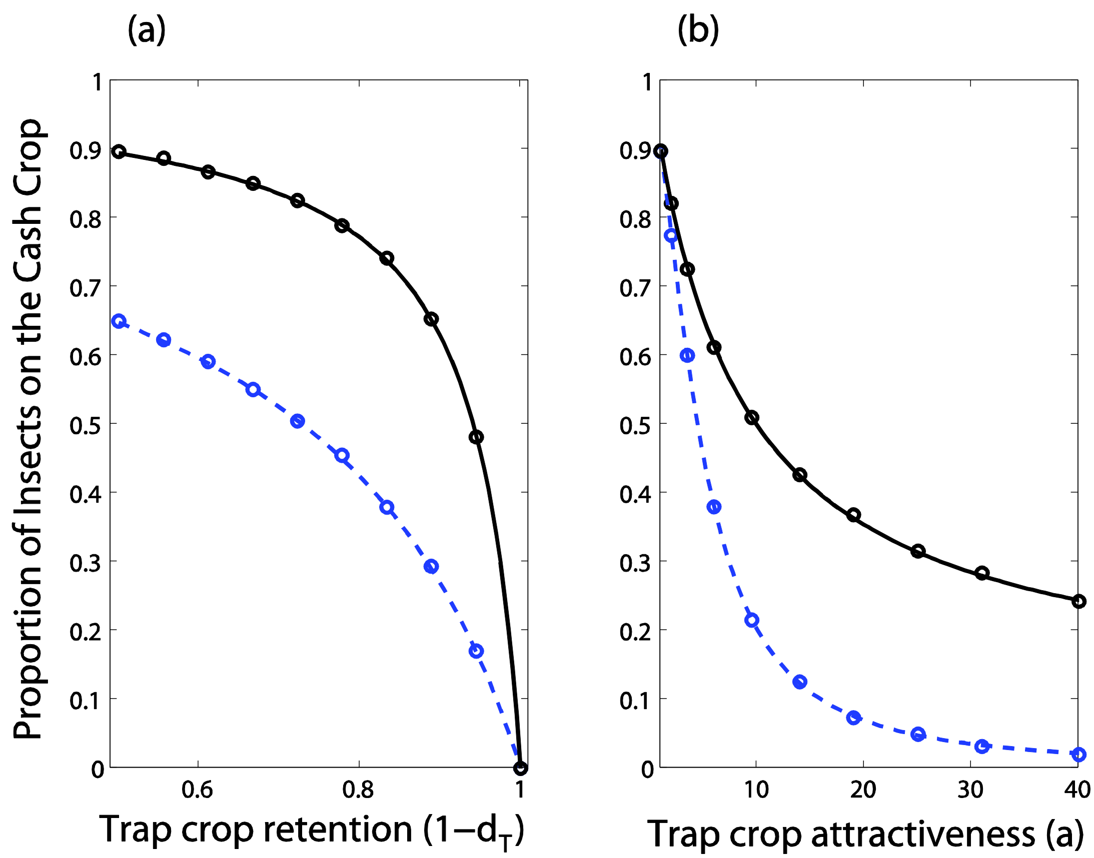

Figure 4. A plot of the proportion of the insects on the cash crop versus (a) trap crop retention and (b) trap crop attractiveness. The circles represent the results from the simulation after 1,000 time steps and the lines are the corresponding analytic approximation. The dashed line is for the clumped landscape and the solid line is for the landscape with uniformly spread out trap plants. Both plots use a 40 x 40 landscape with 16 traps, with cash crop retention and insect dispersal distance fixed at 0.5 and three respectively. For (a) attractiveness is fixed at 10. For (b) trap crop retention is fixed at 0.95.

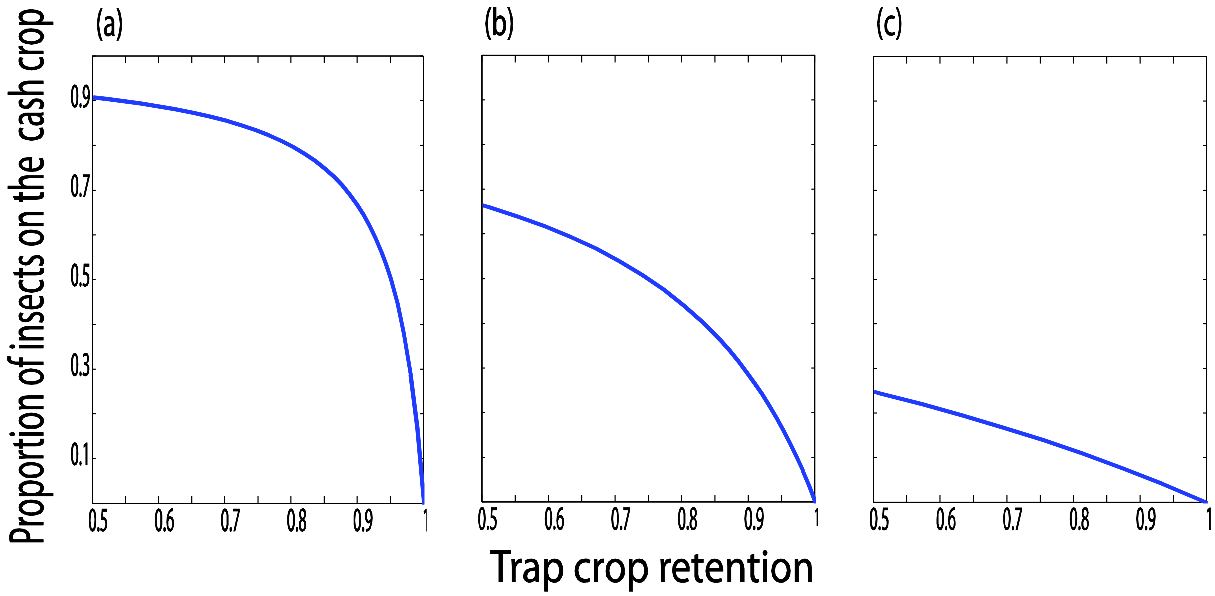

Figure 5. Examples of the equilibrium proportion of insects on the cash crop versus trap crop retention when the attractiveness of the trap crop times the ratio of trap plants to cash plants, *an*, is (a) 0.1, (b) 0.5, and (c) 3.

Supporting Information:

Additional supporting information may be found in the online version of this article.

Appendix S1: Mathematical Analysis